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Morphological and molecular diversity of Nordic oat through one hundred years of breeding

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Summary

Genetic diversity in microsatellites and development of agronomical characters in Nordic oat cultivars (*Avena sativa*) from the 20th century, ranging from landraces to new cultivars, were studied. A clear development in agronomical characters has taken place in this period: Straw length has been reduced, harvest index has increased and heading date has declined. The persistent oat breeding effort in the northern part of the region was indicated by the data, since cultivars from this region showed higher harvest index. Also adaptation to shorter summers was apparent in cultivars from the most northern part of the area. When comparing cultivars released after 1940 to the landraces, the loss of diversity revealed for the agronomical characters was also indicated by the molecular data. This indicates that a more general loss of diversity has taken place in the period, possibly due to random factors during the breeding process (bottleneck effect). The reduction in diversity revealed by recent cultivars at an agronomical as well as a molecular level emphasises the importance of implementing a conservation strategy for older material in order to secure genetic diversity for future oat breeding efforts.

Introduction

During the last century, cereal breeding practices led to abandoning of landraces and to utilization of highly uniform cultivars improved through cycles of hybridisation, selection and inbreeding. Concern has been raised that intense agronomic improvements, lead to erosion of the genetic diversity (Vellve, 1993; Clunier-Ross, 1995; Tripp, 1996; FAO, 1996; Smale, 1997). Much effort has been directed towards evaluating and maintaining existing landraces and cultivars of crop plants like e.g. tea, barley, wheat and potato (Wachira et al., 1995; Demissie & Bjørnstad, 1997; Gregová et al., 1997; Smale, 1997; Huamán, 1998), since these constitute an easily accessible, primary genepool for the species (Harlan & de Wet, 1971). Recent research suggests that breeding efforts do not necessarily lead to continuous diminishing of genetic diversity in the cultivated material. Studies on wheat (Donini et al., 2000; Christiansen et al., 2002; Soleimani et al., 2002), barley (Koebner et al., 2003) and maize (Lu & Bernardo, 2001) indicate that genetic diversity has been stabilized in today's material. Systematic breeding of oat (*Avena sativa*) started in the late nineteenth century in Scandinavia (Åkerman, 1948) in response to demands for quality feed to the growing livestock population. In Sweden the breeding company "The Swedish Seed Association" in Svalöf (Åkerman, 1948) initiated breeding of oat, and today almost 400 Nordic accessions of common oat from various periods are stored in the Nordic Gene Bank (www.ngb.se). Historically, oat was an important crop in the Nordic area,

particularly as a fodder crop, but also as a healthy food supplement for human consumption (Anderson et al., 1984; Truswell, 2002; Chronakis et al., 2004). In recent years, oat has been widely abandoned in favour of other higher yielding crop species, but in the northern part of the region, production and breeding of oat is still important.

Oat breeders have targeted breeding towards agronomical desirable traits such as shorter straw length, higher yield and disease resistance (Rekunen, 1988; Moore-Colyer, 1995). However, the effects of breeding on the general diversity need investigation. Canadian researchers have studied the development in Canadian oat varieties (Fu et al., 2003, 2004) using molecular markers (microsatellites and AFLP markers, respectively). The two studies resulted, however, in conflicting results concerning the variability of Canadian oat. Also Finnish researchers (Peltonen-Sainio, 1990; Peltonen-Sainio & Järvinen, 1995) have investigated the diversity of oats, by analysing some of the agronomically important traits, and found a significant change in the varieties towards types with more desirable traits. Ahokas and Manninen (2000) compared regenerated seeds from a single seed sample, tagged as a landrace, with recent cultivars, and found large differences. However, a thorough analysis of the development of diversity in agronomical and molecular characters of Nordic oat to illuminate the consequences of the long term oat breeding in the area has never been performed.

Here we present an analysis of Nordic oat material ranging from landraces to recent cultivars. Results from field trials are compared with analysis of genetic diversity within seven microsatellite loci. To replicate the climatic conditions similar to the ones where oat is grown and bred extensively, we conducted the field trials at Bjørke field station, Norway, which has short summer periods with long days.

Methods and materials

Field trials

Plant material consisted of 64 oat cultivars and 17 landraces, obtained from the Nordic Gene Bank, which were evaluated in field trials at Bjørke field station in Norway (60 °57′N, 10 °55′E) (Tables 1 and 2). Three agronomical characters were scored during three consecutive years (2001, 2002 and 2003) with two replicates each year. 'Heading date' measured as number of days from sowing to heading in 50% of the plot, 'straw length' measured as an average for the plot and 'harvest index', being the fraction of dry weight made up of grain. In addition 'thousand grain weight' (TGW), was measured in 2002 and 2003.

Data analysis

Apart from the group of landraces, cultivars were divided into groups representing 20 years of breeding: landraces (17 accessions), age 1898–1920 (7 acc.), age 1921–1940 (17 acc.), age 1941–1960 (17 acc.), age 1961–1980 (13 acc.), and age 1981-today (10 acc.).

The Shannon Weaver diversity index (Shannon & Weaver, 1962) was calculated to estimate diversity of phenotypic traits with a Java based program. Observations for each trait were grouped into N classes, where N is the square root of the number of observations in the sample. Standard deviations for estimates of deviance were calculated from 5000 bootstrap datasets.

Analysis of variance (ANOVA) was performed on data from 'heading date', 'straw length', 'harvest index' and 'TGW'. No transformation of data was needed except in the case of 'harvest index' which was subjected to arcsine sqrt transformation to obtain variance homogeneity (Hopkins, 2000). Models removing effects of 'age-group', 'country of origin', 'experimental year' and their second order interactions were tested and non-significant parameters were removed from final models. Analyses were performed using the GLM procedure in the SAS software version 8.02 (The SAS institute, Cary, NC, USA). Least Square Means (LSMeans) with standard errors were calculated with the same software.

The component of 'between cultivar' variation was estimated with the PROC MIXED routine in the SAS software version 8.02 with cultivars as a random and 'experimental year' as a fixed effect. Total variation was calculated as the sum of the genetic and the error component and the genetic determination was calculated as the fraction of the genetic component of the total variation.

Correlation between agronomical data and release year of the six age-groups was tested using Spearman's correlation analyses performed with GraphPad Prism software (Ver. 3.02 GraphPad Software Inc.). This analysis makes it possible to include landraces, even if they do not have a specific 'age of introduction' since the age-groups are included on an "interval scale".

Table 1. The *Avena sativa* accessions included in the study. Range and mean for each character is shown for individual age groups

Age group	Country of origin	No. of accessions	Genetic determination	Straw length 39.8%	Harvest index 49.3%	TGW 64.7%	Heading date 81.4%
1 (Landraces)	Sweden	12	Mean	107	42	31.8	56
	Denmark	1	(Range)	(60–140)	(29.0–60.3)	(19.0–41.4)	(45–69)
	Finland	4					
	Norway	0					
2 (1898–1920)	Sweden	5	Mean	110	41	33.2	59
	Denmark	2	(Range)	(75–140)	(28.5–53.5)	(24.9–41.6)	(51–69)
	Finland	0					
	Norway	1					
3 (1921–1940)	Sweden	16	Mean	107	42	33.9	56
	Denmark	0	(Range)	(65–135)	(30.4–56.7)	(25.0–40.0)	(46–68)
	Finland	0					
	Norway	0					
4 (1941–1960)	Sweden	10	Mean	103	44	34.8	55
	Denmark	4	(Range)	(55–190)	(29.1–60.7)	(28.3–41.7)	(46–63)
	Finland	1					
	Norway	2					
5 (1961–1980)	Sweden	10	Mean	90	46	33.3	55
	Denmark	1	(Range)	(55–130)	(28.9–63.4)	(26.5–40.7)	(47–64)
	Finland	1					
	Norway	1					
6 (1981–today)	Sweden	2	Mean	86	47	33.6	53
	Denmark	0	(Range)	(55–120)	(31.2–63.8)	(24.1–45.7)	(44–61)
	Finland	2					
	Norway	3					
	Non-Nordic	3					
Total		81					

Molecular markers

DNA extraction

Leaf material from the accessions grown in field trials was lyophilised and DNA was extracted using the CTAB extraction method of Doyle and Doyle (1990). Individual samples were adjusted to a final concentration of 50 ng/μl DNA. Equal amounts of DNA from 30 individuals of each accession were pooled to represent the cultivar in marker analysis.

Microsatellites

Seven microsatellite loci (Table 3) were amplified as described by Li et al. (2000). PCR primers were synthesised by MWG (MWG-biotech.com, forward primers were labelled with 5′ IRD 700 dye), and taq-polymerase and PCR buffer derived from Promega (Promega.com).

PCR products were separated according to size in a denaturing 6% polyacrylamide gel containing 7M urea, using a LI-COR® 4200 series Automated DNA Sequencer with florescent dye detection of labelling. Fragment lengths in basepairs were estimated using the Kodak® ID v.3.6 (Kodak 2002) software. LI-COR® size standard IRDye™, 700 50–350 bp was used for reference.

Analysis

Discriminatory power of the investigated microsatellite loci (the polymorphic information content, PIC value) was calculated for each locus (Weir, 1996) according to

Table 2. The names, year of introduction, country of origin and accession numbers of the included *Avena sativa* cultivars. * not included in field trial

Species name	Cultivar name	Year of introduction	Assigned age-group	Country of origin	Accession number
A. sativa	Landsort fra Ribe	Landrace	1	DAN	NGB- 8703
A. sativa	Juuka	Landrace	1	FIN	NGB- 220
A. sativa	Ylitornio	Landrace	1	FIN	NGB- 4883
A. sativa	NFinnish	Landrace	1	FIN	NGB- 4479
A. sativa	Rajala	Landrace	1	FIN	NGB- 227
A. sativa	Korgen*	Landrace	1	NOR	"Graminor", N
A. sativa	Ångermanland	Landrace	1	SWE	NGB- 4881
A. sativa	Värmland	Landrace	1	SWE	NGB- 4878
A. sativa	Kopparberg	Landrace	1	SWE	NGB- 4879
A. sativa	Probsteier Skånsk	Landrace	1	SWE	NGB- 4890
A. sativa	Bohus	Landrace	1	SWE	NGB- 4877
A. sativa	Roslags	Landrace	1	SWE	NGB- 6212
A. sativa	Jönköping	Landrace	1	SWE	NGB- 4875
A. sativa	Svartebäck	Landrace	1	SWE	NGB- 4884
A. sativa	HGotland	Landrace	1	SWE	NGB- 6200
A. sativa	Spethavre från Småland	Landrace	1	SWE	NGB- 6199
A. sativa	Jämtland	Landrace	1	SWE	NGB- 4880
A. sativa	Avlsberg	Landrace	1	SWE	NGB- 9765
A. sativa	Plym Svart tatarisk	1898	2	SWE	NGB- 6187
A. sativa	Guldregn I	1903	2	SWE	NGB- 4893
A. sativa	Gul Nesgård	1905	2	DAN	NGB- 9738
A. sativa	Seger	1908	2	SWE	NGB- 2709
A. sativa	Klock II	1909	2	SWE	NGB-6190
A. sativa	Hedehavre Lyngby	1913	2	DAN	NGB- 9722
A. sativa	Kron	1915	2	SWE	NGB- 4895
A. sativa	Grenader	1920	2	NOR	NGB- 2111
A. sativa	OdalVit	1926	3	SWE	NGB- 4887
A. sativa	Klock III	1926	3	SWE	NGB- 6191
A. sativa	Guldregn II	1927	3	SWE	NGB- 2710
A. sativa	Stjärn	1927	3	SWE	NGB- 6202
A. sativa	Orion II	1927	3	SWE	NGB- 4872
A. sativa	Diamant WW	1928	3	SWE	NGB- 8723
A. sativa	Plym	1930	3	SWE	NGB- 6188
A. sativa	Örn	1931	3	SWE	NGB- 6203
A. sativa	Engelbrecht II	1931	3	SWE	NGB- 4867
A. sativa	Stormogul II	1932	3	SWE	NGB- 4866
A. sativa	Sirius I	1932	3	SWE	NGB-6194
A. sativa	Klock Extra I	1933	3	SWE	NGB- 4868
A. sativa	Ligowo III	1934	3	SWE	NGB- 8253
A. sativa	Primus I	1938	3	SWE	NGB- 4889
A. sativa	Sol I	1939	3	SWE	NGB- 4898
A. sativa	Vidar	1940	3	SWE	NGB- 4888
A. sativa	Dansk*	1940	3	DAN	NGB- 6976
A. sativa	Same	1941	4	SWE	NGB- 6198
A. sativa	Sol II	1942	4	SWE	NGB- 2711
A. sativa	Minor Abed	1943	4	DAN	NGB- 6343

(*Continued on next page*)

Table 2. (*Continued*)

Species name	Cultivar name	Year of introduction	Assigned age-group	Country of origin	Accession number
A. sativa	Trio WW	1943	4	SWE	NGB- 9782
A. sativa	Opub Borris	1945	4	DAN	NGB- 8735
A. sativa	Palu Abed	1945	4	DAN	NGB- 4741
A. sativa	Sirius II	1947	4	SWE	NGB- 4869
A. sativa	Bambu II	1949	4	SWE	NGB- 9805
A. sativa	Blenda	1950	4	SWE	NGB- 4900
A. sativa	Rex	1954	4	DAN	NGB- 6989
A. sativa	Klock Extra II	1954	4	SWE	NGB- 6193
A. sativa	Blixt	1954	4	SWE	NGB- 8256
A. sativa	Seger II	1954	4	SWE	NGB- 4892
A. sativa	Nip	1954	4	SWE	NGB- 4873
A. sativa	Kyrö	1957	4	FIN	NGB- 4486
A. sativa	Moholt	1960	4	NOR	NGB- 11309
A. sativa	Tempo	1960	4	NOR	NGB- 2123
A. sativa	Hannes	1964	5	FIN	NGB- 366
A. sativa	Sörbo	1964	5	SWE	NGB- 4903
A. sativa	Titus	1964	5	SWE	NGB- 4909
A. sativa	Linda	1965	5	SWE	NGB- 4902
A. sativa	Regal Pj	1966	5	DAN	NGB- 5117
A. sativa	Selma	1968	5	SWE	NGB- 2649
A. sativa	Weikus	1969	5	SWE	NGB- 2645
A. sativa	Risto	1970	5	SWE	NGB- 4904
A. sativa	Pol	1974	5	NOR	NGB- 2120
A. sativa	Sang	1974	5	SWE	NGB- 2713
A. sativa	Svea	1976	5	SWE	NGB- 2715
A. sativa	Nema	1978	5	SWE	NGB- 4906
A. sativa	Hedvig	1978	5	SWE	NGB- 2648
A. sativa	Ogle	1981	6	USA	From breeders
A. sativa	Rise*	1982	6	DAN	From breeders
A. sativa	Veli	1982	6	FIN	NGB- 374
A. sativa	Newman	1988	6	CAN	From breeders
A. sativa	Martin	1988	6	NOR	NGB- 9958
A. sativa	Virma	1990	6	FIN	NGB- 4466
A. sativa	Biri	1997	6	NOR	NGB- 13583
A. sativa	Bikini	1997	6	NOR	NGB- 13582
A. sativa	Revisor	1998	6	GER	From breeders
A. sativa	Belinda	1998	6	SWE	NGB- 13588
A. sativa	Stork	2000	6	SWE	NGB- 13587

the formula $\mathrm{PIC} = 1 - \Sigma P_i^2$ where P_i is the frequency of the ith allele in the data set.

To test for independence between age group of cultivars and number of alleles observed in each microsatellite primer pair we used Fisher's exact test. The likelihood of data assuming independent segregation was compared with likelihood of the best possible model for the data with a likelihood ratio approach.

The number of lost and gained alleles relative to landraces for each breeding period were calculated for each microsatellite locus. Statistical significance of the loss or gain of alleles from landraces to modern cultivars was tested using a permutation analysis (Fu et al., 2003), simulating artificial cultivars and averaging with 10 000 permutations (PROC IML performing in SAS software version 8.02). Genetic diversity measures for

Table 3. Number of alleles scored in six different age-groups of *Avena sativa*. PIC values (Polymorphic information content). Number of lost and gained alleles scored in relations to allele number in the landraces. E-Total: The expected number of alleles in cultivars for each breeding period, with standard deviations (E-SD). Asterisks refer to the level of significance ($^{*} = p < 0.05, ^{**} = p < 0.01$)

			Number of alleles					
				Period of release				
Primer set	No. of alleles	PIC value	Landraces	1898–1920	1921–1940	1941–1960	1961–1980	1981–2000
Am1	17	0.88	11	7	8	10	10	8
Am2	15	0.88	10	8	9	7	5	5
Am3	16	0.83	11	5	8	9	4	5
Am25	2	0.49	2	2	2	2	2	2
Am31	11	0.71	8	5	7	4	3	4
Am38	4	0.63	3	3	3	3	3	4
Am40	1	0	1	1	1	1	1	1
	$\Sigma = 66$	Total	46	31	38	36	28	29
		Lost		22	16	19	23	24
		New		7	8	9	5	7
		E-Total	40.32	28.13	39.38	39.33	35.21	32.77
		E-SD	3.12	3.11	3.19	3.15	3.14	3.08
		Prob (E > 0)		0.309	0.092	0.039*	0.006**	0.029*

the microsatellite data were calculated as Nei's simple diversity estimate (Nei, 1978) averaged over all loci with a Java based program. Standard deviations of diversity estimated were calculated from 5000 bootstrap datasets.

Results

Analysis of variance of the phenotypic data (Table 4) showed highly significant differences between cultivars for 'heading date', 'straw length', 'harvest index' and 'thousand grain weight' with high genetic determination for 'heading date' and 'TGW', (81.4% and 64.7%, respectively) and somewhat lower determinations for straw length (39.8%) and harvest index (49.3%) (Table 1).

Partitioning of the cultivar SS (Sum of Squares) showed significant differences between countries for all four quantitative variables. Corrected means (LSMeans) showed that cultivars from the most southern country, Denmark, had a later average heading date (58.81 ± 0.42 days) than cultivars from all other Nordic countries. Swedish cultivars had intermediate heading date (56.2 ± 0.17 days), while cultivars from Norway and Finland both had earlier average heading dates of 53.5 days (± 0.44 and 0.41 respectively). A similar north-south gradient was indicated for 'harvest index': Danish cultivars had the lowest average 'harvest index' (0.696 ± 0.0051), Swedish cultivars were intermediate (0.721 ± 0.0021) while Norwegian and Finnish cultivars had the highest 'harvest index' (0.729 ± 0.0055 and 0.737 ± 0.0051, respectively). Country effects of cultivars for 'TGW', however, showed lowest average values for Norwegian and Danish cultivars of 31.07 ± 0.73 and 32.01 ± 0.69, respectively, while Swedish and Finnish cultivars on average had heavier kernels of 33.709 ± 0.280 and 34.187 ± 0.683, respectively. No significant differences between countries were indicated for straw length.

Also partitioning of cultivar SS according to age-group showed highly significant differences for 'heading date', 'straw length', 'harvest index' and 'TGW' (Table 4). These cultivar differences between age-groups were studied with a Spearman correlation analysis, which showed that 'heading date' and 'straw length' were significantly reduced through breeding during the period, while 'harvest index' had been increased (Figure 1). The significant differences in 'TGW' between age-groups were not reflected as a clear trend in the correlation analysis.

Microsatellite analysis revealed 66 alleles from the seven loci studied among the 84 cultivars and landraces (Table 3). One locus (Am40) did not show polymorphism among the cultivars (Table 3). PIC values for the six polymorphic microsatellite loci were high, between

Table 4. Results from ANOVA with 81 accessions of *Avena sativa*

	Model tested	R^2-value	MS	F-value	Pr > F
Heading date	Total	72.9	867.2	115.8	< 0.0001
	Experimental year		3722.4	496.9	< 0.0001
	Country		227.9	30.4	< 0.0001
	Age-group		141.3	18.9	< 0.0001
Straw length	Total	62.6	16373.7	114.3	< 0.0001
	Experimental year		39678.7	277.1	< 0.0001
	Age- group		7051.7	49.2	< 0.0001
Harvest index	Total	87.0	0.3236	289.5	< 0.0001
	Exp. year		1.6578	1483.2	< 0.0001
	Country		0.0095	8.5	< 0.0001
	Age-group		0.0298	26.6	< 0.0001
TGW	Total	33.3	89.30	8.02	< 0.0001
	Experimental year		250.17	22.47	< 0.0001
	Country		117.79	10.58	< 0.0001
	Age-group		100.43	9.02	< 0.0001
	Age-group*country		89.42	8.03	< 0.0001

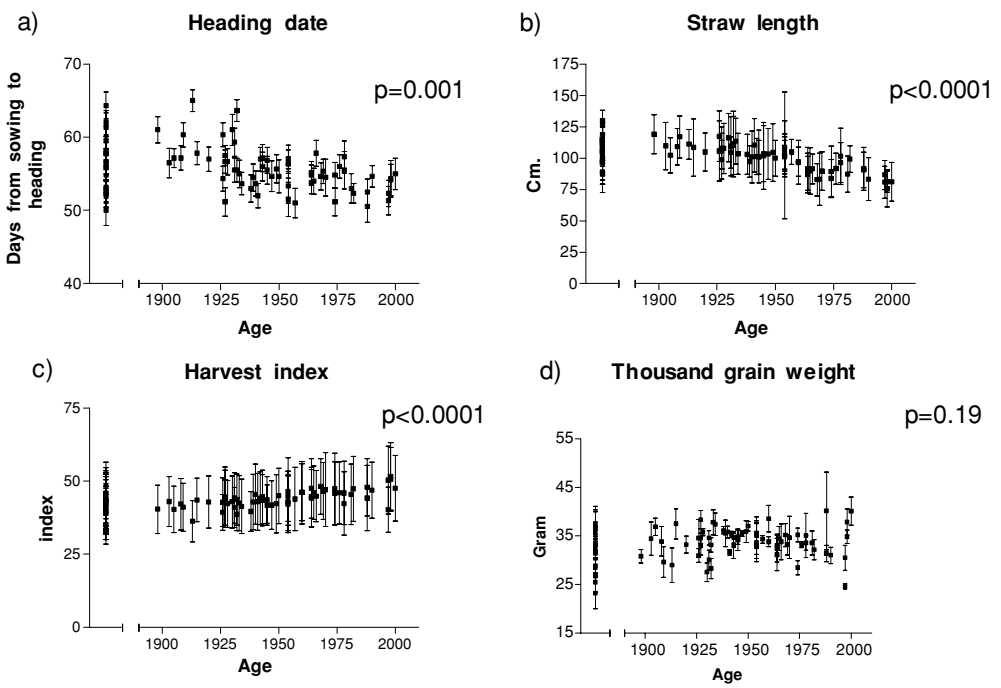

Figure 1. (a–b) Development of major agronomical traits of oat during time. Bars represent standard error. P-values indicate significance of trends from Spearman correlations.

0.49 and 0.88, indicating high information value. Only two of the seven microsatellite markers (Am1 and Am 25) have been mapped previously and were shown to segregate independently in linkage groups OM1 and OM2, respectively (Zhu & Kaeppler, 2003).

Compared to the landraces all other age-groups revealed a smaller number of alleles in the six polymorphic microsatellite loci. Statistical analysis of loss and gain of alleles among the five age groups of bred cultivars relative to the landraces, showed that loss of alleles

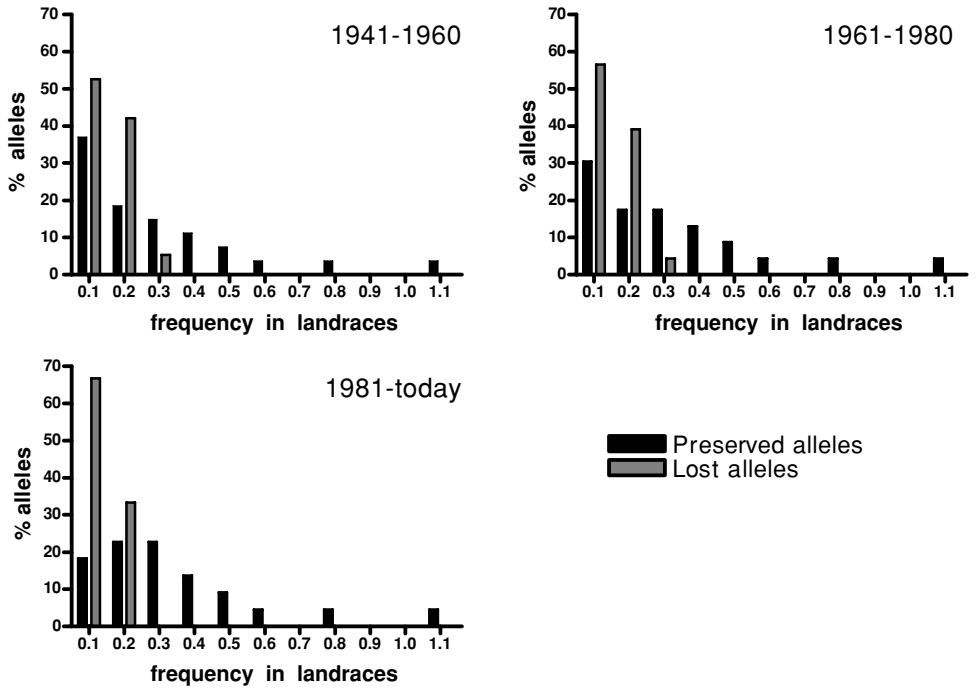

Figure 2. (a–c) Percentages of alleles lost and preserved relative to their original frequencies in landraces, for the age-groups that were found to have a significant loss of alleles (4, 5 and 6, respectively).

was significant for the three most recent age groups (Table 3). The group of landraces that were analyzed revealed 46 different alleles, however, in the bred cultivars released after 1940 a statistically significant reduction in this number of alleles was apparent; the three age-groups representing this period had lost 19, 23 and 24 alleles, respectively. Also, new alleles not found in the landraces were revealed among bred oat cultivars, although more alleles were lost than gained through the period. Seven alleles were exclusively found in landraces. Alleles in landraces, present or absent, in the recent three age-groups, were studied relative to their original frequencies in the landraces (Figure 2a–c). This showed that for all the three most recent age-groups, alleles with low frequencies in the landraces were the ones generally not found in the recent bred cultivars. The test for independence for number of alleles in each microsatellite locus for each cultivar age group with Fisher's test was not significant. It indicates that the loss of alleles during the period is a general phenomenon, which is not related to one or a few of the microsatellite markers studied.

The diversity index (Shannon-Weaver) (Figure 3a) for phenotypic characters over age-groups showed a sudden decline in diversity from around 1950 onwards, with age-group 2 (1898–1920) as an outlier with very low diversity. The molecular marker diversity index (Nei's diversity) (Figure 3b) showed a similar although less distinct trend indicating a decline in diversity from the middle of the last century.

Discussion

Results from this study show that considerable breeding progress has been achieved in Nordic oat cultivars during the last hundred years of breeding. A major change in the characteristics of the oat cultivars took place as a consequence of the transition from cultivation of traditional genetically and morphologically heterogeneous landraces to more uniform "line" cultivars. As also documented by Ahokas and Manninen (2000), a large variation is revealed in the landraces, and a subsequent loss of diversity during the transition to purified cultivars. The original landraces were apparently substituted by cultivars that were later flowering, had considerably longer straw and higher TGW. The changes in these characteristics in cultivar types over a short period of time may to some extent be the result of indirect demands of high yield and uniformity, which

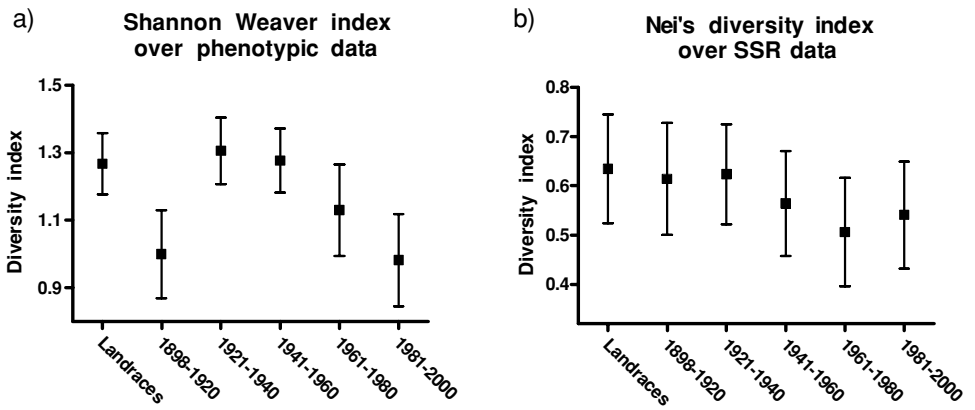

Figure 3. Trends in diversity development of Nordic oat cultivars during hundred years of breeding. (a) The mean Shannon Weaver index of agronomical characters. (b) Nei's simple diversity estimate from microsatellite allele frequencies. Bars represent standard deviation.

could not be met effectively with the traditional heterogeneous cultivars. Higher yield may result from later blooming cultivars. Longer straw in the initially purified cultivars could be preferred as a response to weedy fields where the crops have to compete for light, water and nutrition. The smaller kernel size of the landraces, which might have been a competitive advantage in the heterogeneous population, was exchanged with heavier uniform kernels in the new more homogeneous cultivars. During the subsequent 80 years of breeding, some of these initial breeding shifts towards later heading date and higher plants have gradually been modified towards earlier types with shorter straw. This development has clearly been intensified during the last 50 years probably related to introduction of mechanization and use of fertilizers and pesticides. In contrast, harvest index of the oat cultivars has steadily increased during the entire period, while a trait like TGW seems to have reached an optimum level soon after the initial transition to modern cultivars. Our data are in accordance with the data from Rekunen (1988), who reported a decrease in straw length and heading date but a constant TGW for Finnish oat.

Our data showed a geographical gradient in the plant material according to country of origin. Cultivars from Finland and Norway displayed earlier heading dates, suggesting adaptation to short summer periods, while cultivars from Sweden and particularly Denmark had later heading dates suggesting less constraint from day length and temperature. A similar gradient was reflected in the harvest index, where Norwegian and Finnish cultivars had a higher index compared with Danish and Swedish material. This may result from the more persistent or intense breeding in the northern part of the region. Such geographical gradients, however, may also be created because cultivars from the Northern area are better adapted to the climatic and geological conditions of the evaluation site.

Generally, a comparison of phenotypic or adaptive traits between older cultivars and landraces with modern cultivars is a challenge, since the older material is not adapted to modern production methods. Application of fertilizer is the major problem, since high dose application of fertilizer can lead to elongation of straws followed by lodging. However, Ortiz et al. (2003) in spring wheat, and Peltonen-Sainio et al. (1993) in oat, reported that grain weight and heading date were little affected by nitrogen fertilizer rate.

The microsatellite study shows that breeding of Nordic oat has clearly resulted in a decline in number of alleles from landraces to recent cultivars, a tendency also reported previously for Canadian oat by Fu et al. (2003). A corresponding loss of alleles was found in bread wheat from France by Roussel et al. (2004), as allelic richness between the landrace-period and all other decadal periods was always significant. Like in the French bread wheat accessions (Roussel et al., 2004), we also found that the alleles not represented in modern oat cultivars were, in fact, rare in the landraces. If breeding material is selected as a restricted sample of a large population, there is likely to be a decline of rare alleles in all loci, as a consequence of random factors (a bottleneck) (Charlesworth et al., 1993). In the 1940's and 1950's when modern breeding became more efficient, it is likely that relatively few high performing cultivars formed the basis for most breeding programs, hence creating a bottleneck. Alternatively, a reason for the loss of rare alleles may be that they

had deleterious effects in the material (Allard, 1996; Roussel et al., 2004). However, in this case it would require linkage of the examined microsatellite loci to genomic locations under agronomical pressure. Since the loss of alleles seems to be a general phenomenon for the 6 marker loci studied, the results support the idea of a bottleneck mechanism.

In the present study of oat both agronomical and molecular data indicated a decline in diversity from landraces to recent cultivars. In wheat, barley and maize, DNA-marker results (Donini et al., 2000; Lu & Bernardo, 2001; Christiansen et al., 2002; Soleimani et al., 2002; Koebner et al., 2003) showed a stabilized or unchanged genetic diversity of cultivars from recent years. However, in contrast to our analysis, only few of these studies included a comparison to landraces. The breeding of a crop may reach a point where new diversity must be added in the breeding population to reach new goals. Rasmusson and Phillips (1997) argued that emergence of *de novo* variation by random events like mutations may be sufficient to maintain levels of diversity among cultivars during intensive breeding. In contrast, in this material of oat we find a significant loss in number of alleles since 1940, and therefore it is important to consider conservation strategies to support future breeding programs.

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