Seed size variation and predation of seeds produced by wild and crop–wild sunflowers[1]

Helen M. Alexander,[2] Charity L. Cummings,[2] Lisa Kahn,[2] and Allison A. Snow[3]

[2]Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045 USA; and [3]Department of Evolution, Ecology, and Organismal Biology, Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210 USA

The movement of pollen between crop and wild sunflowers (both *Helianthus annuus*) has led to concerns about the possible introduction of crop transgenes into wild populations. The persistence of crop traits in wild populations will depend in part on the relative fitness of crop–wild hybrid vs. wild plants. Using seeds from two large experimental field plots, we found that seeds produced by crop–wild plants were twice the size of wild seeds and differed in coloration. Head diameter, date of flowering, identity of mother plant, and levels of predispersal predation explained some variation in mean seed size. We hypothesized that postdispersal vertebrate seed predation would be affected by seed size, with hybrid seeds preferentially eaten. In each of three field trials, significantly more hybrid seeds were eaten (62% of hybrid seed; 42% of wild seed). Within the category of wild seeds, larger seeds were preferentially eaten; however among hybrid seeds, predation was not significantly related to seed size. In this study, differential predation thus reduces hybrid fitness and would presumably slow the spread of transgenes into wild populations.

Key words: Asteraceae; crop–wild hybrid; *Helianthus annuus*; predation; seed size; sunflower.

A consequence of the increased use of transgenes in crop breeding is that such genes may move from crops to wild relatives via gene flow. This process could potentially lead to increased weediness of wild plant species if transgenes confer a fitness advantage to the wild plant through, for example, herbivore or pathogen resistance (Raybould and Gray, 1994; Parker and Kareiva, 1996; Snow and Morán Palma, 1997). An important step in studying this problem is measurement of fitness components of wild plants and crop–wild hybrids (e.g., Langevin, Clay, and Grace, 1990; Klinger and Ellstrand, 1994; Arriola and Ellstrand, 1997; Snow et al., 1998). In the majority of studies to date, plant survival and reproduction have been examined without explicit examination of the effects of herbivores and pathogens on crop–wild hybrid and wild plants (but see Cummings, Alexander, and Snow, 1999).

One reason to study the effects of herbivores on fitness of hybrid and wild plants would be if there were a priori reasons to expect differential predation. In the case of postdispersal seed predation, the ecological literature reveals many examples of differential predation on larger seeds, usually in the context of comparisons among species or studies that relate seed size to other seed characters (Mittelbach and Gross, 1984; Kelrick et al., 1986; Hulme, 1994). One of the few studies that examined size-specific seed predation within a species also found differential predation on larger seeds (Moegenburg, 1996). Given that crop seeds are often larger than those of their wild relatives (Table 1) and that hybrid characters are often intermediate between the parental forms, we hypothesized that seeds produced by crop–wild hybrid plants may be larger in size than wild seeds and thus potentially more prone to postdispersal predation.

We examined seed size variation and its relationship to predation with the common sunflower, *Helianthus annuus*. Sun-flower is considered a high-risk species in terms of transgene escape, because of the presence of both crop and wild sunflowers (the same species) over large areas in the central United States and because of the ease of crosses between crop and wild plants (Whitton et al., 1997; Linder et al., 1998; Snow et al., 1998). Sunflower achenes are commonly referred to as "seeds"; crop sunflower seeds are over six times larger in mass than wild sunflower seeds (Table 1). Postdispersal predation can be considerable for this species; for example, seed predation on wild *H. annuus* averaged 48% for a 7-mo period in eastern Nebraska (Teo-Sherrell, 1996). Our objectives were to: (1) quantify variation in the size of seeds produced by crop–wild hybrid and wild sunflowers, (2) explore whether characteristics of sunflower heads are associated with variation in seed size within a cross type (i.e., crop–wild hybrid vs. wild), and (3) compare postdispersal seed predation on seeds produced by crop–wild hybrids and wild plants and determine whether differential predation by size occurs within each cross type.

MATERIALS AND METHODS

Sunflower seed used in this study came from two experimental populations (Sites 1 and 3) of wild and crop–wild hybrid sunflowers (50:50 mixture) grown in 1997 in northeastern Kansas (for details, see Cummings, Alexander, and Snow, 1999). No crop transgenes were present in the plant material. A wild seed or head is defined as being produced on a wild maternal plant and a hybrid seed or head is defined as being produced on a maternal plant that is the product of a crop × wild cross. In the latter case, the seeds are effectively the F₂ generation since most hybrid plants flowered prior to wild plants and thus there was little back-crossing with wild plants (Cummings, Alexander, and Snow, 1999). Seed size is defined as the product of maximum seed length and maximum seed width (caliper measurement to the nearest 0.05 mm; all measurements done by one person for consistency).

We determined the correlation between seed size and seed mass on randomly chosen seeds from both hybrid and wild heads (30 seeds per cross type). Seed size was first determined; seeds were then dried for 2 d in a 90°C oven and then individually weighed. To determine the degree to which a randomly chosen seed from hybrid and wild sunflowers differed in visual characteristics that may alter predation, we determined seed size, coloration,

TABLE 1. Seed size for selected crop, hybrid, and wild species. Seed (or achene) measured unless otherwise indicated. Dashes indicate where data were not available.

Crop	Hybrid (F₁)	Wild	Trait measured
Chenopodium quinoa		*C. berlandieri*	fruit diameter[1]
2.3 mm	—	1.3 mm	
Cucurbita pepo subsp. *ovifera*		*C. pepo* subsp. *ovifera*	mass[2]
variety *ovifera*		variety *ozarkana*	
94 ± 3 mg	30 ± 2 mg	35 ± 1 mg	
Raphanus sativus		*R. sativus*	mass[3]
—	0.03 ± 0.001 g	0.03 ± 0.002 g	
Helianthus annuus		*H. annuus*	mass[4]
47.92 ± 0.62 mg	8.85 ± 0.28 mg	7.09 ± 0.10 mg	
Oryza sativa		*O. sativa*	length × width[5]
23.8 mm²	—	25.7 mm²	
Sorghum bicolor		*S. halepense*	length × width[6]
15.1 mm²	—	7.9 mm²	

[1] Based on measurements of photographs of single fruits (Figs. 2 and 3 in Wilson, 1980).

[2] Each mean is based on 20 samples of five seeds each; except for the crop, each sample is from a separate mother plant (L. J. Spencer, personal communication).

[3] Means reported in Klinger and Ellstrand, 1994.

[4] Each mean is based on 25 samples of 50 seeds each. Crop data are for USDA 894, the source of crop genes in this study. Wild data are for wild genotypes from Kansas, which were also used to create the F₁ hybrids.

[5] Means calculated for two rice cultivars and five red rice types; data in Table 5 of Diarra, Smith, and Talbert, 1985.

[6] Based on measurements of photographs ($N = 3$ per species, Plates 44 and 519 in Martin and Barkley, 1961).

and striping/dot patterns for 100 hybrid and 100 wild seeds (seed came from bulk collections derived from 33 randomly selected hybrid heads and 185 randomly selected wild heads from Site 1).

In addition to the above seed measurements, seed size was measured for a large seed collection because of our interest in whether or not characteristics of individual plants or heads affected mean seed size per head. We thus measured a total of 2120 undamaged seeds (ten seeds per head for randomly chosen hybrid [N = 94] and wild [N = 118] heads) from Sites 1 and 3. For plants in the data set with multiple heads/plant, we used nested ANOVAs to assess the effects of site, plant, and head as factors explaining variation in seed size within each cross type. Given the significant effect of plant, we then randomly chose one head/plant for subsequent analyses (750 hybrid seed; 880 wild seed). Multiple regression was used to explore the relationship between mean seed size per head and four head characteristics. We focused on two traits (head diameter and date of flowering of head) that are likely to determine resources available to the seed. Two other traits (two types of damage to the head by predispersal predators) could be associated with mean seed size per head if insect predators preferred certain kinds of heads or if high predation resulted in a compensatory increase in the size of remaining seeds (Charlet and Miller, 1993). These traits were proportion of seeds affected by "top damage" predispersal predation (likely caused by red or gray sunflower weevil or sunflower moth) and proportion of seeds affected by "bottom damage" predispersal predation (likely caused by banded sunflower moth) (see Cummings, Alexander, and Snow, 1999, for details on head characteristics). Separate regressions were done for each cross type since hybrid and wild heads differed greatly in flowering time and head diameter (Cummings, Alexander, and Snow, 1999). In analyses, we first explored correlations among parameters and then chose a "best subsets" regression model (SAS, 1989; proc stepwise, option maxr) using the criterion that the mean square error was minimized, subject to the constraint that all variables had significant partial F statistics.

Three postdispersal seed predation trials were performed (5 March, 23 April, and 19 May 1998). Each trial consisted of setting out 20 sand-filled trays (52 × 26 cm; 2 cm depth of sand) in an open field. Twenty hybrid and 20 wild seeds were mixed into the sand of each tray (seed came from bulk collections derived from 33 randomly selected hybrid heads and 185 randomly selected wild heads from Site 1). Trays were arranged at 5-m intervals, 5 m from a forest edge. After ~10 d in the field, trays were removed and surviving seeds were recovered by sieving. Surviving seeds were assigned to cross type by comparison of size, color, and stripe/dot pattern to known seeds; see RE-SULTS for description of cross type seed comparisons. Only seven of 1073 recovered seeds could not be reliably identified. Size of each surviving seed

was recorded for Trials 1 and 2. For the first trial, some trays were visited by small rodents (*Mus musculus* [house mouse] and *Peromyscus maniculatus* [deer mouse]) when stored in a field laboratory building and thus some seed predation probably did not occur in the field. For each trial we used a paired *t* test to determine if the numbers of uneaten hybrid and wild seed per tray were consistent with a 50:50 ratio, as expected under the null hypothesis of no differential predation.

We also explored whether or not larger seeds were differentially eaten within a cross type. Recording individual seed size for all 2400 seeds used in the three trials would have been prohibitive, so direct comparisons of sizes of eaten and uneaten seeds were not possible. Instead, for each cross type, we compared size measurements for uneaten seeds for Trials 1 and 2 with mean size from our large seed collection (750 hybrid seed; 880 wild seed; see above). In the absence of size-specific predation, we hypothesized that the mean size of uneaten wild seeds in each tray would be equally likely to be larger or smaller than our best estimate of mean wild seed size based on the large seed collection. To analyze these data, we used a paired *t* test to determine whether there were significant deviations from the mean values of uneaten wild seed per tray and the mean wild seed size based on our large seed collection. An analogous hypothesis and statistical test were used to determine whether there was size-specific predation for hybrid seed.

RESULTS

The average hybrid seed was approximately twice as large as the average wild seed, whether based on the smaller seed collection samples (mean ± 1 SE, hybrid: 18.00 ± 0.572 mm², $N = 100$; wild: 8.42 ± 0.204 mm², $N = 100$; $F_{1,198} = 385.78$, $P < 0.0001$) or the larger seed collection (hybrid: 14.56 ± 0.144 mm², $N = 750$; wild: 7.98 ± 0.067 mm², $N = 880$; $F_{1,161} = 298.25$, $P < 0.0001$). Hybrid seed were darker brown with a longitudinal white stripe while wild seeds were lighter brown with a pattern of brown spots. Seed size was strongly correlated with seed mass ($r = 0.96$, $N = 60$, $P < 0.0001$). Separate nested ANOVAs on mean seed size for both wild and hybrid heads revealed no effect of experimental site, but significant effects of plant (hybrid: $F_{10,15} = 5.12$, $P < 0.005$; wild: $F_{21,29} = 2.15$, $P < 0.05$) and head (hybrid: $F_{15,243} = 22.17$, $P < 0.0001$; wild: $F_{29,468} = 21.49$, $P < 0.0001$).

Multiple regression analyses were used to determine which

TABLE 2. Final multiple regression models for hybrid and wild seed. Regression models were used to determine what variables explain variation in mean seed size per head. Analyses were originally run with four predictor variables (head diameter, date of flowering of head, and "top" and "bottom" predispersal seed predation); variables that were not statistically significant (or marginally significant) were subsequently dropped from the model. See text for details.

a) Hybrid seed size (mm²)

Term	df	SS	MS	F	P
Regression	3	0.480	0.160	3.46	0.0207
Error	71	3.278	0.046		
Total	74	3.758			
$R^2 = 0.1276$					

Model	Parameter estimate	df	F	P
Intercept	2.569	1,71	1134.71	0.0001
Diameter	0.008	1,71	4.59	0.0355
Top damage	−0.355	1,71	5.01	0.0283
Bottom damage	−0.255	1,71	3.48	0.0661

b) Wild seed size (mm²)

Term	df	SS	MS	F	P
Regression	2	1.556	0.778	26.87	0.0001
Error	85	2.461	0.029		
Total	87	4.018			
$R^2 = 0.3873$					

Model	Parameter estimate	df	F	P
Intercept	2.796	1,85	279.44	0.0001
Date	−0.015	1,85	44.39	0.0001
Diameter	0.008	1,85	7.03	0.0095

traits were most strongly associated with variation in mean seed size per head. We used a data set with one head/plant. For hybrid heads, the final multiple regression model explained 12.76% of variation in mean seed size with three predictor variables (Table 2). Head diameter was positively related to mean seed size while proportions of top and bottom damaged seeds were negatively related to mean seed size. For wild heads, the final multiple regression model explained 38.73% of variation in mean seed size with two predictor var-

Fig. 2. Frequency distribution of sizes (mm²) of uneaten wild seed for Trials 1 and 2. Arrows indicate expected average seed size for wild seed prior to predation based on the large seed collection. Uneaten seeds were significantly smaller than the average wild seed size for both trials (Trial 1, $P = 0.05$; Trial 2, $P < 0.0002$; see text for details).

iables (Table 2). Seeds from larger and earlier heads tended to be larger. Virtually identical results were obtained when head area was used in the analyses instead of head diameter.

Over the three predation trials, an average of 62.3% of hybrid seeds (=12.5 seeds) were eaten per tray compared to 41.7% of the wild seeds (=8.3 seeds) (Trial 1, $F_{1,19} = 46.27$, $P < 0.0001$; Trial 2, $F_{1,19} = 25.97$, $P < 0.0001$; Trial 3, $F_{1,19} = 17.21$, $P < 0.0005$) (Fig. 1). Differential predation on hybrid seeds was strongest when overall predation levels in a tray were low. For example, the ratio of proportion of hybrid seed eaten/proportion of wild seed eaten was negatively correlated with total proportion of all seeds eaten (Trial 1: $r = −0.40$, $N = 19$, $P = 0.09$; Trial 2: $r = −0.46$, $N = 20$, $P < 0.05$; Trial 3: $r = −0.51$, $N = 18$, $P < 0.05$). The mean size of uneaten wild seeds per tray was smaller than the mean size of wild seeds from the large head collection, suggesting differential predation on larger seeds (Trial 1, $F_{1,18} = 4.26$, $P = 0.05$; Trial 2, $F_{1,19} = 21.40$, $P < 0.0002$; Fig. 2). Uneaten hybrid seeds were not significantly different from the mean size of hybrid seeds from the large head collection. Concurrent trapping in an adjacent old field revealed moderate population sizes of *Microtus ochrogaster* (prairie vole) and *Reithrodontomys megalotis* (western harvest mouse) and lower numbers of *Peromyscus leucopus* (white-footed mouse) (N. Slade, personal communication). The latter two rodents are likely seed predators of *H. annuus,* with *M. ochrogaster* occasionally consuming seeds (N. Slade, personal communication).
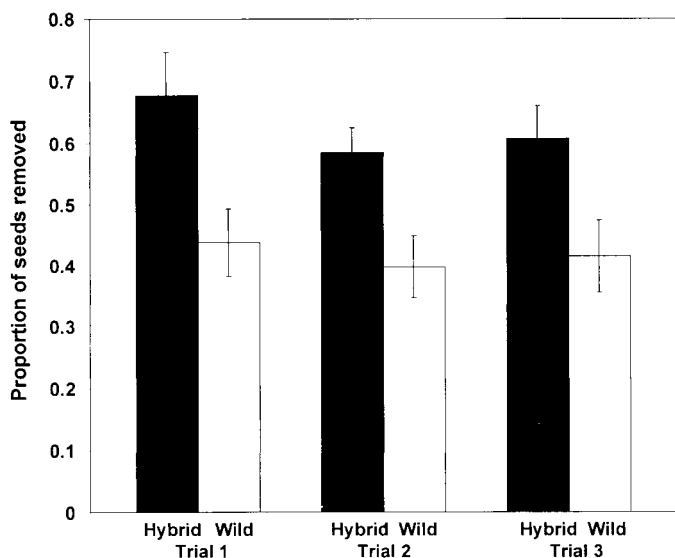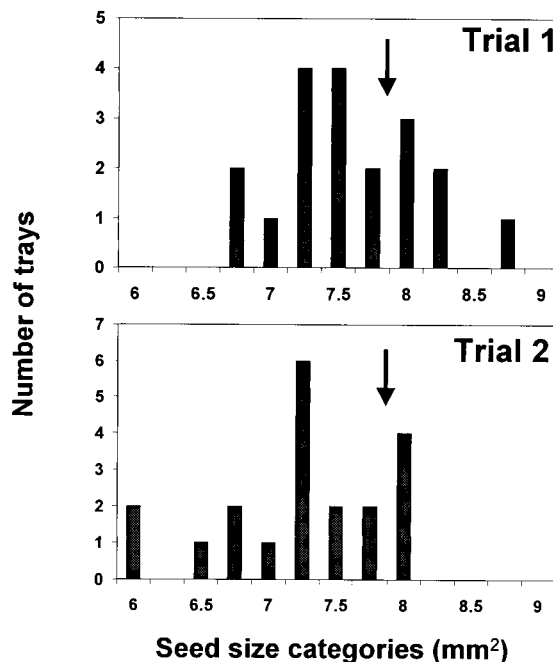

Fig. 1. Percentage removal (presumed predation) of hybrid and wild seed for three trials. Standard error of the mean is indicated. Differences are significant at the $P < 0.001$ level for all trials; see text for details.

DISCUSSION

Seeds produced by crop–wild hybrid plants were usually twice as large as wild seeds, whether based on linear mea-

surements or mass. Within each cross type, most of the variation in average seed size occurs at the level of the head (as opposed to individual plant or site differences). Relationships between seed size and date or diameter suggest the importance of resource allocation in seed size variation. For example, wild heads that were produced late in the season had smaller seeds, as might be expected if most resources had already been expended by this time. Similar temporal changes in seed size have been reported previously for both wild and cultivated sunflower (Seiler, 1983) and for other species (Cavers and Steel, 1984; Kane and Cavers, 1992). Both wild and hybrid heads with larger diameters produced larger seeds. This relationship also suggests the importance of resource allocation if plants with more resources produce larger heads. Since hybrid heads with low levels of predispersal damage had larger seeds, it appears that predispersal predators do not choose heads with larger seeds, nor is there evidence for compensatory responses to damage (Charlet and Miller, 1993).

Seeds from crop and wild sunflowers are eaten by diverse postdispersal predators including quail, cotton rats, and foxes (Michael and Beckwith, 1955; Robel and Slade, 1965; Robel et al., 1974; Sargeant, Allen, and Fleskes, 1986; Teo-Sherrell, 1996). In our trials, postdispersal predators preferred hybrid seed over wild seed with the preference strongest at relatively low predation levels. Seed size is not the only factor that differs between hybrid and wild seed; as noted, seeds of the two types also differ in coloration and patterning of the seed coat. These coat characteristics seem unlikely to affect predation in our trials; the rodents at our study site are nocturnal feeders (N. A. Slade, personal communication) and at least to our eyes, there was no difference in apparency of the seed against the substrate. Avian species such as quail, however, are visual predators, and thus it is possible that they have search images for particular traits. It is also true that crop sunflower seed can have $1.5\times$ the average oil content of wild seed (Seiler, 1983), suggesting that other traits may also differ between hybrid and wild seed. However, the finding of size-specific predation in wild seed (and the absence of such an effect for hybrid seed) suggests that a primary reason why hybrid seed are differentially eaten is their larger size, with the smallest wild seeds more likely to escape predation.

Results from our study are consistent with the general concept of an "optimal" seed size in wild sunflowers. Larger seeds were differentially selected by vertebrates (this study), while studies of many other species have shown that smaller seeds may be at a disadvantage during seed germination and establishment (e.g., Baskin and Baskin, 1998). To understand how seed differences and patterns of predation affect crop-to-wild gene flow and gene persistence, one needs to consider many ecological and genetic factors. Our experimental protocol, for example, used a 50 : 50 hybrid : wild seed mixture and 296 seeds/m². An equal frequency of hybrid and wild seeds may be common in wild populations soon after contact with crop populations. For instance, Whitton et al. 1997 report 42% hybrids at the crop margin after one generation of hybridization. The seed density we used, however, is likely to be lower than in many wild sunflower populations; C. L. Cummings (unpublished data) found that 1768 seeds/m² is typical for Kansas roadside populations. We do not know how differential foraging behavior on wild vs. hybrid seeds would be affected by other seed densities and frequencies.

We are aware that wild and hybrid sunflower seeds differ in other traits besides size (for example, dormancy character-

istics (Snow et al., 1998)) and that predispersal seed predation can be higher on seeds of F_1 hybrids as compared to seeds on wild plants (Cummings, Alexander, and Snow, 1999). In addition, F_1 hybrids typically produce fewer seeds per plant than wild plants (Snow et al., 1998). Although these ecological data suggest that crop gene flow may be impeded, it is well demonstrated by long-term studies involving molecular markers that crop genes can introgress and persist in wild sunflower populations (Whitton et al., 1997; Linder et al., 1998). After many decades, wild populations adjacent to crop populations consisted of advanced generation hybrids (Linder et al., 1998). We would expect that such heterogeneous wild–crop hybrid plants would have variable seed sizes and patterning. Thus we predict that the preference of seed predators for hybrid seeds would have its largest effects in slowing gene flow from crop to wild sunflower in early hybrid generations, when seed size differences are likely to be more distinct and have more subtle effects on genetic composition in later years.

LITERATURE CITED

ARRIOLA, P. E., AND N. C. ELLSTRAND. 1997. Fitness of interspecific hybrids in the genus *Sorghum*: persistence of crop genes in wild populations. *Ecological Applications* 7: 512–518.

BASKIN, C. C., AND J. M. BASKIN. 1998. Seeds. Academic Press, San Diego, California, USA.

CAVERS, P. B., AND M. G. STEEL. 1984. Patterns of change in seed weight over time on individual plants. *American Naturalist* 124: 324–335.

CHARLET, L. D., AND J. F. MILLER. 1993. Seed production after floret removal from sunflower heads. *Agronomy Journal* 85: 56–76.

CUMMINGS, C. L., H. M. ALEXANDER, AND A. A. SNOW. 1999. Increased pre-dispersal seed predation in sunflower crop–wild hybrids. *Oecologia* 121: 330–338.

DIARRA, A., R. J. SMITH, JR., AND R. E. TALBERT. 1985. Growth and morphological characteristics of red rice (*Oryza sativa*) biotypes. *Weed Science* 33: 310–314.

HULME, P. E. 1994. Post-dispersal seed predation in grassland: its magnitude and sources of variation. *Journal of Ecology* 82: 645–652.

KANE, M., AND P. B. CAVERS. 1992. Patterns of seed weight distribution and germination with time in a weedy biotype of proso millet (*Panicum miliaceum*). *Canadian Journal of Botany* 70: 562–567.

KELRICK, M. I., J. A. MACMAHON, R. R. PARMENTER, AND D. V. SISSON. 1986. Native seed preferences of shrub-steppe rodents, birds, and ants: the relationship of seed attributes and seed use. *Oecologia* 68: 327–337.

KLINGER, T., AND N. C. ELLSTRAND. 1994. Engineered genes in wild populations: fitness of weed–crop hybrids of *Raphanus sativus*. *Ecological Applications* 4: 117–120.

LANGEVIN, S. A., K. CLAY, AND J. GRACE. 1990. The incidence and effects of hybridization between cultivated rice and its related red rice (*Oryza sativa* L.). *Evolution* 44: 1000–1008.

LINDER, C. R., I. TAHA, G. J. SEILER, A. A. SNOW, AND L. H. RIESEBERG. 1998. Long-term introgression of crop genes into wild sunflower populations. *Theoretical and Applied Genetics* 96: 339–347.

MARTIN, A. C., AND W. D. BARKLEY. 1961. Seed identification manual. University of California Press, Berkeley, California, USA.

MICHAEL, V. C., AND S. L. BECKWITH. 1955. Quail preference for seed of farm crops. *Journal of Wildlife Management* 19: 281–296.

MITTELBACH, G. C., AND K. L. GROSS. 1984. Experimental studies of seed predation in old-fields. *Oecologia* 65: 7–13.

MOEGENBURG, S. M. 1996. *Sabel palmetto* seed size: causes of variation, choices of predators, and consequences of seedlings. *Oecologia* 106: 539–543.

PARKER, I. M., AND P. KAREIVA. 1996. Assessing the risks of invasion for genetically engineered plants: acceptable evidence and reasonable doubt. *Biological Conservation* 78: 193–203.

RAYBOULD, A. F., AND A. J. GRAY. 1994. Will hybrids of genetically modified crops invade natural communities? *Trends in Ecology and Evolution* 9: 85–89.

ROBEL, R. J., R. M. CASE, A. R. BISSET, AND T. M. CLEMENT, JR. 1974. Energetics of food plots in bobwhite management. *Journal of Wildlife Management* 38: 653–664.

———, AND N. A. SLADE. 1965. The availability of sunflower and ragweed seeds during fall and winter. *Journal of Wildlife Management* 29: 202–206.

SAS. 1989. SAS/STAT user's guide, version 6, 4th ed., vol. 1. SAS Institute, Cary, North Carolina, USA.

SARGEANT, A. B., S. H. ALLEN, AND J. P. FLESKES. 1986. Commercial sunflowers: food for red foxes in North Dakota. *Prairie Naturalist* 18: 91–94.

SEILER, G. J. 1983. Effect of genotype, flowering date, and environment on oil content and oil quality of wild sunflower seed. *Crop Science* 23: 1063–1068.

SNOW, A. A., AND P. MORÁN-PALMA. 1997. Commercialization of transgenic plants: potential ecological risks. *BioScience* 47: 86–89.

———, ———, L. H. RIESEBERG, A. WSZELAKI, AND G. J. SEILER. 1998. Fecundity, phenology, and seed dormancy of F_1 wild-crop hybrids in sunflowers (*Helianthus annuus,* Asteraceae). *American Journal of Botany* 85: 794–801.

TEO-SHERRELL, C. P. A. 1996. The fates of weed seeds. Ph.D. dissertation, Department of Agronomy, University of Nebraska, Lincoln, Nebraska, USA.

WHITTON, J., D. E. WOLF, D. M. ARIAS, A. A. SNOW, AND L. H. RIESEBERG. 1997. The persistence of cultivar alleles in wild populations of sunflowers five generations after hybridization. *Theoretical and Applied Genetics* 95: 33–40.

WILSON, H. D. 1980. Artificial hybridization among species of *Chenopodium* sect. *Chenopodium. Systematic Botany* 5: 253–263.