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Can achene selection in sunflower crop–wild hybrids by pre-dispersal seed predators hasten the return to phenotypically wild sunflowers?

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Abstract Bird attack is a serious limitation to sunflower yield in several regions of the world, but it could also cause selection. The wild *Helianthus annuus,* naturalized in several regions of the world, hybridizes with the crop and produces crop–wild offspring. It is unknown how the selective force of seed predation by birds could drive evolution after a hybridization event. After two generations of natural selection exerted by birds (mostly by Eared Dove and Monk Parakeets), achene and plant traits of the crop–wild hybrid progeny were compared with the same hybrid progeny without any selection by birds. After two generations of bird selection the achene width, thickness and weight decreased by an average of 18.5, 26.7 and 49.2 %, respectively. Also in response to bird selection there was a correlated increase in the plant height, stem diameter, number of heads and a reduction in head diameter and the number of achenes per head. The phenotype of crop–wild plants selected by birds resembles wild plants, whereas the plants without any selection were intermediate between the parents. These results indicate that selection exerted by birds could result in the rapid evolution of crop–wild sunflower populations.

Introduction

Many crop species (like oilseed rape, radish, rye, cotton, sugarbeet, wheat, sorghum) give rise to self-perpetuating populations that have escaped from cultivation and grow in an unmanaged environment (Warwick and Stewart 2005; Bagavathiannan and Van Acker 2008; Ellstrand et al. 2013). However, little is known about the selective pressures driving the major changes in those populations.

Natural selection preserves favourable and rejects unfavourable variation. Individuals with more favourable traits will have a higher survival probability and a higher probability to pass on their genes to descendants (Darwin 1859; Bonner 1988).

If there is any genetic variation in the traits affecting the rate of seed predation from one individual plant to another, then there is potential for the evolution of seed defenses (Crawley 2000). Granivory is common and often intense and seed consumers are selective; for example, predation pressure on large seeds, especially those with thin seed coats, is generally severe and much higher than on small or tough seeds (Louda 1989). Furthermore, granivory

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erradicates individuals, whereas other forms of herbivory result in partial removal of tissue from individual plants. Granivory is expected to impose a strong selection on the plants (Hulme and Benkman 2002). Seed predators impose selection on a particular plant trait when differences in the magnitude of seed predation among individual plants are correlated with differences in this trait (Kolb et al. 2007).

Seed-predators are initially attracted by general features that can be easily detected by vision or olfaction (Hulme and Benkman 2002). A study comparing post-dispersal seed predation between crop and wild hybrid and wild sunflowers concluded that a primary reason why hybrid seeds were consumed differentially was their larger size, since small wild seeds are more likely to escape from predation (Alexander et al. 2001). A further example is provided by Mediterranean birds, which are known to preferentially feed on darker and less chromatically colored fruit; traits highly correlated with high lipid content (Schaefer et al. 2014). Similarly, tephrid flies select for larger capitula in Asteraceae species, possibly because they provide greater food rewards for a given amount of search effort (Fenner et al. 2002).

The linkage between genes that are experiencing selection can play a role in introgression. For example, in early-generation hybrids, a large proportion of the chromosomes could be transferred intact from wild to crop (or vice versa) and the persistence of specific traits (alleles) would depend on whether this chromosomal segment imparts a significant fitness cost to the hybrids (Whitton et al. 1997; Linder et al. 1998). For example, plant height, stem diameter, head diameter and achene number have previously been found to be correlated and subjected to natural selection in crop–wild sunflower crosses (Baack et al. 2008; Gutierrez et al. 2011). Also, traits such as achene mass, achene number, plant height and flowering date were found to be located in the same linkage groups (Baack et al. 2008). Alleles linked to highly advantageous alleles can spread quickly through the population (Ellstrand 2003). Moreover, sunflower domestication research has shown that selection (particularly strong selection for increased achene size) acted on a large number of loci resulting in a rapid phenotypic response (e.g. increase in apical dominance, an increase in seed size, and the loss of natural seed dispersal, seed dormancy, and self-incompatibility) (Burke et al. 2002; Wills and Burke 2007). This suggests that the transition of populations from crop-like to wild-like, aided by birds, could be fast and in a short period of time the morphological traces of the crop could be minimal.

Helianthus annuus is native to North America but nowadays it is widely distributed throughout several continents with reports from North and South America, Europe, Africa and Australia (Heiser 1954; Dry and Burdon, 1986; Poverene et al. 2002; Muller et al. 2009; Ribeiro et al. 2010). Hybridization between wild and domesticated sunflower is possible (Arias and Rieseberg 1994; Ureta et al. 2008) and crop genes have contributed to increase weediness (Muller et al. 2011; Casquero et al. 2013). Granivorous birds are one of the major impediments to sunflower production; they feed on sunflower as the achenes are easily obtained and the seeds have a high nutritional value. Avian seed predators include tiny sparrows (*Passeridae*) to large species such as crows (*Corvidae*) and parrots (*Psittacidae*) (Linz and Hanzel 1997; Cummings et al. 1999). In Argentina, the Eared Dove (*Zenaida auriculata* Des Murs) is the most prevalent granivorous bird and it can cause serious damage to sunflower. Also Monk Parakeets (*Myiopsitta monachus* Boddaert) are considered a serious pest to sunflower (Mott 1973; Bucher and Ranvaud 2006). Both species nest in shrubs and trees and they may fly several kilometers to obtain food (Humphrey and Peterson 1978; Bucher and Ranvaud 2006). These bird species were present during this study and were presumably the main agents of selection on the achenes. We hypothesised that at some distance from the plants, the diameter of the sunflower head will be more important for visual food plant selection, while at close range individual fruit size will influence food selection. In addition, Eared Doves and Monk Parakeets perch on the sunflower heads and reach over the edge to remove the achenes (Mott 1973). It might be easier to perch on larger than on smaller heads.

Based on 10 years of observations, we tentatively conclude that the offspring of crop–wild (sunflower) hybrids tends to progressively resemble wild plants. We wonder why crop traits are lost and what the main forces are that cause a change in phenotype. Here, we focus on a crop–wild sunflower hybrid subjected to two generations of pre-dispersal predation by birds as compared to the same advanced generation hybrid without any selection, with the aim of evaluating changes in the distribution of achene traits by bird selection and their correlation with other plant traits.

We hypothesised that selection (predation) by birds of some cultivated traits (such as large inflorescences and achenes) of the crop–wild populations would eliminate crop-like individuals and lead to individuals with phenotypes that resemble wild populations. Our outcomes will allow an understanding of the role of selection of achene features by birds and their impact on morphological traits in crop–wild plants.

Materials and methods

Plant material

Experimental plants were represented by a wild population (*H. annuus* ssp. *annuus*) from Colonia Barón (BAR; S 36°10′, W 63°53′), a domesticated sunflower (*H. annuus* var. *macrocarpus*; DK3880CL) and a crop–wild hybrid between these two cross types.

During the 2008/2009 growing season, the wild population achenes were placed on wet paper at 5 °C for one week (ISTA 2004) and then were planted in trays on sphagnum peat-based substrate. Seedlings were grown in the greenhouse at 20–25 °C for one month, then transplanted at the 4-6 leaf stage in a common garden at the UNS Agronomy Department (S 38°41′38″, W 62°14′53″) in Bahia Blanca, Argentina. The sunflower cultivar DK3880CL was sown directly in the same experimental field.

The F1 (crop × wild) achenes were produced by hand-pollination between the wild biotype (as male) and the sunflower cultivar DK3880CL (as female) according to Jan and Seiler (2007). Ten heads of sunflower were emasculated in the morning and pollinated with pollen from more than 20 wild plants in the late afternoon.

Experimental design

During the first generation of selection, more than 30 F1 plants were established at 0.30 m apart in a row. At the R4 stage (Schneiter and Miller 1981), heads were bagged and at flowering they were hand-pollinated between siblings. At physiological maturity, half of the plants were uncovered to allow predation by birds and plastic trays were placed on the soil around the plants (covering an area of 0.23 m^2 per plant), to collect any achenes that fell after shattering. The trays were covered with a thin layer of soil to simulate the soil surface and wire nets were placed over them to avoid predation in the trays. After the plants were completely mature, which corresponded with the end of bird activity, the achenes left on the maternal plant and those dropped into the trays were collected. In addition, the achenes on the bagged heads were collected.

A second generation of bird selection was undertaken on a pool of 30 plants from each group (with and without selection). Within the group of plants without selection, the pool of achenes was made from the sum of a relative achene contribution of each F1 plant (achene per plant: total achene production). Within the group of plants with selection, the pool of achenes was made from the sum of all achenes left on the maternal plant and those collected from the trays. Natural selection by birds was managed as in the first stage of the selection process.

During the third year, F3 plants (with and without selection, hereafter F3 predation, F3 no predation) obtained following the same procedure were characterized morphologically in the experimental field in a completely randomized design. A group of 30 plants from the parental wild population (hereafter wild) and 20 plants from the parental domesticated cultivar (hereafter crop) were included as controls.

Width, length, thickness and weight of 30 achenes of one representative disc from each plant were measured. In addition, each plant was characterized morphologically with the following descriptors: quantitative traits of individual plants included: plant height (cm), stem diameter at mid-height (cm), number of heads, leaf width (cm), leaf length (cm), petiole length (cm), number of leaves, phyllary width (cm), phyllary length (cm), phyllary number, head diameter (cm) and the number of achenes per head. Qualitative traits of individual plants included: branching type (0: not branched, 1: basal branched, 2: apical branched and 3: fully branched), the presence of a main head (0: without main head, 1: with main head), stem anthocyanin (0: without anthocyanin, 1: with anthocyanin), and disc flower color (1: yellow disc flower, 2: red disc flower). This combination of characters was selected because of their taxonomical value for detecting differences between crop and wild germplasm (Presotto et al. 2011).

During the two cycles of selection, large populations of Eared Doves (*Zenaida auriculata*) and Monk Parakeets (*Myiopsitta monachus*) came from a

neighboring windbreak of *Eucalyptus globulus*, where they nest annually. Doves and parakeets were seen in this area throughout the life cycle of the wild sunflower, from September to April. There birds were presumably the main seed predators as remnants of pericarp and bird faeces were found below the plants. No filled achenes remained on the plant where the birds had access to the flower heads; all the collected achenes were found in the trays below the plants.

Statistical analysis

In order to determine the effects of seed predation on plant traits, the F3 plant traits with and without selection were compared and they were also compared with their parents. Achene traits were treated in a completely randomized design where the seeds were replicates nested in each head, and the biotypes (F3 no predation, F3 predation) were considered as the source of variation. Quantitative and qualitative plant traits were analyzed in a completely randomized design where the plants were replicates and the biotypes (F3 no predation, F3 predation, wild and crop) were considered as the source of variation. The quantitative data were ln-transformed to improve normality and homoscedasticity. Quantitative transformed data were analyzed using the General Linear Model with the biotype and heads nested within biotypes as categorical variables (achene traits), and the biotype as a categorical variable (rest of the quantitative traits). Qualitative data that did not follow the normal distribution curve were analyzed by the non-parametric Kruskal–Wallis test. Plant quantitative data were analyzed by a principal components analysis (PCA) to explore the similarity between the biotypes. The variables were standardized (transformed into standard-deviation units) prior to performing the PCA. In addition, a hybrid index was obtained for the qualitative data. The index of each plant was the sum of the scores for the four traits. For branching type, the score was on a scale of 0–3 (0 = crop-like to 3 = wild-like). For presence of main (larger) head, the score was on a scale of 0–1 (0 = wild-like to 1 = crop-like). For stem anthocyanin and disc flower color, the scores were on a scale of 0–1 or 2–3, respectively (0 or 2 = crop-like to 1 or 3 = wild-like). Pearson correlation coefficients (r) were generated for all trait combinations for the cross types (F3 no predation, F3 predation, and parental wild population and crop)

grouped together in order to examine the between-trait relationships. Two units of evolution were utilized to quantify the response to selection. Both units estimate the rate of change based on the number of years elapsed since the ancestral population gave rise to the descendant population. The first unit is darwins (d), which is expressed in powers of *e* per million years (Haldane 1949). The second unit is the haldane (h) (Gingerich 1993); (Hendry and Kinnison 1999), which is expressed as standard deviation units per generation:

$$d = (\ln(X_2) - \ln(X_1))/Dt, \qquad (1)$$

$$h = (X_2/S_p) - (X_1/S_p)/g, \qquad (2)$$

in which X_1 and X_2 are the mean trait values of the F3 no predation and F3 predation populations, respectively, Dt is the time interval between the two populations, g is the number of generations, S_p is the pooled standard deviation of the populations' trait values. In this study, as *H. annuus* is an annual species, Dt is equal to g and equal to 2 (years of selection). All analyses were performed using Infostat (Di Rienzo et al. 2014).

Results

The dimensions of the achenes shifted after two generations of bird selection. Mean width (F = 10.6; p < 0.001), thickness (F = 11.2; p < 0.001) and weight (F = 16.4; p < 0.001) were smaller after selection, but the achene length was not significantly different (F = 2.4; p = 0.13). The achene width shifted from 3.2 mm to 2.7 mm (18.5 %), achene thickness shifted from 1.9 to 1.5 mm (26.7 %) and achene weight shifted from 27.9 mg to 18.7 mg (49.2 %). The frequency distributions moved to lower values (Fig. 1) even though the range of each parameter was similar.

Significant differences between biotypes were detected in 14 out of 16 plant traits. The F3 exposed to predation were taller, with larger stem diameter, larger number of heads, smaller head diameter and fewer achenes per head, but more heads per plant than the F3 plants not exposed to predation. The F3 exposed to predation had five out of 16 morphological traits similar to the wild plants, whereas the F3 plants not exposed to predation had three similar metric traits.

Fig. 1 Histograms of the achene traits (width, length, thickness and weight) in plants exposed to bird selection (F3 predation) and plants not exposed to bird selection (F3 no predation)
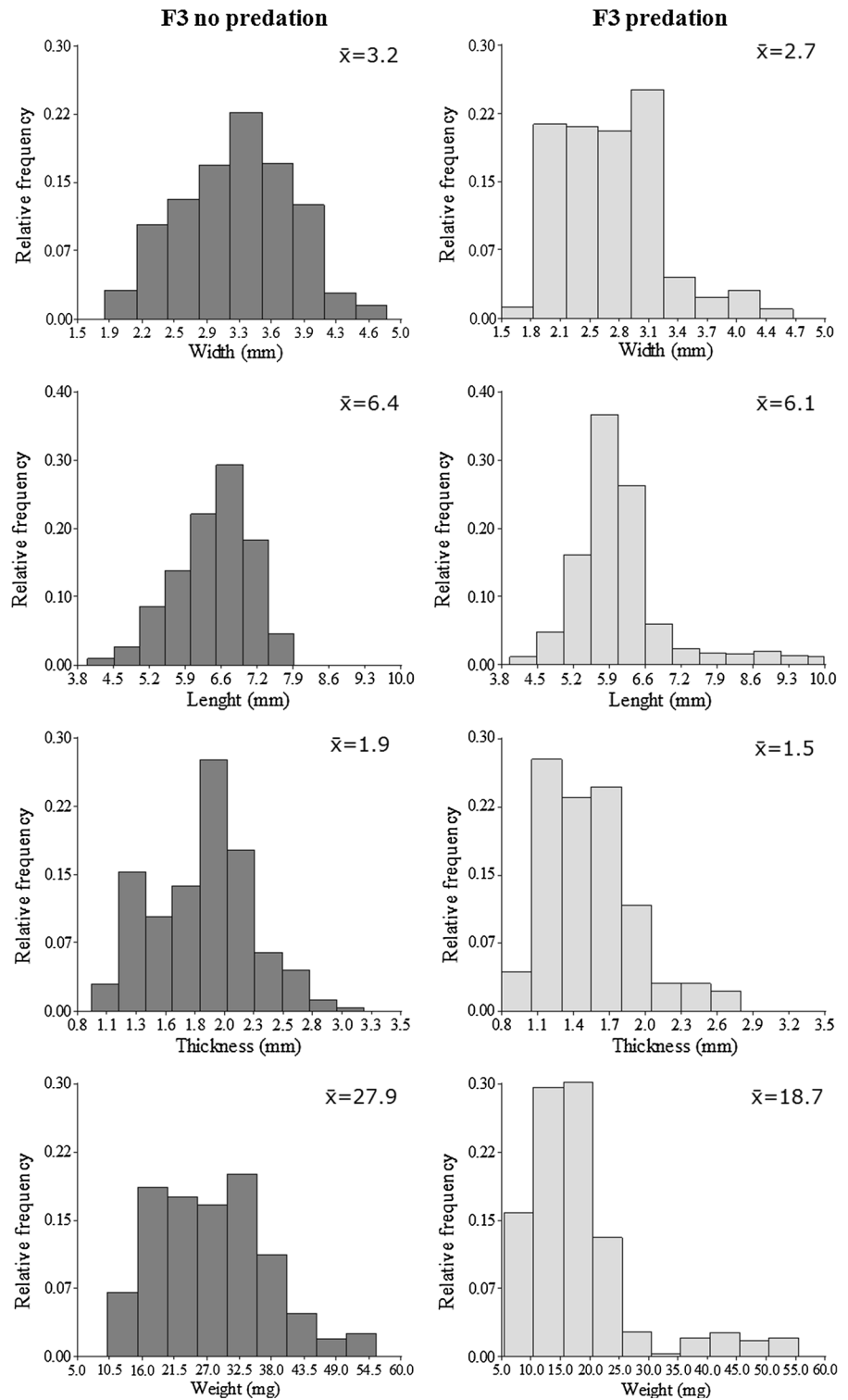
Table 1 Morphological traits (mean ± *SE*, quantitative traits) of plants from seeds of plants exposed to bird selection (F3 predation), plants from seeds of plants not exposed to bird selection (F3 no predation), wild *H. annuus* population (Wild) and sunflower (Crop)

Trait	Wild	F3 predation	F3 no predation	Crop	F or H, *p* value
Plant height (cm)	202.7 ± *6.3* b	217.4 ± *7.8* b	144.1 ± *8.8* a	140.9 ± *1.4* a	30.9, <0.001
Stem diameter (cm)	1.9 ± *0.1* b	2.0 ± *0.1* b	1.6 ± *0.1* a	2.1 ± *0.1* b	20.4, <0.001
Head (n°)	85.6 ± *4.3* d	25.9 ± *3.4* c	8.7 ± *1.7* b	1.0 ± *0.0* a	311.7, <0.001
Leaf width (cm)	18.8 ± *0.5* b	16.2 ± *0.6* a	16.7 ± *0.7* ab	24.6 ± *0.6* c	44.9, <0.001
Leaf length (cm)	21.7 ± *0.7* b	18.6 ± *0.7* a	20.1 ± *1.0* ab	24.5 ± *0.7* c	11.4, <0.001
Petiole length (cm)	15.2 ± *0.7*	17.0 ± *0.5*	15.3 ± *0.7*	14.6 ± *0.6*	3.9, >0.05
Leaf (n°)	22.3 ± *1.0*	26.1 ± *1.3*	22.8 ± *1.3*	24.0 ± *0.3*	2.5, >0.05
Phyllary width (cm)	0.8 ± *0.0* a	1.0 ± *0.1* ab	1.6 ± *0.1* b	3.7 ± *0.1* c	220.5, <0.001
Phyllary length (cm)	2.0 ± *0.1* a	3.3 ± *0.1* b	3.0 ± *0.2* b	5.3 ± *0.2* c	190.9, <0.001
Phyllary (n°)	32.9 ± *1.0* a	37.2 ± *1.1* ab	38.6 ± *1.2* b	60.3 ± *1.3* c	104.6, <0.001
Head diameter (cm)	4.1 ± *0.1* a	5.7 ± *0.3* b	7.7 ± *0.3* c	17.7 ± *0.3* d	363.0, <0.001
Achenes per head (n°)	189.0 ± *12.0* a	393.1 ± *25.0* b	517.2 ± *52.6* c	1082.3 ± *60.6* d	92.5, <0.001
Branching type (0–3)	3.0 c	2.0 b	1.2 b	0.0 a	85.1, <0.001
Main head (0–1)	0.1 a	0.8 b	0.9 b	1.0 b	54.7, <0.001
Stem anthocyanin (0–1)	0.8 b	0.6 b	0.7 b	0.0 a	44.5, <0.001
Disc flower color (1–2)	2.0 c	1.5 b	1.7 b	1.0 a	56.4, <0.001

The *SE* of the quantitative traits are written in italics

Different letters within each variable indicate significant differences according to Tukey–Kramer or Kruskal–Wallis (p < 0.05). Statistics (F or H) with their p value are shown

Plant height, stem diameter, phyllary width and phyllary number of the wild plants were similar to the F3 exposed to predation, whereas leaf width and leaf length of the wild plants were similar to the F3 plants not exposed to predation (Table 1). Stem anthocyanin did not differ between wild, F3 exposed and not exposed to predation.

This combination of traits in the descendants after bird selection gave rise to plants that resemble wild plants (Fig. 2). Plants, which had been exposed to bird selection, were grouped next to wild plants, with no overlapping with sunflower crop plants. On the other hand plants, which had not been exposed to bird selection, were grouped within the parental plants and overlapped with both groups. PC1 was mainly correlated with phyllary traits, head diameter and achenes per head, and PC2 was mainly correlated with stem diameter, plant height and head number (Fig. 2). Moreover, the frequency of qualitative traits in plants exposed to selection was more similar to the wild parental type than to plants not exposed to bird selection. The hybrid index demonstrated that a large proportion of plants experiencing selection had similar values to the wild plants (Fig. 3). Correlations were
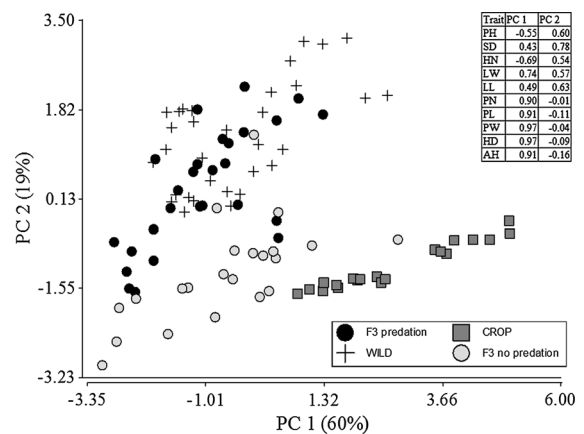

Fig. 2 Principal component analysis of plants with and without bird selection and the parental wild population and sunflower cultivar. PC 1 and PC 2 loadings are shown in the *upper right* part of the figure. *PH* plant height; *SD* stem diameter; *HN* head number; *LW* leaf width; *LL* leaf length; *PN* phyllary number; *PL* phyllary length; *PW* phyllary width; *HD* head number; *AH* achenes per head

positive between the achene traits and leaf width, phyllary traits, head diameter and achenes per head, and negative between the achene traits, plant height and head number (Table 2).

The evolutionary change, measured in haldanes and darwins, was variable with each trait and unit and were mostly selected negatively. The median absolute value (and range) were 0.37 (0.07–0.89) h or 0.09 (0.01–0.55) d. Both measures provided similar relative rankings. The values were highest for head diameter, head number, plant height and phyllary number showed the highest values. The value for achene weight was the highest among the achene traits (Table 3).
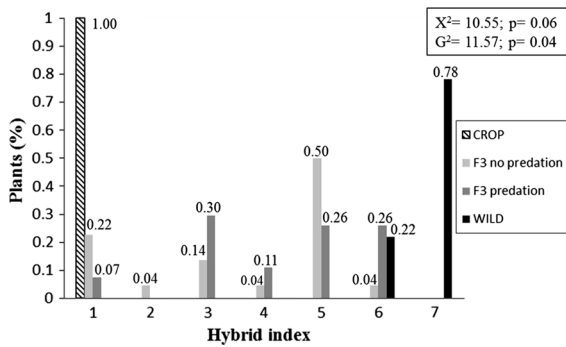
Fig. 3 Hybrid index based on qualitative traits of plants exposed to bird selection (F3 predation), plants not exposed to bird selection (F3 no predation), wild *H. annuus* population (Wild) and domesticated sunflower (Crop). Analysis of contingency: Pearson's Chi square (X^2) and likelihood ratio Chi square (G^2) between F3 predation and F3 no predation (H_0: the proportions of each category are the same for F3 predation and F3 no predation), are shown in the *upper right* part of the figure

Discussion

The selection exerted by birds on crop–wild hybrids caused evolutive changes in the frequency of phenotypes in the population, and in two generations the phenotype converged to that of the wild type sunflower. Predation by birds shifted the achene features of the crop–wild descendants to lower values as compared to plants without selection. It is possible that larger heads, with larger achenes which derive from plants with apical dominance, were more visually attractive and easy to perch. The shift in achene features was linked to changes in the morphology of other plant traits. Seeds exposed to bird predation gave rise to taller plants, with thicker stems, smaller heads but more abundant and fewer achenes per head than seeds that had not been exposed to seed predation (Table 1). The indirect selection would be explained by the strong correlation found between achene traits and plant traits (Table 2). This correlation could be explained by the linkage between genes and the persistence of large segments of the intact chromosomes transferred from wild to crop, conferring a fitness advantages (Whitton et al. 1997; Linder et al. 1998). Since wild sunflowers exhibit higher-fitness traits, the consequence of this linkage was plants phenotypically similar to wild individuals.

This study demonstrates direct evidence of directional selection on sunflower crop–wild hybrids, driven by birds. So far, post-dispersal seed predation in crop, wild, and crop–wild hybrids had focused on

Table 2 Pearson correlation coefficients (correlations below diagonal, significances above diagonal) among traits in F3 no predation, F3 predation, wild and crop

Trait	PH	SD	HN	LW	LL	PeL	LN	PN	PL	PW	HD	AH	AL	AW	AT
PH		**	**	ns	ns	**	**	**	**	**	**	**	**	**	**
SD	**0.38**		ns	**	**	**	*	**	*	**	*	ns	ns	*	*
HN	**0.50**	0.19		ns	ns	ns	ns	**	**	**	**	**	**	**	**
LW	−0.14	**0.53**	−0.04		**	*	ns	**	**	**	**	**	**	**	**
LL	−0.11	**0.40**	0.05	**0.79**		**	ns	*	**	**	**	**	*	**	**
PeL	**0.38**	**0.42**	0.13	0.21	**0.30**		ns	ns	ns	ns	ns	ns	ns	ns	ns
LN	**0.38**	0.26	−0.05	0.11	0.11	0.21		ns	ns	ns	ns	ns	ns	ns	ns
PN	**−0.38**	**0.34**													

Highly significant correlations are in bold

** $p < 0.01$, * $p < 0.05$, ns $p > 0.05$

PH plant height; *SD* stem diameter; *HN* head number; *LW* leaf width; *LL* leaf length; *PeL* petiole length; *LN* leaf number; *PN* phyllary number; *PL* phyllary length; *PW* phyllary width; *HD* head number; *AH* achenes per head; *AL* achene length; *AW* achene width; *AT* achene thickness

Table 3 Estimated rates of evolution expressed as haldanes or darwins, for each quantitative trait. MAV is the median absolute value

Trait	Haldanes	Darwins
Plant height	0.89	0.21
Stem diameter	0.52	0.13
Head number	0.66	0.55
Leaf width	−0.07	−0.01
Leaf length	−0.18	−0.04
Petiole length	0.30	0.05
Leaf number	0.25	0.07
Phyllary width	−0.62	−0.21
Phyllary length	−0.23	−0.05
Phyllary number	−0.14	−0.02
Head diameter	−0.71	−0.16
Achenes per head	−0.30	−0.13
Achene width	−0.45	−0.09
Achene length	−0.18	−0.02
Achene thickness	−0.44	−0.10
Achene weight	−0.50	−0.21
MAV	0.37	0.09

seed trait selection by rodents (Alexander et al. 2001; Dechaine et al. 2010). Selection (predation) targeted larger seeds or seeds with higher oil and lower fibre content. Despite of different feeding habits, birds and rodents seem to select in the same direction – preference for crop-like seeds—and therefore, similar results could be expected between both granivores and even stronger selection levels if both agents act together.

Most species have relatively low mean pre-dispersal seed predation but a few species suffer from high levels of damage and this predation is variable in space and time (Kolb et al. 2007). Sunflower is one of the latter species because bird damage is higher than in other crops (e.g. maize). However the damage is related to local and landscape variables (Peer et al. 2003; Canavelli et al. 2014). This study shows the results of intense selection, which is characteristic of agricultural land near to or surrounded by trees and shrubs, places where birds can nest, roost and breed (Canavelli et al. 2014). This means that these results could not be extrapolated to environments where pre-dispersal seed predation is absent or low. On the other hand, other granivores (e.g. rodents) could be acting and driving the selection with similar strength and direction.

The rates of evolution, as measured by darwins (d) and haldanes (h) confirmed that the intensity of selection was high. Usually, selection intensities are in the range of 0.1–0.3 h (Gingerich 2009), 0–0.81 h or 0–1.37 d (Bone and Farres 2001). Our data revealed rates of 0.07–0.89 h or 0.01–0.55 d, which were similar to rates due to herbicide or artificial selection (Bone and Farres 2001). However, these rates possibly over-estimate long-term rates because of the small number of generations used. Also because in early-generation hybrids, chromosomal blocks could be transferred intact from crop to wild without complete recombination (Linder et al. 1998). Nevertheless, these results indicate the high efficiency of selection (predation) by birds and also that sunflower is a species that rapidly returns to wild phenotype.

Uncontrolled sunflower crop–wild hybrids—as a result of crop pollination by nearby wild population–could establish in the agro-ecosystem which could initially have disadvantageous traits inherited from the crop, such as no branching, large heads, and large achenes. Specifically, early life-history traits with strong maternal effect (such as negligible achene dormancy, large achene size) could initially constrain evolution because they increase the percentage of decayed seedlings and consequently limit the number of adult plants (Alexander et al. 2014). However, birds rapidly select against some of these traits and so, indirectly, select characters that could favor a wild phenotype, such as branching, small heads and achenes, and also a correlated trait, seed shattering (Wills and Burke 2007; Chapman et al. 2008). We confirm that the change caused by selection exerted by birds is related to fitness, the ability of the plants to survive and produce seed. This change produces, after hybridization, a phenotype that largely mimics the wild phenotype caused by natural selection, in a fast convergent selection driven by granivory. In addition, the crop is not only contributing with maladaptive traits but also with traits that could increase invasiveness (Casquero et al. 2013), such as fast growth, early flowering (Mercer et al. 2007) or self-pollination. Furthermore, the chances of a crop–wild progeny becoming a problematic weed are higher than if both hybridizing parents are wild species (Ellstrand 2003). However, if these populations were growing together with wild populations, granivores would reduce the number of crop-like individuals and consequently mitigate the spread of crop alleles to the wild (Dechaine et al. 2010).

In comparison with previous studies, the response to selection was rapid and after two generations the sunflower crop–wild progenies were undistinguishable from wild populations. The outcome of our study provides an understanding of the role of bird selection of achene features and their impact on morphological traits in crop–wild plants.

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