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# The wild ancestry of the cultivated artichoke

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## Summary

The genetic affinities between the cultivated artichoke *Cynara cardunculus* L. var. *scolymus* (L.) Fiori (= *C. scolymus* L.) and its wild relatives were tested by means of a crossing programme. The following wild taxa were involved: (i) wild cardoon *C. carcundulus* L. var. *sylvestris* (Lamk) Fiori, (ii) *C. syriaca* Boiss., (iii) *C. cornigera* Lindley, (iv) *C. algarbiensis* Cosson, (v) *C. baetica* (Spreng.) Pau (= *C. alba* Boiss.), and (vi) *C. humilis* L. Only the wild cardoon was found to be fully cross-compatible and fully infertile with the crop. In contrast, all other five wild *Cynara* species turned to be almost fully—or fully—cross-incompatible with the crop, and the few interspecific $F_1$ hybrids recovered were partly or almost fully sterile. These finds establish the wild cardoon as the wild ancestor of the cultivated vegetable.

## Introduction

Artichoke is a traditional vegetable crop of the Mediterranean basin, containing two principle cultivated types: (i) Artichoke (globe artichoke), *Cynara cardunculus* L. var. *scolymus* (L.) Fiori (= *C. scolymus* L.), grown for its fleshy capitules. (ii) Cultivated cardoon, *C. cardunculus* var. *altilis* DC., grown for its succulent young leaves. Today only artichoke is grown on a commercial scale. However also the leafy cardoon is still locally appreciated in several Mediterranean countries.

*Cynara* L. is a relatively small genus of the daisy family *Compositae* comprising seven or eight wild taxa (Table 1) and the two cultivated vegetables (artichoke, cardoon). The species of *Cynara* growing in Europe were surveyed by Franco (1976), and more recently Wiklund (1992) carried out a taxonomic revision of the wild members of this genus. All wild members of *Cynara* are prennial thistles with characteristic large, spiny capitules. All are native to the Mediterranean basin and some are narrow endemics. All *Cynara* taxa tested up to date were found to be diploid 2n=34, self compatible but predominately cross-pollinated. Allogamy is maintained by protandry. Table 1 enumerates the wild taxa recognized by us in *Cynara* and gives information on their distribution.

*Table 1.* Wild taxa in *Cynara* L. and their distribution

| Species | Geographic distribution |
|---|---|
| 1. *C. cardunculus* L. (wild forms) | West and Central parts of the Mediterranean basin, Canary Islands and Madeira. |
| 2. *C. syriaca* Boiss. (including *C. aurantica* Post) | Near East 'arc'. |
| 3. *C. cornigera* Lindley (= *C. sibthorpiana* Boiss.) | Crete and several adjacent Aegean islands, Cyprus. |
| 4. *C. algarbiensis* Cosson | South Portugal and neighbouring areas in Spain. |
| 5. *C. baetica* (Spreng.) Pau (= *C. alba* Boiss.) | South Spain, Marocco. |
| 6. *C. cyrenaica* Maire & Weiller | Cyrenaica. |
| 7. *C. humilis* L. | Southern parts of Spain and Portugal, Marocco. |

Already Alphonse de Candolle (1886) stressed the close relationship between the cultivated artichoke and

the cultivated cardoon. He also surveyed the wild *Cynara* taxa known at his time, and concluded that both these cultivated types were derived from the wild cardoon, *C. cardunculus* L. var. *sylvestris* (Lamk) Fiori, (= *C. sylvestris* Lamk). This supposition was subsequently shared by several other botanists, but was not critically tested experimentally.

The aim of this paper is to further clarify the relationships between the crop and its wild relatives, and to re-examine the wild ancestry of the cultivated artichoke. We assembled a living collection of wild *C. cardunculus* and five other wild *Cynara* species. Their affinities with the globe artichoke were tested by crossing experiments and evaluation of (i) crossability between the wild taxa and the crop and (ii) the fertility of their interspecific $F_1$ hybrids.

## Materials and methods

Details on the various accessions used in the crossing programme are given in Table 2. The plants were grown in Talpiot experimental farm of the Hebrew University, Jerusalem. For protection from unwanted pollination the parental plants were covered (during flowering) by insect-proof mesh tents. Pollination was carried out when styles in the heads of the mother plants became elongated and pollination was usually repeated 24–48 hrs later. For details on pollination techniques see Foury (1967, 1987) and Foury et al. (1978).

Crosses between the cultivated artichoke and the wild *Cynara* taxa were facilitated by the availability of male-sterile artichoke clones (Basnizki & Zohary, 1994). Seeds produced by these mother plants were all hybrid seeds. By use of such mother plants, seed-set in the various cross-combination could be compared, and the cross-compatibility between the crop and the various wild relatives could be assessed.

In crosses between the wild species this advantage (male-sterile plants) was not available. To minimize selfing we washed the flowers of the mother plants with water 12-48 hrs before the application of pollen—but with little success. The progeny obtained from all these crosses were overwhelmingly selfing products, with only rare interspecific hybrids.

$F_1$ interspecific hybrids in all cross combinations could be easily detected (and separated from selfing products) by their intermediate morphology and by tell-tale traits characteristic of their male parent.

The fertility of the various $F_1$ hybrids was examined in two ways: (i) pollen picture and (ii) seed set.

*Table 2. Cynara* collections used in crosses

| Species or clone | Accession number | Origin |
|---|---|---|
| 1. Male-sterile clones of cultivated artichoke | 90/250 sco | Bred by J. Basnizki & D. Zohary |
| | 113/3 sco | ditto |
| | 204/2 sco | ditto |
| 2. Pollen donor clones of cultivated artichoke | 153 sco | Bred by J. Basnizki & D. Zohary |
| | 155 sco | ditto |
| 3. Wild *C. cardunculus* | 331 car | Pirgos, Peloponnessus, Greece (Col. D. Zohary). |
| | 332 car | Near Huelva, Spain (Col. B. Valdés) |
| | 470 car | Syracuse, Sicily (Col. G. Mauromicale) |
| 4. *C. syriaca* | 001 syr | Beit Guvrin, Judean foothills, Israel (Col. J. Basnizki). |
| 5. *C. cornigera* | 471 syr | Melambas, Crete, Greece (Col. O. Fargman & O. Cohen). |
| 6. *C. algarbiensis* | 340 alg | Huelva province, Spain (Col. B. Valdés). |
| | 341 alg | ditto |
| 7. *C. baetica* | 346 bae | Cadiz province, Spain (Col. B. Valdés) |
| 8. *C. humilis* | 333 hum | Cadiz province, Spain (Col. B. Valdés) |
| | 334 hum | ditto |

Pollen grains from dehiscing anthers were stained with 2% aceto-carmine. A grain was considered normal when its wall was well developed and when its contents stained well. All pollen parents we used scored 95%–99% normally stained pollen.

Seed set was scored in mature dry heads 45–60 days after pollination. The standard for comparison were the seed set values in the male-sterile clones—upon ordinary pollination with cultivated artichoke pollen (100–250 seeds per head). Seed set in the various $F_1$ hybrids could be assessed in the following ways: (i) After selfing of the $F_1$ hybrid. (ii) After its pollination by its male parent pollen. (iii) After its pollination by

*Table 3a.* Results obtained upon pollination of heads of male-sterile clones of cultivated artichoke with pollen of the various wild *Cynara* taxa

| Cross combination | Number of heads pollinated | Average seed set per head | Percentage of seed that produced viable hybrids |
|---|---|---|---|
| 113/3 sco × 331 car | 4 | >100 | >95% |
| 113/3 sco × 332 car | 4 | >100 | >95% |
| 90/250 sco × 470 car | 4 | >100 | >95% |
| 90/250 sco × 001 syr | 13 | 1.3 | 6% |
| 113/3 sco × 471 cor | 9 | 0 | |
| 113/3 sco × 341 alg | 4 | 0 | |
| 90/250 sco × 340 alg | 2 | 5.5 | 28% |
| 113/3 sco × 346 bae | 8 | 0 | |
| 90/250 sco × 346 bae | 13 | 0 | |
| 204/2 sco × 334 hum | 4 | 6.5 | 15% |
| 113/3 sco × 333 hum | 1 | 4.0 | 0% |

*Table 3b.* Crosses between the various wild *Cynara* taxa

| Cross combination | Number of heads pollinated | Number of $F_1$ hybrids recovered |
|---|---|---|
| 331 car × 001 syr | 4 | 1 |
| 332 car × 001 syr | 3 | 0 |
| 470 car × 340 alg | 7 | 0 |
| 331 car × 346 bae | 4 | 1 |
| 470 car × 334 hum | 3 | 0 |
| 001 syr × 341 alg | 2 | 0 |
| 001 syr × 332 car | 1 | 0 |
| 340 alg × 001 syr | 3 | 2* |
| 340 alg × 332 car | 2 | 0 |
| 340 alg × 346 bae | 5 | 0 |
| 341 alg × 334 hum | 1 | 0 |
| 346 bae × 001 syr | 1 | 1 |
| 346 bae × 340 alg | 2 | 0 |
| 346 bae × 332 car | 1 | 0 |
| 333 hum × 001 syr | 1 | 0 |
| 333 hum × 341 alg | 3 | 0 |

*Did not come to flower in the first year

its female parental line's pollen. (iv) By examination of seed set in male-sterile cultivated artichoke after pollination with the $F_1$ hybrid's pollen.

## Results

### *I. Crosses between male-sterile cultivated artichoke and the wild* Cynara *taxa*

Crosses were attempted between cultivated artichoke and the six wild *Cynara* taxa listed in Table 2. They were facilitated by the availability of male-sterile clones of cultivated artichoke developed by Basnizki & Zohary (1994). The cross-combinations attempted and the results obtained are presented in Table 3a, and the fertility scores of the $F_1$ hybrids are brought up in Table 4. They can be summarized as follows:

(1) *Scolymus* × wild *C. cardunculus.* The three accessions of wild *C. cardunculus* (Table 2) turned out to be fully cross-compatible with the crop. Hundreds of well developed seeds were set by the male sterile artichoke mother plants upon pollination with wild cardoon pollen (Table 3a). Several dozens of $F_1$ hybrids grown from these cross-combinations turned out to be fully fertile (Table 4). Practically all their pollen grains stained normally, and their seed set was full (more than 100 seeds per head) upon selfing, upon back crossing by their pollen parent, as well as upon the application of their pollen to the male-sterile *scolymus* parental clone. In addition, several reciprocal (wild *cardunculus* × *scolymus*) $F_1$ hybrids (not recorded in Table 4) exhibited similar full fertility.

(2) *Scolymus* × *C. syriaca.* Thirteen heads of male-sterile *scolymus* plants were pollinated with *C. syriaca* pollen. They set the total of 17 seeds (Table 3a) of which only one grew to maturity. Only 60% of the pollen grains produced by this inter-specific hybrid stained normally. The hybrid set few seeds both upon selfing and upon backcrossing (Table 4). Previous crosses (Zohary & Basnizki 1975) also resulted in rare *scolymus* × *syriaca* hybrids, and showed that this hybrid is almost fully fertile.

(3) *Scolymus* × *C. cornigera.* Nine heads of male-sterile *scolymus* were pollinated with *C. cornigera* pollen. No seeds were set after this pollination.

(4) *Scolymus* × *algarbiensis.* Six heads of male-sterile *scolymus* were pollinated with *C. algarbiensis* pollen (Table 3a) and they set the total of 12 seeds. Three germinated and flowered. Normally stained pollen in all these three *scolymus* × *algarbiensis* $F_1$ hybrids was about 95%. The relatively high fertility values were repeated in seed-sets, both upon selfing and upon backcrossing (Table 4).

*Table 4.* Pollen picture and seed set in the various interspecific $F_1$ hybrids

| $F_1$ hybrids and pollination tests performed on them | Percent of normal pollen in $F_1$ hybrids | Number of heads pollinated | Average number of seed per head in $F_1$ hybrids |
|---|---|---|---|
| *scolymus* × *cardunculus* | 99% | | |
| (113/3 sco × 331 car) selfed | | 2 | >100 |
| (113/3 sco × 332 car) selfed | | 2 | >100 |
| (90/250 sco × 470 car) selfed | | 2 | >100 |
| 113/3 sco × (113/3 sco × 331 car) | | 4 | >100 |
| 113/3 sco × (113/3 sco × 332 car) | | 4 | >100 |
| 90/250 sco × (90/250 sco × 470 car) | | 4 | >100 |
| *scolymus* × *syriaca* | 60% | | |
| (90/250 sco × 001 syr) selfed | | 4 | 4 |
| 90/150 sco × (90/250 sco × 001 syr) | | 4 | 0 |
| 204/3 sco × (90/250 sco × 001 syr) | | 2 | 14 |
| *scolymus* × *algarbiensis* | 95% | | |
| (90/250 sco × 340 alg) selfed | | 3 | >100 |
| (90/250 sco × 340 alg) × 155 sco | | 1 | 26 |
| (90/250 sco × 340 alg) × 340 alg | | 1 | 6 |
| 90/250 sco × (90/250 sco × 340 alg) | | 8 | >100 |
| *scolymus* × *humilis* | 52% | | |
| (204/2 sco × 334 hum) selfed | | 3 | 26 |
| (204/2 sco × 334 hum) × 153 sco | | 3 | 1 |
| 204/2 sco × (204/2 sco × 334 hum) | | 8 | 1 |
| *cardunculus* × *syriaca* | 28% | | |
| (331 car × 001 syr) selfed | | 1 | 18 |
| (331 car × 001 syr) × 331 car | | 1 | 1 |
| (331 car × 001 syr) × 001 syr | | 1 | 4 |
| 113/3 sco × (331 car × 001 syr) | | 4 | 1 |
| *cardunculus* × *baetica* | 25% | | |
| (331 car × 346 bae) selfed | | 2 | 5 |
| (331 car × 346 bae) × 331 car | | 2 | 5 |
| (331 car × 346 bae) × 346 bae | | 1 | 10 |
| 113/3 sco × (331 car × 346 bae) | | 8 | 0 |
| *baetica* × *syriaca* | 55% | | |
| (346 bae × 001 syr) selfed | | 4 | 4 |
| (346 bae × 001 syr) × 346 bae | | 2 | 0 |
| (346 bae × 001 syr) × 001 syr | | 1 | 9 |
| 113/3 sco × (346 bae × 001 syr) | | 7 | 0 |

(5) *Scolymus* × *C. baetica.* Twenty one heads of male-sterile *scolymus* were pollinated with *C. baetica* pollen. No seeds were set.

(6) *Scolymus* × *C. humilis.* Five heads of male-sterile scolymus were pollinated with *C. humilis* pollen (Table 3a) resulting in 30 seeds. Four seeds germinated and developed normally. The $F_1$ hybrids turned out to be semi-sterile with ca 52% normally stained pollen grains, they set several seeds upon selfing, and rare seeds upon backcrossing (Table 4).

*II. Crosses between the wild Cynara taxa:*

Crosses were attempted also between the six wild *Cynara* species. Altogether fifteen cross-combinations were made (Table 3b). The crosses yielded only very rare interspecific hybrids. The great majority of many dozens of seedlings raised from these crosses turned out to be selfing products. Faced with such meagre results it is clear that also the crossability between all the tested six wild taxa is low.

Only three $F_1$ interspecific hybrids, each representing a different cross combination, come to flower at the end of the growing season. The fertility scores of these hybrids are brought up in Table 4 and can be summarized as follows:

(1) Wild *C. cardunculus* × *C. syriaca.* This interspecific $F_1$ hybrid was characterized by relatively low pollen score (28% normally stained pollen grains). Upon selfing it still set relatively numerous seeds (25 per head).

(2) Wild *C. cardunculus* × *C. baetica.* Also this inter-specific $F_1$ hybrid was characterized by low pollen score (25% normally stained pollen grains) and by relatively poor seed set, both upon selfing and upon backcrossing.

(3) *C. baetica* × *syriaca.* This single interspecific $F_1$ hybrid had purple-blue flowers, that could have come only from its male parent. The pollen score was 55%. Seed set was poor both upon selfing and after backcrossing.

## Discussion

The main outcome of this study is the demonstration that the wild forms of *Cynara cardunculus* are fully cross-compatible and fully interfertile with the cultivated artichoke. In contrast, the five other wild *Cynara* species tested, namely, *C. syriaca*, *C. cornigera*, *C. algarbiensis*, *C. baetica* and *C. humilis*, were found to be almost fully—or fully—cross-incompatible with the crop. Only very few viable interspecific hybrids between the crops and these five wild relatives have been recovered, and all manifested reduced fertility.

The close affinities between the cultivated artichoke and the wild cardoon are also indicated by isozyme comparisons, the results of which are published elsewhere (Rottenberg et al., 1995). Very high identity values (0.92—0.96) were found between their isozymes. In contrast, the genetic identity values between the crop and the five other wild *Cynara* species were very much lower (0.68–0.74).

These facts strongly indicate that the wild cardoon *C. cardunculus* var. *sylvestris* is the wild progenitor of the cultivated artichoke. In terms of breeding, this wild thistle should be regarded as part of the primary gene pool (Harlan & De Wet, 1971) of the crop. The five other wild relatives are more remote. All are reproductively isolated from the crop (and from its wild progenitor) by strong barriers of crossability. Furthermore, $F_1$ hybrids—when recovered—manifested partial or even strong hybrid sterility. We suspect that cross incompatibility between the cultivated artichoke and *all* these five wild relatives is not complete and that by repeated crossing one could obtain rare hybrids also between the crop and *C. cornigera* and *C. baetica*. We therefore tentatively regard all these five wild *Cynara* species as belonging to the secondary gene pool of the crop. Because *C. humilis* is morphologically rather distant from all other wild taxa, we suspected that this species would be the hardest to cross. This did not materialize; and also *C. humilis* obviously belongs to the secondary gene pool of the crop.

The data obtained have also taxonomic implications. The finds confirm that the cultivated artichoke, the cultivated cardoon and their closely related wild cardoon comprise a single species, *Cynara cardunculus* L. There is no justification to maintain the cultivated artichoke as an independent binomial (*C. scolymus* L.).

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