8-1-2015

A comparative study of the population dynamics of four Amaranthaceae species

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A COMPARATIVE STUDY OF THE POPULATION DYNAMICS OF FOUR AMARANTHACEAE SPECIES

by

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A Dissertation
Submitted in Partial Fulfillment of the Requirements for the
Doctor of Philosophy Degree

Department of Plant Biology
in the Graduate School
Southern Illinois University Carbondale
August 2015

DISSERTATION APPROVAL

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May 11, 2015

AN ABSTRACT OF THE DISSERTATION OF

LAUREN M. SCHWARTZ, for the Doctor of Philosophy degree in PLANT BIOLOGY, presented on May 11, 2015, at Southern Illinois University, Carbondale.

TITLE: A COMPARATIVE STUDY OF THE POPULATION DYNAMICS OF FOUR AMARANTHACEAE SPECIES

MAJOR PROFESSORS: Dr. David Gibson, Dr. Bryan Young, Co-Chair

Some of the most problematic agricultural weeds found in the Midwest United States are found in the Amaranthaceae family, such as *Amaranthus palmeri* and *A. tuberculatus*. These summer annual weeds are troublesome due to their competitive ability, high seed production, and resistance to herbicides from several modes of action which complicates management in field crops and has led to significant yield loss. *Achyranthes japonica* and *Iresine rhizomatosa* are two perennial species in the same family as *A. palmeri* and *A. tuberculatus* that occur in similar habitats as one another, but differ in invasiveness. *Achyranthes japonica* is a non-native, invasive species that is becoming a threat to forested areas and has been observed along agricultural field margins. *Iresine rhizomatosa* also occurs in forest habitats but is an endangered species in Illinois. This research seeks to determine the comparative life history and relative competitiveness of closely related weedy species when challenged with a dominant species. Specifically, select, closely related weedy species in the Amaranthaceae plant family that occur in southern Illinois were compared, i.e., *Achyranthes japonica*, *Amaranthus palmeri*, *Amaranthus tuberculatus*, and *Iresine rhizomatosa*. The first study examined the life history characteristics of *A. japonica* in regards to survivorship, growth and fecundity at two sites in southern Illinois (Chapter 2). *Achyranthes japonica* is a relatively new invasive species that has been poorly studied. This experiment showed that regardless of site, environmental factors had a significant

effect on seedling emergence and seed viability, which decreased from 2012 to 2013 during a drought year and rebounded from 2013 to 2014 following flooding. On average, individuals at the driest site had higher performance and fecundity, regardless of year. The second experiment tested the relative competitive effect and response of the Amaranthaceae species to *Glycine max*, first in a greenhouse study that tested shading and nitrogen resource drawdown for each species, and second in a controlled field experiment that tested intraspecific competition (Chapter 3). In addition, *A. japonica* seedlings were planted as either unmanipulated seedlings (uncut *A. japonica*) or as a seedling cut back to the soil surface at the four-node stage (cut *A. japonica*) at which point seedlings have reached a perennial growth stage. The greenhouse experiment showed that the four species each drew down light significantly, but not nitrogen. Shading decreased the aboveground biomass of the species in comparison to unshaded controls. Supplemental nitrogen, however, increased the aboveground biomass of *A. palmeri* and *A. japonica*. The supporting controlled field experiment showed that the competitive response of the weed species to the presence of *G. max* showed a reduction in height compared to the weed species grown in monocultures. *Glycine max* and the weed species, except *I. rhizomatosa*, showed a similar competitive effect and response when aboveground biomass was measured. *Achyranthes japonica* attained the highest belowground biomass when grown as a monoculture and in the presence of *G. max*. A competitive effect ranking was determined to be *A. palmeri* > *A. tuberculatus* > cut *A. japonica* = uncut *A. japonica* = *I. rhizomatosa* with the competitive response ranking being the inverse. The third study implemented an integral projection model (IPM) to determine the population growth rate of each species and how they compared to one another (Chapter 4). This experiment

showed that *A. palmeri, A. tuberculatus* and *A. japonica* each had a population growth rate greater than one indicating rapidly growing populations. By contrast, *I. rhizomatosa* had a population growth rate less than one indicating a declining population. The results suggest that *A. japonica* has not yet shown the ability to escape management strategies in agricultural fields implemented by farmers, but it is still an aggressive invasive species that farmers and land owners need to be able to identify. This species has many similar characteristics to the *Amaranthus* species, such as the ability to colonize in areas with limiting resources, continual flushes of germination throughout the growing season, the ability to outcompete other weed species, and high fecundity but, *A. japonica* also is a perennial species that can withstand removal of shoot material and has a high germination rate. Based on these results, only early detection and rapid response methods should be relied on to keep these species out of areas in and around agricultural fields. *Iresine rhizomatosa*'s performance in these studies was consistent with its rarity.

DEDICATION

I would like to dedicate this to Brice Lazaro who has been with me from the start and whom will be with me until the end. Thank you for always being by my side.

ACKNOWLEDGEMENTS

I would like to thank my two co-advisors, Dr. David Gibson and Dr. Bryan Young, for their endless support and advice, which I would have been lost without. Thank you for imparting your knowledge and expertise so that I could grow as a scientist. Thank you for providing endless opportunities to help me achieve my dreams, even when I am not always sure what they are. I also would like to thank Drs. Loretta Battaglia, Sedonia Sipes, and Andrew Wood for their input and encouragement throughout this journey. Each person offered something unique to this project and made new territory manageable.

I would like to thank Julie Young for helping me tackle what seemed like an impossible task at times and for always believing in me. Her technical support and outside perspective was an invaluable resource for me. I also extend my gratitude to Joe Matthews, Eric Miller, and Emily Edler for their assistance in organizing and carrying out day to day operations and to Ron Krausz for his witty banter and advice that has made me a better person both personally and professionally. This project would not have been possible without the support from the Plant Biology and Plant, Soil, and Agricultural Systems Departments and from John Miller for use of the greenhouse facilities.

I will never be able to express my gratitude enough to the countless graduate and undergraduate students who have been with me through revisions, long field days, and countless adventures. A special thank you to the Gibson gals Katie Smith, Lindsay Shupert, and Kelsey Martinez and the Young guns Joe Wuerffel, Lucas Franca, and Nick Harre for being there through the ups and downs both in and out of school. Your friendships mean everything to me.

Finally, I would like to thank my family for their endless love and support throughout this chapter in my life. I would not have been able to accomplish so much without you being there for me. This has truly been an unforgettable experience for all of us. Thank you!

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CHAPTER 1

INTRODUCTION

LITERATURE REVIEW

Plant Life Histories

Communities can be classified on the basis of several aspects, i.e. physiognomy, species composition, dominance, and habitat (Whittaker 1960, 1970). Plant life history characteristics can provide insight to the nature of communities and species interactions. These characteristics include age or size specific fecundity and survival, number and size of offspring, time to reproduction, frequency of reproduction, longevity and senescence (Boutin and Harper 1991).

Biotic factors and abiotic factors have a direct effect on individuals through their action on germination, growth, reproduction and death. The consequences, however, appear at the population level (Boutin and Harper 1991). The emergence, mortality, immigration, and emigration rates within a population, determine population size in a community (Bierzychudek 1982). The regulation of community structure is related to the population size of the component species (Klank et al. 2010). Demographics is an approach that is necessary to assess the magnitude and effect of these factors that operate within and among species (Harper and White 1974; Werner and Caswell 1977; Solbrig 1980). The determination of birth and death rates is necessary, as well as fecundity rates to accurately analyze demographics (Boutin and Harper 1991).

Many studies have used stage or size-based, as opposed to age-based, classification schemes to quantify population dynamics (Silvertown and Charlesworth 2001). Stage-

based schemes are morphological characteristics that tend to not correlate with age after germination (Lefkovitch 1965; Gatsuk et al. 1980; Caswell 2001; Silvertown and Charlesworth 2001). Each successive stage is characterized by changes in morphological structure, such as leaves, tiller density, and reproduction. Quantitative (i.e. growth, longevity, fecundity, height) changes are continuous during the life cycle, and normally follow a unimodal distribution curve (Gatsuk et al. 1980).

The demographics of various taxa are diverse from region to region. Species react to stochastic abiotic and biotic disturbances on small spatial and temporal scales. The diversity of life history characteristics is associated with species that are a result of long evolutionary responses to natural selection over larger scales. Understanding life history characteristics is important because they allow researchers to observe and understand how species behave in relation to their environment, and how species interact with one another. Also, studies of closely related species may be informative in this respect. For example, Boutin and Harper (1991) did a comparative study of five species of *Veronica* in terms of their population dynamics. They found that the species could be ranked in terms of their growth, their ability to form adventitious roots, their reduced degree of self-pollination, and openness of their habitats. Each species had varying life cycles and life history traits.

Integral Projection Modelling: A way to understand population dynamics

Matrix population models (MPM) (Caswell 2001) provide an important and powerful tool for population ecologists to establish parameters that are important to population dynamics by modelling demographic data based off of stage/age transitions (Metcalf et al.

2013). Using commonly collected data MPMs have limitations primarily due to biases or the lack of an ability to input various stochastic variables (Metcalf et al. 2013; Merow et al. 2014a) and may omit complexities of tradeoffs in resource allocation that vary across different environments (Merow et al. 2014b). Other limitations of MPM include the limited capabilities to incorporate variation among individuals within a size/age category and the outputs (i.e. lambda and elasticity values) are very sensitive to various categories, which include but are not limited to environmental and demographic stochasticity (Zuidema et al. 2010).

Integral projection models (IPM), however, offer tools that can incorporate stage, age, and continuous size/age states into a similar analysis of population dynamics (Easterling et al. 2000). Additionally, IPMs accommodate for both discrete and continuous variables as opposed to only discrete stages like MPMs. Other differences between MPMs and IPMs are that IPMs require fewer parameters than MPMs because IPMs are fitted to simple regressions, and IPMs allow for mechanistic insights into population-level patterns by modelling the ecological factors that influence various vital rates (i.e., survivorship, growth, fecundity) (Merow et al. 2014a). The development of an IPM, for a given population, allows for predictions to be made about changes in structure and population numbers and to learn about the sensitivity of these predictions. A straightforward IPM considers growth, survival, and fecundity of a particular species, typically as a function of size.

The multi-species IPM is an extension of the single-species model. This model allows for changes of interacting coexisting individuals to be predicted. These interactions are typically from negative effects on demographic functions, such as reduced survival

probability, reduced growth, or reduced fecundity. It is important to note that competitive interactions may also have positive effects on these demographic functions. Multi-species IPMs have been used to determine the effects of niche differences on coexistence (Adler et al. 2010) and by determining the relative importance of those differences in order to determine when it is necessary to use multi-species models as opposed to single species models (Adler et al. 2012). Other extensions of the basic IPM include complex demography through kernel dependence on other variables affecting demography (Ellner and Rees 2006) and the incorporation of environmental stochasticity (Rees and Ellner 2009; Childs et al. 2004).

In a simple IPM formulation for a single-species, the population is assumed to depend on a continuous variable x. The model maps a population distribution n(x; t) to the next time t + 1 using an integral operator

$$n(y, t+1) = \int_L^U k(x, y) n(x, t) dx.$$

The size of an individual (x) at time t and y is the size of an individual at time $t + 1$ (Rees et al. 2014). To describe these processes, two kernels are defined: P and F. The P kernel represents survival and growth and F represents fecundity. The function F is equivalent to the mean number of offspring from an individual in a specific size class and is the probability distribution of offspring size y for a reproductive individual of size x. Thus, the net result of survival and reproduction can be summarized by the function k, the IPM kernel (Rees et al. 2014). The k kernel acts as the projection matrix in the model that simulates the projected population growth of a population forwards in time. From the k kernel, the population growth rate (λ).

Plant Interactions

There are many types of plant interactions. This study focuses on the competitive response and effect of plant interaction.

Competitive Response and Effect

Competition has been defined as "the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space" (Grime 1979). Competitors are species with adaptations allowing them to maximize their relative growth rate (RGR) (Gibson 2009). Competitors quickly will make use of both the above and belowground resources.

Competition can be compared between species in two ways: first, in their competitive effect or their ability to suppress other individuals, and second in their competitive response or their ability to avoid being suppressed (Goldberg and Landa 1991; Violle et al. 2009; Zhang and Lamb 2011). Newman (1973) and Tilman (1987, 1988) argued that competition is equally important throughout productive gradients, although the resources concerned may differ (Goldberg and Novoplansky 1997). Thus, in unproductive environments, competition is primarily for belowground resources (i.e. nutrients and water), while in productive environments competition is primarily for light (Wilson and Tilman 1993; Goldberg and Novoplasky 1997).

Competitive response and effect abilities vary with each life-stage (Wang et al. 2010). Zhang and Lamb (2011) showed that competitive ability is correlated with traits such as plant height, plant size, leaf shape, and RGR. The C_4 photosynthetic pathway has been associated with a greater competitive ability than plants with a C_3 photosynthetic pathway (Black 1971). Competitive response rankings, however, are more difficult to

predict (Zhang and Lamb 2011). Biomass may be important in determining the adult competitive response ranking in some plants (Weigelt et al. 2002), and time until flowering and root length ratio may be used to determine the competitive response ability in plants with a rosette growth form (Wardle et al. 1998). Juvenile plants have three broad competitive response strategies: (1) persistence to maintain a slow growth rate until resources become available, (2) rapid growth to overreach surrounding vegetation, and (3) foraging for patchy resources as they become available (Keddy et al. 1998; Zhang and Lamb 2011).

The form of competition, effect or response, is important in determining a positive or negative relationship between competitive response and effect (Zhang and Lamb 2011). A negative relationship between competitive response and effect ability could result from size-asymmetrical competition coming from either competition for light (Weiner 1986) or from root-shoot competition interactions (Cahill 2002; Lamb et al. 2009). In this form of asymmetrical interactions, size related traits (i.e., RGR) will allow for a strong competitive effect ability whereas, traits unrelated to size could be associated with a species' ability to survive (Zhang and Lamb 2011). Examples of these traits include the ability to reproduce at a small size even with competitive suppression from other species (Chambers and Aarssen 2009) and the formation of a seed bank (Thompson et al. 1998). In contrast, a positive relationship between competitive response and effect is the product of size-symmetrical competition for limiting resources (Cahill and Casper 2000; Zhang and Lamb 2011). In this form of symmetrical competition, investment in size is a strategy for both dominant and subordinate species (Zhang and Lamb 2011). This investment strategy suggests that a positive relationship between competitive response and effect ability is more likely to be

found in species growing in communities with greater belowground biomass than aboveground biomass (Zhang and Lamb 2011), such as grasslands and tundras (Mokany et al. 2006). Negative relationships between competitive response and effect abilities can be found in old-field and wetland species from communities that can have higher aboveground biomass and stronger shoot competition than root competition (Goldberg and Landa 1991; Keddy et al. 1994; Frasier and Miletti 2008). There are some studies that do not fit either pattern, as these studies found consistent relationships among annual crop and weed species and early-succession old-field species (Goldberg and Fleetwood 1987; Miller and Werner 1987). These are community types with strong aboveground biomass competition (Zhang and Lamb 2011).

Tilman's R Model: an approach to quantify competitiveness*

All plants require light, water, and the same set of approximately 15 essential elements (i.e. N, C, K, P, Ca, Mg, S) (Gibson 2009). The individual growth rate within a population, which is usually best measured in terms of the specific rate of biomass change (Kruger-Magold et al. 2006), depends on the concentration of these resources in a habitat. The growth rate of an individual is determined by the one resource at the lowest availability relative to the plant's requirement for all resources; this is known as the plant's limiting resource (Tilman 1982, 1988, 1997; Lehman and Tilman 2000). In general, the specific rate of biomass change of a species is an increasing function of the environmental condition of its limiting resource (Kruger-Mangold et al. 2006). The growth of a plant would decrease in the presence of a neighboring plant if these plants consumed the same limiting resource (Tilman 1997).

There are two main elements to the Lotka-Volterra hypothesis that underlie Tilman's model: interspecific competition for resources and the long-term pattern of supply of limiting resources (Tilman 1985, 1997). The resource-ratio hypothesis of succession states that individual plant species are dependent upon varying proportions of a limiting resource (i.e., light and nitrogen). In addition, the composition of the surrounding plant community is affected whenever the availability of a limiting resource is altered (Tilman 1980; Miller et al. 2005). Thus, if resource levels are sufficient, then consumers will have a positive growth, which will eventually drive down resource levels and lead to a reduction in population growth (Miller et al. 2005). Since plant species use the same resources, then the resource-ratio hypothesis predicts that the species that can maintain a positive growth rate at the lower resource level will be the better competitor for that resource (Lehman and Tilman 2000). This relationship is expressed in terms of R*. The minimum resource level that can support a producer population is known as the zero net growth isocline (ZNGI).

Invasive Species

An invasive species can be defined as a species that is not native to the ecosystem under consideration and is harmful to the environment. Non-native species, or exotic species, are defined as species from other "continents arriving in North America after the time of Columbus" (Great Plains Flora Association 1986). Not all invasive species are exotic, and not all exotic species are invasive. Invasive species can quickly evolve in areas of disturbance through founder effects and hybridization by responding to selection pressures in the environment (Sakai et al. 2001). Variables that can influence a rapid

invasion include life history, latitude, climate, interactions with new species, and release from competitive species and pathogens in the original habitat (Sakai et al. 2001).

Predicting whether or not a species will become invasive is difficult. Williamson's Tens Rule, however, states that only 10% of invasive species survive introduction into a new ecosystem and that only 10% of those species that survive will become invasive (Williamson 1996). Some common characteristics that invasive species have include: broad-niched, self or wind pollination or non-specialized pollinators, rapid growth to reproductive maturity, high allocation of resources to reproduction, short life cycle, resistance or opportunistic response to disturbance, ability to spread rapidly, prolific vegetative reproduction, an ability to outcompete natives, and a rapid response to resource availability (Baker 1965; Bazzaz 1986; Simberloff et al. 1997). Few invasive species possess all or most of these characteristics. Possession of these characteristics, however, does not necessarily mean that a plant will become invasive (Groves and Burdon 1986; Sakai 2001). There are many additional factors that contribute to an exotic species becoming invasive to a new environment (i.e., the health of the ecosystem, climate similarity to original habitat, whether or not predators and pollinators are present, disturbance in the new ecosystem, and the competitiveness of the native species present (Devine 1998; Lonsdale 1999).

Invasive species are introduced into a new ecosystem in many ways. They may arrive accidentally mixed in shipments from overseas (i.e., in lawn or pasture seed) (Baker 1986). Plants can also spread naturally beyond their native ranges, by migratory birds carrying seeds and by water or wind dispersal. Human intervention is the primary method of introduction for invasive species and human disturbance is almost always necessary for a successful invasion by an invasive species because most cannot invade already well-

established locations (Baker 1986; Silvertown and Doust 1993). Invasive species can spread into areas where they were not planted, persist without human interaction, and displace native species (Simberloff et al. 1997). Davis and Thompson (2000) devised a classification scheme to rate the colonization of plants based on three criteria: dispersal distance, origin, and impact on the environment. According to this classification scheme, dispersal distance can be short or long and a colonizer can only be called an invasive species if it is novel to the region being colonized and if it has a great impact on the new environment. From this, Sakai et al. (2001) devised a classification of the steps of invasion process, which include steps for prevention, eradication, and control/restoration.

Invasive species have large ecological impacts on native species, communities, and ecosystems (Elton 1958; Lodge 1993; Simberloff 1997). There are approximately 50,000 invasive species and the number is steadily increasing (Sakai et al. 2001). About 42% of the species on the Threatened and Endangered species list are at risk primarily because of invasive species (Pimentel et al. 2005, Sakai et al. 2001). Invasive species are now viewed as a significant influence on global change (Vitousek et al. 1996). As well as ecological impacts, invasive species have an economic impact. Costs of invasive species are estimated to be almost $120 billion dollars annually (Pimentel et al. 2005). Ecosystem biodiversity has been negatively impacted by the presence of invasive species. Numerous studies have been done on the impacts of invasive species on community and population structure (MacDougall et al. 2009; Stein et al. 2000; Williamson 1996; Simberloff et al. 1997; Parker et al. 1999) which have indicated that invasive species can reduce the amount of resources available for native species, alter soil chemistry, alter fire cycles and hydrological patterns (Vitousek et al. 1996). These changes in the environment can result in the loss of

threatened and endangered species, loss of habitat, loss of food sources for wildlife, and disruption of native plant-animal interactions (i.e., pollination), seed dispersal, and host plant relationships (Vitousek et al. 1996; Sakai et al. 2001).

Resource availability is also important to the location of an invasive species (Seabloom et al. 2003), such that a plant community becomes more susceptible to invasion as the amounts of available resources increase (Davis et al. 2000). This response could be due to a decreased use by the current vegetation or because of an increased supply of resources. Research has suggested, however, that after resource availability has been accounted for, there is no other significant interaction between the native species and the invasive species (Mack 2003; Maron and Marler 2007).

Invasive Species in Illinois

The Illinois Department of Natural Resources (IDNR 1994) reports that the invasion of exotic species is one of the most serious threats to Illinois, especially in forests. Forests in Illinois contain over half of the native flora and over half of the endangered plant species (IDNR 1994). These forests also provide about 75% of the state's wildlife habitat (IDNR 1994).

Illinois, as of 2014, had 1,156 exotic plant species that had escaped cultivation and became naturalized. This number is equivalent to 32.1% of the state's total flora (Mohlenbrock 2014). Of the 32.1%, 78% of the species were introduced from outside of North America (IDNR 1994). One-fifth of the Illinois flora can be classified as non-native invasive species. These plants can alter the ecosystem and decrease the biodiversity (Sakai

et al. 2001). The rate of introduction for exotic species has increased, as well as the rate of exotic species that have become invasive in Illinois (Henry and Scott 1981; IDNR 1994).

The Illinois Exotic Weed Act (IEWA) was passed in 1991 and makes it illegal to buy, sell, distribute or plant seeds, plants, or plant parts of exotic species recognized by Illinois (IDNR 1994). The IEWA defines exotic species as "those plants not native to North America which, when planted, either spread vegetatively or naturalize and degrade natural communities, reduce the value of fish and wildlife and wildlife habitat, or threaten an Illinois endangered species." There are ten species that fit this definition today. These species are Japanese honeysuckle (*Lonicera japonica*), multiflora rose (*Rosa multiflora*), purple loosestrife (*Lythrum salicaria*), autumn olive (*Elaeagnus umbellata*), Japanese stilt grass (*Microstegium vimmineum*), oriental bittersweet (*Celastrus orbiculatus*), garlic mustard (*Alliaria petiolata*), Johnsongrass (*Sorghum halepense*), Chinese yam (*Dioscorea oppositifolia*), and kudzu (*Pueraria lobata*).

Agricultural Weeds

An understanding of the population biology of agricultural weeds assists in developing management protocols, and vice versa, agricultural weeds can provide useful models to test the basic tenets of life history theory. Weeds are a constant limitation to crop production. Most of the attributes that contribute to weed success are common plant characteristics: rapid growth rates, high fecundity, continual flushes of germination, and herbicide tolerance or resistance (Tranel and Trucco 2009).

Seed production is an important part of weed biology, especially for annual species (Holst et al. 2007). Fecundity is not fixed and depends on a variety of factors (i.e., weather,

precipitation, weed density, crop yield, harvest time in relation to weed maturity, as well as other factors) (Holst et al. 2007). In agricultural demography, fecundity is often translated into seedbank input by a fixed survival rate, although several abiotic (climate, precipitation) and biotic (predation, disease, failed germination) factors affect the rate (Snaydon 1980; Holst et al. 2007). Some models determine the seed bank in two or more soil layers, but four layers (to a maximum depth of 20 cm) are usually chosen for the use of soil tillage (Cousens and Moss 1990). Seeds have also been divided into yearly age classes (Kunisch et al. 1990) to describe age-dependent seed survival and germination.

Seedlings can be the most competitive life stage for weedy species in an agronomic habitat. Empirical studies (Mann and Barnes 1947; Bowden and Friesen 1967; Hakansson 1986) and simulation models (Kropff et al. 1993) have demonstrated that an advantage of a few days can shift the competitive ability between crops and weeds. Kasasian and Seeyave (1969) proposed the critical weed-free hypothesis that states that crops require a weed-free period of one-fourth to one-third of their growing period. This hypothesis was confirmed for *G. max* in a study (Nierto et al. 1968) that reported the crop was most susceptible to weed competition during the first 30 days of a 130- to 135-day growth period (Zimdahl 2004). A competition study done by Klingman and Oliver (1994) between *A. palmeri* and *G. max* showed that *G. max* yield was highly correlated with *A. palmeri* biomass and to the weed's density. Within eight weeks, roughly seedling to juvenile growth, *A. palmeri* densitites of 1, 2, and 10 plants/meter of row reduced *G. max* yield 32, 48, and 68 percent, respectively (Klingman and Oliver 1994).

Resistance to various herbicide mode of actions (MOAs) are often developed in weed populations (Holst et al. 2007; Tranel and Trucco 2009). As of 2012, 372 unique

herbicide-resistant weed species have been confirmed worldwide. The U.S. has 139 of these weed species, with 1 to 19 in most other countries with intensive agriculture (Vencill et al. 2012). Each of these species is resistant to at least one herbicide MOA, and many MOAs have selected for a number of resistant weeds. For example, 116 weed biotypes are resistant to the acetolactate synthase (ALS)-inhibiting herbicides and 21 glyphosate-resistant biotypes (13 of them in the U.S.) (Vencill et al. 2012).

Amaranthaceae

Amaranthaceae (pigweed family) is a widely established plant family consisting of annual or perennial herbs (Blunden et al. 1999). There are about 71 genera worldwide and about 900 species in the family (Pai et al. 2011). Species are primarily found in the tropics and subtropics, but can be found worldwide. Several species are grown as ornamentals or for their grains (Flora of North America 2015).

Species in this family are highly variable: leaves can be alternate, opposite, simple or entire, monoecious or dioecious (Flora of North America 2015). Both monoecious and dioecious species can be highly successful invaders. Inflorescences are often arranged into spikes, which are often aggregated into panicles, or glomerules. A single plant can produce well over 100,000 seeds even when growing in competition with a crop; species can average several thousand seeds per plant (Massinga et al. 2001; Steckel and Sprague 2004; Tranel and Trucco 2009). Fruits are either dehiscent or indehiscent (Flora of North America 2015).

Amaranthaceae species invade a variety of habitats, including most agricultural systems, pastures, rangelands, waste areas, and fence-rows and are highly adaptable. These

species also are notorious for evolving a resistance to herbicides (Tranel and Trucco 2009; Heap 2012). These characteristics make Amaranthaceae a model family to study and understand the population dynamics of closely related species.

Phylogeny

Amaranthaceae (Schinz 1893) and Chenopodiaceae (Bentham and Hooker 1883) have been considered closely related within the Order Caryophyllales (Takhtajan 1997; Sanchez del-Pino et al. 2009), and this was confirmed by morphological and molecular phylogenetic analysis (Rodman 1990; Downie and Palmer 1994; Cuenoud et al. 2002). This two-family treatment differs from the proposed APGII (2003) to merge both families under the name Amaranthaceae. Relationships between the two families are still unresolved, although the monophyly of Amaranthaceae has been shown convincingly (Kadereit et al. 2003; Muller and Borsch 2005; Sage et al. 2007).

Phylogenetic analysis using *rbc*L and *matK/trnK* sequences have been used to better resolve the relationships within Amaranthaceae. Muller and Borsch (2005) used *matK/trnK* sequences to uncover previously unknown clades. Kadereit et al. (2003) used *rbc*L sequences to detemine three independent origins of C_4 photosynthesis in this family. Gene sequencing was used to determine three major clades: Gomphrenoids, Alterantheroids, and Iresinoids by using *trnL-F* and *rpl16* sequencing analysis (Sanchez del-Pino 2009).

A majority rule parsimony tree based on *matK/trnK* sequence data depicted the relationship in Amaranthaceae with nine clades: Achyranthoids, Gomphrenoidea, Aervoids, Allmaniopsis, Psilotrichum, Amaranthoids, Celosieae, Charoentiera, and Bosea. The two annual species of this study, *A. palmeri* and *A. tuberculatus*, fall within the Amaranthoids

clade. *Achyranthes japonica* falls within the Achyranthoids clade and *I. rhizomatosa* falls within the Gomphrenoideae clade, which are sister clades (Sage et al. 2007).

Amaranthus L.

Amaranthus is comprised of 70 species (Mosyakin and Robertson 2003). The *Amaranthus* species are widely distributed, abundant, and among the worst weeds in the world (Tranel and Trucco 2009). This genus includes grain and ornamental species, but is best known for its weedy species (Table 1.1).

The various *Amaranthus* species can be difficult to distinguish (Horak et al. 1994) and there are documented cases of misidentification (Sauer 1953; Ahrens et al. 1981). Much of the difficulty in identifying species can be attributed to seedlings that look morphologically similar (Cai et al. 1998). Diagnostics of the floral structure or a larger individual can be used to distinguish each species (Tranel and Trucco 2009). These characteristics are the basis for the three subgenera that are currently recognized: *Amaranthus*, which includes monoecious weeds and crop species; *Acnida*, which includes dioecious weeds; and *Albersia*, which includes many of the poorly characterized species (Tranel and Trucco 2009).

Subgenus *Amaranthus*

The subgenus *Amaranthus* includes weeds and crop species (primarily consisting of grains). Most of the species are agronomic weeds. They are primarily summer annual, monoecious species capable of competing with crop plants (Moysakin and Robertson 2003). *Amaranthus* species express high plasticity to environmental changes, and ensure

their fitness by producing a large amount of seeds (Zimdahl 2004). The seeds are typically very small (averaging 1 mm in diameter), making them easily dispersed by wind and water. Seeds may also be transported long distances by humans, through machinery, animal feed and clothing, and birds (Weaver and McWilliams 1980).

Amaranthus palmeri L.

Amaranthus palmeri (Palmer amaranth) is a native, weedy dioecious C_4 summer annual (Ehleringer 1983; Horak and Loughin 2000; Sellars et al. 2003). Prior to 1955, this species was found from southern California to central Texas and from the Texas-Oklahoma border to central Mexico (Sauer 1957). Today, *A. palmeri* is distributed in 29 states and has moved beyond its native range to invade the midsouth, midwest (including Illinois), and southeastern United States (Webster 2005; Sosnoskie et al. 2009).

This species can grow erect up to 2 to 3 meters tall (Horak et al. 1994; Wax 1995) and produces unbranched terminal seedheads that can produce anywhere from 60,000 (Bensch et al. 2003) to 500,000 seeds m^{-2} (Sellars et al. 2003), depending on the density and plant size. Seed germination is typically high, compared to other *Amaranthus* species, with maximum germination occurring within three days at 30°C (Steckel et al. 2004; Jha et al. 2010). *Amaranthus palmeri* has a terminal spike inflorescence (Culpepper et al. 2006). Compared with *Amaranthus tuberculatus*, *A. retroflexus*, and *A. albus*, *A. palmeri* had the greatest values for plant volume, dry weight, and leaf area (Horak and Loughin 2000). In addition, *A. palermi* grew 24 to 62% greater than the other *Amaranthus* species each day (Horak and Loughin 2000). The rooting structure for this species is a shallow taproot.

However, in heavily disturbed areas this plant can produce thick lateral roots for stabilization (Moore and Franklin 2011).

Amaranthus palmeri commonly invades disturbed habitats, waste places, railroads, streambanks, sandy areas, and agricultural fields (Guo and Al-Khatib 2003; Moore and Franklin 2011). The species has spread to become one of the primary competitive crop weeds in the United States (Horak 2000; Culpepper 2006). *Amaranthus palmeri* reduced corn (*Zea mays* L.) yields 11 to 91% with 0.5 to 8 plants per m^{-1} (Massinga et al. 2001; Massinga and Currie 2002) and reduced soybean (*Glycine max* L.) yield 17 to 68% with 0.33 to 10 plants per m^{-1} (Klingman and Oliver 1994). In addition, cotton yields, in Texas, decreased from 13 to 54% as *A. palmeri* increased from 1 to 10 plants per 9.1 m^{-1} (Morgan et al. 2001).

As of 2012, *A. palmeri* has exhibited resistance to five different herbicide mechanisms of action (MOAs): ALS-inhibiting herbicides, dinitroanilines, triazines, glyphosate, and HPPD inhibitors (Heap 2012). In addition, numerous *A. palmeri* populations that have been reported as having evolved resistance to multiple herbicide modes of action. For example, in 2013 and 2014, Illinois, Florida, Maryland and Delaware all had reports of populations showing resistance to both ALS-inhibiters and glyphosate in *Glycine max* populations (Heap 2015).

***Amaranthus tuberculatus* L.**

Amaranthus tuberculatus is an annual, dioecious C_4 weed species that has rapid growth characteristics and extended seedling emergence (Horak and Loghin 2000; Duff et al. 2009). This species can grow up to 2 m tall. *Amaranthus tuberculatus* has an elongated

taproot, erect, slender stems and unisexual flowers (Mohlenbrock 2014). Native to North America, *A. tuberculatus* is believed to have been introduced into the Chicago, Illinois region (Swink and Wilhelm 1994). Today, *A. tuberculatus* ranges from Michigan to South Dakota, south to New Mexico, Texas, and Arkansas, and is moving into the eastern United States (Mohlenbrock 2014). The habitat includes moist, disturbed soils and sandy riverbanks (Mohlenbrock 2014). This species flowers from July to October (Mohlenbrock 2014). Without competition, *A. tuberculatus* can produce more than 1 million seeds per plant (Nordby et al. 2007). A study done by Sellars et al. (2003) found that *A. tuberculatus* produces more than 1.5 times more seed than other Amaranthaceae species with the same seed size.

Amaranthus tuberculatus is a weedy species for several reasons. First, reduced tillage systems in corn and soybean fields have been adopted and is more favorable for small-seeded weed species, such as *A. tuberculatus* and *A. palmeri* (Trucco and Tranel 2009). Secondly, populations of *A. tuberculatus* are resistant to many herbicide modes of action, including glyphosate, PSI-inhibiting herbicides, dinitroanilies, acetolactate synthase (ALS)-inhibiting herbicides, and protoporphyrinogen oxidase (protox) (PPO)-inhibiting herbicides (Duff et al. 2009; Hartzler et al. 2004; Mayo et al. 1995; Shoup and Al-Khatib 2004). In addition, Heap (2015) reports that biotypes of *A. tuberculatus* show resistance to multiple modes of action simultaneously in the United States. For example, in 2009 Illinois had a population that was resistant to ALS-inhibitors, PPO-inhibitors, glyphosate and PSII inhibitors. Furthermore, in 2011 Iowa also had a population that showed resistance to four MOAs (ALS-inhibitors, HPPD-inhibitors, glyphosate and PSII-inhibitors).

Finally, *A. tuberculatus* emerges later in the growing season, and emergence occurs during a longer period than many other summer annual weedy species (Hartzler et al. 1999). The delayed and prolonged emergence is advantageous under current weed management systems that rely less on residual herbicides and cultivation (Hager et al 1997; Hartzler et al. 2004). Late emergence, however, places this weed at a competitive disadvantage with the crop (Hartzler et al. 2004). Species emerging at the V2 to V3 soybean stages were approximately 25% as competitive as plants emerging with the crop (Cowan et al. 1998). Seedling emergence of *A. tuberculatus* is also greatly affected by the emergence period of the crop, with reductions ranging from 15,000 to 32,000 seeds per plant^{-1} when emerging up to the four-leaf stage of corn to about 5,000 seeds or less per plant^{-1} when emergence was delayed to the four to seven-leaf stage of corn (Knezevic et al. 1994).

There has been some controversy over *A. tuberculatus* (tall waterhemp) and *A. rudis* (common waterhemp) being the same or different species. Pratt and Clark (2001) proposed that *A. rudis* and *A. tuberculatus* be considered as one species due to their high degree of hybridization, their sympatric geographic distribution, and that their morphological characteristics are very similar, making differences subtle if not indistinguishable. Nevertheless, some scientists consider the two species to be different. For the purposes of this dissertation *A. tuberculatus* will be used to refer to both waterhemp species.

Achyranthes L.

Achyranthes consists of 15 species that are distributed primarily in tropical and subtropical regions of the word (Pai et al. 2011). These species can be perennials or annuals and

consist of herbs. Leaves are opposite with perfect flowers. The seeds are generally oblong and lenticular (Shu 2003). All of the species within this genus have the C_3 photosynthetic pathway (Sage et al. 2007).

Achyranthes japonica (Miq.) Nakai

Japanese chaff flower, *Achyranthes japonica* (Miq.) Nakai (syn. *A. bidentata* var. *japonica* Miq.), is a perennial, C_3 herb that is native to Korea, China and Japan (Sage et al. 2007; Choi et al. 2010; Evans and Taylor 2011). This species is a member of the Amaranthaceae family and is one of the two species in the *Achyranthes* genus that is found in the United States (along with *Achyranthes aspera*) (Evans and Taylor 2011).

Achyranthes japonica is considered to be an exotic, weedy species in the United States and on many Korean islands as well (Choi et al. 2010). This species competes with native herbs and increases the mortality rates and breeding failure rates among seabirds, particularly the Swinhoe's Storm Petrel (*Oceanodroma monorhis*) by its seeds attaching to the birds feathers (Lee et al. 2009). In addition, *A. japonica* is widely used in traditional Asian medicines and as a food additive (Choi et al. 2010; Jung et al. 2008).

This species was first discovered in the United States on the 16th of August 1981 along the banks of the Tug Fork of the Big Sandy River at Warfield, Martin County, Kentucky (Evans and Taylor 2011; Medley et al. 1985). In 2010, a survey conducted by the River to River Cooperative Weed Management Area (CWMA) and by the IDNR found that it was present in every county adjacent to the Ohio River in Illinois and is commonly found in floodplain forests alongside the river (Evans and Taylor 2011). Currently, *A. japonica* has

been identified in over 50 counties in 9 states (Alabama, Georgia, Illinois, Indiana, Kentucky, Missouri, Ohio, Tennessee, and West Virginia) (Schwartz et al. 2015a, 2015c).

Achyranthes japonica is a perennial, herbaceous species that can grow up to three meters high and is easy to identify (Schwartz et al. 2015c). It becomes perennial at an early growth stage by the time it reaches three or four nodes. *Achyranthes japonica*'s leaves are opposite and simple (Mohlenbrock 2014). The stem at ground level and nodes are red, which is a characteristic that is seen in other members of the pigweed family the flowers occur on erect spikes at the end of the stems and upper branches. The flowers, which lack petals, occur in tight clusters and diverge at nearly a right angle, which gives the flowers a bottle-brush look. As the fruits mature, the spikes elongate and the fruits lay flat against the spike. The fruits have two stiff bracts that help in dispersal by attaching to clothing, shoes, hair, or animal feathers and fur. Populations that have been browsed by deer or damaged by insects will resprout and it will overcompensate its growth and amount of seeds produced (Schwartz et al. 2015a). *Achyranthes japonica* can be found growing in areas with partial sun and moist soils, but can also grow in heavily shaded and dry areas. Populations of this species have been found in bottomland and upland forests, along riverbanks, along agricultural field margins, and in roadside ditches.

Achyranthes japonica starts growing in late spring and flowers in the late summer (Schwartz et al. 2015a). Flowers can continue to develop into the early fall, even when seed is starting to be produced. The seeds are mature in mid to late fall. As the plants die off in late fall or early winter, the stems and remaining seed turn an orange-brown color. The dead plant stand can remain erect even into the winter until heavy snow, ice, or floods cause the stems to break. The high germination rate (~ 62% in drought years and ~94% in

average years) and the high seed output (up to 2,000/plant) of this species make it a strong competitor for the following year (Schwartz et al. 2015c). Additionally, about 60% of new seedlings survive to produce seed-bearing adult plants. *Achyranthes japonica* can reach densities over 80 stems per meter squared (which is over ~16,000 seeds). This species has continual germination throughout the growing season and the ability to outcompete other native and invasive species (i.e., *Microstegium viminuem*). Dense populations of *A. japonica* allow very little to grow underneath it (Schwartz et al. 2015a).

Iresine P. Browne

Iresine is comprised of about eighty species that are primarily found in subtropical and tropical America (including the Galapagos Islands), Asia, and West Africa (Flora of North America 2015). There are five species found in North America, which include *I. leptoclada*, *I. palmeri, I. diffusa, I. rhizomatosa*, and *I. heterophylla* (Flora of North America 2015). These five species are found in seventeen states (Alaska, Arkansas, Florida, Georgia, Illinois, Indiana, Kansas, Kentucky, Louisiana, Maryland, Mississippi, Missouri, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, and Virginia) (Flora of North America 2015). Species in this genus can be annual or perennial, monoecious or dioecious herbs. The leaves are opposite and simple, and the flowers are perfect or unisexual. Flowers are crowded into spikes arranged in panicles (Flora of North America 2015). In Illinois and Maryland, there is only one species that is endangered *I. rhizomatosa* (bloodleaf or Juda's bush). In Indiana, *I. rhizomatosa* is considered to be a rare species. There is one species of *Iresine* that occurs in Illinois, *I. rhizomatosa* (Mohlenbrock 2014).

***Iresine rhizomatosa* Standl.**

Iresine rhizomatosa is a C_4, perennial dioecious herb. This native species has erect stems and can grow up to 1.5 m tall (Gibson and Schwartz 2014; Flora of North America 2015). The rhizomes are considered to be slender. This species is distinguished by its opposite leaves, its silvery-white unisexual inflorescences, and the long white hairs that subtend the sepals in the pistillate flowers (Flora of North America 2015). *Iresine rhizomatosa* is found in wet wooded areas and flowers from August to October (Gibson and Schwartz 2014). This species native range is Maryland to Kansas and south to Texas and Virginia. In Illinois, this state-listed endangered species is only found in four counties (Crawford, Massac, Pulaski, and Wabash) (IDNR 1994).

RESEARCH OBJECTIVES AND HYPOTHESES

The overall objective of this study was to determine the comparative life history and relative competitiveness of closely related species when challenged with a dominant species. Specifically, select closely related species in the Amaranthaceae family that occur in southern Illinois were compared, i.e., *Achyranthes japonica*, *Amaranthus palmeri*, *Amaranthus tuberculatus*, and *Iresine rhizomatosa*. These species consist of perennials and annuals, native and exotic species, and weedy and non-weedy species (Table 1.2). This study was conducted because these closely related species vary in life cycle, invasiveness, habitat and ecological research and understanding which characteristics are most important can lead to furthering our knowledge of the poorly researched species and possibly developing management or conservation strategies.

The first objective of this study was to assess the importance of seed survivorship in the soil of *A. japonica* and to compare survivorship, fecundity, and morphological characteristics within populations at two different sites in southern Illinois. The hypothesis (H_1) for this objective was that the two sites would differ in their characteristics based on environmental factors and habitat.

The second objective of this study was to determine the relative competitive effect and response of *A. japonica*, *A. palmeri*, *A. tuberculatus*, and *I. rhizomatosa* to *G. max* as a consistent competitor that has relevance for the *Amaranthus* species, and could potentially be relevant for *A. japonica*, with *Iresine* rhizomatosa versus *G. max* acting as a 'control'. The first hypothesis (H_2) for this objective was that the perennials, *A. japonica* and *I. rhizomatosa*, will have the lower requirement than the annual Amaranthus species for limiting resources when competing with interspecific neighbors, thereby enabling them to displace competitor species. The second hypothesis (H_3) was that the competitive effect and the competitive response rankings will be inversely related among the four species. The competitive effect ranking was predicted to be: *A. tuberculatus* > *A. palmeri* > *A. japonica* = *I. rhizomatosa* whereas the competitive response ranking will be the opposite.

The third objective was to undertake a comparative life history analysis of *A. japonica*, *A. palmeri*, *A. tuberculatus*, and *I. rhizomatosa* in habitats where they occur (including crop fields for species in agricultural settings). The first hypothesis (H_4) for this objective was that the population growth rate (λ) for *A. japonica* will be similar to the *Amaranthus* species and greater than *I. rhizomatosa*. The second hypothesis (H_5) was that the population growth rate (λ) will be higher for the exotic species rather than the native species, because of differences in the demographic process (i.e., growth and fecundity being

more important for invaders; whereas for the natives, survivorship is likely the most important life history trait).

Table 1.1. Major *Amaranthus* agricultural weeds in North America (Tranel and Trucco 2009).

Species	Common Name
A. albus	Tumble pigweed
A. arenicola	Sandhills amaranth
A. australis	Giant amaranth
A. blitoides	Prostrate pigweed
A. hybridus	Smooth pigweed
A. lividus	Livid amaranth
A. palmeri	Palmer amaranth
A. powellii	Powell amaranth
A. quitensis	Yuyo colorado
A. retroflexus	Redroot pigweed
A. spinosus	Spiny amaranth
A. tuberculates var. *rudis*	Common waterhemp
A. tuberculates var. *tuberculates*	Tall waterhemp
A. viridus	Slender amaranth

Table 1.2. Life history characteristics of study species.

Species	**Perennial/ Annual**	**Invasive/ Non-Invasive**	**Native/ Exotic**	**C_3/ C_4**	**Monoecious/ Dioecious**
Achyranthes japonica	Perennial	Invasive	Exotic	C_3	Monoecious
Amaranthus palmeri	Annual	Invasive	Native	C_4	Dioecious
Amaranthus tuberculatus	Annual	Invasive	Native	C_4	Dioecious
Iresine rhizomatosa	Perennial	Non-Invasive	Native	C_4	Dioecious

CHAPTER 2

LIFE HISTORY OF *Achyranthes japonica* (AMARANTHACEAE): AN INVASIVE SPECIES IN SOUTHERN ILLINOIS

Introduction

Invasive species are an ever increasing threat to natural plant communities (Simberloff et al. 2005). In Illinois, non-native species make up about 33.6% of the flora and many are invasive posing a serious threat to natural areas (Mohlenbrock 2014). Demographic processes, such as survival, growth, and reproduction, can inform us about potential invasion risks, extinction risks of native species, and trade-offs in life history strategies. Long-term dynamics of plant invasions and their impacts on the surrounding native plant community and ecosystem may be determined by these demographic processes. The diversity of life history characteristics associated with a species are the result of long evolutionary responses to natural selection over large scales (Merow et al. 2014). Thus, understanding the life history characteristics of invasive species is fundamental for land managers to develop management and control methods (Meyers and Bazley 2003). Japanese chaff flower, *Achyranthes japonica* (Miq.) Nakai (Amaranthaceae) is an exotic species, originally from Japan, Korea, and China (Jussien 2014), that is a relatively new to North America where it was first discovered in 1981 in Martin County, Kentucky (Medley et al. 1985). Since then, this species has been found in every county along the Ohio River down to the Mississippi River confluence. By 2014, this species had been confirmed in nine states (West Virginia, Tennessee, Kentucky, Indiana, Ohio, Illinois, Missouri, Alabama, and Georgia) and over 50 counties (EDDmapS 2014). The actual distribution of *A. japonica* is

most likely much greater than this. The lack of public awareness and land managers limits the knowledge of this species actual distribution. The primary mode of dispersal is through water and animals (Schwartz, personal observation).

Management tactics are lacking for *A. japonica* due primarily to poor public awareness and to the lack of literature on this relatively new invader. In addition, there are limited ecological studies that have been conducted on *A. japonica*. Many of the ecological studies on *A. japonica* in the United States have been strictly observational (Medley et al. 1985; Evans and Taylor 2011; Schwartz et al. 2015a) with one quantitative study (Smith 2013). Previous studies outside of the United States have reported the distribution of *A. japonica* seeds by migratory birds on Korean islands (Choi et al. 2010) and its allelopathic and antimicrobial properties (Kim et al. 1993, Kim et al. 2004).

The overall objective of this research was to assess the importance of seed survivorship in the soil for *A. japonica* and to compare survivorship, fecundity, and performance measurements between populations at two different sites in southern Illinois.

Materials and Methods

Study Species. *Achyranthes japonica* is a perennial, herbaceous species that can grow up to three meters in height. This species becomes established as a perennial capable of regrowth at an early growth stage (three or four nodes) (Smith 2013). *Achyranthes japonica*'s leaves are opposite and simple. The stem at ground level and the nodes have a reddish hue, which is a characteristic consistent with other members of the Amaranthaceae family. The flowers occur on erect inflorescences at the end of the stems and upper branches (Evans and Taylor 2011). The flowers, which have five reflexed tepals (Flora of

North America 2015; or sepals *sensu* Mohlenbrock 2014), occur in tight clusters and diverge at nearly a right angle. As the fruits mature, the spikes elongate and the fruits lay flat against the inflorescence branches. The fruits have two stiff bracts that help in dispersal by attaching to various materials such as clothing, hair, animal feathers or fur (Schwartz et al. 2015a). Plants browsed by deer or damaged by insects will re-sprout and overcompensate in terms of growth and seed production (Smith 2013). *Achyranthes japonica* can be found growing in areas with partial sun and moist soils, but it can also grow in heavily shaded and dry areas (Evans and Taylor 2011; Schwartz 2014). Populations of this species have been found in various habitats including bottomland and upland forests, riverbanks, agricultural field margins, and roadside ditches.

Achyranthes japonica starts growing in late spring and flowers in the late summer, but can continue to develop flowers into the early fall. Flowers can still form when the seeds mature in the mid to late fall (Schwartz et al. 2015a). Plants typically die off in the late fall or early winter, but the dead plant stand can remain erect even into the winter. Dense populations of *A. japonica* allow very little to grow underneath them (Schwartz et al. 2015a) displacing native plant species and altering soil nutrient levels (Yates et al. 2004; Zedler and Kercher 2004).

Experiment Sites. The primary focus was on two abundant populations of *A. japonica* at the Bellrose Waterfowl Reserve in Union County and Chestnut Hills Nature Preserve in Pulaski County in Illinois. Species at each site differed but did have some overlap (Schwartz 2015: Appendix A). Although there were similar species at each site, the sites differed in habitat type. The Bellrose Waterfowl Reserve is considered to be a bottomland hardwood

forest or wetland and Chestnut Hills Nature Preserve is an upland forest that is located near the Ohio River and receives some flooding in lowland areas.

The Bellrose Waterfowl Reserve (BWR: 37°17'N, 89°06'W) site is a part of the Cypress Creek National Wildlife Refuge (CCNWR) found within the Cache River wetlands system. The population studied was within 15 meters of the banks of the Cache River (Smith 2013). This site was historically bottomland hardwood forest (McLane et al. 2012). Regular flooding occurs at BWR primarily through the winter and spring seasons creating scour on the forest floor and allowing only minimal organic matter accumulation. The soil type is a wheeling silt loam (USDA Soil Survey 2015). Hardwood trees such as *Quercus palustris* Münchh. and *Acer saccharum* Marshall dominate the canopy with a large amount of *Taxodium distichum* (L.) Rich. (McLane et al. 2012; Smith 2013). Dominant ground layer species found within the *A. japonica* population include *Toxicodendron radicans* (L.) Kuntze., *Urtica dioica* L., *Tradescantia virginiana* L. and *Polygonum hydropiperoides* Michx..

The Chestnut Hills Nature Preserve (CH: 37°11'N, 89°3'W) site is an 86 hectare upland forest (IDNR 1994). This preserve has several unique features include a rare eroding river bluff community and several rare plants and animals (i.e., *Halesia diptera* Ellis, dusky salamander [*Desmognathus fuscus* Conanti.]), and wintering bald eagle [*Haliaeetus leucocephalus* L.]. This upland forest has a menfro silt loam soil (USDA Soil Survey 2015). The overstory community is dominated by *Fagus grandifolia* Ehrh., *Quercus rubra* L., and *Acer saccharum* Marshall; whereas, the understory community is dominated by *A. japonica*, *Toxicodendron radicans* and *Urtica dioica*.

Populations and Plot Establishment. At each site, a population of *A. japonica* was sampled for three consecutive years (2012 to 2014). Within each population, ten 1 m^2 plots were established in October/November. In addition to the annually established plots, the previous years' plots remained for observations (i.e., 2012 = 10 plots/site; 2013 = 10 new plots/site + 2012 plots/site; 2014 = 10 new plots/site + 2012/2013 plots/site). Additionally, five seedlings per plot (for a total of 50 plants per site per year) were tagged and monitored by taking node counts every two weeks throughout each growing season and the following years where applicable. Tagged plants were classified into stage groups based on node counts: 1 to 4 nodes were seedlings, 5 to 7 nodes were juveniles, and 8+ nodes were adults. Adult plants were further classified into reproductive and non-reproductive plants. Mortality was recorded, but the reason for mortality was not determined (i.e., mammal browsing or natural death from environmental conditions). The same tagged plants were monitored the following years.

Seedling Emergence. *Achyranthes japonica* occurred in the plots established in 2012. In subsequent years, additional plots were seeded in October/November to simulate natural seed rain and the overwintering of seeds (i.e., initial measurements were made in 2012, in the fall of 2012 the plots for 2013 were established and seeded). Seeds were collected from plants at each site to use for the seeded treatment plots. Seven of the ten plots (seeded treatment plots) were each seeded with 1,000 seeds and the remaining three plots were not seeded and are considered to be unseeded controls. These control plots allowed for a baseline to be established to determine seedling emergence from the soil seed bank and did not previously have *A. japonica* present in the plots. The number of seedlings and regrowth of plants from previous years were recorded within each plot every other week. The 2012

field season ran from April 1 through November 2 (216 days); whereas the 2013 and 2014 field seasons ran from June 16 through October 16 (122 days) and from May 23 through September 13 (113 days), respectively. The difference in field season length depended on weather conditions and seedlings were monitored as soon as they emerged until after the first frost date of that year. Sites were monitored weekly until seedlings emerged.

Seed Viability. Seed bags each containing 100 seeds each were buried in all ten plots, regardless of seeding, just below the soil surface at the end of each growing season and were retrieved at the beginning of the following growing season. Seed bags were kept in place in the soil by the wire from a stake wire flag, which also aided in retrieval of the bags. The retrieved seeds were tested for viability using a Tetrazolium test (1% 2,3,5-Triphenyl-2H-Tetrazolium Chloride from MP Biomedicals). The seed coats and surrounding bracts were removed and the seeds were dampened in a wet paper towel over night. The next day, a dissecting pin was used to puncture the seed coat under a dissecting microscope. Then, the seeds were placed in a dark place in a Petri dish to soak in the tetrazolium solution overnight. The following day, the seeds were observed under the dissecting microscope to determine viability. Seed viability was based on the amount of dark purple stained areas, which indicated living tissue. However, light pink areas represented unstained, dead tissue (Grabe 1970). More than half of an individual seed had to be stained dark purple to be considered living.

Plant Performance. Flowering of *A. japonica* was measured each year at each site. Morphological characteristics and fecundity of twenty randomly selected flowering plants outside of plots was recorded. Seed production was assessed by counting seed on these

twenty randomly chosen plants. In all years, each of the twenty plants was measured and the height, inflorescence length (cm), and number of nodes, stems, and inflorescences were recorded.

Data Analysis. A two-way mixed model (SAS Institute, 2003) was used to determine the effects of site and year on performance measurements (plant height, number of nodes, number of stems, inflorescence length, and number of inflorescences) and seed viability and fecundity. Seedling emergence was analyzed using a repeated measures mixed model in SAS (PROC MIXED, SAS Institute, 2003) to determine significant differences in site or year. Significance was assessed at $P < 0.05$. A Tukey's test was used to determine significant differences among means.

Results

Performance of *A. japonica* varied between sites. At CH, the mean plant height in 2012 was 64.7 ± 3.7 cm, while at BWR mean height in the same year was 84.4 ± 5.9 cm (Table 2.1). The following year, mean height decreased by 7.1 cm at CH, but increased by 24.5 cm at BWR. In 2014, plants at CH showed an increase in mean height of 32.3 cm, whereas plants at BWR only increased in height by 0.4 cm, when compared to 2013. The number of nodes and the number of stems also varied between sites and years (Table 2.1). The mean number of nodes at CH and BWR, pooled over years, was 8.7 ± 2.2 and 10.7 ± 3.5 per plant, respectively; while the mean number of stems was 9.7 ± 1.7 per m^2 and 9.3 ± 1.6 per m^2, respectively (Table 2.1). Overall, at the CH site plant size, seed viability and plant density dropped in 2013, but was consistently high in 2014. By contrast height, stem and

inflorescence number, and fecundity per plant at BWR consistently increased all three years.

There was a highly significant interaction between seeding treatments and years ($P = 0.0001$) with a mean of 17.5 ± 2.5 seedlings per m^2 emerging in 2013 and 4.1 ± 0.9 seedlings per m^2 emerging in 2014. Seedling emergence at CH increased from a mean of 20.4 ± 2.7 seedlings per m^2 in 2013 to 52.5 ± 5.1 seedlings per m^2 in 2014 (Figure 2.1a). The BWR site, however, had no emergence in 2013 and had a mean of 19.3 ± 2.7 seedlings per m^2 emerge in the seeded plots in 2014 with 9.7 ± 1.4 seedlings per m^2 emerging in the unseeded plots (Figure 2.1b). Seed viability corresponded with seedling emergence at each site. Regardless of site, there was a decline in seed viability from 2012 to 2013, with viability decreasing 24% and 31% at CH and BWR, respectively (Table 2.1). An increase in seed viability was apparent at both sites from 2013 to 2014 with seeds from plants at CH increasing in viability by 44% and seeds from plants at BWR increasing by 47%.

End of growing season survivorship of tagged seedlings at CH was the lowest in 2012 with an overall seedling survivorship of 62% (Figure 2.2a). In 2013 and 2014, seedling survivorship at CH was 96% and 100%, respectively. At BWR there was a much lower overall seedling survivorship over the three-year experiment. In 2012, seedling survivorship at BWR was 52% (Figure 2.2b). The following years, seedling survivorship was 46% and 60%, respectively. At both sites regardless of year, seedlings that survived became reproductive at the end of the growing season. Additionally, tagged seedlings in 2012 and 2013 were monitored through the end of the 2014 growing season (Table 2.2). Overall, the highest seedling survival to reproduction was at CH regardless of the year the seedlings were initially tagged. For example at CH, 44% of the 2012 tagged seedlings

survived through 2014, whereas 26% survived at BWR. In addition, of the seedlings tagged the following year 74% and 38% survived through 2014, at CH and BWR respectively.

Fecundity differed among years (Table 2.1) with an annual increase regardless of site (Figure 2.3). There was about a five times increase from 2012 to 2014, regardless of site. However, the inflorescence number (4.3 ± 1.1) and average length (CH: 10.0 ± 1.7 cm; BWR: 13.7 ± 3.2 cm) relatively did not change much. The density of plants at CH was 53% greater than at BWR (CH: 22.6 ± 3.7 m^2; BWR: 12.0 ± 2.0 m^2).

Discussion

A simple schematic model summarizing the seed dynamics of *A. japonica* was developed based on our observations of seed viability, seedling emergence, seedling survival to reproduction, and plant fecundity from both sites (Figure 2.4). This model shows that there is a large potential input of *A. japonica* seeds into the seedbank from reproductive plants, but only a small percentage of seeds emerge the following spring (CH: 0.43%; BWR: 0.82%); it should be noted that this low emergence of seedlings does not take into account seed loss. The longevity of seed in the seedbank is unknown and research is needed to understand this part of the life history. This model provides context for the following interpretation of results from CH and BWR in 2012 to 2014.

This study demonstrates the highly variable nature of *A. japonica* plant performance within and among sites and between years in southern Illinois. Variation in performance of this invasive plant had not been demonstrated quantitatively before this study. However, a previous observational study (Evans and Taylor 2011) showed relatively similar seed germination (65%), seed viability (almost 100%) and fecundity (16,000 seeds/m^2) of *A.*

japonica albeit with a higher density of plants (70 plants/m^2).Variation in performance can be partially attributed to environmental factors. In 2012, southern Illinois underwent a drought in which over the growing season (May-October) 33 cm of rainfall occurred; whereas in 2013 and 2014, southern Illinois received 47 cm and 54 cm, respectively, of rainfall (National Weather Service 2015). In addition to the drought year that was experienced in 2012, there were also higher mean temperatures in 2012 compared with 2013 and 2014. The mean growing season temperature in 2012 was 25°C; whereas in 2013 and 2014, the mean growing season temperature was 22°C both years. Both of these environmental factors likely increased plant stress in 2012, which is potentially why seedling survival was lower in 2012 compared with 2013 and 2014. The young seedlings were susceptible to drought. Thus, reallocation of plant resources for survival, in terms of vegetative and root growth, rather than fecundity likely occurred during these periods of environmental stress (Grime 1979). Several previous studies report variable performance of invasive species related to environmental stress. For example, Gibson et al. (2002) showed that the invasive exotic grass *Microstegium viminium* (Trin.) A. Camus had decreased fecundity in drought years. However, demographic buffering is provided to *A. japonica* by a seedbank through between-year survival. Between-year survival offers different resource allocation approaches to perennial species than to annual species, like *M. viminium*. Additionally, an experiment on the invasive shrub *Anthriscus caucalis* M. Bieb. demonstrated that spatial variance of survival varied among types of communities that the shrub was invading (Wallace and Pranther 2013). Fecundity of the invasive shrub was lowest in grazed sites (a trampling effect) in drought years. In this study, fecundity and seedling survivorship were lowest, regardless of site, in 2012 compared to the following

years, whereas seed viability was lowest in 2013. These trends could be attributed to environmental stresses.

Habitat type was another variable that could have influenced plant performance since the BWR population was located within 15 meters of the banks of the Cache River, which was stagnant with a high risk for flooding. In 2011 and 2013, this site was heavily flooded with low species diversity and a lot of bare ground (Smith 2013). Frequent disturbance at BWR led to compacted soils and bare ground that ultimately could have affected the ability of *A. japonica* seeds to germinate limiting competition with other species; thus, allowing for a greater amount of resources to become available. An increase is resources may have allowed the plants to grow taller at BWR than at CH. The BWR plants had reduced fecundity compared with plants at CH possibly due to lower light levels and more frequent disturbance. The CH site was located in a forest that had a higher species diversity than BWR and limited disturbance. Since the CH Nature Preserve is 'landlocked' by surrounding private land on three sides and the Ohio River to the south, it is not easily accessed by the public and the site is rarely used. The presence of the state endangered dusky salamander (*Desmognathus fuscus*) also limits disturbance at CH because the site was protected.

Achyranthes japonica has shown the ability to re-sprout and overcompensate in areas that are browsed or mowed (Smith 2013; Schwartz et al. 2015a), which allows for an increase in seed output. Little information is known about *A. japonica*'s ability to persist in the soil seedbank. However, from this study and from other studies conducted on other species in the Amaranthaceae family (Schwartz et al. 2015b), one can hypothesize that with its large seed size, in comparison to other species in the family, *A. japonica* seeds may not

persist in the soil as long as smaller-seeded members of the Amaranthaceae family. However, large-seeded species may show enhanced survival during seedling establishment compared with small-seeded species (Moles and Westoby 2004). Thompson et al. (1993) proposed a method to predict seed persistence in the soil based upon the variance of fruit length, width and depth, and weight. Accordingly, we examined 50 *A. japonica* fruits and determined a mean weight of 126 mg and a total variance of 0.207 (L.M. Schwartz, unpublished data), implying seed persistence in the soil seedbank for less than five years.

Seedling survivorship at both sites in 2012 appeared to exhibit a Type II survivorship curve which indicates a constant mortality risk throughout the life of the cohort (Gibson 2014). This type of survivorship curve is typical for some herbaceous perennial plant species (Gibson 2014). For example, Meyer and Schmid (1999) found a Type II survivorship curve for the perennial invasive species *Solidago altissima* when determining the transitions between various reproductive stages to assess colonization potential to new habitats by seed. Survivorship in 2013 and 2014 appeared to be moving more towards a Type I survivorship curve which indicates that mortality risk increases as the maximum life span is reached (Gibson 2014). The constant mortality risk associated with 2012 is more than likely due to the extreme drought that southern Illinois underwent. Early season conditions, in 2013 and 2014, were conducive for seedling survivorship possibly due to a higher amount of precipitation, than in 2012, and a colder winter that could be important for the seeds in the soil seedbank. Understanding how the mortality of this species couples with high fecundity, germination, and seed viability provides a foundation to further investigate the persistence and establishment of *A. japonica*. This reasoning can lead to the suggestion that it may not be worth trying to control seedlings or

that if seedlings cannot be controlled, then natural mortality could help control the remaining survivors (i.e., land managers should prioritize managing reproductive plants over seedlings). Although percent emergence is low, this species compensates for it with very high propagule pressure and relatively high seed viability. Populations of the invasive exotic *Microstegium vimineum* had similarly high propagule pressure and low seedling emergence rate supporting the findings of this study (Cheplick 2010).

Arguments have been expressed against the need for population biology to be a fundamental tool in early detection rapid response (EDRR) situations (Simberloff 2003). These arguments have been based on many unsuccessful eradications that typically only provide an additional problem (i.e., *Hydrilla verticallata* (Langeland 1996)) or that do not address the entire problem at hand. However, understanding the basic knowledge of a new invader, such as *A. japonica*, is fundamental in taking the first step towards a comprehensive and effective management plan without risking the surrounding ecosystem. It is important to understand that there is a distinct difference between a new invasion site within a state for a species that was introduced into the United States 150 years ago, where there is an abundance of information, versus the first comprehensive study to document the life history of a relatively new invasive species. This study is not comparing existing management strategies of a well-studied species to what can and should be implemented for the control of *A. japonica*. Rather, this study demonstrates the invasive nature of a poorly studied species that should be of concern in many naturalized areas. Stopping or limiting the spread of a new invasive species is important from an economic and ecological stand point.

This study is the first to empirically assess the invasibility of *A. japonica* in terms of general survivorship, fecundity, and performance measurements. *Achyranthes japonica* has been the subject of relatively few investigations, which justifies further research on the basic life history characteristics and competitive abilities. For example, this study showed that 0.4% to 0.8% of the viable seeds produced by mature plants in a year emerge as seedlings; this leads to several additional questions 1. What happens to the remaining seeds, do they persist in the existing seedbank or do they die, 2. How long do seeds persist in the soil seedbank, and 3. How much does anthropogenic disturbance truly affect this species? However, the schematic model (Figure 2.4) does not account for seed loss which could be due to seed predation, decay, dissemination, hitch hiking on people or animals, or environmental factors such as flooding. Thus, the actual number of viable seeds in the soil is likely less than number of seeds produced shown in Figure 2.4. In addition, this research suggests that the age of the plant plays a major role in fecundity, which is further effected by disturbance and environmental stochasticity.

Achyranthes japonica is an aggressive invasive species that quickly spreads and can invade high quality natural areas. We have already seen it invade into the Cache River watershed which is considered to be the last remaining high quality wetland in southern Illinois (Suloway and Hubbell 1994). How far this species can spread both geographically and into various habitat types is still unknown. More knowledge is needed on this species to generate a more rapid and efficacious management strategy that can be implemented to better control this species in the future.

Table 2.1. Mean morphological and seed characteristics of *A. japonica* at Chestnut Hills Nature Preserve (CH) and Bellrose Waterfowl Reserve (BWR) in southern Illinois from 2012 to 2014. The F and P values are associated with the interaction between site, year and seed/plant characteristic. Different letters indicate significant difference among years between sites.

	CH			BWR			
	2012	**2013**	**2014**	**2012**	**2013**	**2014**	**F_{df}, *P***
Plant Height (cm)	64.7±3.7^{c}	57.6±4.6^{c}	89.9±6.1^{b}	84.5±5.9^{b}	109.1±7.4^{a}	108.5±7.7^{a}	4.97 $_{5,48.5}$, 0.0063
Number of Nodes	8±2^{b}	8±2^{b}	10±3^{ab}	10±3^{ab}	11±3^{a}	10±3^{ab}	2.24 $_{5,33.4}$, 0.0031
Number of Stems	11±3^{a}	10±2^{b}	8±1^{bc}	7±1^{c}	11±3^{a}	10±2^{b}	1.89 $_{5,33.4}$, 0.0047
Inflorescence Length (cm)	7.4±0.9^{c}	8.0±1.2^{c}	14.7±3.1^{a}	12.1±2.8^{b}	14.5±3.4^{a}	14.6±3.3^{a}	2.23 $_{5,38.5}$, 0.0013
Number of Inflorescences	3±0.4^{bc}	5±1^{b}	5±1^{b}	2±0.3^{c}	4±1.2^{bc}	7±2.1^{a}	4.55 $_{5,33.8}$, 0.0128
Seed Viability (%)	78±7^{b}	54±18^{c}	98±3^{a}	67±17^{c}	36±28^{d}	83±6^{b}	5.19 $_{5,65.1}$, 0.0021
Fecundity (seeds/plant)	151±17^{c}	264±9^{b}	632±23^{a}	112±21^{c}	263±8^{b}	564±32^{a}	3.35 $_{5,65.1}$, 0.0001
Density of Plants (m^2)	15±3^{bc}	18±3^{b}	35±5^{a}	13±2^{c}	6±1^{d}	17±3^{b}	8.27 $_{5,44.2}$, 0.0001

Table 2.2. Percentage of seedlings that survived to reproduction of *Achyranthes japonica* (seedlings that survived to flower/seedling mortality) at Chestnut Hills Nature Preserve (CH) and Bellrose Waterfowl Reserve (BWR) in southern Illinois from 2012 to 2014. Fifty seedlings were tagged and monitored at each site for each for the three years.

	CH			**BWR**		
	2012*	**2013**	**2014**	**2012***	**2013**	**2014**
2012+	62% 31/19	-	-	52% 26/24	-	-
2013	94% 29/2	96% 48/2	-	65% 17/9	256% 8/22	-
2014	76% 22/7	77% 37/11	100% 50/0	76% 13/4	68% 19/9	60% 30/20

* Indicates the establishment of original cohort of seedlings
+ Indicates the year the original cohort was continually monitored

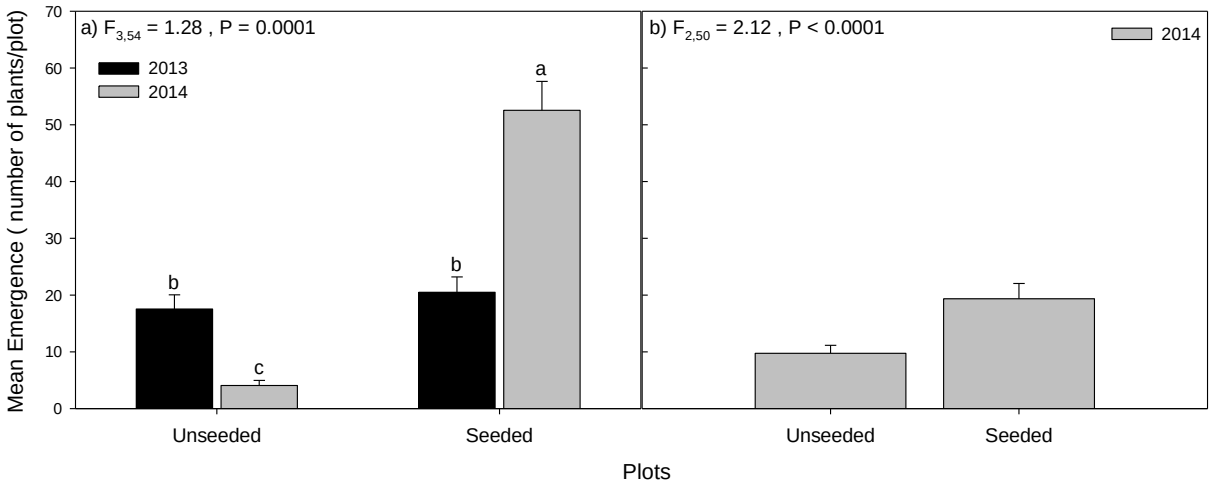

Figure 2.1. Emergence of *A. japonica* at a) Chestnut Hills Nature Preserve (CH) in 2013 and 2014 and at the b) Bellrose Waterfowl Reserve (BWR) in 2014. Zero seedlings emerged at BWR in 2013. Mean values with the same letters are not significantly different at $\alpha = 0.05$.

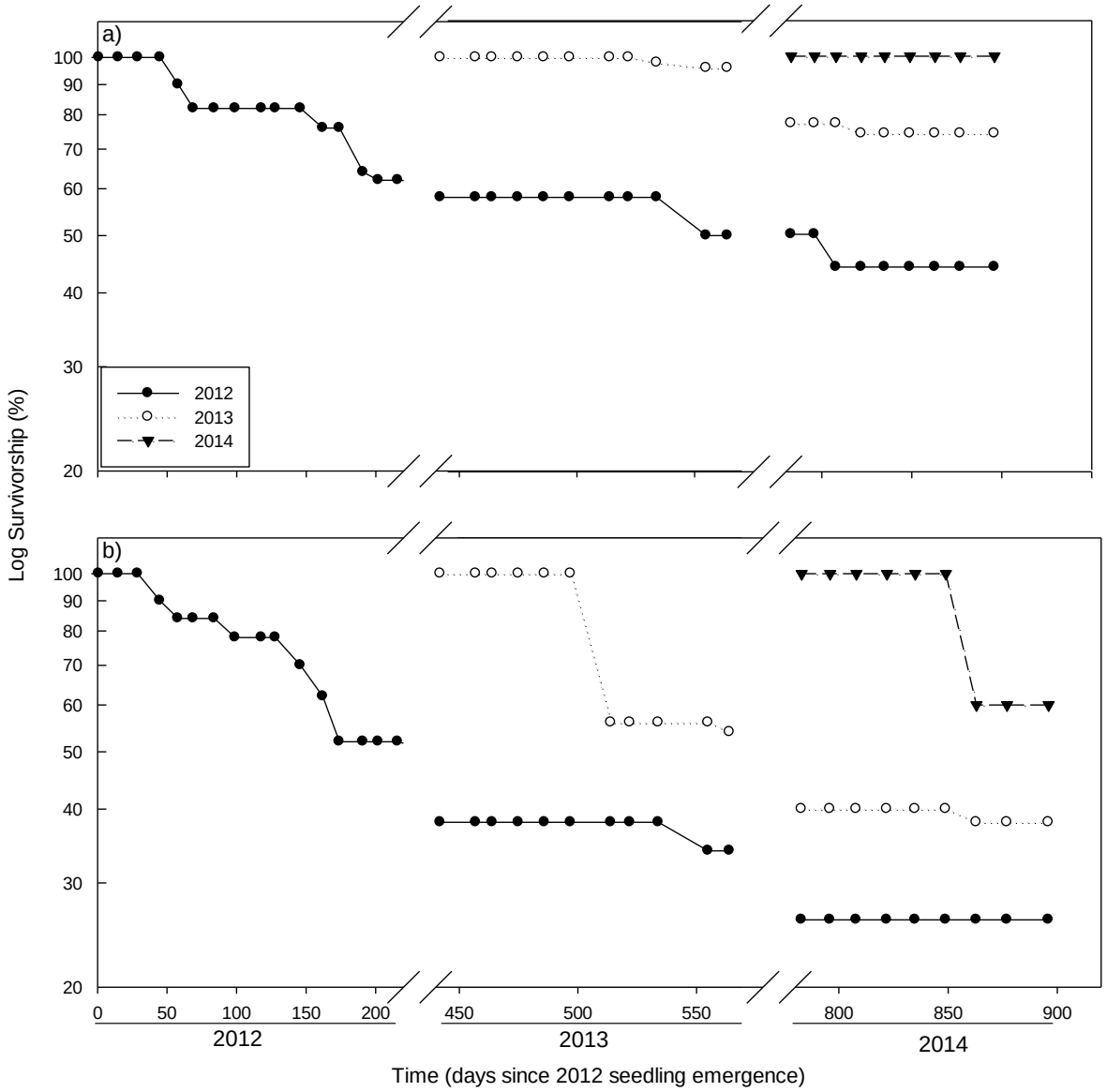

Figure 2.2. Seedling survivorship of *A. japonica* at a) Chestnut Hills Nature Preserve (CH) and the b) Bellrose Waterfowl Reserve (BWR) in southern Illinois from 2012 to 2014. Fifty seedlings were tagged and monitored at each site for each of the three years. Closed circles = 2012 cohort of seedlings that were followed through the 2014 field season; Open circles = 2013 cohort of seedlings that were followed through the 2014 field season; Closed triangles = 2014 cohort of seedlings.

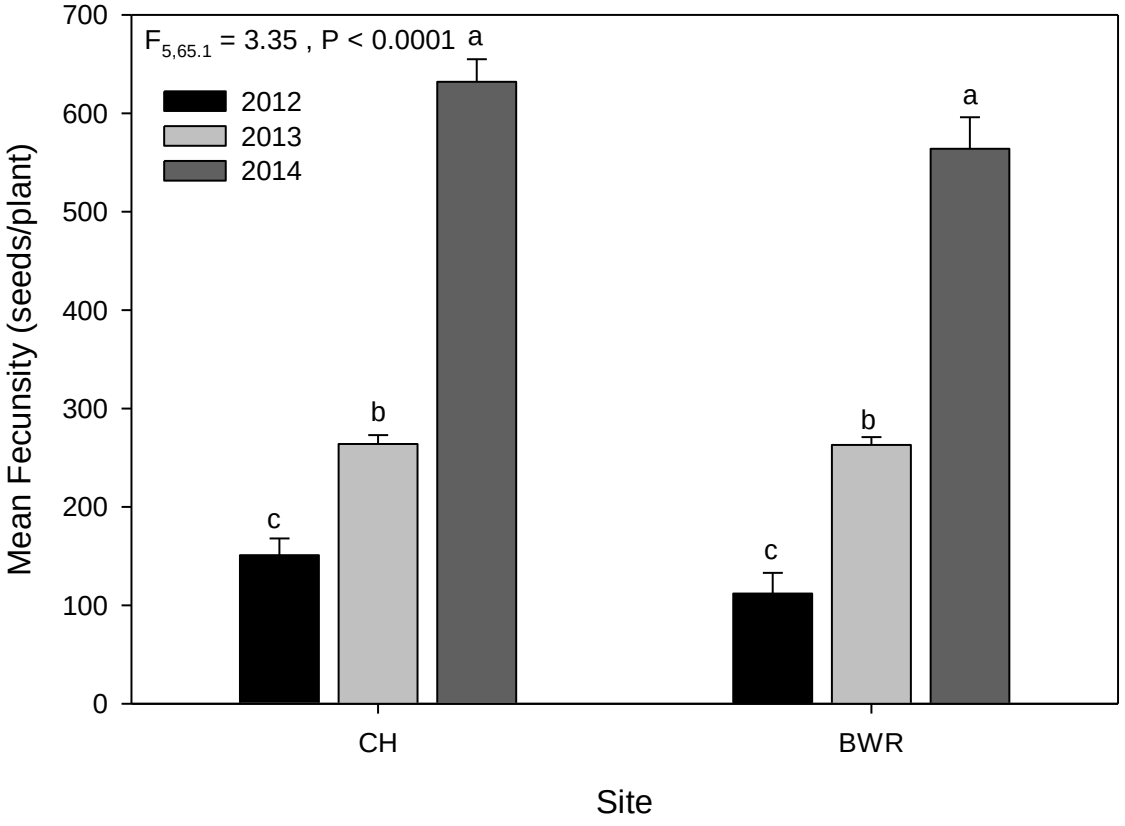

Figure 2.3. Fecundity, from 2012 to 2014, for twenty plants at the Chestnut Hills Nature Preserve (CH) and the Bellrose Waterfowl Reserve (BWR) in southern Illinois. Mean values with the same letters are not significantly different at $\alpha = 0.05$.

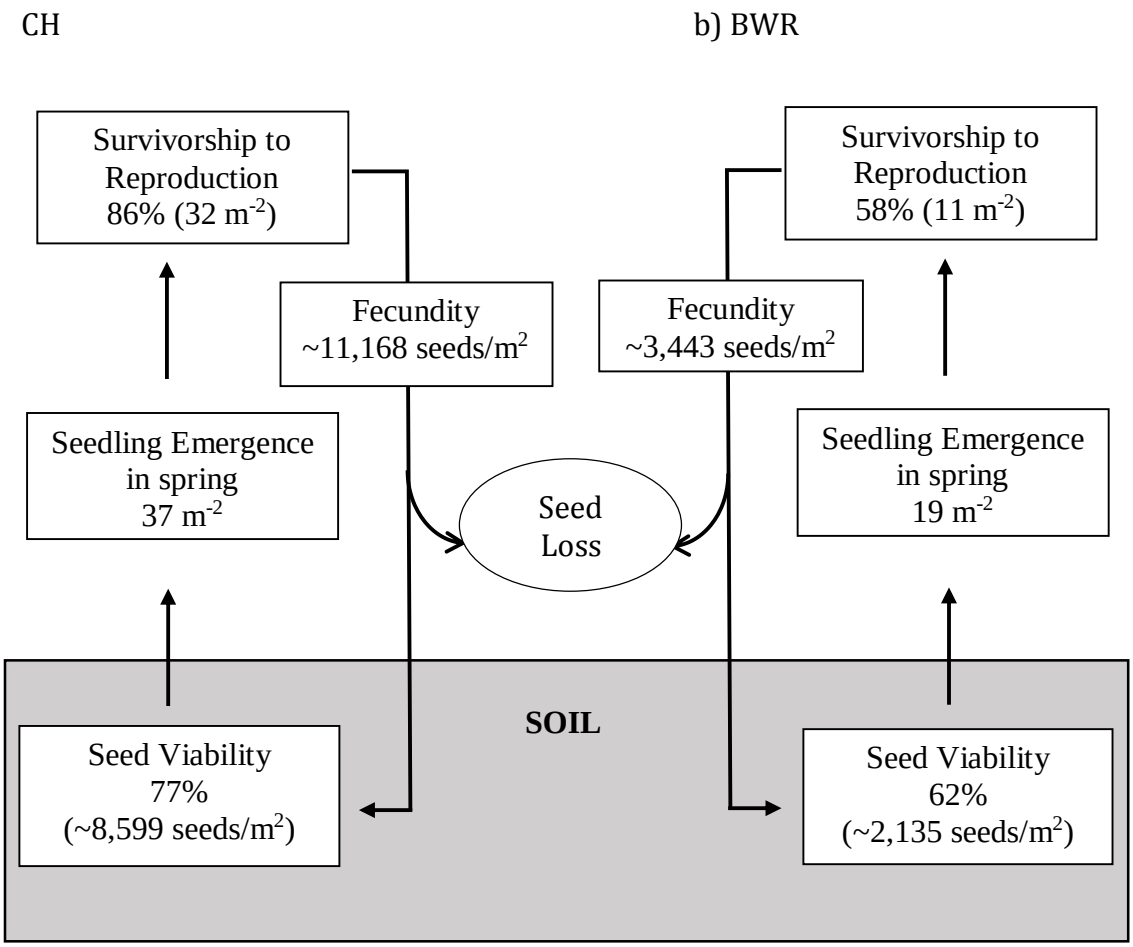

Figure 2.4. Schematic model illustrating seed dynamics of *Achyranthes japonica* at a) Chestnut Hills Nature Preserve (CH) and the b) Bellrose Waterfowl Reserve (BWR) from 2012 to 2014.

CHAPTER 3

THE COMPETITIVE EFFECT AND RESPONSE OF SEEDLINGS OF FOUR AMARANTHACAEAE SPECIES ON SOYBEAN (*Glycine max*)

Introduction

Weeds and crops interact by competing for shared resources such as light, nutrients, and water. There is a long history of studying this competitive interaction in soybean (Stoller et al. 1987; Zimdahl 2004) spanning from investigations of the effects of weed density (Hyvönen and Salonen 2002), weed diversity (Gibson et al. 2008; Kruger et al. 2009), environmental factors such as geography (Schwartz et al. 2015a), and herbicide resistance (Dill et al. 2008). The competitive ability can be compared between species in two ways: first, in the competitive effect of plants or the ability to suppress other individuals, and secondly in the competitive response of plants or the ability to avoid being suppressed (Goldberg and Landa 1991; Violle et al. 2009; Zhang and Lamb 2011). Competitive response and effect traits are correlated with each life-stage (Wang et al. 2010) and with traits such as plant height, plant size, leaf shape, and relative growth rate (Zhang and Lamb 2011), which are important in developing management tactics for cropping systems.

Mechanistically, crop-weed competition can be understood in terms of Tilman's resource ratio model that predicts that the growth rate of an individual is determined by the two resources at the lowest availability relative to the plant's requirement for all resources (Tilman 1982, 1987, 1997; Lehman and Tilman 2000). In general, the specific rate of biomass change of a species is an increasing function of the environmental condition of its limiting resources (Tilamn 1985; Kruger-Mangold et al. 2006). The growth of a plant

would decrease in the presence of a neighboring plant if these plants consumed the same limiting resources (Maron and Marler 2007; Tilman 1988, 1997). While Tilman's resource ratio model has been widely used in natural systems, it is less widely applied in crop systems although the model still applies (Miller et al. 2005; Zimdahl 2004).

The Amaranthaceae family contains important agricultural weeds, invasive exotics, and rare native plants. In the United States Midwest region, Palmer amaranth and tall waterhemp have been widely established as two of the prominent agricultural weeds. These species have many characteristics that make them very successful weeds including the ability to grow 2 to 3 m in height (Horak and Loughin 2000; Tranel and Trucco 2011) and extended seed germination and seedling emergence late into the row-crop growing season (Hartzler et al. 1999). Competition of 8 plants m^{-2}, starting at crop emergence, resulted in Palmer amaranth reducing soybean yields by 78% compared with 56% for tall waterhemp (Bensch et al. 2003). Furthermore, soybean yield was reduced by 10% when plants emerged at the V4 growth stage of soybean (Steckel and Sprague 2004; Steckel et al. 2004; Steckel 2008). Palmer amaranth and tall waterhemp have been found not only to be very competitive with row crops but with other pigweed species as well.

Japanese chaff flower is a member of the Amaranthaceae family and represents a relatively recent introduction spreading across the Ohio River Valley. This perennial, C_3 herb is native to Korea, China and Japan (Sage et al. 2007; Choi et al. 2010; Evans and Taylor 2011; Schwartz 2014). Japanese chaff flower is generally found in areas with some shade and moist soil. However, the species can also grow in drier areas in sun, and in densely shaded areas (Schwartz 2014). Dense patches of Japanese chaff flower have been found in bottomland forests, riverbanks, field edges, and in ditches and swales (Evans and

Taylor 2011; Schwartz 2014; Schwartz et al. 2015b). Large patches of Japanese chaff flower have shown indications of deer browsing and insect feeding but the plant will release new shoot growth from previously dormant axillary buds and overcompensate (Schwartz et al. 2015b). Apart from anecdotal observations, little has been reported on this species and only recently has an aggressive educational campaign been launched to learn more about this species. The occurrence of Japanese chaff flower in row-crop field margins in southern Illinois has prompted concern about its potential competitive effects on crops. By contrast, bloodleaf is classified as endangered in Illinois and Maryland and is considered to be rare in Indiana (IDNR 1994; Gibson and Schwartz 2014). Despite its endangered and rare status, very little ecological work has been conducted on this species (Gibson and Schwartz 2014).

The objective of this study was to determine the relative competitive effect and response of Japanese chaff flower, Palmer amaranth, tall waterhemp, and bloodleaf to soybean. This comparison has relevance for the *Amaranthus* species, and could potentially be relevant for Japanese chaff flower, with bloodleaf versus soybean acting as a non-weed benchmark 'control'. Two hypotheses were tested: 1) the perennial species, Japanese chaff flower and bloodleaf, will have a lower requirement than the annual *Amaranthus* species for a single limiting resource when competing with interspecific neighbors, as measured by resource drawdown, and 2) a competitive effect ranking is predicted to be Palmer amaranth < tall waterhemp < cut Japanese chaff flower = Japanese chaff flower = bloodleaf. The competitive response rankings will be inversely related among the four species.

Materials and Methods

The hypotheses were addressed by conducting two experiments. A resource drawdown experiment was conducted to test how each species utilizes an above- and belowground resource (test of hypothesis 1), and a field experiment was conducted to determine the competitive effect and response of the study species on soybeans at varying densities and soybean row spacing (test of hypothesis 2).

Resource Drawdown Experiment

Experimental Design. The drawdown of light and soil nitrogen of each species was determined in field soil under greenhouse conditions at the Southern Illinois University Tree Improvement Center (TIC) greenhouse. Seed of each of the four Amaranthaceae species were collected from populations within 161 km of Carbondale, IL each year. The Japanese chaff flower site was located at Chestnut Hills Nature Preserve (CH: 37°11'N, 89°3'W) located in Pulaski county, IL and bloodleaf seeds were collected from Beall Woods Nature Preserve (BW: 38°20'N, 87°49'W). Seeds of the two annual *Amaranthus* species (Palmer amaranth (located at the Belleville Research Center (BRC 9B: 38°30'N, 89°50'W)) and tall waterhemp (located at BRC T4: 38°31'N, 89°50'W) were collected from glyphosate susceptible populations and underwent a bleach (5.25% sodium hypochlorite) scarification process to ensure maximum possible seed germination. The soybean, Japanese chaff flower, and bloodleaf seeds did not require pre-treatment. Seeds of each species were sown into separate flats with potting soil and allowed to germinate. Seeding rates and timing were determined based on the germination rate (based on already known germination rates/species) and the expected time to establishment for each species (i.e., Japanese chaff

flower was seeded ten days before tall waterhemp). When seedlings of each species had emerged, five seedlings per species were transplanted into each experimental pot.

Field soil (0 to 15 cm depth) was collected from Southern Illinois University Agronomy Research Center (ARC). Soil was characterized as having a topsoil of silt loam (0 to 0.25 m) and subsoil (0.25 to 1.30 m) of silt clay loam (Herman et al. 1976). Field soil was sterilized and mixed in the ratio of 1:1 with sterilized sand to dilute the N concentration and aid in permeability while watering. The mixed soil was placed into 15-cm pots. The average greenhouse conditions included a photoperiod of about 8 to 12 h per day, which were determined by supplemental lights in the greenhouse, and a temperature of 31 ± 5 C. Two soybean (Asgrow Brand AG3832 plot seed, Illinois origin) seeds were planted in each pot for a density equivalent to soybeans grown in a 38-cm row spacing in agricultural fields.

Resource manipulation treatments of nitrogen addition and light reduction (shading) were implemented. Nitrogen was added as granular ammonium nitrate applied at 1 g per pot prior to transplanting the seedlings. Shading treatments were implemented by surrounding the pots with a frame and then covering the frame with a 60% shade cloth to simulate forested canopies. A frame constructed of PVC pipe was placed around the non-shaded pots to eliminate shade effects produced by the frames. Pots were watered twice daily with 75 mL. A saucer was placed under each pot to ensure a closed system and reduce leaching. Liquid accumulation in the saucer was added back to the soil surface when applicable. There were five replicates (plus one unseeded control pot) of each treatment with two temporal replicates. Control pots were not sown with seeds to establish a baseline for resource drawdown values. The temporal replicates averaged four weeks and ran

during the months of February and March 2013. Pots were placed in the greenhouse in a randomized complete block design.

Sampling. Light intensity drawdown was measured under the plants at the soil surface using a LI-COR Light Meter (LI-COR, Lincoln, Nebraska. Model LI-250) for each pot twice per week (Schwartz 2015: Appendix C). Light quality was measured one time at the end of the experiment using an International Light 1400A radiometer/photometer (IL1400A, International Light, Inc., Newburyport, MA) using white, blue, red, and far-red filters below the leaves. Light quality was performed on a separate set of pots that did not undergo the nitrogen or light treatments.

Performance measurements (height and number of nodes) were recorded twice weekly to use as an indicator of early seedling growth (Schwartz 2015: Appendix B). Above- and belowground biomass were harvested from each pot when the seedlings of each species had reached four nodes, which was indicative of early seedling growth. Biomass was oven dried (48 h, 55 C) and weighed (Schwartz 2015: Appendix D). Inorganic nitrogen was measured in the soil of each pot using ion-exchange resin bags (Binkley 1984; Schwartz 2015: Appendix E). Resin bags were constructed from nylon hose and consisted of 5 g of equal amounts of an anion (Dowex 1 x 8, 50 to 100 mesh; Acros Organics) and a cation (Dowex 50W x 8, 50 to 100 mesh; Acros Organics) resin. In the laboratory, the resin was extracted with 75 mL of 2N KCl after shaking for 1 h at 200 rpm, filtered through a 0.4 µm filter membrane, and the filtrate analyzed for NH_4-N and NO_3-N on a Flow IV Solution Autoanalyzer (O.I. Corporation, College Station, Texas, USA). Total N was determined by adding the NH_4-N and NO_3-N values.

Seedling Competitive Effect and Response Experiment

Study Site. Experimental plots were established at the Southern Illinois University, Carbondale Tree Improvement Center (TIC) in Jackson County, IL (37°42'N, 89°16'W). The soil at the site was a silt clay loam, with a topsoil of silt loam and subsoil of silt clay loam (Herman et al. 1976). The experiment was conducted annually for three years (2012 to 2014), with 2012 being a preliminary experiment (data not reported).

Experimental Design. Seeds, which were collected in southern Illinois that year and were from the same seed source as the resource drawdown experiment, were planted in sterilized pots (15 cm diameter by 15 cm depth) filled with a silt clay loam soil that was collected from the TIC field. The soil was prepared as in the resource drawdown experiment. The soybean, Japanese chaff flower, and bloodleaf seeds did not require pre-treatment. However, as in the resource drawdown experiment, the two *Amaranthus* species (Palmer amaranth and tall waterhemp) were scarified with bleach solution to promote germination. After seedling emergence, the seedlings were transferred to the field and the pots were submerged into excavated holes so the soil surface in the field and pots were equivalent. Pots were used to prevent the release of Japanese chaff flower into the field, since at the time of this experiment this species had not been found in Jackson county, IL. In addition, the planting of an endangered species such as bloodleaf is heavily regulated and the pots provided containment. Volunteer plant seedlings were removed continually throughout the experiment. Each year (2012 to 2014), the experiment was conducted until the plants reached the end of the seedling stage (denoted by the majority of each species reaching the four node stage) to seek consistent results. Plants in this experiment were not

grown beyond the seedling stage because control of agronomic weeds is frequently targeted at this stage.

Each of the four invasive species (n=5 for invasive species treatment including cut- and uncut-Japanese chaff flower, see below) were either planted as a monoculture (control) or with soybean (n=2 for soybean treatment) (Asgrow Brand AG3832 plot seed, Illinois origin). Japanese chaff flower seedlings were planted as either un-manipulated seedlings (referred to as uncut-Japanese chaff flower, ACHJA), or as seedlings cut back to the soil surface at the four node stage (cut Japanese chaff flower, ACHJA-C) at which point seedlings have reached a perennial growth stage (Smith 2013). The cut Japanese chaff flower plants represent perennial plants that may have survived the previous winter or regrowth from the application of a non-systemic herbicide typically applied prior to commercial soybean planting. Upon emergence, the Amaranthaceae seedlings were thinned down to the desired seedling densities per pot (10, 30, and 90 for 38-cm rows (trial 1) and 10 and 30 for 76-cm rows (trial 2)). One or two equidistant (~4 cm) soybean seedlings were planted in each pot to simulate typical planting densities of soybean (Bensch et al. 2003) with the Amaranthaceae densities chosen to allow for agricultural conditions of crowding and competition around the soybean plants. One soybean per pot represented a 76-cm row spacing for soybeans (trial 2), whereas, 2 soybean per pot represented a 38-cm row spacing (trial 1).

This experimental design was an additive (AD) design with repeated measures (Gibson et al. 1999, Gibson 2015). The treatment design was a fully factorial combination of the four Amaranthaceae species including two stages of Japanese chaff flower (see below) (n=5), four or three different densities (n=4 (38-cm rows) or n=3 (76-cm rows)), presence

or absence of a soybean cultivar (n=2), and four or three replications (n=4 (38-cm rows) or n=3 (76-cm rows)) for a total of 5 x 4 x 2 x 4 = 160 experimental units (pots) for the 38 cm rows and 5 x 3 x 2 x 3 = 90 experimental units (pots) for the 76-cm rows; for a grand total of 250 pots (50 pots per species).

Sampling. Height (cm), number of branches, nodes and leaves were measured twice a week for each individual to determine performance (Schwartz 2015: Appendices F-I). All seedlings in each pot were harvested when the majority of the individuals had reached the 4-node stage, oven dried at 55 C, and both above- and belowground biomass weighed (g) (Schwartz 2015: Appendices L-M). Light intensity and soil moisture were measured twice per week in each pot using a LI-COR Light Meter (Model LI-250; LI-COR, Lincoln, Nebraska) and ECH_20 Decagon Soil Moisture meter (Decagon Devices, Inc., Pullman, Washington), respectively (Schwartz 2015: Appendices J-K).

Statistical Analysis

For the resource drawdown experiment, a three-way mixed model (SAS Institute[1]) was used to determine the effects of treatment (nitrogen, light), density, and plant species. Light quality was analyzed using a two-way mixed model testing the effects of light wavelength and plant species on light reduction. The competition experiment was analyzed using a repeated measures three-way mixed model in SAS (PROC MIXED, SAS Institute) to detect treatment effects (weed density [n=2],soybean presence or absence [n=2], and weed species [n=5]) on the performance (height, branch numbers, nodes, and leaf numbers), light intensity, and soil moisture. Aboveground and belowground biomass were analyzed for the Amaranthaceae species and soybean separately using a two-way mixed model to

determine the effect of biomass and density or soybean presence or absence. Significance were assessed at $P < 0.05$. A Tukey's test was used to determine significant differences among means with significant treatment effects. Based on weed species and soybean performance, a competitive effect and response ranking was proposed (after Bensch et al. 2003; Zhang and Lamb 2011).

Results and Discussion

Resource Drawdown. In comparison to the controls (pots with no plants), the four Amaranthaceae species each drew down light, but not nitrogen when treatments were compared (Table 3.1, Figure 3.1). In terms of light drawdown, bloodleaf drew down the least amount of light, indicating that this species had the least amount of plant material shading the soil surface. Palmer amaranth and soybean drew down the greatest amount of light; and tall waterhemp and Japanese chaff flower drew down an intermediate level of light in comparison to the other species. The low drawdown of light by bloodleaf may contribute to the slow growth of this perennial species with a poor ability to colonize, and may have contributed to its endangered status in Illinois, Maryland, and Indiana (Gibson and Schwartz 2014).

There was no significant difference for aboveground biomass between nitrogen treatment levels and species, except for Japanese chaff flower and Palmer amaranth (Table 3.1, Figure 3.2a). A significant aboveground biomass interaction occurred between species and shading treatment (Figure 3.2b). Each species produced more aboveground biomass without the shading than under the 60% shading treatment, except bloodleaf. Again, Japanese chaff flower produced a similar amount of aboveground biomass (0.75 ± 0.03

g/pot) to both Palmer amaranth (0.6 ± 0.04 g) or tall waterhemp (0.55 ± 0.02 g) without shading. Soybean produced the most aboveground biomass (2.5 ± 0.03 g), which was expected from a dominant crop; whereas, bloodleaf produced the lowest amount (0.3 ± 0.01 g), possibly due to its slow seedling growth which again might contribute to its endangered status. Belowground biomass was affected by the shade treatment (Table 3.1), and there was a trend towards an increase for the *Amaranthus* species and a decrease for Japanese chaff flower and soybean in belowground biomass with additional soil nitrogen (Figure 3.2c). A greater amount of belowground biomass was attributed to the nitrogen addition for all species, especially Japanese chaff flower (2.7 ± 0.3 g). Belowground biomass of Palmer amaranth and tall waterhemp were similar regardless of soil nitrogen treatment without shading.

The resource drawdown variation, among the four species, can be explained by R* theory. An R* value simply is the concentration of a resource that a species requires to survive (Krueger-Mangold et al. 2006). The species with the lowest R* value will outcompete a species with a higher R* for that specific resource (Tilman 1982, 1988). Under the conditions of this experiment, seedlings of Japanese chaff flower and Palmer amaranth drewdown the limiting resources in a similar manner, which indicates that at the early growth stage testing in this experiment Japanese chaff flower could potentially affect a dominant crop (i.e., soybeans) in a similar way as Palmer amaranth. Thus, these species would likely displace a species such as bloodleaf that show low rates of resource drawdown when grown in mixture.

An interaction between wavelength and species ($P < 0.0001$) was evident for the mean reduction in light quality (Figure 3.3). Bloodleaf (60.7 ± 1.5%) and soybeans (57.2 ±

2.9%) had the largest far-red (FR) light reduction through shading; whereas Japanese chaff flower had the least (97.3 ± 0.5%). The *Amaranthus* species had a similar reduction of FR light (AMAPA: 54.5 ± 1.1%; AMATA: 52.4 ± 2.7%). Holt (1995) proposed that the FR wavelength was reflected by nearby leaves, which allowed for an early detection of neighboring species that signaled oncoming competition during canopy development. Thus, as the seedlings in this study were growing, FR reflection among neighbors could have been signaling competition and initiating competitive responses through the FR/R photoreceptor also known as phytochrome (Smith 1994). Novoplansky (1991), demonstrated *Portulaca oleracea* L. seedlings avoiding growth in the direction of species with higher reflected FR light. Thus, Japanese chaff flower having the lowest reduction in FR light implies that neighboring species would avoid growing towards it. The only species that had a reduction in red (R) light quality was Japanese chaff flower (57.0 ± 1.1%).

Plants growing in the shade of neighboring taller vegetation are usually receiving reduced light intensity with a decreased R/FR ratio (Yang et al. 2014). Thus, plants grown under such conditions exhibit shade avoidance responses (i.e., elongated stem growth and little new leaf growth) (Smith 2000). Similar responses to decreased light intensity during growth has been reported for Palmer amaranth, where plasticity in acclimation to changing light conditions enabled Palmer amaranth to develop in shade regions (i.e., under a crop canopy) and to achieve high rates of growth if suddenly exposed to high light (Patterson 1985). In this study, the R/FR ratios were comparable (P = NS) for all of the species: bloodleaf 1.37 ± 0.58, Japanese chaff flower 1.51 ± 0.45, Palmer amaranth 1.51 ± 0.64, tall waterhemp 1.56 ± 0.82, and soybean 1.43 ± 0.56. Light intensity at the soil surface coupled

with light quality provides important insight for understanding competitive mechanisms and aids in the development of weed management tactics.

Competitive Effect and Response. The competitive response of the study species to soybean was similar between trials within the same year. In 2013 for both trials plant height was related to species, density, and days after planting (Table 3.2). Tall waterhemp grew the tallest at densities of 10 and 30 seedlings per pot in both trials, with Palmer amaranth and uncut Japanese chaff flower growing to a similar height (Figure 3.4a and 3.4b). Both Palmer amaranth and uncut Japanese chaff flower were not affected by density; whereas tall waterhemp was density sensitive. The cut Japanese chaff flower plants were the shortest regardless of trial. In trial 1 at the 90 seedling density, both *Amaranthus* species reached the same height by the final day after planting (DAP) (Figure 3.4a). In 2014, however, there was an interaction between species, day after planting and soybean (Table 3.2). Regardless of the trial, when soybeans were present, the height of bloodleaf was reduced (Figure 3.4c and 3.4d). This reduction, irrespective of soybean presence, could be due in part to the density of the species in each pot and to a general competition for resources. However, by DAP 23, both monocultures in both trials showed that the seedlings of the two *Amaranthus* species were the largest, with both Japanese chaff flower treatments only 1 cm shorter. Bloodleaf was the shortest in both trials, which is possibly due to its slow seedling growth again reflecting its rare status. The competitive response between years, regardless of trial, was comparable to each other. This similarity in response could be due, in part, to the very similar environmental factors during the month of May, when both trials were conducted. The precipitation levels did vary with 9 cm of precipitation in the month of May in 2013 and 12.5 cm in 2014. Temperature is an important ecological

factor in determining species growth and productivity. Palmer amaranth and tall waterhemp exhibit their highest germination rate of 30 and 50%, respectively, when mean air temperatures are at 25 C (Guo and Al-Khatib 2003).

The competitive effect of the study species on soybeans was only apparent in trial 2 in 2013 (Figure 3.5a) and trial 1 in 2014 (Figure 3.5b). There was an interaction between species and density in both trials. Trial 2 in 2013 ($P = 0.015$) the highest density of cut Japanese chaff flower reduced the height of soybean the most, followed by the two *Amaranthus* species, uncut Japanese chaff flower and bloodleaf. When the density was 10 seedlings per pot, the cut Japanese chaff flower again reduced the height of the soybeans the most, followed by uncut Japanese chaff flower and Palmer amaranth. Although the reduction in height was relatively small (1.8 to 3.1 cm), both uncut Japanese chaff flower and the cut Japanese chaff flower reduced the height of soybean in a similar manner to the two *Amaranthus* species with bloodleaf having no effect at all three densities. The same trend in soybean height reduction across all densities occurred in Trial 1 in 2014: the presence of tall waterhemp caused the greatest height reduction, followed by the cut Japanese chaff flower and uncut Japanese chaff flower, with Palmer amaranth reducing the height the least. Consistency in results between trials and years supports intrinsic differences among species rather than short-term environmental variability (phenotypic plasticity)

There was an interaction between DAP, density, and soybean (Table 3.2) affecting soil moisture in 2013. The soil moisture in the pots with densities of 10, 30 or 90 were relatively similar regardless of trial (Figure 3.6). In 2014, however, there was an interaction between DAP and soybean. In both trials at DAP 10, the monocultures had a

slightly lower mean soil moisture than soybean, but on all other consecutive DAPs, the opposite was apparent. Mean light intensity at the soil surface for all years and trials, except trial 2 in 2013 (Figure 3.7), had an interaction between density and soybean. Overall, light intensity at the soil surface decreased with an increase in the density (Figure 3.7).

Aboveground biomass was affected by study species and soybean presence in the 2014 trials (Figure 3.8c and 3.8d) but not the 2013 trials (Figure 3.8a and 3.8b). In both 2014 trials, the study species monocultures generally had a greater biomass than the mixtures with soybean. Among the study species monocultures, Palmer amaranth had the greatest biomass (3.7 ± 0.7 g/pot). The cut Japanese chaff flower (trial 1: 3.4 ± 0.6 g) and Japanese chaff flower (trial 2: 2.5 ± 0.4 g) had the next largest biomass. In trial 2, Tall waterhemp showed the opposite effect with greater biomass when soybean was present. Data on the number of branches, nodes and leaves are not reported since these variables showed similar results to height.

Competitive Rankings. Neighbor species identity had a direct effect on soybean biomass. Aboveground biomass of soybean was affected by the interaction between study species and density in only 2014 (2013: P = NS; 2014: P = 0.01). Regardless of year and density, the highest soybean biomass was in the presence of bloodleaf indicating that it affected soybean the least of the species (Figure 3.9a and 3.9c). In 2013, the ranking of study species effects on soybean varied with density (Figure 3.9a). For density 10 the rank order was tall waterhemp > Palmer amaranth > uncut Japanese chaff flower > cut Japanese chaff flower. At a density of 30 plants per pot, the rank order was the cut Japanese chaff flower > tall waterhemp > uncut Japanese chaff flower > Palmer amaranth. The highest density (90

seedlings) had the same rank order as a density of 30 seedlings except the *Amaranthus* species were switched. In 2014, the order was the same for all of the densities: tall waterhemp > cut Japanese chaff flower > uncut Japanese chaff flower > Palmer amaranth. This effect was also examined by Bensch et al. (2003), in which the effect of various densities of *Amaranthus* species on soybean yield loss was quantified. They determined that weed species emerging with soybeans were more competitive that weed species emerging later. However, the highest weed biomass affected yield loss with Palmer amaranth having the greatest effect followed by tall waterhemp (Horak and Loughin 2000; Bensch et al. 2003). Differences among the competitive abilities of species in the Amaranthaceae family, specifically the *Amaranthus* genus, are varied but many of those species can have a large effect on crop production.

An overall competitive effect and response ranking among the study species was developed from this research. The competitive effect ranking was determined to be: tall waterhemp > Palmer amaranth = cut Japanese chaff flower ≥ uncut Japanese chaff flower > bloodleaf. The competitive response ranking was the inverse. This ranking is novel because the species that are being compared are within the same plant family, but are found in different habitats, and their competitiveness varies. In addition, competitive abilities have been based off of more than one trait (Andrew et al. 2015). Rankings based on competitive abilities has been used in several other studies that range from closely related weeds (Andrew et al. 2015), to less closely related weeds (Horak and Loughin 2000; Bensch et al. 2003; Hock et al. 2006), or to cultivars of a single weed (Hansen et al., 2008; Andrew et al., 2015). Although Japanese chaff flower may not be fully suited to be the newest weed species in agriculture by escaping management strategies implemented by farmers, (e.g.

current susceptibility of Japanese chaff flower to herbicides; Smith 2013, Schwartz et al. 2015b), it is still an aggressive weed that farmers and land owners need to be able to identify. This species has many similar characteristics to the *Amaranthus* species, such as the ability to colonize in areas with limiting resources, continual flushes of germination throughout the growing season, the ability to outcompete other weed species, and high fecundity; but, Japanese chaff flower also is a perennial species that can withstand removal of shoot material and has a high germination rate (Schwartz et al. 2015b). Only early detection and rapid response methods can be relied on to keep Japanese chaff flower out of areas in and around agricultural fields. If this species evolves resistance to various herbicide modes of action as have other taxa in the Amaranthaceae (Heap 2014), it may well become a prominent weed in agriculture.

Table 3.1. F and *P* statistics for above and belowground biomass (g), in the greenhouse experiment, for nitrogen and light for the four Amaranthaceae species and soybean.

Treatment/Variable	Aboveground Biomass		Belowground Biomass	
	F	*P*	F	*P*
Shading[a]	17	<0.0001	71.35	<0.0001
Nitrogen[b]	17	<0.0001	61.05	<0.0001
Shading*Nitrogen	3.71	0.0864	9.39	0.0069
Species[c]	59.9	<0.0001	19.89	<0.0001
Species*Shading	3.94	0.0064	6.26	0.0003
Species*Nitrogen	2.19	0.0799	4.12	0.0051
Species*Shading*Nitrogen	59.9	0.6753	3.68	0.0092

[a] Shading: treatments with and without the 60% shade cloth (N=2)

[b] Nitrogen: treatments with and without the addition of ammonium nitrate (N=2)

[c] Species: all study species (N=5)

Table 3.2. Significant effects and interactions among groups based upon Amaranthaceae species competitive effect and response (field experiment) to soybean presence/absence. Only significant differences are shown within a variable. Pooled over species.

Variable/Effect	N[a]	F	*P*
Soil Moisture			
T1[b]-2013: Species[d]*Soybean[e]*DAP[f]	60	1.76	0.0366
T1-2013: Density[g]*Soybean*DAP	36	4.66	< 0.0001
T1-2014: DAP	6	214.87	< 0.0001
T1-2014: Density*Soybean	6	3.04	0.0548
T2[c]-2013: Species*DAP	30	2.88	< 0.0001
T2-2013: Density*Soybean*DAP	48	3.89	< 0.0001
T2-2013: Species*Density*Soybean	40	1.92	0.0034
T2-2014: Species*DAP	30	2.19	0.0062
T2-2014: Soybean*DAP	12	2.06	0.0459
Light Intensity at the Soil Surface			
T1-2013: Species*Density*Soybean	30	2.17	0.0351
T1-2014: Species*Density*DAP	90	1.52	0.0513
T2-2014: Species*Density	20	4.54	< 0.0001
T2-2014: Density*Soybean	8	7.74	0.0007
T2-2014: Species*DAP	30	1.75	0.043
Weed Species Height			
T1-2013: Density*Soybean	6	4.62	0.0379

T1-2013: Species*Density*DAP	90	2.23	0.0063
T1-2013: Species*DAP*Soybean	60	2.94	0.0003
T1-2014: Species*DAP*Soybean	60	8.27	< 0.0001
T1-2014: Species*Density*DAP	90	3.52	0.0012
T2-2013: Species*Density*DAP	120	2.66	< 0.0001
T2-2014: Species*DAP*SB	60	1.73	0.027
Soybean Height			
T1-2013: Species*Density	15	3.09	0.0151
T1-2014: Species*DAP	30	1.94	0.0345
T2-2013: DAP*Density	24	5.06	< 0.0001
T2-2013: Species	5	2.92	0.0305
T2-2014: DAP	6	31.88	< 0.0001
T2-2014: Species*Density	20	1.98	0.0406
Weed Species Aboveground Biomass			
T1-2013: Species*Density	15	3.37	0.0186
T1-2014: Species*Soybean	10	4.92	0.0067
T2-2013: Species*Density*Soybean	40	2.66	0.0016
T2-2014: Species*Soybean	10	5.02	0.0013
Soybean Aboveground Biomass			
T1-2013: Density	3	6.40	0.0051
T1-2014: Species	5	15.01	< 0.0001
T2-2013: Species*Density	20	1.79	0.0757
T2-2014: Species*Density	20	3.75	0.001

Belowground Biomass			
T1-2013: Species*Density	15	3.53	0.0026
T1-2014: Species*Density*Soybean	30	3.10	0.0361
T2-2013: Species*Density	15	3.35	0.0004
T2-2014: Species*Density*Soybean	30	3.75	0.001

[a] N = the number of groups in a treatment or variable
[b] T1 =Trial 1
[c] T2 = Trial 2
[d] Species = Weed species
[e] Soybean = soybean(s) present
[f] DAP = Day after planting
[g] Density = Weed species density (T1: 10, 30, 90; T2: 10, 30)

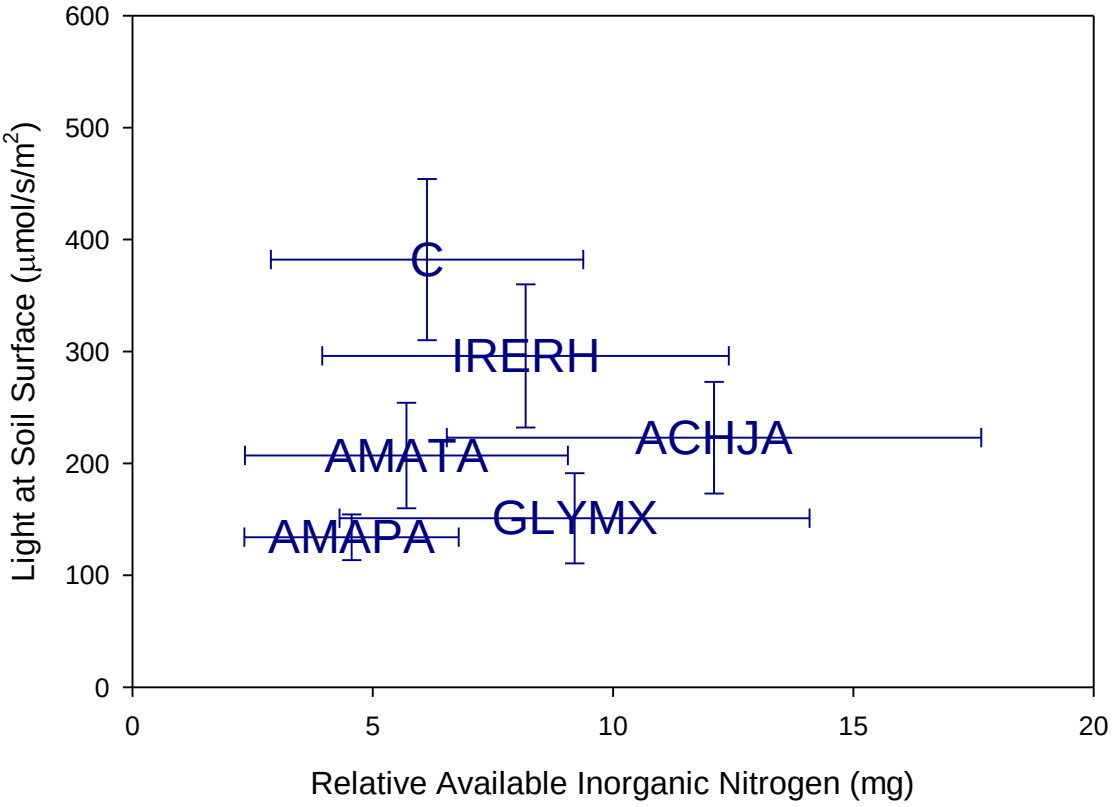

Figure 3.1. Relative resource drawdown for total nitrogen and light intensity at the soil surface for bloodleaf (IRERH), Japanese chaff flower (ACHJA), Palmer amaranth (AMAPA), waterhemp (AMATA), soybean (GLYMX), and control (C) with 95% confidence intervals.

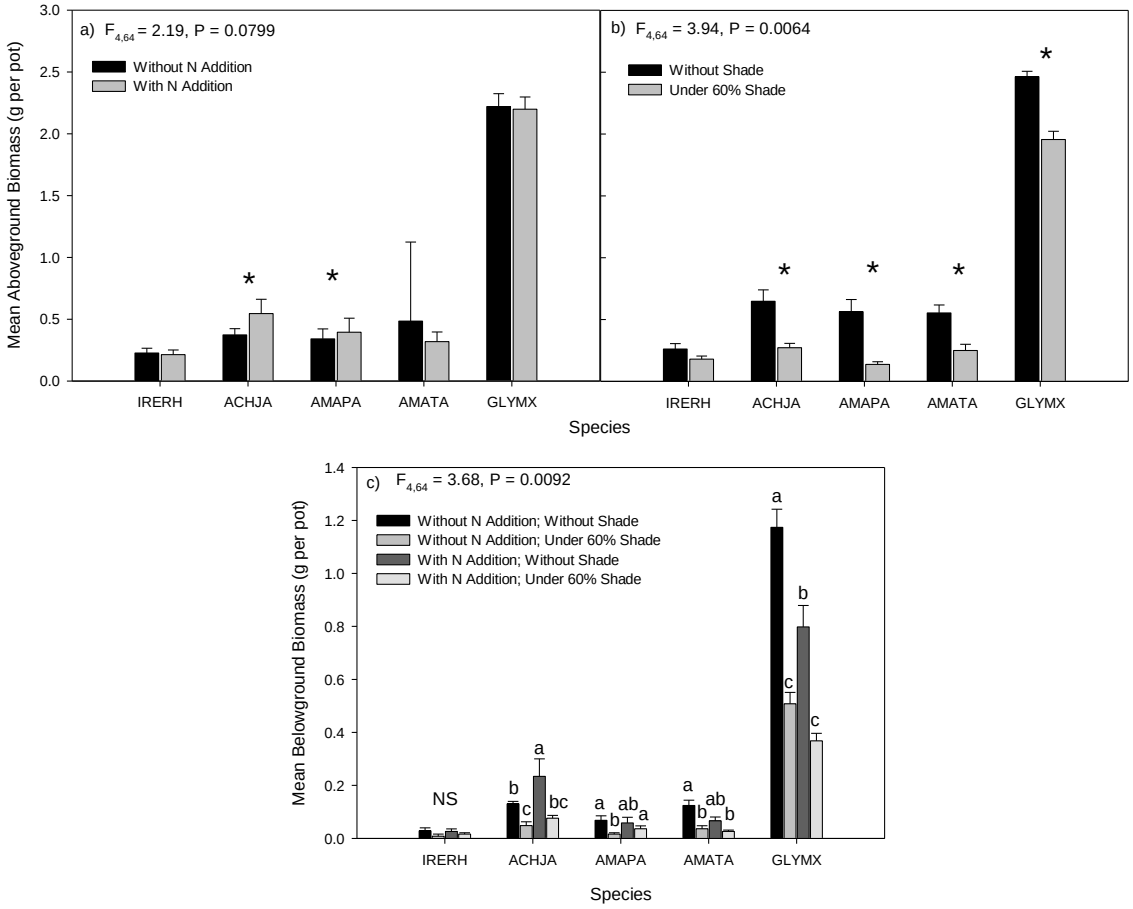

Figure 3.2. Mean (± se) aboveground biomass in response to a) nitrogen and b) light treatments, and c) below ground biomass in response to the interaction between nitrogen and light treatments. Mean values with the same letters are not significantly different at α = 0.05 within a species.

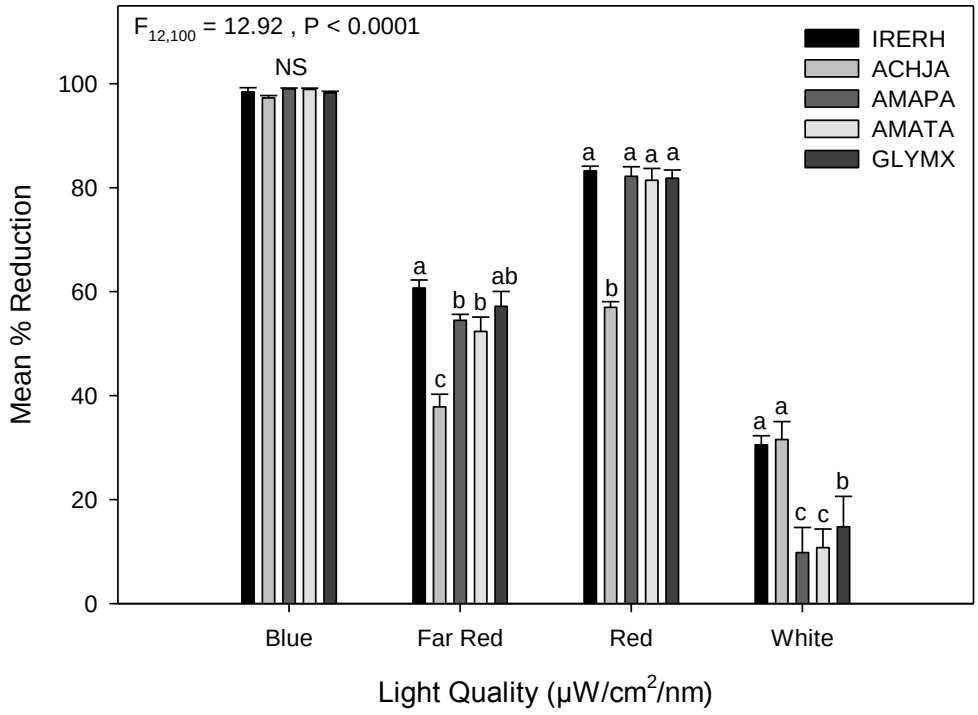

Figure 3.3. Mean (± se) percent reduction of light quality in response to the species and soybean. Species nomenclature is as follows: bloodleaf (IRERH), Japanese chaff flower (ACHJA), Palmer amaranth (AMAPA), waterhemp (AMATA), and soybean (GLYMX). Mean values with the same letters are not significantly different at $\alpha = 0.05$ within a species.

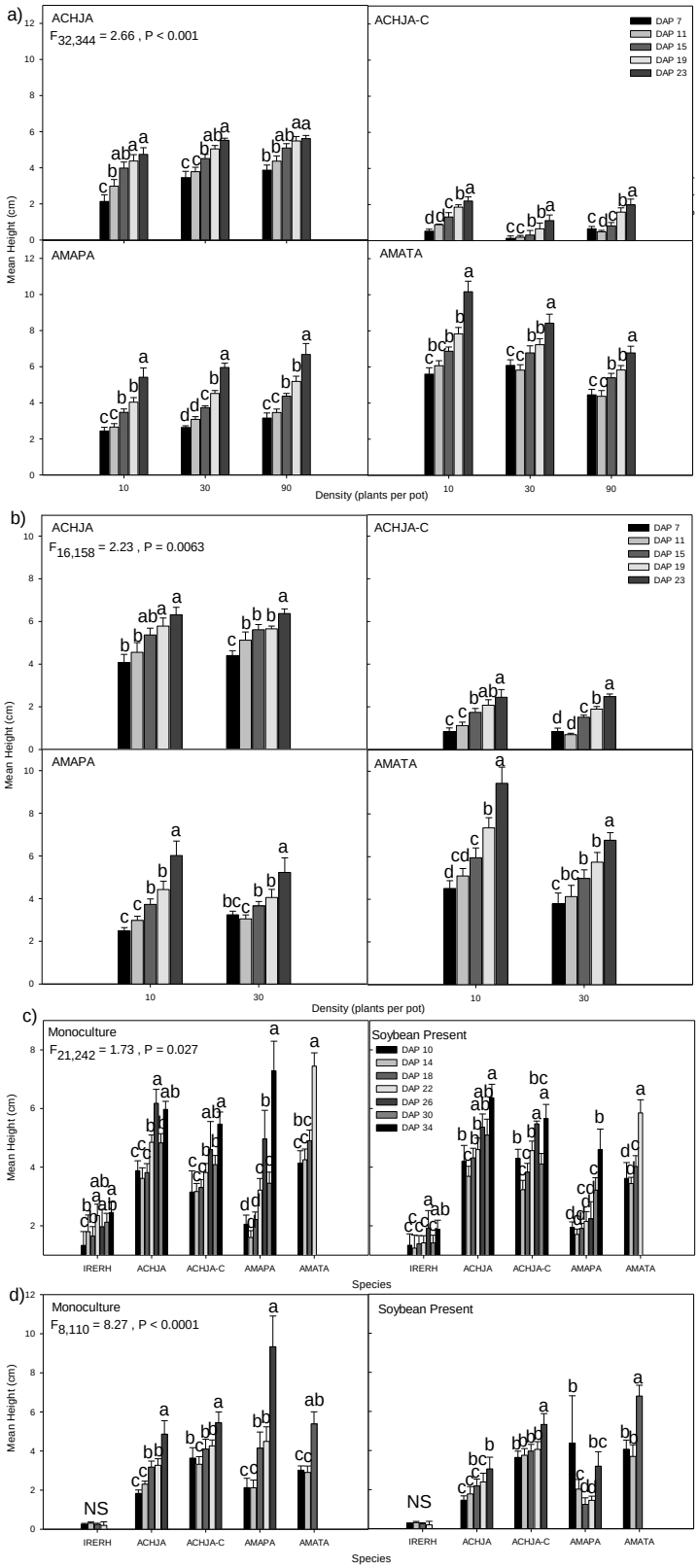
a)
ACHJA
$F_{32,344}$ = 2.66 , P < 0.001
ACHJA-C
DAP 7
DAP 11
DAP 15
DAP 19
DAP 23
AMAPA
AMATA
Mean Height (cm)
Density (plants per pot)
b)
ACHJA
$F_{16,158}$ = 2.23 , P = 0.0063
ACHJA-C
AMAPA
AMATA
Mean Height (cm)
Density (plants per pot)
c)
Monoculture
$F_{21,242}$ = 1.73 , P = 0.027
Soybean Present
DAP 10
DAP 14
DAP 18
DAP 22
DAP 26
DAP 30
DAP 34
Mean Height (cm)
IRERH
ACHJA
ACHJA-C
AMAPA
AMATA
Species
d)
Monoculture
$F_{8,110}$ = 8.27 , P < 0.0001
Soybean Present
NS
Mean Height (cm)
Species

Figure 3.4. The competitive response of the species mean (± se) height for a) trial 2 2013, b) trial 1 2013, c) trial 2 2014, and d) trial 1 2014 to soybean. Species nomenclature is as follows: bloodleaf (IRERH), uncut Japanese chaff flower (ACHJA), cut Japanese chaff flower (ACHJA-C), Palmer amaranth (AMAPA), and waterhemp (AMATA). DAP is equal to day after planting. Mean values with the same letters are not significantly different at $\alpha = 0.05$ within a species.

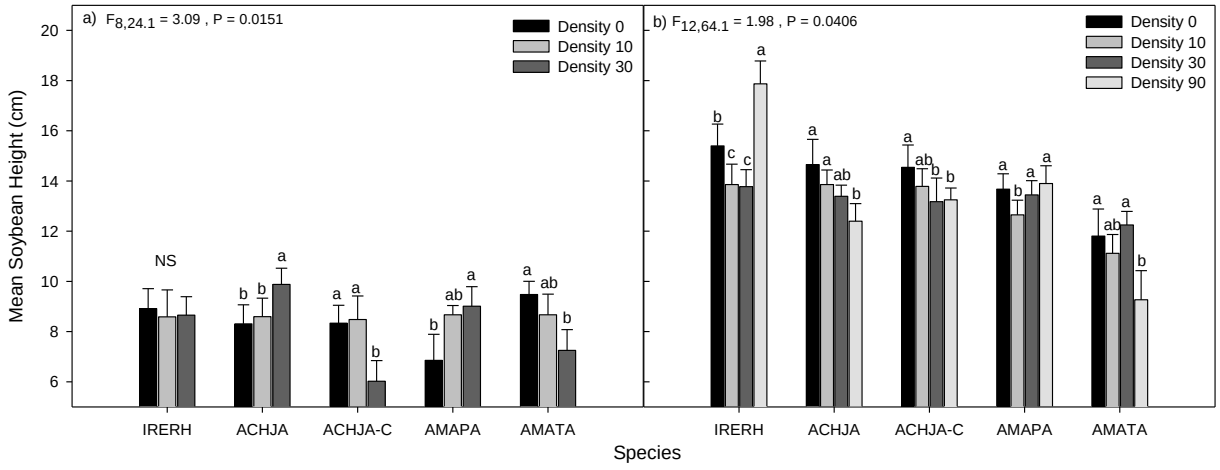

Figure 3.5. Competitive effect of soybean mean (± se) height for a) trial 1 2013 and b) trial 2 2014 in response to the species bloodleaf (IRERH), uncut Japanese chaff flower (ACHJA), cut Japanese chaff flower (ACHJA-C), Palmer amaranth (AMAPA), and waterhemp (AMATA). Mean values with the same letters are not significantly different at $\alpha = 0.05$ within a species.

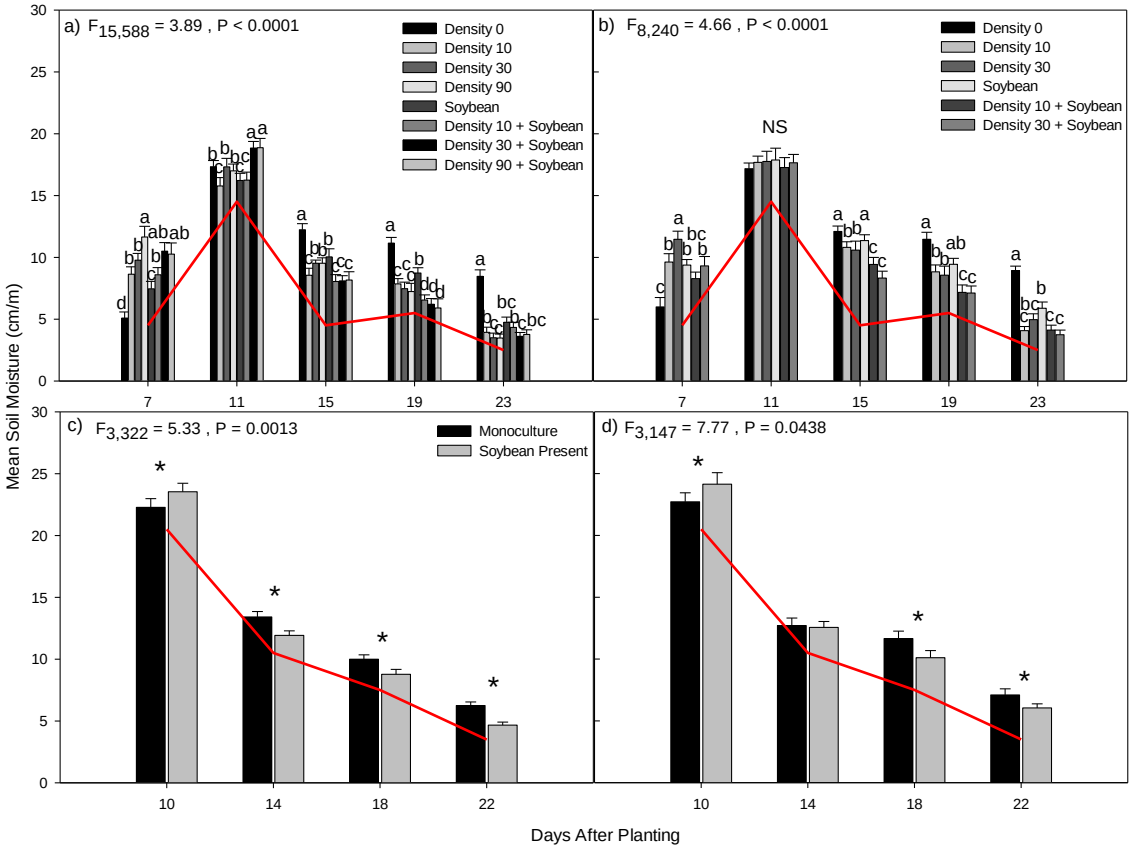

Figure 3.6. Mean (± se) soil moisture for a) trial 2 2013, b) trial 1 2013, c) trial 2 2014, and d) trial 1 2014. Red lines are indicative of daily average soil moisture. Mean values with the same letters are not significantly different at α = 0.05 within a species.

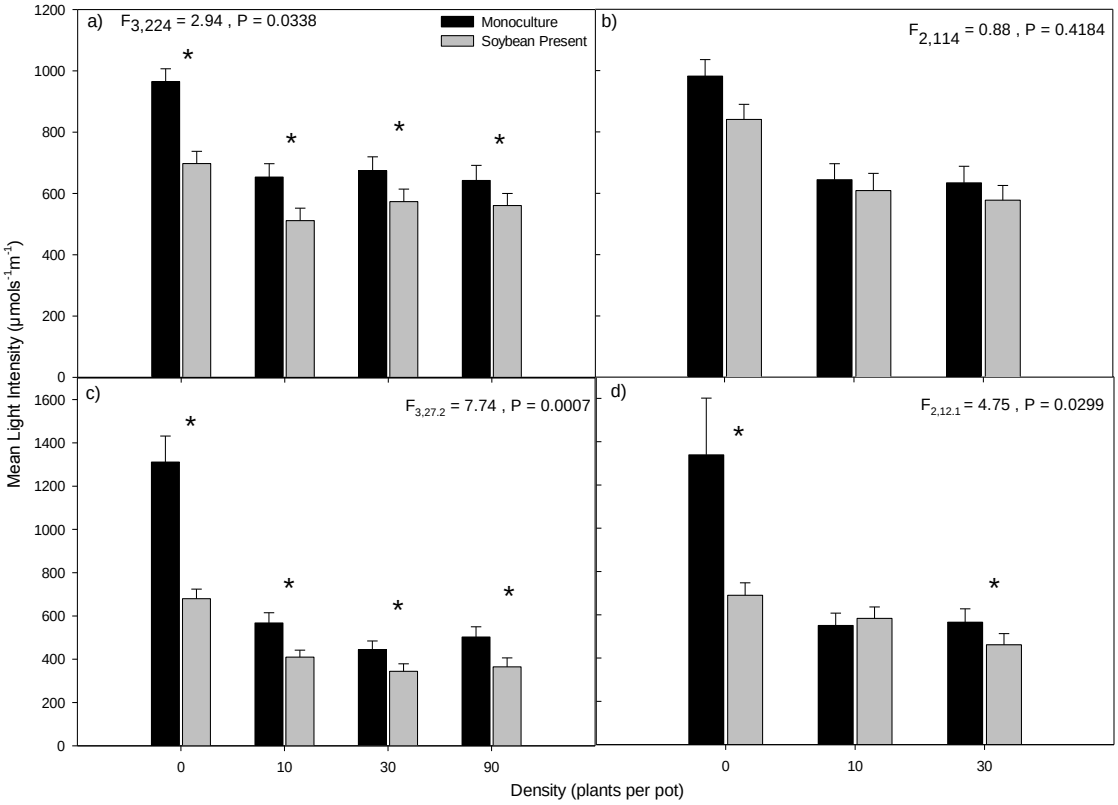

Figure 3.7. Mean (± se) light intensity at the soil surface for a) trial 2 2013, b) trial 1 2013, c) trial 2 2014, and d) trial 1 2014. Mean values with the same letters are not significantly different at $\alpha = 0.05$ within a species.

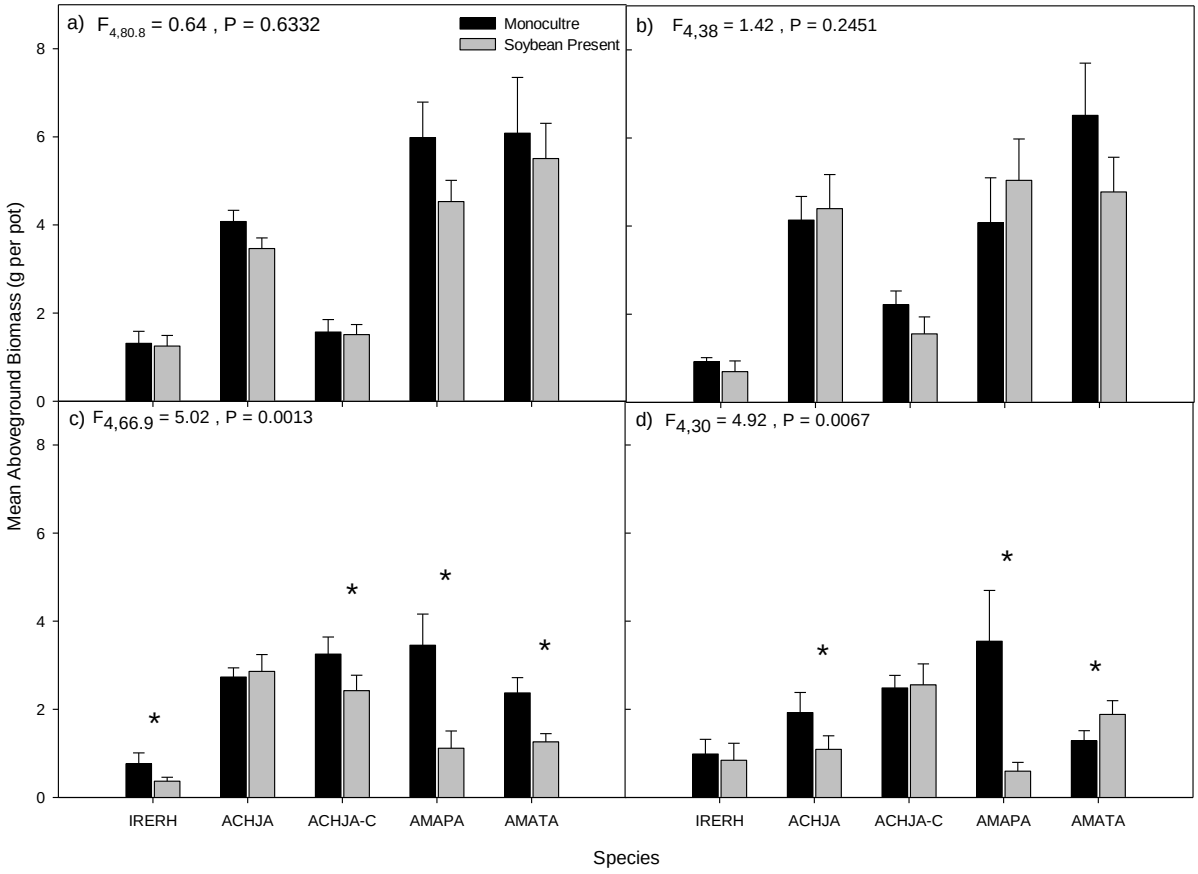

Figure 3.8. Mean (± se) aboveground biomass for the species bloodleaf (IRERH), uncut Japanese chaff flower (ACHJA), cut Japanese chaff flower (ACHJA-C), Palmer amaranth (AMAPA), and waterhemp (AMATA) in response to soybean for a) trial 2 2013, b) trial 1 2013, c) trial 2 2014, and d) trial 1 2014. Mean values with the same letters are not significantly different at $\alpha = 0.05$ within a species.

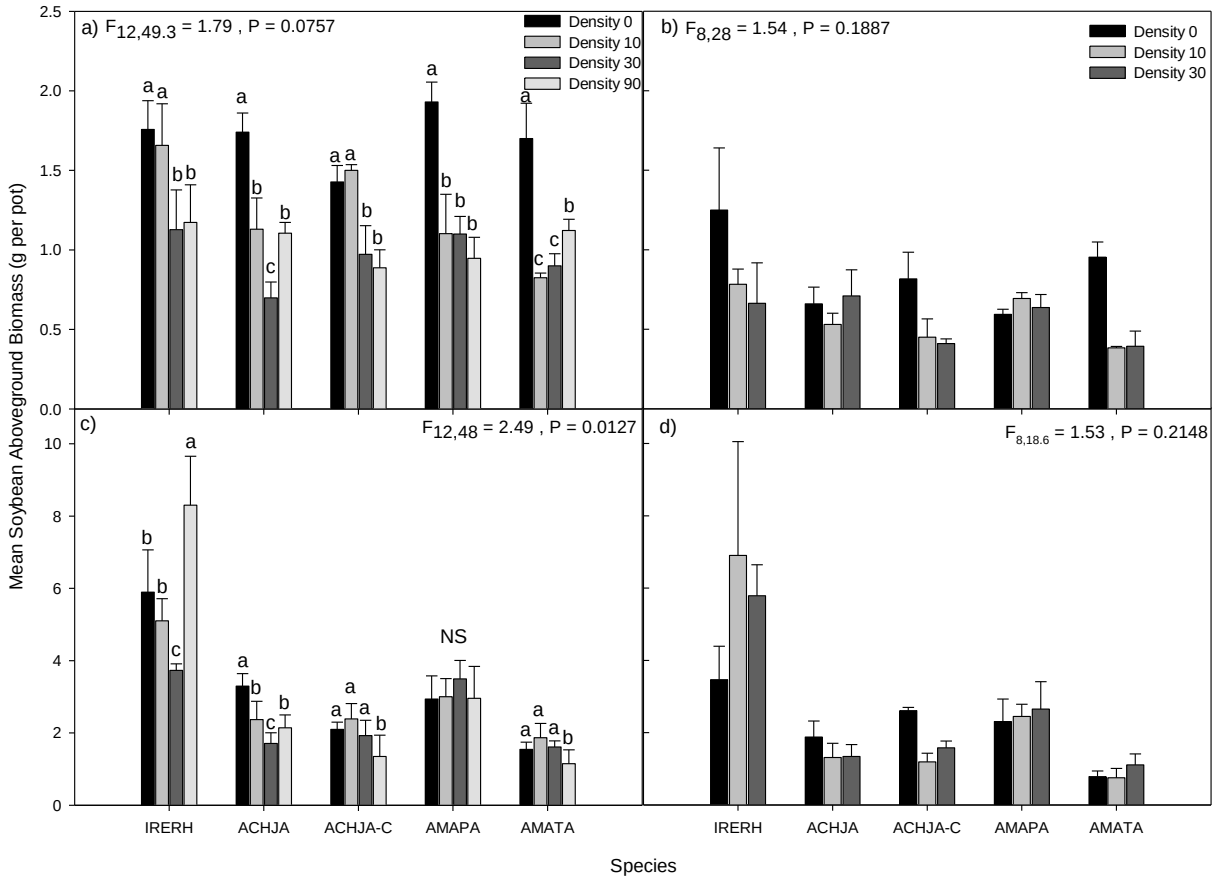

Figure 3.9. Mean (± se) aboveground biomass for the soybean in response to the species bloodleaf (IRERH), uncut Japanese chaff flower (ACHJA), cut Japanese chaff flower (ACHJA-C), Palmer amaranth (AMAPA), and waterhemp (AMATA) for a) trial 2 2013, b) trial 1 2013, c) trial 2 2014, and d) trial 1 2014. Mean values with the same letters are not significantly different at $\alpha = 0.05$ within a species.

CHAPTER 4

USING INTEGRAL PROJECTION MODELS TO COMPARE POPULATION DYNAMICS OF FOUR CLOSELY RELATEED SPECIES

Introduction

Demographic processes, such as survival, growth, and reproduction, can inform us about invasion risk, extinction risk, trade-offs in life history strategies. Demography links the processes that affect individuals to population and community level patterns (Merow et al. 2014b). The diversity of life history characteristics associated with a species are the result of long evolutionary responses to natural selection over large scales. Studies of closely related species, such as species in the same family, may be informative in this respect. Matrix population models (MPM) (Caswell 2001) provide an important and powerful tool to establish parameters that are important to population dynamics by modelling discrete, demographic stage or age data (Metcalf et al. 2013). Using commonly collected demographic data, MPMs have limitations primarily due to biases or they may omit the complexities associated with resource allocation that vary across different environments (Merow et al. 2014b). In addition, MPMs require a lot of parameters to incorporate stochasticity because they have to estimate stochasticity for each stage separately. Another important limitation of MPMs is that they may be inappropriate for small sample sizes (Salguero-Gómez and Plotkin 2010).

In integral projection models (IPM), fewer parameters are used because the model is fit based on only one descriptor, the state variable, instead of using many stages. (Metcalf et al. 2013; Merow et al. 2014a). Integral projection models can incorporate continuous

stage and age variables into a similar analysis of population dynamics (Easterling et al. 2000; Gibson 2014). Although both MPMs and IPMs allow for mechanistic insights into population-level patterns by modelling the ecological factors that influence various vital rates (i.e., survivorship, growth, fecundity), IPMs require fewer parameters than MPMs because IPMs are fitted to simple regressions (Merow et al. 2014a). The development of an IPM, for a given population, allows for predictions to be made about changes in structure and population numbers (both on a short-term and longer term scale), and to learn about the sensitivity of these predictions to parameters and inputs.

The Amaranthaceae family contains important agricultural weeds, invasive exotics, and rare native plants. In the United States Midwest region, *Amaranthus palmeri* (S.) Watson and *A. tuberculatus* (Moq.) Sauer have been widely established as two of the prominent agricultural weeds. These species have many characteristics that make them very successful weeds including the ability to grow 2 to 3 m in height (Horak and Loughin 2000; Trucco and Tranel 2011) and extended seed germination and seedling emergence late into the row-crop growing season (Hartzler et al. 1999). *Achyranthes japonica* (Miq.) Nakai is a relatively recent introduction spreading across the Ohio River Valley. This perennial, C_3 herb is native to Korea, China and Japan (Sage et al. 2007; Choi et al. 2010; Evans and Taylor 2011; Schwartz 2014). *Achyranthes japonica* is generally found in areas with some shade and moist soil. However, the species can also grow in drier areas in sun, and in densely shaded areas (Schwartz 2014). Dense patches of *A. japonica* have been found in bottomland forests, riverbanks, field edges, and in ditches and swales (Evans and Taylor 2011; Schwartz 2014; Schwartz et al. 2015). Apart from anecdotal observations, little has been reported on this species and only recently has an aggressive educational

campaign been launched to learn more about this species. *Iresine rhizomatosa* Standl. is classified as endangered in Illinois and Maryland and is considered to be rare in Indiana (IDNR 1994; Gibson and Schwartz 2014). Despite its endangered and rare status, very little ecological work has been conducted on this species (Gibson and Schwartz 2014).

A demographic study was conducted to examine the population dynamics of four closely related species to determine which vital rate(s) contributed most to population growth rate to further develop appropriate management and conservation programs. This study analyzed the population dynamics of each species over a three-year period. Integral projection models were used to evaluate the demographic performance and identify the life history stage most critical for population growth rate (λ). The objective of this study was to evaluate the demographic patterns of each of the four species using an IPM to compare vital rates.

Materials and Methods

Study Sites. Demographic observations were made at two sites per species across southern Illinois. The sites were located within 145 km or less of each other (Table 4.1). Variation occurred in environmental factors over the three-year study. In 2012, southern Illinois underwent a drought in which over the growing season (May-October) only 3.3 cm of rainfall occurred; whereas in 2013 and 2014, southern Illinois received 9.1 cm and 9.9 cm, respectively, of rainfall (National Weather Service records). In addition to the drought year that was experienced in 2012, there were also higher mean temperatures in 2012 compared with 2013 and 2014. The mean growing season temperature in 2012 was 24.6 C; whereas in 2013 and 2014, the mean growing season temperature was 22 C both years.

Field Methods. The two populations were monitored for three consecutive years (2012 to 2014) at each site. Within each population, ten 1-m^2 plots were established randomly in sites where the species was known to be present in April 2012. Populations of each species were pooled and observed species were in an area of 200 m^2. Seedlings were tagged and monitored by taking node counts every week throughout each growing season and the following years where applicable (i.e., the perennial *A. japonica* and *I. rhizomatosa*). Height measurements were taken at the various stages and used as the state variable. Adult plants were further classified into reproductive and non-reproductive plants. Individuals were followed for three years or until death. Demographic parameters were measured each year monthly from May to October. The difference in field season length depended on weather conditions and seedlings were monitored as soon as they emerged until after the first frost date of that year.

Flowering of each individual species was measured in October of each year. In all years, each plant was measured in terms of plant height, number of nodes and stems; as well as the inflorescence length and number of inflorescences. Seed number per plant was determined by cleaning the seed to remove any chaff, then counting ten lots of 1,000 seeds per sample per site per species, and finally weighing the entire sample. The ten lots of 1,000 seeds were averaged to determine the final seed count.

Seed viability and germination tests were conducted for each species at each site annually. To determine seed viability, seed bags containing 100 seeds each were buried in all plots, just below the soil surface at the end of each growing season and were retrieved at the beginning of the following growing season. The retrieved seeds were tested for viability using a Tetrazolium test (1% 2,3,5-Triphenyl-2H-Tetrazolium Chloride from MP

Biomedicals). The seed coats and surrounding bracts were removed and the seeds were dampened in a wet paper towel over night. The next day, a dissecting pin was used to puncture the seed coat under a dissecting microscope. Then, the seeds were soaked in the tetrazolium solution overnight in a Petri dish placed in the dark. The following day, the seeds were observed under the dissecting microscope to determine viability. Seed viability was based on the amount of the seed stained. Dark purple areas on the seed indicated stained, living tissue and light pink areas represented unstained, dead tissue (Grabe 1970). More than half of an individual seed had to be stained dark purple to be considered living. Germination tests were performed by hand seeding 10,000 seeds onto the soil surface for each field population in the fall and counting the number that germinated the following spring. The germination test was conducted each year.

Data Analysis. Individuals can move to the next size, reduce in size, or die between times t and $t + 1$; they can also produce recruits. The size of an individual (z) at time t and z^1 is the size of an individual at time $t + 1$ (Rees et al. 2014). To describe these processes, two kernels are defined: $P(z^1,z) = s(z)G(z^1,z)$ and $F(z^1,z) = F_1(z^1)\ F_2(z^1,z)$. $P(z^1,z)$ represents survival and growth (Schwartz 2015: Appendices N and O) and $F(z^1,z)$ represents fecundity (Schwartz 2015: Appendices P-R). $G(z^1,z)$ is the probability of a size-z individual growing to be size z^1. For all years, the survival function $s(z)$ was estimated by logistic regression of survival on size z (Figure 4.1). The growth function $G(z^1,z)$ was first plotted using the relationship between individual sizes at time t and time $t + 1$. A linear model was determined to be suitable for describing the relationship between size at time t and size at time $t + 1$ (for the slope: $P < 0.05$).

The fecundity function $F(z^1,z)$ was estimated in a similar manner to the P kernel (Table 4.2). The function $F_1(z^1)$ is equivalent to the mean number of offspring from an individual in a specific size class, whereas $F_2(z^1,z)$ is the probability distribution of offspring size y for a reproductive individual of size x. The mean number of offspring was estimated from the germination trials and was fitted using a Poisson linear regression on adult size ($P < 0.05$ for all years, Figure 4.2).

Thus, the net result of survival and reproduction can be summarized by the function: $K(z^1,z) = P(z^1,z) + F(z^1,z)$; where K is the IPM kernel (Rees et al. 2014). The K kernel acts as the projection matrix in the model that simulates the projected population growth of a population forwards in time. From the K kernel, the population growth rate (Λ), or dominant eigenvalue can be calculated. Corresponding to Λ are the dominant right and left eigenvectors $w(z)$ and $v(z)$, respectively. The right eigenvector determines the stable size distribution and the left eigenvector determines the size-specific reproductive values (Caswell 2001).

The implementation of IPMs requires calculating the integrals, which is most practically conducted by applying fine categorization (Metcalf et al. 2013). The limits of integration were determined from the variance of growth (described in Easterling et al. 2000). The maximum and minimum limits of integration was set by adding or subtracting three standard deviations of the growth increment based on the maximum and minimum observed sizes. Alternative statistical relationships for growth, survivorship, and fecundity as functions of plant size were calculated, then model selection methods based on the Akaike Information Criterion (AIC) were used to determine which provided the best fit to the data. Finally, for the analyses, we determined the population growth rate (λ), the P

and *F* kernels, and the elasticity analysis. Models were fitted using the R program *IPMpack* (Metcalf et al. 2013; Schwartz 2015: Appendix S), and the significance of nonlinear terms was tested using an ANOVA function with a χ^2 test statistic (Metcalf et al. 2013).

Elasticity is the proportion of λ resulting from the transition of each matrix element. Thus, the elasticity formula is

$$e(z_1, z_2) = \frac{K(z_1, z_2)}{\lambda} \times \frac{v(z_1)w(z_2)}{[w, v]}$$

The elasticity function sums to unity (1) in the matrix projection model (Ferrer-Cervantes et al. 2012).

Results

Overall in 2012, on average, 1,334 individuals of *A. japonica* (density: 35 ± 4 individuals/m^2), 9,564 individuals of *A. palmeri* (density: 77 ± 6 individuals/m^2), 11,002 individuals of *A. tuberculatus* (density: 106 ± 11 individuals/m^2), and 928 individuals of *I. rhizomatosa* (density: 9 ± 2 individuals/m^2) were found. The following census range, 2013 to 2014, showed that there was an overall decline in the density for all species. The density of individuals per m^2 was 29 ± 4 for *A. japonica*, 61 ± 5 for *A. palmeri*, 92 ± 9 for *A. tuberculatus*, 5 ± 1 for *I. rhizomatosa*. The germination experiments resulted in an average germination rate of 86 ± 4.2% for *A. japonica*, 12 ± 2.8% for *A. palmeri*, 14 ± 2.2% for *A. tuberculatus*, and less than 1 ± 0.3% for *I. rhizomatosa* (Table 4.2).

The population growth rates (λ) for *A. japonica*, *A. palmeri*, and *A. tuberculatus* were all close to or greater than one for each census period (Table 4.3). These values of λ indicate that the populations were growing. By contrast, *Iresine rhizomatosa*, however, had

λ values less than one (2012: 0.53; 2013: 0.68) over both census periods indicating that the populations were in decline.

The *P* and *F* kernels are shown separately (Figure 4.3) and not as the full *K* kernel because the scales were so different and it was difficult to visualize together when the full kernel was implemented. The *P* kernel for *A. japonica* shows that there is the highest survivorship probability for juvenile and adult plants, but there is not much growth of individuals between time *t* to time *t* + 1 (Figure 4.3a). The two *Amaranthus* species again showed a similar result in that survivorship increased with the growth of the plant (i.e., larger plants had a high survivorship) (Figure 4.3b and 4.3c). The endangered *I. rhizomatosa* has a similar *P* kernel to *A. japonica* in terms of relatively little growth that occurs from one year to the next and that large-sized reproductive individuals have the highest survivorship probabilities (Figure 4.3d). Juvenile plants seem to have the lowest survivorship. All of the *F* kernels indicated that the larger the individual, the higher the fecundity. The *Amaranthus* species, however, can reproduce over a wide range of plant sizes; whereas, *I. rhizomatosa* needs to be large in size to reproduce.

In this experiment, the survival/growth functions made a greater contribution to λ than the fecundity function. The elasticity values varied among species and the *Amaranthus* species showed similar results (Figure 4.4). *Achyranthes japonica* and the *Amaranthus* species had higher values, than *I. rhizomatosa*, for the growth and survival transitions of small and intermediate-sized individuals. *Iresine rhizomatosa*, however, had high elasticity values for the growth and survival transitions of largest sized individuals had the best chance of survival compared with small, young individuals. The elasticity values are shown for only 2013 to 2014 because the pattern was similar the prior year.

Discussion

The four closely related Amaranthaceae species showed similar IPM outputs related to life cycle or invasiveness. The two perennial species both had similar *P* and *F* kernels showing that the largest plants were the drivers of survival. The annual weedy *Amaranthus* species and the perennial *A. japonica*, the invasive species, were similar in survival from time *t* to time *t* + 1 and in fecundity, although on different temporal scales. The similarities between the invasive species and the annual life forms provide insight into management and conservation efforts. According to our results, the small-sized to intermediate-sized individuals are the most critical for controlling populations of the invasive species, which corresponds with several other studies (especially in agriculture) (Horak and Loughin 2000; Trucco and Tranel 2011; Zimdahl 2004). This early growth stage is detrimental to the survival of the endangered species as well. Understanding the dynamics of these species individually can only enhance our knowledge when comparing species within a family and projecting the rate of population growth. This knowledge allows land managers to be pre-warned about life-stage sensitivity of a potential new invasive species coming into an area. Thus, this knowledge allows some time to develop an appropriate management plan.

There were however, differences in seedling density, survivorship, and fecundity between species and years. This response could be due, in part, to varying environmental factors. In 2012, southern Illinois underwent a drought in which over the growing season (May-October) only 3.3 cm of rainfall occurred; whereas in 2013 and 2014, southern Illinois received 9.1 cm and 9.9 cm, respectively (National Weather Service records 2015). In addition to the drought year that was experienced in 2012, there were also higher mean

temperatures in 2012 compared with 2013 and 2014. The mean growing season temperature in 2012 was 24.6 C; whereas in 2013 and 2014, the mean growing season temperature was 22 C both years. The small individuals were susceptible to drought, especially for *I. rhizomatosa*. Thus, reallocation of plant resources for survival, in terms of vegetative and root growth, rather than fecundity likely occurred during these periods of environmental stress (Grime 1979). Temperature is an important ecological factor in determining species growth and productivity. For example *A. palmeri* and *A. tuberculatus* exhibit their highest germination rate of 30 and 50%, respectively, when mean air temperatures are at 25 C (Guo and Al-Khatib 2003).

Habitat type and management strongly influences plant performance (Schwartz et al. 2015). Although reasons of mortality were not recorded, disturbances such as flooding, herbicide drift, herbivory, and general human traffic resulted in high mortality of individuals at some sites. Furthermore, the endangered status of *I. rhizomatosa* is enhanced by anthropogenic disturbances. These types of disturbances have also increased seedling mortality for other endangered species, such as *Mammillaria gaumeri* (Britton & Rose) Orcutt, by altering the composition of the surrounding plant community and fragmenting its already restricted habitat (Ferrer-Cervantes et al. 2012).

The population growth rate for three of the study species was greater than one, which was expected for agricultural weeds and an invasive species. Lower lambdas, as seen in the *I. rhizomatosa* populations, during some years can be attributed partially to the higher mortality of individuals in those years, which relates to its endangered status. For example, in 2012, there was a higher mortality, than in other years, for all species due to

the extreme drought in southern Illinois. In the following years, the population remained more stable than in the previous year.

Elasticity analysis on the whole IPM kernel includes survival, growth, and reproduction and has been used to separate these demographic functions to lambda from different size classes (Easterling et al. 2000). In general, the vital rates effect lambda the most because they represent a larger proportion of the stable stage distribution. However, this is altered by the assumption that smaller plants contribute almost no recruits to the next generation. The elasticity values in this study show that population growth of *I. rhizomatosa* and the *Amaranthus* species depends strongly on the retention and survival of larger individuals; whereas, growth of *A. japonica* populations are affected most by demography of smaller individuals. On this basis, management and conservation methods can be developed to target specific life history stages. A similar approach was used to develop long-term management strategies for *Polygonum cuspidatum* Siebold & Zucc., which targeted the largest plant sizes (Dauer and Jongejans 2013). Our current knowledge of *A. japonica* and *I. rhizomatosa* demography is limited to two sites with different data on growth, survival, and fecundity (Gibson and Schwartz 2014; Schwartz et al. 2015). There continues to be a need to more widely measure and model the demography of these closely related species to make generalizations about vital rates.

Although the data set was relatively small, Ramula et al. (2009) showed that IPMs produce less bias than MPMs for small data sets. They showed that for large data sets both MPMs and IPMs produced the same λ estimates. However, for small data sets IPMs produced a smaller bias and variance for λ than MPMs. In addition Gonzales et al. (2012) determined that the same demographic transitions were contributing to the greater

changes in λ. The major differences between MPMs and IPMs were due to generality in the fecundity functions. The demographic attributes of a species must be thoroughly researched and incorporated into the model so that IPMs can accurately determine the demographic processes that affect population growth rate the most. Thus, making IPMs a dependable tool for developing management or conservation strategies for the future.

As this study demonstrates, IPMs are useful for understanding population-level patterns that could not be determined from data solely on demographic measurements (Merow et al. 2014a). This approach leads to a more basic understanding of populations and potentially will allow for better predictions of population dynamics in an ecological context (Smallegange and Coulson 2013). IPMs can be a powerful tool that can utilize vital rate models and make inferences at the population level.

Table 4.1. Site characteristics for each species. Data pooled over years.

Species	Site Name	Location	Soil Type[a]	Land Cover	Mean Temp (C)[b]	Mean PPT (cm)[b]
Achyranthes japonica	Chestnut Hills	37°11'N 89°3'W	Menfro silt loam	Forest	22.9	27.5
Achyranthes japonica	Cypress Creek	37°17'N 89°06'W	Wheeling silt loam	Forest	22.9	27.5
Amaranthus palmeri	BRC: 9B	38°30'N 89°50'W	Bethalto silt loam	Agriculture Field	24.5	28.6
Amaranthus palmeri	Rend Lake	38°7'N 88°54'W	Wynoose silt loam	Agriculture Field	23.4	27.2
Amaranthus tuberculatus	BRC: T4	38°31'N 89°50'W	Bethalto silt loam	Agriculture Field	24.5	28.6
Amaranthus tuberculatus	DeSoto	37°47'N 89°15'W	Hurst silt loam	Agriculture Field	23.5	27.3
Iresine rhizomatosa	Beall Woods 1	38°20'N 87°49'W	Birds silt loam	Forest	23.9	28.3
Iresine rhizomatosa	Beall Woods 2	38°21N 87°50'W	Birds silt loam	Forest	23.9	28.3

[a] Source: USDA Soil Survey 2015

[b] Source: National Weather Records 2015

Table 4.2. Mean fecundity of *A. japonica*, *A. palmeri*, *A. tuberculatus*, and *I. rhizomatosa*. Measurements were averaged from 2012 to 2014 and pooled over sites per species.

	Mean Seeds/Plant	Mean Germination Rate	Probability of		
			Seedling - Juvenile	Juvenile - Adult	Seed Viability
Achyranthes japonica	331	0.86	0.67	0.72	0.93
Amaranthus palmeri	15,880	0.12	0.55	0.80	0.64
Amaranthus tuberculatus	63,441	0.14	0.48	0.77	0.71
Iresine rhizomatosa	1,000	0.01	0.31	0.45	0.23

Table 4.3. Lambda values (λ) for the period 2012 to 2014 for all species. Populations are pooled by species.

	λ	
	2012-2013	2013-2014
Achyranthes japonica	1.37	1.79
Amaranthus palmeri	1.15	1.22
Amaranthus tuberculatus	0.97	1.18
Iresine rhizomatosa	0.53	0.68

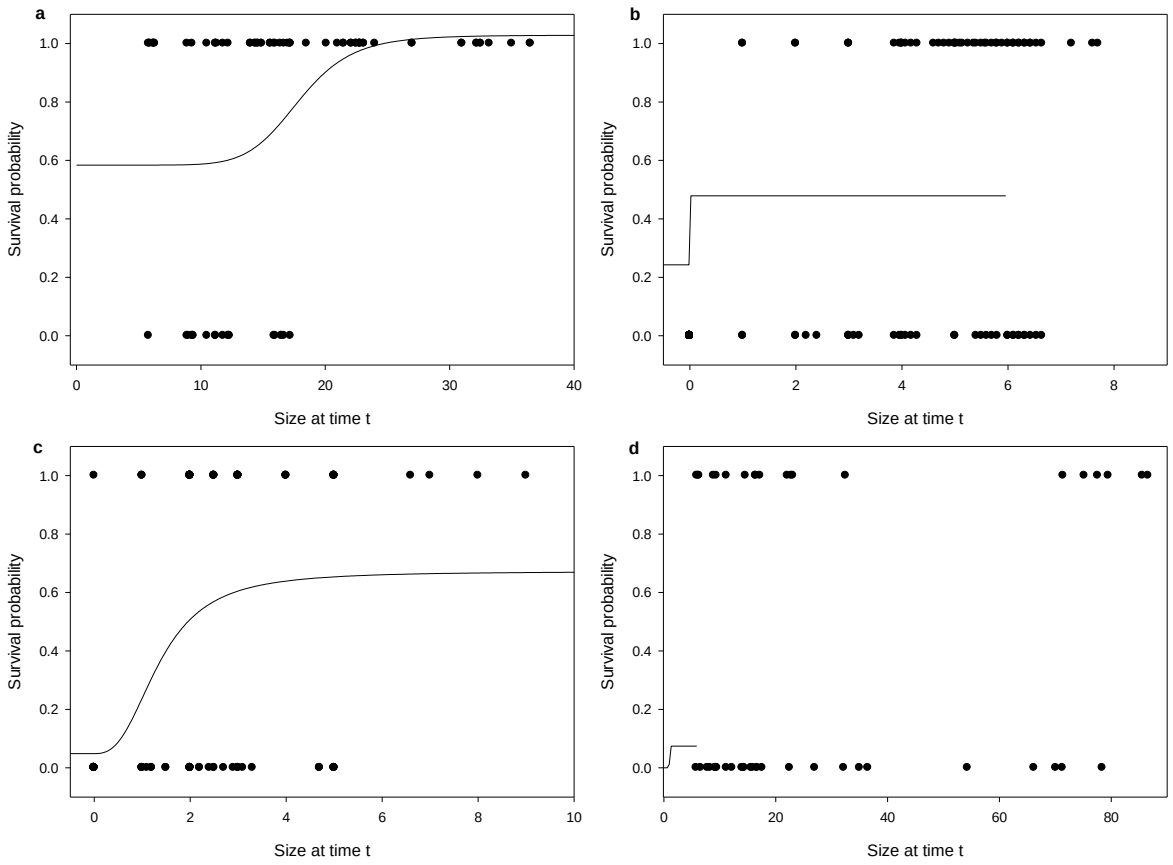

Figure 4.1 Fitting of survival function to each species 2014 data for a) *A. japonica*, b) *A. palmeri*, c) *A. tuberculatus*, d) *I. rhizomatosa*. The survival data are plotted (0 = death; 1 = survival) as a function of individual size *x* (plant height in cm). The figures represent data grouped over two sites per species. The x-axis scales are different among the panels.

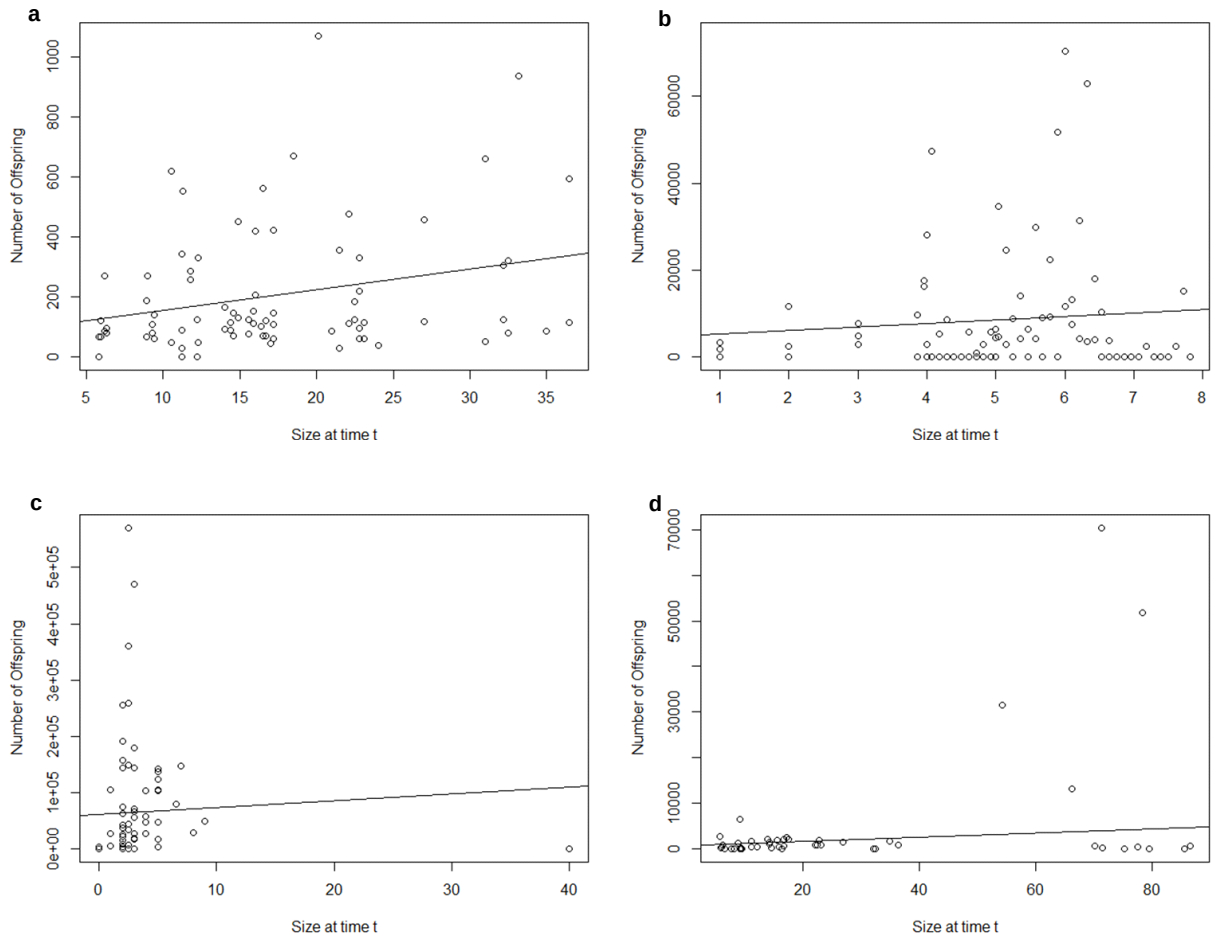

Figure 4.2 Number of offspring as a function of individual size (plant height (cm)), along with the linear regression for the mean number of offspring for to a) *A. japonica*, b) *A. palmeri*, c) *A. tuberculatus*, d) *I. rhizomatosa*. Data pooled over years. The y-axis scales are different among the panels.

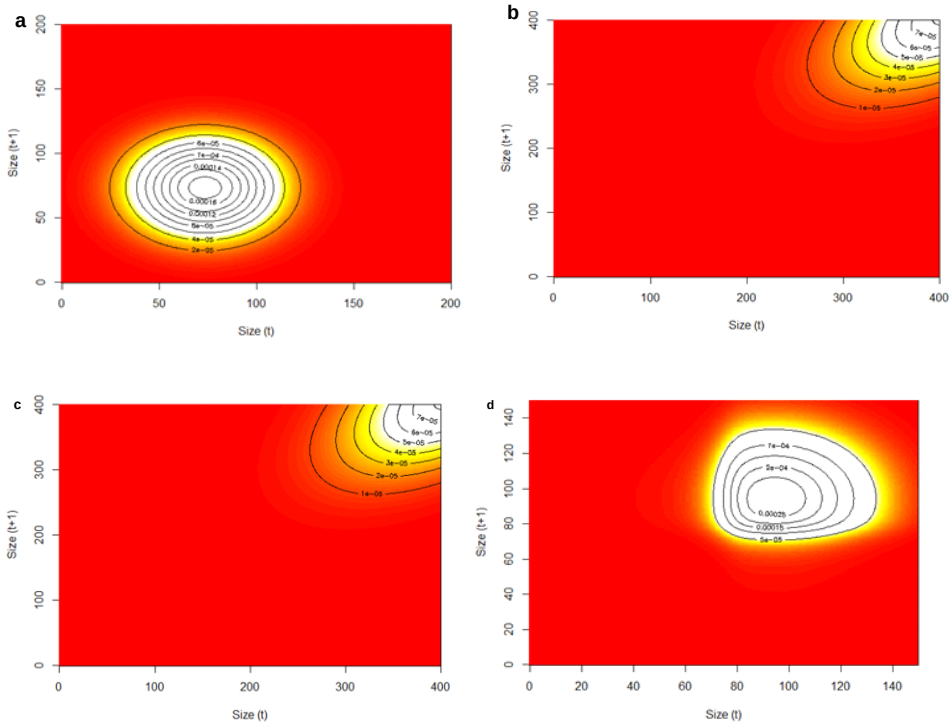

Figure 4.3 Elasticity surface for the integral projection model fitted to a) *A. japonica*, b) *A. palmeri*, c) *A. tuberculatus*, d) *I. rhizomatosa* in 2013 to 2014. The y-axis scales are different among the panels.

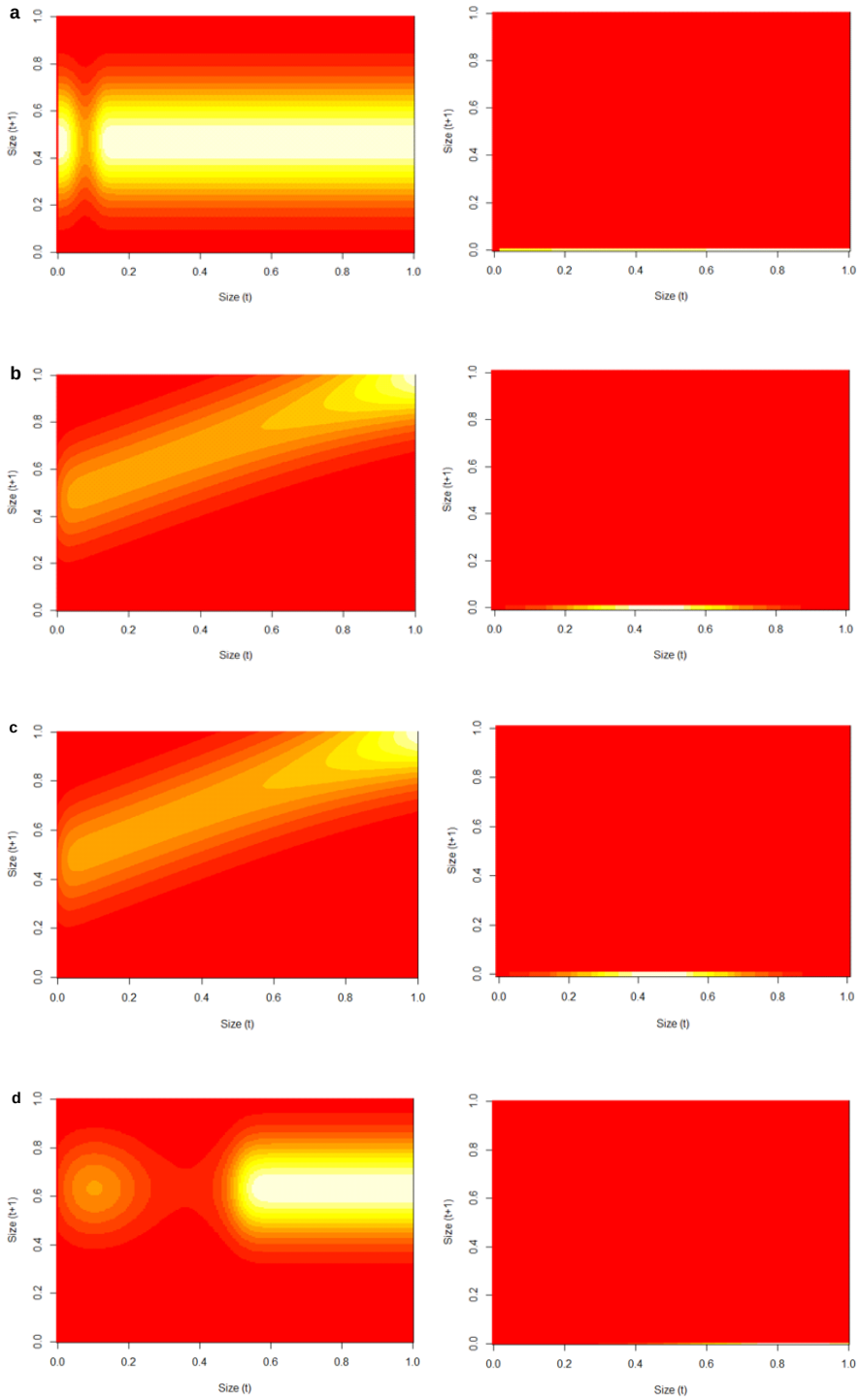

Figure 4.4 *P* and *F* kernels for a) *A. japonica*, b) *A. palmeri*, c) *A. tuberculatus*, d) *I. rhizomatosa* from 2013 to 2014.

CHAPTER 5

SUMMARY AND CONCLUSIONS

This final chapter first revisits the objectives and hypotheses posed at the start of this dissertation (Chapter 1), then briefly summarizes each data chapter (Chapters 2 – 4) before providing an integrated overall summary of the whole study in the context of the literature on invasive and weed species, competition, resource use, integrated pest management, and management implications.

Objectives and Hypotheses

Objectives

Objective 1: Assess the importance of seed survivorship in the soil of *A. japonica*, and to compare survivorship, fecundity, and morphological characteristics within populations at two different sites in southern Illinois.

Objective 2: Determine the relative competitive effect and response of *A. japonica*, *A. palmeri*, *A. tuberculatus*, and *I. rhizomatosa* to *G. max.*

Objective 3: Undertake a comparative life history analysis of *A. japonica*, *A. palmeri*, *A. tuberculatus*, and *I. rhizomatosa* in habitats where they occur (including crop fields for species in agricultural settings).

Hypotheses

Hypothesis 1: The two sites would differ in their characteristics based on environmental factors and habitat. [Objective 1]

Hypothesis 2: The perennial species, *A. japonica* and *I. rhizomatosa*, will have the lower requirement than the annual *Amaranthus* species for limiting resources when competing with interspecific neighbors enabling them to displace competitor species. [Objective 2]

Hypothesis 3: The competitive effect ranking was predicted to be: *A. tuberculatus* > *A. palmeri* > *A. japonica* = *I. rhizomatosa*. The competitive response ranking will be the opposite. [Objective 2]

Hypothesis 4: The population growth rate (λ) for *A. japonica* will be similar to the *Amaranthus* species and greater than *I. rhizomatosa*. [Objective 3]

Hypothesis 5: The population growth rate (λ) will be higher for the exotic species rather than the native species, because of differences in the demographic process. [Objective 3]

Chapter 2: Life history characteristics of *Achyranthes japonica* [Objective 1]

Summary

This study was the first to empirically assess the invasibility of *A. japonica* in terms of general survivorship, fecundity, and performance measurements. Environmental factors had a significant effect on seedling emergence and seed viability, which decreased from 2012 to 2013 during a drought year and rebounded from 2013 to 2014 following flooding. On average, individuals at the drier CH site had higher performance and fecundity when compared to BWR, regardless of year. The results of this study can help establish management protocols for *A. japonica* and to hopefully limit its spread.

Chapter 3: Competitive effect and response [Objective 2]

Summary

The greenhouse experiment showed that the four species each drew down light significantly, but not nitrogen. Shading decreased the aboveground biomass of the species in comparison to unshaded controls. Supplemental nitrogen, however, increased the aboveground biomass of *A. palmeri* and *A. japonica*. In the field experiment, a competitive effect ranking was determined to be *A. palmeri* > *A. tuberculatus* > cut *A. japonica* = *A. japonica* = *I. rhizomatosa*; with the competitive response ranking being the inverse. These results suggest that under ideal conditions *A. japonica* may be as competitive with *G. max* during early vegetative growth as the two *Amaranthus* species; thus, *A. japonica* has the potential to cause *G. max* yield loss. On this basis, *A. japonica* requires unique management practices as it is a potential economic threat if it is able to colonize agricultural fields.

Chapter 4: Comparative demography [Objective 3]

Summary

Demographic processes, such as survival, growth, and reproduction, can inform us about invasion risk, extinction risk, trade-offs in life history strategies. The *Amaranthus* species and *A. japonica* had an estimated population growth rate > 1, projecting increases in population size. By contrast, λ was < 1 for *Iresine rhizomatosa*, projecting a decline in population size reflecting its endangered status. Germination rates and seed viability were dependent on species and varied over time. Elasticity analyses showed that survival and growth contributed most to λ for the perennial species; whereas, for the annual species, population dynamics were driven primarily by survival.

Overall Summary

The comparative population dynamics of four closely related Amaranthaceae species were both qualitatively and quantitatively examined. All of the research conducted supports the highly invasive nature of *A. japonica* (Chapter 2) in comparison to the *Amaranthus* species, and the endangered status of *I. rhizomatosa,* in terms of resource drawdown (Chapter 3), competitive effect and response to a dominant crop (Chapter 3), and life history characteristics (Chapter 4). In addition, the use of IPMs gave an insight into the population growth rate of these species, which determined specific growth stages for management; whether it be for the removal of invasive species or for conservation efforts for an endangered species. Invasion status appeared to be more important than the plant's life cycles when comparing these species overall.

Although future research directions are still needed to more clearly understand the population dynamics of these closely related species, this research provides several insights into the Amaranthaceae family. First, another Amaranthaceae species, *A. japonica*, has shown the potential to become an aggressive invasive species with the ability to outcompete not only native species, but other invasive species as well (Schwartz et al. 2015a). The fact that this species shows similar invasive characteristics as the two *Amaranthus* species in this study (i.e., continuous germination throughout the growing season, adaptability, and high fecundity) allows for concern (Trucco and Tranel 2011). The high germination rate, large seed size, and the greater amount of root growth appears to give *A. japonica* a competitive advantage that the *Amaranthus* species do not possess. However, *A. japonica* grew more slowly than the annual species, which is reflective of a perennial life cycle. Thus, invasive species in this family should not be underestimated.

Secondly, competitive interactions can be broken down into a few general underlying principles: the duration of competition, weed density, biomass (both above and belowground), germination rate and the hardiness, or survival under harsh conditions of the plant (Zimdahl 2004). In *G.* max, the duration of competition with *A. palmeri* and *A. tuberculatus* is about six weeks after emergence (Feltner et al. 1969) before yield loss becomes inevitable. Also, the critical weed-free period has been determined to be anywhere from nine to thirty-eight days after emergence, or until the V-2 stage (Van Acker et al 1993). This study exhibits how the above mentioned principles demonstrated by the study species (except *I. rhizomatosa*), reduce the height of *G. max* within this six-week period.

Additionally, resource use (i.e., water, light, nutrients, and space) is critical to plant growth and to competitive interactions between species. A plant community becomes more susceptible to invasion as the amounts of available resources increase (Hobbs 1989; D'Antonio 1993). Thus, if resource levels are sufficient, then competitors will have a positive growth rate, which will eventually drive down resource levels and lead to a reduction in population growth of the other species (Miller et al. 2005). Plants growing in the shade of neighboring taller vegetation are usually receiving reduced light intensity with a decreased R/FR ratio (Yang et al. 2014). Thus, plants grown under such conditions exhibit shade avoidance responses (Smith 2000). Similar responses have been reported for soil properties, such as water and nutrients, where invasive species can alter or outcompete native species for these valuable resources (Davis et al. 2000; Davis and Thompson 2000). Therefore, the only driving factor between native and invasive species is resource availability (Mack 2003; Maron and Marler 2007).

Finally, this research provides important insight into potential management strategies, especially for invasive/weedy species. The general principles of control are broken down into three categories: prevention, eradication and control (Sakai et al. 2001). To implement these principles, a grower or land manager must be able to correctly identify an invasive/weedy species at an early vegetative growth stage, have knowledge about the species life history traits, and be able to implement the appropriate control method (Zimdahl 2004). The use of integrated pest management (i.e., mechanical, cultural, biological and chemical control) is the most effective way to control current and emerging invasive species in any system (Swanton and Weise 1991).

Mechanical control methods include hand pulling, mowing, herbivore grazing, smothering through mulches or plastic, burning, and tillage. Mechanical methods are usually expensive and time consuming depending on the area of control (Van Der Weide et al. 2008). Unfortunately, mechanical control methods are not always reliable because roots may not be pulled completely, which is important for perennial species, an overcompensation response could be triggered, and it is not always practical. Cultural control methods include planting date, seeding rate, irrigation, fertilization, crop row width, crop rotation, and the use of cover crops. These methods are primarily used in, but are not restricted to, horticultural and agricultural systems. Biological control is the use of natural enemies to control invasive/weedy species. Biological control is more effective on perennial species than annual species, but is not always effective because the biological agent (i.e., insect, pathogen, or animal) may not thrive in the new habitat or will thrive on a native species (Simberloff 2012). Chemical control utilizes herbicides which kills or inhibits plant growth through various modes of action. This method is cost effective and can be

selective (i.e., grass, broadleaf, or sedge species) or non-selective. The drawbacks associated with this control method are that there can be potential injury to non-target species, shifts in species composition (i.e., grasses to broadleaf weed/invasive species), and the development of herbicide resistant species (Johnson et al. 2012; Young et al. 2013).

This research serves as an indication that the functional traits of closely related species can be very similar, especially when comparing between invasion status (Garnier and Navas 2012). The invasive species of this study, *A. palmeri*, *A. tuberculatus*, and *A. japonica*, all exhibited similar competitive and general life history traits to one another. Thus, inferences from the very well-studied *Amaranthus* species could provide for further insight into the poorly studied *A. japonica*. Furthermore, *A. japonica* can potentially invade other habitats, such as agricultural or open fields, given the right conditions. While an *A. japonica* invasion into agriculture fields is currently improbable, predetermined evolutionary traits, as seen in other Amaranthaceae species (Vencill et al. 2008), to develop herbicide resistance is an evolutionary stepping stone for this species. Undoubtedly, specific management tactics implemented by individual growers or manager has a significant influence on the rate that herbicide resistance could occur for *A. japonica*.

Overall, better weed control tactics and early detection and rapid response methods are imperative to preventing the spread of any weedy or invasive species. These precautionary tactics also aim to preserve natural areas and enhance the growth of native and endangered or threatened species. Invasive species management will only be improved by understanding the basic biology and population dynamics of an individual species and those species that are closely related.

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Dissertation Title

A comparative study of the population dynamics of four Amaranthaceae species.

Major Professors: Dr. David Gibson and Dr. Bryan Young

Publications: Peer reviewed journal

Schwartz, L.M., D.J. Gibson, and B.G. Young. 2015. Using integral projection models to compare population dynamics of four closely related species**.** Population Ecology. *In review.*

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