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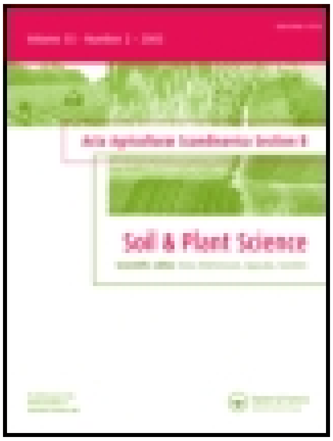

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Diversity in Nordic spring wheat cultivars (1901-93)

Rodomiro Ortiz [a b] , Sten Madsen [a] & Sven Bode Andersen [a]

[a] Department of Agricultural Sciences , The Royal Veterinary and Agricultural University , 40 Thorvaldsensvej, Frederiksberg C, DK-1871, Denmark

[b] ICRISAT , Patancheru, Andhra Pradesh, 502 324, India

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Diversity in Nordic Spring Wheat Cultivars (1901–93)

Ortiz, R., Madsen, S. and Andersen, S. B. (The Royal Veterinary and Agricultural University, Department of Agricultural Sciences, 40 Thorvaldsensvej, DK-1871 Frederiksberg C, Denmark). Diversity in Nordic spring wheat cultivars (1901–93). Accepted December 3, 1998. Acta Agric. Scand., Sect. B, Soil and Plant Sci. 48: 229–238, 1998. © 1998 Scandinavian University Press.

Nordic plant breeders have selected superior genotypes and released new spring wheat cultivars throughout this century. However, the extent of phenotypic diversity that exists in this improved germplasm has not been accurately investigated. This study phenotypically assessed 75 selected cultivars released to farmers in Denmark, Finland, Norway and Sweden within the last 10 decades. Grouping of cultivars was not related to their geographical origin or decade of release. The respective within-cluster variances were always larger than the among-cluster variances. The average phenotypic diversity for Nordic spring wheat germplasm was 0.22, which was not surprising because some newer cultivars were derived from older cultivars. There was a significant influence of geographical origin on days to heading, straw, grain and biomass weight, and kernel number. Likewise, the country × decade of release interaction was significant for all characteristics except plant height. These findings suggest that irrespective of location, Nordic breeders have reduced plant height in recently released cultivars at a rate of -0.5 cm year^{-1}, thereby reducing lodging in this germplasm. There was no significant change in biomass, straw and kernel weight between old and new cultivars. Nonetheless, relative genetic gains in this germplasm during this century were significant for agronomic characteristics, such as days to heading (8%), plant height (36%), grain yield (20%), harvest index (19%), and number of kernels per unit area (18%). On average, the absolute genetic gain for grain yield was about 18.5 kg ha^{-1} year^{-1}. Negative changes in days to heading (at a rate of -0.06 year^{-1}) and plant height, and positive changes in harvest index (0.06% year^{-1}), and kernels m^{-2} (45 year^{-1}) were associated with gains observed in grain yield, i.e. an early flowering plant with short straw, but many fertile tillers, had high grain yield. This sustained genetic gain could result from the accumulation of favourable alleles and intergenomic interactions between homologous loci during systematic plant breeding for grain yield.

Rodomiro Ortiz*, Sten Madsen and Sven Bode Andersen

The Royal Veterinary and Agricultural University, Department of Agricultural Sciences, 40 Thorvaldsensvej, DK-1871, Frederiksberg C, Denmark

Key words: cultivar, genetic grain, phenotypic diversity index, *Triticum aestivum*.

Introduction

Accurate estimation of genetic diversity in germplasm collections is important for conservation and management of genetic resources. A direct comparison between and within cultivars of different national

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* New address: ICRISAT, Patancheru 502 324, Andhra Pradesh, India.

origin may help us to understand how breeding has been focused within each cultivar pool. In this way, useful characteristics associated with this improvement could be identified. Also, with the aid of a phenotypic diversity index based on agronomic characteristics, the extent of phenotypic variability and the available genetic base in different germplasms for further breeding work may be determined.

Wheat yields in Scandinavia are relatively high (4–7 t ha^{-1}). Spring wheats are popular in Finland, Norway and Sweden. Bred cultivars have been released since the early 1900s in Sweden, from 1920s onwards in Norway and Finland, and more recently in Denmark. A comparison of genetic improvement within each gene pool over time could show the benefits of plant breeding, and provide a means of determining changes in morphotype, quality and pest resistance, arising from artificial selection. Peltonen-Sainio & Karjalainen (1991) compared genetic gains of 22 widely grown spring wheat cultivars based on long-term trial data collected in Finland (1920–88). The average annual yield gain was 0.38–0.45% in spring wheat. Similar results with Swedish spring wheat were obtained by MacKey (1994), who indicated that in excess of 50% of the total gain can be attributed to plant breeding. Peltonen-Sainio & Karjalainen (1991) suggested that grain yield gains were the result of higher harvest indices. However, as these authors stated, calculation of genetic gains on yield based on long-term yield trials may be biased by the cultivation techniques used throughout the testing period.

Partial data of agronomic, quality, and pest resistance in 66 spring wheat cultivars were compiled by the Nordic Gene Bank (Nordic Gene Bank, 1992). A preliminary examination of this database confirms a slight improvement in grain weight in Swedish spring wheat cultivars (Evans, 1993) and shortening of their plant height. Most Swedish spring wheat cultivars have maintained moderate levels of mildew resistance (2–4 on a 1–9 scale) throughout the release period. Similarly, gains in grain weight and shortening of plant height seem to be associated with improvement of grain yield in Norwegian spring wheat cultivars. However, the data deposited in the Nordic databases were provided by many scientists and plant breeders. This heterogeneity of data does not allow a proper analysis. Likewise, data transformation (standard 1–9 scale) does not necessarily reflect the same absolute value in the original database. Hence, the objective of this research was to assess the phenotypic diversity in Nordic spring wheat cultivars released from 1901 to 1993, and examine the relationship of these cultivars with their origin and decade of release.

Table 1. Sample of Nordic spring wheat cultivars released from 1901 to 1993 by country and decade of release

Decade of release	Country			
	Denmark	Finland	Norway	Sweden
1900s				Kolben, Vårparl
1910s				Extra Kolben
1920s			Ås	Diamant, Rubin, Extra Kolben II
1930s		Tammi	Fram, Snøgg	Atle, Diamant II, Drott
1940s		Apu, Kimmo	Ås II, Fram II, Skirne, Snøgg II	Brons, Progress
1950s	Peko[d]	Touko	Nora, Norrøna Tautra, Trym	Atson, Blanka, Fylgia, Fylgia II, Karn, Karn II, Pondus, Rival, Safir, Svenno
1960s		Ruso	Møystad, Rollo	Pompe, Prins, Rang, Ring, Snabbe
1970s	William[c]	Taava, Tahti, Ulla	Lanor, Reno, Runar	Amy, Drabant, Saffran, Sappo, Sonett, Trippel, Walter
1980s	Timmo[c]	Luja	Baastian[a]	Canon, Dragon, Fagott, Nemares, Sober, Sunnan,
1990s	Troll[c]			Boru, Dacke, Kadett, Sport, Tjalve
Unknown				Tilly[b]

[a] First semi-dwarf cultivar in this country (K. Ringlund, NLH, Norway, pers. comm.).

[b] Probably never marketed in Scandinavia, but was released in England in 1972 (G. Svensson, SLU, Sweden, pers. comm.).

[c] Bred in southern Sweden by Weibullsholm's Plant Breeding Institute (Landskrona).

[d] Originally bred in Germany.

Materials and methods

A total of 75 Nordic spring wheat cultivars (Table 1) from Denmark (4), Finland (9), Norway (17) and Sweden (45) were included in this research. All cultivars but one (Peko) were released by Nordic breeders from 1901 to 1993, and their seed was obtained from the Nordic Gene Bank (Alnarp, Sweden). The cultivars were grown in a randomized complete block with two replications in 1997 at Højbakkegård (55° 40′ N, 12° 20′ E) in Taastrup (Denmark). This location has a fine, sandy, moraine, humic soil, with a pH of ~ 7. Weather data are available upon request from the authors. The plant characteristics recorded were days to heading, height (cm), lodging, total biomass weight at harvest (BW), straw weight, grain yield (GY), weight of 1000 grains, and average number of kernels per plot. The harvest index was calculated as 100*GY/BW.

Each experimental plot consisted of ~ 70 seeds sown in six rows of 1.2 m length. The distance between rows was 0.20 m. All plots were hand harvested 123 days after sowing. Their stems were cut at ground level. Plants were fertilized with N–P–K at a rate of 80 kg N ha^{-1}, 11.4 kg P ha^{-1}, and 38 kg K ha^{-1}. This amount of fertilizer was applied to avoid bias towards progress resulting from modern cultural practices rather than genetic gains. The chosen fertilizer rate could have been adequate for cultivars released in the 1970s, but high for old cultivars, especially those showing lodging in this experiment, and low to show the yield potential of the cultivars bred in the 1990s (G. Svensson, SLU, Sweden, pers. comm.). All plots were sprayed with a recommended commercial fungicide to control mainly leaf diseases that could occur during the experiment, and to allow all cultivars, irrespective of their host plant resistance or susceptibility, to show their phenotypic potential.

A phenotypic distance matrix was created by calculating the difference between each pair of accessions for each characteristic. The diversity index was calculated by averaging all the differences in the phenotypic value for each descriptor divided by the respective range (Johns et al., 1997). The analyses of variance for the phenotypic diversity index, based on morphological descriptors, considered the variation between and within Nordic country clusters, and between and within decade of release clusters. Thus, the between-cluster mean squares ($ó^2_{\mathrm{Bi}}$) was divided by the total mean squares ($\sigma^2_{\mathrm{Bi}} + \sigma^2_i$), where σ^2_i was the within-cluster mean squares. A ratio close to 1 (maximum) indicates greater partitioning of the population into sub-groups (either country or decade of release). Further analysis considered the average phenotypic distance for each Nordic cultivar as deviations from the population mean for all Nordic spring wheat cultivars, and the sum of their squared deviations as a variance (σ^2_{C}). Similarly, the squared deviations for each pair comparison from the average phenotypic distance for a particular cultivar were calculated to obtain σ^2_{W}. A ratio (hereafter Φ_{ST}) was calculated by dividing the among cultivars mean square by the total-mean square ($\sigma^2_{\mathrm{W}} + \sigma^2_{\mathrm{C}}$). Average linkage cluster analysis was performed on the phenotypic distance matrix to study the pattern of variation and relationship between wheat cultivars according to their known year of release and geographical origin.

Variation due to genotypes was split into country of origin, decade of release and the interaction between these factors. A single degree of freedom was used from the decade of release to perform a linear regression analysis to determine the rate of annual genetic improvement throughout this century. The independent variable was year of release and the dependent variable was the phenotypic variation for each specific characteristic. Absolute rates of genetic improvement were divided by the mean of each characteristic to calculate the relative genetic gain during the period 1901–93 for those characteristics that showed a significant regression slope. Cultivar means for each decade of release within each country were compared by the least significant difference at the 5% level. Phenotypic correlations between all characteristics were calculated using individual plot means to establish which phenotypic changes were associated with grain yield improvement during this century. Contingency tables were tabulated for lodging vs. other morphological characteristics and year of release, to perform chi-square tests. All statistical analyses were performed either with MSTATC (Anonymous, 1989) or SAS (Anonymous, 1996).

Results

The widest range of phenotypic diversity was often observed between, rather than within, country clusters (Table 2). Diamant II and Drott, both developed and released in Sweden in the 1930s, were the two closest cultivars as determined by the phenotypic diversity index (0.0285) based on agronomic characteristics. Within the other country clusters, the closest phenotypic resemblance was observed between the cultivars William and Timmo from Denmark, between Apu and Ulla from Finland, and between Møystad and Nora from Norway (Table 2). These pairs of cultivars released in Denmark and Norway were within two consecutive decades (Table 1).

The most phenotypically distinct cultivar with respect to the other Nordic cultivars was Tahti, which was released in Finland in 1972. The average phenotypic diversity index of this cultivar was 0.4384. The

Table 2. Range (minimum in upper line and maximum in lower line) of the phenotypic diversity index based on agronomic characteristics between (above diagonal) and within (in italics on diagonal) Nordic spring wheat cultivars according to origin

Country	1	2	3	4
Denmark	*0.0646*	0.1485	0.0747	0.0461
	0.3697	0.5514	0.4098	0.4687
Finland		*0.0689*	0.0521	0.0600
		0.4354	0.5759	0.6328
Norway			*0.0465*	0.0567
			0.4781	0.5032
Sweden				*0.0285*
				0.4663

largest phenotypic distance (0.6328) among two cultivars was recorded between Tahti and Rang (Sweden, 1968). The most phenotypically different Norwegian cultivars were Ås and Baastian, and Vårparl and Boru in Sweden, which are among the oldest and newest cultivars for either country in this investigation (Table 2). Similarly, the most phenotypically distinct cultivars released in Denmark are Peko and William, which were originally developed in Germany and southern Sweden, respectively. However, neither time nor geographic origin accounts solely for phenotypic differentiation between Nordic cultivars. For example, Taava and Tahti are the most different cultivars released in Finland, but within the same decade (1970s).

Table 3 lists the ranges of the phenotypic diversity index according to decade of release. There was overlap of ranges among decades. The range of phenotypic diversity was smallest at the beginning of the century, and widest among cultivars released in the 1970s. It seems that phenotypic diversity consistently enlarged in this Nordic spring wheat pool until the 1970s, but has lessened since.

The lack of distinct pattern for phenotypic diversity according to country of origin or release decade was confirmed by the between and within cluster variances. The latter was always larger than the former. For example, the between country cluster variance was 0.0002, while the respective within country cluster variance was 0.0071. Similarly, the between and within decade of release cluster variances were 0.0006 and 0.0067, respectively. The ratios between/within cluster variances were smaller than 0.10, indicating that there was little multivariate phenotypic differentiation between decades of release or country of origin.

The phenotypic diversity index variance among Nordic cultivars (σ^2_C) was 0.0019, while the within variance (σ^2_W) was 0.0066. Thus, Φ_{ST} was calculated as 0.2229. Fig. 1 shows the average linkage cluster analysis performed on the phenotypic distance matrix. The average phenotypic diversity index among Nordic cultivars at the 95% probability level was

Table 3. Range (minimum in upper line and maximum in lower line) of the phenotypic diversity index based on agronomic characteristics between (above diagonal) and within (in italics on the diagonal) Nordic spring wheat cultivars according to decade of release

Decade	1	2	3	4	5	6	7	8	9	10
1900s	*0.1053*	0.1763	0.0741	0.0984	0.0770	0.1143	0.1909	0.1570	0.2454	0.2515
			0.2339	0.2786	0.3595	0.4088	0.4523	0.4687	0.4557	0.4663
1910s		—	0.0890	0.1149	0.0973	0.1222	0.2344	0.1926	0.2882	0.3060
			0.1777	0.2918	0.3283	0.3019	0.3771	0.4374	0.3980	0.3732
1920s			*0.0724*	0.0412	0.0339	0.0459	0.1152	0.0615	0.1739	0.1082
			0.2319	0.3172	0.3272	0.3415	0.3988	0.4381	0.4781	0.4435
1930s				*0.0285*	0.0596	0.0477	0.1072	0.0596	0.1107	0.1401
				0.2532	0.3941	0.3543	0.4039	0.3838	0.3769	0.4657
1940s					*0.0655*	0.0612	0.0702	0.0689	0.0830	0.0963
					0.4377	0.3908	0.5079	0.5662	0.5032	0.4932
1950s						*0.0486*	0.0465	0.0512	0.0921	0.0856
						0.3176	0.3779	0.5759	0.4371	0.3725
1960s							*0.0562*	0.0531	0.0887	0.0857
							0.4025	0.6328	0.4563	0.4063
1970s								*0.0644*	0.0600	0.0715
								0.5514	0.5374	0.5745
1980s									*0.0605*	0.0820
									0.3040	0.3977
1990s										*0.0836*
										0.3095

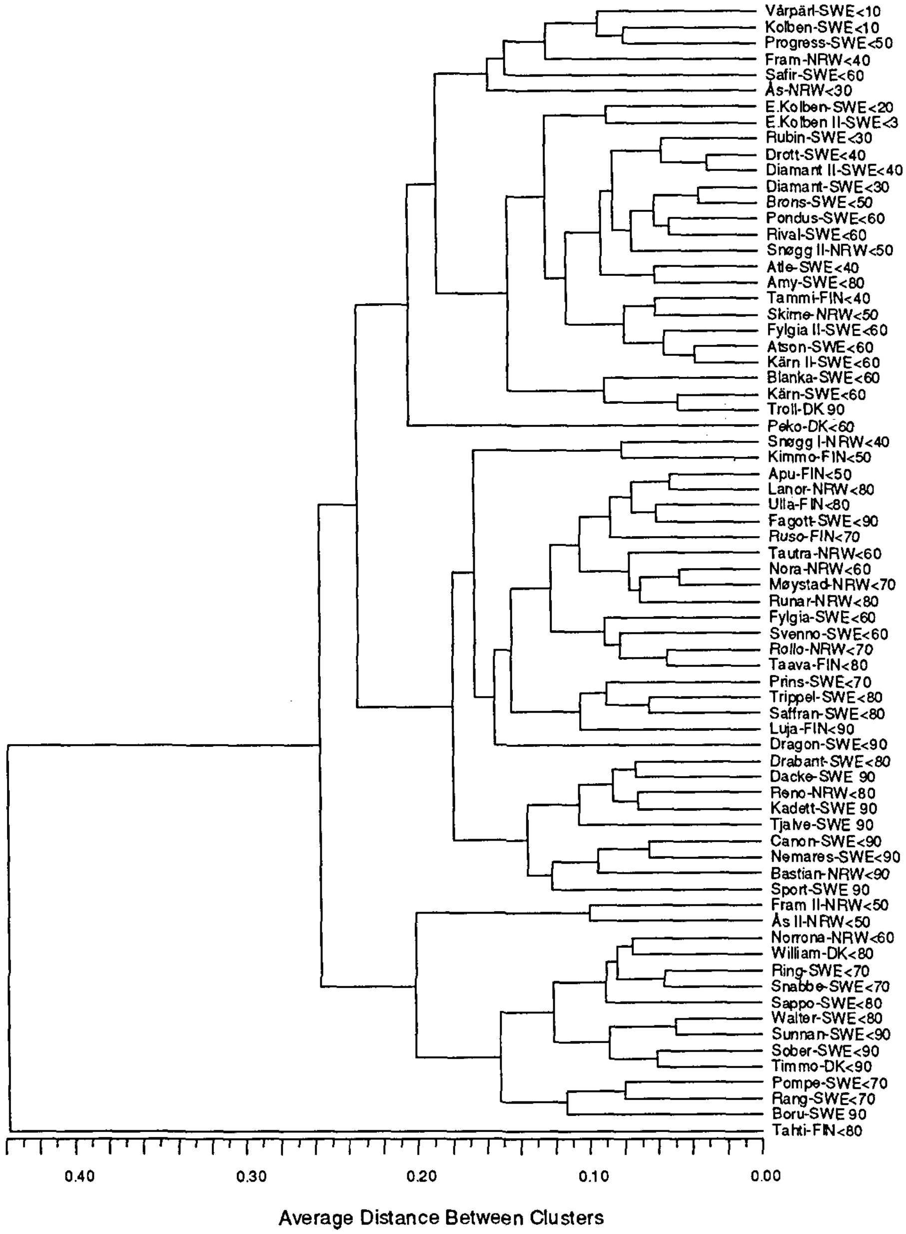

Fig. 1. Dendrogram of clusters resulting from the phenotypic diversity index for Nordic spring wheat cultivars. Cultivar name followed by country (SWE = Sweden; NOR = Norway; FIN = Finland; DK = Denmark) and decade of release (< 10 = decade of release from 1901 to 1909, < 20 = 1910–19, etc.). A distance in excess of 0.0191 was significantly different at the 5% level.

0.2175 ± 0.0191. The values for Φ_{ST} and the average phenotypic diversity index were not surprising, because some newer cultivars were derived from older cultivars. For example, Extra Kolben was the common parent of Progress, Brons, Atle and Diamant. The phenotypic diversity index between these cultivars and the common parent ranged from 0.1375 to 0.1725, while this index ranged from 0.0339 to 0.2132 among the half-sibs. The phenotypic diversity index was always smaller than 0.25 for most pair comparisons between parent–offspring and grandparent–offspring, or among half- and full-sibs. It was interesting to note that the phenotypic diversity index between Ruso and its ^{60}Co mutant Taava was 0.0879, which suggested close similarity between both cultivars. The mutant had slightly higher grain yield in this experiment, owing to improved tilling and heavier grains than its parent, but earliness, plant height and harvest index were similar.

There were significant differences between Nordic cultivars for all agronomic characteristics (Table 4). Genotypes accounted for in excess of 75% of the total sum of squares in the analysis of variance. Most of the variation observed in the agronomic characteristics was significantly affected by country of origin (C) of the cultivar, except for plant height, harvest index and thousand-kernel weight. The decade of release (D) affected significantly days to heading, plant height and harvest index, while the C × D interaction was significant for all characteristics except plant height. This analysis suggests that Nordic breeders have selected short, newer cultivars irrespective of their working location.

On average, early flowering cultivars were bred in Finland and Norway, whereas the cultivars developed in southern Scandinavia exhibited high biomass and straw weight, and had the highest yield, harvest index and number of kernels per unit area (Table 5). Results for grain yield agreed with national average yields in the Nordic region, i.e. highest yields were recorded on farmers' fields in Denmark, followed by Sweden, Norway and Finland. The improving trend in the Nordic germplasm across time for days to heading, plant height, grain yield, harvest index, and kernels per area became clear after splitting this century into five periods of 20 year intervals (hereafter breeding era). Furthermore, the rates of phenotypic improvement across time for these characteristics were significant as shown by the respective regression analyses (Table 6). The relative genetic gain during this century ranged from almost 8% for days to heading to 36% for plant height. Grain yield was improved at a rate of 18.5 kg ha^{-1} $year^{-1}$ from 1901 to 1993 in Scandinavia.

Lodging was observed in 16 Nordic cultivars in this experiment. There was a significant association between lodging and days to heading, plant height and release year (Table 7). Lodging was more frequent among old releases, owing to their taller plant height compared with modern cultivars. Phenotypic correlations were significant for half of the pairs between characteristics (Table 8). On average, tall cultivars exhibited later flowering, had higher straw weight, and showed lower harvest index than short cultivars. Straw weight was positively correlated with both grain yield and number of kernels per unit area, whereas grain yield was significantly associated with both harvest index and number of kernels per unit area. The latter was also positively correlated with total biomass weight and harvest index, but negatively correlated with thousand-kernel weight. These significant phenotypic correlations suggest that the improvement of grain yield in the Nordic germplasm was the result of selection for short, early flowering plants, bearing many fertile tillers.

Discussion

The results suggest that there was a geographic pattern of diversity for days to heading, straw and biomass weight, grain yield, and kernel number (Table 4). Cultivars released in the most northern latitudes headed significantly earlier, but had significantly lower grain yield and number of kernels at the southern Scandinavian site of this experiment. However, the ranges of the phenotypic diversity index (Table 2), as well as the analysis of between- and within-cluster mean squares, indicated that the within cluster variation was the most important. Therefore, differentiation between Nordic populations was relatively low, suggesting that plant breeders have been selecting spring wheat cultivars with similar characteristics in the region arising from the same regional adaptation patterns. Much of the phenotypic diversity among decades of release was also attributable to within-cluster diversity. Similarity between cultivars released in different decades could be ascribed to genotypes sharing common ancestors. For example,

Table 4. Percentage of sum of squares and significance for each source of variation for agronomic characteristics between Nordic spring cultivars (1901–93)

Source of variation	DH	PH	SW	GY	BW	HI	TKW	K/P
Replications	8***	6***	0	0.5	0	6***	0	1
Genotypes	80***	86***	76***	78***	77***	76***	92***	79***
Country (C)	23*	1	39*	42**	43*	10	20	34*
Release decade (D)	51*	90***	20	30	20	68**	36	23
C × D interaction	26*	9	41**	28*	37**	22**	44***	43***
Error	12	8	24	21	23	18	8	20
Coefficient of variation (%)	2.0	4.5	11.3	12.2	11.3	4.3	3.6	11.9
Mean	71.6	116.8	2415.5	1011.7	3427.2	29.5	36.9	27479.3

*, **, *** Significance at 5%, 1% and 0.1% levels, respectively.

DH = days to heading; PH = plant height (cm); SW = straw weight (g $plot^{-1}$); GY = grain yield (g $plot^{-1}$); BW = total biomass weight at harvest (g $plot^{-1}$); HI = harvest index (%); TKW = thousand-kernel weight (g); K/P = average number of kernels $plot^{-1}$.

Table 5. Agronomic characteristics according to origin and period of release

Country/Period	N	DH	PH	SW	GY	BW	HI	TKW	K/P
Country									
Denmark	4	72	113	2704	1178	3882	30	41	29936
Finland	9	70	115	1973	807	2781	29	37	21887
Norway	17	70	120	2444	978	3422	29	35	27701
Sweden	45	72	117	2457	1045	3502	30	37	28250
Period									
1900–19	3	76	138	2372	860	3231	26	36	23778
1920–39	10	73	127	2429	930	3358	28	35	26367
1940–59	24	72	124	2496	1017	3513	29	38	26989
1960–79	22	71	111	2353	1024	3377	30	37	27598
1980 onwards	15	70	103	2357	1069	3426	31	36	29910
$LSD_{0.05}/[1/N_1+1/N_2]^{1/2}$		3	10	545	247	770	2	3	6529

N = number of cultivars; DH = days to heading; PH = plant height (cm); SW = straw weight (g $plot^{-1}$); GY = grain yield (g $plot^{-1}$); BW = total biomass weight at harvest (g $plot^{-1}$); HI = harvest index (%); TKW = thousand-kernel weight (g); K/P = average number of kernels $plot^{-1}$.

the early Swedish cultivars Extra Kolben and Extra Kolben II are parents of other cultivars released later in the century. The above observations were confirmed by the average linkage cluster analysis (Fig. 1). The grouping of cultivars in different clusters was related to neither their geographic origin, nor their decade of release. This phenotypic clustering indicated the existence of large variability among cultivars belonging to either the same country or similar decade of release.

The values of the phenotypic diversity index suggest that Nordic plant breeders should consider the utilization of other sources of variation to incorporate in their spring wheat breeding populations to broaden the genetic base. However, Allard, (1996) indicated that 'the most useful genetic resources are modern elite cultivars and their close relatives, especially materials that are adapted in the local environment or closely similar environments'. Likewise, he recommends that favorable multi-allelic interactions developed for a given habitat should be preserved and enhanced. Hence, Nordic breeders may consider obsolete cultivars when searching for desired phenotypes to be incorporated in their current breeding populations, because these old Nordic cultivars already have the required adaptation to this northern latitude. A broad base population may be developed by choosing as parents old and new released cultivars with desired characteristic(s) but distinct morphotypes, as determined by the average linkage cluster analysis (Fig. 1).

The range for the phenotypic diversity index was significantly correlated with the number of cultivars in the respective decade of release cluster ($r = 0.770$, $P = 0.008$). Likewise the maximum values for the phenotypic diversity index within the same cluster were associated with the number of cultivars in respective decade of release ($r = 0.762$, $P = 0.009$), while the minimum values for the phenotypic diversity index within the respective cluster were negatively associated with the number of cultivars from the same country ($r = -0.943$, $P = 0.028$). These results

Table 6. Phenotypic change per year of release and relative genetic gain from 1901 to 1993

Characteristic	Phenotypic change (unit $year^{-1}$)	Genetic gain (% in period)
Days to heading	-0.060 ± 0.012 ($R^2 = 25.2\%$, $P < 0.001$)	7.8
Plant height (cm)	-0.453 ± 0.035 ($R^2 = 70.3\%$, $P < 0.001$)	36.1
Straw weight (g $plot^{-1}$)	-1.610 ± 1.863 ($R^2 = 1.1\%$, $P = 0.390$)	nd
Grain yield (g $plot^{-1}$)	2.223 ± 0.880 ($R^2 = 8.5\%$, $P = 0.014$)	20.4
Biomass weight (g $plot^{-1}$)	0.613 ± 2.697 ($R^2 = 0.1\%$, $P = 0.821$)	nd
Harvest index (%)	0.059 ± 0.007 ($R^2 = 51.4\%$, $P < 0.001$)	18.6
Thousand kernel weight (g)	0.010 ± 0.018 ($R^2 = 0.5\%$, $P = 0.553$)	nd
Kernels $plot^{-1}$	53.782 ± 24.689 ($R^2 = 6.4\%$, $P = 0.033$)	18.2

nd, not calculated because there was no significant phenotypic change.

Table 7. Contingency χ^2 tests between lodging and agronomic characteristics or year of release in Nordic spring wheat

Classes	Non-lodging	Lodging	χ^2	P
Days to heading				
68–69	14	1		
70–71	18	0		
72–73	11	4		
74–75	14	9		
76–77	2	2	13.358	0.0097
Plant height (cm)				
95–104	9	0		
105–114	21	2		
115–124	18	3		
125–134	8	6		
135–140	3	5	17.194	0.0018
Year of release				
1901–20	2	1		
1921–40	5	7		
1941–60	16	6		
1961–80	24	0		
1981 onwards	11	2	17.120	0.0018

suggest that the range of the phenotypic diversity index depended on the sample size. Hence, the higher the number of cultivars released in a country or within a decade, the greater the phenotypic diversity among cultivars. This finding demonstrates that cultivar development by plant breeders could have widened the phenotypic diversity, thereby broadening its germplasm base, in Nordic spring wheats during this century.

The range of the phenotypic diversity index across decades could be also associated to the number of breeding programmes active in respective period. At the beginning of this century only one programme was breeding spring wheat in Sweden, while from the 1940s until the 1970s the highest number of wheat breeding programmes were active in the Nordic region. In recent decades breeding programmes merged and only a few are still active nowadays. Likewise, in the 1980s and 1990s the backcross method was an important tool to breed new cultivars with specific disease resistance (G. Svensson, SLU, Sweden, pers. comm.). Such a breeding approach could lead to the development of related cultivars.

No levelling off of the tendency for progress in wheat breeding in Sweden has been reported (MacKey, 1994). Our results (Table 3) confirmed this observation, but for the whole Nordic region. Disomic polyploidy enables alleles allocated to different homologous loci to interact at the same time as they become homozygous in each of the respective genomes (MacKey, 1970). In selfing species, such as spring wheat, this means that heterosis via 'overdominance' between homologous loci can be fixed (MacKey, 1987). Furthermore, Rasmusson & Philips (1997) claimed that 'elevated epistasis' arising from de novo non-allelic interactions may account for genetic gains within narrow gene pools.

The improvement in spring wheat performance this century could be due to changes in cultural practices (including fertilizer) as well as to the development of genetically superior cultivars (Kuhr et al., 1985). These results show that there has been a significant increase in the genetic yield potential of Nordic spring wheat, though the average rate of genetic improvement of grain yield was generally lower than reported elsewhere except India (Slafer & Andrade, 1991; Pecceti & Annicchiarico, 1998). Nevertheless, the absolute rate of genetic improvement (18.5 kg ha^{-1} year^{-1}) was higher than those reported in most countries except Italy (Canevara et al. 1994), Mexico (Waddington et al., 1986; Bell et al., 1996) and UK (Austin et al., 1980, 1989). In this century Nordic breeders focused strongly on improving baking quality in spring wheat as well as in selecting early cultivars, which could have indirectly affected the rate of grain yield betterment in this germplasm.

Total plant biomass, straw weight, and thousand-kernel weight did not change significantly between decades, indicating that short plant height, early flowering, and increased grain yield, harvest index, and kernel number per area could occur at the expense of the former characteristics that remained unchanged. Similar associations were observed in German spring wheat (Feil & Geisler, 1988), and British winter

Table 8. Phenotypic correlations (ρ) between agronomic characteristics in Nordic spring wheat

Characteristic	PH	SW	GY	BW	HI	TKW	K/P
Days to heading	0.605***	0.216	−0.060	0.130	−0.462***	0.018	−0.061
Plant height (PH)		0.326**	−0.108	0.190	−0.710***	0.099	−0.155
Straw weight (SW)			0.845***	0.983***	0.010	0.206	0.731***
Grain yield (GY)				0.928***	0.537***	0.205	0.882***
Total biomass weight at harvest (BW)					0.190	0.213	0.809***
Harvest index (HI)						0.059	0.501***
Thousand kernels weight (TKW)							−0.270*
Average number of kernels per plot (K/P)							

*, **, *** Significance at 5%, 1% and 0.1% levels, respectively.

wheat (Austin et al., 1980). Slafer & Andrade (1991) indicated that changes in grain yield in wheat were mostly associated with changes in number of kernels per area rather than with changes in kernel weight. They reported that although the source: sink ratio was high during kernel filling in old cultivars but more balanced in new cultivars, grain yield could be sink-limited during kernel filling. Hence, a compromise between straw weight and grain yield would be required to achieve further sustained gains in the improvement of yield potential in spring wheat. In this regard, Wallace et al. (1993) have suggested that efficient breeding for higher yield should rely on simultaneous selection of three characteristics, namely biomass accumulation, yield *per se* to achieve a high harvest index, and time to harvest maturity adjusted to specific growing season in respective location(s).

The gain for improving grain yield in Nordic spring wheat appears to be correlated with a change in the composition of the total biomass weight, i.e. a higher harvest index, and resistance to lodging owing to short plant height. Furthermore, this negative association between grain yield and plant height could arise either due to pleiotropic competitive effects or due to genetic linkage. In this regard, Bourlag, (1997) suggested that dwarfing genes are apparently ‘master genes’ because ‘at the same time they reduced plant height, and improved standability, they also increased tillering and the number of florets and the number of grains per spike (harvest index)’.

Our calculation of genetic gain in the Nordic spring wheat germplasm may have been influenced by field testing in one location, fungicide spraying and intermediate fertilizer inputs. For example, genetic gains may be greater in high input environments (Austin et al., 1989). Hence, an assessment of Nordic spring wheat cultivars across locations and with distinct cultural practices may be needed to determine whether the current observations reflect genetic gains across distinct agro-ecological environments in this region of northern Europe.

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