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Domestication via hybridization of the wild tetraploid oats *Avena magna* and *A. murphyi*

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Abstract The wild tetraploid (2n = 28) oat species *Avena magna* and *A. murphyi* have been domesticated by having been transferred from the common oat, *A sativa* (2n = 42), the characteristics of non-shedding spikelets glabrous and yellow lemma, and reduced awn formation. Domestication has been achieved by crossing the common oat with either of the tetraploid species and then backcrossing the pentaploid hybrids with pollen of the tetraploid wild parent. Among the BC plants obtained only a few produced some seeds. Fertile tetraploids exhibiting the domesticated syndrome have been selected for in the F_2 generation. Although morphologically they were almost indistinguishable from the common oat, they were tetraploids. Wild × domesticated *A. magna* hybrids were vigorous and fertile. They retained their spikelets at maturity, lemma color and pubescence were intermediate between the parental lines, and awns were formed only on the lower floret of the spikelet. Each of these characteristics segregated in a 3:1 fashion, indicating single gene control, as in the common oat. These four characteristics formed a linkage group in one F_2 family and two linkage groups in the other two families. The usefulness of the domesticated tetraploids for oat research and production has been discussed. Taxonomically, the domesticated tetraploids were ranked as subspecies: *A. magna* ssp. *domestica*, and *A. murphyi* ssp. *rigida*.

Key words Gene introgression · Genetics · Linkage · Taxonomy

Introduction

Plant domestication is the process of selecting characteristics that have been favored under cultivation but are usually of low adaptive value, or even lethal, in the wild. Archaeological evidence suggests that most of the major crop plants were domesticated as far back as 5,000–10,000 years ago. In grain crops, the selection for types which had lost their seed dispersal mechanism marks the beginning of domestication and expansion of the crop. Selection of these types is also a prerequisite in modern crop domestication, as in the case of lupin (Schwanitz 1966; Gladstones1967). Rare mutations have provided the raw material for both prehistoric and modern domestication and while these were selected for unintentionally for the most part by the Neolithic farmer, they are prime targets for modern plant domesticators.

This paper reports on the domestication of two wild tetraploid oat species not by selection of rare mutations, but by the transfer into them of the domesticated syndrome of the cultivated oat through hybridization.

The common oat, *Avena sativa*, is an allohexaploid, 2n = 6x = 42, originating from the *A. sterilis–A. fatua* complex of wild and weedy forms (2n = 42) that are interfertile with the common oat. The diploid and tetraploid ancestors of the hexaploid oats have not yet been identified (Ladizinsky 1995). Although the recently discovered tetraploid, 2n = 28, oats, *A. magna* (Murphy et al. 1968) and *A. murphyi* (Ladizinsky 1971) are morphologically akin to *A. sterilis*, neither of them can be regarded to be the tetraploid progenitor of the hexaploid oats. In the last few years *A. magna* have been treated as a synonym of an older taxon, *A. maroccana* (Baum 1977), but recent evidence has shown that the two are separate biological entities (Ladizinsky 1993) and that *A. magna* is the correct epithet for this tetraploid oat. *A. magna* and *A. murphyi* show resistance to rust and powdery mildew and are exceptionally rich in protein. This genetic diversity could be exploited by introgressing it into the common oat, or by reverse introgression of the domesticated syndrome of the common oat into these tetraploids (Ladizinsky and Fainstein 1977). Morphological characteristics of the common oat such as non-shedding spikelets, lack of awns, and glabrous and yellow lemmas are each controlled by a single gene

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(Marshall and Shaner 1992), the transmission of which to the tetraploid species can apparently be achieved.

Among other factors, massive introgression of that kind is conditioned by the degree of homology, or homoeology, between the chromosomes of the species involved. The proportions of the tetraploid genomes that could be affected by introgression is estimated by the number of chiamata in the pentaploid hybrids involving each of the tetraploids and the common oat as compared with their numbers in the tetraploid species. Accordingly, about 75% and 62% of *A. magna* and *A. murphyi* genomes, respectively, can be affected by introgression from *A. sativa* (Ladizinsky 1992).

Materials and methods

In selecting common oat cultivars for the hybridization experiments, an attempt was made to include those that have unique characteristics. The following cultivars and lines have been involved: 'Ogle', '86-4189', '86-4467', '86-5698', all with some tolerance to barley yellow dwarf virus (BYDV); 'Dolphin', a dwarf variety; and 'Tibor' and 'Pennuda', both naked types.

Two *A. magna* accessions were utilized in the initial crosses: M and M3-1. The former is the first collection of this species in Morocco, and the second one was received from Plant Breeding Station Aberystwyth, UK. Another three accessions, M21, M26, and M29, were employed for hybridization with the domesticated derivaties. Of *A. murphyi*, four accessions were used Cs4471, Cs4096, Cs40/1 and Cs43/2, all were received from Aberystwth. The first accession was used for production the pentaploid hybrids and the latter in the backross experiments.

In all crosses the common oat served as the female parent. Reciprocal crosses never yielded viable hybrid seeds. Hybrid seeds were significantly smaller than those produced by selfing and any contamination could be eliminated by sizing at harvest. Backcrosses were accomplished by planting the pentaploid hybrids among the pollen donor plants, thereby allowing natural cross-pollination to occur.

Chromosome numbers of the backcross plants and of the F_2 derivatives were examined in root tips that had been first given a24-h treatment of cold water, then fixed in 3:1 absolute ethanol-glacial acetic acid, and thereafter stained with Feulgen reagent. Meiotic chromosomems were examined in pollen mother cells (PMC) fixed in 3:1 absolute ethanol-glacial acetic acid and stained by acetocarmine.

Pollen fertility was examined in mature anthers following acetocarmine staining. Darkly stained and regularly shaped grains were considered to be viable. Seed fertility was determined as the number of seeds per spikelet. It was very low for the F_1 plants and was estimated in the segregating generations.

For the statistical analysis the LINKAGE-1 program (Suiter et al. 1983) was used to test the fit to 3:1 segregation ratio and two-point linkage.

Results

Production of domesticated *A. magna*

First hybridization cycle

The *A. sativa* × *A. magna* pentaploid hybrids were raised in 1989. They were totally self-sterile when kept in the greenhouse. Pollen stainability was less than 1%, and the anthers did not dehisce. When grown in the field among the *A. magna* plants they were heavily infected by BYDV, though less so that the tetraploid plants. Consequently, some of the tetraploid plants died as early as the vegetative stages, and only a few flowering tillers emerged and dispersed their pollen. Spikelet morphology of the pentaploid hybrids was intermediate between that of their parents. Spikelets remained attached to the pedicels at maturity, as in the common oat. Lemma color was brownish-gray and partially pubescent, and awns were formed only on the lower floret of the spikelet. Although the pentaploid hybrids were highly sterile, they did produce a few seeds. At maturity a seed-bearing spikelet could be distinguished from a sterile one by its greener glumes and darker lemma color. Altogether 33 backcross seeds were collected from the pentaploid hybrids.

The BC plants

These plants were grown in autumn 1989 in the greenhouse, and they exhibited variation in chromosome number, morphology and fertility. The tetraploid chromosome number ($2n = 28$) was observed in 3 plants, but chromosome numbers of $2n = 29$ to $2n = 33$ were most common. A few plants had the pentaploid or even the hexaploid chromosome number. Spikelet morphology varied considerably among the BC plants, and about one-half of the plants dropped their spikelets at maturity as the wild parent does. This was expected because spikelet shedding is governed by a single gene in the hexaploid oats, and spikelet shedding among the BC plants was similar to that of a testcross. The BC plants also varied with respect to lemma color, lemma pubescence and degree of awn development. Nearly all of the BC plants were sterile. Although pollen stainability varied considerably (10% – 89%), only 3 plants set seeds. A plant designated Aa2 ($2n = 32$) had the highest pollen stainability and produced 47 seeds. The other 2 plants, also aneuploids, produced 2–4 seeds.

$F_2 - BC$

Progeny of the Aa2 plant were grown in a nethouse during winter-spring 1990. Thirty-five seeds germinated and 33 plants reached maturity. The chromosome number was checked in 16 plants, of which 11 were tetraploids. At maturity, 25 plants retained their spikelets as does *A. sativa*, and 8 dropped them like the wild parent. Segregation of spikelet shedding fit a single-gene 3:1 ratio, $\chi^2 = 0.01$, $P = 0.9$, indicating the Aa2 BC plant to be heterozygous. Four F_2 plants were morphologically almost indistinguishable from the common oat and possessed the following four main characteristics of the domesticated syndrome: non-shedding spikelets, glabrous lemma, yellow lemma, and a weakly developed awn on the lower floret or no awns at all (Fig. 1). By progeny testing, 2 plants appeared to be homozygous and 2 heterozygous for spikelet shedding.

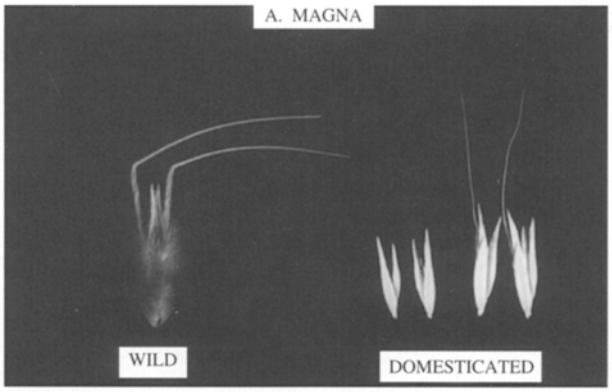

Fig. 1 Spikelets, glumes excluded, of wild and domesticated *A. magna*

Crossing between wild and domesticated *A. magna*

To study the genetic nature of the domesticated *A. magna* and to obtain a deeper insight into the introgression process, the domesticated and wild forms were crossed. Three domesticated lines, Aa2-3, Aa2-13, and Aa2-16, and three wild *A. magna* accessions, M21, M26, and M29 were involved in these crosses. Hybrid seeds were easily obtained in both cross directions. Three F_1 combinations were grown. The plants developed normally and they retained their spikelets at maturity. Lemma color and pubescence were intermediate to that of the parents. Chromosome pairing at meiosis was normal in all three hybrids, and 14 bivalents were regularly formed. Pollen stainability was in the range of their parents, and seed set was normal.

Spikelet shedding, lemma color, lemma pubescence, and awn formation segregated in all three F_2 families. The various characteristics were grouped as follows: lemma color was classified as yellow or as various degrees of coloration; lemma pubescence as glabrous or as various degrees of hairiness; and awn formation as two awns per spikelet, absence of awns, or a single awn per spikelet. Each of the four characteristics segregated as a single gene in the M21 × Aa2-3 and A2-16 × M26 families. Spikelet shedding and number of awns per spikelet also segregated as single genes in the M29 × aA2-13 family, but lemma color and lemma pubescence deviated significantly from the expected 3:1 ratio (Table 1). In the common oat, spikelet shedding, lemma color, lemma pubescence, and awn formation are each controlled by a single gene which are designated *Ba*, *Lc*, *Lp* and *A*, respectively. This gene disignation can also be adopted for the domesticated *A. magna*.

The four loci were linked to one another in the Aa2-16 × M26 family. Lemma pubescence was excluded from this linkage group in the M21 × Aa2-3 family, and in the M29 × Aa2-13 family spikelet shedding and awn formation formed one group and lemma color and lemma pubescence another group (Table 2). The different linkage grouping in the three F_2 families was unexpected because all of the domesticated lines originated from the same BC plant in which meiosis was normal. Meiosis also was normal in the three F_1 hybrids. The discrepancy could be explained by assuming that the parental lines of the F_2 families differed by intercalary translocations that could not be detected at metaphase I of meiosis. The average recombination values of the four genes in the three F_2 families suggest a tight linkage of 1.4 map units between the *Ba* and *A* genes and a linkage of 8 units between *Lc* and *Lp*. The gene order seems to be *Ba-A-Lc-Lp*. *Ba* is equally distant from *Lc* and *Lp* (19.1 units), whereas *A* is closer to *Lc* than to *Lp* (13.6 and 17.6, respectively).

Second hybridization cycle

Fertile tetraploid hybrid derivatives exhibiting the domesticated syndrome were utilized in the second hybridization cycle with selected lines of the common oat. Also here, hybrid seeds were obtained only when the hexaploid lines served as the female parent. In the winter of 1992 the pentaploid hybrids were grown in a greenhouse to protect them from BYDV and were surrounded by plants of the domesticated line Aa2-3, which served as pollen donor. The F_1 plants were tall and vigorous and produced 6–25 panicles per plant. The total yield of backcross seeds was much higher this time, and 593 seeds were collected. However, the proportion of fertile florets remained very low. Fertile florets were also plumper and their lemmas darker than those of the sterile florets. On average, 8.9 seeds were obtained per plant, but hybrids of some combinations did not produce even a single seed, while others produced more than 20 seeds

Table 1 Segregation of four spikelet characteristics in F_2 families of hybrids between wild and domesticated *A. magna* (χ^2, 3:1)

Family	Spikelet shedding		Lemma color		Lemma pubescence		Awn/spikelet	
	Shedding	Non Shedding	Yellow	Dark	Glabrous pubescence		2	1
M21 × Aa2-3	37	93	36	94	29	101	37	93
	$\chi^2 = 0.83, P = 0.36$		$\chi^2 = 0.50, P = 0.46$		$\chi^2 = 0.50, P = 0.46$		$\chi^2 = 0.83, P = 0.36$	
M29 × Aa2-13	41	97	17	121	17	121	41	97
	$\chi^2 = 1.63, P = 0.20$		$\chi^2 = 11.83, P = 0.00$		$\chi^2 = 11.83, P = 0.00$		$\chi^2 = 1.63, P = 0.20$	
Aa2-16 × M26	46	119	33	132	32	133	44	121
	$\chi^2 = 0.72, P = 0.39$		$\chi^2 = 2.20, P = 0.13$		$\chi^2 = 2.76, P = 0.09$		$\chi^2 = 0.24, P = 0.62$	

Table 2 Linkage of spikelet characteristics in *A. magna* wild × domesticated F_2 families

Characteristic & families	χ^2	*df*	*P*	*r*	SE
Spikelet shedding-lemma color					
M21 X Aa2-3	12.38	1	0.00	0.216	0.083
M29 × Aa2-13	2.79	1	0.09	0.428	0.068
Aa2-16 × M26	12.66	1	0.003	0.166	0.075
Spikelet shedding-lemma pubescence					
M21 X Aa2-3	0.02	1	0.98	0.494	0.060
M29 × Aa2-13	2.79	1	0.09	0.428	0.067
Aa2-16 × M26	12.09	1	0.000	0.169	0.075
Spikelet shedding-awn formation					
M21 X Aa2-3	12.38	1	0.000	0.007	0.087
M29 × Aa2-13	13.80	1	0.000	0.000	
Aa2-16 × M29	13.68	1	0.000	0.035	0.007
Lemma color-awn formation					
M21 X Aa2-3	11.01	1	0.010	0.220	0.083
M29 × Aa2-13	3.48	1	0.062	0.421	0.069
Aa2-16 × M29	11.78	1	0.000	0.172	0.075
Lemma color-lemma pubescence					
M21 × Aa2-3	0.03	1	0.846	0.490	0.060
M29 × Aa2-13	13.80	1	0.000	0.000	
Aa2-16 × M29	5.12	1	0.023	0.172	0.074
Lemma pubescence-awn formation					
M21 X Aa2-3	0.008	1	0.929	0.498	0.060
M29 × Aa2-13	3.48	1	0.062	0.421	0.069
Aa2-16 × M26	11.25	1	0.000	0.176	0.074

(Table 3). The number of florets per panicle in the pentaploid hybrids varied in the range of 80 to 120, and an average of 100 florets is a reasonable estimate. If an average of 15 panicles per F_1 plant is assumed the estimated seed set on these hybrids was 8.9/1,500, or about 0.5%.

BC_2

Four hundred backcross seeds were germinated in the autumn of 1992, and chromosome numbers were counted in 237 of them. Although chromosome number in the majority of the seedlings was in the range of 2n = 28 to 35, the tetraploid number was found in only 15% of them (Table 4). The BC plants developed normally and, as expected, they all exhibited the domesticated syndrome. The BC plants were highly sterile, pollen stainability was usually less than 30%, and the anthers did not dehisce. Low pollen stainability was also common in 2n = 28 plants. Of the 380 growing BC plants, only 4 produced seeds and these all were tetraploids. A small number of F_2 derivatives were grown from each of the 4 fertile BC plants. They exhibited some

Table 3 Backcross seeds collected on pentaploid hybrids naturally pollinated by Aa2-3 (2n = 28)

Hybrids	Number of plants	Total no. seeds	Seeds/plant
86-6404 × Aa2-3	5	7	1.4
86-6404 × Aa2-13	7	91	13.0
86-4407 × Aa2–13	7	133	19.0
86-4407 × Aa2-16	8	92	11.5
86-5698 × Aa2-3	3	17	5.6
86-5698 × Aa2-13	2	43	21.5
86-5698 × Aa2-16	8	76	9.5
Dolphin × Aa2-3	3	13	4.3
Dolphin × Aa2-16	10	0	0
Tibor × Aa2-3	5	113	22.6
Pennuda × Aa2-3	8	8	1.0
Total	66	593	8.9

Table 4 Frequency distribution of chromosome numbers among BC plants of the second hybridization cycle involving *A. magna*

Family	28	29	30	31	32	33	34	35	36-52	Total
10[a]	5	5	4	3	6	5	7	5	7	47
11	8	8	6	9	4	5	2	3	4	49
12	4	4	6	9	7	2	4	3	3	42
13	6	4	4	3	2	1	4	4	2	30
14	11	9	12	3	5	4	3	0	0	47
15	1	4	4	1	2	0	4	3	3	22
Total	35	34	36	28	26	17	24	18	19	237

[a] 10 = (86 − 6404 × Aa2 − 13) × Aa2 − 2, 11 = (86 − 4407 × Aa2 − 16) × Aa2 − 3, 12 = (86 − 56498 × Aa2 − 16) × Aa2 − 3, 13 = (Tibor × Aa2 − 3) × Aa2 − 3, 14 = (86 − 4407 × Aa2 − 13) × Aa2 − 3, 15 = (86 − 56984 × Aa2 − 13) × Aa2 − 3

variation in glume size and panicle shape, and were as fertile as their tetraploid parents.

Domesticating *A. murphyi*

A. murphyi domestication was performed according to the experimental procedure used for *A. magna*. Hybrid seeds were also obtained only when the hexaploid parent was used as the female. Accession no. 4471 of *A. murphyi* was crossed with the cultiviated lines 'Ogle' and 86-6404, and the F_1 hybrids were grown in the field surrounded by plants of the wild parents, accession nos. 4471 and 4096. The *A. murphyi* plants were severely infected with BYDV, and many of them died at the vegetative stages. The F_1 hybrids were more tolerant to BYDV, but they also showed severe symptoms. As a result, only 12 BC seeds were collected on the pentaploid hybrids. Morphologically, the pentaploid hybrids were characterised by non-shedding spikelets, a single awn per spikelet, and glabrous yellow lemmas. Another attempt to develop domesticated forms of *A. murphyi* was made in 1991. Cultivars 'Ogle' and '86-4189' were crossed with accession no. 4471 of *A. murphyi*. Forty-five pentaploid hybrids were grown in the greenhouse to protect them from BYDV, and they were surrounded by *A. murphyi* plants, accessioins nos. 4771 and 4096, as the pollen source. The F_1 hybrids were vigorous but highly sterile, and only 102 seeds were collected from them, about 2 seeds per plant.

The BC seeds were germinated in the autumn of 1992, and chromosome numbers were counted in 41 seedlings. None of these had the tetraploid chromosome number, a single plant had $2n = 29$, and in the remainder of the plants, the chromosome number varied from $2n = 30$ to $2n = 35$. Despite their uneven chromosome numbers, 6 plants produced a few seeds. Among them, plants Ai1-5 and Ai1-7 had $2n = 33$ and $2n = 32$, respectively, Ai2-29 had $2n = 35$, and Ai2-35 had $2n = 31$.

Spikelet shedding segregated, as expected, among the BC plants. At maturity, 39 plants shedded their spikelets while in 36 plants the spikelets remained attached to the pedicels. This segregation fit the 1:1 ratio of a monohybrid testcross ($\chi^2 = 0.12$, $P = 0.90$). Among the partially fertile BC plants which retained their seeds were Ai2-29, Ai2-34, Ai2-35, and Ai2-39, and these were used for further selection of domesticated *A. murphyi*. Additional spikelet characteristics of these plants were glabrous and yellow lemmas and a single awn per spikelet, always on the lower floret. Plants with shedding spikelets always had two awns per spikelet, and they developed as in the wild parent.

The F_2 families

Chromosome numbers varied within each of the four F_2 families and between them. In Ai2-35, which was derived from a $2n = 31$ plant, individuals with $2n = 28$ were most common (Table 5). Most interesting, however, is the Ai2-29 family that originated from a $2n = 35$ plant. Here again, about one-third of the plants were tetraploids. Spikelet shedding segregated in each of the four F_2 families, indicating the heterozygous state of the respective BC plants. The fertility of the F_2 plants also varied considerably. Plants with the tetraploid chromosome number exhibited the whole range, from complete sterility to nearly normal seed set (Table 6). By progeny testing of the most fertile F_2 plants, which also retained their spikelets at maturity, a number of fertile domesticated lines were selected (Fig. 2).

Fertile domesticated forms of the Ai2-29 and Ai2-35 families were crossed with wild *A. murphyi*, no. 4471. The F_1 hybrids developed normally and were fully fertile. Their spikelets did not shed at maturity, lemmas were yellow and glabrous, and the awns were developed only on the lower floret of the spikelet.

Table 5 Frequency distribution of chromosome numbers among F_2 families of (*A. sativa* × *A. murphyi*) × *A. murphyi*

	2n						
Family	27	28	29	30	31	32	Total
Ai2-29 (2n = 35)	–	6	4	2	7	1	20
Ai2-34	–	4	1	1	–	1	7
Ai2-35 (2n = 31)	1	23	20	9	1	–	54
Ai2-39	–	1	4	2	1	–	8

Table 6 Ranges of number of seeds per spikelet ($n = 20$) in plants having the same chromosome number in F_2 families of the (*A. sativa* × *A. murphyi*) × *A. murphyi* cross

	2n				
Family	28	29	30	31	32
Ai2-29	0–2.57	0–1.90	0	0–1.44	–
Ai2-34	0–0.32	0	0	–	0
Ai2-35	0–2.50	0–2.70	0–1.96	1.47	–
Ai2-39	1.90	0–1.10	0.67	0.18	–

Fig. 2 Spikelets, glumes excluded, of wild and domesticated *A. murphyi*

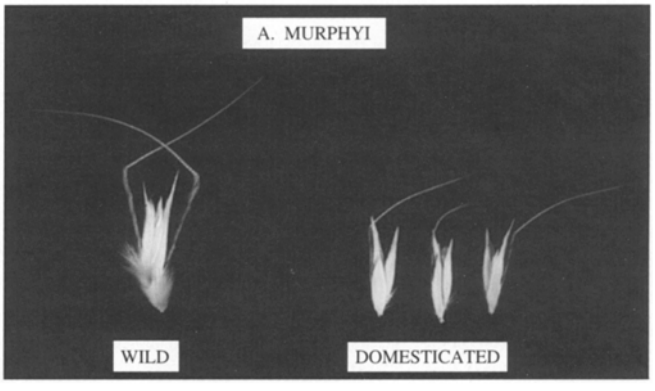

Table 7 Protein content in parental species and tetraploid derivatives

Species & line		Seed weight (g)	Protein (%)
A. sativa	86-6404	0.608	18.75
	Ogle	0.523	18.05
A. magna	M1 (wild)	0.525	24.75
	M3 (wild)	0.517	24.40
	Aa2-3 (domesticated)	0.555	23.19
	Aa2-13 (domesticated)	0.532	23.30
	Aa2-16 (domesticated)	0.552	19.89
	Ba 13-13 (domesticated)	0.523	24.07
	Ba 14-10 (domesticated)	0.526	24.02
A. murphyi	4771 (wild)	0.519	23.69
	Ai2-35 (domesticated)	0.490	18.39

Protein content of the domesticated tetraploids

Protein content of some of the domesticiated tetraploids and their parental lines, all of which grew under uniform conditions, was examined in the summer of 1994 (Table 7). Protein contents of the two *A. sativa* lines were 18.05% and 18.75%, while those of *A. magna* and *A. murphyi* were up to 24.71% and 23.69%, respectively. The three magna-derivatives that were examined had protein contents that fell in the range of those of their wild parent. In a single *murphyi*-derivative, however, groat protein content was similar to that of the common oat.

Discussion

The present study demonstrates how the domesticated syndrome of a crop plant can be transferred into its wild relatives, which are members of the crop's secondary gene pool and also have a different chromosome number. The main obstacles to gene flow, as demonstrated here, between the hexaploid common oat and the two wild tetraploids are as follows: (1) hybrid seeds can be produced only when the common oat is the female parent, (2) extremely low seed set on the pentaploid hybrids, even when they were pollinanted by the parental species, and (3) a low proportion of BC plants produce seeds.

Since hybrid seeds can only be produced when the hexaploid species serves as the female parent, all of the tetraploid derivatives contain the *A. sativa* cytoplasm. Repossession of the tetraploid cytoplasm can be achieved at a later stage by hybridizing the tetraploid derivatives with their respective tetraploid wild form as female parent. The production of hybrid seeds only in the (6X) × (4X) cross direction, in the second hybridization cycle as well, suggests that no cytoplasmic or genetic factors affect seed set, but there is a difference in number of genomes in the endosperm of the hybrid seeds. The smaller size of the hybrid seeds compared with those produced by selfing also indicates slow endosperm development.

Complete self-sterility of the pentaploid hybrids is due to irregular chromosome distribution at anaphase I of meiosis and low pollen fertility, which does not enable anther dehiscence and release of the few viable pollen grains. Chromosome numbers in viable female gametes of the pentaploid hybrids can be deduced by subtracting the pollen chromosome number, 14, from the 2n of the BC plants. It appears that gamete viability, at least that of female gametes, is not conditioned by a specific chromosome number but apparently by the genetic content of the individual chromosomes. Furthermore, the chromosome constitution that confers gamete viability on the pentaploid hybrids will not necessarily guarantee fertility of the resultant BC plant. Partially fertile aneuploid plants evidently contained the complete set of 14 pairs, which allowed the appearnace of stable tetraploids in the F_2 generation.

In addition to depending on the fertility of the interspecific hybrid and hybrid derivativies, introgression also depends upon the degree of homology and potential of crossing-over between the chromosomes of the species involved. The recombination potential between the common oat and *A. magna* or *A. murphyi* is relatively high, 75% and 62%, respectively (Ladizinsky 1992). These values, however, do not predict the possibility of introgressing a specific gene or characteristic from the hexaploid common oat to either of the wild tetraploids. The recovery of stable, fertile tetraploid derivatives exhibiting the domesticated syndrome of the common oat indicates that the genes controlling the relevant characteristics reside in chromosome segments that are considerably homologous to one another in the common oat and both tetraploids. Each of the characteristics spikelet shedding, lemma color, lemma hairiness and awn formation is controlled by a single gene in the common oat. This has also been found in domesticated *A. magna*. Furthermore, several studies have shown that these four spikelet characteristics are linked to one another in the common oat (Marshall and Shaner 1992). Linkage between these four characteristics was found in the Aa2-16 × M26 family of domesticated *A. magna*. Lemma hairiness was removed from the linkage group in the M21 × Aa2-3 family, and in the Aa2-13 × M29 family spikelet shedding and awn formation formed one linkage group and lemma color and lemma hairiness another group. Since chromosome pairing was normal in the F_1 of these three families, it is likely that two of them were heterozygous to a reciprocal translocation that was too small to cause a detectable quadrivialent at metaphase I of meiosis.

Potential use of the domesticated tetraploids

The production of domesticated forms of *A. magna* and *A. murphyi*, naturally raises the question of their usefulness with respect to oat research and production. At the

moment, their impact may be visualized in three different areas: (1) they may become crops in their own right, (2) they may be used to synthesize new hexaploid oat types, and (3) they may be an effective tool for gene transfer from diploid species to the common oat.

It is premature to assess the potential of the domesticated tetraploids as new crops. Much work is needed before the first commercial tetraploid oat variety can be released. This endeavor must include the transfer of additional diversity of agronomic value from the common oat and the initiation of breeding within each of the domesticated tetraploids. It is also difficult to predict any advantages of these tetraploids over the common oat. In this regard, however, wheat is an encouraging model. Both hexaploid and tetraploid wheat cultivars are extensively grown, usually for different purposes and in different areas. The hexaploid wheat is grown mainly for bread-making, and it is common in cooler areas, whereas the tetraploid wheat is used for pasta and grows in warmer areas. Both *A. magna* and *A. murphyi* grow naturally in warm habitats in Morocco and Spain. In such habitats their domesticated derivatives may be more successful than the common oat. High protein content is another potential characteristic of the domesticated tetraploids. Accessions of the wild tetraploids have the reputation of having 25%–40% more protein content in the groat than the leading common oat cultivars. The high protein content maintained in some of the domesticated lines suggests that high protein content may be one of the main features of domesticated tetraploid cultivars.

The common oat is an allohexaploid, but the diploid and tetraploid ancestors of the common oat, as with all other hexaploid oats, have not yet been identified. Similarly, there is no way of knowing if the genomic composition of the common oat is optimal for achieving the highest possible performance in this crop. The domesticated tetraploid forms enable, for the first time, the synthesis and testing of new hexaploids with different genomic combinations. We have produced such as synthetic hexaploid involving domesticated *A. magna* and var 'Saia' of the diploid *A. strigosa*. The performance of this synthetic hexaploid suggests that it can be used, almost immediately, as a crop, and the details will be published elsewhere.

Utilization of the genetic diversity of diploid oat speices for improving the hexaploid common oat offers problems because of crossability barriers. The diploid oat species, on the other hand, are cross-compatible with the tetraploids *A. magna* and *A. murphyi*, and the F_1 hybrids are vegetatively normal but sterile. Fertility is then resotred by chromosome doubling, and the synthetic hexaploids could easily be hybridized with the common oat in a reciprocal fashion. When the domesticated forms of such tetraploids are available for producing synthetic hexaploids, the F_1 hybrids with the common oat and their derivatives possess most of the main characteristics of domesticated oats, enabling easier selection of desirable types in the segregating generations.

Since the domesticated forms of *A. magna* and *A. murphyi* will apparently, have some impact on oat research and production, they need to be distinguished in some way, and their taxonomic status is therefore a relevant question. According to te International Code of Botanical Nomenclature (1983), a hybrid between representatives of two or more taxa are nothotaxa and may receive a name (article H.3.1); the epithet of a nothotaxon is a collective name (article H.3.3); a nothotaxon has the same rank as its postulated or known parent taxa (article H.5.1).

It seems that these regulations and recommendations cannot simply be applied for establishing the taxonomic status of the domesticated tetraploid oats for the following reasons: (1) these types are not hybrids but hybrid derivatives; (2) although they have resulted from hybrids between two distinct species, they do not deserve species rank because they are fully interfertile with their respective tetraploid wild parent.

Crop plants and their wild progenitors traditionally have been treated as two different species. In oat, for example, the common oat *A. sativa* and its wild progenitor, *A. sterilis* or *A. fatua*, are considered as two separate species (Baum 1977). Modern taxonomy of crop plants, however, regards a crop plant and its wild progenitor as subspecies of the same species because the two are interfertile and the domesticated form has resulted from human selection. This recommendation may also be adopted with regard to the domesticiated tetraploid oats and they too should be ranked as subspecies, and are described as such here:

1) *Avena magna* Murphy et Terrel ssp. *domestica* Ladizinsky subsp. nov. Similis *Avena sativa*, spiculae non-deciduae, lemma glabra vel pubescentia, arista absentes vel rudimentales, $2n = 28$, plantae interfertilis cum ssp. *magna* (holo, HUJ).

2) *Avena murphyi* Ladizinsky ssp. *rigida* Ladizinsky subsp. nov. Similis *Avena sativa*, spiculae non-deciduae, lemma glabra, arista presentes vel absentes, $2n = 28$, plantae interfertilis cum ssp. *murphyi* (holo. HUJ).

Ranking the domesticated forms as subspecies also requires new intraspecific classification in both *A. magna* and *A. murphyi*, and the following classification is proposed:

1) *A. magna* Murphy et Terrell, ssp. *magna* Murphy et Terrell, wild., ssp. *domestica* Ladizinsky, domesticated.

2) *A. murphyi* Ladizinsky, ssp. *murphyi* Ladizinsky, wild, ssp. *rigida* Ladizinsky, domesticated.

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