

Palmer Amaranth (*Amaranthus palmeri*) Damage Niche in Illinois Soybean Is Seed Limited

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Palmer amaranth, a dioecious summer annual forb, originating in Sonoran desert washes, compromises crop yields in much of the southern United States and its range is expanding northward. Appropriate tactics for managing this weed proactively in the Upper Midwest will depend on characterizing its damage niche, the geographic range in which it can reduce crop yields. We implemented a common garden study in 2011 and 2012, planting eight accessions of Palmer amaranth from the southern and midwestern United States, into soybean crops in southern, central, and northern Illinois, at a population density of 8 plants m⁻² with a biocontainment protocol. Once Palmer amaranth plants initiated flowering, they were removed and burned. Weed survival, flowering, and weed biomass were measured, in addition to soybean yield and weather data. Analyses indicated that Palmer amaranth's damage niche in Illinois soybean was independent of weed genotype or maternal environment. Despite competing only briefly, Palmer amaranth reduced soybean yields in all site-years, indicating its damage niche in Illinois, and much of the Midwest, is limited primarily by seed immigration rate. These results highlight the urgent need for weed managers to learn Palmer amaranth identification, prevent seed introduction, and maintain a policy of zero seed return.

Nomenclature: Palmer amaranth, *Amaranthus palmeri* S. Wats.; soybean, *Glycine max* (L.) Merr.

Key words: Common garden experiment, genetic and environmental variation, geographic range expansion, global change, weed–crop interference.

At the midpoint of the previous century, the University of Wisconsin botanist J. D. Sauer made a perceptive observation about the dioecious amaranths (*Amaranthus* spp.), which now seems prescient. He noted that those species originating in desert washes and riparian areas, such as Palmer amaranth and tall waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer], were preadapted for dispersal into agricultural systems because of their ongoing exposure to heavy soil disturbance and nutrient pulses, whereas species adapted to interior and coastal sand dunes, such as greenstripe (*Amaranthus acanthochiton* Sauer) and Watson's amaranth (*Amaranthus watsonii* Standl), were unlikely to colonize agricultural systems because they had evolved under low-disturbance, oligotrophic conditions (Sauer 1957). This prediction has been

borne out during the subsequent decades by the invasion of both tall waterhemp and Palmer amaranth into arable habitats in the Midwest and the southern United States, respectively (Bensch et al. 2003; Ward et al. 2013). Colonization of new habitats, driven by preadaptation, allows for in-filling of a weed species' bioclimatic niche, given sufficient dispersal (Pinto and MacDougall 2010).

The bioclimatic niche of a weed species, the set of biophysical conditions under which it can complete its life cycle, represents the maximum geographic range that a weed species can occupy. However, this type of information alone is insufficient to aid weed managers in prioritizing species when developing weed management strategies. Weeds can be present in the local environment without interfering with crop yields; for example, Palmer amaranth has been detected in Champaign County, IL, agricultural habitats, for more than 30 yr without presenting significant challenges to producers (L. Wax, personal communication). More useful is the concept of the *damage niche*, introduced by McDonald et al. (2009) to define the geographic area in which a given weed species can cause economic yield loss within fields of a given crop species. Ongoing, anthropogenic change of the global environment, combined with long-distance seed

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transport through commerce, has made scientific understanding of this concept particularly timely. Widespread soil disturbance and elimination of competitor species through strong chemical control allowed Palmer amaranth and tall waterhemp to make their first range expansion from disturbed natural habitats to arable ones, thus initializing the damage niche of these species (Wax 1995). Now, global climate change, coupled with increased propagule pressure through long-distance grain, feed, machinery, and transport, raise the possibility of rapid northward expansion of the damage niches of these weed species (McDonald et al. 2009).

Our article focuses on factors affecting potential expansion of the damage niche of Palmer amaranth into the Midwest United States. Throughout this region, tall waterhemp, which evolved near the confluence of the Mississippi and Ohio Rivers (Sauer 1957; Wax 1995), has already thoroughly colonized arable habitats and is now a challenge to producers because of resistance to multiple herbicides (Bell et al. 2013). Although Canadian weed scientists may consider conducting an investigation of the potential damage niche of tall waterhemp in their agricultural landscape, a more pressing concern for the Midwest United States is whether Palmer amaranth will be able to not only complete its life cycle in this region but also compete with soybean, which is highly susceptible to interference from amaranth weeds (Bensch et al. 2003; Klingaman and Oliver 1994).

Palmer amaranth is a dioecious summer annual forb that evolved in desert washes of the Sonoran desert of North America (Sauer 1957; Ward et al. 2013). Whereas in the mid-20th century, Palmer amaranth was a common weed of field crops in Oklahoma, Texas, and Mississippi (Wax 1995), during the past few decades, its range has continued to expand into the southeastern United States and northward into Kansas, Missouri, and Arkansas, with many populations exhibiting herbicide resistance (Bensch et al. 2003; Burke et al. 2007; Klingaman and Oliver 1994; Norsworthy et al. 2008; Peterson 1999; Sosnoskie and Culpepper 2014). Because of the rapid growth rate, prolific seed production, and very high competitiveness of this weed (Ward et al. 2013), it is able to overrun agricultural fields in only a few years if not properly controlled (Norsworthy et al. 2014). Farmers in the Midwest regard this weed with trepidation and want to know whether the geographic

limits of its competitive range will include their farm (Sprague 2014; Wines 2014).

Plant range expansion may be driven by the local environment, the genotype, propagule dispersal, or some combination of the three factors (Colautti et al. 2006; Moloney et al. 2009; Pinto and MacDougall 2010). If abiotic environments are already receptive to a given species that is not well-represented in a region, then the simplest explanation for low abundance of the species may be low propagule pressure (Colautti et al. 2006). Alternatively, low abundance of a particular species may reflect the prevalence of genotypes poorly suited for rapid spread in a region. Repeated selection in agricultural environments can result in the evolution of particularly competitive or hard-to-control weeds, and thus, there may be some weed genotypes that have much larger damage niches than others do. Given the hypothesis by McDonald et al. (2009)—that increased global average temperatures may result in northward expansions of the damage niches of many weed species—our group wanted to investigate the relative importance of genetic and environmental factors in determining the geography of Palmer amaranth interference in Illinois soybean, and by extension, much of the Midwest.

We undertook a common garden study to disentangle questions of environmental vs. genetic limitation of Palmer amaranth's damage niche in Illinois soybean. Our research objectives were framed by the following hypothesis: The potential damage niche for Palmer amaranth in Illinois soybean is governed by local adaptation of various genotypes and is, thus, subject to both environmental and genetic variation. Under this scenario, we predicted that soybean yield under Palmer amaranth competition would be dependent on either weed genotype or soybean growing environment, or both, such that (1) Palmer amaranth would exert less competitive pressure on soybean in cooler climates (higher latitudes), and that (2) Palmer amaranth accessions adapted to warmer climates would be less likely to interfere with soybean yield in higher latitudes than those accessions adapted to cooler climates. Our null hypothesis, in contrast, was that Palmer amaranth competition with soybean would not be conditioned by either weed genotype or soybean environment, thereby indicating that the damage niche of Palmer amaranth in Illinois soybean is limited by propagule pressure (Colautti et al. 2006).

Table 1. Collection locations of Palmer amaranth seed accessions.

Seed source ^a	Latitude °N	Longitude °W	Elevation m	30-yr annual weather means	
				Air temperature C	Precipitation mm
Fayetteville, AR	36.09336	94.1726	438	14.2	1169
Jenkins, GA	32.80001	81.8668	72	18.3	1120
Urbana, IL	40.0656	88.2520	224	11.3	1036
Manhattan, KS	39.12503	96.6083	310	12.4	873
Columbia, MO	38.9500	92.3200	226	12.7	1065
Stoneville, MS	33.4230	90.9150	39	17.3	1132
Garrison, NE	41.15021	97.1002	487	10.4	727
Las Cruces, NM	32.3200	106.7700	1184	16.9	241

^a All seed accessions collected in Fall 2009 from active field crop production sites.

Materials and Methods

Seed Collection and Increase. Mature seeds of Palmer amaranth were collected from the margins of agricultural fields in September 2009 at the eight locations listed in Table 1, avoiding glyphosate-resistant populations of Palmer amaranth. At each location, mature infructescences of a single, large, female plant were shaken gently over a paper bag to collect a single accession of at least 200 seeds matured in the maternal environment (termed *source accessions*). Source accessions were stored at -20 C in airtight containers until March of 2010. At that time, seeds of each accession were mixed into a colloidal suspension of laponite (Rockwood Additives Ltd., Cheshire, U.K.) in water, 1:10 v/v and were stored in sealed glass vials at 4 C for 2 mo, until planting. Storage in laponite suspension reduced levels of seed dormancy and increased the proportion of germinable seed (Jha et al. 2010).

To eliminate confounding maternal environment effects on seeds to be used in the common garden study because we were interested in only genotypic differences among the accessions, we grew source accessions of Palmer amaranth for seed increase at a single location in Savoy, IL, managed by the University of Illinois Crop Sciences Research and Education Center, in summer 2010. The nursery area had previously been in a long-term grass sward. The collections of seed produced under a single environment were termed *study accessions*.

We took several precautions against unintended gene flow when growing the source accessions for seed increase. First, to avoid introducing a seedbank of nonlocal Palmer amaranth genotypes, we transplanted seedlings that were started from single seeds in compressed soil blocks. For each source accession, on May 15, approximately 100 seeds that had been stored in a laponite suspension, as mentioned previously, were extruded from a syringe onto

moistened filter paper in a petri dish. Seeds were then incubated under a diurnal temperature/light cycle of 28/20 C day/night temperature (14/10 light/dark) until seedling radicles protruded 1 mm from seed coats, after approximately 36 h. Germinated seeds were transferred to 0.125-cm^3 soil blocks freshly made from LC1 synthetic soil mix (SunGro Horticulture, Agawam, MA) with a stand-up 20-unit soil blocker (Johnny's Selected Seeds, Albion, ME), one seed to a block, and were covered with a 0.5-cm layer of soil mix. Plastic flats containing soil blocks with pregerminated seeds were then placed outside under woven row cover (Agribon+ AG-19, Johnny's Selected Seeds) to prevent desiccation and were then watered daily until seedlings produced their first true leaves. Seedlings were then transplanted into the field nursery in holes 6 cm in diameter by 5 cm deep prepared with a handheld bulb corer. Edges of the planting holes were gently pressed against the sides of the soil blocks to provide good soil contact. Seedlings of each accession were arranged in groups of two at eight planting stations spaced 0.5 m apart within 4.5 m long rows. Plants were watered as needed until they had three or more true leaves, at which time seedlings were thinned to one plant every 0.5 m (8 plants m^{-2}).

Once the first inflorescences began to form, nonterminal inflorescences were clipped as they appeared, and all plants were covered in floating row cover to prevent pollen flow among accessions or into surrounding environment. Polyethylene film was placed under all the plants from a given maternal line to collect any dispersed seed for subsequent removal and destruction. Once seeds had turned dark brown, indicating maturity, we clipped the terminal inflorescences of eight plants per source accession and placed them in an open paper bag to dry at 35 C in a forced air oven for

2 wk. Dry inflorescences were then threshed by hand using a wooden block against a corrugated rubber surface. The threshed material was processed on a seed cleaner to remove chaff and light seed. Clean seed was stored in airtight, plastic containers at 4 C until use. As a final measure to hinder gene flow in this experimental phase, we returned the seed increase nursery to permanent sod, monitored to confirm the absence of Palmer amaranth seedling recruitment.

Common Garden Study. We implemented our study as a hierarchical, nested design, with four replicate blocks of accession and competition level (weedy or weed-free) nested within common garden location and year in the following nesting order: year(location{block[accession(competition level)]}). In 2011 and 2012, soybean was grown either weed-free or in competition with each of eight study accessions of Palmer amaranth (see previous section, and Table 1), in three field-plot locations chosen to span much of the latitudinal gradient of Illinois.

Field plots for common garden experiments were located in southern, central, and northern Illinois. Southern field plots were located at the Dixon Springs Agricultural Research Center (37.424608°N, 88.662602°W; elevation: 121 m above sea level [a.s.l.]) in Simpson, IL, in 2011 and at the Southern Illinois University Agronomy Research Center (37.698133°N, 89.242912°W; elevation: 138 m a.s.l.) in Carbondale, IL, in 2012. Central field plots were located at the University of Illinois Crop Sciences Research and Education Center (40.049023°N, 88.237647°W; elevation: 217 m a.s.l.) in Savoy, IL, in both 2011 and 2012. Northern field plots were located at the University of Illinois Northern Illinois Agronomy Research Center (41.8400009°N, 88.865580°W; elevation: 268 m a.s.l.) in Shabbona, IL, in both 2011 and 2012. Soil types at the Simpson, Carbondale, Savoy, and Shabbona, IL, locations were, respectively, Sharon silt loam (coarse-silty, mixed, active, mesic, Oxyaquic Dystrudepts), Weir silt loam (fine, smectitic, mesic Typic Endoaqualls), Raub silt loam (fine-silty, mixed, superactive, mesic Aquic Argiudoll), and Elpaso silty clay loam (fine-silty, mixed, superactive, mesic Typic Endoaquoll). Study plots were chisel-plowed in fall after harvest of corn (*Zea mays* L.) and managed according to local agronomic recommendations.

Local choice of soybean cultivar varies by latitude, with growers at higher latitudes typically choosing cultivars in shorter-season maturity groups. To avoid confounding soybean morphology

and competitive ability with maturity group, we chose soybean cultivars with appropriate phenology for each of the locations, but in a common genetic background. The cultivars grown at the southern, central, and northern locations were, respectively, 'Pioneer 94Y40', 'Pioneer 93Y51', and 'Pioneer 93Y13'. Soybean was planted in 76-cm-wide rows at a population of 370,500 seeds ha⁻¹. Planting occurred as soon as local soil temperature and moisture conditions were conducive to soybean germination and permitted seedbed preparation with a combination soil finisher. In 2011, planting occurred on May 23, May 16, and May 27 at Dixon Springs, Urbana, and De Kalb, IL. In 2012, planting occurred on May 14, May 22, and May 30 at Carbondale, Urbana, and De Kalb, IL. Each 6m wide (eight rows spaced 76 cm apart) by 24-m-long replicate block was subdivided into eight plots, one for each study accession. Each plot was further divided into two adjacent, 3-m-wide by 3-m-long subplots in which soybean was grown with (*weedy*) or without (*weed-free*) competition from Palmer amaranth.

Concurrent with soybean planting at each location, Palmer amaranth seeds were pregerminated for seedling establishment using the single-seed soil block method described previously. When all seedlings for a location had at least one pair of true leaves, they were transplanted into the soybean row of weedy plots, spaced 0.5 m between seedlings, and received a single watering. Each seedling was flagged, with its own identification number, to facilitate a final plant inventory at the study's end to ensure that no plants were left in the field. When Palmer amaranth seedlings were 10 cm tall (approximately 14 d after planting), they were covered with 1-L, plastic, food service containers to permit an application of glyphosate (1.27 kg ae ha⁻¹) and S-metolachlor (2.14 kg ai ha⁻¹) to the entire field. Additional hand labor removed remaining nonstudy weeds for the duration of the experiment.

Field plots were checked daily for plant growth stage. When new Palmer amaranth male and female inflorescences began to form at a given study location, accession, and ID of the reproductive plants were noted, and all inflorescences were clipped and removed on a daily basis until it was no longer feasible to do so, approximately 5 to 7 weeks after transplanting. At that point, all Palmer amaranth plants were clipped 5 cm below the soil surface, removed from the field, weighed, and burned. Soybean plants were permitted to reach full maturity and were then hand-harvested for grain

yield from 1.5-m row lengths in the two central rows in each subplot. Percentage of soybean yield loss to weed interference was calculated for each accession at subplot level as $[(yield_{weedfree} - yield_{weedy})/yield_{weedfree}] \times 100$. At the time of weed removal, soybean plants were generally at the R1 to R3 stage, with several weeks of growth and maturation left; thus, yield loss estimates in this study were quite conservative compared with full-season competition.

To examine relationships between study-site environments and source-accession environments, we assembled 30-yr, growing-season means of daily air temperature and precipitation for each of the source environments from data obtained through the National Oceanic and Atmospheric Administration National Climatic Data Center (<http://www.ncdc.noaa.gov/>) and the growing-season means for each of the study site-years from on-farm weather stations at each location. We also calculated the difference in air temperature between the study and source environments during the study period.

Statistical Analyses. Data were analyzed in two stages, using general linear mixed-effects models and structural equation models (SEMs). Mixed-effects models provided a means of examining direct sources of genotypic and environmental variation in yield of soybean grown with weed competition, whereas SEMs allowed us to test for the presence of both direct and indirect effects of genotype and environment on yield of soybean yield (Grace 2006). General linear models (GLMs) included soybean yield as the dependent variable; independent variables included terms for Palmer amaranth accession and competition level as fixed effects and year[location(block)] as random effects. For analysis of proportion data, including yield loss, plant survival, proportion of flowering individuals, generalized linear models were used, with binomially distributed error terms (Crawley 2007). Maximum-likelihood comparisons of candidate models were used to calculate Akaike weights (w_i), indicating the relative support for a given model in a pool of candidate models (Burnham and Anderson 2002). Candidate SEM models included yield of soybean grown with weed competition as an endogenous variable, measures of weed biomass, temperature, and precipitation as exogenous variables, and latent error terms for weedy biomass (Table 2). All variables were standardized (as the difference between an individual observation and the population mean, divided by the standard deviation) before SEM

analysis (Grace 2006). We implemented mixed-effects GLMs, generalized linear models, and SEMs within the nlme, lme4, and lavaan packages of R Version 2.15.2, respectively (R Development Core Team, <http://www.r-project.org/>).

Results and Discussion

Palmer Amaranth Growth and Development are Heat Driven. Palmer amaranth was able to survive to the onset of reproductive maturity and begin to form inflorescences in all site-years. Survival to flowering, proportion of the population flowering, and biomass were all positively associated with the accumulation of thermal time at the study location (Figure 1), with weaker or nonsignificant associations with precipitation and mean temperature at the study location. Maximum-likelihood comparisons of competing linear models with different environmental terms indicated much stronger support for growing degree days ($GDD_{10} = [(minimum\ temperature + maximum\ temperature)/2] - 10\ C$) ($w_i = 1$ for all three variables shown in Figure 1) than any other environmental variable. The most parsimonious generalized linear model for percentage of plant survival to maturity included terms for study accession, thermal time (GDD_{10}) in a given site-year, and their interaction (Akaike information criterion [AIC] = 2,586; GDD_{10} : $P < 0.0001$, accession: $P < 0.01$, $GDD_{10} \times$ accession: $P < 0.0001$). Likewise, the best generalized linear model for percentage of individuals flowering at the time of weed termination included terms for study accession, thermal time (GDD_{10}) in a given site-year, and their interaction (AIC = 2,903; GDD_{10} : $P < 0.0001$, accession: $P < 0.01$, $GDD_{10} \times$ accession: $P < 0.001$). All accessions of Palmer amaranth responded positively to increasing GDD_{10} ; the interaction between accession and GDD_{10} indicated varying positive slopes for the response of survival and flowering to heat accumulation.

Similar to the demographic variables, Palmer amaranth biomass was subject to effects of accession ($F_{7,154} = 9$, $P < 0.001$), GDD_{10} ($F_{1,154} = 112$, $P < 0.001$; $y = -0.69 + 0.0005x$), and their interaction ($F_{7,154} = 4.2$, $P < 0.001$). Palmer amaranth biomass within subplots varied from 0.02 to 0.52 Mg ha⁻¹ across site-years. In comparison to plant survival to reproductive maturity, which appeared to saturate at accumulated thermal time greater than 1,600 GDD_{10} , both percentage of flowering and biomass (and variations

Table 2. Structural equation models relating seed yield of soybean grown in competition with Palmer amaranth to abiotic and biotic environmental variation.^a

Model	Environmental variables ^b		Parameter values ^c			Model performance		
	Variable 1	Variable 2	b_1	b_2	cov _{1,2}	R^2	AIC	w_i
1	Mean T	$\Delta T_{\text{study vs. source}}$	-0.69***	0.12	0.72***	0.34	1416	1
2	Mean T	$\Delta \text{Latitude}_{\text{study vs. source}}$	-0.63***	-0.07	-0.49***	0.36	1504	0
3	Mean T	Weed biomass	-0.56***	-0.20*	0.20*	0.40	1539	0
4	Mean T	Total rainfall	-0.75***	0.25**	-0.64***	0.39	1452	0
5	Total rainfall	Weed biomass	0.23*	-0.32**	0.02	0.15	1612	0
6	Total rainfall	$\Delta \text{Latitude}_{\text{study vs. source}}$	0.17*	0.20*	0.28**	0.09	1609	0
7	Total rainfall	$\Delta T_{\text{study vs. source}}$	0.074	-0.34***	-0.45	0.15	1570	0

^a Abbreviation: AIC, Akaike information criterion; w_i , Akaike weight.

^b Explanation of environmental variable names: mean T, mean temperature (C) during study period; $\Delta T_{\text{study vs. source}}$, difference in temperature (C) among study locations during study year and 30-yr average for seed accession collection location; $\Delta \text{latitude}_{\text{study vs. source}}$, difference in latitude between study location and seed accession collection location; weed biomass, dry biomass (g) of Palmer amaranth at termination of study; total rainfall, cumulative rainfall (mm) during the study period.

^c Explanation of parameter abbreviations and model structure given in Figure 2.

within these parameters) continued to rise with increasing GDD₁₀ over the study conditions represented here (Figure 1). Palmer amaranth is a heat-tolerant plant, with origins in the Sonoran Desert (Sauer 1957). Although it appears to survive to reproductive maturity in northern Illinois, there was a rapid drop-off in flowering and growth in response to reduced accumulation of heat units in this area. Does this mean that Palmer amaranth in northern Illinois is near the northern tip of its geographic range? Not necessarily, because recently established, yet persistent, populations of Palmer amaranth have been reported as far north as southeast Michigan (Sprague 2014).

The Palmer amaranth plants in this study originated from seedlings that were raised under controlled conditions. Thus, results reflect plant survival without consideration of genotype and environmental effects on seed germination and PRE seedling growth. Nonetheless, the broad range of temperatures that stimulates Palmer amaranth germination (Guo and Al-Khatib 2003) suggest that the environmental requirements for Palmer amaranth germination can be fulfilled in the U.S. Midwest. In addition, to prevent accidental spread of herbicide-resistant biotypes, this study used seeds collected from populations susceptible to glyphosate. Demographic results from this study are thought to be applicable to Palmer amaranth populations resistant to glyphosate because previous research determined that resistant and susceptible populations did not differ in growth and fecundity (Giacomini et al. 2014).

Soybean Yield Loss Scales to Local Environment.

Yields of soybean grown in competition with

Palmer amaranth varied widely within and among locations and years (Figure 2), with mean soybean yields of different accession subplots ranging from 2.5 to 3.6, 2.3 to 3.7, and 3.6 to 4.4 Mg ha⁻¹ in southern, central, and northern Illinois study locations. Weed-free soybean yields varied far less within locations than did yields of soybean grown with weed competition; mean yields of weed-free soybean at these locations were, respectively, 3.5 ± 0.07 , 3.6 ± 0.15 , and 4.4 ± 0.13 Mg ha⁻¹. Although Palmer amaranth plants were removed from the field soon after first inflorescences began to form (for a maximum of 5 wk of interference against soybean), weed interference, nonetheless, did reduce soybean yields (main effect of competition level: $F_{1,270} = 55$, $P < 0.0001$), with losses ranging between 2 and 30% (Figure 2). Our estimate of Palmer amaranth interference with soybean was likely conservative; in comparison, full season competition of Palmer amaranth with soybean can cause yield losses ranging from 20%, at moderate weed-population densities, to 80% at high infestations (Bensch et al. 2003; Klingaman and Oliver 1994).

The competitive effect of Palmer amaranth on soybean was mediated by site-year, but not by weed genotype. Significant interactions were observed between competition level and site-year ($F_{2,270} = 7.3$, $P = 0.0009$), but there was no interaction between weed accession and competitive effect ($F_{7,270} = 0.48$, $P = 0.85$). To clarify the spatiotemporal interaction term, we examined weed competitive effect on soybean yield in individual regions of the state by year. Results for proportional yield loss of soybean to Palmer amaranth followed a similar pattern, and will not be discussed

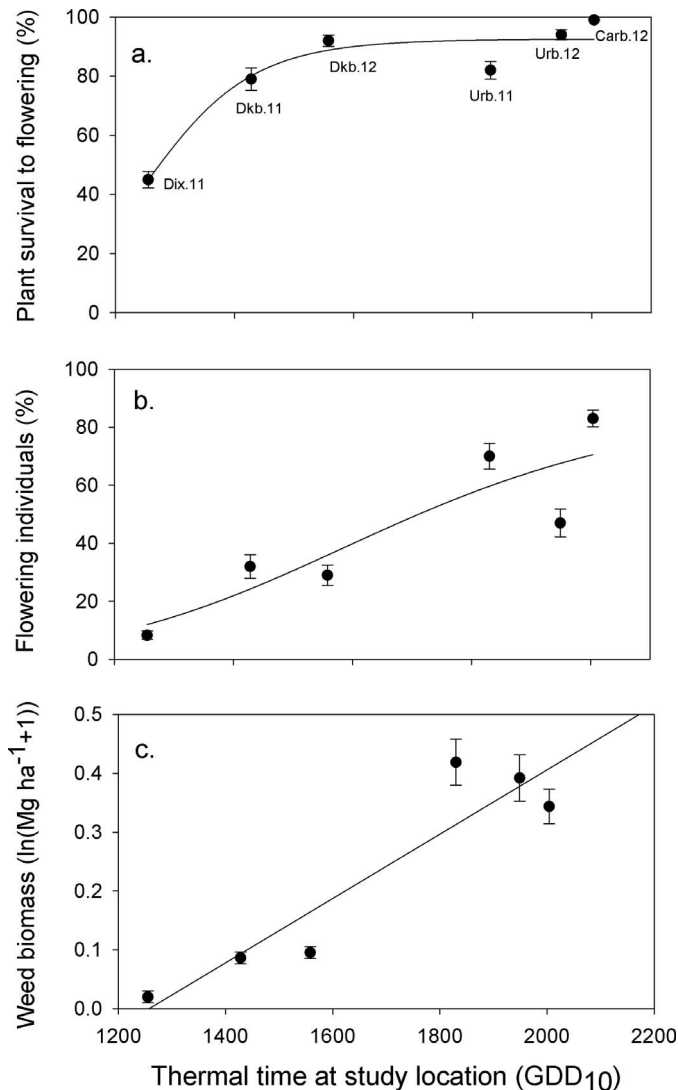


Figure 1. Palmer amaranth demography (a) survival, (b) reproduction, and growth and (c) weed biomass were positively associated with accumulated heat units across site-years. Symbols represent means (\pm SE), across accessions, of four replicates per site-year. Data labels represent site-years, in 2011 and 2012. Abbreviations: Dix, Dixon Springs; Carb, Carbondale; Dkb, DeKalb; Urb, Urbana.

separately. In 2011, there was a significant main effect of competition level in southern ($F_{1,45} = 35$, $P < 0.0001$) and central ($F_{1,45} = 29$, $P < 0.0001$), but not northern, Illinois ($F_{1,45} = 1.7$, $P = 0.19$). Weed interference was observed at all locations in 2012, with a significant main effect of competition level in southern ($F_{1,45} = 10$, $P = 0.004$), central ($F_{1,45} = 62$, $P < 0.0001$), and northern Illinois ($F_{1,45} = 13$, $P = 0.0009$). There were no significant interactions between competition level and accession in either year within any of the study locations. A single degree-of-freedom contrast of soybean yield loss in northern Illinois, compared with southern and central locations, revealed a significant difference among regions ($F_{1,364} = 12$, $P = 0.0007$);

mean soybean yield losses in the northern portion of the state ranged between 0 and 10%, compared with losses ranging from 3 to 30% in the central and southern portions of the state.

These results offer partial support for the central hypothesis of this study, in that the damage niche of Palmer amaranth in soybean appears to be affected by local growing conditions, but not by Palmer amaranth genotype. The competitive effect of Palmer amaranth on soybean yield was lower in northern Illinois than it was in southern and central Illinois. However, there were no hypercompetitive accessions of Palmer amaranth to be especially cautious about, and weed genotype was not a reliable predictor of the yield of soybean grown under weed competition.

Study-site mean air temperature during the growing season was negatively associated with the yield of soybean grown with or without Palmer amaranth competition (Figure 3). When comparing rainfall, air temperature, and latitude for the study site and accession source locations, the most parsimonious general linear mixed-effects model for soybean yield contained terms for weed competition level ($F_{1,358} = 126$, $P < 0.0001$), mean temperature during the growing season at the study site ($F_{1,11} = 29$, $P = 0.0002$), and the interaction of these terms ($F_{1,358} = 9$, $P = 0.003$). Higher temperatures were associated with reduced soybean yields in both levels of competition, but the presence of Palmer amaranth exacerbated the effect of increasing temperature on soybean yield (Figure 3), with a greater negative slope in the weedy treatment than in the weed-free treatment (weed-free: yield = $6.9 - 0.16 \times \text{study temperature}$; weedy: yield = $7.9 - 0.23 \times \text{study temperature}$). The greater explanatory power of higher air temperatures on soybean yield, compared with rainfall, is somewhat unexpected given the large negative effect of soil moisture stress on soybean yield (Mishra and Cherkauer 2010). A strong negative correlation was observed between mean air temperature and cumulative rainfall during the growing season for the site-years included in this study ($r = -0.63$, $P < 0.0001$), and rainfall was positively correlated with soybean yield in both weedy ($r = 0.23$, $P < 0.01$) and weed-free ($r = 0.16$, $P < 0.05$) conditions; nonetheless, temperature was retained as a better predictor during model selection in both the GLM and SEM approaches, as discussed below. Because rainfall during the 2011 and 2012 growing seasons was very low, averaging from 490 and 340 mm, respectively, there may have

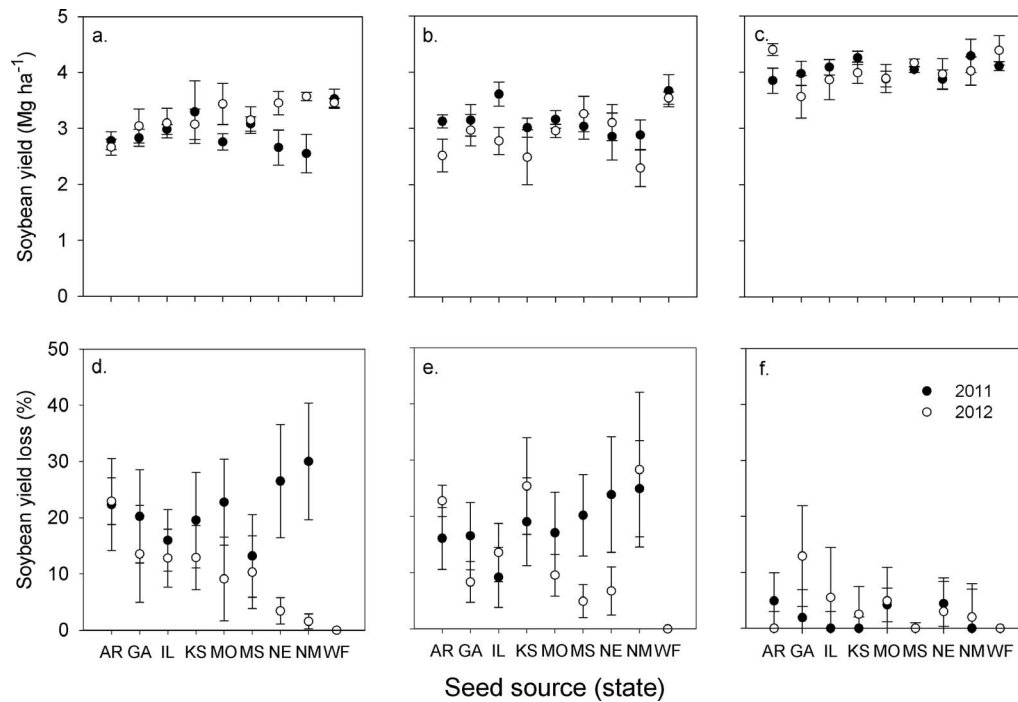


Figure 2. Seed yield and yield loss to weed interference of soybean grown with or without competition from Palmer amaranth in (a and d) southern, (b and e) central, and (c and f) northern Illinois in 2011 and 2012. Symbols represent the mean (\pm SE) of four experimental replicates per site-year. Abbreviations: Palmer amaranth seed source is represented by two-letter state abbreviations, with the exception of WF, soybean grown without Palmer amaranth.

been insufficient variation in this variable to drive statistical models, leaving air temperature as a more information-rich proxy for evapotranspiration stress in soybean.

As a complement to data analysis with GLMs, in which site-year, competition level, and genotype were treated primarily as categorical factors, we also took a SEM approach (Figure 4) to understanding the effect of quantitative variation in these variables on yield of weedy soybean. Candidate models (Table 2) examined the relative effect of local conditions at the study site in comparison to measures of local adaptation and biomass production by the various Palmer amaranth accessions. The most parsimonious SEM for yield of soybean under weed competition (as measured by minimizing AIC in Table 2) contained mean study-location temperature during the growing season and the difference in mean growing season temperature between the study location and accession source locations. These variables were allowed to covary, as well as have direct relationships to soybean yield (Figure 4). In the fitted model, study-location mean temperature during the growing season had a significant negative association with soybean yield, whereas the degree of similarity of the study environment to the environment from which the study accessions were taken did not have a significant relationship to

soybean yield. The Akaike weight for the most parsimonious model was 1, compared with 0 for the other models, indicating that other proposed models were far less informative for explaining variation in

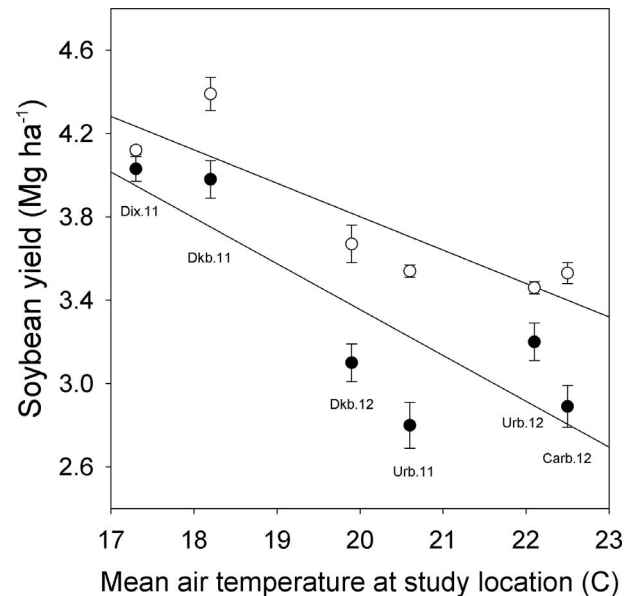


Figure 3. Yield of soybean grown with or without interference from Palmer amaranth was negatively related to mean temperature during the study period across site-years and accessions. Symbols represent the mean (\pm SE) of four experimental replicates per site-year. Data labels represent site-years, in 2011 and 2012. Abbreviations: Dix, Dixon Springs; Carb, Carbondale; Dkb, DeKalb; Urb, Urbana.

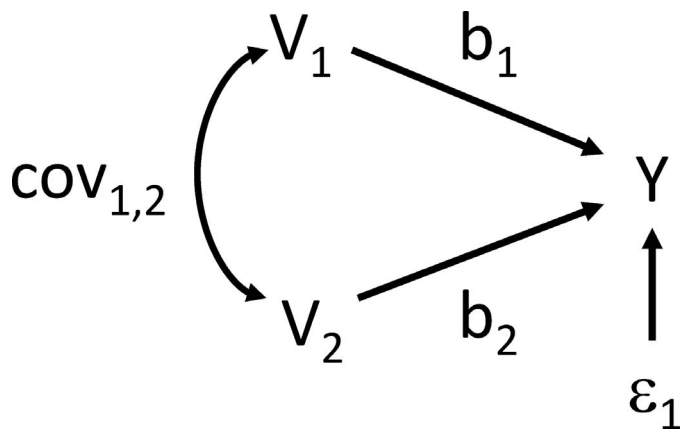


Figure 4. Parameters for structural equation models presented in Table 2 were related to each other as shown here. Abbreviations: V_1 , V_2 , manifest independent variables 1 and 2; Y , dependent variable (seed yield of soybean grown in competition with Palmer amaranth); b_1 , b_2 , standardized regression coefficients for regressions between V_1 and Y , and V_2 and Y , respectively; $cov_{1,2}$, covariance between V_1 and V_2 ; ε_1 , latent error (variance in Y unexplained by model parameters).

soybean yield under weed competition. The results of SEM analyses support the GLM results: local environmental variation is more important than weed accession characteristics in determining the competitive effect of Palmer amaranth on soybean in Illinois. If Palmer amaranth was present, higher temperatures at the study site increased its ability to interfere with soybean yield.

The importance of local environmental conditions in driving Palmer amaranth demography and growth corroborates the findings of a north-central U.S. regional study of giant ragweed (*Ambrosia trifida* L.) and common sunflower (*Helianthus annuus* L.) (Wortman et al. 2012), and more broadly, a study of the potential range of Chinese tallowtree [*Triadica sebifera* (L.) Small], an invasive tree of the southeast United States (Pattison and Mack 2008). Similarly, the strength of interference of both velvetleaf (*Abutilon theophrasti* Medik.) and giant foxtail (*Setaria faberi* Herrm.) with corn across the north-central region have been found to vary with local environment (Lindquist et al. 1996, 1999). Our results contrast with those of Andersen et al. (1985), who observed a relationship between velvetleaf demography and the similarity of common garden environmental conditions during their study to maternal environment; our study did not detect scaling of Palmer amaranth interference against soybean to maternal environment of the various study accessions. This may be due to the much broader range of environments (Weslaco, TX; Rosemount, MN; and Fairbanks, AK) with which Andersen et al. challenged their velvetleaf accessions.

Whereas their study contained a 38° latitudinal difference between the most southerly and northerly gardens, our study examined environmental suitability over a 4.4° latitudinal gradient in Illinois.

Prevention a Key Priority for Weed Managers.

The results presented in this study offer a simple message to weed managers in the upper Midwest United States: It is not a matter of if, but when, Palmer amaranth arrives at a nearby farm. With no genetic barriers to establishment, growth, survival, and interference, and only modest mitigation of these factors by local environments, the primary hindrance to widespread invasion of cropping systems in the northern corn belt by Palmer amaranth appears to be low propagule pressure, the *null model for biological invasions* (Colautti et al. 2006; Pinto and MacDougall 2010). Current low abundance of Palmer amaranth seed in this region is likely temporary. A growing number of field reports from farmers and scientists (Sprague 2014; Wines 2014; Yates 2014) indicate that Palmer amaranth seeds, by means of contaminated feed, equipment, and seed, are repeatedly sampling potential sites of introduction in the upper Midwest. Many of these sites involve livestock production (Sprague 2014), indicating strong potential for secondary dispersal of Palmer amaranth to nearby fields through the land-application of manure.

Weed prevention is a fundamental component of multitactic integrated weed management, with an emphasis on reducing weed demographic success by limiting seed dispersal, persistence, recruitment, and fecundity (Jordan 1996). At a field scale, prevention may take the form of consistent scouting, with an emphasis on early identification and eradication of any individuals found; there is no control threshold for this species (Hager 2014; Norsworthy et al. 2014). Established populations, before seed formation, should be prioritized for complete control through hand-labor or tillage. At crop harvest, patches should be avoided by harvest machinery, to prevent spreading Palmer amaranth seed from the patch to the field scale (Humston et al. 2005; Norsworthy et al. 2014; Woolcock and Cousens 2000), although new machinery may offer the potential for in-crop weed seed destruction at harvest (Walsh et al. 2013). Cleaning machinery when moving between fields may help prevent interfield seed dispersal for a single operator. However, at higher spatial scales, including county, regional, and interregional levels, a coordinated screening effort at multiple stages in feed, seed, and

machinery transport chains may be necessary to prevent widespread introductions of this species. Future efforts to identify key dispersal pathways for Palmer amaranth into the upper Midwest, in combination with outreach efforts to disseminate best management practices for managing this weed, will be crucial to curtailing its spread.

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