

Article

Characteristics of Progenies Derived from Bidirectional *Avena sativa* L. and *Avena fatua* L. Crosses

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Abstract: Crossing genetically distant forms is widely used in breeding programs and allows the introduction of beneficial features from the wild into cultivated species. In this study, agronomic traits of two F_2 segregating populations derived from crosses in both directions between *A. sativa* cv. Sam and *A. fatua* '51532', as well as their parental forms, were phenotyped and statistically compared. Almost all mean values of the analysed features in the populations ranged between the values of the two parental forms. In both F_2 populations, high variability of the traits was observed. The plant height was strongly correlated with the length of the first internode below the panicle in all populations except parental form '51532'. An intermediate correlation between the plant height and the panicle length could be observed only for 'Sam' and 'Sam' $\times$ '51532'. The segregation of non-shattering to shattering phenotypes of the progeny confirmed a single gene inheritance of the trait. Additionally, in both combinations, transgressive forms in terms of some phenotypic traits were observed. The direction of crosses had no impact on the values of characterised parameters. During the interspecific crosses, new breeding lines and cultivars are obtained, enriched with specific qualitative and quantitative properties. The genetic distinctness between crossed species often prevents the formation of desired hybrids but also enables obtaining superior genotypes with traits exceeding the parental forms. Even though efficient crossbreeding with *A. fatua* is demanding, looking for new germplasm in wild ancestors is crucial for expanding the *Avena* genetic pool and developing long-term strategies beneficial to modern oat breeding.



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Keywords: *Avena fatua*; *Avena sativa*; interspecific hybrids; phenotyping; wide crossing; oat

1. Introduction

A. fatua is a hexaploid *Avena* species belonging to the family Poaceae, with genome AACCCD and a chromosome count of $2n = 6x = 42$ [1,2]. *A. fatua* may easily adapt to different environmental conditions because of special morphological features, high seed production and a unique germination ecology [3]. This widespread wild oat is one of the 10 worst annual weeds of cereal crops in agricultural regions [4], with increasing resistance to herbicides [5–7]. *A. fatua* causes significant economic danger to crop yield due to the seed shattering allowing achieving long-distance dispersal, the ability of seed dormancy, enabling the seeds to remain viable for several years in the soil and competitiveness at the seedling stage [8,9]. At the same time, it may be widely used in breeding programs as a new source of useful genes since *A. fatua* genotypes can be crossed quite easily with oat cultivars.

Many researchers have proven that wild *A. fatua* is a rich source of useful genes and has tremendous potential for oat varieties improvement. Briggles and Youngs [10] indicated that this wild oat contains disease-resistance genes and other valuable properties such as early maturity, rapid growth rate, seed dormancy, high seed protein and high groat percentage. Another advantage of *A. fatua* is its good adaptation to difficult growing conditions. It grows in equal amounts on alkaline and acidic soils, both nutrient-rich and poor. Luby and

Stuthman [11] established that *A. fatua* might contribute to *A. sativa* valuable agronomic and grain quality traits, such as increased oil content (9.2%), which is associated with increased grain energy. *A. fatua* contained the highest level of esterase and lipase among species of Gramineae; therefore, it was considered a good feedstock for these enzymes in industry production [12]. The grain of *A. fatua* contained over 20% of protein, 8% of lipid and 55% of starch and was rich in essential minerals and vitamins [13]. Moreover, *A. fatua* was a source of dwarfing genes crossed into cultivated oat for increased lodging resistance [14] and resistance to barley yellow dwarf virus (BYDV) [15]; however, it remains underexploited as a fungal resistance gene donor.

A. fatua, widely available and richly gathered in global collections, can still be a valuable source of new gene alleles for the improvement of cultivated oat. The most recent studies indicate that *A. fatua* may be a valuable source of resistance genes to the most damaging fungal diseases of oat. Paczos-Grzęda et al. [16] tested 204 worldwide accessions of *A. fatua* in terms of crown rust reaction using host-pathogen tests with five highly virulent races of *Puccinia coronata* f. sp. *avenae*. Twelve of them, mainly derived from Kenya or Egypt, allowed postulation of the likely presence of novel crown rust resistance genes. Similarly, Okoń et al. [17] tested eleven genotypes of *A. fatua* with the three most virulent isolates of *Blumeria graminis* f. sp. *avenae*, and some of the genotypes presented intermediate resistance.

Previous studies confirm that cultivated oat (*A. sativa*) has a very narrow gene pool [18–24]. In order to extend the genetic variability of oat, interspecies and intergeneric crosses were carried out. As an exotic alleles source, *A. sterilis* and *A. fatua* accessions were used [11,14,15]. There are no crossing barriers between hexaploid species within the genus *Avena*, and hybrids between *A. sativa*, *A. byzantina*, *A. fatua* and *A. sterilis* could be obtained with relatively low effort [25]. Wild and weedy species seeds or spikelets shattering at maturity inherited as a recessive trait is the main obstacle. However, plant breeders, mostly for economic reasons, usually source populations for cultivar development from crosses within regionally adapted *A. sativa* cultivars with good agronomic performance to avoid yield penalties connected with undesirable alleles derived from wild progenitors and linkage drag [24]. Linkage drag is a severe limitation on the use of potentially beneficial alleles accumulated in wild species and may not always be removed, even by multiple backcrossing to the recurrent parents [26]. By narrowing the starting material, breeders do not need to eliminate the undesirable features, significantly speeding up the breeding process, but this attempt leads to meeting only short-term breeding goals and narrowing the cultivated oat gene pool [27]. Therefore, prebreeding programmes are conducted by scientific institutions to support breeders and provide preliminary evaluated and selected lines. During the initial selection, many quantitative traits determining the value of the evaluated forms are taken into account. The most frequently assessed traits, such as plant height, tillering, earliness and fertility of the spikelet or 1000 kernel weight, are determined due to their direct impact on yield, which is still the basic goal of modern oat breeding [28].

Interspecific crosses of Polish *A. sativa* cultivars with *A. sterilis* and *A. fatua* were performed previously [29–31], and within segregating progeny lines, characterising advantageous traits were identified. The best lines were given over to the breeders for further crosses or selection. This study is a continuation of our previous efforts and attempts to determine the influence of *A. fatua* on the extension of genetic variability in cultivated oat based on the assessment of the morphological traits of two hybrid F₂ populations derived from crosses between *A. sativa* and *A. fatua*. This study also investigated whether cross-breeding with *A. fatua* and the crossing direction affects the breeding value of cultivated oat.

2. Materials and Methods

2.1. Plant Material

The study materials were hexaploid oat hybrids of the F₁ and F₂ generations derived from crosses: *A. sativa* L. cv. Sam × *A. fatua* L. ‘51532’ and *A. fatua* L. ‘51532’ × *A. sativa* L. cv. Sam obtained at the Institute of Plant Genetics, Breeding and Biotechnology of the Univer-

sity of Life Sciences in Lublin, Poland, as well as the parental forms of studied populations. ‘Sam’ is a Polish variety of common oat derived from Strzelce Plant Breeding company, with a pedigree (Flamingsnova × Swan mut) × {[Alfred × (Garland × C2)] × Swan mut.}. The ‘51532’ is the accession of wild oat *A. fatua* L. originated from Peru and was obtained from the Polish genebank (National Center for Plant Genetic Resources in Radzików, Poland).

The field experiment was carried out at the Experimental Farm of the University of Life Sciences in Lublin, in Czesławice (Czesławice 51°18′ N, 22°15′ E). Forms intended for crossing, as well as field and laboratory evaluation, were sown on brown soil made of loess, belonging to the 2nd valuation class. The forecrop was potatoes. In late autumn, deep ploughing was performed, and in spring, mineral fertilisation was applied in the amount of 60 N kg · ha^{−1}, 80 P₂O₅ kg · ha^{−1} and 100 K₂O 100 kg · ha^{−1}.

Parental components for the crossing were sown manually on 2-row plots, about 1 m long and 0.6 m wide, in April 2016. As a result of the crossing, F₁ hybrid grains were obtained, which in 2017 were sown on experimental plots to obtain F₂ grains. F₂ generation hybrid grains were harvested from each F₁ plant and sown pointwise at a distance of 10 cm × 20 cm in April 2018. At the beginning of the growing season, maintenance spraying with herbicide (Chwastox D) was carried out, and later, the weeds were removed manually. In addition, spraying by Fastac 10EC was performed against the cereal leaf beetle (*Oulema melanopus*) at the rate of 0.1 L · ha^{−1}.

Plants of the segregating progeny and *A. fatua* were protected against grain shedding by putting cellophane isolators on panicles. Field observations were made during the growing season; afterward, in the phase of full maturity, the plants were harvested for laboratory evaluation of agronomic traits.

2.2. Phenotyping and Data Analysis

Phenotyping was carried out to evaluate the basic agricultural values of plants in field and laboratory conditions. The heading date was recorded in the field as the date on which the base of the panicle had just emerged from the boot and expressed as the number of days from 1st May to the heading date. Plant height (cm) was measured just before harvest as the distance from the soil surface to the apex of the panicle. The following factors were assessed in the laboratory conditions: the number of productive and unproductive tillers; the number of internodes in the main shoot; length of the first internode below the panicle (cm); diameter of the second from the bottom internode in the main shoot (cm) measured with vernier; the main panicle length (cm), from the bottom of panicle to the top of the upper spikelet; the number of spikelets from the main panicle; and number and weight (g) of kernels from the main panicle. In the case of shattering *A. fatua* plants and F₂ progeny, the number of spikelets and kernels were assessed after careful removal of cellophane isolators from the panicles. Additionally, the following were calculated: the fertility of the spikelet (number of grains per one spikelet in the main panicle), 1000 kernels weight (g) (weight of grains per panicle/number of grains from the panicle × 1000) and lodging factor Lc [32] determined based on the ratio of plant height to the diameter of the second internode from the bottom.

For each analysed trait, mean, median, minimum, maximum and standard deviation were calculated. The fit of the traits to a normal distribution was assessed using Shapiro–Wilk’s normality test ($\alpha = 0.05$). The homogeneity of variance was tested using Bartlett’s test. Multiple comparisons among all genotypes were carried out according to Tukey’s test or mean ranks post hoc comparison ($p < 0.05$). Chi-squared (χ^2) analyses of the phenotyping data from F₂ progeny were conducted to test the goodness-of-fit of observed to expected segregation ratios. Two sample test comparison of shattering and non-shattering progeny from the cross *A. fatua* ‘51532’ and *A. sativa* ‘Sam’ was performed by t-test or Mann–Whitney *U* test ($p < 0.05$). The Spearman correlation between analysed phenotypic traits was assessed for all data and divided into populations. The results were statistically analysed using STATISTICA 13.3 [33] and PAST 4.1 software [34].

3. Results

A phenotypic evaluation was carried out for 30 plants of each of the tested parental forms of the combinations, as well as 158 plants of the *A. fatua* L. '51532' × *A. sativa* L. cv. Sam and 152 plants of the *A. sativa* L. cv. Sam × *A. fatua* L. '51532' population.

Analysis of variance results indicated statistically significant differences ($p \leq 0.0011$) among studied populations for all phenotyped traits.

The plant height of studied parental forms ranged from 108 to 143 cm for cv. Sam and 125–155 cm for '51532'. The minimum plant height within the cv. Sam × '51532' population was 65 cm, and the maximum height was 156 cm, while for the '51532' × cv. Sam population, these values ranged from 98 cm to 170 cm (Table 1). The standard deviation for both populations was at the level of 15.5 and 14.4, respectively, showing high variability of the trait (Table 1). The results confirmed a normal distribution of the trait for '51532' × cv. Sam population. Statistically significant differences in height were observed between parental forms. The plants of the cv. Sam × '51532' population were lower than the parental forms and the '51532' × cv. Sam population, while the genotypes of the '51532' × cv. Sam population did not differ significantly from the parental forms (Table 2).

When taking into account the number of productive and unproductive tillers, it was noticed that the 'Sam' parental form differed significantly from other populations, as it developed on average 2.6 and 1.3 of the tillers, respectively. In both parental and F_2 forms, a greater number of productive than unproductive tillers was observed. Both populations developed the same average number of unproductive tillers (2.4) (Table 1). Additionally, a significant increase in the number of productive and unproductive tillers was noted in F_2 populations in comparison to *A. sativa* 'Sam' (Table 2). Both traits did not have a normal distribution for any of the studied populations.

The number of internodes in the main shoot of the 'Sam' cultivar differed from other populations, achieving the highest mean number of 5.7 (Table 2). The mean number of internodes of both analysed populations did not differ from *A. fatua* '51532'. The median of the analysed trait was 5 for the cv. Sam × '51532' population as well as wild form '51532', and for the '51532' × cv. Sam population reached 4. The minimum number of internodes for populations and '51532' was 3; the maximum was 6 for the cv. Sam × '51532' population and '51532', and the maximum was 7 for the '51532' × cv. Sam population (Table 1). The trait distribution was not normal for any of the studied populations.

The average distance between the panicle and the internode below in *A. sativa* cv. Sam was 50 cm and in *A. fatua* '51532', 55.7 cm. A large differentiation of the tested trait was found in the individuals of the '51532' as well as hybrid populations, and the standard deviation ranged from 8.2 to 10 (Table 1). Cv. Sam × '51532' population and 'Sam' cultivar differed significantly from '51532' × cv. Sam population and its maternal form '51532' (Table 2). Normal distribution was observed in the '51532' × cv. Sam population.

The diameter of the second internode in the main shoot measured from the root in both parental forms differed significantly from each other and in both populations (Table 2). In the 'Sam' cultivar, the thickest internodes were observed with an average value of 6.5 cm, while in the wild form '51532', the internodes were much thinner, on average 3.6 cm (Table 1). Individuals of both populations developed internodes of similar thickness; for the cv. Sam × '51532' population, the internode diameter ranged from 2.1 to 7.6, and for the '51532' × cv. Sam population was from 2.9 to 7.7. The trait had a normal distribution in studied F_2 populations.

Table 1. Statistical analysis of agronomic traits of parental forms *Avena sativa* cv. Sam and *Avena fatua* '51532' as well as their F₂ populations.

Parental form/Population		Plant Height	Number of Productive Tillers	Number of Unproductive Tillers	Number of Internodes in the Main Shoot	Length of the First Internode	Diameter of the Main Shoot Second Internode	The Main Panicle Length
<i>A. sativa</i> cv. Sam	Mean	130.0	2.6	1.3	5.7	50.0	6.5	25.9
	Min	108.0	1.0	0.0	5.0	43.0	5.5	22.0
	Max	143.0	4.0	4.0	6.0	58.0	7.5	29.0
	Stand. Dev.	8.8	0.8	1.2	0.5	3.5	0.7	1.6
	Median	130.0	3.0	1.0	6.0	50.0	6.5	25.0
<i>A. fatua</i> '51532'	Mean	139.7	6.3	3.6	4.8	55.7	3.6	23.1
	Min	125.0	1.0	0.0	3.0	27.0	2.9	14.0
	Max	155.0	20.0	8.0	6.0	69.0	4.3	28.0
	Stand. Dev.	7.5	4.2	2.3	0.6	10.0	0.4	2.8
	Median	140.0	6.0	4.0	5.0	58.0	3.5	23.0
51532 × cv. Sam	Mean	135.0	5.6	2.4	4.4	57.3	5.2	25.1
	Min	98.0	1.0	0.0	3.0	31.0	2.9	15.0
	Max	170.0	20.0	10.0	7.0	79.0	7.7	36.0
	Stand. Dev.	14.4	2.9	2.2	0.6	8.2	0.9	3.3
	Median	136.0	5.0	2.0	4.0	57.0	5.3	25.0
cv. Sam × 51532	Mean	121.0	4.7	2.4	4.6	51.0	5.0	23.6
	Min	65.0	1.0	0.0	3.0	22.0	2.1	15.0
	Max	156.0	19.0	11.0	6.0	90.0	7.6	35.0
	Stand. Dev.	15.5	2.8	2.3	0.6	9.1	0.9	3.8
	Median	120.0	4.0	2.0	5.0	52.0	5.0	23.0
Trait distribution among studied populations	A point across the box is depicted as the median. The box indicates the 25th and 75th percentiles, and the whiskers represent minimum and maximum values.							

Table 2. Mean ranks post hoc comparison of agronomic traits among parental forms *Avena sativa* cv. Sam and *Avena fatua* ‘51532’ as well as their F₂ populations. Lowercase letters (a, b, c, d) indicate homogeneous groups ($p < 0.05$).

Population	Plant Height	Number of Productive Tillers	Number of Unproductive Tillers	Number of Internodes in the Main Shoot	Length of the First Internode below the Panicle	Diameter of the Main Shoot Second Internode	The Main Panicle Length	Number of Spikelets from the Main Panicle	Number of Kernels from the Main Panicle	Weight of Kernels from the Main Panicle	The Fertility of the Spikelet	1000 Kernels Weight	Lodging Factor Lc	Number of Days from 1st May to Head Date
cv. Sam	a	a	a	a	a	a	a	a	a	a	a	a	a	a
51532	b	bc	b	b	b	b	b	b	b	b	ab	b	b	b
51532 × cv. Sam	ab	b	bc	b	b	c	a	c	b	c	b	c	c	c
cv. Sam × 51532	c	c	c	b	a	c	b	c	b	c	ab	c	d	c

It was observed that cv. Sam and the '51532' × cv. Sam plants had significantly longer main panicles in comparison to the '51532' and cv. Sam × '51532' (Table 2); however, the differentiation of the measurements was much higher in both populations. The panicles length of the parental forms ranged from 22 to 29 cm in the 'Sam' and from 14 to 28 cm in the '51532' plants. The shortest panicle of plants of both populations was 15 cm long, and the longest measured 35 cm in the cv. Sam × '51532' population and 36 cm in the '51532' × cv. Sam population (Table 1). A normal distribution of the trait was observed in the cv. Sam × '51532' population.

The highest average number of spikelets was observed for the 'Sam' cultivar (103.3) and the lowest (38.7) for the '51532' (Tables 1 and 2). The mean number of spikelets in both of the populations was at a comparable level of 53.2 for the cv. Sam × '51532' and 55.2 for the '51532' × cv. Sam. The trait was very diverse in the progeny and ranged from 15 to 139 in the cv. Sam × '51532' population (standard deviation of 25.6) and from 11 to 131 in the '51532' × cv. Sam population (standard deviation of 23.4) (Table 1), and the measurements exceeded the maximum number of spikelets from the main panicles of cv. Sam (125). The consequence of the variation in the number of spikelets was the variation in the number of kernels and kernel weights of the main panicle. The standard deviation of the number of kernels was at a similarly high level in cv. Sam × '51532' population (47.4) and '51532' × cv. Sam population (41.2). The mean number, as well as the weight of kernels from the main panicle of populations, was slightly higher than that of the parental form '51532'; however, still much lower than that of the 'Sam' cultivar (Table 1). Plants of both populations developed panicles with the same average kernel weight (2.3 g) and a comparable number of kernels, from 10 to 289 in the cv. Sam × '51532' population, and from 12 to 217 in the '51532' × cv. Sam population (Table 2). In both F₂ populations, all three traits had a distribution far from normal.

The fertility of the spikelet differed significantly only between the '51532' × cv. Sam population (1.7) and its paternal form 'Sam' (2.1) (Table 2). In the cv. Sam × '51532' population and paternal form '51532' spikelet fertility was 1.9 and 1.7, respectively (Table 1). The results confirmed the normal distribution of the trait for the '51532' × cv. Sam population.

The analysis of the 1000 kernels weight showed the highest mean (34.9 g) for the 'Sam' variety and the lowest (20.1 g) for the '51532', which was significantly different from the populations and the 'Sam' parental form. The differentiation of the trait in the hybrids was at a high level and ranged from 5.9 to 46.4 g in the cv. Sam × '51532' population and from 2.5 to 38 g in the '51532' × cv. Sam population (Table 1). The distribution of the trait in the populations was not normal.

In terms of the lodging factor, each of the groups was statistically different (Table 2). The lowest coefficient was observed in *A. sativa* 'Sam' (20.2) and the highest in *A. fatua* '51532' (39.6) (Table 1). In parental forms, the trait was less varied than in populations, while in the case of populations, greater differentiation of the trait was observed in the '51532' × cv. Sam population. The distribution of the trait was far from normal within the progeny of studied F₂ populations.

The last statistically analysed trait was the number of days from 1st May to the heading date. The panicles of *A. fatua* '51532' matured at the latest on average 58.7 days from 1st May, which made the group statistically different from other analysed populations (Table 2). In *A. sativa* 'Sam' and populations, the maturation period of the panicles was a few days shorter and amounted to 54.3 days in the cv. 'Sam', 53.5 days in the plants of the cv. Sam × '51532' population and 54.1 days in the plants of the '51532' × cv. Sam population (Table 1). The trait distribution was comparable, but a lack of normal distribution was noted in populations.

The largest number (13) of correlated traits ($r > 0.65$) were noticed in the cv. Sam and the smallest (2) in '51532' × cv. Sam. The number of kernels was correlated with the weight of kernels from the main panicle ($r \approx 0.87$, $p > 0.05$), regardless of whether the entire dataset was analysed or the data were grouped by population; however, the weakest correlation was observed for '51532' ($r = 0.7$). Similarly, the number of spikelets

was positively correlated with the number of kernels from the main panicle as well as the diameter of the second internode was negatively correlated with the lodging factor (Lc) ($r < -0.69$). The plant height was positively correlated with the length of the first internode below the panicle ($r > 0.65$, $p > 0.05$) in all populations except ‘51532’. Additionally, in ‘Sam’ and cv. Sam $\times$ ‘51532’, the diameter of the second internode in the main shoot was correlated with the number of spikelets from the main panicle ($r = 0.71$) (Figure 1).

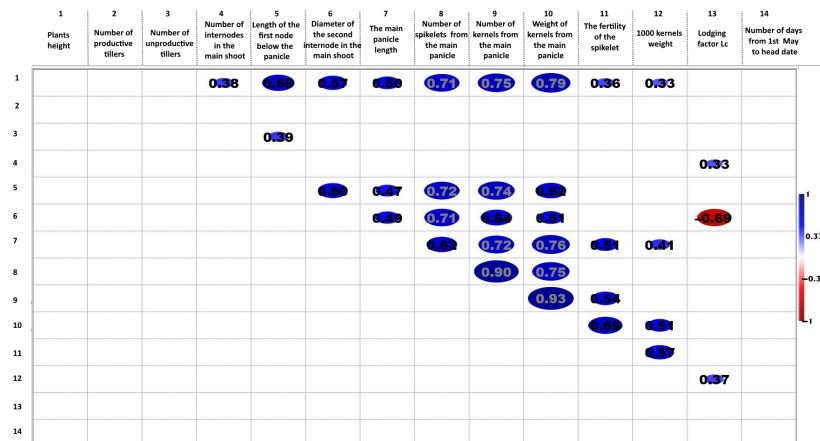
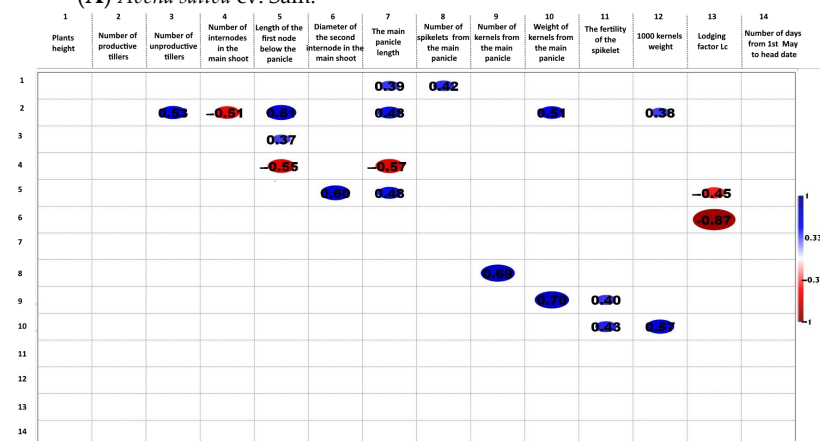
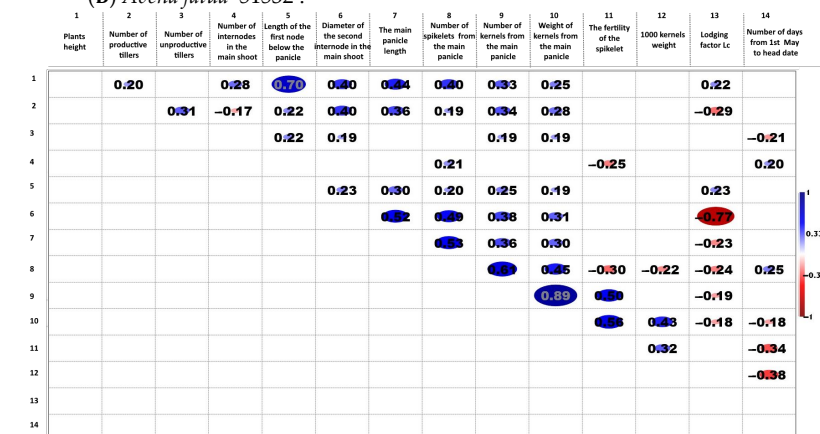
(A) *Avena sativa* cv. Sam.(B) *Avena fatua* ‘51532’.(C) *Avena fatua* ‘51532’ $\times$ *Avena sativa* ‘Sam’.

Figure 1. Cont.

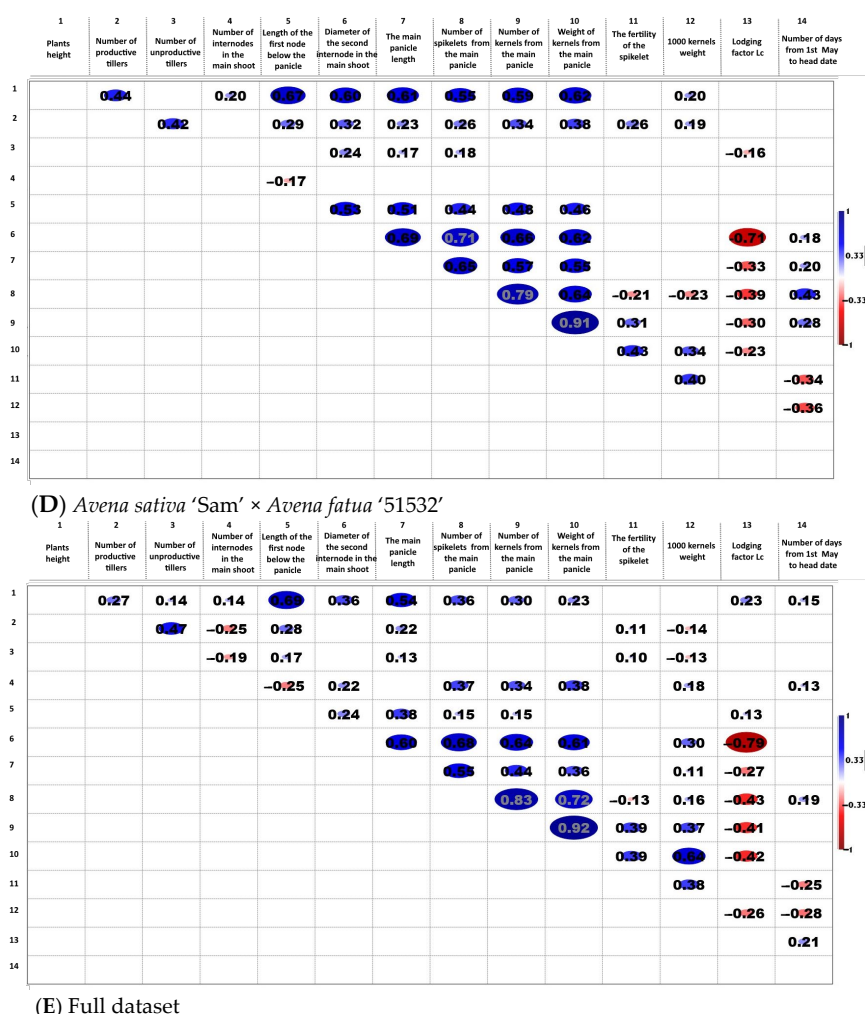


Figure 1. Heatmaps of Spearman's correlation coefficient (r) showing association of agronomic traits evaluated across (A) *Avena sativa* cv. Sam and (B) *Avena fatua* '51532', as well as (C,D) their F₂ populations and (E) full dataset. Blue colours represent positive correlation, while red show negative correlation. R values with $p > 0.05$ are blank. The size of the ellipses corresponds to the correlation level. $R > 7.0$ is in gray.

In both populations the segregation patterns based on Chi-square tests, fit a Mendelian ratio of three non-shattering/one shattering phenotype in F₂ population (*Avena fatua* '51532' × *Avena sativa* 'Sam': $\chi^2 = 0.684$; p -value = 0.408; *Avena sativa* 'Sam' × *Avena fatua* '51532': $\chi^2 = 0.035$; p -value = 0.851) (Table 3). Two sample test comparisons of shattering and non-shattering progeny of the population showed statistically significant differences ($p < 0.05$) between the genotypes of '51532' × cv. Sam in terms of the number of unproductive tillers.

Table 3. Segregation ratios of shattering in F₂ progeny from the cross *Avena fatua* '51532' and *Avena sativa* 'Sam'.

'Celer'/STH9210					
Population	Non-Shattering	Shattering	Ratio	χ^2	p -Value
<i>Avena fatua</i> '51532' × <i>Avena sativa</i> 'Sam'	123	35	3:1	0.684	0.40837
<i>Avena sativa</i> 'Sam' × <i>Avena fatua</i> '51532'	115	37	3:1	0.035	0.85141

4. Discussion

Avena sativa L. is a cereal species cultivated on a global scale with a high range of applications from the food industry to pharmaceuticals and animal feed [28]. Modern oat breeding prioritises high yield and other desirable agronomic traits, including resistance to biotic and abiotic stress. Wild oat progenitors have been proven to be a rich source of useful genes [35–38]; however, all *Avena* spp. are grouped into three gene pools [39], and successful transfer of genes from diploids or tetraploids from the secondary and tertiary gene pool to hexaploid *A. sativa* is more demanding and requires special techniques [40]. Thus hexaploid wild oat species from the primary gene pool, including *A. fatua* L., may be an available source of genetic diversity as they cross relatively easily and produce fertile progeny. In this study, we compared selected phenotypic traits of two populations between *A. sativa* cv. Sam and *A. fatua* ‘51532’ in both crossing directions, as well as their parental forms, to assess whether crossbreeding with *A. fatua* affects the breeding value of cultivated oat.

In this research, traits influencing the agronomic value of the plant related to the yield were selected. Tall plants are prone to lodging, which is one of the major causes of crop losses. Lodging prevents effective vegetation, hinders harvesting, affects the quality of the grain and reduces the usefulness of straw [41]. On average, cv. Sam was 10 cm shorter than ‘51532’, which is typical for cultivated varieties. Interestingly, cv. Sam × ‘51532’ reached a lower average height than cv. Sam; however, in both populations, high variability of the trait was observed since it is the F₂ generation. In our study, plant height was strongly correlated with the length of the first internode below the panicle. Some studies suggest that plant height might be correlated with panicle length [42]; however, in this case, an intermediate correlation could be observed only for ‘Sam’ and ‘Sam’ × ‘51532’. Although usually lower plant height correlates with high yield, several studies showed that yield is reduced when plants are shortened too much with dwarfism genes [43]. Incorporating dwarfism genes into cultivars may cause some yield penalty associated, e.g., with failure of the panicle to fully emerge from the leaf sheath [44] or compact panicle architecture [14,45]

The number of internodes and the diameter of the second internode in the main shoot, as well as the length of the first internode below the panicle, are related to plant height and, thus, are resistant to lodging [46]. In these cases, as in the case of all analysed traits, there was a statistically significant difference between the parental forms. Crossing with *A. fatua* lowered the average number of internodes in the main shoot, and in hybrids, the number was lower than in ‘51532’. Regardless of the direction of crossing, the diameter has reached an average value, while the length of the first internode below the panicle seemed to be inherited from the maternal form. Researchers claim that possible nuclear-cytoplasmic effects could be expected even in less distant crosses of oat, such as enhanced yield of the lines with *A. sterilis* cytoplasm [47] or different levels of disease resistance [48]. Additionally, in *Avena*, significant interactions between the cytoplasm and nuclear genes of groat protein content in interspecific matings of *A. sativa* and *A. sterilis* were reported [49]. However, it should be taken into account that quantitative traits may also be influenced by environmental conditions [50].

In ‘Sam’, the main panicle length was strongly correlated with the number and weight of kernels; a slightly weaker correlation of these traits was observed in the ‘Sam’ × ‘51532’. However, no such correlation was observed in *A. fatua* parental form ‘51532’ as well as the ‘51532’ × ‘Sam’. Almost all values of these traits in the populations ranged between the two parental forms, similar to the number of days from 1st May to the heading date in the assessment of earliness. The selection for short plant height and earliness has been one of the main goals of different oat breeding programs. Oat is particularly susceptible to drought during the flowering time, so the heading date is of fundamental importance in dry summer temperate climates since the early heading date enables drought avoidance [51] and may be crucial for world breeding in a systematically warming climate.

In both studied populations, the segregation of non-shattering to shattering genotypes of the progeny fitting a Mendelian ratio was observed, confirming a single gene inheritance.

Shattering in wild *Avena* progenitors is essential for seed dispersal and enables the survival of the species. The domestication made this process possible to control and allowed for increasing the harvesting efficiency and limiting yield losses. In this study, most of the examined traits did not show any significant correlation with shattering except the number of unproductive tillers in the '51532' $\times$ cv. Sam population in which the non-shattering plants were less tillering.

Some plants of the studied populations were characterised by the value of phenotypic traits exceeding the parental forms. This was in the case of the plant height, the number of unproductive tillers, the length of the first internode below the panicle, the main panicle length, fertility of the spikelet and 1000 kernel weight. The occurrence of a wider range of variability of traits, in comparison to the parental generation, is most likely the result of a large genetic diversity of parental forms, multi-gene inheritance of the examined phenotypic traits and additive gene action [52]. The phenomenon of transgression was observed, e.g., for the chlorophyll fluorescence parameters in sunflower (*Helianthus annuus* L.) [53] and for parameters related to yielding and flowering time in barley [54]. Transgressive segregation and heterosis are the basis of effective plant breeding, enabling obtaining of superior genotypes with traits not found even in parental forms [55].

Studies of oat genetic variation show that diversity within obsolete as well as modern gene pools is quite narrow [18–21,23]. Over the years of selection, some valuable alleles have been lost, so looking for new germplasm in wild ancestors, obsolete cultivars and landraces is crucial for the oat breeding progress [22]. Efficient crossbreeding with wild forms such as *A. fatua* is demanding and requires backcrossing due to the presence of many primitive features in hybrids of the early generations. However, expanding the *Avena* genetic pool is essential for developing long-term strategies beneficial to modern oat breeding.

5. Conclusions

A. fatua is a valuable source of genes for the improvement of cultivated oat. Statistical characteristics of phenotypic traits of progenies derived from bidirectional crosses enabled us to evaluate whether crossing with *A. fatua* reduces the agronomic utility of the resulting hybrids. Almost all mean values of the analysed features in the populations ranged between the values of the two parental forms; however, in both combinations, transgressive, superior genotypes with traits exceeding the parental forms were observed. Especially genotypes with increased fertility of the spikelet and 1000 kernel weight might constitute relevant breeding material. Obtained results also confirmed earlier reports on the correlation between plant height and the length of the first internode below the panicle; however, no strong correlation between the height and the length of the panicle was observed. A unique trait of wild oat species is also the agronomically unfavourable shattering. The conducted research confirmed the potential single-gene inheritance of this trait in *A. fatua* and excluded correlation with most of the analysed traits, except the number of unproductive tillers. Statistical analysis showed no influence of the crossing direction on the agronomic parameters of the studied populations obtained from interspecies crossing.

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