

FECUNDITY, PHENOLOGY, AND SEED DORMANCY OF F_1 WILD-CROP HYBRIDS IN SUNFLOWER (*HELIANTHUS ANNUUS*, ASTERACEAE)¹

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Crop-to-wild hybridization has the potential to introduce beneficial traits into wild populations. Gene flow from genetically engineered crops, in particular, can transfer genes coding for traits such as resistance to herbicides, insect herbivores, disease, and environmental stress into wild plants. Cultivated sunflower (*Helianthus annuus*) hybridizes spontaneously with wild/weedy populations (also *H. annuus*), but little is known about the relative fitness of F_1 hybrids. In order to assess the ease with which crop-to-wild introgression can proceed, we compared characteristics of F_1 wild-crop progeny with those of purely wild genotypes. Two nontransgenic, cultivated varieties were crossed with wild plants from three different regions—Texas, Kansas, and North Dakota. Seed burial experiments in the region of origin showed that wild-crop seeds had somewhat higher germination rates (less dormancy) than wild seeds from Kansas and North Dakota, while no differences were seen in seeds from Texas. Progeny from each type of cross were grown in outdoor pots in Ohio and in a weedy field in Kansas to quantify lifetime fecundity and flowering phenology. Flowering periods of hybrid and wild progeny overlapped considerably, especially in plants from North Dakota and Texas, suggesting that these hybrids are very likely to backcross with wild plants. In general, hybrid plants had fewer branches, flower heads, and seeds than wild plants, but in two crosses the fecundity of hybrids was not significantly different from that of purely wild plants. In Ohio, wild-crop hybrids from North Dakota appeared to be resistant to a rust that infected 53 % of the purely wild progeny, indicating a possible benefit of “traditional” crop genes. In summary, our results suggest that F_1 wild-crop hybrids had lower fitness than wild genotypes, especially when grown under favorable conditions, but the F_1 barrier to the introgression of crop genes is quite permeable.

Key words: Asteraceae; crop-weed hybrids; fecundity; fitness; flowering phenology; gene flow; introgression; seed dormancy; sunflower.

Wild-crop hybridization has the potential to influence the evolutionary ecology of related wild/weedy taxa, but little is known about the persistence or ecological effects of crop genes that enter wild populations via pollen movement (Small, 1984; Rissler and Mellon, 1996; Snow and Moran-Palma, 1997). Weedy relatives are especially likely to acquire genes from commercial cultivars when they co-occur, have overlapping flowering periods, share pollen vectors, and do not have strong reproductive barriers that prevent hybridization and introgression. Examples of crops that can hybridize spontaneously with wild/weedy populations include sunflower (Arias and Rieseberg, 1994), squash (Kirkpatrick and Wilson, 1988), radish (Klinger, Arriola, and Ellstrand, 1992), foxtail millet (Till-Bouttraud et al., 1992), sorghum (Arriola and Ellstrand, 1996), and canola (Crawley et al., 1993; Jørgensen and Andersen, 1995). In sunflower, foraging

bees carried crop-specific genetic markers as far as 1000 m from experimental stands of cultivated sunflower (Arias and Rieseberg, 1994). In addition, the isolation zone required to meet seed purity standards in commercial sunflower seed nurseries is 6.4 km (Smith, 1978). Therefore, pollen from cultivated sunflower is certain to spread to adjacent wild populations due to the movements of foraging bees.

When crop genes move into wild populations, reduced fitness of F_1 progeny may constitute a barrier that blocks or retards the transmission of crop genes to subsequent generations (e.g., Panetsos and Baker, 1967; Barton and Hewitt, 1985). This barrier is expected to weaken when surviving F_1 hybrids backcross with wild plants and may disappear entirely during successive generations of backcrossing. In some cases, an initial F_1 barrier to gene flow may be absent, as documented in radish (Klinger and Ellstrand, 1994) and sorghum \times Johnson grass (Arriola and Ellstrand, 1996, 1997). For some pairs of species, F_1 wild-crop hybrids may even exhibit heterosis, thereby boosting the frequency of crop genes in wild populations. For example, heterosis may be responsible for enhanced growth following wild-crop crosses in rice, radish, and oilseed rape (Langevin, Clay, and Grace, 1990; Klinger and Ellstrand, 1994; Thure Hauser, Copenhagen University, personal communication to A. Snow). In the first study to quantify the relative reproductive success of

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TABLE 1. Sources of wild seeds used in hand-pollinations to produce wild-crop hybrids. Seeds were collected from 25 to 30 widely spaced, open-pollinated plants in each population. Seed burial and excavation dates for germinability experiment are also shown.

Location	Collection number	No. of plants used in crosses	Duration of seed burial
Texas (Karnes County)	L. Rieseberg, no. 1022	23	11 Feb 1995–11 Apr 1995
Kansas (Douglas County)	L. Rieseberg, no. K-1	36	20 Dec 1994–28 Mar 1995
North Dakota (Wells County)	USDA Germplasm, PI 586808	38	2 Dec 1994–21 Apr 1995

wild-crop hybrids, Klinger and Ellstrand (1994) found that wild-crop F_1 radishes (wild *Raphanus sativus* \times cultivated *R. sativus*) exhibited 15% greater lifetime fecundity than purely wild genotypes.

Recently, new interest in wild-crop hybridization has been sparked by concerns about gene flow from genetically engineered crops into wild populations (e.g., Ellstrand and Hoffman, 1990; Raybould and Gray, 1993, 1994). In addition, hybridization has become easier to detect due to the availability of crop-specific DNA markers, such as RAPDs and transgenes (e.g., Frello et al., 1995; Mikkelsen, Andersen, and Jørgensen, 1996). The long-term goals of our research on sunflower are to determine the extent to which crop genes persist in wild/weedy populations and whether beneficial crop traits could cause wild/weedy varieties to become more abundant and invasive.

Here we report results from the first phase of our research on the fitness of hybrids between wild and cultivated sunflower, both *Helianthus annuus*. Wild *H. annuus* is a native, annual weed that is widespread throughout much of the United States (Heiser, 1954, 1976). Natural populations from different regions of the country exhibit a great deal of morphological variation, but distinct subspecies are difficult to categorize (Heiser 1954, 1976). Recent isozyme and molecular surveys suggest that gene flow among populations has been extensive (Rieseberg and Seiler, 1990; Arias and Rieseberg, 1995) and that populations near commercially grown sunflowers harbor crop-specific DNA markers due to wild-crop hybridization (Whitton et al., 1997; Linder et al., in press). These findings are not surprising, given that wild sunflower is a human-dispersed weed that is fully compatible with cultivated varieties.

Wild sunflower is a large, branching plant, typically ~1–3 m tall, which was first domesticated by Native Americans (e.g., Smith, 1989) and now occurs as a wild plant on disturbed sites such as roadsides and agricultural fields (Heiser, 1976; Smith, 1989). Here we refer to free-living populations as wild populations, although others might consider it more appropriate to classify them as weeds. Wild populations are self-incompatible and are pollinated by bees and other insects (Seiler, 1984). In Nebraska, wild plants have annual cycles of seed dormancy that prevent germination in the autumn (Teo-Sherrell, 1996). A portion of each year's cohort remains dormant in the spring as well, and seeds can remain viable for several years in soil seed banks (Teo-Sherrell, 1996).

In contrast to wild plants, modern agricultural breeding has resulted in commercial varieties of *H. annuus* that typically have one large flower head (capitulum), are self-compatible, and have sixfold larger seeds than wild plants, with a seed oil content of ~45% as compared to ~24% in wild seeds (Seiler, 1984). The single flower head trait is controlled by several genes coding for strong apical dominance

(Hockett and Knowles, 1970; Dedio and Putt, 1980). Lack of branching means that the flowering periods of individual plants are much shorter than those of wild plants, which have indeterminate growth. The crop has also been selected to exhibit traits such as rapid and synchronous seed germination, resistance to several diseases (including certain strains of rust), high yields when grown in cultivated conditions, and synchronous seed maturation to facilitate harvesting (Seiler, 1992). In this study we examined several traits that could influence the persistence of crop genes that move into wild populations: seed dormancy, flowering phenology, disease resistance, and lifetime fecundity of wild vs. wild-crop hybrids.

MATERIALS AND METHODS

Source of wild and wild-crop seeds—In order to include geographic variation in F_1 hybrids, we made crosses using wild plants from three regions: Texas, Kansas, and North Dakota (Tables 1, 2; voucher specimens from the Kansas and Texas populations have been deposited at the Indiana University Herbarium; specimens from North Dakota are in the herbarium collection maintained by G. Seiler, USDA). Also, to determine whether there are any major differences between wild-crop hybrids from different cultivated seed sources, wild plants from each region were crossed with two cultivated lines. The cultivated varieties we chose were Triumph Number 565 (Triumph Seed Co., Ralls, TX) and the standard USDA Number 894 used in agronomic sunflower research (seeds provided by G. Seiler, USDA). Both of these cultivated varieties are sold as F_1 "hybrids" from crosses between two inbred lines, as is typical in commercial oilseed sunflowers. Although Triumph 565 has presumably been subjected to more extensive artificial selection for economically important traits, performance tests conducted by university extension agents showed that yield differences between these two cultivars were either small or negligible at most sites in North and South Dakota (Berglund, 1994, 1995; Grady and Lammers, 1994).

Plants from these wild and cultivated seed sources were used in hand-pollinations that were carried out in an insect-free greenhouse during the summer of 1994. Because of space limitations, crosses involving wild plants from Texas, Kansas, and North Dakota were carried out at different times. To imitate the flow of crop pollen into wild populations, wild plants were used as pollen recipients and wild or crop plants were the pollen donors. None of the wild plants set seed autonomously, being self-incompatible, and unintentional cross-pollination was not a problem as evidenced by the fact that only hand-crossed flower heads (= capitula) produced seeds. On each maternal plant, an equal number of flower heads were pollinated with pollen from (1) other wild plants from the region, (2) Triumph 565, or (3) USDA 894 (Table 2). The numbers of wild plants used as pollen donors and/or recipients ranged from 24 to 38 plants from each region (Table 1).

Pollen was applied using a Q-tip at the stage when all of the stigmas on the capitulum were exerted. (Florets are protandrous and mature centripetally, with stigmas exerted until they are pollinated; older florets appear to set seed as effectively as younger ones.) Several weeks later, mature achenes (hereafter referred to as seeds) were collected and stored at room temperature. Seed set from all crosses appeared to be close to

TABLE 2. Characteristics of wild vs. wild-crop hybrids. Within regions, means followed by different superscripts are significantly different at $P < 0.05$ (Tukey tests).

Characteristic		Field site		Outdoor pots	
A) Height (cm)					
Region	Cross type	Mean	SE, <i>N</i>	Mean	SE, <i>N</i>
Texas	× Wild	86 a	3, 36	145 a	3, 38
	× Triumph 565	56 b	3, 38	129 b	4, 37
	× USDA 894	52 b	3, 33	110 c	3, 38
Kansas	× Wild	122 a	4, 34	272 a	6, 39
	× Triumph 565	74 b	2, 23	174 b	5, 40
	× USDA 894	77 b	4, 31	142 c	6, 36
North Dakota	× Wild	92 a	5, 42	131 b	3, 40
	× Triumph 565	103 a	4, 34	147 a	4, 40
	× USDA 894	101 a	3, 38	123 b	3, 40
B) Disk area of primary flower heads (mm ²)					
Texas	× Wild	221 b	18, 36	511 b	39, 38
	× Triumph 565	557 a	51, 38	1257 a	91, 37
	× USDA 894	569 a	41, 33	1207 a	69, 38
Kansas	× Wild	497 b	35, 34	1066 b	80, 39
	× Triumph 565	565 b	71, 23	1992 a	128, 40
	× USDA 894	816 a	87, 31	1825 a	127, 36
N. Dakota	× Wild	272 b	23, 42	629 b	48, 40
	× Triumph 565	551 a	48, 34	2307 a	128, 40
	× USDA 894	531 a	51, 38	2285 a	160, 40
C) Days to flowering					
Texas	× Wild	85 a	3, 36	69 a	0.6, 38
	× Triumph 565	64 b	2, 38	70 a	0.8, 37
	× USDA 894	55 c	1, 33	63 b	0.8, 38
Kansas	× Wild	112 a	2, 34	135 a	1.9, 39
	× Triumph 565	86 b	4, 23	93 b	2.6, 40
	× USDA 894	77 b	3, 31	79 c	2.2, 36
N. Dakota	× Wild	49 a	1, 42	64 b	0.7, 39
	× Triumph 565	56 a	2, 34	70 a	1.1, 40
	× USDA 894	48 a	2, 38	63 b	0.8, 40

100% and will not be considered further. Approximately equal numbers of seeds from the maternal plants used in each of the nine cross types were mixed for subsequent experiments, resulting in at least 2000 seeds per cross type.

Seed mass and germinability—To investigate differences in seed dormancy, germinability was assayed after burying seeds in bridal-veil mesh bags during the winter at agricultural fields in their region of origin (Austin, Texas; Lawrence, Kansas; or Fargo, North Dakota). For each cross type, 25 or 30 bags containing 40 or 50 seeds each were buried at a depth of ~20 cm for 2–4 mo depending on logistical constraints (exact dates given in Table 1). Prior to burial, the seeds (entire achenes) in each bag were weighed as a group to determine effects of cross type on achene mass. Buried bags of seeds from the three cross types were randomly positioned at 0.5-m intervals along three transects of equal length.

The mesh bags were excavated in the spring of 1995 and shipped overnight to Ohio State University. When the bags were washed and opened the next day, some of the seeds had already germinated, but it was easy to quantify percentage germination even if the seedling was gone because we could count the number of achenes that were hollow and open at one end. Ungerminated seeds were placed in trays of moist, sterilized sand at room temperature for ~2 wk, after which time they stopped germinating. The total number of seeds that had germinated by this time was used as an index of germinability. All ungerminated seeds were hard-coated and appeared to be viable, as described in Teo-Sherrell (1996). In addition, a standard tetrazolium test (Delouche et al., 1962) of a sample of 200 ungerminated seeds demonstrated that >95% were

viable. Therefore, we assumed that ungerminated seeds were probably viable but dormant.

Flowering and seed set in common gardens—Freshly germinated seeds from the burial experiments were transplanted to small pots and then used in two common garden field experiments, one in Kansas and one in Ohio. In Kansas, we planted seedlings from all nine cross types ($N = 50$ per cross type) at a recently disked field at the Kansas Ecological Reserves, University of Kansas, Lawrence, Kansas. Seedlings from each region were planted together in a grid design, with 5 m between plants and an alternating arrangement of cross types, in early May. It was not feasible to plant seedlings from all regions within the same grid, but all seedlings were planted in the same large field. These plants were not fertilized or irrigated and were allowed to compete with local weeds (mainly ragweed, *Ambrosia artemisiifolia*). A similar experiment was started in early May in Ohio, but in this experiment the plants were grown outdoors at the Ohio State University campus in an area adjacent to a honeybee research facility ($N = 40$ plants per cross type). These seedlings were transplanted to 5-L pots filled with potting soil. The plants received equal amounts of slow-release fertilizer (Osmocote) and were watered as necessary. Final sample sizes for the two experiments are shown in Table 2.

For plants in both experiments, we recorded survival, date of first flowering, the width of the first flower head, maximum height, and the total number of flower heads per plant at the end of the growing season. In Ohio we were able to carry out more detailed observations as well. Each week we inspected plants for disease symptoms and noted how many of the plants from each cross type were blooming. Seed number

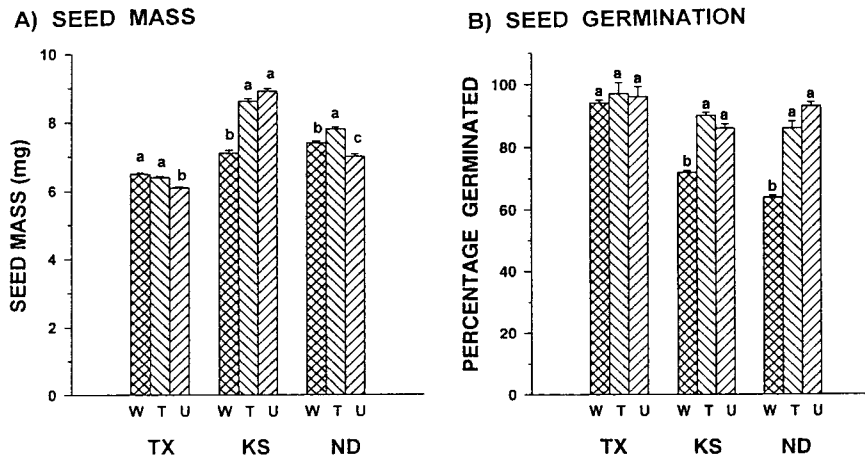


Fig. 1. Average mass of achenes, referred to as seeds (A), and percentage of buried seeds that germinated the following spring (B). Cross types were wild \times wild (W), wild \times Triumph (T), and wild \times USDA (U). Within each region (Texas, Kansas, or North Dakota), means with different superscripts are significantly different at $P < 0.05$ (Tukey tests; percentages were arcsine transformed). $N = 25-30$; error bars represent 1 SE using nontransformed data.

from a subsample of open-pollinated flower heads was determined in order to compare primary, secondary, and tertiary heads from each cross type (see sample sizes in Appendix; maturing seed heads were bagged to prevent seed loss prior to counting). A flower head was designated as primary if it was the first to open on a plant, whereas those on branches off the main stem were designated as secondary heads and those on branches coming off of these branches were considered tertiary heads. Average seed number per head type was multiplied by the numbers of primary, secondary, and tertiary heads per plant to estimate the total numbers of seeds per plant for the Ohio field experiment.

Statistical analyses—Because the timing of hand-pollinations, seed excavation, and planting varied slightly for plants from different regions, data for each region were considered to represent separate experiments and statistical interactions across regions will not be presented. The main result of interest was how the wild plants performed relative to the wild-crop hybrids from the same region. Continuous data were analyzed using the GLM procedure in SAS followed by Tukey tests (SAS, 1994), and percentages were arcsin transformed prior to analysis. Categorical data were analyzed using G tests.

RESULTS

Seed mass and germinability—Crop genes had significant effects on mass and seed germination following burial. We expected that crosses involving wild recipients and crop pollen donors would result in larger seeds than wild \times wild crosses, but this was seen in only three of the six comparisons shown in Fig. 1A. In two comparisons, the hybrids actually had smaller seeds than wild seeds from the same region, although differences among cross types were not great. Wild-crop hybrids from all regions had high seed germination after 2 wk indoors (90–95%), while only 64% of wild seeds from Kansas and 72% of wild seeds from North Dakota germinated (Fig. 1B). In the Texas group, germination rates of wild seeds were similar to those of the F_1 hybrids. The ungerminated seeds from Kansas and North Dakota had hard seed coats, were white inside, and were viable based on tetrazolium staining, so we assumed that these seeds were dormant (see Materials and Methods). We also noticed repeatedly that hybrid seeds germinated earlier than

wild seeds (A. Snow, personal observation), although differences in the timing of germination were not quantified precisely and warrant further investigation. In the experiments described below, all seedlings came from seeds that germinated within the first week after excavation, so differences in emergence times were negligible and did not contribute to differences in lifetime fecundity.

Flowering and seed set in common gardens—Cross type did not affect survival, which was lower in Kansas than in Ohio due to browsing by deer (G tests, see sample sizes in Table 2 and recall that 50 seedlings per cross type were planted in Kansas and 40 in Ohio). In both experiments, flowering times of wild and wild-crop hybrids overlapped extensively, but wild plants from Kansas were much taller than wild-crop hybrids from this region and flowered considerably later (Fig. 2, Table 2). Differences between the flowering phenologies of wild and hybrid plants from North Dakota and Texas were much smaller, especially in Ohio (Fig. 2; Table 2).

Wild plants produced far more branches and flower heads than hybrids when cultivated outdoors in pots, but these differences were less pronounced at the unmanaged field in Kansas (Fig. 3). In the pots, which were watered and supplemented with slow-release fertilizer, wild plants produced up to 100–200 heads per plant, whereas those in Kansas seldom had >10 heads per plant. Due to a lack of extensive branching by wild plants at the Kansas site, differences between wild and hybrid plants were diminished, and in two crosses the difference in flower head production between wild and hybrid plants was not statistically significant (Fig. 3). In both field experiments, hybrids from Nebraska exhibited the smallest differences in flower head production when compared with wild plants. Using number of flower heads as an index of fecundity, it is clear that the relative performance of F_1 hybrids was affected by growing conditions as well as the wild plants' region of origin.

It was difficult to estimate total seed number per plant because flower head size was so variable (see Appendix), and it was not possible to collect or even measure every

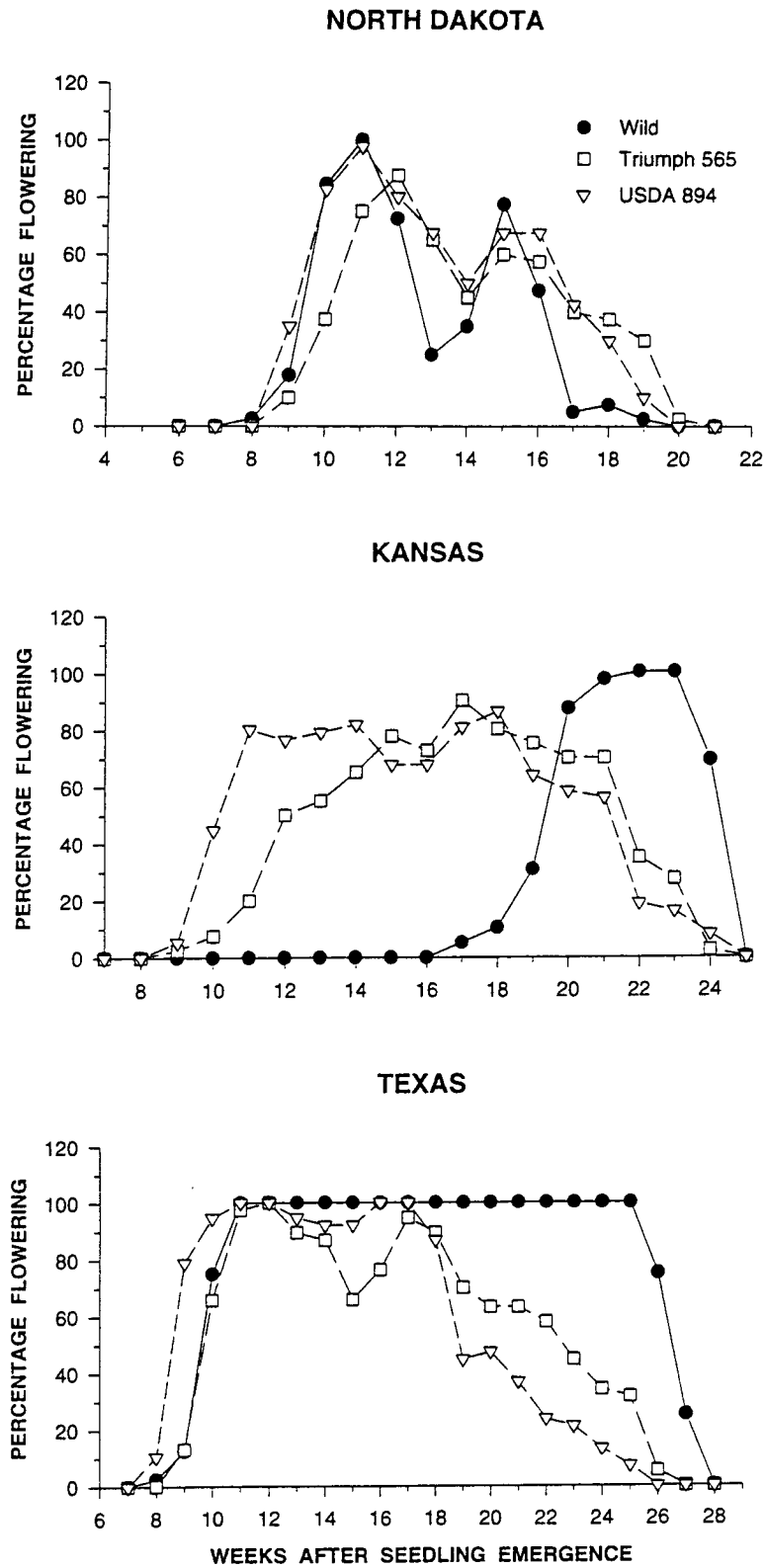
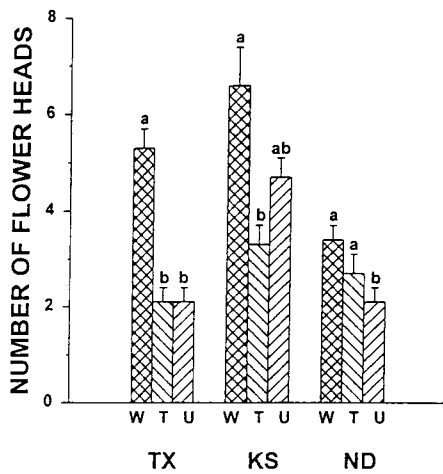


Fig. 2. Flowering phenology of each cross type when grown outdoors in pots in Ohio. The total number of plants in each group was 37-40, as indicated in Table 2.

A) FIELD SITE



B) OUTDOOR POTS

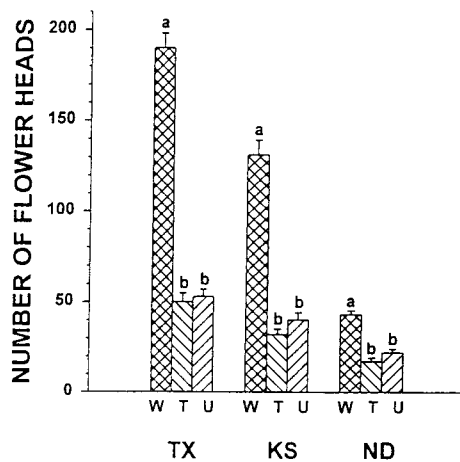


Fig. 3. Mean number of flower heads per plant at (A) the field site (Kansas) and (B) in outdoor pots (Ohio). Labels and statistical tests are as in Fig. 1; see Table 2 for sample sizes.

flower head. Data from Ohio plants showed that when the number of seeds per plant was estimated from subsamples of flower heads (Fig. 4), the F_1 disadvantage was similar to that based on flower head counts (Fig. 3). Thus, even though flower heads of the wild plants were usually smaller and had fewer seeds than those of hybrids (see Table 2 and the Appendix), wild plants produced far more flower heads during their lifetime, so their total seed production was higher.

In Ohio, where summer conditions were quite humid, some of the wild plants from North Dakota were infected by a fungal pathogen that was not observed in the Kansas experiment. By early August, 53% of these plants showed symptoms of rust (small, cinnamon-brown spots on brittle leaves), while none of the wild-crop hybrids showed symptoms ($N = 39-40$). The frequency of rust symptoms seen in wild and hybrid plants from Kansas and Texas ranged

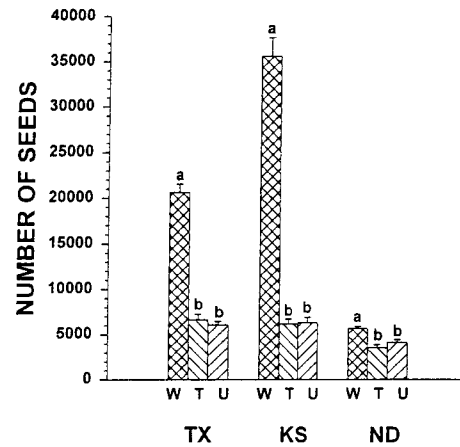


Fig. 4. Estimated number of seeds per plant for potted plants in Ohio, based on numbers of primary, secondary, and tertiary seed heads per plant and the average numbers of seeds per head type as shown in the Appendix. Superscripts and sample sizes are as in Table 2.

from 0 to 3%, so presumably these plants were resistant to the rust. Among the wild plants from North Dakota, those that were free of rust symptoms produced 24% more flower heads than infected plants (means were 46.7 vs. 37.9, $P < 0.02$, t test, $N = 23$ and 17, respectively).

DISCUSSION

In this study we observed regional differences in the relative performance of wild plants vs. F_1 hybrids, while differences in F_1 progeny from the two cultivars were negligible. The regional differences we report should be interpreted cautiously, however, because we studied only one population from each region and in most cases common garden experiments were not conducted in the native region of the parental wild plants (with Kansas being an exception). Nonetheless, our results suggest that hybrids involving wild plants from different parts of the species' range vary in their fecundity and phenology relative to purely wild plants. Part of this variation could be due to different histories of past hybridization. In this regard, it is interesting to note that a study of wild populations near commercial-scale sunflower farms in North Dakota and Canada revealed that all of the plants sampled ($N = 115$) had at least one crop-specific genetic marker (Linder et al., in press). In addition, the Texas population we used is known to possess genes derived from another sunflower species, *Helianthis debilis* ssp. *cucumerifolius* (Rieseberg, Beckstrom-Sternberg, and Doan, 1990).

We found that wild-crop hybrids are very likely to germinate in their first year given suitable environmental conditions. Possible disadvantages of the hybrids include a lack of innate seed dormancy in the F_1 hybrids, whereas 28 and 36% of the wild seeds from North Dakota and Kansas, respectively, appeared to be dormant (seed dormancy was not detected in wild plants from Texas). Similar results were obtained by Teo-Sherrell (1996), who found that ~30-40% of wild seeds from Nebraska are dormant in their first year. Furthermore, he showed that wild seeds have annual dormancy cycles, with very low germinability except in the spring, when ~60-70% of the viable seeds are germinable. After 3 yr of burial at

depths of 10–20 cm, the fraction of original seeds that remained viable was still ~20% in his study. Presumably, these dormancy characteristics allow seed banks to persist for many years so that new populations can become established following local disturbances to the soil.

Reduced dormancy of crop–wild hybrids vs. wild plants has also been reported in two types of canola hybrids: cultivated *Brassica rapa* × wild *B. rapa* (Adler et al., 1993) and cultivated *Brassica napus* × wild *B. rapa*. In the former cross, germination characteristics of F_1 hybrids resembled those of the maternal parent (Adler et al., 1993). This condition would favor the persistence of crop genes in soil seed pools when wild plants are the pollen recipients because innate seed dormancy was high in most wild populations. In contrast, crosses involving *B. napus* as pollen donors and weedy *B. rapa* (= *B. campestris*) as maternal plants resulted in F_1 progeny with very low intrinsic dormancy (Landbo and Jørgensen, 1997; R. Linder, University of Texas, personal communication to A. Snow). The latter situation, which is similar to our results with sunflowers, suggests that local weed control efforts could eradicate F_1 hybrids when these seeds are near the soil surface and are very likely to germinate. This practice could retard the rate at which crop genes accumulate and persist in soil seed pools, although F_1 hybrid seeds at greater depths might not germinate due to a lack of germination cues.

Another disadvantage of hybrids was seen in the flowering times of F_1 hybrids from Kansas, which began flowering 4–8 wk earlier than wild genotypes. This limits opportunities for backcrossing with wild neighbors, although we expect more overlap to occur under natural conditions, where the timing of seedling establishment and individual growth rates would probably be more variable than in our common garden experiments. However, we also observed that F_1 seeds germinated earlier than wild plants, in which case favorable growing conditions might allow them to be even *less* synchronized with wild plants. Nonoverlapping flowering times would force F_1 plants to cross primarily with each other, thereby delaying the immediate introgression of crop genes into wild populations. In contrast, flowering phenologies of plants from North Dakota and Texas showed fewer differences between wild and hybrid genotypes.

The magnitude of fecundity differences between wild vs. wild–crop hybrids was strongly affected by local growing conditions. Without competition, wild plants produced 2–3 times more flower heads than F_1 hybrids when grown in pots in Ohio. In contrast, differences in flower head production were smaller when plants were grown at a weedy field site in Kansas, especially for plants from North Dakota and Texas. Taken together, these disadvantages of wild–crop hybrids suggest that the F_1 generation may act as a weak and temporary barrier to the spread of crop genes after episodes of hybridization. Crop-to-wild introgression will occur most quickly in situations when F_1 fitness is similar to that of wild plants, but even when F_1 plants are at a strong disadvantage, crop-specific alleles will be able to persist when they recombine into a wild-type genetic background. During subsequent generations of backcrossing with wild plants, natural selection should gradually purge highly deleterious crop traits from wild

populations, while selectively neutral alleles would persist, and favorable alleles would spread.

An interesting advantage of hybrid plants was seen in the apparent inheritance of disease resistance that occurred in plants from North Dakota. Wild populations of *H. annuus* are known to vary in their resistance to strains of the rust *Puccinia helianthi* Schw. (Seiler, 1992), and resistance genes from wild plants have been bred into cultivated sunflower (e.g., Quresh, Jan, and Gulya, 1990). In our experiment, it appears that resistance genes may have been lacking in about half of the wild plants from North Dakota, although further studies are needed to confirm this. If this was the case, hybridization with the crop led to protection from disease. Wild plants that were free of rust symptoms produced 24% more flower heads than infected plants, indicating that the rust had a significant effect on lifetime fecundity. This is just one example of the types of advantageous traits that can also be transferred from transgenic plants to wild relatives, thereby increasing the seed production of the wild plants. If wild plants inherit several such fitness-related genes from cultivated relatives, whether transgenic or not, it is possible that these beneficial traits could contribute to weediness of the wild genotypes. Indeed, some of the striking regional variation in the size and morphology of wild sunflowers may be due to varying degrees of wild–crop hybridization that has occurred over the past few decades. In conclusion, the present study and our research involving genetic markers (Arias and Rieseberg, 1994; Whitton et al., 1997; Linder et al., in press) provide convincing evidence that crop genes continually move into wild sunflower populations and persist in these populations for many generations. The next question of interest is whether beneficial traits such as resistance to insect herbivores can affect competitive ability, seed production, and population growth rates under natural conditions. We plan to investigate the ecological effects of beneficial transgenes in the next phase of our research.

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APPENDIX

For plants grown in pots in Ohio, estimates of the total numbers of seeds per plant (Fig. 4) were obtained by counting the numbers of seeds in primary, secondary, and tertiary flower heads and multiplying these averages by the numbers of each type of head on each plant (see Table A-1). We were not able to obtain comparable data for plants grown in the field in Kansas. Also, because the disk areas of primary flower heads in the field in Kansas were about half the size of those from the outdoor pots in Ohio (See Table 1), we could not use the seed counts from Ohio to estimate the total number of seeds per plant at the field site in Kansas.

TABLE A-1. Numbers of seeds in primary, secondary, and tertiary capitula of plants grown in outdoor pots in Ohio. Means within columns and regions were compared using Tukey tests (different superscript signifies significant difference at $P < 0.05$); SE and N shown in parentheses.

Region	Cross type	Primary	Secondary	Tertiary
Texas	× Wild	97 b (10, 20)	87 b (9, 19)	111 a (9, 23)
	× Triumph 565	303 a (18, 20)	157 a (14, 20)	116 a (11, 23)
	× USDA 894	272 a (30, 20)	169 a (7, 19)	96 a (9, 19)
Kansas	× Wild	351 b (24, 18)	317 a (20, 19)	260 a (19, 18)
	× Triumph 565	541 a (25, 21)	193 b (20, 19)	175 b (21, 23)
	× USDA 894	469 a (46, 20)	247 a,b (32, 10)	120 b (17, 18)
N. Dakota	× Wild	308 b (16, 19)	177 b (12, 20)	78 b (12, 19)
	× Triumph 565	557 a (52, 20)	232 a (18, 17)	107 a (20, 18)
	× USDA 894	718 a (51, 20)	231 a (26, 16)	89 a (22, 11)