Genetic Analysis of Sunflower Domestication

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ABSTRACT

Quantitative trait loci (QTL) controlling phenotypic differences between cultivated sunflower and its wild progenitor were investigated in an F_3 mapping population. Composite interval mapping revealed the presence of 78 QTL affecting the 18 quantitative traits of interest, with 2–10 QTL per trait. Each QTL explained 3.0–68.0% of the phenotypic variance, although only 4 (corresponding to 3 of 18 traits) had effects >25%. Overall, 51 of the 78 QTL produced phenotypic effects in the expected direction, and for 13 of 18 traits the majority of QTL had the expected effect. Despite being distributed across 15 of the 17 linkage groups, there was a substantial amount of clustering among QTL controlling different traits. In several cases, regions influencing multiple traits harbored QTL with antagonistic effects, producing a cultivar-like phenotype for some traits and a wild-like phenotype for others. On the basis of the directionality of QTL, strong directional selection for increased achene size appears to have played a central role in sunflower domestication. None of the other traits show similar evidence of selection. The occurrence of numerous wild alleles with cultivar-like effects, combined with the lack of major QTL, suggests that sunflower was readily domesticated.

THE domestication of plants from their wild progenitors has led to the production of a wide variety of crops that share a number of traits. For example, domestication of the major cereals (*i.e.*, maize, millet, rice, sorghum, and wheat) has generated plants with larger grains, increased inflorescence size, and more determinate growth as compared to their wild progenitors. In general, this pattern of transition from small-seeded plants with natural seed dispersal to larger-seeded plants that retain their seeds until harvest applies to all seed crops, not just the cereals. In fact, these parallels transcend the deepest divisions within the angiosperms, with both monocot and dicot crops developing a similar suite of adaptations to human cultivation over the last 10,000 years (collectively known as the domestication syndrome; Harlan 1992).

Over the years, these rapid and dramatic morphological transformations have been the target of a number of genetic analyses (*e.g.*, Beadle 1939; Langham 1940; Ladizinsky 1985; Doebley *et al.* 1990; Doebley and Stec 1991, 1993; Koinange *et al.* 1996). Such studies have been motivated by a desire to link phenotypic changes with the genes that are ultimately responsible. From an agricultural standpoint, the importance of this work is obvious. Understanding the genetic basis of traits that make "good" crops good could greatly expedite crop improvement efforts. Evolutionary biologists, on the other hand, are interested in domestication as a means of understanding the genetic basis of fundamental evolutionary processes. Indeed, in reference to the role of natural selection in evolutionary diversification, Darwin (1859, p. 4) wrote that "a careful study of domesticated animals and cultivated plants would offer the best chance of making out this obscure problem."

Genetic analyses of domestication to date have revealed that the domestication syndrome is often under relatively simple genetic control. For example, quantitative trait locus (QTL) mapping has revealed that the striking morphological differences between maize and teosinte result from the effects of as few as five genomic regions, each of relatively major effect (Doebley *et al.* 1990; Doebley and Stec 1991, 1993). Interest in the number of QTL underlying trait differences as well as the magnitudes of their effects stems from a simple fact: selection response is strongly influenced by genetic architecture. Genetic correlations among traits are, therefore, also of interest. If individual chromosomal regions contribute to multiple traits, selection on one character may influence one or more apparently unrelated characters. These correlations, which result from either the pleiotropic effects of a single gene or physical linkage among multiple genes, can facilitate or constrain adaptation (Lande 1979; Lande and Arnold 1983).

Another question that QTL mapping can answer relates to the identity of traits that were the primary targets

This paper is dedicated to Charles B. Heiser, Jr., for his many contributions to our understanding of sunflowers and their domestication.

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TABLE 1

Comparison of 18 traits between cultivated (cmsHA89) and common (*Helianthus annuus* var. *annuus*) sunflower

Trait	Cultivated sunflower (cmsHA89)	Common sunflower (*H. annuus* var. *annuus*)
Days to flower	48–50	52–68
Stem diameter	1.9–2.1 cm	1.2–1.4 cm
Height	120–136 cm	153–170 cm
No. of main stem leaves	30–32	74–90
Leaf shape (l/w)	1.15–1.25	1.45–1.55
Leaf size (l × w)	300–315 cm^2	180–270 cm^2
Peduncle length	5.4–6.2 cm	5.8–11.8 cm
No. of branches	0	12–16
No. of heads	1	40–50
No. of heads/branch	NA	2.5–4.2
Disc diameter	9.0–11.0 cm	3.0–5.0 cm
No. of ray flowers	30–35	20–30
Ray size (ligule l × w)	9.5–11.5 cm^2	3.5–4.5 cm^2
No. of selfed seeds[a]	NA	NA
Achene weight	55–65 mg	9–10 mg
Achene length	9.5–10.5 mm	5.0–5.2 mm
Achene width	5.0–5.2 mm	2.4–2.6 mm
Shattering	No	Yes

Data were obtained from Heiser *et al.* (1969), Kim and Rieseberg (1999), and from personal observations of greenhouse grown plants. NA, not applicable.

[a] Neither cmsHA89 nor *H. annuus* var. *annuus* are capable of self-fertilization, but for different reasons. cmsHA89 is self-compatible, but male sterile, whereas *H. annuus* var. *annuus* is self-incompatible.

of strong selection during domestication. While QTL studies have been criticized for their inability to detect loci of minor effect, as well as their often biased estimates of effect magnitudes (Beavis 1994), they are generally good at indicating the direction of allelic effects. With these data, it is possible to detect the footprint of directional selection (Orr 1998). Although the primary targets of selection are often known (or at least suspected) in crop taxa, QTL data provide a means of confirmation. Finally, QTL studies can provide insight into the mode of gene action underlying domestication traits. Classical studies on the genetics of domestication have suggested that domestication traits, which often result from the loss of wild-type functions, are largely under recessive control (*e.g.*, Ladizinsky 1985). Because this view is based mainly on work in the major cereals, how well it applies to other crop species is unclear. In fact, recent QTL studies have indicated that recessivity is not necessarily the rule, with numerous instances of additive, or even dominant, gene action being reported (*e.g.*, Paterson *et al.* 1991; Doebley *et al.* 1994).

Along with soybean (*Glycine max*), rapeseed (*Brassica rapa* and *B. napus*), and peanut (*Arachis hypogaea*), the cultivated sunflower (*Helianthus annuus* var. *macrocarpus*) is one of the four most important crops grown for edible oil worldwide (Putt 1997). Derived from the common sunflower (*H. annuus* var. *annuus*), cultivated sunflower is also a major source of confectionery seeds. The weedy, self-incompatible common sunflower is native to North America and found throughout the United States, Canada, and Mexico. It is particularly abundant in the central and western United States (Heiser 1951). Although cultivated sunflower was long thought to have had a single origin in the eastern United States over 4000 years ago (*e.g.*, Heiser 1954, 1955; Rieseberg and Seiler 1990; Crites 1993), Lentz *et al.* (2001) recently reported finding domesticated sunflower achenes of a similar age in central Mexico. Moreover, two recent molecular studies suggest the possibility of multiple origins (S. Tang and S. J. Knapp, unpublished data; A. V. Harter and L. H. Rieseberg, unpublished data).

Although completely interfertile and considered to be members of the same species, cultivated and common sunflower exhibit a number of phenotypic differences (Table 1). In short, common sunflower is characterized by many branches along its entire stem, each with numerous small heads and relatively small achenes (*i.e.*, single-seeded fruits). When disturbed, mature heads release their achenes, or "shatter." In contrast, cultivated sunflower is characterized by an unbranched stem topped by a single, large head. Cultivated sunflower achenes, which are relatively large, are retained in the head until harvest. Both varieties of *H. annuus* are diploid ($n = 17$) annuals. In this article, we report the results of a QTL analysis of these and other traits that differentiate common and cultivated sunflower.

MATERIALS AND METHODS

Mapping population: The entire mapping population described in this study was derived from a cross between a single individual of the cytoplasmic male-sterile cultivar known as cmsHA89 and a single wild *H. annuus* var. *annuus* individual from Keith County, Nebraska (Ann1238). The resulting F_1 individuals were grown to maturity and self-pollinated. Of the >150 F_1 individuals tested, 2 were self-compatible. The single most productive F_1 individual was selected as the founder of the F_2 generation. The F_2 generation was outplanted in Cuernavaca, Mexico, and allowed to produce F_3 seeds. These seeds were nicked with a razor blade and allowed to imbibe ddH_2O on filter paper in petri plates prior to being germinated in flats in the growth chamber. Seedlings were then transplanted into clay pots and grown under 16-hr days in the Indiana University greenhouses. A total of 374 F_3 lines were produced from this crossing program. In an attempt to minimize environmental variation early in the experiment, plants were rotated among beds on a weekly basis until they were too large to move (~6 weeks).

Phenotypic trait measurements: Eighteen quantitative traits that differentiate cultivated and wild sunflower were measured in the F_3 plants (Table 1). In addition, two dominant morphological markers (hypocotyl/disc pigmentation and restoration of male fertility) were scored for each plant. The following traits were measured at the initiation of flowering: days to flower, stem diameter (2.5 cm above the soil line), height of

the main stem, number of leaves along the main stem, length and width of the largest leaf (leaf shape was calculated as l/w, and leaf size was calculated as l × w), peduncle length, disc diameter, number of ray flowers, and the length and width of the ligule of each of three arbitrarily selected ray flowers on the primary head (ray size was calculated as ligule l × w). The primary head on each plant was bagged and allowed to self-pollinate without human intervention. The number of branches and heads were counted at harvest. Following harvest, the primary head was photographed in profile with a digital camera, and the depth and width of the head were measured using NIH Image (developed at the U.S. National Institutes of Health and available at http://rsb.info.nih.gov/nih-image/). These measurements were then used to calculate an indirect measure of shattering, the ratio of mature head depth:width. The rationale for this approach is that shattering in wild sunflower is accompanied by the continued growth of the capitulum, resulting in a convex disc (an increase in the depth:width ratio). In contrast, the nonshattering cmsHA89 retains a relatively flat head at maturity, corresponding to a lower depth:width ratio. Seeds were removed from each head, weighed, and counted. The length and width of five arbitrarily selected achenes from each plant were then measured with digital calipers (achene size was calculated as l × w).

All traits were tested for deviations from normality using the Shapiro-Wilk test as implemented by JMP 4 (SAS Institute, Cary, NC). Where necessary, non-normal traits were transformed using the Box-Cox tranformation (Box and Cox 1964). To test for environmental variation, each trait was then analyzed as a one-way ANOVA with blocks (*i.e.*, greenhouse beds) as the main effect. Eight traits (stem diameter, height, leaf size, number of branches, number of heads, number of heads per branch, disc diameter, and shattering) showed significant variation among blocks (sequential Bonferroni-adjusted $P \leq 0.05$; data not shown). To control for environmental variation in these eight traits, we performed all further analyses on the residuals from the one-way ANOVA, rather than on the raw trait values. All phenotypic trait measurements are available upon request.

DNA isolation and genotyping: Total genomic DNA was isolated from 200 mg of fresh leaf tissue using the DNeasy plant mini kit (QIAGEN, Valencia, CA) and quantified using a TKO-100 fluorometer (Hoefer Scientific Instruments, San Francisco). A subset of 88 F_3 DNA samples was then genotyped with a series of 202 simple sequence repeat (SSR, or microsatellite) primers developed by Tang *et al.* (2002). The majority of these primers produced easily interpretable, single-locus, codominant banding patterns. The remainder produced more complex banding patterns, often with multiple unlinked dominant loci. Reactions were run in 10 μl total volume with 10 ng template DNA, 10 pmol of the forward and reverse primers, and a final concentration of 2 mm $MgCl_2$, 30 mm Tricine, 50 mm KCl, 100 μm each dNTP, and 0.5 units of *Taq* polymerase. In each reaction, the forward primer was 5′-labeled with one of three fluorophores (6FAM, HEX, or NED). To reduce nonspecific amplification, we used touchdown PCR (Don *et al.* 1991) with an initial denaturation of 95° for 3 min followed by 1 cycle of 94° for 30 sec, final annealing temperature (T_A) + 10° for 30 sec, and 72° for 30 sec. The annealing temperature was reduced by 1° per cycle during each of the 9 following cycles, at which time the products were amplified for 30 cycles at 94° for 30 sec, T_A for 30 sec, and 72° for 30 sec with a final extension of 20 min at 72°. Final annealing temperatures varied between 54° and 60°. All PCRs were run in 96-well format on MJ Research (Watertown, MA) PTC-100 and tetrad thermalcyclers.

Genotypes were resolved on an ABI 3700 (Applied Biosystems, Foster City, CA). A total of 3–12 PCR products were multiplexed in each lane by running separate PCRs, which were then combined and diluted 20-fold in ddH_2O. Samples were then prepared by mixing 1 μl of the diluted PCR pool with 9.8 μl ddH_2O and 0.20 μl GenSize R500 ROX size standard (GenPak, St. James, NY). The samples were heated for 5 min at 95°, chilled for 5 min on ice, and placed on the ABI 3700. Run results were analyzed using GeneScan 3.5 and Genotyper 3.6 (Applied Biosystems).

Map construction: A preliminary map was produced from the subset of 88 F_3 individuals using MAPMAKER 3.0/EXP (Lander *et al.* 1987; Lincoln *et al.* 1992). Markers were initially divided into groups using the "group" command with LOD > 5.0, $\theta < 0.20$. The remaining markers were then assigned to groups by reducing the stringency to LOD > 3.0, $\theta < 0.25$. Map orders were explored using the "compare" and "ripple" commands, and a final set of 105 markers that (1) spanned the 17 linkage groups and (2) could be ordered unequivocally (LOD > 3.0) were selected for use in the entire mapping population. The remainder of the mapping population was then genotyped for the selected markers and the final map was constructed as above. Recombination fractions were translated into centimorgan (cM) distances using Kosambi's (1944) mapping function.

QTL analysis: All QTL analyses were performed using composite interval mapping (CIM; Zeng 1993, 1994) as implemented by the program Zmapqtl (model 6) of the software package QTL Cartographer version 1.15d (Basten *et al.* 1994, 2001). This approach tests the hypothesis that an interval between two adjacent markers harbors a QTL affecting the trait of interest while controlling for the effects of other QTL segregating outside the region of interest. CIM was run with a 10-cM window and five background cofactors. Tests were performed at 2-cM intervals, and cofactors were selected via forward-backward stepwise regression using the program SRmapqtl. Genome-wide threshold values ($\alpha = 0.05$) for declaring the presence of QTL were estimated from 1000 permutations of each phenotypic trait (Churchill and Doerge 1994; Doerge and Churchill 1996). A likelihood-ratio decline of ≥9.21 (equivalent to a LOD decline of ≥2.0) between adjacent peaks on a linkage group was taken as evidence of multiple, linked QTL. One-LOD support limits for the position of each QTL were calculated from the CIM results.

In addition to testing for the presence of a QTL in an interval of interest, Zmapqtl also provides an estimate of the additive (a) and dominance (d) effects of the cmsHA89 allele. The degree of dominance of the cmsHA89 allele was calculated as d/a, such that the expected value under purely additive gene action is 0. For purely dominant and purely recessive gene action, the expected values are 1.0 and −1.0, respectively. Values >1.0 or below −1.0 are a result of over/underdominance. The following arbitrary thresholds were used to classify the mode of gene action at each QTL: underdominant ≤ −1.25 < recessive ≤ −0.75 < partially recessive ≤ −0.25 < additive < 0.25 ≤ partially dominant < 0.75 ≤ dominant < 1.25 ≤ overdominant.

RESULTS

Linkage analysis: The SSR and morphological markers coalesced into the expected 17 linkage groups (Figure 1). These groups were cross-referenced with those of Tang *et al.* (2002) and were found to be in good agreement. The linkage group nomenclature presented in Figure 1, therefore, follows that of Berry *et al.* (1997), Gedil *et al.* (2001), and Tang *et al.* (2002). Overall, the two maps had 65 markers in common. Of these, only 3

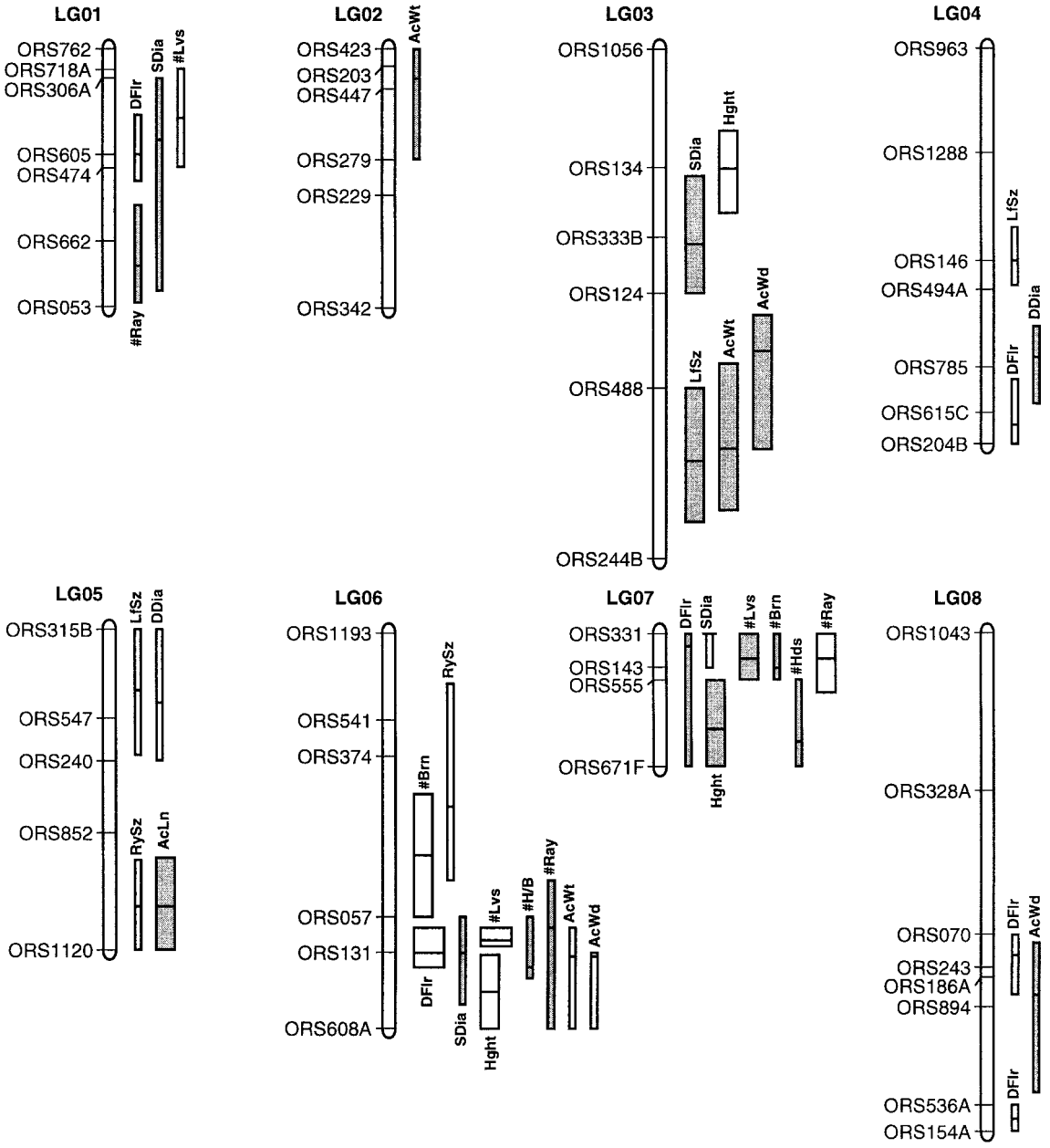

FIGURE 1.—Linkage map derived from the cultivated (cmsHA89) × wild (*H. annuus* var. *annuus*) sunflower F_3 mapping population. Marker names are listed to the left of each linkage group, and boxes to the right of each linkage group indicate QTL positions/magnitudes. A horizontal bar marks the most likely position of each QTL within the 1-LOD support limits, and QTL with effects in the expected direction are shaded. Marker names ending in a letter refer to dominant loci, whereas all others are codominant.

produced noncongruent results: ORS1056, ORS541, and ORS261 mapped to LG03, LG06, and LG11, respectively, rather than to LG13, LG10, and LG05, respectively. The most likely explanation for this noncongruence is that the loci produced by the primers in question were paralagous to those mapped by TANG *et al.* (2002). The total map distance covered was 972.6 cM, with an average intermarker interval of 11.1 cM. The map length reported here is thus considerably shorter than both the 1566.7 cM reported by TANG *et al.* (2002) and the estimated full length of the *H. annuus* genome (1650 cM; GENTZBITTEL *et al.* 1995). This is likely due, at least in part, to incomplete genome coverage. The magnitude of this difference is, however, somewhat misleading. A comparison of shared markers indicates relatively shorter map distances (~70% as long) across presumably equal physical distances in this map when compared to that of TANG *et al.* (2002). Correcting for this discrepancy, this map covers an estimated 84% of the full 1650 cM *H. annuus* genome.

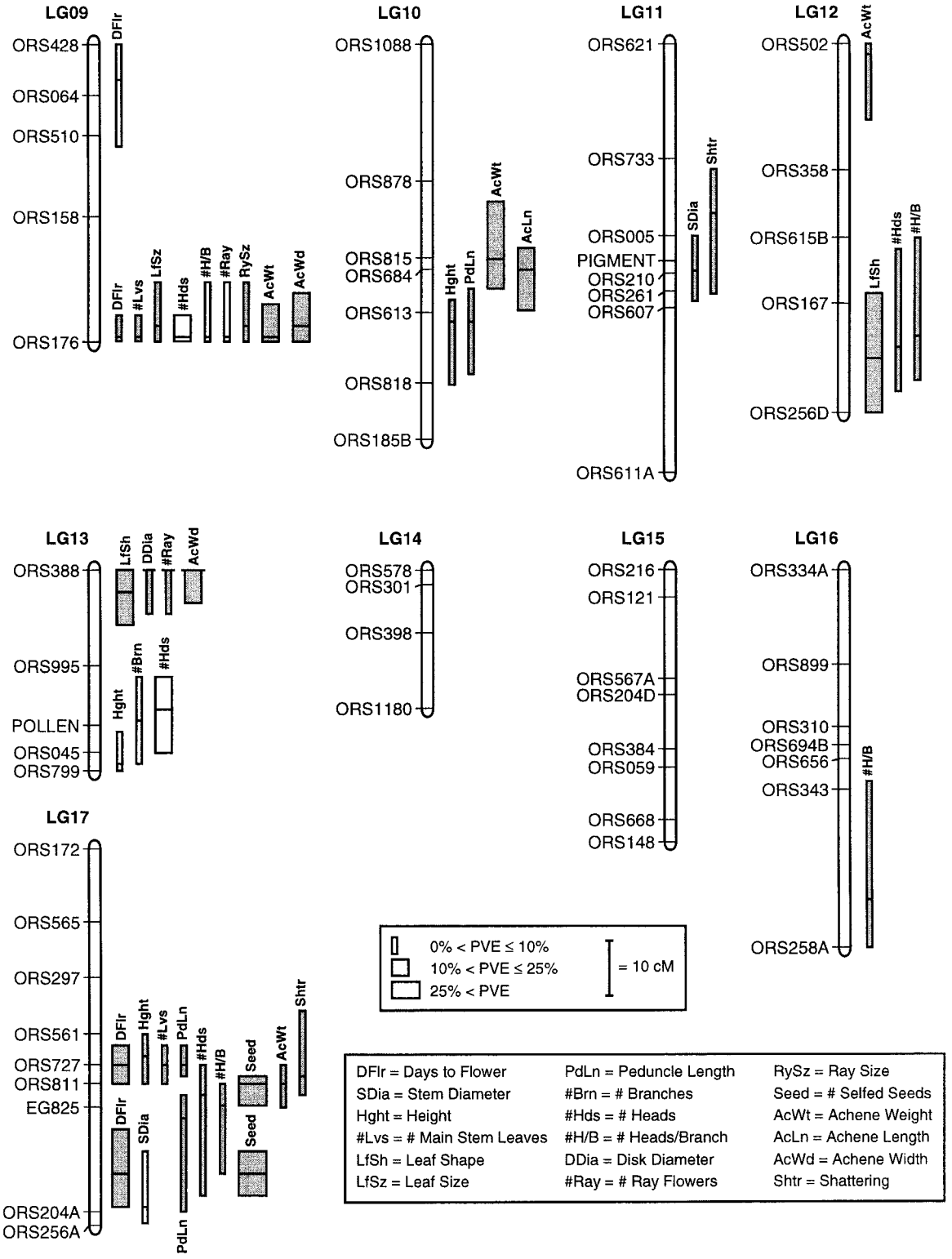

FIGURE 1.—*Continued.*

QTL analysis: Results of the QTL analysis are reported in Table 2 and presented graphically in Figure 1. Composite interval mapping revealed the presence of 78 QTL affecting the 18 quantitative traits of interest. The 1-LOD support limits, which give an approximate confidence interval for the location of each QTL, ranged from 4.0 to 34.7 cM, averaging 14.1 cM. The number of QTL mapped for a given trait ranged from 2 to 10 (mean = 4.3), and 3 traits (days to flower, peduncle length, and number of selfed seeds) had >1

TABLE 2

Putative QTL positions, effect magnitudes, and modes of action for 18 traits using composite interval mapping in an F_3 population of cultivated (cmsHA89) × wild (*H. annuus* var. *annuus*) sunflower

Trait	Linkage group	Position[a]	1-LOD interval[b]	PVE[c]	Mode of action[d]	Degree of dominance[e]
Days to Flower	LG01	17.2	10.8–21.5	3.0	A	−0.05
	LG04	61.3	53.9–64.4	6.5	U	−15.63
	LG06	52.2	48.2–54.6	28.0	A	−0.08
	LG07	2.0	0.0–21.7	9.5	r	−0.34
	LG08	52.7	49.3–59.0	5.5	A	−0.12
	LG08	79.3	77.0–81.3	6.4	d	0.34
	LG09	11.3	0.0–18.8	5.6	A	−0.08
	LG09	53.5	49.5–54.3	3.3	A	0.14
	LG17	39.2	35.6–42.6	19.9	d	0.38
	LG17	58.9	50.9–64.9	21.8	d	0.52
Stem diameter	LG01	14.8	4.8–39.5	7.8	A	−0.06
	LG03	31.9	20.7–39.9	13.4	r	−0.27
	LG06	52.2	46.4–60.6	4.4	d	0.45
	LG07	0	0.0–5.5	3.9	R	−0.90
	LG11	41.5	35.1–47.0	4.5	O	3.27
	LG17	64.9	54.9–67.8	7.6	d	1.51
Height	LG03	19.3	13.3–26.7	11.3	d	0.28
	LG06	58.6	52.6–64.6	22.5	r	−0.25
	LG07	15.6	7.6–21.7	15.6	U	−11.0
	LG10	50.7	46.7–62.2	5.3	r	−0.55
	LG13	35.5	29.6–36.8	5.1	A	0.11
	LG17	37.6	33.6–42.6	9.2	A	0.19
No. of main stem leaves	LG01	10.8	3.3–19.2	4.6	d	0.31
	LG06	50.2	48.2–52.2	28.1	A	0.09
	LG07	4.0	0.0–7.5	13.3	r	−0.29
	LG09	53.5	49.5–54.3	5.2	d	0.27
	LG17	39.2	35.6–42.6	9.8	d	0.26
Leaf shape	LG12	57.4	45.6–67.3	10.2	D	1.05
	LG13	4.0	0.0–10.0	21.0	A	0.15
Leaf size	LG03	67.2	55.3–77.2	11.9	O	2.23
	LG04	34.6	29.1–38.6	5.0	r	−0.28
	LG05	10.0	0.0–20.6	8.3	R	−1.15
	LG09	51.5	43.5–54.3	7.9	O	16.3
Peduncle length	LG10	50.7	44.7–60.2	7.0	r	−0.65
	LG17	39.2	35.6–41.2	4.7	d	0.62
	LG17	48.9	44.6–65.8	5.7	D	0.85
No. of branches	LG06	36.4	26.4–46.4	11.3	A	0.12
	LG07	5.5	0.0–7.5	8.8	U	−1.41
	LG13	27.6	19.6–35.5	7.0	r	−0.63
No. of heads	LG07	17.6	7.5–21.7	9.4	R	−1.23
	LG09	53.5	49.5–54.3	10.4	O	1.45
	LG12	55.4	37.6–63.4	8.0	U	−1.35
	LG13	25.6	19.6–33.5	11.4	r	−0.74
	LG17	44.6	39.2–62.9	8.6	U	−2.36
No. of heads/branch	LG06	54.6	46.4–64.6	6.5	r	−0.28
	LG09	53.5	43.5–54.3	4.9	D	1.00
	LG12	53.4	35.6–61.4	7.3	r	−0.48
	LG16	60.1	38.6–68.9	7.6	r	−0.53
	LG17	46.6	42.6–58.9	8.4	R	−0.85
Disc diameter	LG04	51.9	45.3–57.9	4.6	O	9.42
	LG05	12.0	0.0–21.5	5.7	r	−0.70
	LG13	0	0.0–8.0	6.0	d	0.58
No. of ray flowers	LG01	35.5	25.5–41.5	7.8	A	0.04
	LG06	48.2	40.4–64.6	7.2	d	0.46
	LG07	4.0	0.0–9.6	10.1	r	−0.69
	LG09	53.5	43.5–54.3	5.9	d	0.55
	LG13	0	0.0–8.0	6.9	A	0.25

(*continued*)

TABLE 2

(Continued)

Trait	Linkage group	Position[a]	1-LOD interval[b]	PVE[c]	Mode of action[d]	Degree of dominance[e]
Ray size	LG05	45.3	37.7–52.3	9.0	U	−1.29
	LG06	28.4	8.3–40.4	7.7	A	−0.16
	LG09	51.5	43.5–54.3	8.7	D	1.10
No. of selfed seeds	LG17	42.6	41.2–46.6	42.7	r	−0.29
	LG17	58.9	54.9–62.9	68.0	r	−0.55
Achene weight	LG02	4.8	0.0–18.0	5.9	A	0.06
	LG03	65.2	51.3–75.2	15.0	D	5.32
	LG06	52.6	48.2–64.6	5.6	r	−0.67
	LG09	53.5	47.5–54.3	13.7	d	0.45
	LG10	39.3	28.8–44.7	12.4	D	0.87
	LG12	2.0	0.0–14.0	5.7	D	0.97
	LG17	42.6	39.2–46.9	5.4	A	0.10
Achene width	LG03	49.3	43.3–65.2	10.2	D	2.07
	LG06	52.6	52.2–64.6	7.4	R	−0.81
	LG08	59.1	50.7–75.0	9.2	A	0.03
	LG09	51.5	45.5–54.3	17.8	D	1.13
	LG13	0	0.0–6.0	11.0	d	0.66
Achene length	LG05	45.3	37.3–52.3	16.9	r	−0.72
	LG10	41.3	37.3–48.7	10.7	D	1.05
Shattering	LG11	31.0	23.0–45.7	6.6	d	0.76
	LG17	41.2	29.4–44.6	5.0	d	0.44

[a] Absolute position from left telomere in centimorgans.
[b] Refers to the region flanking each QTL peak in which LOD scores decline by one.
[c] Percentage of phenotypic variation explained by each QTL using CIM. Note that PVE values are not additive across multiple QTL in CIM and, as such, they may sum to >100%. PVE values for QTL with effects in the direction of the cultivated phenotype (see Table 1) are underlined.
[d] Refers to mode of action of the cmsHA89 allele. U, underdominant; R, recessive; r, partially recessive; A, additive; d, partially dominant; D, dominant; and O, overdominant.
[e] Refers to the degree of dominance (d/a) of the cmsHA89 allele.

QTL on a single linkage group. Although the detected QTL are distributed throughout the genome, with 15 linkage groups carrying at least 1 QTL, a substantial amount of clustering is apparent (Figure 1). Of the 13 linkage groups carrying multiple QTL, all show some degree of overlap (based on 1-LOD support limits), with as many as 9 QTL overlapping in range of position (see LG09). Only 6 of the 78 QTL do not overlap with at least one other QTL.

Individual QTL explained 3.0–68.0% of the phenotypic variation of any particular trait (Table 2). Using arbitrary thresholds of 10 and 25% to delineate "minor," "intermediate," and "major" QTL, it appears as if the majority of traits are conditioned by minor and intermediate factors, with only 3 traits (days to flower, number of main stem leaves, and number of selfed seeds) affected by major QTL (Table 2; Figure 1). In terms of directionality, 51 QTL (65%) produced the expected effect based on the trait differences outlined in Table 1. In other words, for these QTL, the cmsHA89 genotype produced a more cultivar-like phenotype, and the Ann1238 genotype produced a more wild-like phenotype. Moreover, for 13 traits (72%), the majority of QTL had an effect in the expected direction. Of the remaining 5 traits, 2 (height and leaf size) had an equal number of QTL in the right/wrong direction, and 3 (days to flower, number of branches, and ray size) had a minority of QTL in the expected direction. Finally, several of the chromosomal regions that influence multiple traits carry QTL with antagonistic effects (*e.g.*, the bottom of LG06, top of LG07, and bottom of LG09). In other words, these regions produce a more cultivar-like phenotype for some traits, and a more wild-like phenotype for others.

The degree of dominance of the cmsHA89 allele ranged from −15.63 to 16.31 (mean = 0.14). On the basis of the criteria outlined in MATERIALS AND METHODS, nearly a quarter of all QTL (18 of 78) behaved in an additive fashion (Table 2; Figure 2). In contrast, the cmsHA89 allele showed some degree of recessivity at 22 QTL, some degree of dominance at 24 QTL, and under or overdominance at 6 and 8 QTL, respectively.

DISCUSSION

Perhaps the most surprising result of this study was the paucity of major QTL detected. Only 4 of 78 QTL (corresponding to only 3 of 18 traits) explained >25%

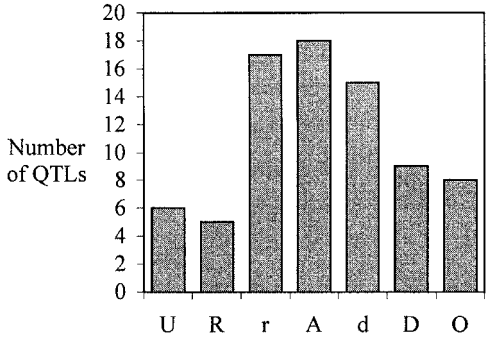

FIGURE 2.—Distribution of the mode of gene action for the 78 QTL detected in this study. U, underdominant; R, recessive; r, partially recessive; A, additive; d, partially dominant; D, dominant; and O, overdominant. Criteria used in defining the mode of gene action of each QTL are outlined in MATERIALS AND METHODS.

of the phenotypic variation in the mapping population (Table 2; Figure 1). In contrast, other recent studies on the genetic basis of domestication have revealed that domestication traits often have a relatively simple genetic basis. In maize, for example, 6 of the 10 domestication traits analyzed by DOEBLEY and STEC (1991) were conditioned by one major QTL each, accompanied by 3–6 modifiers of minor to intermediate effect. Similarly, KOINANGE *et al.* (1996) identified major QTL for 8 of 10 traits involved in the domestication of the common bean. The observed lack of major QTL in our study suggests that the phenotypic transition from wild to domesticated sunflower was relatively smooth, with very few (if any) major leaps. Moreover, this lack of dependence on major alleles suggests that sunflower domestication may have occurred much more readily than if it had required the fortuitous occurrence of multiple major mutations.

The observed lack of major QTL is also somewhat surprising given the results of prior studies in sunflower (reviewed in MILLER and FICK 1993). For example, PUTT (1940) identified a single, dominant gene (*Br*) that controls branching. Two decades later, PUTT (1964) reported recessive control of branching due to alleles at another locus (*b1*). HOCKETT and KNOWLES (1970) reported the existence of two additional duplicate genes (*Br2* and *Br3*) with dominant effects, as well as two complementary genes (*b2* and *b3*) that produce a fully branched plant when both are homozygous recessive. More recently, KOVACIK and SKALOUD (1990) verified the existence of two genes that exhibit dominant control of branching, as well as two additional genes that produce a branched plant when either is homozygous recessive. Finally, GENTZBITTEL *et al.* (1999) found that top branching and basal branching are controlled by two different loci, both of which are located on the same linkage group. Thus, although there is some support for the existence of major genes, our results suggest that the control of branching is genetically complex.

Of the three traits influenced by major QTL in this mapping population, the number of selfed seeds is conditioned by two such loci that are linked on the lower half of LG17. Although cultivated sunflower is generally self-compatible and wild sunflower is self-incompatible, it is unclear if either (or both) of these QTL correspond to loci involved in the recognition and rejection of self-pollen. Rather, the selection of a self-compatible F_1 may have led to the founding of a completely self-compatible mapping population. Because the heads were left unmanipulated, it thus is possible that these regions correspond to loci that influence autogamy independent of the self-incompatibility system. Along these lines, GEORGE and KLUNGNESS (1980) reported that variation in selfing ability can be influenced by factors such as floret density and stigma orientation, which alter the degree of contact between the anthers and stigmas of adjacent flowers on a head. Pollen agglutination (*i.e.*, the tendency of pollen to form sticky masses) also influences selfing rate in sunflower through its effects on pollen mobility (SEGALA *et al.* 1980). The issue of locating and identifying self-incompatibility loci is an important one in that patterns of variation at these highly variable loci may provide a great deal of information on the dynamics of sunflower domestication as well as insight into the question of multiple origins.

Given that the QTL magnitudes presented here contrast so strongly with those from other studies of domestication, alternative explanations must be considered. One possibility is that, because QTL magnitudes were expressed in terms of the percentage of phenotypic variation explained (PVE), increased variation due to environmental effects would lead to a reduction in QTL magnitude. As discussed in MATERIALS AND METHODS, however, environmental variation was controlled for in two ways. First, plants were rotated among greenhouse beds early in their development. Second, all traits were tested for variation among blocks and, where necessary, subsequent analyses were performed on the residuals after accounting for block effects, rather than the raw trait values. Environmental variation is not, therefore, a likely explanation for the paucity of major QTL. Another possibility is that numerous major QTL exist, but were missed due to incomplete genome coverage. The map covers an estimated 84% of the sunflower genome, however, making this explanation also unlikely. Finally, it is possible that defining the magnitude of QTL on the basis of PVE is somewhat misleading. Rather, it may be more appropriate to express effects in terms of the proportion of the phenotypic difference between the parental taxa that is explained by a given QTL. In this case, however, the overall conclusions that can be drawn from such a comparison are much the same. For example, the two QTL detected for achene length (located on LG05 and LG10) account for 16.9 and 10.7% of the phenotypic variance in the mapping population, respectively (Table 2). By comparison, the phenotypic

effects of these loci correspond to ~10 and 5% of the phenotypic gap between cultivated and common sunflower (Table 1). Thus, it appears that the lack of major QTL is a biologically real phenomenon. Although it is possible that a substantial amount of the phenotypic variance is conditioned by epistasis, significant interactions among QTL were detected for only two traits, heads per branch and ray size (data not shown). In both cases, the interactions accounted for only a small proportion of the total variance (5.2 and 4.7%, respectively). It therefore seems likely that most traits are controlled by the additive effects of numerous loci of small to moderate effect.

Because domestication presumably results from strong selection, the expectation would be for cultivar alleles to produce a cultivar-like phenotype and wild alleles to produce a wild-like phenotype. Although our data largely conform to this expectation, there are exceptions. At over one-third of all QTL detected (27 of 78), the cmsHA89 allele had a wild-like phenotypic effect and, perhaps most notably, three traits (height, number of branches, and ray size) had a minority of QTL in the expected direction (Table 2). The fact that many wild alleles have crop-like effects suggests that common sunflower may be a rich source of germplasm for continued crop improvement. The occurrence of numerous crop-like alleles in the wild also supports our contention that sunflower may have been readily domesticated. Indeed, if large reserves of suitable variation were already present in the ancestral population(s), then sunflower domestication needed only the intervention of humans to proceed.

The presence of crop-like alleles in the wild also suggests that there may be multiple paths to the domesticated phenotype. This, in turn, makes multiple origins all the more feasible. In contrast, if domesticated taxa are built on novel variation, mutation will be the rate-limiting step, and the recurrent evolution of domesticated taxa will be relatively unlikely (*e.g.*, Doebley 1990). It would therefore be interesting to compare the genetic architecture of domestication (more specifically, the directionality of allelic effects) in taxa with single *vs.* multiple origins of domestication. Multiple independent origins of domesticated plants have been documented in barley, bitter vetch, lima beans, common beans, chili peppers, and rice (Blumler 1992; van Raamsdonk 1993; Diamond 1997; Zohary 1999; reviewed in Levin 2001). Unfortunately, the data necessary for such a comparison do not currently exist.

The frequent occurrence of QTL with effects in the "wrong" direction, combined with the relatively low magnitudes described above, indicates that, at least for some traits, a large fraction of the phenotypic difference between cultivated and common sunflower cannot be accounted for. One possible explanation is that there may have been QTL of small effect that went undetected (Beavis 1994). Alternatively, incomplete sampling of the wild genome may have created this effect. Common sunflower is highly heterozygous, but the crossing design employed here permitted the introduction of only a single wild allele per locus into the mapping population. All possible alleles from the wild parent, as well as the interactions among these alleles, were therefore not represented. Thus, additional crosses between the same parental lines might reveal additional QTL, thereby accounting for a greater proportion of the phenotypic difference between cultivated and common sunflower.

Although the genomic locations of QTL identified in this study are relatively widespread, a considerable amount of clustering is apparent (Figure 1). Clearly, some of this clustering is due to the inclusion of multiple measures of what might be considered a single trait. For example, achene length, width, and weight might all be considered measures of "achene size," and QTL for these traits sometimes coincide (see LG03, LG06, LG09, and LG10). However, there is also considerable clustering of QTL across apparently unrelated traits. This pattern of genetic correlations across traits has been documented in other cases of domestication as well. In the common bean and maize, QTL underlying domestication traits are largely restricted to three and five genomic regions, respectively (Doebley *et al.* 1990; Doebley and Stec 1991, 1993; Koinange *et al.* 1996). Although linkage among QTL influencing domestication traits is predicted to evolve under strong selection, especially in allogamous species (Le Thierry D'Ennequin *et al.* 1999), relatively little attention has been paid to the role of pleiotropy in domestication. Thus, further characterization of the genetic basis of these correlations (*i.e.*, linkage *vs.* pleiotropy) would be illuminating.

Regardless of the ultimate cause of genetically correlated traits, the end result is much the same. Antagonistic correlations will constrain adaptive evolution, whereas concordant effects will facilitate adaptation (Lande 1979; Lande and Arnold 1983). The main difference is that under physical linkage, as opposed to pleiotropy, unfavorable relationships can be disrupted, potentially freeing up advantageous alleles that were previously housed in maladaptive chromosomal blocks. This issue is especially interesting in light of the observed directionality of allelic effects. Although the majority of trait correlations were concordant, there were numerous instances of antagonistic correlations across the genome (Figure 1). For example, 7 of the 10 QTL on LG06 have effects in the wrong direction, including 2 QTL affecting achene size, a trait that was clearly under selection during domestication (see below). This pattern could result from either the chance fixation of a maladaptive chromosomal block during domestication or strong selection favoring one or a few QTL that have antagonistic effects on other domestication traits. With respect to the former, chance fixation would be more likely if sunflower experienced a strong domestication bottleneck (*i.e.*, a period of restricted population

size during domestication). Although little is known about the dynamics of sunflower domestication, this sort of bottleneck has been documented in maize (Eyre-Walker *et al.* 1998). In the latter case, one might expect such selectively important QTL to be of relatively major effect. It is therefore possible that the trait driving the evolution of this region was not included in the present analysis. One possibility is that this region harbors one or more loci with effects on seed oil content or composition.

The ratio of alleles with effects in the "right" *vs.* "wrong" direction can also be used to investigate the role of selection in trait divergence (Orr 1998). The mere existence of alleles in one direction or the other is not, however, sufficient to implicate the effects of selection. For example, because cultivated sunflower has larger achenes than its wild progenitor, we know *a priori* that the cultivar must harbor at least some "plus" alleles. Thus, we must ask if the ratio of plus:minus alleles is more extreme than expected by chance, given the observed phenotypic difference (Orr 1998). In this case, 14 QTL affect some aspect of achene size (length, width, or weight). Of these, 12 have the expected effect (*i.e.*, the cmsHA89 allele produces larger achenes). Inspection of Figure 1 reveals that these 14 QTL map to only 10 unique chromosomal regions. Of these 10 regions, 9 produce the expected effect. Applying Orr's (1998) test to these data, our results are consistent with directional selection favoring increased achene size ($P = 0.04$). In view of the fact that sunflower is a seed crop, this result is not necessarily surprising. What is more interesting is that none of the other traits analyzed show similar evidence of selection. Traits relating to plant architecture, for example, may not have been targets of strong directional selection. This conclusion must be tempered with the realization that the power of this test is closely associated with the number of QTL detected. For traits such as shattering, therefore, we fail to reject the null hypothesis of neutral divergence even though all of the QTL detected (in this case only 2) had effects in the expected direction.

Finally, our data contradict the view that domestication traits are largely under recessive genetic control (*e.g.*, Ladizinsky 1985). Inspection of Figure 2 reveals that the majority of QTL are, in fact, nonrecessive. These findings are in accord with those of Paterson *et al.* (1991) in tomato and Doebley *et al.* (1994) in maize. Once again, this finding suggests that sunflower was readily domesticated and that selection during domestication likely resulted in a rapid phenotypic response.

The goal of this study was to examine the genetic basis of traits that differentiate cultivated and wild sunflower. The lack of major QTL, combined with both the occurrence of numerous wild alleles with cultivar-like effects and largely nonrecessive gene action, suggests that sunflower was readily domesticated. Moreover, our data suggest that wild sunflower may be an important source of germplasm for continued crop improvement. Looking across the genome, there was a considerable amount of clustering among QTL influencing multiple, apparently unrelated traits. Whether this pattern results from linkage or pleiotropy remains unclear. The first step to resolving this issue will be fine mapping these regions in an attempt to further refine QTL locations. Finally, a major sunflower cDNA sequencing effort is currently underway. The logical next step in the study of sunflower domestication will therefore be to begin identifying and mapping candidate genes underlying the traits of interest. The characterization of nucleotide variation at these adaptively important loci promises to provide a wealth of information on factors such as the strength and timing of selection during domestication. This approach will also open the door for comparative analyses of the domestication syndrome across widely disparate taxa.

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