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Pollen-Mediated Gene Flow in Common Lambsquarters (*Chenopodium album*)

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Common lambsquarters is highly competitive in many cropping systems and has demonstrated resistance to several herbicide mechanisms of action. However, predicting the spread of resistance is difficult due to limited information about gene flow. We conducted research to determine the potential for movement of resistance alleles in common lambsquarters under field conditions. *Chenopodium giganteum* (a member of the *C. album* aggregate) that has a dominant magenta phenotypic marker was used as a pollen parent in gene flow experiments. A wild-type accession of common lambsquarters was used as a seed parent. Seed parents were grown in a soybean field and arranged in concentric circles 2 to 15 m from a center which contained 24 pollen parents. The concentric circles were divided into eight directions. Pollen movement was estimated by determining the percentage of progeny with the magenta phenotype from seed parents. Average cross-pollination across directions was greatest (3.0%) at 2 m and decreased to low levels (0.16%) 15 m from the center, consistent with observations of other primarily self-pollinated species. Cross-pollination was greatest ($P < 0.10$) in the south-southwest, west-southwest, and west-northwest directions, approximately 180° from the prevailing wind direction during the time of pollen shed. Since common lambsquarters does not have an active dispersal mechanism for seeds, pollen-mediated gene flow may play an important role in the transfer and frequency of resistance alleles within and between populations.

Nomenclature: Common lambsquarters, *Chenopodium album* L. CHEAL; magenta spreen, *C. giganteum* D. Don; soybean, *Glycine max* (L.) Merr.

Key words: Cross-pollination, herbicide, inheritance, phenotypic marker, resistance.

Common lambsquarters is considered one of the world's worst weeds due in part to its global occurrence (Holm et al. 1977) and evolved resistance to photosystem II inhibitors, acetolactate synthase inhibitors, and synthetic auxins (Heap 2011). Further, common lambsquarters has shown variable or inconsistent responses to glyphosate across a wide geographical range in the United States (Hite et al. 2008; Kniss et al. 2007; Sivesind et al. 2011; Westhoven et al. 2008). Common lambsquarters is highly competitive with many crop species, including corn (*Zea mays* L.) (Moechnig et al. 2003a,b) and soybean (Conley et al. 2003; Kruger et al. 2009). Plants have a high rate of seed production (Gramig and Stoltenberg 2009; Harrison 1990) and seeds can remain viable in the soil for 30 to 40 yr (Conn and Deck 1995; Holm et al. 1977). It is a hexaploid ($2n = 54$) (Bhargava et al. 2006; Darmency and Gasquez 1990) and is predominantly self-pollinating (Holm et al. 1977). However, the degree of cross-pollination and the rate of pollen-mediated gene flow are poorly understood (Gasquez 1985).

Evolved weed resistance to herbicides is typically a nuclear trait (Powles and Preston 2006) and as such would be expected to travel in pollen. Pollen dispersal in wind-pollinated species can be affected by plant morphology and environmental factors such as prevailing winds, wind speed, temperature, and precipitation, as well as the relative population sizes of pollen donors and recipients (de Vries 1971, 1972; Matus-Cadiz et al. 2004; Waines and Hegde 2003).

Pollen-mediated gene flow has been shown to be important for movement of resistance traits in both weed and crop populations. In a study of chlorsulfuron-resistant kochia (*Kochia scoparia* [L.] Schrad.), a primarily self-pollinating weed species with some wind-pollination, Mulugeta et al. (1994) estimated that 25% of pollen would be deposited within 1.3 m of a resistant source population, based on nonlinear regression analysis using the Weibull function. Furthermore, the function predicted that 99% of resistant kochia pollen grains would be deposited within 154.4 m of the source population. Stallings et al. (1995) demonstrated that pollen-mediated gene flow from sulfonylurea-resistant kochia plants to sensitive plants was between 4 and 13.1% at 1.5 m and between 0.01 and 1.4% at 28.9 m. Gene flow in kochia appears to be intermediate between that of imazethapyr-resistant common sunflower (*Helianthus annuus* L. HELAN), a primarily insect-pollinated and outcrossing weed species, and that of acetyl-coenzyme A carboxylase inhibitor-resistant giant foxtail (*Setaria faberi* Herrm.), a primarily self-pollinating weed species. In sunflower, gene flow was 29% at 5.5 m and approached 1% at 30 m (Marshall et al. 2001). In giant foxtail, gene flow ranged from 0.24 and 0.73% among plants grown 36-cm apart (Volenberg and Stoltenberg 2002). In primarily self-pollinating crop plants such as wheat (*Triticum aestivum* L.) (Matus-Cadiz et al. 2004) and rice (*Oryza sativa* L.) (Rong et al. 2007), gene flow was less than 1% at distances greater than 5 m, although very low rates (< 0.01%) were detected for rice and wheat at the maximum distances sampled (27 and 300 m, respectively).

Despite the increasing occurrence of common lambsquarters resistance to herbicides, allele movement in this species is poorly understood. Gene flow from herbicide-resistant common lambsquarters could provide an initial source of resistance alleles in previously sensitive populations. Mathematical models predict that the time required for resistance alleles to become fixed in a population is especially dependent on the initial frequency of resistance alleles and the selection intensity created by the herbicide (Jasieniuk et al. 1996; Neve 2008). Basic knowledge of common lambsquarters biology and ecology is needed for the development of successful resistance management strategies. Therefore, the objective of this research was to determine the frequency of pollen-mediated gene flow in common lambsquarters in a typical cropping system.

Materials and Methods

Plant Materials. *Chenopodium* seedlings homozygous for a magenta leaf axil phenotypic marker were collected from a

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farm field outside of Darlington, WI, in 2007. By use of morphological markers, the plants were identified as magenta spreen (*C. giganteum* D. Don), a member of the *C. album* aggregate (Rahiminejad and Gornall 2004; USDA-NRCS 2012). *Chenopodium giganteum* is a hexaploid ($2n = 54$) as is *C. album* (Rahiminejad and Gornall 2004). Results of preliminary greenhouse experiments demonstrated that *C. album* and *C. giganteum* hybridized readily and that the magenta marker was dominant with leaf axils of F_1 progeny from wild-type by *C. giganteum* crosses bearing the magenta phenotype (data not shown). However, the lack of molecular markers made it unclear whether the two taxa outcross as freely with each other as they do within their respective taxa, and we are unaware of any studies that have investigated this. We assumed equal outcrossing frequencies for the current study. If outcrossing frequency is reduced between taxa, our data would be expected to slightly underestimate gene flow within and among wild-type *C. album* populations. Nevertheless, the ability to unambiguously identify F_1 plants from crosses between *C. album* and *C. giganteum* made the magenta marker ideal for studying gene flow. Therefore, *C. giganteum* was used as a pollen parent and wild-type *C. album* was used as a seed parent in our experiments.

Experimental Approach and Design. The experimental approach was to investigate the effects of both distance and direction on the potential for gene flow (Marshall et al. 2001). Wild-type common lambsquarters plants were grown in soybean fields in concentric circles at 2, 3, 4, 6, 10, and 15 m from a center containing 24 *C. giganteum* plants. The concentric circles were divided into sectors representing eight intercardinal directions: north-northeast (NNE), east-northeast (ENE), east-southeast (ESE), south-southeast (SSE), south-southwest (SSW), west-southwest (WSW), west-northwest (WNW), and north-northwest (NNW) (Figure 1). Each sector contained three *C. giganteum* plants and 17 wild-type plants: one at 2 and 3 m, two at 4 m, three at 6 m, four at 10 m, and six at 15 m. Pollen movement was estimated by sampling seed from wild-type plants and quantifying the percent of F_1 progeny displaying the magenta marker. The percentage of magenta F_1 progeny from those plants was determined for each distance and sector. Two separate experiments were conducted using the same experimental setup.

General Field and Greenhouse Procedures. Field experiments were conducted in 2009 at the University of Wisconsin, Arlington Agricultural Research Station, near Arlington, WI. The soil type was a Plano silt loam (fine-silty mesic Typic Argiduoll) with 3.3% organic matter and pH 7.0. Soil was chisel-plowed in the fall and cultivated in the spring for seedbed preparation. Glyphosate-resistant soybean seed 'Asgrow 2108' was planted at a rate of 380,000 seeds ha^{-1} in rows spaced 76-cm apart and oriented in a north–south direction on May 29 (experiment 1) and June 4 (experiment 2). Experiments were located approximately 0.9 km apart.

For field experiments, common lambsquarters seedlings were grown in the University of Wisconsin-Madison Walnut Street Greenhouse and transplanted at the cotyledon stage to in situ field locations. Seeds were sown and covered with 2-mm commercial potting media (Metro Mix 300 potting medium, Scott-Sierra Horticultural Products Co., Marysville, OH) in individual pots (166 cm^3) (Jiffy Strips, Jiffy Products of America Inc., Lorain, OH). Potting media was watered daily to prevent moisture deficiencies and was maintained at ambient temperature and photoperiod until seedling emergence. Wild-type plants were established within soybean rows to facilitate tillage for weed control. Two sets of wild-type plants were established at each in situ location 1 wk apart (VC and V2 soybean, respectively) and were watered daily during the first 2 wk following transplanting. At the time of floral initiation in *C. giganteum*, one wild-type plant per in situ location whose time of floral initiation was best synchronized was chosen as a seed parent and any competing wild-type plants at that location were removed. Soybean plants that shaded common lambsquarters transplants were cut at the soil surface and removed by hand. All in situ common lambsquarters within 50 m of experiments were treated with glyphosate applied POST or were removed by hand to avoid competition for pollination sites in seed parents.

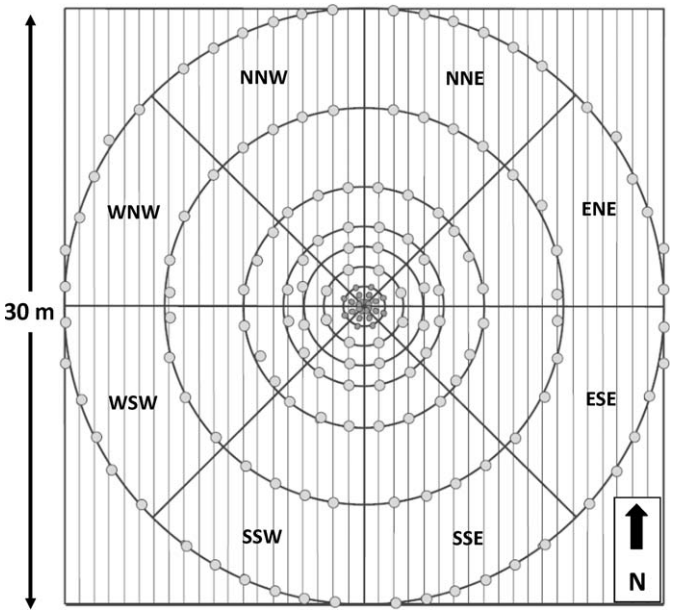

Figure 1. Field design for the planting arrangement of wild-type *Chenopodium album* (seed parents, ○) relative to a dense central planting of *C. giganteum* (pollen parents, ●) in gene flow experiments at the University of Wisconsin Arlington Agricultural Research Station near Arlington, WI, in 2009. Vertical lines represent rows of soybean. Concentric circles represent distances of 1, 2, 3, 4, 6, 10, and 15 m from the center of the experiment. The experiment is divided into sectors representing eight intercardinal directions: north-northeast (NNE), east-northeast (ENE), east-southeast (ESE), south-southeast (SSE), south-southwest (SSW), west-southwest (WSW), west-northwest (WNW), and north-northwest (NNW). Distances are to scale.

Data Collection and Statistical Analysis. Dates corresponding to three stages of floral development were noted for common lambsquarters plants in each experiment, including the beginning of pollen shed (one open flower), maximum pollen shed (50% open flowers), and the end of pollen shed (no open flowers). Data were expressed as a percentage of the plant population on a daily basis. The progress of each stage was described using a sigmoid logistic function:

$$Y_i = d_i / 1 + \exp[-b_i(x_i - t_i)] \quad [1]$$

for $i = 1$ to N where N is the number of stages, y_i is the percentage of the plant population at a given stage of pollen

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shed, d_i is the corresponding maximum percentage, x_i is the current day, t_i is the day when 50% of the plant population reaches each stage of pollen shed, and b_i is the relative slope around t_i (Lizaso et al. 2003).

At the end of anther dehiscence, a mesh bag (16 by 30 cm^2) (Pollination bag, Vilutis and Company, Inc., Frankfort, IL) was placed on inflorescences of each seed parent to prevent seed loss. Bagged inflorescences were harvested when seeds reached physiological maturity. Seeds were separated from plant tissue by hand and stored at −18 to 0 C for 3 mo to break dormancy. Seed parents were sampled at each distance within a sector and progeny were combined to form a composite sample (Marshall et al. 2001). In the greenhouse, approximately 1,000 seeds from each composite sample were sown and covered with 2-mm commercial potting media in separate 265- by 265- by 55-mm (length by width by height) plastic trays. Seedlings were watered daily and fertilized (Peter's Professional Fertilizer, Everris International B.V., Geldermalsen, The Netherlands) weekly to prevent moisture or nutrient deficiencies. Plants were maintained at a 16/24 C day/night temperature regime with a 16-h photoperiod of natural light supplemented with artificial light (1000W HPS, P.L. Light System, Inc., Beamsville, ON).

The number of *C. album* progeny to evaluate at each distance in order to have 90% power of detecting F_1 plants was estimated from previous studies of gene flow in wheat (Matus-Cadiz et al. 2004; Waines and Hegde 2003), a primarily self-pollinated species. Ad hoc estimates were generated in PROC POWER of SAS 9.1 (SAS Institute, Cary, NC). Within each sector, 22, 37, and 110 randomly selected progeny from composite samples were evaluated at distances of 2, 3, and 4 m, respectively, whereas 434 progeny were evaluated at distances of 6, 10, and 15 m since cross-pollination was expected to reach its lower asymptote at 6 m.

The effect of direction on the frequency of cross-pollination was tested (Marshall et al. 2001) using a randomized complete block design with sector across distance as a treatment effect and experiments as replicates (blocks, $n = 2$). The effect of distance on the frequency of cross-pollination was tested also (Marshall et al. 2001) using a randomized complete block design with distance within sector as a treatment effect and sectors as replicates (blocks, $n = 8$). Cross-pollination data for tests of direction and distance were subjected to ANOVA to generate F and P values using PROC MIXED. The Shapiro-Wilk test was conducted in PROC UNIVARIATE to test the assumption of normality. The Levene's test was conducted in PROC GLM to test the homogeneity of variance assumption among sectors and distances. Sector or distance data with heterogeneous variances were subjected to repeated measures ANOVA (Wolfinger 1996). Experiment by treatment interactions were tested for significance in PROC MIXED. Experiment by sector interactions were tested using the sector by experiment error term as an estimate of the variance. Experiment by distance interactions were tested using the distance by sector error term as an estimate of the variance. Cross-pollination data within sector or distance were pooled when interactions were not significant. Means were separated using Fisher's LSD test at P = 0.10 for sector and P = 0.05 for distance using preplanned contrasts.

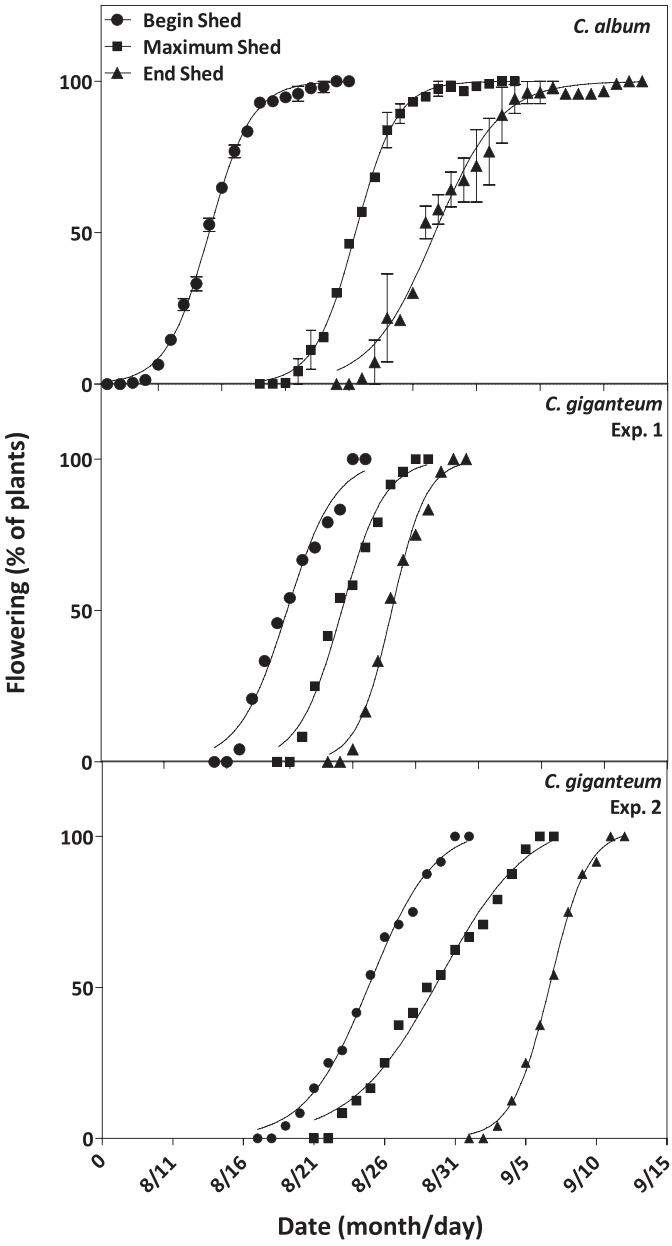

Figure 2. Percent flowering (± SEM) for wild-type *Chenopodium album* and *C. giganteum* in gene flow experiments at the University of Wisconsin Arlington Agricultural Research Station near Arlington, WI, in 2009. Dates corresponding to three stages of floral development are represented, including the beginning of pollen shed (one open flower), maximum pollen shed (50% open flowers), and the end of pollen shed (no open flowers). Floral synchrony did not differ between experiments for *C. album*, justifying the pooling of data. Floral synchrony differed between experiments for *C. giganteum* such that data for each experiment are shown separately.

Results and Discussion

Floral Synchrony and Wind Direction. Floral synchrony did not differ between experiments for wild-type plants, so data were pooled for analysis; however, floral synchrony differed between experiments for *C. giganteum* such that data for each experiment are reported separately (Figure 2). Differences between experiments for *C. giganteum* floral synchrony may have been due to the smaller numbers of plants per experiment (24) compared to wild-type plants (136). Wild-type common lambsquarters pollen shed began

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Table 1. Meteorological data for the beginning to end time of pollen shed of *Chenopodium giganteum* (pollen parents) in gene flow experiments at the University of Wisconsin Arlington Agricultural Research Station near Arlington, WI, in 2009. The bolded text (August 22 to September 3) corresponds to the time of maximum pollen shed. Reported averages are based on 24-h observations.

Date	Direction of prevailing wind[a]	Average wind speed	Average temperature	Average relative humidity	Total daily precipitation
		km h^{-1}	C	%	mm
August 17	WSW	3.2	20.3	96.6	10.9
August 18	WSW	10.8	18.3	81.2	0
August 19	SSE	10.8	17.8	87.0	3.1
August 20	WSW	15.1	18.0	90.8	6.4
August 21	WNW	11.4	16.1	87.5	3.1
August 22	**NNW**	**9.9**	**14.3**	**84.8**	**0**
August 23	**SSW**	**1.8**	**15.0**	**85.9**	**0**
August 24	**SSW**	**12.1**	**17.7**	**83.7**	**0**
August 25	**SSW**	**8.7**	**19.8**	**92.3**	**5.3**
August 26	**ENE**	**11.9**	**19.0**	**79.5**	**0**
August 27	**ESE**	**9.6**	**15.5**	**88.9**	**1.3**
August 28	**NNW**	**5.8**	**16.6**	**81.1**	**4.1**
August 29	**NNW**	**21.2**	**12.7**	**87.8**	**1.3**
August 30	**NNW**	**10.3**	**11.3**	**79.9**	**0**
August 31	**WNW**	**3.0**	**11.5**	**79.4**	**0**
September 1	**SSW**	**1.6**	**12.7**	**80.1**	**0**
September 2	**ESE**	**2.5**	**13.1**	**79.9**	**0**
September 3	**ENE**	**2.8**	**13.9**	**81.0**	**0**
September 4	NNE	2.2	14.8	81.0	0
September 5	ESE	3.1	15.4	78.9	0
September 6	ESE	2.8	15.8	83.9	0
September 7	ENE	4.6	15.9	79.9	0
September 8	ENE	6.1	16.1	79.5	0
September 9	ENE	4.9	17.4	85.1	0
September 10	ESE	6.5	18.5	84.1	0
September 11	ESE	4.8	18.0	80.4	0
2009 average[b]	ESE	2.0	16.0	83.9	1.4
20-yr average[b]	SSW	2.1	18.8	81.7	2.4

[a] Abbreviations: NNE = north-northeast; ENE = east-northeast; ESE = east-southeast; SSE = south-southeast; SSW = south-southwest; WSW = west-southwest; WNW = west-northwest; NNW = north-northwest.
[b] The 2009 and 20-yr (1989 to 2008) average wind speed, temperature, relative humidity, and precipitation are based on observations between August 17 and September 11. Prevailing wind is the direction with the highest frequency over that time period (23% in 2009 and 19% over 20 yr).

on August 9, while *C. giganteum* began approximately 1 wk later on August 17. However, all plants reached maximum pollen shed between mid-August and early September and pollen shed ceased by September 18. Average daily prevailing winds during the time of pollen shed were from the ESE and ENE (Table 1) with a frequency of 23 and 19% during that time period, respectively.

Experiment by sector interactions were not significant such that cross-pollination data for each sector were pooled across experiments. Gene flow corresponded to the down-wind

Table 2. Percent cross-pollination to wild-type *Chenopodium album* (seed parents) at various distances and directions from *Chenopodium giganteum* (pollen parents) at the University of Wisconsin Arlington Agricultural Research Station near Arlington, WI, in 2009.

	Cross-pollination								
	Wind direction[a]								
Distance (m)[b]	NNE	ENE	ESE	SSE	SSW	WSW	WNW	NNW	Average
	%								
Experiment 1									
2	0	0	0	0	7.5	8.3	0	0	2.00
3	0	0	2.3	0	0	1.5	0	2.3	0.76
4	0.89	0	1.6	0	0.79	2.2	0	0	0.69
6	0.59	1.1	0	0.87	0.41	0.67	0.22	0.38	0.53
10	0	0.17	0	0	0	0.28	0.32	0	0.10
15	0.22	0.21	0	0	0.41	0.30	0	0	0.14
Average	0.28	0.25	0.65	0.14	1.5	2.2	0.09	0.45	
Experiment 2									
2	2.6	3.6	1.5	7.7	0	8.3	8.6	1.2	4.20
3	0	0	0	1.4	4.7	1.7	0	0.93	1.50
4	0	0	0	0.57	0.74	1.3	1.1	0.55	0.53
6	0.20	0.37	0	0.61	0.37	0.23	0.22	0.21	0.28
10	0.23	0	0.21	0	0.20	0	0.19	0.16	0.12
15	0	0	0	0	0.88	0.20	0.20	0.19	0.19
Average	0.51	0.66	0.28	1.7	1.1	2.0	2.1	0.54	

[a] Abbreviations: NNE = north-northeast; ENE = east-northeast; ESE = east-southeast; SSE = south-southeast; SSW = south-southwest; WSW = west-southwest; WNW = west-northwest; NNW = north-northwest.
[b] Distance from the center of the experiment in meters.

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direction of the prevailing winds and was greatest (2.1% cross-pollination, across distances) to the WSW, intermediate to the SSW (1.3%) and WNW (1.1%), and least in all other directions (< 1.0%) (Table 2). While pollen-mediated gene flow in wind-pollinated species is often correlated with wind direction, it is not always the case, indicating that caution should be used when estimating expected gene flow rates based on experiments oriented in only one direction from the agent of pollination (Matus-Cadiz et al. 2004). Our results support this because maximum gene flow was roughly 180° from the predominantly ENE and ESE winds during the pollination period, not the prevailing WNW and NNW winds typical of southern Wisconsin (Wisconsin State Climatology Office 2009).

Distance from Pollen Source. Experiment by distance interactions were not significant such that cross-pollination data for each distance were pooled across experiments for analysis; however, experiments are presented separately (Table 2). Pollen-mediated gene flow was greatest at 2 m (3.0%); intermediate at 3 m (0.9%), 4 m (0.6%), and 6 m (0.4%); and least (< 0.3%) at 10 and 15 m ($P < 0.05$). Maximum cross-pollination observed across experiments at 2 m was 8.6% and at 15 m was 0.2%. A negative exponential function was fitted to the data to describe the maximum observed cross-pollination between wild-type *C. album* and *C. giganteum* based on the two highest values of cross-pollination at each distance. These values were observed in the SSW, WSW, and/or WNW sectors of each experiment (Figure 3). The function predicted gene flow at 1 and 15 m to be 12 and 0.3%, respectively.

Gene flow in primarily self-pollinating crops such as wheat and rice, and weeds such as kochia and giant foxtail, decreases to low levels at short distances from pollen donors. Specifically, 0.93% gene flow at 1 m from pollen donors has been observed in wheat (Matus-Cadiz et al. 2004) and 0.088% has been reported in rice (Rong et al. 2007). In these studies, both species' gene flow was less than 1% at distances greater than 5 m, although very low rates (< 0.01%) were detected for rice and wheat at the maximum distances sampled (27 and 300 m, respectively). Gene flow in giant foxtail averaged 0.49% among plants grown 36-cm apart in greenhouse studies (Volenberg and Stoltenberg 2002). Gene flow was slightly greater in kochia, between 4 and 13.1% at 1.5 m from source populations and between 0.01 and 1.4% at 28.9 m (Stallings et al. 1995). These gene flow estimates are in contrast to those observed in primarily outcrossing, wind-pollinated species such as corn and outcrossing, insect-pollinated species such as sunflower. Gene flow estimates between 25% (Jones and Brooks 1952) and 82% (Ma et al. 2004) immediately adjacent to pollen donors have been observed in corn (Halsey et al. 2005), comparable to the 29% observed in sunflower at a distance of 5.5 m (Marshall et al. 2001). The distances required to reduce gene flow to less than 1% ranged from 23 m (Bateman 1947) to 200 m (Jones and Brooks 1950) for corn (Halsey et al. 2005) and more than 30 m for sunflower (Marshall et al. 2001). Observed gene flow in common lambsquarters was most similar to that of kochia, with a maximum of 8.6% gene flow at 2 m from the center of experiments (1 m from the outer edge of the area occupied by pollen donors), and less than 1% gene flow at distances beyond 6 m. By comparison to the gene flow rates of wheat, rice, maize (*Zea mays* L.), and sunflower, we conclude that common lambsquarters is primarily self-pollinating in a typical cropping system, although somewhat less so than wheat or rice.

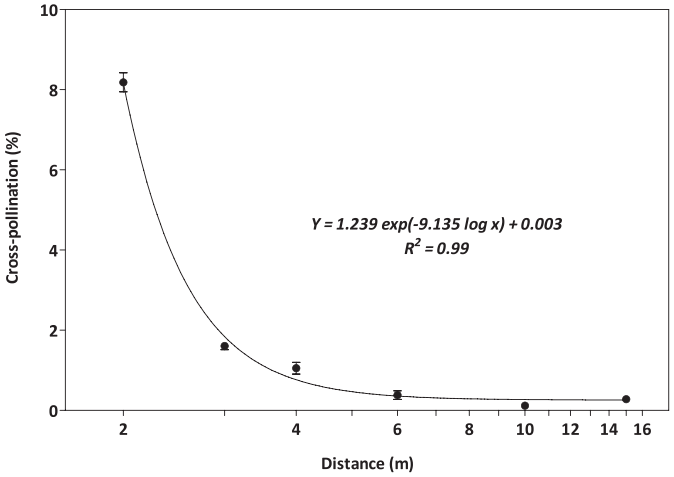

Figure 3. Empirical model of pollen-mediated gene flow in common lambsquarters at the University of Wisconsin Arlington Agricultural Research Station near Arlington, WI in 2009. A negative exponential function describing the maximum observed cross-pollination percent at each distance between wild-type *Chenopodium album* and *C. giganteum* was developed using the two highest values at each distance from the SSW, WSW, and/or WNW sectors (generally 180° from the prevailing wind direction during the time of pollen shed) of each experiment. Mean values of the maximum cross-pollination percent (± SEM) are shown, as determined by ordinary least squares analysis.

Potential for Gene Flow of Resistance Alleles. Gene flow is an important evolutionary force affecting plant populations because it can introduce new genes to different environments (Barton and Dracup 2000; Newman and Tallmon 2001; Tallmon et al. 2004). In the case of weeds, plants that have resistance alleles show increased fitness under selective pressure by herbicides relative to plants with wild-type alleles (Jasieniuk et al. 1996) because they survive exposure and set more viable seed.

To our knowledge, only one study has investigated the relative fitness of glyphosate-tolerant and -susceptible common lambsquarters in the absence of selection by glyphosate (Westhoven et al. 2008). Tolerant biotypes grew taller, amassed more leaf area and dry mass, and advanced through growth stages more rapidly than sensitive biotypes during the early portion of the growing season, but had lower dry mass at maturity. Tolerant biotypes initiated flower primordia approximately 6 to 8 wk after transplanting, while sensitive biotypes required 12 wk. The authors concluded that reduced relative fitness in the absence of glyphosate was not associated with tolerance to glyphosate based on seed production estimates; however, they noted that it is possible that the earlier flowering phenology could reduce the flowering overlap with the wild type, thus reducing cross-pollination and gene flow.

Mathematical models have been developed to describe putative changes in allelic frequencies of herbicide resistance traits in weed populations based on genetic and weed management parameters (Jasieniuk et al. 1996; Neve 2008). Jasieniuk et al. (1996) in particular noted that gene flow of resistance traits via pollen or seed may provide an initial source of resistance genes in the population that may confer a

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selective advantage in the presence of herbicides. Neve (2008) developed a model that accounted for multiple biological parameters involved in the evolution of weed resistance to glyphosate, including seed bank dynamics, weed seedling survival, seed production, genetic variability for susceptibility to herbicides, weed management tactics, resistance management strategies, weed breeding system, and the initial frequencies of resistance alleles. Simulations based on high glyphosate use frequency that would be expected to exert strong selective pressure on weed populations demonstrated the importance of the initial frequency of herbicide resistance alleles in a population. Since common lambsquarters is associated with very high seed production (Moechnig et al. 2003a), a single tolerant or resistant individual surviving exposure to glyphosate and setting seed can serve as an initial source of resistance alleles, ensuring that their subsequent loss by genetic drift is highly unlikely. Therefore, relatively low levels of pollen-mediated gene flow in common lambsquarters may nevertheless be sufficient to ensure the long-term persistence of resistance alleles in the landscape, and likely constitutes an important mechanism of allele transfer in a species otherwise lacking a seed dispersal mechanism.

In summary, our methods for investigating the pollen-mediated gene flow between wild-type *C. album* and *C. giganteum* demonstrated a primarily self-pollinating breeding system. The high degree of mechanical disturbance in agricultural systems would make gene flow of herbicide resistance traits by seed immigration on farm machinery a more likely means of movement, especially over distances greater than 15 m. However, since common lambsquarters has no active seed dispersal mechanism, pollen-mediated gene flow may play a significant role in the transfer and frequency of resistance alleles within and among populations.

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