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Comparative analysis of Palmer amaranth (*Amaranthus palmeri*) and waterhemp (*A. tuberculatus*) in Iowa

by

Rebecca Suzanne Baker

A thesis submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Crop Production and Physiology (Weed Science)

Program of Study Committee:
Robert Hartzler, Major Professor
Prashant Jha
Ajay Nair

The student author, whose presentation of the scholarship herein was approved by the program of study committee, is solely responsible for the content of this thesis. The Graduate College will ensure this thesis is globally accessible and will not permit alterations after a degree is conferred.

Iowa State University

Ames, Iowa

2021

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DEDICATION

In memory of my grandparents, Dr. Charles and Mary Blair Johnson, Myron and Shirley Hudson Schulze, uncle Jim Johnson, and aunt Marie Johnson.

In memory of my mother-in-law, Debra Jo Wheatley Baker. Happy trails.

For my parents, Bob and Merry Johnson, who taught me the importance of being inquisitive and chasing down answers, and who gave me the opportunity and motivation to go to college. It was always the dream and now it is a reality. Thank you, and I love you.

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ABSTRACT

Waterhemp (*Amaranthus tuberculatus* [Moq.] J.D. Sauer), a native to the Midwestern United States, is difficult to control in crops and has become resistant to several herbicides. Emergence and growth of waterhemp have been studied extensively in Iowa. Palmer amaranth (*A. palmeri*) is a relative of waterhemp, but it is native to the southwestern United States. It has evolved resistance to several herbicides and was recently introduced to Iowa in its northward expansion through the United States. The objectives of this research were to understand seed bank dynamics, growth, and competitive ability of Palmer amaranth compared to waterhemp. Short-term seed persistence of Iowa Palmer amaranth, Kansas Palmer amaranth, and Iowa waterhemp populations were compared, with seeds left on the soil surface or buried at 15-cm depth in the soil. The Kansas Palmer amaranth population and the Iowa waterhemp population were more persistent than the Iowa Palmer amaranth population at the soil surface, with up to 55% of seeds remaining viable after one year; all populations maintained over 50% viability at 15 cm burial depth. Emergence patterns of the populations were studied using an artificial seed bank. Emergence differed between years, with differences between populations only occurring in 2019. Waterhemp reached 50% emergence 1 to 2 weeks earlier than Palmer amaranth. Both species demonstrated abilities to establish persistent seed bank and sustain season-long emergence. A common garden study compared the growth, biomass, and seed production capabilities of Iowa waterhemp and the two populations of Palmer amaranth, Iowa and Kansas. Across years, females were 24% taller than males. Plant growth rate in 2019 showed differences between species early in the season with Iowa waterhemp having higher relative growth (0.05 cm cm^{-1} day^{-1}) than Palmer amaranth (0.03 to 0.035 cm cm^{-1} day^{-1}). Maximum growth occurred on July 9 at around 0.07 cm cm^{-1} day^{-1}. Palmer amaranth produced 50 to 100% more biomass than waterhemp in 2019 with values of 1,000 g plant^{-1} for waterhemp and up to 2,000 g plant^{-1} for Palmer amaranth. Palmer amaranth reached 50% flowering 2 weeks earlier than waterhemp. Seed production was similar between the species due to high variability. Average seed production for Iowa Palmer amaranth, Kansas Palmer amaranth, and Iowa waterhemp was 60,000, 120,000 and 100,000 seeds plant^{-1}, respectively. Waterhemp produced more seed per gram of dry biomass compared to Palmer amaranth, 45,000 and 25,000 seed g biomass^{-1}, respectively, indicating larger seed size for Palmer amaranth than for waterhemp. A greenhouse replacement study compared the competitive abilities of Iowa waterhemp and Iowa Palmer amaranth in five ratios: 100% Palmer amaranth; 100% waterhemp; 75% Palmer amaranth, 25% waterhemp; 50% Palmer amaranth, 50% waterhemp; and 25% Palmer amaranth, 75% waterhemp. After six weeks of growth, Palmer amaranth produced twice as much biomass than waterhemp, 3 and 1.5 g plant^{-1}, respectively, regardless of planting ratio. Relative yield of the species was calculated by dividing biomass produced in mixture with a similar proportion of biomass produced in monoculture. When the species grow similarly in mixture and in monoculture, relative yield is equal to one. Values greater than one indicate greater productivity in mixture, and values less than one indicate decreased productivity in mixture relative to monoculture. Biomass of Palmer amaranth was not affected by competition with waterhemp (relative yield = 1.24), but waterhemp biomass was decreased by competition with Palmer amaranth (relative yield = 0.75). Greenhouse temperatures were greater than early-season field conditions which might have favored the growth of Palmer amaranth over waterhemp. These studies provide evidence that Palmer amaranth is not yet well-adapted to growing conditions in Iowa, especially early in the growing season, and indicate that further introductions and spread of the species should be avoided and carefully managed.

CHAPTER 1. GENERAL INTRODUCTION

Thesis organization

This thesis is organized in four chapters. The first chapter includes a literature review of Palmer amaranth and waterhemp and an introduction to the studies included in this thesis. The second and third chapters are research manuscripts formatted for submission to a scientific journal. The second chapter, titled "Seed Bank Characteristics of Palmer Amaranth (*Amaranthus palmeri*) and waterhemp (*A. tuberculatus*) in Iowa," is suitable for submission to Weed Technology. "Comparative Growth of Palmer Amaranth (*Amaranthus palmeri*) and Waterhemp (*A. tuberculatus*) Under Competitive and Non-Competitive Conditions," the third chapter of this thesis, is also formatted for submission to Weed Technology. Chapter four is a general conclusion, including recommendations for future research.

***Amaranthus* genus**

The genus *Amaranthus* contains crop, ornamental, and weedy species (Sauer 1957, 1967). Cultivated varieties are used for grain and pigment, and grain varieties were selected for weak bracts, large inflorescences, and light-colored seed (Sauer 1967). Some species, such as *Amaranthus hybridus*, have both weedy and cultivated biotypes (Adhikary and Pratt 2015). Amaranth seed has been gathered for food by many cultures across the world for centuries (Sauer 1967). Young shoots have been gathered and boiled for food.

Before humans spread the genus, there were about 60 species native to North America and 15 native to the eastern hemisphere (Sauer 1967). Native habitats of the genus in North America were often disturbed marshes or riverbanks, and prolific seed production appears to have always been a characteristic trait. Phenotypic plasticity, primarily color and growth habit, have also been recognized for decades, being mentioned by Sauer (1967) as a complication in the identification of genetically similar species. Flower parts appear to segregate more strongly between species and can serve as a primary visual identifier. Species within the genus, both mono- and dioecious, have been found to cross-pollinate, which complicates identification of species (Nie et al. 2019; Oliveira et al. 2018; Sauer 1955). Hybridization contributes to amaranths success as weeds by introducing genetic diversity, which can transfer traits such as drought or herbicide resistance between populations. The ability of amaranths, primarily waterhemp (*Amaranthus tuberculatus* [Moq.] J. D. Sauer) and Palmer amaranth (*Amaranthus palmeri*), to develop resistance to herbicides has contributed to their dominance as weeds of crop fields (Steckel 2007).

Waterhemp biology

Waterhemp is native to the Midwestern United States, including Iowa, and is known for its ability to evolve herbicide resistance. Waterhemp is sometimes referred to as the waterhemp complex because it was previously considered two distinct species, *A. tuberculatus and A. rudis*, which were thought to exist separately with many hybrids (Pratt and Clark 2001; Steckel 2007). Pratt and Clark (2001) proposed that there were never two unique species, just one with highly variable phenotypes. This phenotypic plasticity is widely recognized as a unique trait of waterhemp. Characterized typically by lanceolate-shaped leaves and glabrous stems, often having a reddish color, waterhemp plants are highly variable in appearance. In general, plants are erect and can reach heights of 3 m (Sauer 1955). Female waterhemp plants can produce up to 290,000 seeds that can remain dormant in the soil for up to 5 years (Sellers et al. 2003; Steckel et al. 2007). The prolific seed production allows waterhemp to rapidly establish or sustain a large seed bank when plants escape control. The amount of waterhemp seed remaining in the soil seed bank from 0 to 20 cm was 39%, 28%, 10%, and 0.004% after 1, 2, 3, and 4 years, with no new seed contributions (Steckel et al. 2007). The seed bank decreased more rapidly in the first year under no-till than in systems using tillage. No-till leaves the seed closer to the soil surface, promoting germination versus moving the seed into the soil where it can avoid environmental cues for germination. In an artificial seed bank study, 12% of waterhemp seed remained viable in the soil after four years of burial at 0 to 5 cm (Buhler and Hartzler 2001).

Waterhemp emergence typically begins in early to mid-May in Iowa, with peak emergence occurring from late May through mid-July (Hartzler et al. 1999). Werle et al. (2014) developed models for seed emergence using thermal time, hydrothermal time, and day of year. The best fitting model for waterhemp used only day of year, which suggests that factors other than average daily temperature and moisture may be a better predictor of waterhemp emergence (Leon et al. 2004; Werle et al. 2014).

Waterhemp exhibits relatively strong primary dormancy, with germination below 10% immediately following seed maturation (Wu and Owen 2015). Dormancy gradually decreased while waterhemp seed was in storage; seed reached peak germination of 80% after 4 months. Germination of waterhemp peaked in the second year of a four-year artificial seed bank study, with 5% germination in the first year followed by 7%, 1%, and 2% germination in subsequent years (Buhler and Hartzler 2001). Alternating temperatures of ±40% of constant temperature have been found to release primary dormancy of seeds. Waterhemp can emerge at temperatures as low as a mean of 5 C when temperatures are alternating, compared to a constant temperature of 10 C (Steckel et al. 2004).

The late-season decline in germination may be due to the induction of secondary dormancy rather than a depletion of the soil seed bank. Waterhemp germination declined after 6 to 8 months of storage, indicating that time, as well as environmental conditions, may be a factor in induction of secondary dormancy (Wu and Owen 2015). After 3 years of burial at a 20-cm soil depth, where seeds were not exposed to temperature and light cues for germination, 7% of waterhemp seeds were viable (Burnside et al. 1996). The same study found that 3% of waterhemp seeds were viable and germinated after 17 years of burial.

Timing of seed germination plays an important role in the success of the resulting plant. When waterhemp was planted at three different dates, May, June, and July, the May planting date had greatest biomass and seed production, but seeds produced by the July planting were larger (Heneghan and Johnson 2017). Sufficient seed was produced by July-planted populations to sustain the soil seed bank; plants established in July produced 276,258 seeds plant^{-1} compared with 926,629 and 828,905 seeds plant^{-1} in May and June plantings, respectively. Large reductions in biomass, seed production, and survival occur when waterhemp emerges after a soybean crop, especially if the crop is planted in narrow rows (Steckel and Sprague 2004). Waterhemp plants emerging as late as the early reproductive stages of a soybean crop are still capable of producing up to 300 seeds. Waterhemp plants that emerged in 38-cm-row corn had biomass reductions of 20% compared to plants in 76 cm rows, and seed production was up to 48,400 seeds (Nordby and Hartzler 2004). Waterhemp that emerged at the V3 stage of corn produced 9,000 seeds, and plants emerging at the V5 stage produced only 600 seeds.

The majority of waterhemp emerges after typical crop planting dates in the Midwest, so emerged waterhemp plants are often not affected by soil disturbance caused by seedbed preparation and planting operations. A single preemergence followed by a postemergence herbicide application may fail to completely control waterhemp due to the prolonged emergence period. Waterhemp has evolved resistance to seven herbicide sites of action, and most biotypes are resistant to several sites of action (Shergill et al., 2018; Heap, 2020). A six-way resistant biotype was identified in Missouri with resistance to 2,4-D, atrazine, chlorimuron, fomasafen, glyphosate, and mesotrione (Shergill et al. 2018).

Palmer amaranth biology

Palmer amaranth is a summer annual weed known for fast growth, prolific seed production, and interference with cropping systems. It is characterized by glabrous stems; ovate-shaped leaves, often with watermarks; and large seed heads with sharp bracts on female plants (Sauer 1955). Seeds are small, round, shiny, and dark-colored, and a single plant can produce hundreds of thousands of seeds. The seeds of Palmer amaranth exhibit dormancy that allows them to survive in the soil for several years (Jha et al. 2010a). A single Palmer amaranth plant can produce 250,000 to 1.5 million seeds (Sellers et al. 2003; Smith et al. 2012). Palmer amaranth emerges from early May through July, with some seeds emerging into late October (Jha and Norsworthy 2009).

Native to the southwestern United States and northwestern Mexico, Palmer amaranth moved eastward across the southern United States where it now threatens crop yields (Sauer 1957). Yield reductions have been observed in soybean, corn, peanut, and cotton; the magnitude of loss is related to both the density and timing of Palmer amaranth emergence in relation to crop emergence (Burke et al. 2007; Klingaman and Oliver 1994; Massinga et al. 2001; Norsworthy et al. 2016). Sweet potato yield was reduced by up to 95% by a season-long interference of Palmer amaranth (Smith et al. 2020). Palmer amaranth emerging at the same time as corn reduced the corn yield up to 91%. When the weed emerged at V4 or later stages of corn, the yield loss was 7 to 35% (Massinga et al. 2001). In a study that simulated allowing one glyphosate-resistant Palmer amaranth to produce seed, cotton yield was reduced as much as 17 kg ha^{-1} two years following seed dispersal (Norsworthy et al. 2014). Seeds and plants spread to all areas of the field within two years following seed dispersal, and after three years, Palmer amaranth infested

100% of the field and caused 100% crop yield loss. Soybean planting density had an effect on Palmer amaranth plants emerging up to 2 weeks following soybean emergence, but not on plants emerging later in the season (Korres et al. 2020). Plants emerging late, however, still produced up to 3,500 seeds plant^{-1}.

The spread of Palmer amaranth across the southern United States has been well-documented (Sauer 1957). Palmer amaranth was termed an “up-and-coming troublesome weed” in the South in a 1995 survey (Webster and Coble 1997). From 1994 to 2009, Palmer amaranth increased in importance as a weed in corn, and by 2009, Palmer amaranth was one of the top-five most troublesome weeds in the South (Webster and Nichols 2012). The same survey identified Palmer amaranth as the second most important weed in soybean. Because Palmer amaranth produces very small seeds, it can be easily dispersed in a number of ways. Movement of seeds may introduce the weed to new areas or new biotypes to previously infested areas which may present new challenges to management.

Because Palmer amaranth plants are still standing and have not shed seed at the time of cotton harvest, seed can be present in cotton seed and gin trash, which is often shipped to other states as cattle feed, in densities from 0 to 40,000 seeds per metric ton (Norsworthy et al. 2009). Migrating ducks and geese can also carry ingested seed from areas with established infestations and introduce Palmer amaranth in new areas. Seed removed from the digestive tracts of these birds was found to be viable, meaning that deposited seeds could germinate and establish (Farmer et al. 2017). Palmer amaranth seed, along with waterhemp seed, has been found in commercially available birdseeds (Oseland et al. 2020). The seed was often germinable, and some samples contained seed from glyphosate-resistant biotypes. In Arkansas, a glyphosate-resistant biotype was confirmed in a flood plain of the Mississippi River and this caused concern for spread of the resistant biotype via flood waters (Norsworthy et al. 2008).

In August 2013, Palmer amaranth was confirmed in Harrison County, Iowa, the first report in the state (Hartzler 2013a). Later in 2013, two more infestations were discovered: another in Harrison County and one on the eastern side of the state in Muscatine County (Hartzler 2013b). By the end of 2013, Palmer amaranth had been identified in two more counties: Fremont and Page, both in southwest Iowa (Hartzler 2014). Palmer amaranth was introduced across the state of Iowa in 2016 when contaminated cover crop seed was used to plant native perennials in conservation areas (Anderson and Hartzler 2016; Hartzler 2016a). By April 2017, Palmer amaranth had been added to the Iowa noxious weed law and recipients of potentially contaminated seed were notified of the problem (Hartzler 2017). Palmer amaranth is currently listed as a primary noxious weed in Iowa, and special requirements are articulated in the noxious weed law for the control of Palmer amaranth on conservation reserve program lands (WEEDS, §317.1A 2020). Efforts in Iowa have focused on containing and eradicating the weed before it becomes a permanent component of the weed flora.

There have been several reports of resistance to multiple herbicides beginning in 2008, with recent studies in Kansas reporting populations with resistance to five (Kumar et al. 2020) and six herbicides: 2,4-D, ALS-inhibitor, PSII-inhibitor, EPSPS-inhibitor, PPO-inhibitor, and HPPD-inhibitor (Shyam et al. 2021). There is evidence of transfer of herbicide resistance alleles between species of the same genus (i.e., Palmer amaranth and waterhemp) which may contribute to the rapid spread of herbicide resistance (Jhala et al. 2020). The site of the first known infestation was found to have greatly reduced populations in 2018 and to be free of Palmer amaranth in 2019 (Hartzler 2018, 2019). It appears that proper management, including handrogueing of adult plants prior to seed shatter, chemical control of seedlings, and planting of perennials in waste areas, is, at this time, limiting the spread of Palmer amaranth in Iowa.

A proactive approach to management of Palmer amaranth in Iowa involves seed bank management. Palmer amaranth seeds must be located near the soil surface in order to germinate (Jha et al. 2010a). Seeds that are located in the upper 5 cm may germinate, be eaten by granivores, or be degraded by environmental processes. Palmer amaranth seed in the upper 5 cm of the soil were reduced by up to 99% after one year of management using conventional tillage and glyphosate (Norsworthy 2008). While conventional tillage may move seeds deeper into the soil profile, only 0.03% of Palmer amaranth seeds buried from 0 to 10 cm were viable after 4 years (Jha et al. 2014). Seed viability does not appear to be affected by glyphosate resistance when compared with glyphosate-susceptible biotypes (Sosnoskie et al. 2013).

Seed bank management

Effective weed management can lead to significant decreases in seeds in the soil seed bank, which can lead to reductions in inputs required for control. Significantly greater numbers of *Amaranthus* spp. seeds emerged in no-till than tilled treatments in the first year following seed dispersal (Egley and Williams 1990). Soil disturbance via tillage was associated with an increase in germination of redroot pigweed (*Amaranthus retroflexus*) seeds located in the soil seed bank, leading to a decrease in the soil seed bank (Mulugeta and Stoltenberg 1997). Up to 5.3% of Palmer amaranth and waterhemp seeds remained viable across depths of 0 to 15 cm after 3 years of burial in a multi-state study (Korres et al. 2018). Redroot pigweed, when buried at 8 cm, emerged at rates less than 10%, compared to almost 90% at 0 to 2 cm (Benvenuti et al. 2001). Germination was suppressed by 100% at the 10 to 12 cm depth. Redroot pigweed emergence was maximized at the 1.25-cm-depth and was reduced by soil crusting (Wiese and Davis 1967). There is some evidence that soil texture may influence survival of Palmer amaranth seeds, with seed damage being greater in sandy loam soil compared to silt loam soil, 41% and 36%, respectively (Franca et al. 2020).

Seed degradation processes are more active near the soil surface, but also occur deeper in the soil profile. Soil macro- and microorganisms use weed seeds as food sources. Fungi colonize weed seeds and use them as a carbon source (Chee-Sanford 2008). This can either destroy the seed or reduce its viability. Soil conditions influence the activity of soil fungi with water being a key factor. Saturating the soil decreased the viability of weed seeds in the soil, but when fungicide was added, seed viability was preserved (Schafer and Kotanen 2003). This indicates that it is not soil moisture alone that degrades seeds, but soil moisture increases activity of fungi that degrade seeds. Palmer amaranth seeds have also been found to be targeted as food sources by rodents and arthropods (Sosnoskie et al. 2013). Up to 75% of seed was consumed by granivores over 7 days. Redroot pigweed seeds were eaten by ground beetles and crickets in greater quantity, compared to velvetleaf and giant foxtail seed (White et al. 2007). Similar amounts of seed biomass of the different species were consumed, suggesting that more redroot pigweed seeds were eaten due to small seed size. Emergence of redroot pigweed was reduced by the presence of seed predators. Redroot pigweed seeds located at the 0 to 3 cm depth were significantly reduced in the presence of ground beetle larvae (Hartke et al. 1998).

Persistent seeds remaining in the soil seed bank often exhibit seed dormancy. Dormant seeds have one or more mechanisms that prevent germination when conditions are favorable for germination and seedling survival. This ensures that weed seeds are not only dispersed through space, but through time (Foley 2001). There are five classes of seed dormancy, not including undifferentiated embryos (Baskin and Baskin 2004). These classes are: physiological dormancy, morphological dormancy, morphophysiological dormancy, physical dormancy, and combination dormancy. Within these classes are defined levels and types described in detail by Baskin and Baskin (2004).

Palmer amaranth and waterhemp seed both germinated at higher rates with alternating versus constant temperatures (Steckel et al. 2004). Seed dormancy may be influenced by the environment in which the mother plant grows (Jha et al. 2010b; Karimmojeni et al. 2014). Seeds of redroot pigweed that developed under well-watered conditions, as well as seeds that developed with adequate nitrogen fertilization, showed greater dormancy than seeds that developed under stressful conditions. This is contrasted by the findings of Fawcett and Slife (1978). Common lambsquarters (*Chenopodium album*) seeds produced by plants fertilized with ammonium nitrate or composted manure had less dormancy than seeds from plants in the control plots which received only water. In Palmer amaranth, shading of the mother plant and position of the seed on the mother plant influenced germination of seeds (Jha et al. 2010b). Seeds that developed on a shaded mother plant had lower germination, and seeds that developed on the lower third of the plant germinated at lower rates. Palmer amaranth seed germination also appears to be influenced by water stress conditions under which seeds develop on the mother plant (Matzrafi et al. 2020). Seeds developed under drought conditions exhibited less dormancy and required less water for germination.

Seeds of some species also have secondary dormancy. This occurs when dormancy is initially lifted, but conditions become unfavorable before the seed germinates, and the seed then re-enters dormancy until conditions are again favorable for germination. Secondary dormancy often occurs during summer when high temperature and soil moisture become limiting factors for germination and establishment of seedlings. Using a hydrothermal model, changes in mean base water potential was the primary factor promoting secondary dormancy of downy brome, *Bromus tectorum* (Hawkins et al. 2017). While mechanisms for secondary dormancy are not known, it is thought that they are similar to mechanisms responsible for primary dormancy (Foley 2001). Soltani et al (2017) suggest that secondary dormancy may be less important to seed persistence than deep burial of seeds.

Plant competition

Cultural weed management strategies focus on creating an unfavorable environment for weed germination and increasing the competitiveness of the crop. Row-spacing influences crop competitiveness, with a goal of increasing the speed which the crop fills the space between rows, or canopy. Once the crop has canopied, it uses more of the available light earlier in the season. Increased soybean population decreases the number of days from crop emergence to crop use of 95% of solar radiation (Shibles and Weber 1966). Row spacing has effects on both crop yield and weed management. In barley (*Hordeum vulgare*), narrow row spacing and increased seeding density increased crop yield and decreased weed biomass (Kirkland 1993). Narrow rows reduced weed competition with corn crop when used in combination with high planting density and banded fertilizer (Anderson 2000). Combining management strategies to make crops more effective competitors against weeds is important when considering an integrated approach to weed management.

While it may be intuitive that larger plants are better competitors, it was found that this is only true in competition for light (Wilson 1988). Sheep’s fescue (*Festuca ovina*) size was determined by counting the number of tillers at the beginning of the study; small plants experienced higher relative growth rates and competed successfully belowground. This may be applied to Palmer amaranth and waterhemp, with Palmer amaranth being known as a larger plant than waterhemp. While studies have not yet been done on the competition between waterhemp and Palmer amaranth, it could be hypothesized that both plants may compete effectively. Both species have proven their ability to adapt to adverse growing conditions. Due to the differences in adaptations between the species, it is possible that they may compete for resources differently and can coexist. Waterhemp competes successfully with crop plants but Palmer amaranth has a greater negative effect on crop growth and yield. When both waterhemp and Palmer amaranth were grown in competition with soybean, models predicted that Palmer amaranth reduced soybean yield by 78.7%, whereas waterhemp reduced yield by 56% (Bensch et al. 2003). At high weed density, waterhemp produced more seed than Palmer amaranth, with maximum seed production for the species totaling 51,800 seeds m^{-2}. Palmer amaranth produced more seed than waterhemp at low weed density.

When the two species were grown under the same conditions, they produced a similar number of seed (Sellers et al. 2003). Palmer amaranth dry biomass was greater than waterhemp at all sampling dates except one, at 12 weeks after planting, when biomass was similar. Palmer amaranth plant height was greater than that of waterhemp throughout the growing season. Seed production was similar between the two species due to high variability of seeds per plant, but waterhemp produced more seeds per gram of dry plant biomass. Palmer amaranth also has a higher rate of growth, plant volume, and leaf area than waterhemp (Horak and Loughin 2000). When the species emerged at two dates during the 1994 growing season, Palmer amaranth maintained greater leaf area, dry biomass, and number of primary branches compared to waterhemp. Heights of Palmer amaranth and waterhemp were similar throughout the growing season, but Palmer amaranth was significantly taller at the end of the season. In 1995, growth of the two species was similar, indicating that environmental factors differently affect the growth of Palmer amaranth and waterhemp. More GDD were accumulated in the early part of the season in 1995, and precipitation patterns differed between years as well, with large, sporadic precipitation events occurring in 1994 and smaller, more frequent precipitation in 1995. Relative growth rates were generally higher for Palmer amaranth than waterhemp early in the season, but waterhemp relative growth rate was greater mid- to late-season; these rates also differed between years. Sellers et al. (2003) determined that Palmer amaranth was faster-growing, but delayed emergence and/or slower early-season development may favor waterhemp. Horak and Loughin (2000) concluded that the traits that characterize Palmer amaranth contribute to its success as an invasive weedy species, but since waterhemp shares many of those characteristics, it is likely comparably competitive.

There are generally two types of plant competition: intraspecific and interspecific. Intraspecific competition is defined as competition between plants of the same species, and interspecific competition is competition between plants of different species. Within these categories, there are other types of competition that may be referenced, such as interbiotypic, which is competition within two or more biotypes of the same species (Anderson et al. 1996). Reduction of weed seed production due to competition with a crop at low weed densities would be considered interspecific competition, while reduced seed number at high weed densities where weeds compete with both the crop and other weeds would be inter- and intraspecific competition (Massinga et al. 2001). When Palmer amaranth and waterhemp were grown at different densities in competition with soybean, both experienced a decrease in dry biomass when weed density reached 2 plants m^{-1} row (Bensch et al. 2003). The reduction in productivity at densities greater than 2 plants m^{-1} row likely is due to intraspecific competition among the weeds. Waterhemp produced more biomass at higher densities than Palmer amaranth at one location, and waterhemp produced more seed than Palmer amaranth at both locations (Bensch et al. 2003). The authors suggest that this was due to differences in the competitive abilities of the plants, which can be attributed to differences in plant characteristics.

As evidenced by many studies that compare Palmer amaranth and waterhemp, it is not clear which of the two plants is the more successful competitor, and the reason for that may be simple: their competitive strategies cannot be compared. One principle of plant competition by Clements et al. (1929), as cited in Zimdahl (2004), states: “Competition is keenest when individuals are most similar and make the same demands on the habitat and adjust themselves less readily to their mutual interactions.” The two plants have apparently different strategies for competing with other plants for resources. Palmer amaranth has extremely high rates of growth, grows to heights greater than crop plants, and produces large amounts of biomass and leaf area, making its appearance match the severity of its competition; this growth strategy was defined by Connell (1990) as direct interference. Waterhemp is more subtle about its competition, with relatively shorter heights and smaller amounts of biomass and leaf area, but still being a successful competitor. The key to these plants’ success may be explained by the last part of Clements’ principle: “…adjust themselves less readily to their mutual interactions.” Weedy *Amaranthus* spp. are highly plastic, adapting readily to the environmental conditions in which they are growing. Waterhemp and Palmer amaranth both are adapted to growing in shade (Jha et al. 2008; Steckel et al. 2003), waterhemp adapts to growing in high plant densities (Bensch et al. 2003), and both have demonstrated an incredible ability to evolve resistance to herbicides. Six-way resistant biotypes of both species have been documented (Shergill et al. 2018; Shyam et al. 2021). Because the survival of the weed is dependent upon seed production rather than crop yield reduction, and both species accomplish this under a variety of adverse conditions, it can be concluded that both species are successful.

No studies have compared the two in a competitive setting. Studies have compared biotypes of waterhemp that are resistant to herbicide with susceptible biotypes. Differences were not found between competitive abilities of PPO-resistant and –susceptible waterhemp, but differences were observed between triazine-resistant and –susceptible, with susceptible being more competitive (Anderson et al. 1996; Duff et al. 2009). A fitness cost associated with evolved resistance of waterhemp to 2,4-D, atrazine, glyphosate, and PPO-inhibitor herbicides was observed when plants were grown in competition with soybean (Butts et al. 2018). There may be evidence for a slight glyphosate-resistant-associated fitness cost in Palmer amaranth (Chandi et al. 2012). In a non-competitive setting, it was concluded that multiple herbicide resistance (MHR) did not affect plant fitness (Jones et al. 2019). MHR biotypes of waterhemp were found to have similar biomass production, and seed production was not found to be influenced by MHR traits. No fitness cost was reported for glyphosate-resistance via amplification of the EPSPS gene in Palmer amaranth (Giacomini et al. 2014; Vila-Aiub et al. 2014). Glyphosate-resistant Palmer amaranth grown in high-nitrogen environments had higher nutrient-use efficiency than a susceptible biotype (Bravo et al. 2018), and both glyphosate-resistant and ALS-resistant biotypes of Palmer amaranth were found to be more drought-tolerant than susceptible biotypes (Chandi et al. 2013).

Summary and research objectives

Palmer amaranth has proven itself to be a highly adaptable weed species capable of reducing crop yields, hindering harvest, and evolving resistance to herbicides. Its spread across the southern United States has been well-documented, as well as crop losses associated with Palmer amaranth infestations. Since it was introduced to Iowa in 2016, it has not become a prominent weed in the cropping system. Waterhemp, native to Iowa, has been the primary weed concern in Iowa for approximately 25 years. It is important for growers and land managers to understand the nature of Palmer amaranth before it takes hold in crop fields across the state. Management systems must be diverse and well-thought-out to avoid furthering the resistance of Palmer amaranth, as well as waterhemp, to herbicides. These management decisions must be informed by timing of emergence, and it must be recognized that Palmer amaranth can emerge throughout the growing season and adapt to growing in shade. Time of emergence is influenced by seed persistence in the soil, so this is also important information for management.

Effective management of any weed requires a basic understanding of the biology and ecology of the weed in relation to the environment. This knowledge is lacking for Palmer amaranth recently documented in Iowa.

The objectives of this research are to:

1. Compare emergence patterns of populations of Palmer amaranth relative to waterhemp, which is generally well-understood in Iowa.
2. Determine the persistence of populations of Palmer amaranth relative to waterhemp at both shallow and deep levels of burial in the soil to understand the impacts of tillage on the soil seed bank of Palmer amaranth and waterhemp in Iowa.
3. Compare the growth of populations of Palmer amaranth and waterhemp in two typical Iowa soils to understand impacts of different environments on height, biomass, and seed production.
4. Understand the competitive abilities of Palmer amaranth and waterhemp when grown in competition to determine if presence of waterhemp in a crop field influences success of Palmer amaranth in that field.

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CHAPTER 2. SEED BANK CHARACTERISTICS OF PALMER AMARANTH (*AMARANTHUS PALMERI*) AND WATERHEMP (*A. TUBERCULATUS*)

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Abstract

Waterhemp (*Amaranthus tuberculatus*) is a weedy species native to the Midwestern United States, whereas Palmer amaranth (*A. palmeri*) is native to the southwestern United States and was recently introduced in Iowa. Because of its recent introduction, seed bank dynamics of Palmer amaranth are not understood in Iowa. The goals of these studies were to better understand seed persistence and seedling emergence. Seed of a Kansas Palmer amaranth and waterhemp population were more persistent than an Iowa Palmer amaranth population at the soil surface with viability up to 54% after one year. Persistence of the Iowa Palmer amaranth and waterhemp populations were approximately double at 15 cm than at 1 cm, whereas no difference in survival at the two depths was observed in the Kansas Palmer population. In 2019, time to 50% emergence was different among all populations; 50% emergence values were 12, 19, and 25 days, respectively, for waterhemp, Iowa Palmer amaranth, and Kansas Palmer amaranth. In 2020, time to 50% emergence was similar among populations, approximately 19 days. Differences between persistence and emergence of the two species varied, but the data indicates Palmer amaranth should be capable of establishing persistent seed banks in Iowa.

Introduction

Waterhemp (*Amaranthus tuberculatus* [Moq.] J. D. Sauer) is a dioecious summer annual native to the Midwestern United States (Sauer 1957). It is characterized by lanceolate leaves, glabrous stems, high fecundity, and small seed. Foliage of this weed is bright green with stems often having reddish coloration (Sauer 1955). Waterhemp typically begins emerging in late spring once soil temperatures reach 10 to 12 C, regardless of accumulated growing degree days and precipitation (Steckel et al. 2004, 2007). Peak emergence occurs in early summer and often coincides with precipitation events (Hartzler et al. 1999). Waterhemp forms a persistent seed bank with a majority of seed lost after four years of burial. Seed buried at a greater depth survived longer than seeds near the soil surface (Steckel et al. 2007). Seeds are considered persistent if they survive the first germination season and can germinate in subsequent seasons (Thompson and Grime 1979; Walck et al. 2005). In a four-year study, waterhemp emerged at rates of 1 to 7% per year with the greatest emergence occurring in the first two years (Buhler and Hartzler, 2001). Waterhemp has evolved resistance to seven herbicide sites of action, with many biotypes exhibiting resistance to multiple sites of action (Heap 2021). A biotype found in Missouri was resistant to six distinct herbicide sites of action: auxinic mimics and inhibitors of PSII, ALS, PPO, EPSPS, and HPPD (Shergill et al. 2018).

Palmer amaranth (*Amaranthus palmeri* S. Watson) is also a dioecious summer annual, but is native to the southwestern United States and northern Mexico (Sauer 1957). Female plants are characterized by large, sharp bracts associated with reproductive structures. Palmer amaranth is also glabrous (Bond and Oliver 2006; Horak and Peterson 1995; Steckel 2007; Ward et al. 2013). The period of emergence stretches from early spring through mid-summer, and large flushes often follow precipitation (Jha and Norsworthy 2009). Germination began at alternating temperatures as low as 5 C, but maximum germination occurred at alternating temperatures centering around 30 C (Steckel et al. 2004). Palmer amaranth forms a persistent seed bank, with about 1% of seeds remaining viable after one year of burial and up to 0.03% remaining after four years (Jha et al. 2014). These percentages are small, but considering the high fecundity of Palmer amaranth, many seeds may remain viable in the soil for germination in future seasons. A single plant can produce 250,000 to 1.5 million seeds (Sellers et al. 2003; Smith et al. 2012). Seeds germinate at relatively low percentages, ranging from 0.5% the first year following burial to 0% at 4 years after burial (Jha et al. 2014).

Management of both waterhemp and Palmer amaranth is complicated by herbicide resistance. Palmer amaranth has evolved resistance to many herbicide sites of action. A biotype from Kansas was recently identified with resistance to six sites of action: auxinic mimics, and inhibitors of ALS, PSII, EPSPS, PPO, and HPPD (Shyam et al. 2021). When postemergence options are limited due to resistance, producers must rely on other methods of weed management, including hand-weeding, cultivation, preemergence soil residual herbicides, and deep tillage (Sosnoskie and Culpepper 2014). Timing of weed emergence relative to crop planting and emergence is vital information when implementing weed management. Typical Iowa crop planting dates range from mid-April to mid-May (Elmore 2012). Compared to this, waterhemp germination is late, beginning in early- to mid-May and peaking through the month of June (Hartzler et al. 1999). Late-emerging waterhemp seedlings often avoid control by preemergence herbicides and tillage passes, so producers rely on postemergence herbicides and shading by the crop canopy to control waterhemp.

Weed emergence patterns are also important when considering competitive interactions between crops and weeds. When Palmer amaranth emerged at the same time as corn, corn yield was decreased up to 91%, and Palmer amaranth produced up to 514,000 seeds m^{-2} (Massinga et al. 2001). When Palmer amaranth emerged after the corn crop, yield loss was reduced, but plants still produced up to 91,000 seeds m^{-2}. Though seed production was reduced, sufficient seed was produced to sustain the soil seed bank. It was determined that timing of weed emergence affected competitiveness of Palmer amaranth more than weed density. Palmer amaranth that emerged with a soybean crop reduced yield 31% more than Palmer amaranth that emerged 8 weeks after soybean emergence (Korres et al. 2020). Season-long competition between soybean and waterhemp reduced soybean yield by 40%. Yield reduction was less than 10% when waterhemp emerged at the V4/V5 stage of soybean (Steckel and Sprague 2004).

In 2016, Palmer amaranth was widely introduced to Iowa via planting of contaminated seed mixes for conservation plantings (Hartzler and Anderson 2016). Native seed mixes were contaminated with Palmer amaranth seed, causing the weed to become established in at least 35 counties. The contamination was thought to be caused by increased demand for native seed mixes, which led to an increase in use of seed from states with established populations of Palmer amaranth. Prior to 2016, Palmer amaranth had been identified in five Iowa counties along the state borders. Because Palmer amaranth was recently introduced to Iowa, seed persistence and emergence pattern have not been studied and are thus not well understood. This research aims to increase knowledge of Palmer amaranth seed bank dynamics in Iowa by comparing seed persistence and emergence to that of waterhemp, which is well-understood in Iowa. The persistence and emergence of two Palmer amaranth populations, collected from Iowa and Kansas, were compared with an Iowa waterhemp population. It was hypothesized that Palmer amaranth seed would be shorter lived than waterhemp due to differences in soil type and moisture between its native range and Iowa, and the emergence of Palmer amaranth would begin earlier and last longer than waterhemp.

Materials and Methods

Plant material

Waterhemp seed used in this experiment was collected from the Iowa State University Horticulture Farm near Gilbert, Iowa in September 2018. Palmer amaranth seed was collected from established stands in Pottawattamie County, Iowa and Riley County, Kansas in August 2018. Seed was dried at room temperature, manually threshed, and cleaned using sieves and an air column separator.

Seed was tested for germination using a warm germination test and viability using a tetrazolium test at the Iowa State University Seed Testing Laboratory (Ames, Iowa). A warm germination test began on October 29, 2018 and September 12, 2019 using small blotter boxes and moistened blotter papers. Four replications containing 100 seeds of each population, Iowa Palmer amaranth, Kansas Palmer amaranth, and Iowa waterhemp, were placed in the boxes using a vacuum seeder, and boxes were placed in incubation carts. Conditions were light with temperature oscillating between 20 and 25 C, day and night, respectively (Guo and Al-Khatib 2003). Initial germination counts were performed 8 days following planting and a second count was made three to five days later. Seeds were counted as germinated if the radicle was >1 mm in length and removed after counting. Greater germination was observed in 2019 than in 2018, likely due to after-ripening of seeds in cold storage (Table 2-1).

Table 2-1. Germination of Iowa Palmer amaranth (ApIA), Kansas Palmer amaranth (ApKS), and Iowa waterhemp (AtIA) seed prior to planting in 2018 and 2019. Seed was collected from Iowa State University Horticulture Research Station. Germination tests were conducted in a growth chamber with fluctuating temperatures of 25 C and 20 C, day and night, respectively (Guo and Al-Khatib 2003).

Population	2018	2019
	---------------------------%	-------------------------
ApIA	29	49
ApKS	25	46
AtIA	2.5	5.3

Seed persistence

Field experiments were established on November 15, 2018 and November 6, 2019 at the Iowa State University Horticulture Research Farm near Gilbert, Iowa. Soil type was Clarion loam with 2 to 6% slope (Soil Survey Staff 2021). Clarion soil is moderately well-drained, and the parent material is fine-loamy till. Seeds were prepared for burial by counting 100 seeds, mixing with 20 grams of fine sand, and placed into 8 cm by 8 cm, 500-micron opening nylon mesh bags (Elko Filtering, Miami, Florida) (Korres et al. 2018; Sosnoskie et al. 2010). Mesh bags filled with seed and sand were planted at 1 cm and 15 cm depths in the soil. Plots were arranged in a randomized complete block design with five replications. The area was blocked from north to south to account for changes in slope.

Bags were retrieved and placed in a cooler at 6 C on August 19, 2019 and 2020 until enumeration. Bags were opened and contents were poured into an Erlenmeyer flask containing a flotation solution. The flotation solution consisted of 40 g of $MgSO_4$ and 250 ml of tap water (Malone 1967). The solution containing the seeds was poured over a fine mesh sieve to retrieve the seeds, samples were washed 3 to 4 times to ensure retrieval of all seeds.

Seeds were then placed in petri dishes on moistened filter paper to determine percent germination. Dishes containing seeds were placed in a growth chamber at alternating temperatures of 25/20 C with 14 hours of light (Guo and Al-Khatib 2003). Dishes were checked periodically, and germinated seeds were removed. Seeds were considered germinated if the radicle had reached a length of at least 1 mm (Buhler and Maxwell 1993; Steckel et al. 2004). Dishes remained in the growth chamber for 21 days and seeds that did not germinate were subjected to a crush test to determine viability (Borza et al. 2007; Jha et al. 2010a; Sawma and Mohler 2002). Seeds were considered viable if the seed was firm, resisted crushing with gentle pressure from forceps, and when crushed, tissue appeared light-colored and oily (Sawma and Mohler 2002).

Seedling emergence

Field experiments were established on October 29, 2018 and October 28, 2019 at the same site as the persistence experiments. This site was selected for a low likelihood of a waterhemp seed bank due to previous use for vegetable and perennial cropping systems. Redroot pigweed was present at low numbers.

Circular plots measuring 0.74 m^2 were established by burying landscape edging (Terrace Board, Master Mark Plastics, Paynesville, MN), leaving approximately 5 cm above the soil surface to prevent seed movement outside of the plot area. The top 0.5 cm (3,730 cm^3) of soil was removed and placed in a plastic tub, 3,700 seeds $plot^{-1}$ were added, and the soil mixed thoroughly to ensure even distribution of seeds through the soil (Buhler and Hartzler 2001). Seed counts were determined by weight. An error in weighing resulted in an approximate 10% discrepancy in seed numbers in 2018, preventing calculation of percent emergence during the first year of the experiment. The soil/seed mixture was then added back to the plots and spread evenly across the surface, maintaining 5 cm of landscape edging above the soil surface; a 2.5 cm border of soil without added seed was maintained along the edge of plots to minimize microclimate effects caused by the dark-colored landscape edging. Plots were arranged in a randomized complete block design with five replications. The experiment was blocked from north to south to account for changes in slope.

Beginning on May 20, 2019 and May 15, 2020, seedlings were counted as ‘emerged’ when the first true leaf was approximately 0.5 cm in length and then removed. Seedlings were counted twice weekly at intervals of 3 to 4 days until August 12, 2019 and August 6, 2020. After these dates, plots were counted weekly. Other weed seedlings were also removed from the plots at each emergence count timing. Field experiments were terminated on October 9, 2019 and September 23, 2020 by removing the top 5 cm of soil from the plots and replacing it with soil surrounding the plots that was not seeded the previous fall. This was done to ensure that any seeds that emerged the following spring were from the 2019 seeding date and not 2018.

Data analysis

Data were analyzed using SAS® software version 9.4, and significance was determined at the α=0.05 level. No differences were found between years in the seed persistence data, so data were pooled across years. Germinable seed and any non-germinated seed determined to be viable using the crush test were combined into one category termed 'viable.'

All emergence data was converted to percentage of cumulative emergence in each plot to account for differences in number of seeds planted in 2018 and 2019. Seedlings were not identified beyond genus *Amaranthus* and control plots were established. Plots were assumed to contain the same number of 'native' *Amaranthus* spp. seed in the soil seed bank. The number of emerged *Amaranthus* spp. seedlings in the control plot of each block was subtracted from observations in the other plots in the block to account for native *Amaranthus* spp. seed in the soil. Average emergence from control plots ranged from 0 to 4.6 per sampling date compared with 0 to 302.6 in treatment plots. On some sampling dates, more seedlings were present in the control plot than in the treatment plot, so some numbers became negative. Differences were found between years, so 2019 and 2020 data were analyzed separately using the drc package in *R* (Ritz et al. 2015). A 3-parameter log-logistic model was used for nonlinear regression of the data and time to 10%, 50%, and 90% emergence were calculated. Day 0 was determined to be the day that emergence was first observed in any plot, and day as represented on the x-axis is number of days following day 0.

Climate data was obtained from the Iowa State University Iowa Environmental Mesonet National Weather Service COOP Network (Table 2-2). The station selected was IAC005 Iowa –

Central Climate Division which is located about 15 miles east of Ames in Sherman, Iowa. This station is the closest to the research plots, and the distance and direction from the plots to the station are 18 miles east-southeast. Growing degree days (GDD) were calculated by averaging the daily high and low temperatures and subtracting the base temperature, which was 10 C. This temperature was chosen because it is a standard base temperature for crop plants and *Amaranthus* spp. (Guo and Al-Khatib 2003). Days with a negative value after the subtraction of the base temperature defaulted to 0 GDD. Accumulation of GDD began on April 1 of each year and continued through the growing season.

Table 2-2. Cumulative growing degree day (GDD, base 10 C) and rainfall (cm) for Iowa Central Climate Division, Iowa Environmental Mesonet Station IAC005, April 1 through August 31, 2019 and 2020.

	GDD		Rainfall	
Date	2019	2020	2019	2020
	----(base 10C)----		----(cm)----	
April 1-15	52	37	1.9	2.9
April 16-30	126	110	3.0	0.9
May 1-15	182	179	5.8	2.3
May 16-31	314	303	15.4	11.1
June 1-15	481	505	0.6	1.3
June 16-30	660	708	9.5	2.7
July 1-15	880	917	7.7	5.6
July 16-31	1090	1141	4.0	1.5
Aug 1-15	1281	1318	1.1	2.5
Aug 16-31	1444	1518	2.2	0.1

Results & Discussion

Year was not significant in the analysis of seed persistence, so data were pooled across 2019 and 2020. Population, depth, and their interaction were significant for seed persistence of the three *Amaranthus* spp. populations: ApIA = Iowa Palmer amaranth; ApKS = Kansas Palmer amaranth; AtIA = Iowa waterhemp. Seed of ApIA and AtIA were more persistent at 15-cm than 1-cm soil depths, whereas ApKS persistence was not affected by the burial depth (Figure 2-1). At the 1 cm depth, viability was 22, 54, and 43% for ApIA, ApKS and AtIA, respectively. Viability of seeds buried at 15 cm depth was 55, 60, and 72% for ApIA, ApKS, and AtIA, respectively. ApIA was less persistent than ApKS and AtIA at the 1 cm depth, but was only less persistent than AtIA at 15 cm. Seed characteristics can vary widely among populations within a species (Korres et al. 2018), but these data suggest Palmer amaranth, like waterhemp, is capable of establishing persistent seed banks in Iowa.

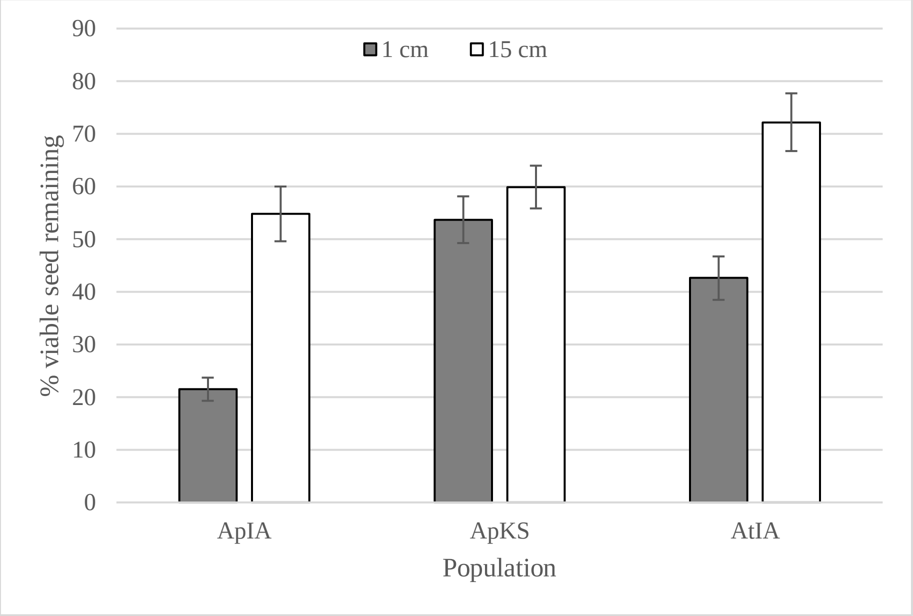

Figure 2-1. Viability of Iowa Palmer amaranth (ApIA), Kansas Palmer amaranth (ApKS), and Iowa waterhemp (AtIA) seeds buried at 1 and 15 cm depths in the soil approximately 9 months after burial, pooled across 2019 and 2020. Error bars represent standard error of the mean.

For 2019 emergence, slope of the model differed between ApIA and both ApKS and AtIA; ApKS and AtIA were similar (Figure 2-2, Table 2-3). ED50, the time to 50% emergence, differed between populations (Table 2-4). ED50 for ApIA, ApKS, and AtIA were 18.7, 25.0, and 12.3 days, respectively. Waterhemp reached 50% cumulative emergence approximately 1 to 2 weeks earlier than Palmer amaranth, suggesting it is adapted to cooler soil temperatures at the beginning of the growing season than Palmer amaranth. The time to 10% emergence, ED10, was also calculated for all three populations. ED10 was 12.5, 10.3, and 5.2 days, respectively, for ApIA, ApKS, and AtIA. Emergence for all populations began on day of year (DOY) 140, or May 20, 2019.

Table 2-3. Log-logistic model parameter estimation for 2019 and 2020 Iowa Palmer amaranth (ApIA), Kansas Palmer amaranth (ApKS), and Iowa waterhemp (AtIA) seedling emergence. ED_{50} represents time to 50% emergence.

	Population	**2019**		**2020**	
		Estimate	StdErr	Estimate	StdErr
Slope	ApIA	-5.39	0.59	-12.39	1.96
	ApKS	-2.49	0.19	-7.95	0.67
	AtIA	-2.56	0.19	-7.83	0.63
Upper limit	ApIA	97.47	0.98	98.32	0.49
	ApKS	103.4	2.13	96.08	0.52
	AtIA	100.1	1.13	97.74	0.52
ED50	ApIA	18.70	0.36	18.95	0.18
	ApKS	24.98	0.84	19.16	0.17
	AtIA	12.26	0.45	19.42	0.17

Table 2-4. Differences between population parameters estimated by log-logistic model for 2019 and 2020 Iowa Palmer amaranth (ApIA), Kansas Palmer amaranth (ApKS), and Iowa waterhemp (AtIA) seedling emergence.

	Comparison	**2019**		**2020**	
		Estimate	p-value	Estimate	p-value
Slope	ApIA/ApKS	2.17	6.40e-05	1.56	0.05
	ApIA/AtIA	2.11	8.75e-05	1.58	0.04
	ApKS/AtIA	0.97	NS	1.02	NS
ED_{50}	ApIA/ApKS	0.75	9.213-16	0.99	NS
	ApIA/AtIA	1.53	6.25e-15	0.98	0.05
	ApKS/AtIA	2.04	<2.2e-16	0.99	NS

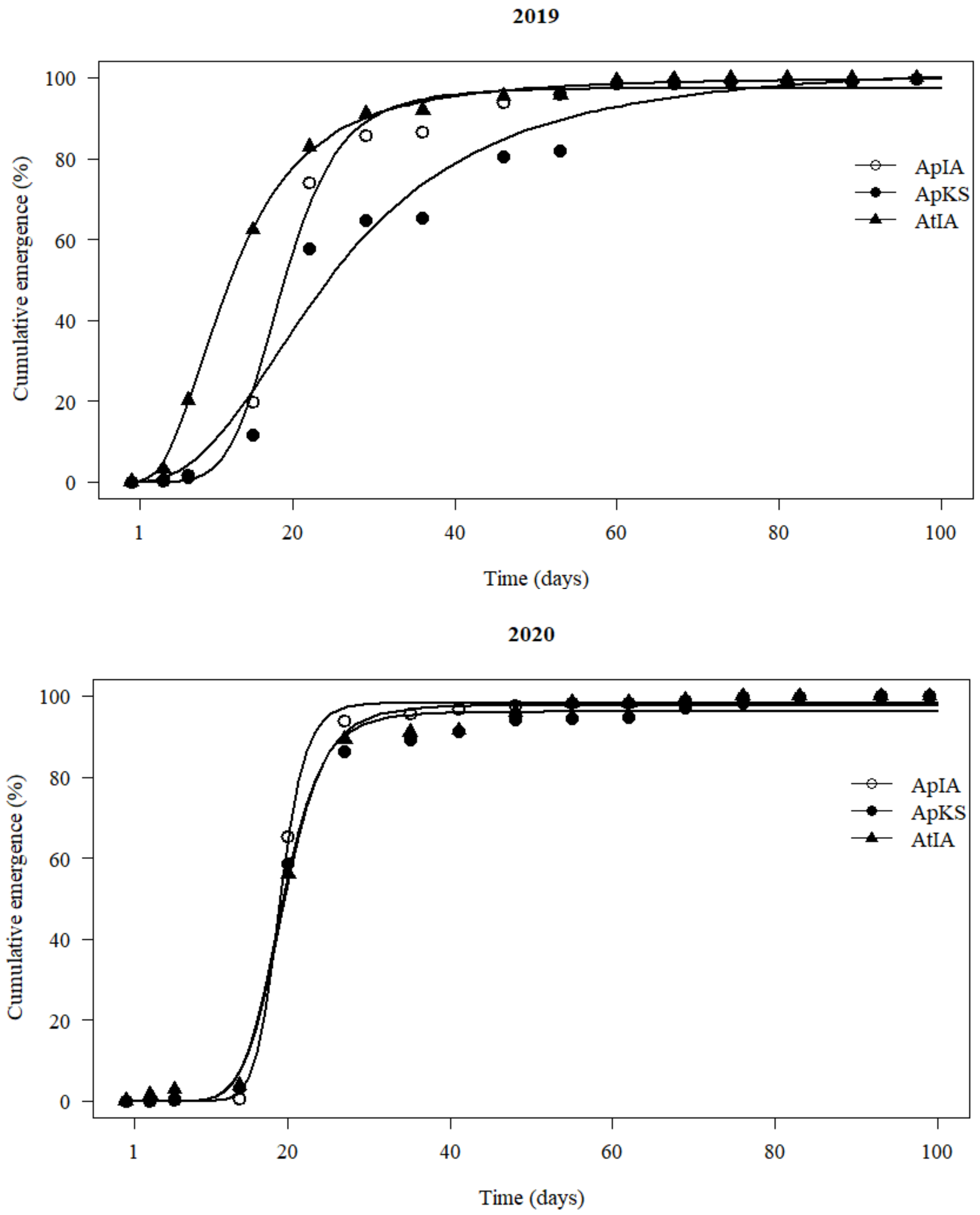

Figure 2-2. Nonlinear regression using log-logistic model for emergence, plotting cumulative emergence by days from initiation of emergence (day 0) for Iowa Palmer amaranth (ApIA), Kansas Palmer amaranth (ApKS), and Iowa waterhemp (AtIA). Day 0 was the day that emergence began in any plot each year; day 0 in 2019 was DOY 140 and in 2020 was DOY 136.

Emergence began on DOY 136, or May 15, in 2020. Initial emergence was three days earlier in 2020 that in 2019, even though there had been fewer accumulated GDD at the time of initial emergence. Similar to 2019, the slope of the emergence models differed among populations in 2020 (Figure 2-2, Table 2-4). ApIA slope was different than the slopes of ApKS and AtIA, whereas ApKS and AtIA were similar. ED50 differed between ApIA and AtIA, but other values were similar. ED50 was 18.9, 19.2, and 19.4 days, respectively, for ApIA, ApKS, and AtIA (Table 2-3). ED10 was 15.9 days for ApIA, 14.5 days for ApKS, and 14.7 days for AtIA. In 2020, waterhemp emergence was about 7%, and emergence of Palmer amaranth ranged from 9% for the Kansas population to 19% for the Iowa population. Germination rates were similar for 2019. These numbers are similar to what has been reported for waterhemp in other experiments (Buhler and Hartzler 2001; Leon and Owen 2006). Palmer amaranth also germinates at low percentages, with up to 0.8% of buried seeds emerging from a 10 cm burial depth over four years (Jha et al. 2014). Deeper burial likely led to lower rates of germination, even with soil disturbance, than was observed when seed was mixed into the upper 0.5 cm of soil. Emergence of Palmer amaranth in the greenhouse was greater at 0.6 to 2.5 cm burial depths than at 5 to 7 cm (Keeley et al. 1987). About 40% of seed planted at the shallow depth emerged after four weeks, compared to 7% at 5 to 7 cm.

Although seed persistence among populations was variable, more than 50% of seed of all populations buried at 15 cm were viable at the end of the growing season. Persistent seed complicates management since multiple years of effective control are required to deplete the seed bank. An area for further research would be to repeat the persistence study at two locations with different soil types. Palmer amaranth seeds have been found to be less persistent in silt loam than they are in sandy loam (Franca et al. 2020). Other areas for expansion include testing seed viability after two or more years of burial, including more burial depths or populations of both species, and testing for germinability after differing periods of burial.

Due to differences between the emergence of the two populations of Palmer amaranth, it is unclear whether the two species vary in emergence patterns. Differences between the two populations of Palmer amaranth could be due to genetic differences or differences in environmental conditions during seed maturation. The environment in which the mother plant grows, develops, and reproduces affects the dormancy and germination of seeds produced by that plant (Jha et al. 2010b; Karimmojeni et al. 2014; Matzrafi et al. 2020). Differences between 2019 and 2020 emergence could be due either to after-ripening of the seed in cold storage or environmental differences between 2019 and 2020. Germinability of the seeds was higher prior to planting for 2020 than in 2019. Accumulation of GDD began earlier in 2019 than in 2020; precipitation was also greater at the start of the season in 2019 than in 2020.

Although there were statistical differences in emergence patterns between the species, the differences probably would not warrant changes in approaches to management. The emergence patterns of all populations would be considered prolonged, which complicates management. Management strategies currently used for waterhemp will likely control Palmer amaranth, although differences in herbicide resistance among populations could influence results. Integrated management systems which combine chemical control with cultural and mechanical strategies will provide the most consistent and durable management of the weedy *Amaranthus* species.

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CHAPTER 3. COMPARATIVE GROWTH OF PALMER AMARANTH (*AMARANTHUS PALMERI*) AND WATERHEMP (*A. TUBERCULATUS*) UNDER COMPETITIVE AND NON-COMPETITIVE CONDITIONS

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Abstract

Studies compared the growth and competitive abilities of a native *Amaranthus* species, waterhemp (*A. tuberculatus*), and two populations of Palmer amaranth (*A. palmeri*), a species native to the southwest US that has recently invaded Iowa. A common garden study compared the growth, biomass, and seed production of an Iowa waterhemp population and Palmer amaranth populations from Iowa and Kansas. Under non-competitive conditions, Palmer amaranth produced more biomass than waterhemp in one of four trials but had no advantage in number of seed produced. Palmer amaranth initiated flowering approximately two weeks earlier than waterhemp. A greenhouse replacement study compared the competitive abilities of waterhemp and Iowa Palmer amaranth at five proportions (0:4, 1:3, 1:1, 3:1, 4:0). Average daily high temperature was 29 C in the greenhouse, which would favor growth of Palmer amaranth over waterhemp. Palmer amaranth produced twice as much biomass as waterhemp in the first six weeks of growth, regardless of planting proportion.

Introduction

Palmer amaranth (*Amaranthus palmeri* S. Watson) is native to the southwestern United States and northern Central America (Sauer 1957). Mature plants typically reach one m in height but can grow as tall as three m (Sauer 1955). Palmer amaranth was identified as an “up-and-coming troublesome weed” in the southern United States in a 1995 survey (Webster and Coble

1997) and was on the list of the top-five most troublesome weeds in the South in 2009. From 1994 to 2009, Palmer amaranth had one of the greatest increases in importance as a weed in corn crops (Webster and Nichols 2012). The same survey identified Palmer amaranth as the second most important weed in soybean. There have been reports of herbicide resistance beginning in 1992, with a recent study reporting a Kansas population with resistance to six sites of action: synthetic auxin, ALS-inhibitor, PSII-inhibitor, EPSPS-inhibitor, PPO-inhibitor, and HPPD-inhibitor (Gossett et al. 1992; Shyam et al. 2021).

Palmer amaranth is highly competitive, causing farmers to tailor management to control this weed. Rapid growth and large leaf area allow Palmer amaranth to shade crop plants, and yield loss is probable if the weed is not appropriately controlled. In response to shading, Palmer amaranth plants were able to increase their specific leaf area up to 43% as shading increased to 87% (Jha et al. 2008). Corn yield was reduced up to 91% with eight Palmer amaranth plants m^{-1} (Massinga et al. 2001), and cotton lint yield was reduced 54% by ten plants m^{-1} (Morgan et al. 2001). Many aspects of sorghum harvest were affected negatively by Palmer amaranth, including harvest efficiency, foreign material contamination, seed loss, grain grade, and grain yield (Moore et al. 2004).

Waterhemp (*Amaranthus tuberculatus* [Moq.] J. D. Sauer) is another problematic, dioecious amaranth. Plants are often described as relatively short when compared to Palmer amaranth, but can achieve heights up to three m (Sauer 1955). Waterhemp decreased soybean yield by 40% when it emerged before the V5 stage and competed for the whole season (Steckel and Sprague 2004). When compared to weed free treatments, soybean that competed with waterhemp for 10 weeks experienced a 43% reduction in seed yield (Hager et al. 2002). The effects of waterhemp on corn varied from 11 to 74% yield reduction when waterhemp was allowed to compete season-long (Steckel and Sprague 2006). Herbicide resistance contributes to management problems for waterhemp in the Midwest, with some biotypes resistant to five sites of action (Evans et al. 2019).

Differences in competitive ability among weeds are often due to differences in plant architecture. In general, Palmer amaranth is a larger plant, capable of producing greater biomass and leaf area than waterhemp. In a study comparing the species in Kansas, Palmer amaranth had higher growth rate, greater height, more primary branches, larger leaf area, and greater dry weight (Horak and Loughin 2000). A similar study in Missouri reported Palmer amaranth emerged earlier in the season than waterhemp which allowed it to accumulate greater height and biomass (Sellers et al. 2003). Waterhemp produced more seeds than Palmer amaranth, but Palmer amaranth seed was larger.

When plants were grown in competition with soybean, Palmer amaranth again emerged earlier than waterhemp (Bensch et al. 2003). Waterhemp produced more seed per square meter than Palmer amaranth at high weed densities, but Palmer amaranth produced more seeds at low weed density, indicating greater seed production per plant. Palmer amaranth caused greater losses in soybean yield than waterhemp at all weed densities. Palmer amaranth dry biomass and seed production were decreased when emergence was delayed by two weeks relative to soybean emergence, but late-emerging Palmer amaranth plants still produced up to 3,500 seeds plant^{-1} (Korres et al. 2020).

The purpose of these studies is to compare the growth and reproduction of waterhemp and Palmer amaranth in Iowa. It is hypothesized that Palmer amaranth will be a larger plant with higher seed production when grown separately from other plants in the common garden study. When plants are competing intra- and/or interspecifically in the replacement study, it was hypothesized that waterhemp will be the more successful plant due to its adaptation to Iowa soil and weather.

Materials and Methods

Plant material

Waterhemp seed used in this experiment was collected from the Iowa State University Horticulture Farm near Gilbert, Iowa in September 2018. Palmer amaranth seed was collected from Pottawattamie County, Iowa and Riley County, Kansas in August 2018. Seed was hand threshed and cleaned using a series of sieves and an air column blower (Seedburo Equipment Company, Des Plaines, IL). Seed was stored at 6 C. Prior to planting, seeds were primed to remove dormancy by soaking in water for at least 14 days at 6 C and then drying at 50 C for 24 hours. The 2018 seed was used for both 2019 and 2020 to reduce genetic variability between years.

Plants were started in the greenhouse on May 15, 2019 and May 5 and 12, 2020. Seeds were planted in soilless potting media (Sun Gro Horticulture, Agawam, MA) in Speedling flats (6.5 cm^2, 6.4 cm deep; Speedling, Ruskin, FL). Plants were thinned to one plant per cell.

Common garden study

Experiments were conducted at two locations: Iowa State University Johnson Farm (JF) located south of Ames, Iowa and Iowa State University Applied Sciences Farm (ASF) located north of campus near Squaw Creek. Soil type at Johnson Farm is a well-drained Clarion loam with 2 to 6% slope; soil type at Applied Sciences Farm is moderately drained Hanlon fine sandy loam with 0 to 2% slope (Soil Survey Staff 2021). Plots were established on June 7, 2019 and June 3, 2020. The field was prepared for planting with tillage and application of 1.6 kg ha^{-1} glyphosate and 0.07 kg ha^{-1} imazethapyr on June 5, 2019 and June 2, 2020. Fertilizer with a composition of 12-12-12 was applied in 2020 at a rate of 488 kg ha^{-1}. Seedlings were transplanted on June 7, 2019 and June 3, 2020 at a density of one plant 1.5 m^{-2}. Each location contained twelve blocks, and blocks consisted of one plant of each of the three *Amaranthus* populations.

Dead or missing plants were replaced until July 1, 2019 and 2020 with similar sized plants. Weeds that emerged in plots following transplant were removed by hand as necessary during weekly data collection. Plant height and width were measured weekly starting June 18, 2019 and June 25, 2020 and continued until harvest. Plots were harvested when a majority of plants reached maturity; harvest occurred on August 23 and 30, 2019 and September 2 and 9, 2020. Seedheads were removed and placed in paper bags; the remainder of the plants were cut at soil level and placed in canvas bags for drying. Biomass was dried at 60 C for 7 days. Plants and seedheads were weighed, then seed was threshed manually and cleaned using sieves and an air column blower (Seedburo Equipment Company, Des Plaines, IL). Seed number was determined by weighing lots of 100 seeds and averaging those weights. Plants with low seed number were counted manually.

Greenhouse competition study

A greenhouse competition study was initiated on July 22 and October 7, 2020 in the Iowa State University Agronomy Teaching Greenhouse. Waterhemp seeds were prepared for planting by soaking and chilling at 6 C for at least two weeks prior to planting. Seeds were planted into 21 cm, 6.6 L greenhouse pots filled with moistened, sterile potting media (Nursery Supplies, Inc., Orange, CA; Sun Gro Horticulture, Agawam, MA). Seeds were spaced 8 to 9 cm apart with a planting density of four plants per pot or 115 plants m^{-2} (Anderson et al. 1996; Duff et al. 2009; Soltani et al. 2008). Pots were watered daily, and light was supplemented 12 hours per day. Plants were harvested 40 days after planting by cutting at the soil surface. Biomass was dried at 60 C for 48 hours, and dry biomass was weighed.

Data analysis

Data was analyzed using SAS® software version 9.4. Where necessary, data were transformed using either square-root or logarithmic transformations to meet assumptions of the model. Significance was determined at the α=0.05 level. For heights in the garden study, years were analyzed separately due to differences between 2019 and 2020. Probability of flowering was analyzed in *R* using a log-logistic model in the drc package (Ritz et al. 2015). Year was not significant, so data were pooled across 2019 and 2020. Relative growth rate for plant height was calculated by year, location, and population across the growing season; only 2019 data will be discussed, and values will be pooled across locations. Fecundity was analyzed separately by year. Seed produced per gram of dry biomass per plant (seed/DM) was calculated for female plants; years were analyzed separately.

Greenhouse competition study biomass data were compared using an analysis of variance (ANOVA) and used to calculate relative yield (RY), an index commonly used to compare the competitiveness of plants in mixture. Relative yield were calculated for each species at each ratio by dividing yield in mixture by the appropriate proportion of yield in monoculture (Williams and McCarthy 2001; De Wit 1960). RY values were compared using ANOVA. A one-sample t-test was used to compare RY values to a null-hypothesis value of 1.

Climate data was obtained from the Iowa State University Iowa Environmental Mesonet National Weather Service COOP Network (Table 3-1). The station selected was IAC005 Iowa – Central Climate Division which is located about 15 miles east of Ames in Sherman, Iowa. This station is the closest to the research plots, and the distance and direction from the plots to the station are 18 miles east-southeast. Growing degree days (GDD) were calculated by averaging the daily high and low temperature and subtracting the base temperature, which was 10 C. This temperature was chosen because it is a standard base temperature for crop plants and *Amaranthus* spp. Days with a negative value after the subtraction of the base temperature defaulted to 0 GDD. Accumulation of GDD began on April 1 of each year and continued through the growing season.

Table 3-1. Cumulative growing degree day (GDD, base 10 C) and rainfall (cm) for Iowa Central Climate Division, Iowa Environmental Mesonet Station IAC005, June 1 through August 31, 2019 and 2020.

	GDD		Rainfall	
Date	2019	2020	2019	2020
	--(base 10 C)--		----(cm)----	
June 1-15	481	505	0.6	1.3
June 16-30	660	708	9.5	2.7
July 1-15	880	917	7.7	5.6
July 16-31	1090	1141	4.0	1.5
Aug 1-15	1281	1318	1.1	2.5
Aug 16-31	1444	1518	2.2	0.1

Results & Discussion

Common garden study

Environmental conditions were more challenging in 2020 than in 2019. The beginning of the season was hot, dry, and windy, resulting in higher seedling mortality in 2020 than in 2019. Furthermore, there was a severe windstorm known as a derecho that occurred on August 10, 2020. Plants were blown over and some branches were partially separated from the main stem. Vascular connections remained and allowed seed fill to continue. The damage likely contributed to the variability in 2020 growth rate, biomass and fecundity, thus only height and biomass were analyzed for 2020 to demonstrate differences between years. Location was the only factor significant in the analysis of plant height in 2019 (Figure 3-1, Table 3-2). All populations were taller at ASF than JF. In addition to soil differences between the sites, the ASF is a low-lying area with a tree line approximately 20 to 100 m on three sides that would provide shelter from wind. In 2020, the population by location interaction was significant. ApKS was taller at JF than it was at ASF. There were no differences between populations within locations. Across years, females were an average of 24%, or 33.7 cm, taller than males (data not shown).

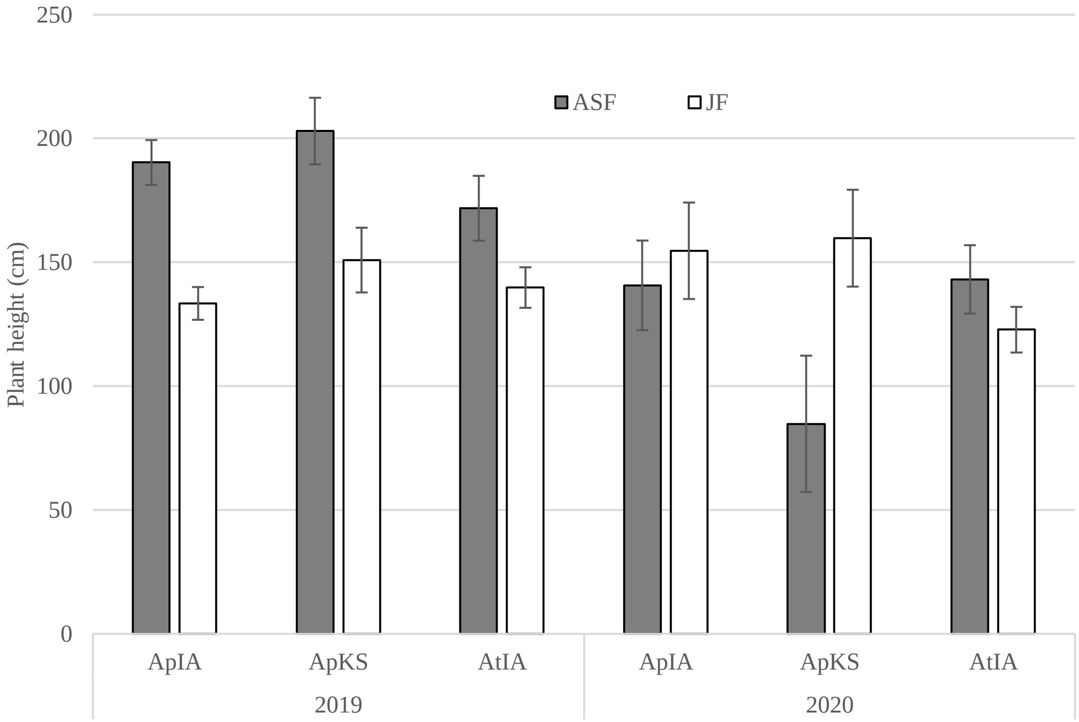

Figure 3-1. End-of-season plant height of Iowa Palmer amaranth (ApIA), Kansas Palmer amaranth (ApKS), and Iowa waterhemp (AtIA) grown at two locations, Applied Science Farm (ASF, fine sandy loam soil) and Johnson Farm (JF, loam soil) in central Iowa in 2019 and 2020. Error bars represent standard error of the mean.

Plant relative growth rates (RGR; cm cm^{-1} day^{-1}) in 2020 were affected by environmental conditions, so only 2019 values will be discussed. Across sampling dates and locations, waterhemp had higher RGR than both populations of Palmer amaranth (data not shown). On day of year (DOY) 176, or June 25, waterhemp had higher RGR than Palmer amaranth (Figure 3-2). On DOY 182, or July 1, RGR for waterhemp was higher than for ApIA; ApKS was similar to both. On DOY 190, or July 9, ApKS had lower RGR than both ApIA and waterhemp. Plant sex did not have an effect on RGR. Maximum RGR for all populations were between 0.06 and 0.08 cm cm^{-1}day^{-1} and occurred on DOY 190. Early-season differences indicate an advantage of waterhemp over Palmer amaranth under cooler temperatures. As the season progressed and more GDD accumulated, differences between the species became statistically insignificant, and Palmer amaranth RGR did not surpass waterhemp RGR. In contrast to these observations, Palmer amaranth is usually characterized by greater RGR (g g^{-1}day^{-1}) than waterhemp, with maximum values of 0.32 and 0.31, respectively (Horak and Loughin 2000). This difference indicates that management strategies should focus primarily on Palmer amaranth due to high RGR. In Iowa, however, management decisions should still be tailored for control of waterhemp.

Table 3-2. Results of ANOVA for end-of-season height, end-of-season dry biomass, fecundity, and seed weight in common garden studies, 2019-2020. Populations were Iowa Palmer amaranth, Kansas Palmer amaranth, and Iowa waterhemp; locations were Applied Science Farm (ASF, fine sandy loam) and Johnson Farm (JF, loam).

	Height		**Biomass**		**Fecundity**	**Seed weight**
Variable	2019	2020	2019	2020	2019	2019
	---------cm---------		---------g---------		--seed plant^{-1}--	seed g biomass^{-1}
Population	NS	NS	0.0014	NS	NS	NS
Location	0.0003	NS	<.0001	NS	NS	0.0499
Population x Location	NS	0.0461	NS	NS	NS	NS

In 2019, both location and population affected biomass. Both Palmer amaranth populations produced more biomass than waterhemp, and plants at ASF were 380% more productive than plants at JF (Figure 3-3, Table 3-2). In 2020, only plant sex had a significant effect on plant weight. The population by location interaction had a p-value of 0.0662, but some differences within this interaction were significant, as shown in Figure 3-3. At JF, ApKS produced more biomass than AtIA; ApIA biomass value was similar to both ApKS and AtIA. Female plants weighed an average of 87%, or 619.8 g, more than male plants in both years (data not shown).

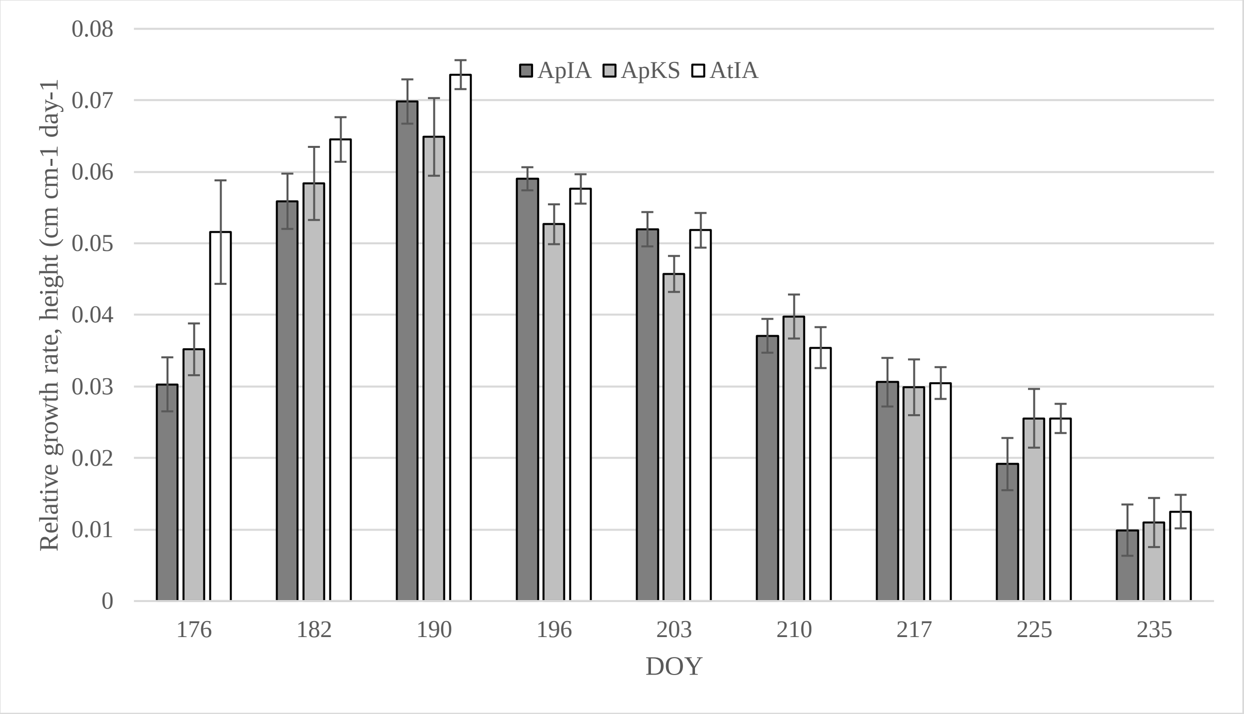

Figure 3-2. Relative growth rate (cm cm-1 day-1) of Iowa Palmer amaranth (ApIA), Kansas Palmer amaranth (ApKS), and Iowa waterhemp (AtIA) by day of year (DOY) in 2019. Error bars represent standard error of the mean. DOY 176 was June 25; DOY 203 was July 22; DOY was August 23.

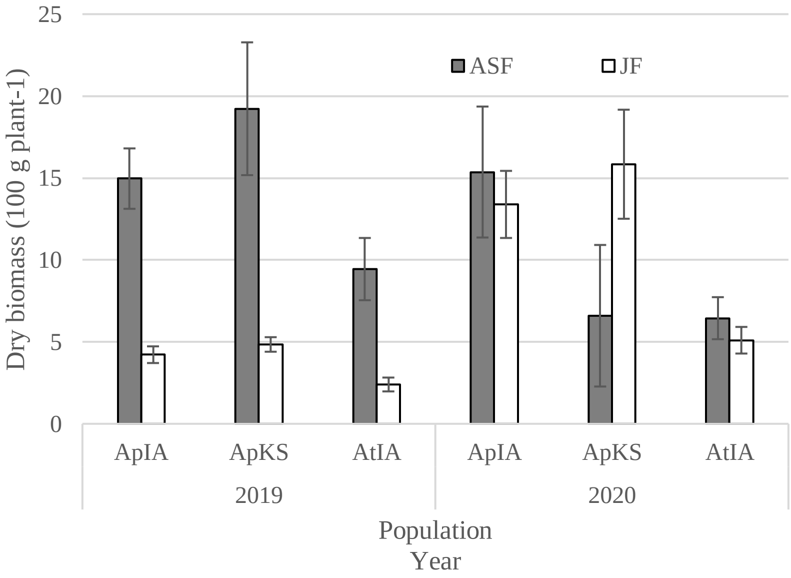

Figure 3-3. Dry biomass of Iowa Palmer amaranth (ApIA), Kansas Palmer amaranth (ApKS), and Iowa waterhemp (AtIA) grown at two locations, Applied Science Farm (ASF, fine sandy loam soil) and Johnson Farm (JF, loam soil) in central IA in 2019 and 2020. Error bars represent standard error of the mean.

Plants in the competition study were expected to have a sex ratio of 1:1, male to female. Observed ratios were 1.75:1 for ApIA, 2.15:1 for ApKS, and 2.40:1 for AtIA. When these values were compared to the expected ratio, 1:1, there were no differences (data not shown). Palmer amaranth sex ratio has been found to vary with plant density, ranging from 0.6:1 at a low density to 1.9:1 at a high density (Korres and Norsworthy 2017). The sex ratio of Palmer amaranth has been reported to be as low as 0.55:1 (Lemen 1980). Waterhemp sex ratio varied with the addition of compost fertilizer, from 1.1:1 to 1.4:1 (Menalled et al. 2004). Seeds could not be selected by sex and so distribution of females and males is random, as indicated by inconsistent differences between observed and expected ratios. Plant sex was identified at flowering and confirmed at harvest. Due to differences in ratios of sexes, and differences in growth of female and male plants, average heights and weights could be affected by the sex ratio of populations at individual sites.

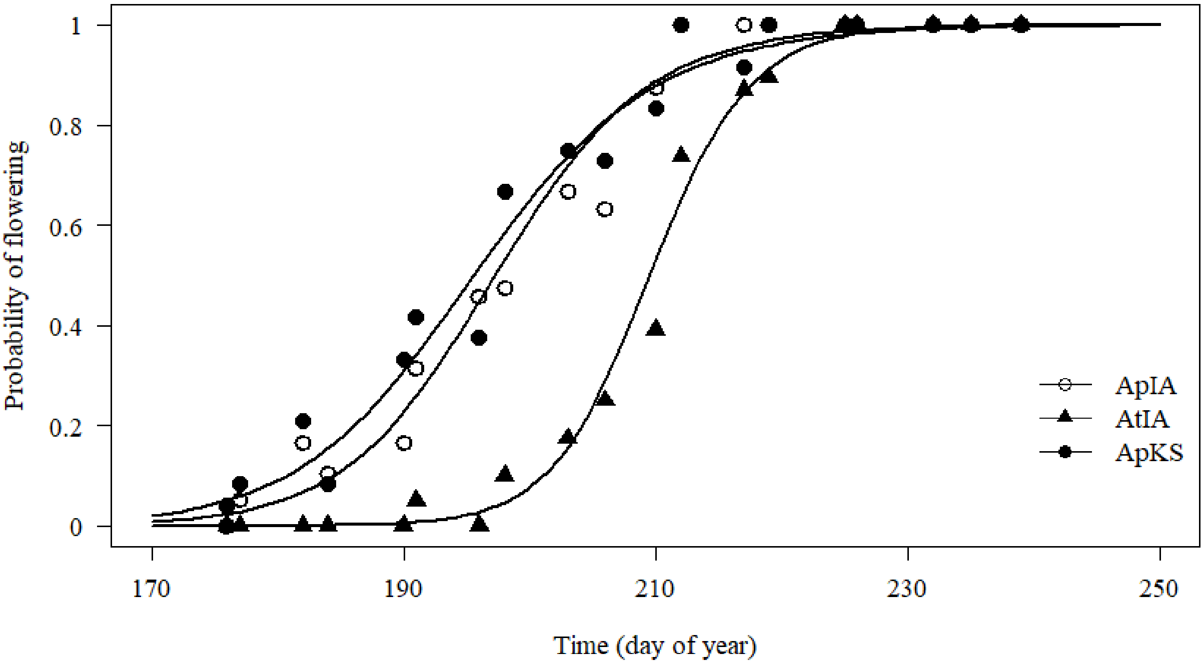

Figure 3-4. A 3-parameter log-logistic model plotting the probability of Iowa Palmer amaranth (ApIA), Kansas Palmer amaranth (ApKS), and Iowa waterhemp (AtIA) flowering by Julian day of year for 2019 and 2020, combined.

Both Palmer amaranth populations reached 10 and 50% flowering before waterhemp, with the two Palmer amaranth populations reaching 50% flowering approximately two weeks earlier than waterhemp (Figure 3-4). Amaranths are short-day plants; flowering is initiated by shortening photoperiod (Wu and Owen 2014). In a common garden study involving cocklebur (*Xanthium strumarium*) biotypes from several Midwestern USA locations, later flowering biotypes produced more biomass than earlier flowering biotypes (Lee and Owen 2003). A similar response has been observed in wild radish (Ashworth et al. 2016). Plants selected for early flowering had reduced plant biomass compared with late-flowering plants. The early flowering of Palmer amaranth observed in these studies could reduce their productivity in Iowa compared to southern states where they are better adapted.

Physical breakage of plants by the derecho in 2020 is thought to have affected seed production, so only 2019 data are presented. Fecundity was highly variable among populations and locations, and no differences were observed (Figure 3-5, Table 3-2). Seed weights of both populations of Palmer amaranth were greater than waterhemp, as indicated by the number of seeds per gram (data not shown). Waterhemp produced more seed per gram of biomass than Palmer amaranth (Figure 3-6, Table 3-2). Waterhemp has been found to produce twice as many seeds per gram of dry biomass, compared to Palmer amaranth, while Palmer amaranth produced larger seed than waterhemp (Sellers et al. 2003).

Results of these field experiments indicate that Palmer amaranth is adapted to Iowa conditions and could pose a threat to agricultural production. In 2019, both Palmer amaranth populations produced approximately 85% more biomass than waterhemp. In 2019, all populations accumulated more height and biomass at the site with a well-drained, sandy soil (ASF) compared to the site with a loam soil (JF). ApIA and AtIA had greater biomass at ASF than JF in 2020. Location did not affect seed production of any population. It was hypothesized that Palmer amaranth would be more productive on the well-drained, sandy soil, and this was found to be true, but waterhemp was more productive on the sandy soil as well.

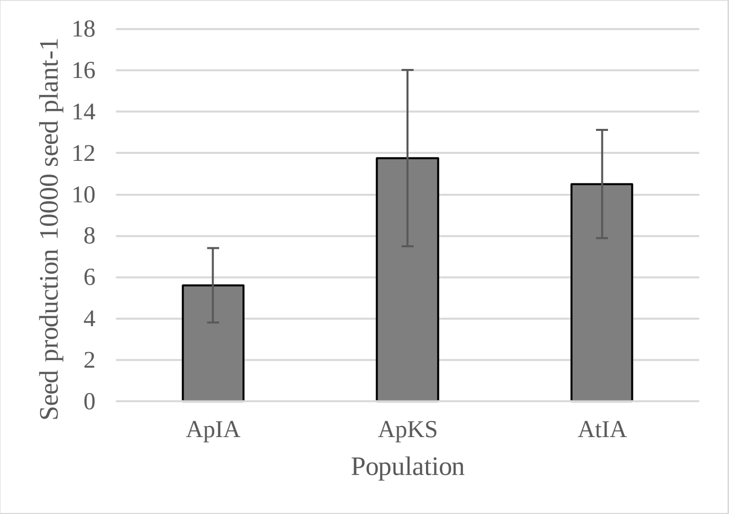

Figure 3-5. Fecundity of Iowa Palmer amaranth (ApIA), Kansas Palmer amaranth (ApKS), and Iowa waterhemp (AtIA) grown at two locations, Applied Science Farm (ASF, fine sandy loam soil) and Johnson Farm (JF, loam soil) in central IA in 2019. Error bars represent standard error of the mean.

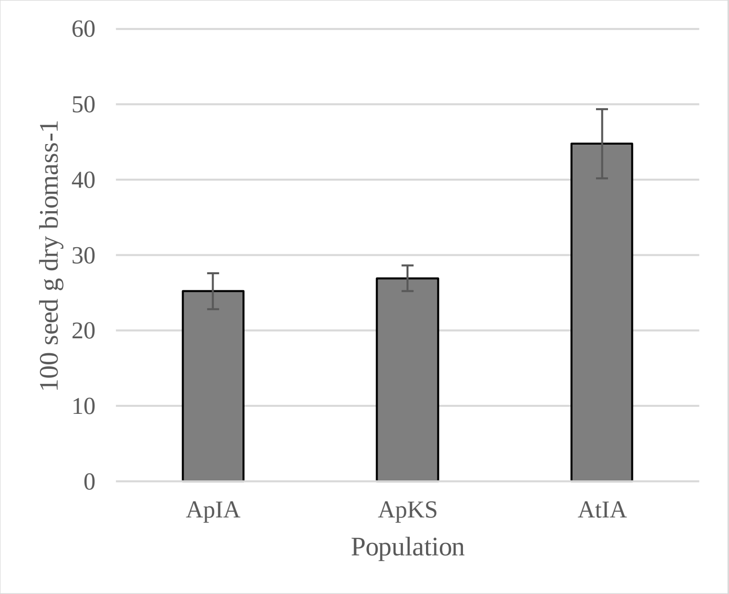

Figure 3-6. Seed weight (seed per gram of dry biomass) of Iowa Palmer amaranth (ApIA), Kansas Palmer amaranth (ApKS), and Iowa waterhemp (AtIA) grown at two locations, Applied Science Farm (ASF, fine sandy loam soil) and Johnson Farm (JF, loam soil) in central IA in 2019. Error bars represent standard error of the mean.

Greenhouse competition study

Palmer amaranth (ApIA) produced twice as much biomass as waterhemp (AtIA), 3.0 g plant^{-1} compared to 1.5 g plant^{-1} (Figure 3-7). The ratio of the two species contained in a pot did not affect growth of either ApIA or AtIA.

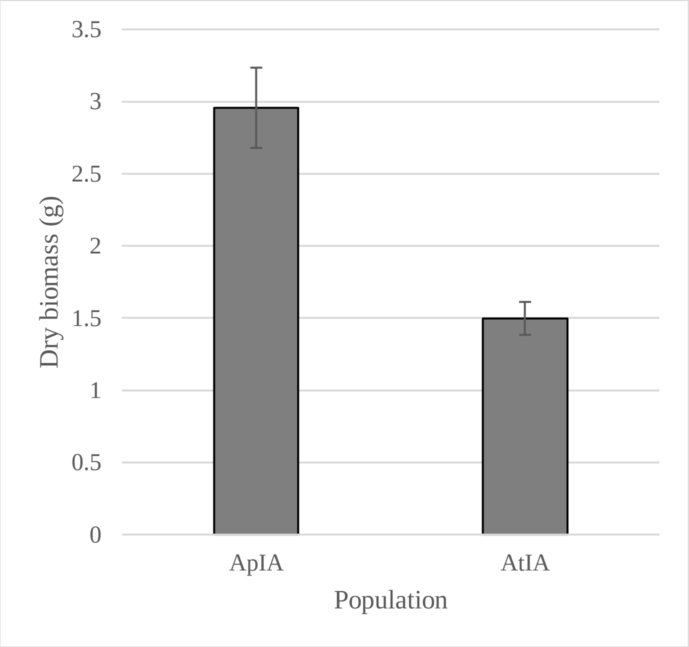

Figure 3-7. End-of-season dry biomass (gram plant^{-1}) of Iowa Palmer amaranth (ApIA) and Iowa waterhemp (AtIA) in a greenhouse replacement series study (Anderson et al. 1996, Duff et al. 2009). Error bars represent standard error of the mean.

Relative yield (RY) for ApIA was 1.24 and 0.75 for AtIA (Figure 3-8). The T-test for RY compared calculated values to the null hypothesis value of 1. ApIA RY value did not differ from 1; however, AtIA RY value was different from 1 with a p-value of 0.0021. RY values less than one indicate that the species does better in monoculture than it does in mixture with the other species. The reduction in RY for waterhemp indicates that Palmer amaranth was more competitive than waterhemp under greenhouse conditions.

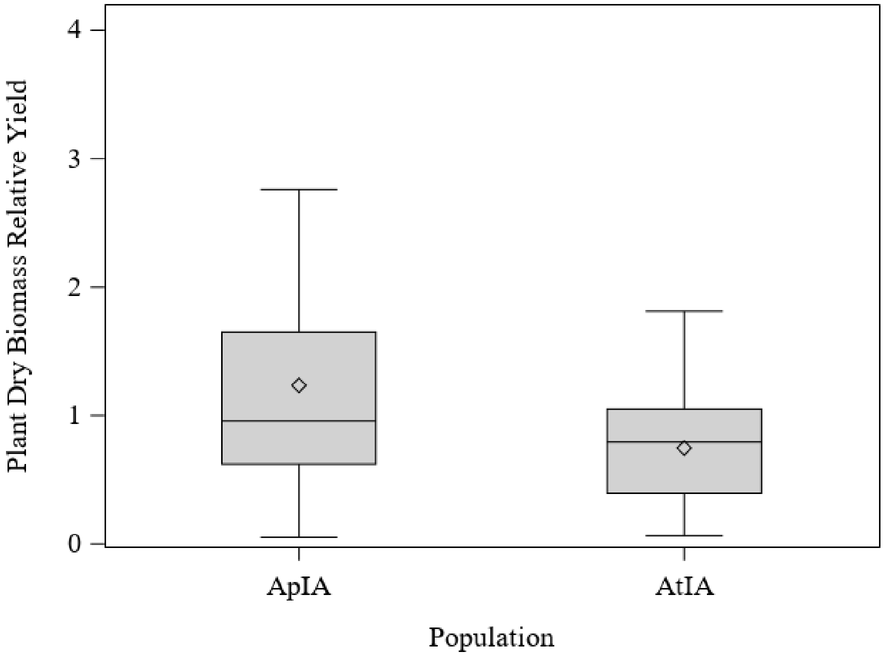

Figure 3-8. Box and whisker plots for relative yield (RY) calculated for end-of-season plant dry biomass (gram plant^{-1}) of Iowa Palmer amaranth (ApIA) and Iowa waterhemp (AtIA) in a replacement series study (Anderson et al. 1996, Duff et al. 2009). When yield in mixture > yield in monoculture, RY > 1.

Greater competitive ability in Palmer amaranth is supported by the findings of Bensch et al. (2003), Klingaman and Oliver (1994), and Hager et al. (2002) which found that Palmer amaranth reduced soybean yield 20% more than waterhemp. This is consistent with yield reduction of corn by Palmer amaranth and waterhemp; waterhemp reduced yield up to 74% and Palmer amaranth reduced yield up to 91% (Massinga et al. 2001; Steckel and Sprague 2006). If plants had been established at a higher density in the pots, it is likely that competition would have begun at earlier growth stages which could lead to greater differences in RY between ApIA and AtIA.

Greenhouse temperatures averaged 29 C, with spikes up to 36 C or higher (data not shown). These temperatures are generally higher than those present early in Iowa growing seasons, when waterhemp and other annual weeds emerge following planting. High greenhouse temperatures may have favored Palmer amaranth, therefore allowing it to suppress waterhemp and reduce AtIA RY. Palmer amaranth produced more biomass than waterhemp when both species were grown at alternating temperatures of 35/30 C; whereas waterhemp produced more biomass at 15/10 C (Guo and Al-Khatib 2003). Palmer amaranth was also more heat-tolerant than waterhemp, with 50% of Palmer amaranth plants surviving 10 days at 45/40 C, compared to 10% of waterhemp.

The field studies under non-competitive conditions did not indicate a consistent advantage for Palmer amaranth over waterhemp in terms of biomass or seed production. In both years, ApIA produced 62 to 240% more biomass than AtIA; however, this increased production by ApIA was not reflected in greater seed production. Early flowering of Palmer amaranth in Iowa may divert resources from vegetative growth and therefore reduce reproductive potential. Under greenhouse conditions, early vegetative growth for Palmer amaranth was twice that of waterhemp. This advantage for Palmer amaranth may have been facilitated by higher temperatures than are typically encountered early in the growing season. This research indicates Palmer amaranth is adapted to Iowa, but Iowa’s environment may not provide it the competitive advantage observed in warmer regions of the country.

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CHAPTER 4. GENERAL CONCLUSIONS

The first objective of this research was to determine short-term persistence of Palmer amaranth relative to waterhemp. Viability of seeds after one year of burial at the soil surface was variable, and consistent differences were not found between populations of Palmer amaranth and waterhemp. Both species had similar survival at 15 cm, with more than 50% of seeds remaining viable after one year. Palmer amaranth demonstrates that it can establish a persistent seed bank in Iowa, similar to waterhemp.

The second objective was to compare emergence patterns of Palmer amaranth to waterhemp. Waterhemp emerged earlier in 2019 than Palmer amaranth, suggesting that it is better adapted to cooler early-season temperatures experienced in Iowa than Palmer amaranth. Differences were less clear in 2020, possibly due to differing environmental conditions or after-ripening of the seed in cold storage. Both species exhibited prolonged emergence, requiring approximately two to three weeks to reach 50% cumulative emergence. Prolonged emergence complicates management of both species due to the need to extend control tactics later in the season. The primary concern in management of both waterhemp and Palmer amaranth in Iowa is their propensity to evolve herbicide resistance. Integrated management will provide the most reliable control.

The third objective of these studies was to compare growth of Palmer amaranth and waterhemp in two Iowa soils, a loam and a sandy loam. Only 2019 results are considered reliable due to environmental conditions in 2020 that hindered establishment and resulted in mid-season wind damage. Plant heights were greater at the location with sandy loam soil, and female plants were taller than male plants. Across locations and sampling dates, waterhemp had a higher relative growth rate than both populations of Palmer amaranth. Differences in growth rates between populations were more pronounced early in the season, indicating that waterhemp may have an advantage over Palmer amaranth during cooler temperatures typical of the early growing season in Iowa. Palmer amaranth produced more biomass than waterhemp, and plants were more productive at the site with sandy loam soil than on the loam soil. There were more males than females in the garden study, but male to female ratios were not significantly different from 1:1.

Palmer amaranth flowered up to two weeks earlier than waterhemp, allowing greater time for seed fill and maturation, but shortening the vegetative growth period. Reproductive potential could be reduced by early flowering, but in this study neither species appeared to have an advantage when it came to plant fecundity. Waterhemp produced more seed per gram of dry biomass, which has been reported previously. Palmer amaranth growth and seed production was similar to waterhemp, indicating that it is adapted to Iowa environmental conditions and may threaten agricultural production.

The fourth objective was to compare competitive abilities of Palmer amaranth and waterhemp in a greenhouse setting. Palmer amaranth produced twice as much biomass as waterhemp, regardless of species composition within pots. Relative yield of the species was calculated by comparing biomass produced in mixture with biomass produced in monoculture. Palmer amaranth relative yield did not differ from one when grown in competition with waterhemp; however, relative yield for waterhemp was significantly less than one. These results indicate Palmer amaranth was more competitive than waterhemp under the greenhouse conditions. Growth of Palmer amaranth probably was favored by the high greenhouse temperatures. The study was limited in its scope and ability to predict competitiveness of the species, but it provides a framework for future studies.

Areas for future research include identifying Iowa populations of Palmer amaranth and screening for herbicide resistance. It will be beneficial to re-examine growth of Palmer amaranth in a field setting by including more site-years in a study, as well as compare competitive abilities of Palmer amaranth and waterhemp in the field. Longer-term seed bank studies could provide valuable information on the time required to eradicate current infestations in Iowa. While much remains to be elucidated regarding fitness of Palmer amaranth in Iowa, these studies document that it is currently adapted to the environment and efforts should be taken to prevent further introductions and prevent spread from current infestations.