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Diversity of Polish Oat Cultivars with a Glance at Breeding History and Perspectives

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Abstract: During 120 years of Polish breeding of oats (*Avena sativa* L.), dozens of new varieties have been developed. This study was undertaken to investigate the diversity and population structure of 72 Polish oat cultivars released since 1893. The analysis was based on pedigree data as well as ISSR and REMAP marker polymorphisms. The ancestry of common oat cultivars was traced back to 124 cultivars, breeding lines, and landraces. The five most common progenitors were 'Markische Landsorte', 'selection from Ligowo oat', 'Fransk Svarthavre', 'Blanche de Siberie', and 'selection from Schleswig-Holstein landrace'. We found that at least one of them was present in 78% of analysed objects. The studied cultivars were assigned to four groups according to the period of their breeding (before 1945, 1945–1969, 1970–2000, and after 2000) and six groups according to the breeding company (Strzelce Plant Breeding Company, DANKO Plant Breeding, Station of Plant Breeding in Rogaczewo, Małopolska Plant Breeding Company, Station of Plant Breeding in Borów, and other). A decrease in observed heterozygosity within the groups was observed only in the postwar period (1945–1969). As a result of breeders' efforts and extensive crosses with foreign materials initiated in 1970 and 1980, new alleles were provided to the oat gene pool. The highest number of new varieties came from the Strzelce and DANKO breeding companies. There were no significant differences between modern cultivars derived from different breeding companies. However, very early breeding centres functioning before 1945 had significantly different materials from the modern ones. The population genetic structure of the studied group of cultivars appeared to be quite simple. It was shown that their genetic makeup consisted of two or three distinct gene pools, depending on the method of polymorphism assessment. The performed research proved that Polish oat breeding using traditional breeding methods—such as selection or intraspecific and interspecific crosses—although focused on improving yield and tolerance to biotic and abiotic stress, did not significantly narrow the oat gene pool and has been releasing cultivars that are competitive in the European market.

Keywords: *Avena sativa*; ISSR; REMAP; pedigree; cultivars; oat; diversity

Citation: Koroluk, A.; Paczos-Grzęda, E.; Sowa, S.; Boczkowska, M.; Toporowska, J. Diversity of Polish Oat Cultivars with a Glance at Breeding History and Perspectives. *Agronomy* **2022**, *12*, 2423. https://doi.org/10.3390/agronomy12102423

Academic Editors: Guiquan Zhang and Zhoufei Wang

Received: 29 August 2022
Accepted: 4 October 2022
Published: 6 October 2022

1. Introduction

Within the genus *Avena* L., the self-pollinating allohexaploids *A. sativa* L. and *A. byzantina* C. Koch., (2n = 6x = 42)—known as common and red oats, respectively—are the main cultivated oat species [1]. In some regions, the diploid *A. strigosa* Schreb., called bristle oats, and the tetraploid *A. abyssinica* Hochst., known as Ethiopian oats, are also cultivated [2,3]. The cultivated forms of marginal importance are the diploid species *A. nuda* L., *A. brevis* Rotch., and *A. hispanica* Ard. [2], along with the tetraploid A. barbata Pott. ex link [4].

Avena sativa L. appeared in cultivation several thousand years later than wheat and barley [5]. Initially, it was a weed that polluted these crops [6]. The importance of oats increased as a result of migration from Southeast Asia toward Northern European regions

with a cold and humid climate in the late Bronze Age [7,8]. Non-shattering oat mutants emerged and, as they were less demanding, cold-resistant, and well-adapted, they began to displace wheat, becoming cultivated over time [9]. The area of oat cultivation has continuously declined over the past few decades. This can be partially attributed to the increase in major crops such as maize or wheat. However, in recent years, the demand for oats for human consumption has increased, particularly because of their dietary benefits [10]. Today, the common oat is the seventh most economically important cereal, after maize, wheat, rice, barley, sorghum, and millet [11]. The grain production quantity, after a significant (i.e., almost twofold) drop in the 1980s and 1990s, has been quite stable over the last 20 years (2000–2021), oscillating around 25 million tonnes. Due to low environmental requirements, including cool and wet climates and soils with low fertility, oats are cultivated worldwide [1]. Poland is among the three largest oat-producing countries, after Canada and the Russian Federation. The other important oat suppliers—producing about 1 million tonnes per year—are Spain, Finland, Australia, the United Kingdom, and the United States [11]. Formerly, oats were primarily a fodder cereal; therefore, the basic direction of breeding was to increase the yield and improve the fodder value of grain with a low share of husk and high protein and fat [12]. The introduction of naked oat varieties with a low fibre content increased the attractiveness of growing this species as a fodder plant for monogastric animals [13]. Currently, attempts are being made to create varieties that are resistant to biotic stresses and can easily adapt to abiotic stresses and climate change.

Oat breeding in Poland began in the late 19th century, around the same time as oat breeding in Germany, the United Kingdom, and Sweden [14]. Before the First World War and during the interwar period, seed companies and private breeders were involved in breeding oats. The first Polish varieties of oat were 'Sobieszyński', 'Najwcześniejszy Niemierczański', and 'Teodozja'. The oldest printed description of breed cultivars concerns the 'Sobieszyński' oat, developed by professor Antoni Sempołowski in Sobieszyn in 1893 [15]. Before the First World War and in the interwar period in Poland, mainly domestic cultivars and landraces were cultivated. During the Second World War, almost all achievements of Polish breeders were lost, and after the war, for many years, the register of oat varieties in Poland was based on prewar entities from the 1920s and German varieties cultivated as indemnity for deeds executed during the war. Additionally, immediately after the war, Polish varieties selected from the German ones were created, i.e., 'Przebój I', 'Przebój II', and 'Proporczyk', selected from 'Flämingsgold', 'Flämingstreu', and 'Findling', respectively. At the end of the 1960s, as in the case of other spring cereals, foreign oat varieties were imported, i.e., 'Flamingsweiss II', 'Diadem', and 'Leanda'. Because of the lack of national materials, foreign cultivars and lines were included in the Polish breeding programs. It took over 30 years for Polish oat breeding to recover from the damage caused by the war, and new Polish cultivars did not begin to enter the market until 1977 [16]. From 1979, better and better Polish varieties were entered into the register, among which 'Dragon', 'Komes', and 'Markus' gained the greatest importance in cultivation in the 1980s. The last two decades of the 20th century were marked by numerous successes in oat breeding in Poland. Many very good varieties were developed at the plant breeding stations in Borów, Choryń, Polanowice, Wielopole, and Strzelce. Currently, oat breeding is conducted by three companies at Choryń, Polanowice, and Strzelce.

Plant breeders usually source populations for cultivar development from crosses within regionally adapted germplasm with good agronomic performance. The exchange of lines and cultivars between breeders is common but occurs mainly within certain regions and is rare between continents. As a consequence, European spring oat breeding programs may be reliant on a relatively narrow gene pool for agronomic and quality traits [17]. Over the years of selection, some valuable alleles have been lost, so modern breeding seeks new germplasm in wild ancestors, obsolete cultivars, and landraces [18]. New sources of genes could be useful in the future; therefore, a thorough knowledge of cultivars' genetic diversity and relatedness is highly important for breeders. Molecular

markers are so far the most effective tool widely used to study genetic diversity in the *Avena* genus. Paczos-Grzęda [19] compared RAPD (randomly amplified polymorphic DNA) and simplified ^{PstI}AFLP (amplified fragment length polymorphism) in the diversity evaluation of 19 common oat (*A. sativa* L.) cultivars registered in Poland in the years 1984–2004. Paczos-Grzęda and Bednarek [20] performed a comparative analysis of hexaploid Avena species (*A. sativa* L., *A. fatua* L., and *A. sterilis* L.) using the REMAP (retrotransposon–microsatellite-amplified polymorphism) and ISSR (inter-simple-sequence repeats) methods, and concluded that both techniques were informative enough to differentiate between the species and generated reliable molecular markers for the diversity assessment. ISSR, RAPD, and AFLP were also used by Boczkowska et al. [21] to evaluate the genetic diversity of 23 primary cultivars of common oat bred in Poland before 1939. Comparative analysis of the three molecular markers' systems showed that the set of ISSRs was the most efficient, highly reproducible, and had a relatively low cost. Moreover, only ISSR showed a statistically significant correlation with morphological data, prompting the use of this method to analyse a set of Polish oat landraces [22] and compare the diversity of landraces to selected modern and old Polish cultivars [23]. One of the major findings of the research was the undeniable distinctiveness of the gene pools of the old and modern Polish cultivars; however, none of the previous studies covered a wide set of Polish varieties representing almost the entire history of Polish oat breeding; hence, an attempt was made to conduct such an experiment. The genetic analysis of 72 oat cultivars released from 1893 to 2008 was performed based on ISSR and REMAP markers, the usefulness of which was confirmed in the studies cited above. Additionally, the results were enriched with pedigree data. The aims of this study were as follows: to investigate the changes in the gene pool of the Polish oat cultivars over nearly 120 years of breeding through diversity and population structure analysis; to verify the possibility of genetic discontinuities between obsolete and modern Polish cultivars hypothesised by researchers in the previous oat diversity studies; and to determine the effectiveness of ISSR and REMAP markers in assessing the genetic diversity of *A. sativa*.

2. Materials and Methods

2.1. Plant Material

In this study, 72 Polish *A. sativa* cultivars released between 1893 and 2008 were included (Table 1). The old cultivars dated before 1986 were obtained from a Polish gene bank (the National Centre for Plant Genetic Resources, Radzików, Poland). The seeds of the remaining cultivars (42) were kindly supplied by three Polish breeding companies: Strzelce Plant Breeding, Małopolska Plant Breeding, and DANKO Plant Breeding. The cultivars were assigned to four groups according to their breeding time: before 1945, 1946–1969, 1970–1999, and after 2000.

2.2. DNA Extraction and Genotyping

Extraction of total genomic DNA was carried out from several-day-old leaves of 15–20 seedlings of each of the 72 genotypes, according to the CTAB procedure [24]. Molecular analyses were performed using the ISSR method described by Ziętkiewicz et al. [25], with minor modifications as specified by Paczos-Grzęda et al. [26]. For amplification, 36 ISSR primers were used (Table S1). Cultivar genotyping was also carried out according to the REMAP method described by Kalendar et al. [27] and modified by Paczos-Grzęda and Bednarek [20], using the REMAP-LTR primer (555′ CTAGGGCATAATTCCAACA 333′) directed toward 555′ terminal LTR sequence Bare-1 retrotransposon, combined with 16 random ISSR primers (Table S1). The amplification products were separated on 2.5% agarose gels in 1X TBE buffer (89 mM Tris-borate, 2.5 mM EDTA, 0.1% EtBr).

Table 1. Names, breeding company, pedigree, and information about time of presence in the National Register of Varieties of common oat cultivars.

No.	Cultivar Name	Breeding Company	Pedigree	Accession Number	Donor Identifier	The Year of Entry and Removal from the National Register of Varieties	Group According to the Breeding Time
1	Akt	Strzelce Plant Breeding	Adam × Adamo		Strzelce	1997/2007	1970–1999
2	Antoniński Biały	Sandomiersko-Wielkopolska Plant Breeding in Antoniny	Selection of Sobieszyński	PL51622	NCPGR	1928/-	Before 1945
3	Antoniński Żółty	Sandomiersko-Wielkopolska Plant Breeding in Antoniny	Selection of Von Lochow Gelb	PL51465	NCPGR	1928/-	Before 1945
4	Arab	DANKO Plant Breeding, Choryń	Borys × Jawor	-	DANKO	2004/2014	After 2000
5	Bachmat	DANKO Plant Breeding, Choryń	Dula × Komes	-	DANKO	2001/2007	After 2000
6	Bajka	Strzelce Plant Breeding	KR 8543 × [(Random × KR 316) × Perona]	-	Strzelce	1997/2007	1970–1999
7	Bartek Udycki	'Udycz' Company	Antoniński Żółty × Znajda	PI285552	USDA	Before 1939 /1972	Before 1945
8	Berdysz	DANKO Plant Breeding, Choryń	(Dukat × SV87598) × Bajka	-	DANKO	2008/2018	After 2000
9	Biały Mazur	Małopolska Plant Breeding in Skrzeszowice—Kleszczyńscy	Local variety × Biały Orzeł	PL51466	NCPGR	1928/1973	Before 1945
10	Biały Orzeł	Sveriges Ustadesforenigs Institution, Svalof	Von Lochow Gelb × Sieger	PL51467	NCPGR	Before the war/-	Before 1945
11	Bohun	DANKO Plant Breeding, Choryń	LP 8675 × STH 110/86	-	DANKO	2002/2012	After 2000
12	Borek	Station of Plant Breeding, Borów	(Selma × Avoine Grise D'hiver) × Udycz Żółty	PL50043	NCPGR	1981/1989	1970–1999
13	Borowiak	Station of Plant Breeding, Borów	Góral × Santor	-	MPB	1998/2010	1970–1999
14	Boruta	Station of Plant Breeding, Borów	[Rodney ABDHCR × (Astor × Flamingsweiss II)] × Dula	PL50113	NCPGR	1982/1991	1970–1999
15	Boryna	Station of Plant Breeding, Borów	[Rodney ABDHCR × (Astor × Flamingsweiss II)] × Dula	-	MPB	1990/1999	1970–1999
16	Borys	Station of Plant Breeding, Borów	(Dato × Po.39) × Pinto	-	MPB	1991/1999	1970–1999
17	Breton	DANKO Plant Breeding, Choryń	Szakal × Expander	-	DANKO	2007/2017	After 2000
18	Budrys	DANKO Plant Breeding, Choryń	Adamo × CHD 792	-	DANKO	2001/2005	After 2000
19	Cacko	Strzelce Plant Breeding	Adam × Adamo	-	Strzelce	2000/2010	After 2000
20	Cekin	Station of Plant Breeding, Borów	POB-W-2010/93 × Zlatak	-	MPB	1999/2010	1970–1999
21	Celer	Station of Plant Breeding, Borów	Góral × KR-KOR	-	MPB	2000/2010	After 2000
22	Chwat	Strzelce Plant Breeding	Dukat × (Flamingsnova × Swan)	-	Strzelce	2000/2010	After 2000
23	Cwał	DANKO Plant Breeding, Choryń	Borys × Jawor	-	DANKO	2001/2011	After 2000
24	Deresz	DANKO Plant Breeding, Choryń	Maro × MGH 978.2	-	DANKO	2000/2010	After 2000
25	Dragon	Station of Plant Breeding, Rogaczewo	MGH 6374 × Diadem	PL50117	NCPGR	1982/2004	1970–1999
26	Dukat	Strzelce Plant Breeding	Fagot × KR 2335/74 L.	-	Strzelce	1991/2006	1970–1999
27	Farys	Małopolska Plant Breeding, Polanowice	(Biały Mazur × Astor) × Cebeco 7511	-	MPB	1989/1999	1970–1999
28	Furman	DANKO Plant Breeding, Choryń	Kwant × Jawor	-	DANKO	2006/2016	After 2000
29	German	Strzelce Plant Breeding	Samanta × Alfred	-	Strzelce	1991/2007	1970–1999

Table 1. *Cont.*

No.	Cultivar Name	Breeding Company	Pedigree	Accession Number	Donor Identifier	The Year of Entry and Removal from the National Register of Varieties	Group According to the Breeding Time
30	Gniady	DANKO Plant Breeding, Choryń	Noirine × Tropicale	-	DANKO	2007/2017	After 2000
31	Góral	Strzelce Plant Breeding	Borek × Brutus	-	Strzelce	1988/2007	1970–1999
32	Grajcar	Station of Plant Breeding, Borów	Komes × KR 81-1122	-	MPB	1997/2010	1970–1999
33	Hetman	DANKO Plant Breeding, Choryń	Jawor × Semundo 212.1	-	DANKO	1999/2007	1970–1999
34	Jagiełło	J.Turnau in Mikulicach	Selection of Rychlik Mikulicki	PL51507	NCPGR	Before 1939/	Before 1945
35	Jawor	DANKO Plant Breeding, Choryń	MGH0894.4 × (Mana × Leanda)	-	DANKO	1994/2007	1970–1999
36	Jubileuszowy Więcławicki	Buszczyński and the sons	Selection of Antoniński Żółty	PL52020	NCPGR	Before 1939/	Before 1945
37	Kanarek Mikulicki	J.Turnau in Mikulice	Selection of Jagiełło	PL51510	NCPGR	1923/-	Before 1945
38	Karol	Strzelce Plant Breeding	STH 171 × Brutus	-	Strzelce	1989/1996	1970–1999
39	Kasztan	Station of Plant Breeding, Borów	Dawid × CHD 1685/84 or 83	-	MPB	1999/2010	1970–1999
40	Komes	DANKO Plant Breeding, Choryń	MGH 61649 × Jaycce	-	DANKO	1985/1999	1970–1999
41	Koneser	Strzelce Plant Breeding	Szakal × (Jawor × Dukat)	-	Strzelce	2007/2017	After 2000
42	Kościelecki	Buszczyński and the sons	selection of Marczak Włosciański	PL51933	NCPGR	1923/-	Before 1945
43	Krezus	Strzelce Plant Breeding	Góral × [(Flamingsnova × Swan mut.) × Dukat)]	-	Strzelce	2005/2015	After 2000
44	Kwant	Strzelce Plant Breeding	Alfred × Dula	-	Strzelce	1992/2010	1970–1999
45	Lach	Station of Plant Breeding, Aleksandrówka	Vigor × Flamande de Blanche	PL50122	NCPGR	1980/1987	1970–1999
46	Markus	Station of Plant Breeding, Rogaczewo	Astor × Pendek	PL50118	NCPGR	1979/1988	1970–1999
47	Modzurowski	Kraków Plant Breeding	Sun II × Biały Mazur	PL51319	NCPGR	1969-1972	1945–1969
48	Niemierczański Najwcześniejszy	Buszczyński and the sons	Selection of Włościański z Podola	PL51084	NCPGR	1893/-	Before 1945
49	Pegaz	Małopolska Plant Breeding, Polanowice	Auswuchsfester × Bordeweiss	PL51217	NCPGR	1977/1981	1970–1999
50	Płatek	Strzelce Plant Breeding	(Flamindsgold × Pendek) × Leanda	PL50731	NCPGR	1986/1993	1970–1999
51	Podkowa Dłużewski	Dłużew, Mińsko-Mazowiecki district	-	PL51227	NCPGR	1929/-	Before 1945
52	Polar	Strzelce Plant Breeding	(Ago × Ramiro) × (Płatek × Swan mut) × Caesar	-	Strzelce	2002/2012	After 2000
53	Proporczyk	National Plant Breeding Institutions	Selection of Findling	PL51229	NCPGR	Before 1939/-	Before 1945
54	Przeboj I	National Plant Breeding Institutions	Selection of Flamingsgold	PL52070	NCPGR	1962/-	1945–1969

Table 1. *Cont.*

No.	Cultivar Name	Breeding Company	Pedigree	Accession Number	Donor Identifier	The Year of Entry and Removal from the National Register of Varieties	Group According to the Breeding Time
55	Przeboj II	Station of Plants Selection in Jeżowo-Gola, Gostyń district	Selection of Flamingstreue	PL51924	NCPGR	1974/-	1945–1969
56	Puławski Średniorychły	State Research Institute of Rural Husbandry in Puławy	Selection of Pfiffelbacher Gelb	PL50406	NCPGR	1928/-	Before 1945
57	Rajtar	DANKO Plant Breeding, Choryń	Ramiro × Jawor	-	DANKO	2004/2014	After 2000
58	Rumak	Station of Plant Breeding, Rogaczewo	MGH 6374 × Flamingsweiss II	PL50120	NCPGR	1981/1987	1970–1999
59	Rychlik Oberek	Małopolska Plant Breeding in Skrzeszowice (Kleszczyńscy brothers)	Rychlik Podgórski × Dogold	PL51233	NCPGR	Before 1939/-	Before 1945
60	Sam	Strzelce Plant Breeding	(Flamingsnova × Swan mut) × {[Alfred × (Garland × C2)] × Swan mut.}	-	Strzelce	1999/2010	1970–1999
61	Santor	Strzelce Plant Breeding	Borek × Brutus	-	Strzelce	1989/1999	1970–1999
62	Skrzat	Małopolska Plant Breeding, Polanowice	Komes × Maris Tabard	-	MPB	1996/2004	1970–1999
63	Sławko	Strzelce Plant Breeding	Mustang × Swan mut.	-	Strzelce	1993/2010	1970–1999
64	Sobieszyński	Agricultural Experimental Station in Sobieszyn	Selection of Rychlik Lubelski	PL51261	NCPGR	1923/-	Before 1945
65	Sprinter	Strzelce Plant Breeding	(Flamingsnova × Swan mut.) × Dukat	-	Strzelce	2000/2010	After 2000
66	Stoper	Strzelce Plant Breeding	(Flamingsnova × Swan mut.) × Dukat	-	Strzelce	2003/2013	After 2000
67	Szakal	Strzelce Plant Breeding	(Flamingsnova × Swan mut.) × Dukat	-	Strzelce	2000/2010	After 2000
68	Teodozja	breeded in Łęki by M.Rożański/Czarnecki, Kutnowski district	Selection of Scottish oat	PL50976	NCPGR	1923/-	Before 1945
69	Udycz Biały	Udycz' company in Kwasów	Kanarek Mikulicki × Sieger	PL51051	NCPGR	1925/-	Before 1945
70	Udycz Żółty	Udycz' company in Kwasów	Pflugs Gelb × Von Lochow Gelb	PL51050	NCPGR	Before 1939/1976	Before 1945
71	Ułan	DANKO Plant Breeding, Choryń	WIR 1714 × Diadem	PL51449	NCPGR	1985/1990	1970–1999
72	Zuch	DANKO Plant Breeding, Choryń	Vusch × Szakal	-	DANKO	2008/2018	After 2000

2.3. Molecular Data Mining and Analysis

ISSR and REMAP fragments were converted into binary matrix tables. The matrices were then used to determine the level of primer informativeness measured as polymorphic information content (PIC), which is a relative measure of marker informativeness and depends on the number of alleles of the particular marker, calculated according to the formula described by Roldan-Ruiz et al. [28]; marker index (MI), which provides a convenient estimate of marker utility assessed based on the work of Varshney et al. [29]; and resolving power (RP), which is the coefficient that indicates the discriminatory potential of the markers chosen for the analysis, following the formula of Prevost and Wilkinson [30]. The pedigree of the cultivars was traced back to their ancestors' cultivars or landraces using data available in Polish GenBank databases (https://bankgenow.edu.pl/en/ accessed on 10 June 2022) and POOL (Pedigrees of Oat Lines) (https://triticeaetoolbox.org/POOL/ accessed on 10 June 2022) [31]. The coefficients of parentage (COPs) were computed from a pedigree in MS Excel 2016 for all pairwise combinations of genotypes, as described by Wang and Lu [32]. Distance matrices were developed for molecular data based on the Gower coefficient [33]. A Mantel test was conducted to verify the association between molecular markers and pedigree. The Ward method of clustering was used, and dendrograms were constructed in XLSTAT Ecology [34]. The relationships between the true distances and the distances predicted using the dendrogram were measured as the cophenetic correlation coefficient (CPCC) [35]. Discrimination analysis (DA) was carried out to identify homogeneous groups [34]. Principal coordinate analysis (PCoA) was also conducted based on distance matrices to visualise the grouping pattern and to provide a graphical representation of the relationships between cultivars [34]. The Generalized Procrustes Analysis (GPA) was used to reduce the scale effects and to obtain a consensus configuration of all of the data [34]. Genotypic variations were assessed across groups created based on breeding time and breeding centre using the analysis of molecular variance (AMOVA) in GenAlEx [36]. The AMOVA procedure in GenAlEx follows the methods of Excoffier et al. [37], estimating the proportion of the variance among populations relative to the total variance. When the data are binary, AMOVA calculates the ΦPT value, which is analogous to Fst [38,39]. A ΦPT value of 0 denotes the minimum level of diversity among subpopulations, while a value of 1 denotes the maximum. The significance of the resulting variance and intergroup genetic distances was tested using 999 random permutations. Nei's coefficient [40] was calculated to estimate genetic variation within the abovementioned groups of cultivars.

Population structure was estimated using a Bayesian model-based approach implemented in the program STRUCTURE v. 2.3.4 [41]. An admixture model with correlated allele frequencies was employed. The number of clusters (k) was set from 1 to 11, with five independent runs for each k (10,000 burn-ins and 100,000 iterations). The Cluster Markov Packager Across K (CLUMPAK) was used to find optimal alignments of independent runs, and the output was used for cluster visualisation [42]. Cultivars with a membership coefficient lower than 0.8 were identified as admixed.

3. Results

3.1. Pedigree

The ancestry of Polish common oat cultivars was traced back to 124 cultivars, breeding lines, and landraces. The average number of ancestors per cultivar was 10.2, ranging from 1 to 28, and it increased along with the time of breeding, i.e., the oldest and the most recent cultivars were derived from 1.6 and 15.6 ancestors on average, respectively (Figure 1). The five most common progenitors were 'Markische Landsorte', 'selection from Ligowo oat', 'Fransk Svarthavre', 'Blanche de Siberie', and 'selection from Schleswig-Holstein landrace'. We found that at least one of these was present in 78% of analysed cultivars.

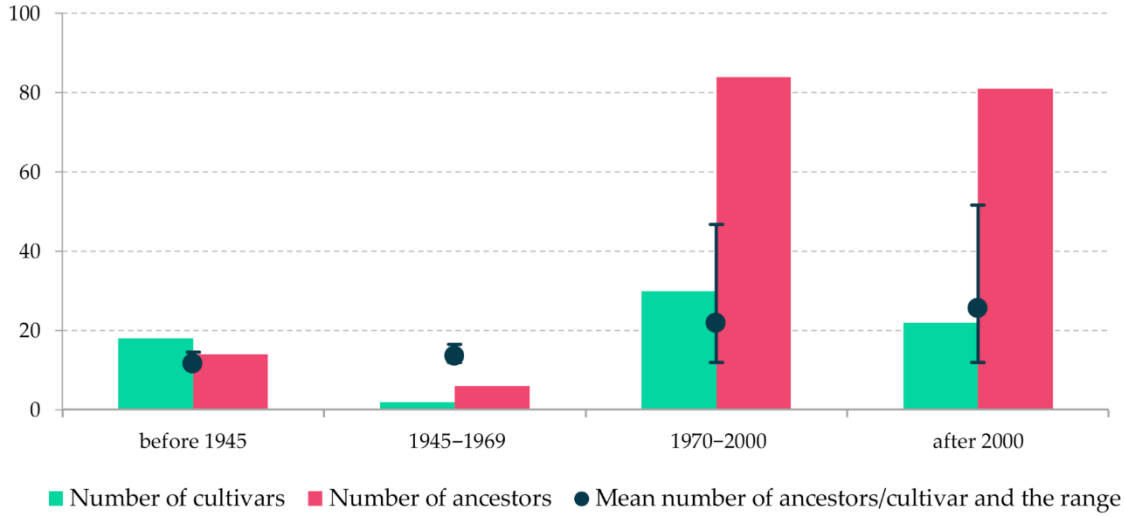

Figure 1. Description of four periods of breeding, including the number of cultivars, number of ancestors, and the mean number of ancestors per cultivar. The range of the number of single cultivar progenitors is also shown.

Eighteen cultivars were bred before 1945, and these were derived from fourteen ancestors. Six of them were descendants of the German landrace 'Markische Landsorte'. Only two cultivars in the study represented the period 1945–1969, and both of them had 'Markische Landsorte' as a progenitor. Thirty cultivars represented the period lasting for the next 30 years (1970–1999). Of 84 identified ancestors, the most common were 'selection from Ligowo oat', 'Markische Landsorte', and 'Fransk Svarthavre', appearing in the pedigrees of 23, 21, and 20 cultivars, respectively. As many as 22 of the most contemporary cultivars—those that were bred after 2000—were predominantly descendants of 'selection from Schleswig-Holstein landrace', 'Markische Landsorte', 'selection from Ligowo oat', and 'Fransk Svarthavre'. In total, 81 ancestors were identified for the latest cultivars. The summary of these data can be found in Figure 1.

Descendants of 'Markische Landsorte' were the result of the Strzelce Plant Breeding Company breeding programs. Only two cultivars—'Sławko'$_{(63)}$ and 'Dukat'$_{(26)}$—did not have it as an ancestor. Another prevailing progenitor was 'selection from Ligowo oat', and only 'Dukat'$_{(26)}$ and its descendants were not connected with it. 'Blanche de Siberie' was present in the pedigree of 14 cultivars bred by the Strzelce Plant Breeding Company. In total, in the breeding of 19 cultivars, 56 progenitors were used. The DANKO Plant Breeding Company mainly used derivatives of 'selection from Ligowo oat' and 'Fransk Svarthavre' in their programs. Four cultivars had a distinct pedigree, i.e., 'Deresz'$_{(24)}$, 'Komes'$_{(40)}$, 'Ułan'$_{(71)}$, and 'Zuch'$_{(72)}$. A total of 75 ancestors were identified for 16 cultivars. In this study, nine cultivars bred by the Station of Plant Breeding in Borów were included. In the pedigrees, four primary sources were found, i.e., 'Markische Landsorte', 'Blanche de Siberie', 'selection from Ligowo oat', and 'Fransk Svarthavre'. Two cultivars had a distinct origin: 'Borys'$_{(16)}$ and 'Grajcar'$_{(32)}$. Borys'$_{(16)}$ resulted from crossing ('Dato' × 'Po.3999') × Pinto, while 'Grajcar'$_{(32)}$ originated from 'Komes' × 'KR 81-112222'. In total, the cultivars were derived from 55 ancestors. The Małopolska Plant Breeding Company was represented in the study by five cultivars, for which 43 progenitors were identified. Their breeding programs, similarly to the previous ones, were based on materials derived from 'selection from Ligowo oat' and 'Markische Landsorte'. Notably, another distinct source ('Milton') was found in three cultivars. It is worth noting that 'Modzurowski'$_{(47)}$ also had a slightly different pedigree; however, it was bred in the earlier period (1945–1969). 'Milton' also appeared in the pedigrees of all three cultivars that were bred by the Station of Plant Breeding in Rogaczewo. Furthermore, 'Markische Landsorte' and 'selection from Ligowo oat' were found among the ancestors of all of them. In total, only 15 progenitors were

identified for this set. The data summarising the Polish breeding companies and stations are presented in Figure 2.

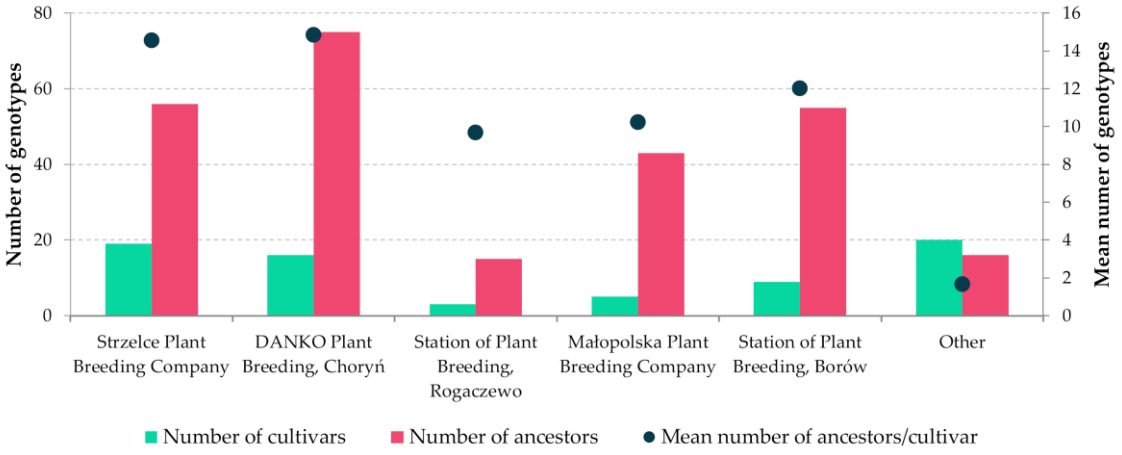

Figure 2. A summary of the breeding centres' activity.

Based on COPs, the pairwise dissimilarity coefficient was calculated, and its average value was 0.81. The dissimilarity matrix was used to perform clustering analysis. Clustering of genotypes based on the Gower coefficient resulted in the detection of three major clusters (Figure 3a) with CPCC equal to 0.568. Cluster 1 was the most numerous and consisted of 37 cultivars that had 87 progenitors. Their breeding time was as follows: 23 cultivars were bred in the years 1970–1999, 10 after the year 2000, 5 before 1945 and, finally, 1 in the period 1945–1969. The cultivars in this cluster were derived mainly from 'Markische Landsorte' or 'selection from Ligowo oat' (37 and 28, respectively). All of the oldest cultivars (bred before 1945) had 'Markische Landsorte' and/or 'Leutewizter Gelb' in their pedigree, which were also the ancestors of 16 other cultivars from this cluster. Among the later cultivars, only three did not have 'Markische Landsorte' as a progenitor, i.e., 'Sławko'$_{(63)}$, 'Boruta'$_{(14)}$, and 'Budrys'$_{(18)}$. The 'selection from Ligowo oat' was the progenitor of 28 cultivars in this cluster; however, it did not occur in the pedigrees of the oldest cultivars or in 'Cekin'$_{(20)}$, 'Ułan'$_{(71)}$, 'Przebój II'$_{(55)}$, or 'Budrys'$_{(18)}$. Cluster 2, composed of only nine cultivars, was the smallest cluster. It contained 'Dukat'$_{(26)}$, which was bred in 1991, and its descendants that were obtained after 2000. Therefore, all cultivars were descendants of the crossing 'Fagot × KR 2335/74 L' maximal in the third generation, and their other ancestry components were quite similar. In total, 33 progenitors were identified for this cluster. *Avena sterilis* L. was the ancestor of seven cultivars (exceptions: 'Dukat'$_{(26)}$ and 'Berdysz'$_{(8)}$). All of them were bred by the two largest Polish breeding companies, i.e., Strzelce and DANKO (6 and 3, respectively). Cluster 3 had 26 cultivars, with the majority having a simple origin, i.e., a short list of progenitors. Thus, the rest of the old cultivars (before 1945) were grouped there. Among other, more contemporary cultivars (i.e., those bred after 1970), the most common ancestors were 'selection from Ligowo oat' and 'Fransk Svarthavre'.

The results of principal coordinate analysis (PCoA) based on pedigree data are presented on scatterplots of the first two principal coordinates in Figure 3b,c. The first and the second principal coordinates explained 15.6% and 12.8% of the variation, respectively. No significant grouping pattern was found, although the points corresponding to the studied cultivars in two-dimensional space were arranged according to the clusters determined by agglomerative hierarchical clustering. When the breeding centre was indicated, the presence of two groups was noted within the cultivars bred by the DANKO Plant Breeding and Małopolska Plant Breeding companies, as well as within those obtained at the Station of Plant Breeding in Borów (Figure 3c).

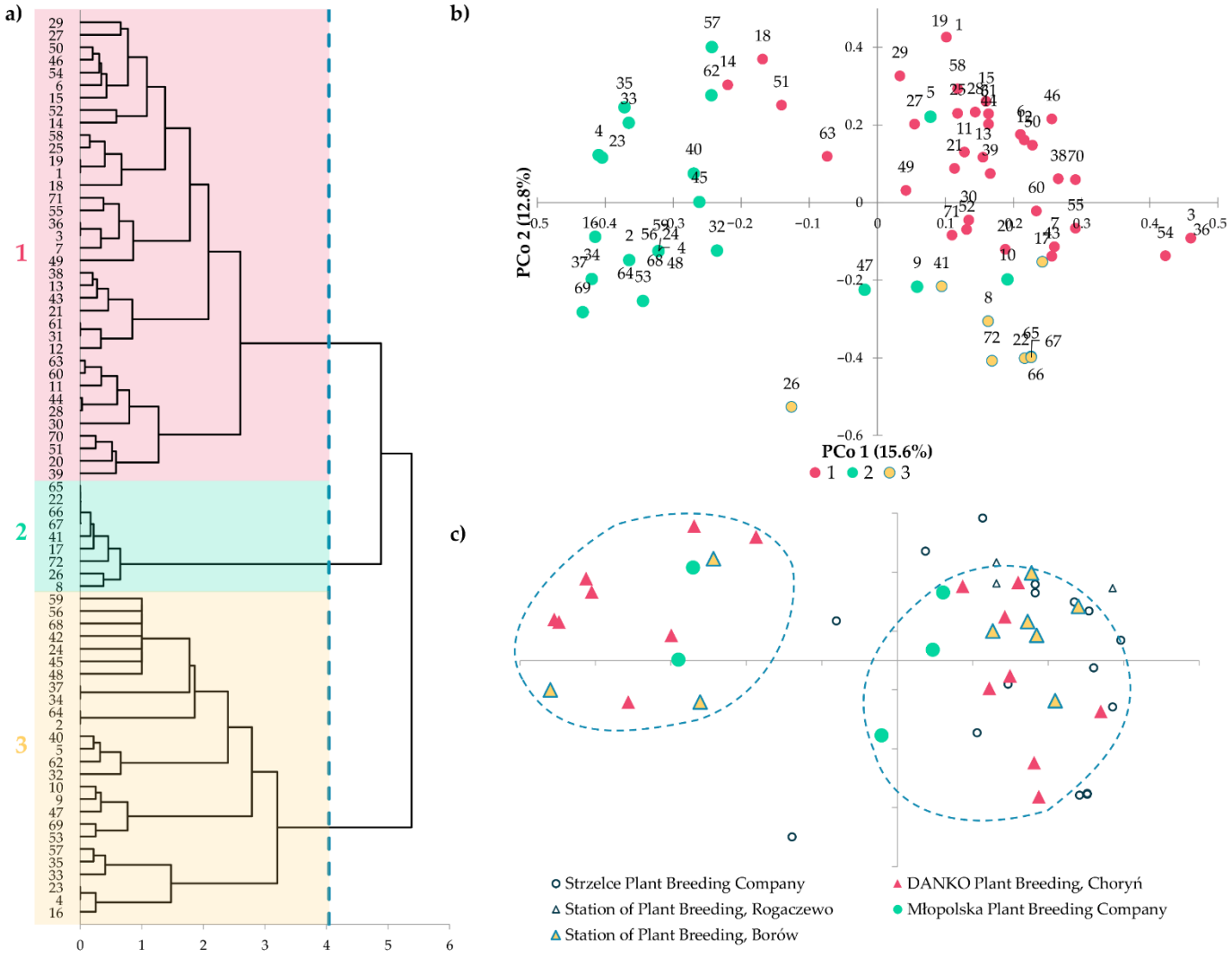

Figure 3. Pedigree: (**a**) A dendrogram of the results of the Ward method of clustering based on the COP. The vertical dashed line indicates the optimal number of clusters based on entropy, which measures how elements are distributed or assigned in each cluster. Low entropy corresponds to better clustering. (**b**) PCoA of the inter–cultivar distances measured using the COP. The colours of the points correspond to the groups marked on the dendrogram ((**a**,**b**) each number represents a single cultivar and is consistent with the numbers in Table 1). (**c**) PCoA plot with the indication of the breeding centre, excluding the group of 'Others'. The two distinct groups are framed by a dashed line.

3.2. ISSR

In this study, 36 ISSR primers were used to amplify 203 fragments, of which 99.5% were polymorphic. On average, a single ISSR generated 5.72 fragments (range: 1–18). The marker informativeness coefficient values ranged as follows: PIC from 0.05 (sr37) to 0.49 (sr32), with a mean of 0.23; MI from 0.0 (sr37) to 0.49 (sr32), with a mean of 0.18; and RP from 0.11 (sr37) to 23.36 (sr60), with a mean of 5.3 (Table S1).

The Nei's unbiased genetic diversity (uHe) derived from the ISSR data was 0.256 (Table 2). It was the highest for cultivars bred between 1970 and 1999 (0.236), while it was the lowest for the preceding period (0.106). The most diverse cultivars were derived from the Strzelce Plant Breeding Company (0.241). The cultivars bred by the Małopolska Plant Breeding Company had the lowest variation.

Table 2. Summary statistics of diversity within groups created based on breeding time and breeding company.

		ISSR					REMAP				
		No. of Fragments	**% Polymorphic Fragments**	**No. of Private Fragments**	**uHe**	**SE**	**No. of Fragments**	**% Polymorphic Fragments**	**No. of Private Fragments**	**uHe**	**SE**
	Total	203	99.51%	-	0.256	0.012	178	87.08%	-	0.308	0.012
Breeding time	Before 1945	170	65.02%	4	0.192	0.014	155	66.29%	2	0.236	0.015
	1945–1969	119	19.21%	1	0.106	0.015	126	28.65%	0	0.158	0.019
	1970–2000	189	85.22%	13	0.236	0.013	173	88.20%	11	0.286	0.014
	After 2000	170	72.41%	1	0.224	0.014	160	81.46%	2	0.289	0.014
Breeding company	Strzelce Plant Breeding Company	179	79.31%	5	0.241	0.014	163	80.90%	5	0.283	0.015
	DANKO Plant Breeding, Choryń	167	67.49%	2	0.214	0.014	158	79.78%	3	0.288	0.015
	Station of Plant Breeding, Rogaczewo	133	38.92%	0	0.173	0.016	135	46.63%	0	0.211	0.018
	Małopolska Plant Breeding Company	141	41.38%	2	0.155	0.015	141	55.06%	0	0.235	0.018
	Station of Plant Breeding, Borów	155	54.19%	0	0.188	0.015	150	64.61%	4	0.244	0.016
	Other	172	67.98%	4	0.198	0.013	155	67.42%	4	0.239	0.015

AMOVA determined that the majority of the observed genetic variability was due to variation within groups formed according to breeding time (91%) or among cultivars within breeding companies (93%). The pairwise matrix of the ΦPT groups showed that the longer the time interval between the breeding of two groups, the greater the differences between them (Table 3). It also indicated that there were no significant differences between cultivars from modern breeding companies/stations. However, very early breeding centres functioning before 1945 had significantly different materials from the modern ones (Table 4).

Table 3. Results of the analysis of molecular variance (AMOVA). Pairwise ΦPT values for groupings according to breeding time ($p < 0.001$) of ISSRs (above diagonal) and REMAPs (below diagonal).

	before 1945	**1945–1969**	**1970–2000**	**after 2000**
before 1945	x	ns	0.091	0.131
1945–1969	ns	x	0.110	0.141
1970–2000	0.116	ns	x	0.047
after 2000	0.109	ns	0.021	x

ns—Not significant.

Table 4. Results of the analysis of molecular variance (AMOVA). Pairwise ΦPT values for groupings according to the breeding company ($p < 0.001$) of ISSRs (above diagonal) and REMAPs (below diagonal).

	Other	Strzelce Plant Breeding Company	DANKO Plant Breeding, Choryń	Station of Plant Breeding, Rogaczewo	Małopolska Plant Breeding Company	Station of Plant Breeding, Borów
Other	x	0.117	0.131	0.114	0.093	0.108
Strzelce Plant Breeding Company	0.104	x	ns	ns	ns	ns
DANKO Plant Breeding, Choryń	0.124	0.020	x	ns	ns	ns
Station of Plant Breeding, Rogaczewo	0.123	ns	ns	x	ns	ns
Małopolska Plant Breeding Company	0.102	ns	ns	ns	x	ns
Station of Plant Breeding, Borów	0.166	0.043	ns	ns	ns	x

ns—Not significant.

The pairwise Gower similarity ranged from 0.936 ('Biały Mazur'$_{(9)}$ vs. 'Sobieszyński'$_{(64)}$) to 0.64 ('Płatek'$_{(50)}$ vs. 'Szakal'$_{(67)}$). The Ward clustering algorithm reflected three main clusters with CPCCs equal to 0.371 (Figure 4a). The first cluster contained 36 cultivars, of which 64% were bred in the period 1970–1999, 31% after 2000, and 2 cultivars were from the oldest group, i.e., 'Kanarek Mikulicki'$_{(37)}$ and 'Podkowa Dłużewski'$_{(51)}$. The second cluster was the smallest one, and it was composed of nine cultivars that were bred after 2000 and two from an earlier period (1970-1999), i.e., 'Sam'$_{(60)}$ and 'Sławko'$_{(63)}$. The cultivars that were grouped in this cluster were derived from two major breeding centres, i.e., Strzelce and DANKO. The third cluster contained 25 cultivars, including the majority of the oldest cultivars (before 1945), 'Modzurowski'$_{(47)}$ and 'Przebój I'$_{(54)}$ that were bred in the period 1945–1969, and also 7 cultivars obtained later. Discriminant analysis indicated that 58.33% of cultivars were assigned to the same group in the analysis of COP and ISSR.

The first two coordinates of PCoA based on the Gower dissimilarity coefficient explained 22.8% of the variance and indicated the presence of three groups (Figure 4b). On the plot below, an association of time of origin with the first coordinate can be observed. The newest and the oldest cultivars were arranged at opposite ends of the axle (Figure 4c).

The genetic structure of 72 oat cultivars was estimated via model-based Bayesian clustering using the STRUCTURE software. Based on the highest Δk values, k = 2 appeared the most probable (Figure 4d). When considering k = 2, the collection was split into two subgroups containing 21 and 28 cultivars, while 23 were admixed (80% level). The oldest cultivars were placed in the first group or were classified as admixed, i.e., 'Kanarek Mikulicki'$_{(37)}$, 'Podkowa Dłużewski'$_{(51)}$, 'Teodzja'$_{(68)}$, and 'Udycz Biały'$_{(69)}$. Both cultivars bred in the period 1945–1969 and four from 1970–1999 were also assigned to the first group. 'Polar'$_{(52)}$, which was bred after 2000, was the only cultivar from that period in this group. The second group was formed of 28 cultivars evenly sourced from the two most recent periods (Figure 4d).

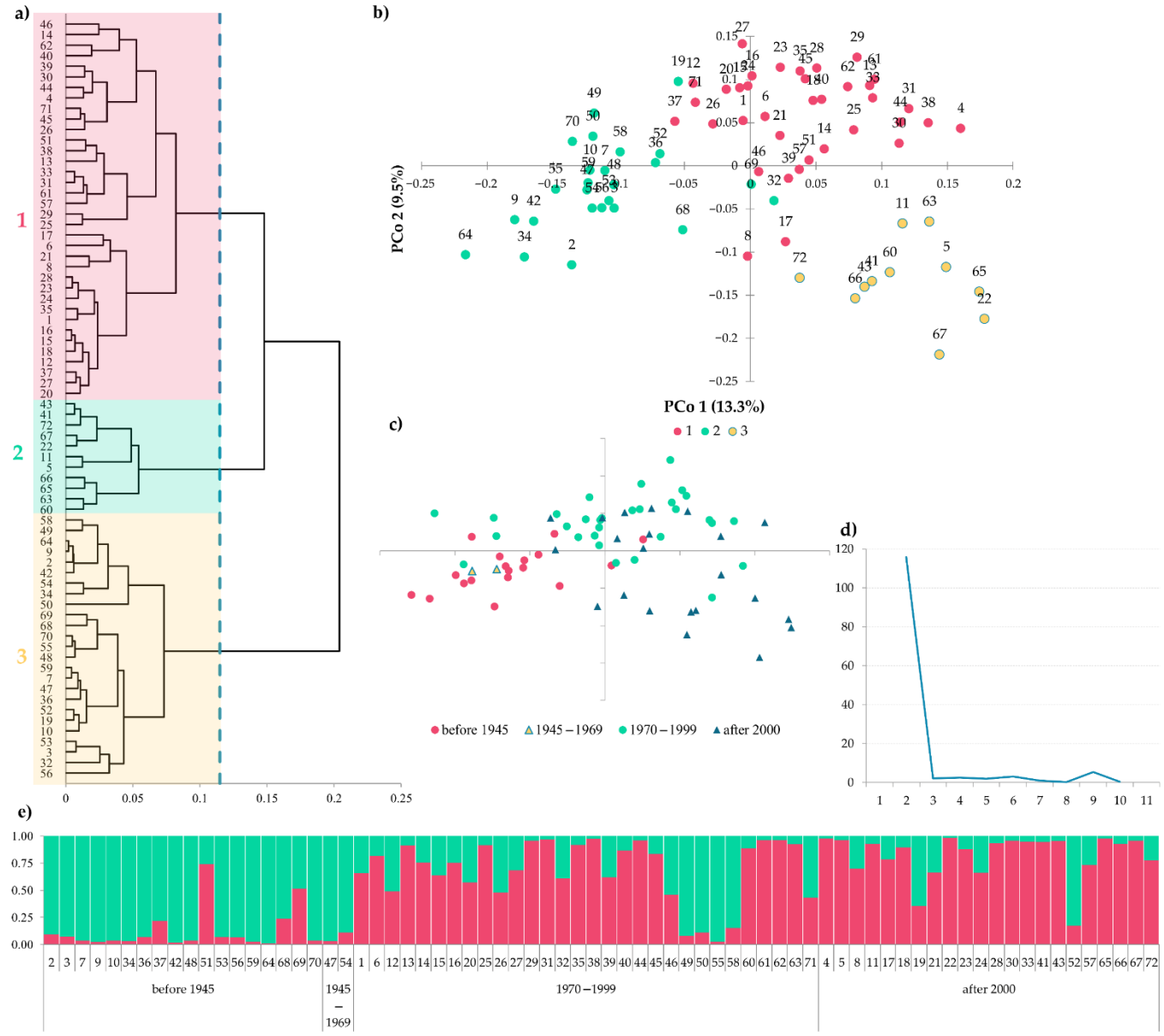

Figure 4. ISSR: (**a**) A dendrogram of the Ward method clustering results based on the Gower dissimilarity coefficient. The vertical dashed line indicates the optimal number of clusters based on entropy, which measures how elements are distributed or assigned in each cluster. Low entropy corresponds to better clustering. (**b**) PCoA of the inter-cultivar distances measured using the Gower dissimilarity coefficient. The colours of the points correspond to the groups marked on the dendrogram. (**c**) PCoA plot with the indication of the breeding time. (**d**) Estimated number of clusters obtained for K values from 1 to 11 using ISSR data based on ΔK. (**e**) Inferred population structure using the model-based program STRUCTURE. Plots were generated based on the Q-matrix consensus permuted across 5 replications for K = 2 using the CLUMPAK software. Each cultivar is represented by a single vertical line, which is partitioned into segments proportional to the estimated membership in the two subpopulations. The likelihood of assignment to a given cluster is on the vertical axis. (**a**,**b**,**e**—Each number represents a single cultivar and is consistent with the numbers in Table 1).

3.3. REMAP

Using 21 REMAP pairs of primers, a total of 178 fragments were obtained, of which 87.1% were polymorphic. On average, a single REMAP reaction yielded 8.48 fragments (range: 2–17). All characteristics of the markers are presented in Table S2. The average value of PIC for REMAP markers was 0.29. The maximum PIC was obtained for the primer pairs

r42, r47, and r54 (0.49), while the minimum value was demonstrated by r6 and r11 (0.03). The highest and the lowest MI values were obtained for the same primers as PIC, and the values were 0.49 and 0.0, respectively. The average RP value for REMAP was 9.05, and for each primer pair it ranged from 0.08 to 32.92 (r6 and r59, respectively), with a mean of 5.3 (Table S2).

The Nei's unbiased genetic diversity (uHe) derived from the REMAPs was slightly higher than that from ISSRs, at 0.308 (Table 2). The group of most recent cultivars were the most diverse (0.289), while cultivars bred between 1945 and 1969 had the lowest diversity coefficient (0.158). The most varied cultivars were bred by the DANKO Plant Breeding Company (0.288) and Strzelce Plant Breeding Company (0.283), while the least diverse ones were bred by the Station of Plant Breeding in Rogaczewo.

The results of AMOVA based on REMAP data were consistent with those obtained for ISSRs and indicated that variability among cultivars within the periods of breeding time was significantly higher than the variation between the breeding periods. Variance among cultivars within breeding companies was also higher than between companies. The pairwise ΦPT of breeding period groups did not support the results of analogous analysis for ISSRs. The difference between the oldest and the newest cultivars was smaller than that between the oldest and those bred in the period 1970–1999 (Table 3). Very small differences were found between contemporary breeding companies/stations. The cultivars derived from historical breeding centres were significantly different from the more modern ones, and this was consistent with the ISSR results (Table 4).

Genetic similarity between samples was calculated based on the Gower coefficient. For REMAP analysis, it was in the range of 0.59–0.88 for the cultivar pairs 'Borek'$_{(12)}$ vs. 'Proporczyk'$_{(53)}$ and 'Boryna'$_{(15)}$ vs. 'Borys'$_{(16)}$, respectively. Based on the genetic distance matrices, Ward's cluster analysis was performed (Figure 5a). The cophenetic correlation was 0.437. A dendrogram created based on these results showed the presence of three major clusters with a strong hierarchical structure containing 27, 11, and 34 cultivars. The oldest cultivars (before 1945), with no exception, were grouped in the first cluster. Apart from them, there were also the two cultivars from the period 1945–1969, six bred in the period 1970–1999, and 'Polar'$_{(52)}$ representing the most modern group. The second cluster was composed of only 11 cultivars, the majority of which were bred after 2000. Two cultivars ('Kasztan'$_{(39)}$ and 'Sławko'$_{(63)}$) of this cluster were obtained earlier, i.e., between the years 1970 and 1999. The third and largest cluster was composed of 34 cultivars, of which 22 were bred in the period 1970–1999 and the remaining 12 came from the most recent period. According to DA, the assignment of cultivars to the groups was identical in as much as 79.17% for REMAP and ISSR analyses, but only in 58.33% when comparing pedigree.

Associations among the 72 oat cultivars revealed by PCoA calculated from REMAP-based Gower dissimilarity estimates are presented in Figure 5b. The first (PCo1) and second (PCo2) principle coordinates accounted for 13.8 and 8.4% of the total variation, respectively. The results were spread across the principal coordinates, and no grouping pattern was found. However, an association of the breeding period with the plot could be noted, as shown in Figure 5c. DA confirmed 68.1% compliance of PCoA with the breeding time.

The STRUCTURE software was also used to determine the REMAP-based genetic structure. The Δ statistical test showed that k = 2 was optimal in this analysis (Figure 5d). At k = 2, 25 and 26 cultivars fell into the two groups, while 21 were marked as putative hybrids (Figure 5e). In general, the participation of the genetic makeup of the first group was higher in the cultivars bred before 1970, while the later ones mostly represented the second group. However, two cultivars from the period 1970–1999 and seven from the most recent period showed similarity with the first group at a level above 80%.

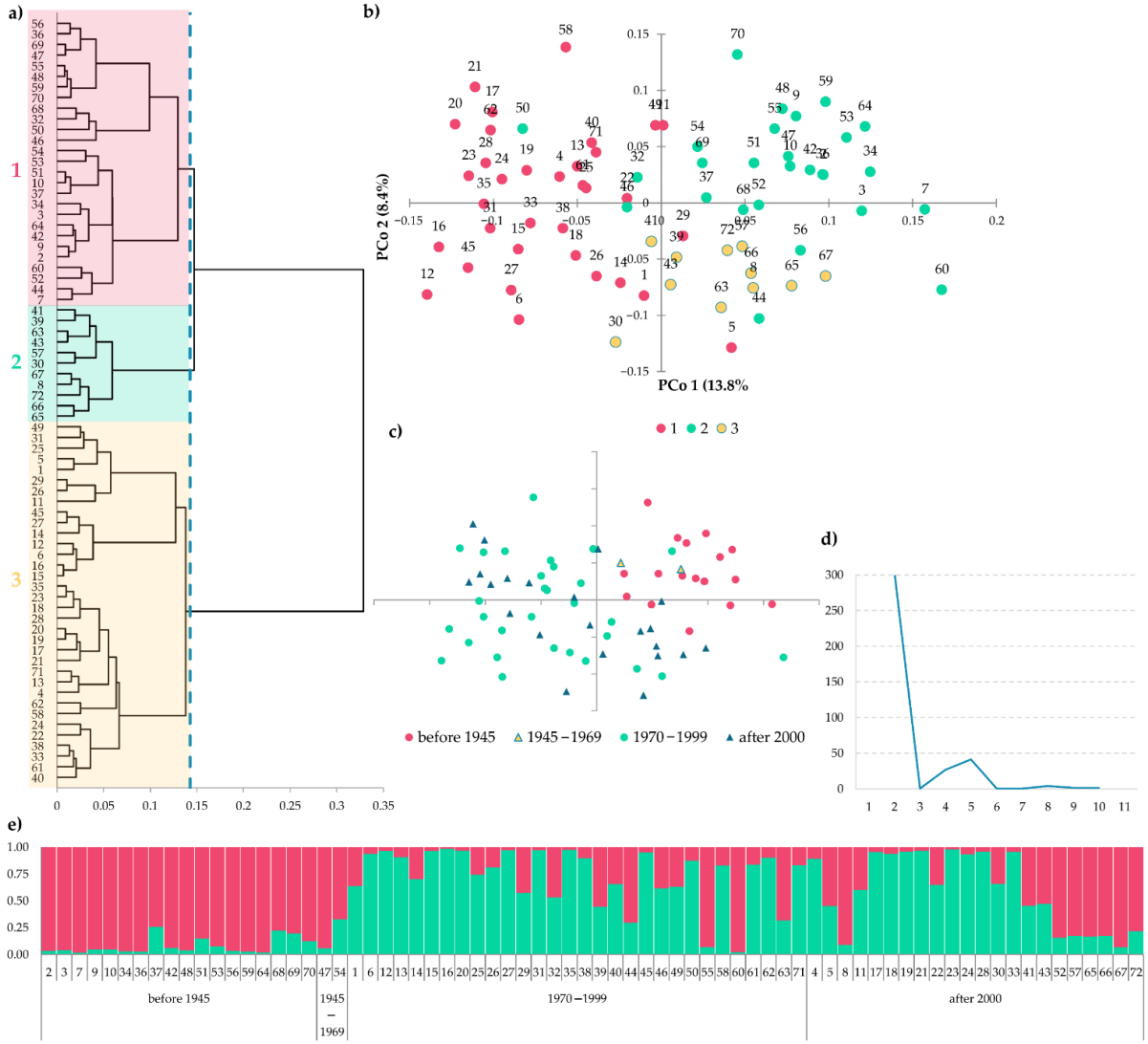

Figure 5. REMAP: (**a**) Results of the Ward method clustering based on the Gower dissimilarity coefficient. The vertical dashed line indicates the optimal number of clusters based on entropy, which measures how elements are distributed or assigned in each cluster. Low entropy corresponds to better clustering. (**b**) PCoA of the inter-cultivar distances measured using the Gower dissimilarity coefficient. The colours of the points correspond to the groups marked on the dendrogram. (**c**) PCoA plot with the indication of the breeding time. (**d**) Estimated numbers of clusters obtained for K values from 1 to 11 using ISSR data based on ΔK. (**e**) Inferred population structure using the model-based program STRUCTURE. Plots were generated based on the Q-matrix consensus permuted across 5 replications for K = 2 using the CLUMPAK software. Each cultivar is represented by a single vertical line, which is partitioned into segments proportional to the estimated membership in the two subpopulations. The likelihood of assignment to a given cluster is on the vertical axis. ((**a**,**b**,**e**)—Each number represents a single cultivar and is consistent with the numbers in Table 1).

3.4. Combined and Comparative Evaluation

A pairwise Mantel test was performed for all combinations of dissimilarity matrices. Statistically significant correlation (r = 0.419, *p*-value < 0.0001) was observed only for the comparison of the ISSR and REMAP matrices.

For the combined binary matrices obtained from the ISSR and REMAP analyses, agglomerative hierarchical clustering (AHC) was performed using the Ward method. It showed the presence of three main clusters that, as before, were strongly hierarchical inside and contained 19, 18, and 35 cultivars, respectively (Figure 6a). Discriminant analysis

showed that the AHC results for the pooled matrices were 77.78% consistent with the clustering derived from the ISSR results and 86.11% consistent with the results derived from REMAP alone. The concordance of the clustering of the combined matrices with the results obtained from the pedigree analysis was 58.33%, which was the same as for each of the molecular analyses separately.

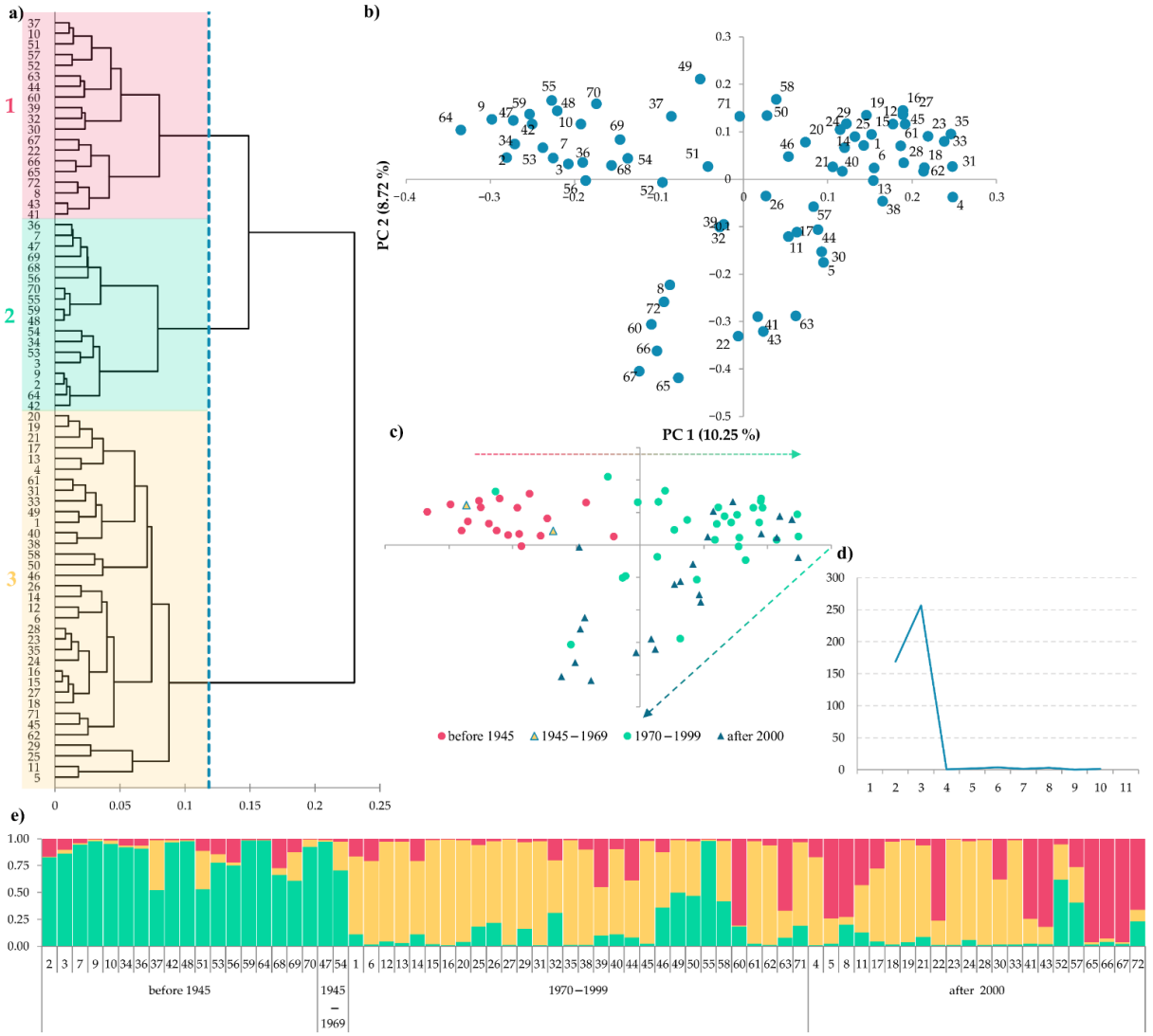

Figure 6. Combined results: (**a**) Results of the Ward method clustering based on the Gower dissimilarity coefficient for ISSR and REMAP. The vertical dashed line indicates the optimal number of clusters based on entropy, which measures how elements are distributed or assigned in each cluster. Low entropy corresponds to better clustering. (**b**) Scatterplot of GPA results for ISSR, REMAP, and pedigree data. (**c**) GPA plot with the indication of the breeding time. (**d**) Estimated number of clusters obtained for K values from 1 to 11 using ISSR and REMAP data based on ΔK. (**e**) Inferred population structure using the model-based program STRUCTURE. Plots were generated based on the Q-matrix consensus permuted across 5 replications for K = 3 using the CLUMPAK software. Each cultivar is represented by a single vertical line, which is partitioned into segments proportional to the estimated membership in the three subpopulations. The likelihood of assignment to a given cluster is on the vertical axis. ((**a**,**b**,**e**)—Each number represents a single cultivar and is consistent with the numbers in Table 1).

A combination of PCoA results obtained from the pedigree, ISSR, and REMAP data was performed using Generalized Procrustes Analysis (GPA). The proportion of total variance explained by the consensus matrix (Rc) for the dataset was high (0.737), and the

permutation test indicated that it was statistically significant ($p < 0.05$), so the agreement within the dataset was strong. The pedigree data gave slightly less consistent results. The first two PCA dimensions (PC1 and PC2) accounted for 18.97 % of the variance in the consensus matrix (Figure 6b). Based on the biplot of the first two dimensions, the presence of three groups was noted. Moreover, a shift and then a change in breeding direction were found (Figure 6c).

Genetic structure was estimated based on combined genetic data using the model-based Bayesian clustering (Figure 6d). Based on the highest Δk values, k = 3 appeared to be optimal. The oldest cultivars represented the first group, with the small participation of other groups (Figure 6e). From 1970 to 1999, the presence of the genotypes representing the second group was higher, while the recent cultivars belonged to both the second and third groups. This reflected the GPA results presented below.

4. Discussion

The dozens of new oat cultivars have been developed over nearly 120 years of Polish breeding of oats (*Avena sativa* L.). In this study, an analysis of the diversity and population structure of 72 oat cultivars released since 1893 was carried out. The pedigree data as well as ISSR and REMAP markers were used for the research. The studied set of cultivars was assigned to the four groups according to the period of their breeding (before 1945, 1945–1969, 1970–2000, and after 2000) and six groups where the breeding company by which they were developed was considered (Strzelce Plant Breeding Company, DANKO Plant Breeding, Choryń, Station of Plant Breeding, Rogaczewo, Małopolska Plant Breeding Company, Station of Plant Breeding, Borów, or other). For historical and geographical reasons, European breeding has had a significant impact on the beginnings of oat breeding in Poland. In this research, the ancestry of Polish common oat cultivars was traced back to 124 cultivars, breeding lines, and landraces, allowing us to establish the influence of foreign varieties on the analysed material.

In our studies, we identified the five most common progenitors of Polish cultivars, which were 'Markische Landsorte', 'selection from Ligowo oat', 'Fransk Svarthavre', 'Blanche de Siberie', and 'selection from Schleswig-Holstein landrace'. We found that at least one of these was present in 78% of analysed cultivars. 'Selection from Markische Landsorte' became the cultivar 'Lochows Gelb', which gave rise to 'Flaminstreue'—a cultivar from the first German oat breeding lineages described by Bickelman (1989). Bickelmann's studies on fatuoid oats enabled him to conclude that the German varieties were derived from several genetic lines, three of which are the most numerous. One of them comes from the cross of the landraces 'Lochows Gelb' and 'Oberschlesische Landsorte Weiβ', which gave rise to 'Flamingstreue' and 'Flamingsgold'. Most of the German breeding materials are descendants of these cultivars. The cross of 'Probstei Type' with 'Lochows Gelb' gave rise to the 'Adler' lineage, to which a series of cultivars can be traced back. The cross of 'Silber' with a 'Fransk Svarthavre' gave rise to 'Minor'—the starting point of a third breeding lineage. Another progenitor of Polish cultivars, 'Selection from Ligowo oat'—a cultivar from Sweden—gave rise to 'Swedish Select', followed by the 'Blanche de Siberie' (or 'White Siberie'). This variety, after crossing with 'Lochows Gelb', gave the 'Flamingsgold' variety (also from the first German lineages). 'Fransk Svarthavre' gave rise to the third German lineage. The common Polish cultivars' progenitor, 'selection from Schleswig-Holstein landrace', took part in the formation of a Probsteir-type oat lineage, which may be related to the second most popular pedigree line of German varieties. This confirms that Polish and German obsolete oat cultivars were derived from a small number of closely related landraces, cultivars, or breeding lines.

Comparing the European cultivars with the North American ones, Achleitner et al. [43] found that oat cultivars originating from European breeding programs showed less diversity than cultivars originating from North and South America. However, in Canadian breeding programs, 130 cultivars released from 1930 to 2001 could be traced back to fewer than 10 parental lines [44]. Similarly, most of the USA germplasm utilised for cultivar

development before 1970 traced back to only seven landrace varieties introduced from Europe: 'Kherson' ('Sixty Day'), 'Green Russian', 'Victory', 'Markton', 'White Russian' ('White Tartar'), 'Red Rustproof', and 'Winter Turf' [7]. The higher diversity of American cultivars was probably the effect of the popularity of the hybridisation of *A. sativa* with *A. byzantina*. Such hybrids were quite rare, especially in North and Central Europe, because *A. byzantina* is a winter-type red oat that is well-adapted to the mild winters typical of the Mediterranean basin as well as the United Kingdom.

Concern has often been expressed that modern intensive plant breeding leads to a reduction in the genetic diversity of crops. Such reductions may have consequences, both for the susceptibility of crops to pests and diseases and their ability to respond to climate change [45]. It is therefore necessary to quantify the changes that have occurred in the genetic diversity of major crops. In this study, the diversity and population structure analyses of 72 oat genotypes were performed to investigate the changes in the gene pool of the Polish oat cultivars over nearly 120 years of breeding. For this purpose, ISSR and REMAP molecular marker systems were used. Large-scale DNA sequencing techniques allow for an increase in the number of polymorphisms identified in a single experiment—mainly SNPs and In/Dels. Nevertheless, many breeding companies and scientists still cannot afford sequential analysis, and traditional polymorphism analysis techniques are a widely used and cheap alternative. PCR-based techniques give a direct measure of genetic diversity and identify a high number of polymorphic loci uniformly distributed through the genome. In our study, both the ISSR and REMAP matrices showed a statistically significant correlation, allowing us to obtain complementary results. Similarly, Dziurdziak et al. [46], examining local barley cultivars, found a high correlation between the results obtained with the ISSR method and DArTseq. The DArTseq relies on the analysis of SNPs by restriction digestion within the reduced representation of the genome. Thus, it can be concluded that the ISSR and related REMAP markers belong to the group of highly informative and reliable markers.

In this paper, the effectiveness of ISSR and REMAP markers was determined by the amount of polymorphism, PIC (polymorphic information content) coefficient, marker index (MI), and resolving power (RI). The highest average number of polymorphic fragments as well as PIC, RI, and MI was characterised by REMAP, in contrast to the results of Paczos-Grzęda and Bednarek [20]. The REMAP method identifies polymorphisms resulting from the distribution of microsatellite sequences and retrotransposons; therefore, a greater polymorphism of REMAP markers seems to be justified. The ISSR method, on the other hand, detects variation in the size of the genomic regions between the two adjacent microsatellite sequences used as the primer binding sites [25]. Most of the studies on *Avena* diversity conducted so far by other authors have been carried out using the ISSR method; however, enriching the results with REMAP polymorphism works in favour of the obtained results, especially since the two methods show a statistically significant correlation. Pedigree analysis is the most misleading method, as it is based on the assumption that parents contribute half of their genome to the progeny and are genetically significantly distinct from one another. Consequently, the differences between genotypes obtained by this method are overestimated.

The genetic diversity of Polish oat cultivars has been analysed in the past using molecular markers such as RAPD and AFLP [19], as well as ISSR [18,20,21,47]. The results obtained in the previous studies indicated differences between old and modern Polish cultivars; however, the diversity within the analysed gene pools was at a low level, which is consistent with the results obtained in this study. Our research indicates that most of the variability is due to the variation within analysed oat groups based on the period of their breeding. The longer the breeding time interval, the greater the differences between the studied gene pools. The distinction of the historical gene pool from that of modern oat cultivars is justified by the destruction of Polish breeding materials during World War II. Historical cultivars from the first half of the 20th century mainly result from selection within landraces. Landraces, usually genetically heterogeneous and adapted to local

conditions, are seen as a source of easily accessible genes that provide better resistance to biotic and abiotic stresses [48]. Landraces, in comparison to cultivars, are considered to be much more genetically diverse, as confirmed by the previous results of a genetic diversity analysis within a collection of common oat landraces originating from the same regions [18,22,23]. The total variation of the collection was relatively low in contrast to the internal variation of the studied landraces. Moreover, the level of oat landraces' internal variation was significantly higher than that found within historical and modern cultivars [23]. In our study, the group of the most recent cultivars was more diverse than most of the compared groups; however, incorporating landraces as well as wild relatives into the modern breeding process would definitely expand the oat gene pool and enrich it with the desired breeding traits. Today, in the modern breeding process—mostly for economic reasons—the exploitation of landraces is replaced by advanced cultivars or breeding lines with a limited genetic makeup. By narrowing the starting material, breeders do not need several backcrossing cycles to eliminate the undesirable traits introduced along with the desirable ones, significantly speeding up the breeding process, but leading to meeting short-term breeding goals.

Currently, attempts are being made to create cultivars that are resistant to new aggressive races of pathogens and easily adapt to abiotic stresses and climate change [13]. This study indicates that historical oat cultivars are genetically distinct from more modern ones and, according to our previous research [49] determining resistance to *Puccinia coronata* f.sp. *avenae* in a set of 63 previously uncharacterised oat cultivars, historical varieties could be a valuable source of useful *Pc* resistance genes discarded during subsequent breeding. A similar role may be played by wild oat progenitors [49–53]; however, all *Avena* spp. are grouped into three gene pools [54], and successful introgression of genes from diploids or tetraploids belonging to the tertiary gene pool to hexaploid *A. sativa* is more demanding and requires special techniques [55]. Attention needs to be paid to integrated efforts in the conservation of oat germplasm and the exploration of new sources of desirable alleles. Continuous diversification of breeding materials and gene introgression from more exotic germplasm would broaden the genetic diversity and allow sustainable oat improvements.

Diversity loss is common in modern crops of major species developed by large breeding programs [56]. The performed research proved that Polish oat breeding using traditional breeding methods, although focused on improving traits defined by market needs, did not significantly narrow the oat gene pool and has been releasing cultivars that are competitive in the European market. A further, more detailed analysis extended with morphological and physiological characteristics is crucial for developing long-term strategies that are beneficial to modern oat breeding.

5. Conclusions

The performed analysis enabled the investigation of the changes in the gene pool of the oat cultivars over nearly 120 years of breeding in Poland. A decrease in observed heterozygosity within the groups was observed only in the postwar period (1945–1969), and new alleles were provided as a result of extensive crosses with foreign materials. The population genetic structure was quite simple, composed of two or three distinct gene pools, depending on the method of polymorphism assessment. ISSR and REMAP analysis support the statement that currently grown cultivars share a very similar genetic background, although they are derived from different breeding companies and their gene pool is significantly distinct from that of older varieties. This confirms the undeniable distinctiveness of the gene pools of old and modern Polish cultivars hypothesised by researchers in the previous oat diversity studies. The pedigree analysis enabled the identification of the five most common progenitors of Polish cultivars and the establishment of the influence of foreign varieties in the analysed material. Comparative analysis of the methods used in the study showed that the set of REMAPs was the most efficient, and since most of the studies on *Avena* diversity conducted so far have been carried out using the ISSR method, enriching

the results with REMAP polymorphism works in favour of the obtained results—especially since the two methods show a statistically significant correlation.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy12102423/s1, Table S1: List of ISSR primers used in the study and values of informativeness coefficients: Polymorphic information content (PIC); Marker Index (MI); Resolving Power (RP); Table S2: List of REMAP primers used in the study and values of informativeness coefficients: Polymorphic information content (PIC); Marker Index (MI); Resolving Power (RP).

Author Contributions: Conceptualisation and methodology, A.K., E.P.-G. and S.S.; investigation, A.K. and J.T.; resources E.P.-G.; writing—original draft preparation, A.K.; writing—review and editing, E.P.-G. and S.S.; visualisation, M.B. All authors have read and agreed to the published version of the manuscript.

Funding: The calculations were performed at the Interdisciplinary Centre for Mathematical and Computational Modelling, University of Warsaw (ICM UW), within the framework of Computational Grant No. G72–19.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

References

1. Stevens, E.J.; Armstrong, K.W.; Bezar, H.J.; Griffin, W.B.; Hampton, J.G. Fodder oats an overview. In *Fodder Oats: A World Overview*; Suttie, J.M., Reynolds, S.G., Eds.; Agriculture Organization of the United Nations: Rome, Italy, 2004; pp. 1–9.
2. Baum, B.R. *Oats: Wild and Cultivated: A Monograph of the Genus Avena L. (Poaceae)*; Monograph; Supply and Service Canada: Ottawa, ON, Canada, 1977.
3. Leggett, J.M. Classification and Speciation in *Avena*. In *Oat Science and Technology*; Marshall, H.G., Sorrells, M.E., Eds.; Agronomy Monograph; American Society of Agronomy, Crop Science Society of America: Madison, WI, USA, 1992; pp. 29–52. ISBN 978-0-89118-225-2.
4. Zeller, F.J. Nutzung des genetischen Potentials der *Avena*-Wildarten zur Verbesserung des Saathafers (*Avena sativa* L.). *J. Appl. Bot.* **1998**, *72*, 180–185.
5. Zohary, D.; Hopf, M. *Domestication of Plants in the Old World*, 2nd ed.; Clarendon Press: Oxford, UK, 1993.
6. Budzyński, W.; Szemplińska, W. Owies (Oat). In *Szczegółowa Uprawa Roślin (Detaild Plant Cultivation)*; Jasińska, Z., Kotecki, W., Eds.; Agricultural Academy: Wrocław, Poland, 2003; pp. 239–258.
7. Coffman, F.A. *Oat History, Identification and Classification*; US Department of Agriculture: Washington, DC, USA, 1977; Volume 1516.
8. Murphy, J.P.; Hoffman, L.A. The Origin, History, and Production of Oat. In *Oat Science and Technology*; Marshall, H.G., Sorrells, M.E., Eds.; American Society of Agronomy: Madison, WI, USA, 1992; p. 27.
9. Leggett, J.M.; Thomas, H. Oat evolution and cytogenetics. In *The Oat Crop*; Welch, W., Ed.; Chapman & Hall: London, UK, 1995; p. 121.
10. Andersson, A.; Börjesdotter, D. Effects of environment and variety on content and molecular weight of b-glucan in oats. *J. Cereal Sci.* **2011**, *54*, 122–128. [CrossRef]
11. FAOSTAT Database. Food and Agriculture Organization of the United Nations. Available online: www.fao.org (accessed on 21 July 2022).
12. Boczkowska, M.; Podyma, W.; Łapiński, B. Oat. In *Genetic and Genomic Resources for Grain Cereals Improvement*; Singh, M., Upadhyaya, H.D., Eds.; Elsevier: Amsterdam, The Netherlands, 2016; pp. 159–225. ISBN 9780128020005.
13. Gorash, A.; Armonienė, R.; Mitchell Fetch, J.; Liatukas, Ž.; Danytė, V. Aspects in oat breeding: Nutrition quality, nakedness and disease resistance, challenges and perspectives. *Ann. Appl. Biol.* **2017**, *171*, 281–302. [CrossRef]
14. Spiss, L. History of oat breeding in Poland. *Biul. Inst. Hod. Aklim. Roślin* **2003**, *229*, 7–11.
15. Arseniuk, E.; Krzymuski, J.; Martyniak, J. *History of Breeding and Seed Production in Poland in the 20th Century*; IHAR Radzików: Radzików, Poland, 2003; ISBN 83-88518-53-4.
16. Świerczewski, A.; Mazaraki, M. Oat breeding. In *Biology and Agrotechnology of Oats*; Mazurek, J., Wojcieska, U., Mazurek, J., Król, M., Eds.; IUNG: Pulawy, Poland, 1993; pp. 129–161.
17. Montilla-Bascón, G.; Sánchez-Martín, J.; Rispail, N.; Rubiales, D.; Mur, L.; Langdon, T.; Griffiths, I.; Howarth, C.; Prats, E. Genetic Diversity and Population Structure Among Oat Cultivars and Landraces. *Plant Mol. Biol. Report.* **2013**, *31*, 1305–1314. [CrossRef]

18. Boczkowska, M.; Łapiński, B.; Kordulasińska, I.; Dostatny, D.F.; Czembor, J.H. Promoting the Use of Common Oat Genetic Resources through Diversity Analysis and Core Collection Construction. *PLoS ONE* **2016**, *11*, e0167855. [CrossRef] [PubMed]
19. Paczos-Grzęda, E. Pedigree, RAPD and simplified AFLP-based assessment of genetic relationships among *Avena sativa* L. cultivars. *Euphytica* **2004**, *138*, 13–22. [CrossRef]
20. Paczos-Grzęda, E.; Bednarek, P.T. Comparative analysis of hexaploid *Avena* species using REMAP and ISSR methods. *Turk. J. Botany* **2014**, *38*, 1103–1111. [CrossRef]
21. Boczkowska, M.; Nowosielski, J.; Nowosielska, D.; Podyma, W. Assessing genetic diversity in 23 early Polish oat cultivars based on molecular and morphological studies. *Genet. Resour. Crop Evol.* **2014**, *61*, 927–941. [CrossRef]
22. Boczkowska, M.; Tarczyk, E. Genetic diversity among Polish landraces of common oat (*Avena sativa* L.). *Genet. Resour. Crop Evol.* **2013**, *60*, 2157–2169. [CrossRef]
23. Boczkowska, M.; Onyśk, A. Unused genetic resources: A case study of Polish common oat germplasm. *Ann. Appl. Biol.* **2016**, *169*, 155–165. [CrossRef]
24. Doyle, J.J.; Doyle, J.L. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull.* **1987**, *19*, 11–15.
25. Ziętkiewicz, E.; Rafalski, A.; Labuda, D. Genome Fingerprinting by Simple Sequence Repeat (SSR)-Anchored Polymerase Chain Reaction Amplification. *Genomics* **1994**, *20*, 176–183. [CrossRef]
26. Paczos-Grzeda, E.; Bednarek, P.T.; Koroluk, A.; Nita, Z.; Banaszak, Z.; Bichonski, A.; Chmiel, M.; Gradzielewska, A.; Nowaczyk, K.; Szolkowska, A.; et al. Genetic similarity assessment among selected naked oat cultivars and breeding lines using ISSR markers. *Not. Bot. Horti Agrobot. Cluj Napoca* **2014**, *42*, 66–72. [CrossRef]
27. Kalendar, R.; Grob, T.; Regina, M.; Suoniemi, A.; Schulman, A. IRAP and REMAP: Two new retrotransposon-based DNA fingerprinting techniques. *Theor. Appl. Genet.* **1999**, *98*, 704–711. [CrossRef]
28. Roldán-Ruiz, I.; Calsyn, E.; Gilliland, T.J.; Coll, R.; Van Eijk, M.J.T.; De Loose, M. Estimating genetic conformity between related ryegrass (Lolium) varieties. 2. AFLP characterization. *Mol. Breed.* **2000**, *6*, 593–602. [CrossRef]
29. Varshney, R.K.; Chabane, K.; Hendre, P.S.; Aggarwal, R.K.; Graner, A. Comparative assessment of EST-SSR, EST-SNP and AFLP markers for evaluation of genetic diversity and conservation of genetic resources using wild, cultivated and elite barleys. *Plant Sci.* **2007**, *173*, 638–649. [CrossRef]
30. Prevost, A.; Wilkinson, M.J. A new system of comparing PCR primers applied to ISSR fingerprinting of potato cultivars. *TAG Theor. Appl. Genet.* **1999**, *98*, 107–112. [CrossRef]
31. Tinker, N.A.; Deyl, J.K. A Curated Internet Database of Oat Pedigrees. *Crop Sci.* **2005**, *45*, 2269–2272. [CrossRef]
32. Wang, S.; Lu, Z. Genetic diversity among parental lines of Indica hybrid rice (*Oryza sativa* L.) in China based on coefficient of parentage. *Plant Breed.* **2006**, *125*, 606–612. [CrossRef]
33. Gower, J.C. A General Coefficient of Similarity and Some of Its Properties. *Biometrics* **1971**, *27*, 857. [CrossRef]
34. *Addinsoft XLSTAT 2019.4.1 Statistical and Data Analysis Solution*; Addinsoft, NY, USA, 2019. Available online: https//www.xlstat.com (accessed on 10 June 2022).
35. Farris, J.S. On the Cophenetic Correlation Coefficient. *Syst. Zool.* **1969**, *18*, 279. [CrossRef]
36. Peakall, R.; Smouse, P.E. GenAlEx 6.5: Genetic analysis in Excel. Population genetic software for teaching and research—An update. *Bioinformatics* **2012**, *28*, 2537–2539. [CrossRef] [PubMed]
37. Excoffier, L.; Smouse, P.E.; Quattro, J.M. Analysis of molecular variance inferred from metric distances among DNA haplotypes: Application to human mitochondrial DNA restriction data. *Genetics* **1992**, *131*, 479–491. [CrossRef]
38. Wright, S. The Interpretation of Population Structure by F-Statistics with Special Regard to Systems of Mating. *Evolution* **1965**, *19*, 395. [CrossRef]
39. Wright, S. Isolation by distance. *Genetics* **1943**, *28*, 114–138. [CrossRef] [PubMed]
40. Lynch, M.; Milligan, B.G. Analysis of population genetic structure with RAPD markers. *Mol. Ecol.* **1994**, *3*, 91–99. [CrossRef] [PubMed]
41. Hubisz, M.J.; Falush, D.; Stephens, M.; Pritchard, J.K. Inferring weak population structure with the assistance of sample group information. *Mol. Ecol. Resour.* **2009**, *9*, 1322–1332. [CrossRef] [PubMed]
42. Kopelman, N.M.; Mayzel, J.; Jakobsson, M.; Rosenberg, N.A.; Mayrose, I. Clumpak: A program for identifying clustering modes and packaging population structure inferences across K. *Mol. Ecol. Resour.* **2015**, *15*, 1179–1191. [CrossRef] [PubMed]
43. Achleitner, A.; Tinker, N.A.; Zechner, E.; Buerstmayr, H. Genetic diversity among oat varieties of worldwide origin and associations of AFLP markers with quantitative traits. *Theor. Appl. Genet.* **2008**, *117*, 1041–1053. [CrossRef] [PubMed]
44. Fu, Y.; Peterson, G.W.; Scoles, G.; Rossnagel, B.; Schoen, D.J.; Richards, K.W. Allelic Diversity Changes in 96 Canadian Oat Cultivars Released from 1886 to 2001. *Crop Sci.* **2003**, *43*, 1989–1995. [CrossRef]
45. Clunies-Ross, T. Mangolds, manure and mixtures: The importance of crop diversity on British farms. *Ecologist* **1995**, *25*, 181–187.
46. Dziurdziak, J.; Gryziak, G.; Groszyk, J.; Podyma, W.; Boczkowska, M. DArTseq Genotypic and Phenotypic Diversity of Barley Landraces Originating from Different Countries. *Agronomy* **2021**, *11*, 2330. [CrossRef]
47. Boczkowska, M.; Harasimiuk, M.; Onyśk, A. Studies on genetic variation within old Polish cultivars of common oat. *Cereal Res. Commun.* **2015**, *43*, 12–21. [CrossRef]
48. Villa, T.C.C.; Maxted, N.; Scholten, M.; Ford-Lloyd, B. Defining and identifying crop landraces. *Plant Genet. Resour.* **2005**, *3*, 373–384. [CrossRef]

49. Sowa, S.; Paczos-Grzęda, E. A study of crown rust resistance in historical and modern oat cultivars representing 120 years of Polish oat breeding. *Euphytica* **2020**, *216*, 1–10. [CrossRef]
50. Okoń, S.M.; Ociepa, T.; Paczos-Grzęda, E.; Ladizinsky, G. Evaluation of resistance to *Blumeria graminis* (DC.) f. sp. *avenae*, in *Avena murphyi* and *A. magna* genotypes. *Crop Prot.* **2018**, *106*, 177–181. [CrossRef]
51. Paczos-Grzęda, E.; Sowa, S.; Koroluk, A.; Langdon, T. Characteristics of resistance to *Puccinia coronata* f. sp. *avenae* in *Avena fatua*. *Plant Dis.* **2018**, *102*, 2616–2624. [CrossRef] [PubMed]
52. Paczos-Grzęda, E.; Sowa, S.; Boczkowska, M.; Langdon, T. Detached Leaf Assays for Resistance to Crown Rust Reveal Diversity Within Populations of *Avena sterilis*. *Plant Dis.* **2019**, *103*, 832–840. [CrossRef]
53. Sowa, S.; Paczos-Grzęda, E.; Koroluk, A.; Okoń, S.; Ostrowska, A.; Ociepa, T.; Chrząstek, M.; Kowalczyk, K. Resistance to *Puccinia coronata* f. sp. *avenae* in *Avena magna*, *A. murphyi*, and *A. insularis*. *Plant Dis.* **2016**, *100*, 1184–1191. [CrossRef] [PubMed]
54. Harlan, J.R.; de Wet, J.M.J. Toward a rational classification of cultivated plants. *Taxon* **1971**, *20*, 509–517. [CrossRef]
55. Aung, T.; Chong, J.; Leggett, M. The Transfer of Crown Rust Resistance *Pc94* from a Wild Diploid to Cultivated Hexaploid Oat. In Proceedings of the 9th International European and Mediterranean Cereal Rust and Powdery Mildews Conference, Lunteren, The Netherlands, 2–6 September 1996; Kema, G.H.J., Niks, R.E., Daamen, R.A., Eds.; Wageningen, European and Mediterranean Cereal Rust Foundation: Lunteren, The Netherlands, 1996; pp. 167–171.
56. Maxted, N.; Dulloo, M.E.; Ford-Lloyd, B.V. *Enhancing Crop Genepool Use: Capturing Wild Relative and Landrace Diversity for Crop Improvement*; CABI: Boston, MA, USA, 2016.