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Weed Seed Pools Concurrent with Corn and Soybean Harvest in Illinois

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At the time of grain harvest, weed seeds can be classed into one of four pools on the basis of dispersal status and location: (1) undispersed, remaining on the mother plant; (2) dispersed in the current year, on the soil surface; (3) dispersed in the current year and collected by harvest machinery; and (4) dispersed in a previous year and persisting within the soil seed bank. Knowledge of the relative sizes of these seed pools for different weed species under different crop environments will be useful for determining the best way to reduce the size of inputs to the soil seed bank. In fall 2004 and fall 2005, four randomly selected commercially managed corn and soybean fields in east-central Illinois were sampled to quantify weed seed pools at time of crop harvest. Thirty randomly located 0.125-m^2 quadrats were placed within each field, the four seed pools mentioned above were sampled for each quadrat, and the species composition and abundance of each seed pool was determined. The magnitude of the weed seed rain varied among species and between years and crops. Twenty-six weed species were found to contribute to at least one of the four seed pools. However, the weed seed pools were consistently dominated by six species: velvetleaf, *Amaranthus* complex (redroot pigweed and waterhemp), ivyleaf morningglory, giant foxtail, prickly sida, and common cocklebur. For each of these species, the ratio of undispersed seeds to seeds in the soil seed bank at harvest time was ≥ 1 in at least one crop during one of the two experimental years, indicating a potential for the soil seed bank to be completely replenished or augmented by that year's seed rain. This analysis demonstrates the urgent need for techniques to limit weed seed inputs to the soil seed bank at the end of the growing season.

Nomenclature: Common cocklebur, *Xanthium strumarium* L. XANST; common waterhemp, *Amaranthus rudis* Sauer AMATA; giant foxtail, *Setaria faberi* Herrm. SETFA; ivyleaf morningglory, *Ipomoea hederacea* (L.) Jacq. IPOHE; prickly sida, *Sida spinosa* L. SIDSP; redroot pigweed, *Amaranthus retroflexus* L. AMARE; velvetleaf, *Abutilon theophrasti* Medik. ABUTH; corn, *Zea mays* L; soybean, *Glycine max* (L.) Merr.

Key words: Seed rain, community structure, risk analysis, seed bank replenishment.

A casual glance at most commercially managed corn and soybean fields while traveling at highway speed through central Illinois would suggest that the struggle against weeds is over. Row after row appear to be weed free, and the rare weed escape is confined to a field margin or wet spot. As most farmers will attest, however, the struggle is not over, and agricultural statistics on herbicide usage support this. Since 2000, with nearly universal adoption in Illinois of glyphosate-resistant soybean, and more recently, corn, fields look cleaner than ever, yet the average application rate of glyphosate has increased steadily by 0.027 and 0.036 kg ae ha^{-1} yr^{-1} in soybean and corn, respectively (NASS 2007). These data suggest that weed infestations in conventionally managed grain fields are not diminishing and could be growing more problematic to control.

On closer inspection of these same fields, especially after crop senescence, it becomes apparent that mature weeds do exist within these fields, not just on the margins, and that they are adding substantial numbers of new seeds to the weed seed bank. The value of managing the seed stage of annual weeds, either by targeting the seed bank directly (Gallandt 2006) or by reducing fecundity (Norris 2007), has received both theoretical and empirical support (Davis 2006; Davis and Williams 2007; Dieleman et al. 1999; Taylor and Hartzler 2000). Few seed bank management tactics have been developed to the point of commercial utility, however, and research in this area lags behind other tactics.

In this paper, I attempt to gauge the extent of the weed fecundity problem (Norris 2007) and the feasibility of capturing and destroying weed seeds in commercial corn and soybean fields at the time of harvest (Slagell-Gossen et al. 1998). Three research questions guided this study: What is the magnitude of the various weed seed pools (undispersed, dispersed, and within the soil seed bank) in corn and soybean at the time of crop harvest? How frequently are weed seed banks replenished or augmented? What proportion of newly produced seeds remain undispersed at the time of crop harvest and therefore potentially could be captured by mechanical adaptations of harvest machinery? These questions were addressed with empirical estimates of population densities for various weed seed pools at the time of grain harvest in central Illinois in commercially managed corn and soybean fields.

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Materials and Methods

Survey Design. A survey of weed seed pools at the time of corn and soybean harvest in central Illinois was conducted in the fall of 2004 and 2005 as a completely randomized design with four replications per experimental run. Four corn and four soybean fields were randomly chosen to be surveyed in each study year from a candidate pool of > 30 fields in Savoy, IL (40°03′24.75″N, 88°13′29.57″W), managed with standard commercial practices for the area by the University of Illinois Crop Science Research and Education Center (CSREC) staff. Each of the survey fields comprised production areas of > 3.2 ha. The dominant soil types for the fields were Drummer silt loam (fine-silty, mixed, superactive, mesic Typic Endoaquoll), averaging 5.2% organic matter and pH 6.6, and Flanagan silt loam (fine, smectitic, mesic Aquic Argiudoll), averaging 3.6% organic matter and pH 6.4.

Field crops were managed by the CSREC farm staff in a manner consistent with surrounding commercial grain crop production fields (M. Kleiss, personal communication). All fields were chisel plowed in late fall after grain harvest, with further seedbed preparation in early April. Synthetic fertilizer applications were made on the basis of soil tests in accordance with University of Illinois Extension recommendations (Hoeft and Peck 2002). Weed management activities in soybean consisted of a preplant incorporated application of and pendimethalin at 0.07 and 0.94 kg ai ha^{-1}, respectively, followed by a single postemergence application of glyphosate at 1.27 kg ae ha^{-1} at the 5- to 10-cm stage of weed growth and, in corn, a single preemergence application of atrazine at 1.12 kg ai ha^{-1} tank-mixed with acetochlor at 2.27 kg ai ha^{-1}.

Collection of Seed Pools. Ongoing communication with the CSREC staff was used to time seed collection within 3 d before harvest for each of the survey fields. For both crops and for both years, harvest dates ranged from late September to mid-October. Within each survey field, 30 sampling locations were randomly chosen by a computer program to generate random combinations of number of crop rows from a field corner and number of paces into the field.

Four seed pools were collected as part of the survey. These consisted of (1) seeds that remained undispersed on standing biomass of the mother plant (ST), (2) seeds dispersed during the current growing season and remaining on the soil surface (SU), (3) seeds within the soil seed bank (SO), and (4) seeds collected by the combine at harvest (CO).

Seeds in the ST pool were collected by placing a 0.125-m^2 quadrat at the sampling location and clipping all weed biomass within the quadrat, sorting to species, and removing seeds as described later. Once standing weed biomass had been removed, a portable wet/dry vacuum[1] was used to gently remove SU seeds from the soil surface and from the surface of fallen plant residue within the quadrat. The device was fitted with an internal nylon sleeve to collect samples as they were vacuumed from the soil surface. After surface seeds were removed, a hand trowel was used to further clear residue from the soil surface and scrape away the top 0.5 cm of soil to prevent contamination of the SO pool with remaining seeds from the SU pool. Seeds in the SO pool were then sampled by removing two 10-cm-diameter by 10-cm-deep (785 cm^3) soil cores from within the quadrat with a golf cup cutter.[2] Whereas collection of seeds from the ST, SU, and SO pools occurred before harvest, seeds in the CO pool were collected by the combine at harvest. Seeds in the CO pool were recovered from the combine by taking 30 periodic 1-kg scoops from the grain cart as the combine was offloading grain. This subsampling technique was an attempt to capture some of the variability in the CO pool within the field. Despite this effort, however, seed mixing within the combine meant that the estimate of seed population density within the CO pool represented a field average, rather than a site-specific sample, as for the other seed pools.

Plant biomass collected for estimating population density of the ST pool was dried to constant weight at 35 C, after which the weed seeds were recovered by hand threshing with a "rub board" (wooden block and ramp coated with ribbed rubber sheeting, rubbed against one another), sieving through a series of standard soil sieves, and processing on a seed cleaner.[3] Seeds in the SU and SO pools were recovered through elutriation (Wiles et al. 1996), dry sieving, and processing on the seed cleaner. Seeds in the CO pool were simply dry-sieved. After seeds were collected for the various seed pools, they were stored in sealed polyethylene bags at 4 C before hand counting and determination of viability via tetrazolium testing (AOSA 2000). Only viable seeds were included in data analysis and presentation.

Statistical Analysis. Analysis of the seed pool data proceeded in a series of levels, from general to more specific. At the most general level, a nested multivariate analysis of variance (Scheiner 2001) was performed to quantify significant factors operating on the four seed pools over the entire data set and to protect further univariate analyses within species ($\alpha = 0.05$). A multivariate analysis of variance (MANOVA) model containing main effects and interactions for Species, Year, and Crop nested within Field was used to analyze population density of seeds in the ST, SU, SO, and CO pools within the GLM (general linear model) subroutine of SYSTAT 11.0.1.[4] Pillai's trace was used as the statistic for determining effect sizes and significance because it is robust to departures from MANOVA assumptions (Scheiner 2001), and the distributions of seed population density for the various seed pools were heavily skewed toward zero. Ecological count data commonly include sparse cells, resulting in zero-inflated distributions that violate usual analysis of variance assumptions (Cunningham and Lindenmayer 2005).

After MANOVA, no further multivariate analyses were employed because the subject of interest in this study was the distribution of seed population densities at time of grain harvest for individual weed species, not community composition. Instead, univariate analyses were performed within species. Generalized linear models (Neter et al. 1996) containing main and interaction effects of Year, Crop nested within Field, and Pool were constructed with a variety of link functions to determine the appropriate underlying statistical distribution for analyzing the data. Performance of four candidate models fit to the master data set with various standard unimodal distributions as link functions (Hilborn and Mangel 1997), including normal, lognormal, negative binomial, and zero-inflated Poisson (Cunningham and Lindenmayer 2005), was evaluated according to minimization of Akaike's Information Criterion (AIC) (Burnham and Anderson 2002). Subsequent to model selection, the best performing link function (log-normal) was used to fit generalized linear models to count data for each species. Models were implemented with the GAMLSS package (Stasinopoulos et al. 2006) for the open source statistical software program R (v.2.5.1).[5]

Weed seed bank replenishment within a given quadrat was defined empirically as $(ST + SU)/SO \geq 1$, where ST, SU, and SO were standardized on a seeds per square meter basis. Because this study did not quantify postdispersal seed losses to predation (Menalled et al. 2006), it was only possible to determine potential inputs to the soil seed bank. However, because cumulative seed predation rates in north-central field crop systems rise slowly to their maximum over a period of several months (Harrison et al. 2003) and because these fields were tilled immediately after crop harvest, it is reasonable to speculate that most of the seeds measured in the ST and SU fractions entered the soil seed bank. On the basis of the above criterion, seed bank population densities were used to assign each quadrat a binary code related to seed bank replenishment. Seed bank replenishment prevalence was quantified for each weed species by building multiple logistic regression models with Crop and Year as candidate variables. Alternative models were evaluated with the *G* statistic (Hosmer and

Table 1. Multivariate analysis of variance of seed pool population density in corn and soybean fields in central Illinois at harvest time in 2004 and 2005. df, degrees of freedom.

Effect	Pillai's trace	F	df_{num}	df_{den}	$P > F$
Species (S)	1.34	3.17	100	624	0.0001
Year (Y)	0.04	1.6	4	153	0.18
Crop{Field} C{F}	0.28	2.99	16	624	0.0001
S × Y	0.49	0.88	100	624	0.79
S × C{F}	1.58	1.01	400	624	0.44
Y × C{F}	0.21	2.16	16	624	0.005
Y × S × C{F}	1.69	1.14	400	624	0.07

Lemeshow 2000). Multiple logistic regression models were implemented with the LOGIT subroutine of SYSTAT 11.0.1.

Seed capture leverage was defined as the ratio of seeds—either on standing plants or collected by the combine—to newly produced seeds, with relevance to possible reduction in inputs of new seed to the soil seed bank by capturing and destroying that seed pool. For the ST and CO seed pools, seed capture leverage values were calculated as ST/(ST + SU) and CO/(ST + SU), respectively. Means and 95% confidence intervals were obtained for leverage values with 10,000 bootstrap iterations (Dixon 2001) within the STATS subroutine of SYSTAT 11.0.1.

Results and Discussion

Weed Seed Pools at Time of Crop Harvest. Multivariate analysis of variance results indicated significant main effects of Species and Crop, and a significant interaction effect between Year and Crop (Table 1). The large amount of variability observed in fecundity was expected because phenology and response to different growing environments is species-specific (Forcella et al. 1996, 2000; Kegode et al. 1999; Norris 2007). The multivariate results also protected further univariate analyses of seed pool population density, examined within Species, Crop, and Year.

A comparison of generalized linear models, fit to the master data set with four different link functions, indicated that a log-normal distribution described the data better than (i.e., minimized AIC compared with) the normal, negative binomial or zero-inflated Poisson distributions (data not shown). Subsequent fits within species were also better described by the log-normal distribution; therefore, univariate analyses were performed on the basis of this link function.

Twenty-six weed species were represented in the surveys, pooled over crops and study years (Figure 1). For the majority of species, many quadrats were empty and seed pool population density was skewed toward zero (box plot was anchored on the x axis). However, for a small number of species, including common waterhemp, giant foxtail, ivyleaf morningglory, and redroot pigweed, seeds were ubiquitous, and median population densities were greater than zero. The *Amaranthus* complex (redroot pigweed and waterhemp) and giant foxtail have long been problematic weeds in Illinois field crops (Knake and Slife 1969; Patzoldt et al. 2002), but it is noteworthy that ivyleaf morningglory was also well represented in the various seed pools, as Illinois grain producers have remarked on its increasing frequency in recent years (Illinois Soybean Association, personal communication). Seeds of common waterhemp, redroot pigweed, and ivyleaf morningglory are all known to be persistent over the long term in the soil seed bank (Burnside et al. 1996; Stoller and Wax 1974), whereas seeds of

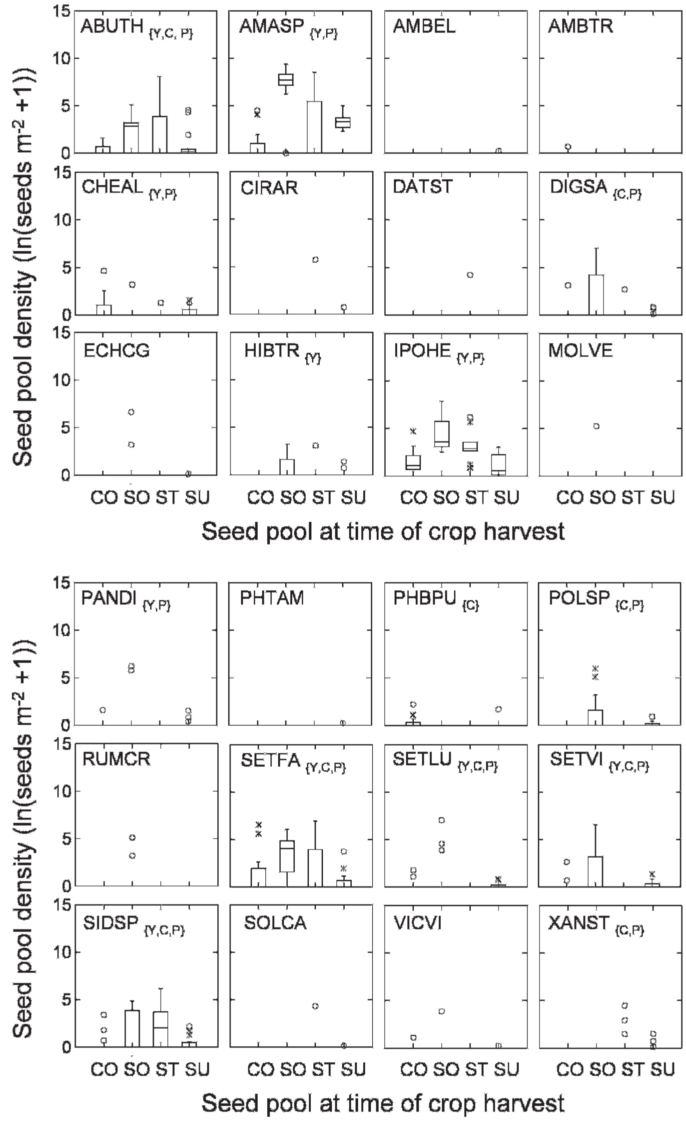

Figure 1. Distribution of population density for four seed pools at time of grain harvest in Savoy, IL, for 26 weed species (data pooled over Crop and Year). Box length, range within which the central 50% of the values fall; horizontal line within box, median; whiskers, values 1.5 times the interquartile range; x and o, outside values and far outside values, respectively. Uppercase letters within curly brackets show significant ($P < 0.05$) effects of Year (Y), Crop (C), and Pool (P). Abbreviations for seed pools: CO, seeds collected by combine harvester; SO, seeds in the soil seed bank; ST, seeds remaining undispersed at time of harvest; SU, dispersed seeds remaining on the soil surface at time of harvest. Bayer codes: ABUTH, velvetleaf; AMASP, common waterhemp and redroot pigweed; AMBEL, common ragweed, *Ambrosia artemisiifolia* L.; AMBTR, giant ragweed, *Ambrosia trifida* L.; CHEAL, common lambsquarters; CIRAR, Canada thistle, *Cirsium arvense* (L.) Scop.; DATST, jimsonweed, *Datura stramonium* L.; DIGSA, large crabgrass; ECHCG, barnyardgrass, *Echinochloa crus-galli* (L.) Beauv.; HIBTR, Venice mallow, *Hibiscus trionum* L.; IPOHE, ivyleaf morningglory; MOLVE, carpetweed, *Mollugo verticillata* L.; PANDI, fall panicum; PHBPU, tall morningglory, *Ipomoea purpurea* (L.) Roth; PHTAM, pokeweed, *Phytolacca americana* L.; POLSP, ladysthumb and Pennsylvania smartweed; RUMCR, curly dock, *Rumex crispus* L.; SETFA, giant foxtail; SETLU, yellow foxtail; SETVI, green foxtail; SIDSP, prickly sida; SOLCA, horsenettle, *Solanum carolinense* L.; VICVI, hairy vetch, *Vicia villosa* Roth; XANST, common cocklebur.

giant foxtail are only persistent in the short term in the soil seed bank (Buhler and Hartzler 2001). High population densities of giant foxtail observed in the soil seed bank were therefore likely to have come from recurrent seed inputs.

Environmental effects on seed pool counts, including Crop and Year, were observed for 18 of 26 species (Figure 1).

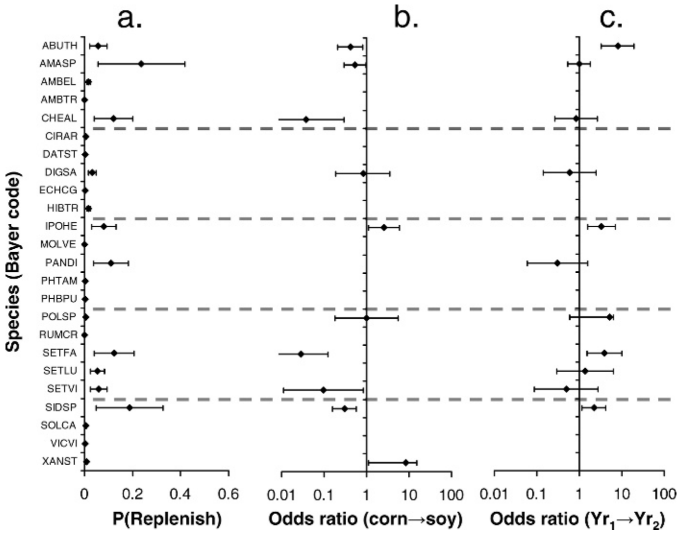

Figure 2. Logistic regression of weed seed bank replenishment rate in corn and soybean fields in Savoy, IL. Within species, panels show estimates with 95% confidence intervals for (a) base seed bank replenishment rate, (b) odds ratio of seed bank replenishment because of difference in crop environment, and (c) odds ratio of seed bank replenishment because of difference between study years.

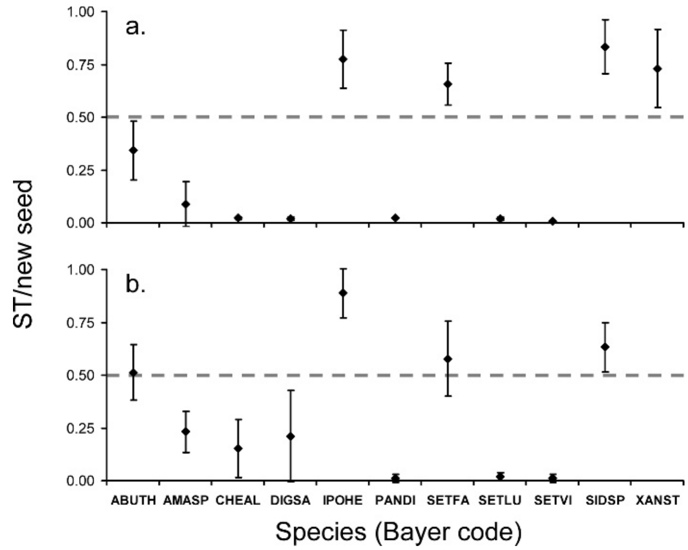

Figure 3. Bootstrapped means and 95% confidence intervals for ratio of seeds remaining on the parent plant at time of (a) corn and (b) soybean harvest (ST pool) compared with all new seeds produced in that growing season (ST + SU pools) for the 11 most abundant weed species in this study.

Variation by year in seed pool population density was more common than variation by crop species. For 14 species, Pool type was also a main effect on seed pool population density. The SO pool had a greater population density ($P < 0.05$), averaged over Crop and Year, than other pools for the *Amaranthus* complex, large crabgrass [*Digitaria sanguinalis* (L.) Scop.], ivyleaf morningglory, fall panicum (*Panicum dichotomiflorum* Michx.), the *Polygonum* complex (ladysthumb [*Polygonum persicaria* L.] and Pennsylvania smartweed [*Polygonum pensylvanicum* L.]), giant foxtail, yellow foxtail [*Setaria glauca* (L.) Beauv.], and green foxtail [*Setaria viridis* (L.) Beauv.]. Soil seed bank population densities within this study are similar to those observed previously for weed seed banks in the north central United States (Forcella et al. 1992).

Seed Bank Replenishment Rates. Averaging seed pool densities across crops, sites, and years, is a convenient way of obtaining an overview of weed seed pools at the time of crop harvest but obscures an important result: At the level of individual quadrats, current seed inputs often exceeded soil seed bank densities. Multiple logistic regression indicated that for over half of the species studied, the risk of seed bank replenishment from a single season's seed rain was greater than zero (Figure 2a). For several species, including velvetleaf, the *Amaranthus* complex, common lambsquarters (*Chenopodium album* L.), ivyleaf morningglory, fall panicum, giant foxtail, yellow foxtail, green foxtail, and prickly sida, seed bank replenishment rate was substantially greater than zero, varying between 5 and 25%. For two species (morningglory and cocklebur), risk of seed bank replenishment was greater in soybean than in corn, whereas for six species (velvetleaf, *Amaranthus* complex, common lambsquarters, giant foxtail, green foxtail, and prickly sida), risk of seed bank replenishment was lower in soybean than in corn (Figure 2b). A combination of specific crop–weed interference intensities (Zimdahl 2004) and differential effects of herbicide chemistry on various weed species under central Illinois conditions (Hager and Nordby 2007) were most likely responsible for differences in replenishment rates.

It is notable that seed bank replenishment rates this high were recorded in intensively managed fields typical of surrounding commercial production systems. Seed bank replenishment at this level could be one factor contributing to ongoing high annual expenditures on herbicides (NASS 2007) and supports recent calls for a greater focus on reducing inputs to the weed seed bank (Buhler et al. 2000; Davis 2006; Norris 2007). Another important ramification of weed seed escapes, especially in the *Amaranthus* complex, is the potential contribution to development of herbicide resistance. It is precisely those plants surviving control measures and producing seed at the end of the growing season that are most likely to represent new herbicide resistance events (Jasieniuk et al. 1996; Maxwell et al. 1990).

Seed Capture Leverage. Weed species with seed bank replenishment rates substantially greater than zero were examined further to determine what proportion of new seed production remains standing at crop maturity and, therefore, potentially captured by harvesting equipment (Shirtliffe and Entz 2005; Slagell-Gossen et al. 1998) or destroyed through spray-topping applications (Medd et al. 1992). For three weed species with high seed bank replenishment rates, ivyleaf morningglory, giant foxtail, and prickly sida, the majority of new seeds (> 50%) remained on the mother plant at the time of harvest in both corn and soybeans (Figures 3a and 3b). Most velvetleaf seeds had dispersed by harvest time in corn fields, whereas most remained undispersed within soybean fields. Cocklebur remained undispersed at corn harvest and was not detected in the soybean fields studied. For the remaining species, > 75% of seeds had dispersed by the time of harvest.

Only a small proportion of newly produced seeds were recovered by harvest machinery for the seven species that had high seed bank replenishment rates and also showed up in the CO pool. Combine seed capture leverage was < 0.10 and 0.15, respectively, in corn and soybeans, for the most abundant weed seed in the harvested grain, common lambsquarters, and < 0.01 for the least abundant species in the harvested grain, the *Amaranthus* complex (Figure 4).

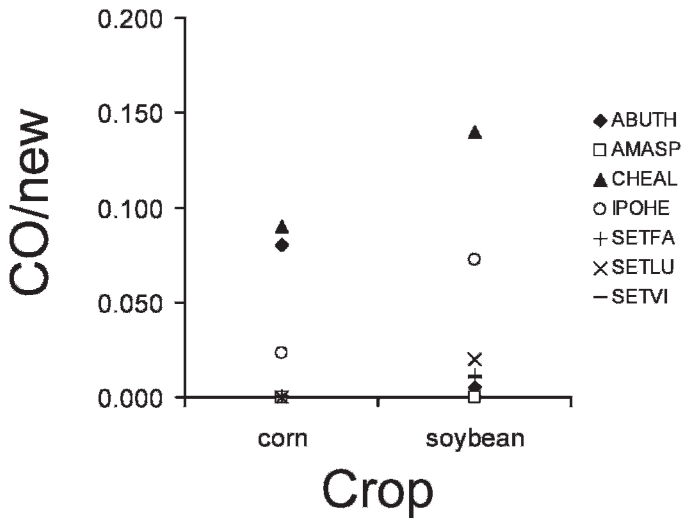

Figure 4. Bootstrapped means and 95% confidence intervals for ratio of seeds collected by combine harvester (CO pool) compared with all new seeds produced in that growing season (ST + SU pools) for the seven most abundant weed species in the CO seed pool.

Implications for Seed Bank Management. The results presented here demonstrate that far from being a rare event, weed seed bank replenishment resulting from a single season's seed rain is a common occurrence, even in a commercial grain production system managed with standard herbicide programs. Mathematical models (Davis 2006) and field studies (Davis and Williams 2007; Taylor and Hartzler 2000) both point to the consequences of high–seed production events for weed population growth and crop yield loss. For species with seeds that are highly persistent in the soil seed bank, such as common lambsquarters and velvetleaf, a single pulse of seeds can persist for decades (Burnside et al. 1996); therefore, seed bank replenishment should not be taken lightly. Yet weed management tactics targeted directly at the weed seed bank or at reducing fecundity remain rare (Gallandt 2006; Norris 2007). This underdeveloped research area has measurable effects on long-term weed management success and potentially is of critical importance to herbicide resistance management. Supplementing early-season tactics targeting weed seedlings with late-season tactics targeting seed rain and the soil seed bank could provide an additional obstacle to resistance development (Maxwell et al. 1990).

The first line of defense against seed production is a competitive crop and stringent weed management practices (Norris 2007). Seed predation, either by granivores living in crop fields (Menalled et al. 2006) or mechanical adaptations of harvest machinery to collect and destroy weed seeds (Slagell-Gossen et al. 1998), offers a direct way of targeting seed production escapes. Spray-topping with herbicides during weed seed formation (Medd et al. 1992) offers another option, although most likely an expensive one, for reducing weed fecundity.

Seed capture leverage values in this study show that for several common weeds in central Illinois grain fields, mechanical collection and destruction of weed seeds at harvest time could be practical. However, for small-seeded, highly persistent species such as common lambsquarters, common waterhemp, and redroot pigweed, the seed capture leverage was so low that seed recovery would require modification to current harvest machinery used in conventionally grown corn and soybean. To capture and destroy weed seeds of any size with modified harvesting machinery would require a substantial engineering effort, with potential additional costs associated with weed seed destruction. Management practices aimed at enhancing pre- and postdispersal predation of these species (Menalled et al. 2007; Nurse et al. 2003) or, better, preventing seed formation in the first place (Norris 2007) are more likely to succeed in reducing fecundity of these species. Developing effective suites of management practices to reduce overall weed fecundity in production fields will be greatly aided by species-level information identifying those tactics that are most appropriate for a given weed flora.

Sources of Materials

[1] DeWalt DC500, DEWALT Industrial Tool Co., 701 E Joppa Road, TW425, Baltimore, MD 21286.

[2] Par Aide Pro Cup Cutter, www.putting-greens.com.

[3] South Dakota seed blower model 757, Seedburo Equipment Co., 1022 W Jackson Boulevard, Chicago, IL 60607.

[4] SYSTAT Software, 501 Canal Boulevard, Suite C, Richmond, CA 94804.

[5] The R Project for Statistical Computing, http://www.r-project.org/.

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