A Century of Breeding – is Genetic Erosion a Reality?

Temporal Diversity Changes in Nordic and Baltic Barley

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Abstract

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Barley (*Hordeum vulgare* L. ssp. *vulgare*) is an important crop in the Nordic and Baltic countries, where it is mainly used for feed and malt. Commercial breeding of barley has been carried out in this region for more than a century, and landraces have been completely replaced by pure line cultivars. There is a concern that plant breeding might lead to a severe reduction of genetic diversity, so-called genetic erosion, since commercial breeding was initially based only on a few successful selections from landraces. The consequences of such erosion would affect plasticity of the crop, which might reduce its ability to adapt to future agriculture and consumption demands and increase the vulnerability to epidemics. The aim of this study was to evaluate the degree of putative genetic erosion and relationships in Nordic and Baltic barley material. A large collection representing landraces and cultivars from the end of the 19th century up to modern material were analysed by isozymes and DNA markers. In addition, field trials were performed in order to observe changes in the diversity of agronomic traits. General indications of a decrease in diversity were observed. A loss of less common alleles was found in molecular markers and a significant decrease of variability was detected for most agronomic traits. However, the molecular markers failed to prove significant diversity changes in the material as a whole. New alleles, not present in Nordic and Baltic landraces and old cultivars, were found in modern material. Differences in the magnitude of diversity varied depending of country and region (North vs South) of origin and row type of the crop. Some of these diversity changes were also significant in the molecular makers, for example a significant decrease in material from the southern part of the region was observed. The two-rowed and six-rowed cultivars of this region were well differentiated not only by agronomic data, but also by DNA markers. They demonstrated differences at chromosome regions distant from the inflorescence determinating genes. While agronomical data separate modern material from landraces and old cultivars fairly well, DNA markers achieved this for most of the countries only when the material was analysed separately by country. The main conclusion of this study is that breeding in Nordic and Baltic countries has decreased diversity at some traits, but overall diversity of the crop has not changed significantly. However, the landraces and old cultivars of the region should still be considered as valuable diversity sources since some of the loci found there are not present in modern materials.

Keywords: genetic diversity, *Hordeum vulgare*, agronomic traits, molecular markers, barley breeding

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Contents

Appendix

Papers I-IV

This thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Kolodinska Brantestam, A., von Bothmer, R., Rashal, I. & Weibull, J. (2003) Changes in the genetic diversity of barley of Nordic and Baltic origin, studied by isozyme electrophoresis. *Plant Genetic Resources Evaluation and Utilization 1*, 143-149.

II. Kolodinska Brantestam, A., von Bothmer, R., Dayteg, C., Rashal, I., Tuvesson, S. & Weibull, J. (2004) Inter simple sequence repeat analysis of genetic diversity and relationships in cultivated barley of Nordic and Baltic region. *Hereditas 141*, 186-192.

III. Kolodinska Brantestam, A., von Bothmer, R., Dayteg, C., Rashal, I., Tuvesson, S. & Weibull, J. Genetic diversity changes and relationships in spring barley germplasm of Nordic and Baltic areas as shown by SSR markers (Submited).

IV. Kolodinska Brantestam, A., von Bothmer, R., Gullord, M., Rashal, I., & Weibull, J. Changes in variation of agronomic traits of Nordic and Baltic spring barley bred during the 20th century (Manuscript).

Introduction

Taxonomy, domestication and distribution

Barley is the fourth largest cereal crop in the world (FAO, 2004). It is globally grown in a wide range of habitats reaching to higher altitudes and latitudes and deeper into semi-arid areas than those of most other crops (Graner *et al*., 2003). Cultivated barley *Hordeum vulgare* L. ssp. *vulgare,* belongs to the genus *Hordeum*, tribe *Triticeae*, family *Poaceae*. Besides *H. vulgare* there are another 31 species in this genus (Bothmer *et al.*, 1995). The progenitor of cultivated barley is *H. vulgare* ssp. *spontaneum* – wild barley which has no crossing barriers to the crop (Asfaw & Bothmer, 1990). According to the genepool concept of Harlan and de Wet (1971) *H. vulgare* ssp. *spontaneum* belongs to the primary barley genepool. All other *Hordeum* species, except *H. bulbosum* (secondary genepool) belong to the tertiary genepool (Fig. 1). *H. bulbosum* shares the basic H genome with cultivated barley, but crosses with some difficulty to the crop (Bothmer *et al*., 2003).

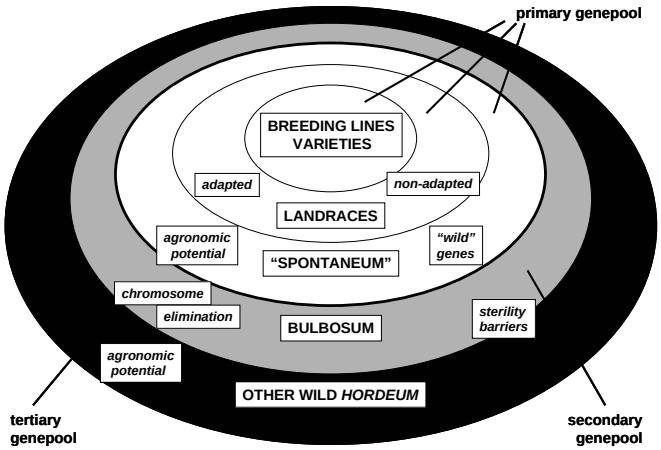

Fig. 1. Genepools in cultivated barley (*Hordeum vulgare* L. ssp. *vulgare*) (Bothmer *et al*., 2003).

Clear evidence of early barley domestication and cultivation dates back approximately 10 000 years in the area of the Fertile Crescent (Zohary & Hopf, 1993; Harlan, 1995), which geographically corresponds to a region extending from Israel and Jordan, through Syria, Lebanon and southern Turkey, into Iraq and Iran (Fig. 2). One of the most important traits of domestication was probably non-brittleness of rachis, which is of benefit for efficient harvesting without loss of grains (Bothmer *et al*., 2003). The two recessive genes *brt1* and *brt2,* each responsible

for non-brittle rachis, arose through natural mutation and were later selected for during domestication (Takahashi, 1987).

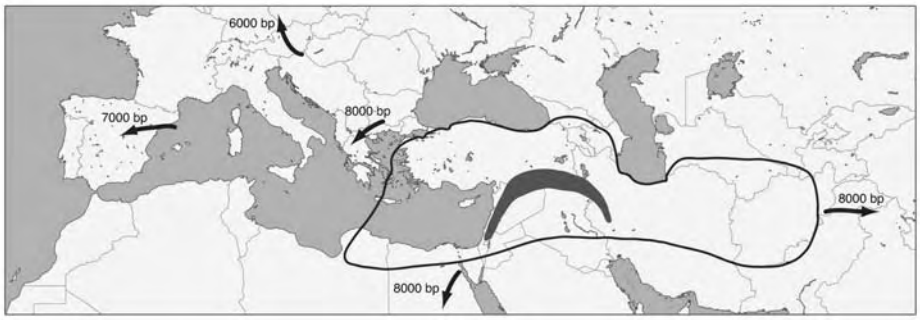

Fig. 2. The Fertile Crescent, the area of early domestication of cultivated barley (*H. vulgare* L. ssp. *vulgare*) in the Middle East, distribution of the wild progenitor of barley (*H. vulgare* L. ssp. *spontaneum*) (within solid line) and approximate time, year before present (BP) for cultivated barley to reach different areas (Bothmer *et al.*, 2003).

The major types of cultivated barley, based on combinations of hulled versus naked kernels and spike type, i.e. two-rowed versus six-rowed ears (Fig. 3), appeared during the early phases of plant cultivation in the Old World (Zohary & Hopf, 1993).

Fig. 3. The two-rowed (a) and six-rowed (b) type of cultivated barley (*H. vulgare* L. ssp. *vulgare*).

The 'naked kernel' and 'six-rowed' types were also spontaneous mutations. Six-rowed barley originated from at least two independent mutations at the *vrs1* locus (Tanno *et al.,* 2002). This type comprised some 90% of cereal crop production in ancient Mesopotamia (Harlan, 1970) and played a major role during later and more far-reaching expansions of agriculture (Fischbeck, 2002; Tanno *et al*., 2002). Only the six-rowed ear type reached Northern Europe during the third and fourth

millennia B.C. (Körber-Grohne, 1987). Two-rowed barley has been cultivated in the Nordic and Baltic regions only since the early to mid 17th century, or in some parts (S Finland) since the 18th century, and became important with the cultivation of spring cultivars at the beginning of the 20th century (Hjelmqvist, 1955; Aikasalo, 1988; Ortiz *et al.*, 2002).

Barley in Northern Europe

Applications and adaptation requirements to regional conditions

Barley is one of the most important crops in northern Europe. Here it was historically used as one of the major food sources for humans. It also became the major source of malt needed by the brewing guilds that were formed in Europe during medieval times, from which modern malting and brewing industries later developed. Cultivation of barley for feed is a more recent development, but despite that most of the barley produced nowadays is used for this purpose. This fact relates to the decreasing importance of barley in food production (Fischbeck, 2002). Today in the Nordic and Baltic countries, the crop is used mainly for the feed and malt. In Denmark, for example, the need for feed barley is related to the pig-based meat export industry. In the south (Denmark, Lithuania, southern Sweden) two-rowed types of barley are mainly grown, and these types are generally preferred by the malting industry (Trolle, 1957; Persson, 1997; Fischbeck, 2002). In the northern part of the region, early maturing, six-rowed types are more common (Ortiz *et al.*, 2002).

In this region the northern limit for barley cultivation extends to high latitudes. Because of warm currents that heat up the waters of the North Atlantic, the annual isotherm of +4 ºC is located further north than in other parts of the world (Fig. 4). This is why arable land extends up to 67 ºN latitude in Finland (Mukula & Rantanen, 1987) and 70 ºN in Norway (Fageria *et al*., 1997).

Fig. 4. Temperature climate around 60 °N latitude for the annual isotherm +4 °C (Kalliola, 1951, *cit* Lomakka, 1958).

There are considerable differences in growing conditions for barley in the Nordic and Baltic countries. In the north, the growing season (> +5 ºC) is only 130-135 days (N Finland) whereas in the south it can be up to 215 days (southern Sweden and Denmark) (Mukula & Rantanen, 1987; Wiberg, 1993). In Norway, Finland, northern Sweden and Estonia, agricultural activities are restricted by a very short vegetation period, but this disadvantage is somewhat alleviated by an excessively extended photoperiod during the growing season (Fischbeck, 2002). In the Nordic and Baltic countries there is also a large variation in soil types (Mukula & Rantanen, 1987; Ortiz *et al*., 2002). Furthermore, there are differences in the requirements for resistance to various diseases. For example, powdery mildew does not rank high for improving barley cultivars grown north of 62 °N, because scald and net blotch are more common diseases at these latitudes (Ortiz *et al.*, 2002).

Current national yield levels of barley in this region range from 19 (Estonia) to 47 metric tons per hectare (Denmark) with an average of 32 tons per hectare (FAO, 2004). Approximately 2.5 million hectares are harvested in the Nordic and Baltic countries per year. However, the annual harvested area during the past 85 years has changed (Fig. 5). In most of the countries in the region, the barley area harvested increased from the 1950s until the 1980s, but it has decreased in recent decades as larger areas are being planted with wheat (FAO, 2004).

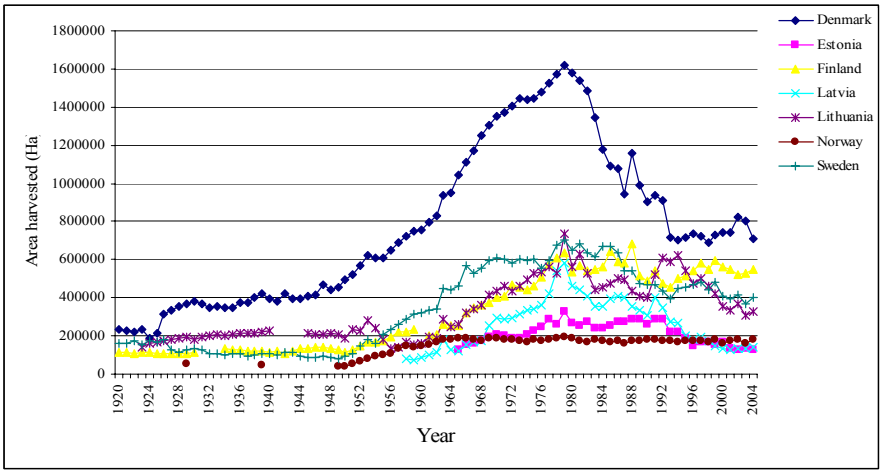

Fig. 5. Annual harvest area (ha) for barley in the Nordic and Baltic countries over 85 years of cultivation (Paatela, 1953; Statistiska Centralbyrån, 1959, 1970; Danmarks statistik, 1968; Statistical Office of Estonia, 1991; FAO 2004, Official Agricultural Statistics Finland, http://www.ssb.no; http://www.stat.ee; http://www.std.lt; http://www.zm.gov.lv).

A brief history of barley breeding in the region

An increase in crop yield per hectare has been a typical trend in Nordic and Baltic agriculture over the past century (Fig. 6). For example, in Sweden during the period 1886-1995 the yield increased 200-300% (Persson, 1997). Sub-surface drainage and mechanization have greatly increased both the efficiency and speed of soil cultivation, so that spring sowing can be accomplished earlier than before.

As a result, the growing time for spring cereals is lengthened, which is of great importance, especially in the northern part of the region. In addition to improved technology, the yield capacity of crops has also improved as a result of plant breeding (Mukula & Rantanen, 1987).

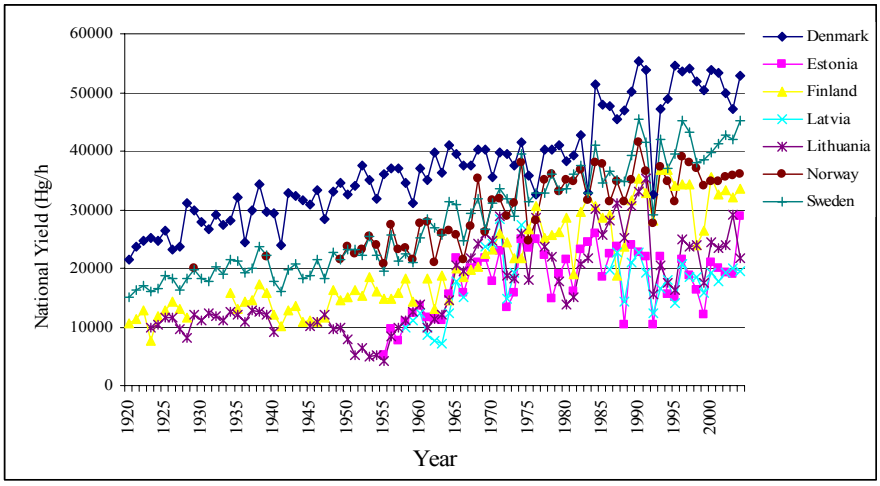

Fig. 6. Annual yield of barley in the Nordic and Baltic countries over 85 years of cultivation (Statistiska Centralbyrån, 1959, 1970; Yllö, 1962; Danmarks statistik, 1968; Statistical Office of Estonia, 1991; FAO 2004, http://www.ssb.no; http://www.stat.ee; http://www.std.lt; http://www.zm.gov.lv).

When commercial barley breeding in the Nordic and Baltic countries began (end of 19th and early 20th century) (Kivi, 1963; Gaike, 1992; Persson, 1997), the initial breeding material and new cultivars were selected from local landraces or introductions of foreign selections. Only a few landraces from the major-growing regions were successfully exploited for the selection of superior genotypes in Europe at that time. These were 'Binder', 'Hanna', 'Hannchen' and 'Kneifel' from Moravia; 'Bavaria' and 'Danubia' from Bavaria; 'Gull' and 'Schonen' from southern Sweden; and 'Archer' and 'Plumage' from England (Fischbeck, 1992). However, in Norway and Finland breeders also used some locally adapted barley landraces ('Bjørneby', 'Jaerbygg' etc.) to improve earliness in their material. Other adaptation traits, for example, resistance to soil acidity in the Finnish cultivar 'Pirkka' and the Swedish 'Vega' (Aikasalo, 1988) probably came from the local landraces in their pedigree. At the end of the 1920s and beginning of the 1930s, the first cultivars obtained through combination breeding were released in this area (Trolle, 1957; Gaike, 1992; Persson, 1997). Later, new cultivars were bred mainly through successive cycles of crosses between established pure lines (Fischbeck, 1992). During these periods of barley breeding, lines could be classified according to their origin from different landraces and/or the contributions from main ancestors (Melchinger *et al.*, 1994) (Fig. 7). From the beginning of 1970, crossings became more complicated (Fig. 8).

During the 1960s and 1970s, the mutation breeding technique was applied and resulted in some new resistance genes, e.g. the M*lo*-resistance (Helms Jørgensen,

1992). It also produced some semi-dwarfing genes, that decreased lodging and increased the harvest index of the crop. One such semi-dwarf gene in Nordic and Baltic material originates from the X-ray irradiation-derived Czech cultivar 'Diamant' (Mlčochova *et al.*, 2004).

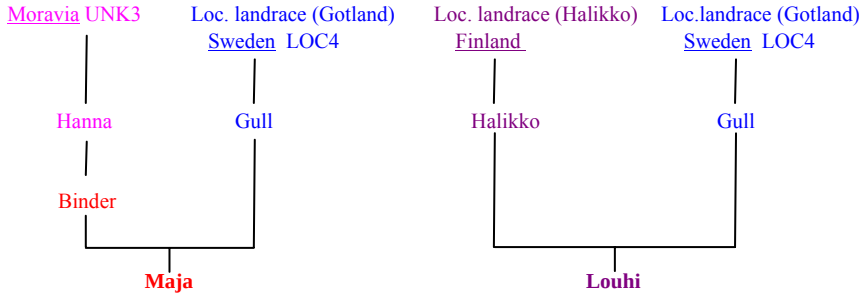

Fig. 7. Pedigree of the Danish cultivar 'Maja' (1927) and the Finnish cultivar 'Louhi' (1934).

Landraces are rich sources of disease resistance, especially those from the centre of origin in the Fertile Crescent and regions where barley cultivation started early, e.g. Ethiopia and North Africa (Jana & Bailey, 1995; Yitbarek *et al.*, 1998; Czembor & Czembor, 2000). For instance, the resistance gene for powdery mildew *mlo-11* from an Ethiopian landrace has been incorporated in many accessions (Helms Jørgensen, 1992; Piffanelli *et al.*, 2004). The actual amount of exotic material incorporated into the Nordic and Baltic barley genome is not known. This is due to the fact that adaptation of the cultivar to the requirements of modern agriculture and regional conditions (Tigerstedt, 1994; Ortiz *et al.*, 2002) needs several cycles of backcrossing to advanced lines. For example, crosses with the landrace *H. vulgare* var. *'laevigatum'* resulted in good mildew resistance from the *Ml-v* resistance gene (Swanston, 1987). *H.vulgare* var. *laevigatum* and the first commercial cultivars carrying the *Ml-v* mildew resistance gene, 'Vada' and 'Minerva' (Swanston, 1987), were also included in breeding programmes in the Nordic and Baltic countries (Fig. 8).

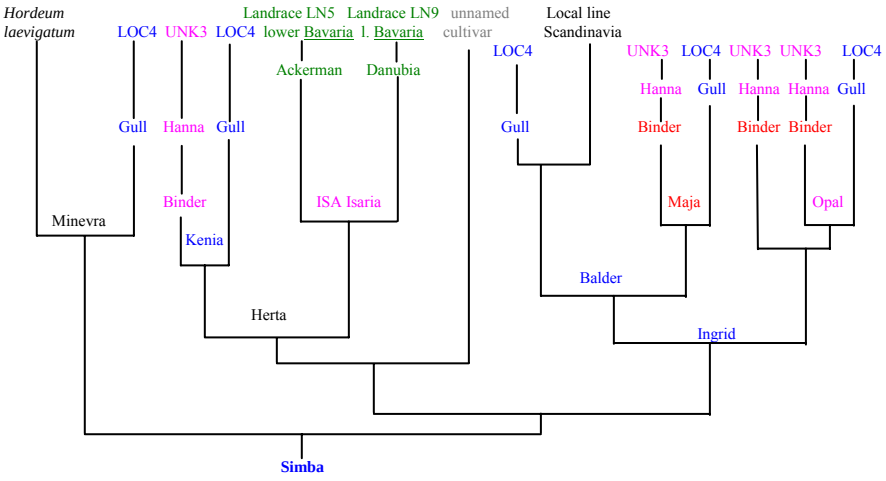

Fig. 8. Pedigree of the Swedish cultivar 'Simba' (1975).

This is a rare exception of incorporation of an exotic gene source requiring fewer cycles of backcrossing and with a good adaptation to modern agriculture; i.e. with high yield values. However, the genes from this exotic source are negatively affecting malt quality (Swanston, 1987) so that cultivars with *H. vulgare* var. *laevigatum* in their pedigree are mainly used as feed barley.

The wild relatives of barley are a rich source of disease resistance. *H. vulgare* ssp. *spontaneum* is a source of useful resistance genes to leaf rust, net blotch, septoria speckled leaf blotch, powdery mildew, barley mosaic virus, scald, etc. (Jahoor & Fishbeck, 1993; Garvin *et al.*, 1997; Fetch *et al.*, 2003). Another potential resource is *H. bulbosum* from the secondary genepool (Fig. 1). This species is a rich source of resistance to important fungal and viral diseases (Milhăilescu & Giura, 2001). However, large phenotypic differences exist between modern cultivars and wild barley, which carries a number of undesirable traits in quality and agronomic performance. The success of favourable character transfer can be obtained by applying a refined system of genetic markers (Forester *et al*., 1997). Such methods were not available in the past and the use of wild relatives in breeding required and still require expensive and laborious prebreeding processes (Lehmann & Bothmer, 1988; Veteläinen, 1994). This is why the use of wild material is restricted in Nordic and Baltic material.

Selection for malting quality has been carried out in the Nordic and Baltic region since the beginning of barley breeding, because beer brewing is economically important (Trolle, 1957; Persson, 1997). The malting quality of barley is a phenotype representing the net effects of a number of interacting component traits (Marquez-Cedillo *et al.*, 2000a; Zale *et al.*, 2000; Ayoub *et al.*, 2002; Prada *et al.*, 2004). The complexity of malting quality improvement has led breeders to work within narrow gene pools. In Nordic and Baltic malting barley there are only a few established lines used in crosses to produce cultivars with good malting quality. For example, excellent malting quality was recognised in the barleys from Moravian 'Hanna' at the end of 19th century (Grausgruber *et al.*, 2002). 'Binder Abed', which is a selection from 'Hanna' barley, was for many years the main barley cultivar in Denmark (Trolle, 1957) and is found in the pedigrees of numerous later Nordic and Baltic cultivars. In later breeding periods 'Trumph' became widely used in the Nordic and Baltic malt barley pedigrees (Fischbeck, 1992).

Feed is another important end-use of barley. However, barley cultivars are often developed and selected on the basis of only agronomic and malting-quality characteristics. There is currently no widely accepted set of criteria for determining barley feed quality as there is for malting quality. Therefore barley breeders have been limited in their ability to develop cultivars improved for feed quality characteristics (Bowman *et al*., 2001). Recent research has identified high starch content, low acid-detergent fibre (ADF), low ruminal dry-matter digestibility (DMD) and large particle size after dry rolling as desirable barley feed-quality characteristics for beef cattle (Hunt, 1996; Surber *et al.*, 2000; Bowman *et al.*, 2001).

Traditional barley breeding skills have served the agricultural industry very well over many years and are likely to retain a significant role in the future. However,

with the employment of novel technologies, the speed and accuracy of selection are enhanced (Swanston & Ellis, 2002). Today, successful results in breeding are achieved through increased knowledge about the barley genome and its diversity.

The barley genome

Barley is a model genome system for *Triticeae* species, because it has a self-fertile, diploid (2n=2x=14) genetic system that has advantages for studies of phenotypic expression of genes and development of homozygous material. The barley chromosomes are homologous to those of cultivated wheat which is polyploid and inbreeding, and of rye which is diploid and outbreeding (Hori *et al.*, 2003). The genome of barley is approximately 5 000 million base pairs (Mbp) in size (Yu *et al.*, 2000). It has been estimated that the average distance between barley genes is 240 kb (based on an estimated genome size of 5,000 Mb and 21000 genes) (Dubcovsky *et al*., 2001). However, the average gene density in some genome regions has approximately one gene every 20 kb, which is 12 times higher than the expected genome average (Panstruga *et al*., 1998; Dubcovsky *et al*., 2001; Druka *et al*., 2002). A very heterogeneous distribution of recombination rates is found along individual chromosomes. Recombination is mainly confined to a few relatively small areas interspersed with large segments in which recombination is severely suppressed (Künzet *et al.*, 2000). A high correlation between marker density and recombination frequency implies that most recombination events occur in gene rich regions corresponding to small chromosomal areas (Künzel *et al.*, 2000). Panstruga *et al*. (1998) conclude that grass genomes are characterized by compositional compartmentalization with gene islands (also termed 'gene space') of 100-200 kb. The base paire composition of these gene-rich regions is not significantly different from the average genome base pair composition in *Triticeae* (Dubcovsky *et al.*, 2001).

Most genes are present in physically small gene-rich regions. Some genes are highly repetitive, such as the 18S-5.8S-25S ribosomal RNA (rRNA) genes and intergenic spacer, together called the rDNA, occurring at the nucleolus organizing regions (NORs) loci on the chromosomes. Major sites of rRNA genes involve hundreds or thousands of copies of the tandem repeat unit, which is about 10 kb long (Linde-Laursen *et al.*, 1997). The gene-rich regions are interspersed by large chromosomal blocks mainly containing repetitive sequences (Barakat *et al.*, 1997). Repetitive DNA comprises >70% of the genome (Barakat *et al.*, 1997). These repetitive DNA-sequence motives, typically 2 to 10 000 bp long, are repeated hundreds or even thousands of times in the genome (Linde-Laursen *et al.*, 1997). For example, the BARE-1 retrotransposons in barley are present in 16.6×10^3 copies and more than 6×10^4 single long terminal repeats (Vicient *et al.*, 1999). Dubcovsky and his co-workers (2001) showed that a large difference in size between the rice and barley colinear gene regions was mainly due to the insertion of different layers of retroelements in the intergenic regions. Retrotransposons, because of their abundance, diversity and widespread distribution, make a major contribution to both the shape and size of plant genomes (Vershinin *et al*., 2002). Vicient *et al*. (1999) suggested that the genome increases and genetic polymorphism in dry environments might be adaptive in the genus *Hordeum* and associated along with either propagation of BARE-1 or inheritance of new copies.

In this regard, transcription or transposition of various retrotransposons is linked to genes for biotic and abiotic stress tolerance (Wessler 1996; Takeda *et al.*, 1998).

Modern tools for barley breeding and their implications

Molecular maps and chromosome library

The use of molecular techniques as diagnostic tools to assist the conventional breeding process demands the construction of linkage maps. Markers evenly spaced on the chromosomes are then used to scan the genome in order to identify associations of markers and traits. Molecular mapping of the barley genome has been facilitated by the development of molecular markers, the ability to develop doubled haploid (DH) lines, the availability of numerous mutants and cytogenetic stocks, particularly the barley-wheat additional lines, and the recent development of large insert libraries. The comprehensive molecular marker linkage maps have provided a powerful and important tool for identifying quantitative trait loci (QTL) for agronomic and qualitative traits in barley (Kleinhofs & Han, 2002). Molecular linkage maps of cereals are being improved rapidly by adding new types of markers, by merging different species-specific maps and by comparative mapping of markers between related genomes. Efficient use of the resulting dense maps, therefore, requires detailed insights into the relationship between genetic and physical distances (Künzel *et al.*, 2000).

Molecular marker linkage maps have been developed using restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), simple sequence repeat (SSR), isozyme and protein markers (Kleinhofs *et al.*, 1993; Becker *et al.* 1995; Langridge *et al.*, 1995; Sherman *et al.*, 1995; Waugh *et al.*, 1997). All these mapping efforts have resulted in the location of several thousands of different molecular markers to the barley genome. These data have been used to merge several maps (Sherman *et al*., 1995; Kleinhofs & Han, 2002). All barley maps appear to be co-linear and easy to integrate with only minor differences in genetic distances between markers. In addition, a barley morphological-marker linkage map containing over 200 loci has been constructed (Franckowiak, 1997) and is integrated with the molecular marker maps (Qi *et al*., 1996; Kleinhofs & Graner, 2001). With a more extensive effort to merge mapping information from different mapping populations, the North American Barley Genome Mapping Project (NABGMP) introduced the BIN Map concept (Kleinhofs & Graner, 2001). Using the 'Steptoe' x 'Morex' (SM) map as a base, the barley genome was divided into approximately 10 cM intervals or Bins, allowing the placement of many markers on different maps in their appropriate Bins. The map integrated RFLP, AFLP and SSR markers, which are mapped in independent linkage studies, by allocating them to 99 evenly spaced BIN groups. However, the average resolution on the physical distance by 1 172 markers in the barley genome is about 4 500 kb/marker in the present map. There is still a large gap between the physical distance and the resolution of the high-density map in barley. Constructing high-density molecular maps in barley has revealed uneven distributions of markers and a strong clustering of markers around the centromere (Becker *et al.*, 1995; Qi *et al.*, 1998; Ramsay *et al*., 2000). Clustering of markers at centromeric regions was also observed on the barley integrated map (Qi *et al.*, 1996).

A bacterial artificial chromosome (BAC) library has been constructed for the cultivar 'Morex' using the cloning enzyme HindIII (Yu *et al*., 2000). The library contains 313 344 clones with an average insert size of 106 kbp. BAC libraries are useful for examining genomic structure and positional cloning of genes (Song *et al.*, 1995). Moreover, the barley BAC library is an important tool for developing physical maps of the gene-rich regions (Yu *et al.*, 2000). High-resolution maps have been prepared for several barley genome regions (Kleinhofs & Han, 2002), for example *lig*, *mlo*, *wx*, *Rpg1* and *Mla* (Jorgensen & Jensen, 1979, Rosichan *et al.*; 1979; Konishi, 1981; DeScenzo *et al.*, 1994; Kilian *et al.*, 1997; Simons *et al.*, 1997).

Quantitative trait loci and marker assisted selection

Mapping and marker development have progressed in recent years for both barley and two related *Hordeum* species. Establishment of synthetic relationships among major grass species, especially at the micro level, has made possible 'map based cloning' of genes from a large genome such as barley by utilising the results of genetic and physical mapping of the small genomes (Kleinhofs & Han, 2002).

A goal of the molecular mapping activity in barley is to locate quantitative trait loci (QTLs) for map-based cloning or to find associated markers for molecular marker-assisted selection (MAS) to supplement ongoing breeding programmes (Hoffman & Dahleen, 2002). The agronomic performance of crop varieties is mainly influenced by complex quantitative traits, for example, yield and quality components (Pillen *et al*., 2003). QTLs are often clustered and a discriminating marker could be located in a region associated with a number of traits. For example, the AFLP marker E36M47.M162 on chromosome 5 is situated in a region associated with plant height, heading data, malt extract, grain protein, diastatic power and the Kohlbach index (Hoffman & Dahleen, 2002). QTL analysis identifies chromosome regions, linked molecular markers, gene effects and QTL x E (environment) and QTL x QTL interactions for a given trait (Zale *et al*., 2000).

QTL mapping in barley has received world-wide attention. The North American Barley Genome Mapping Project has focussed on 'Steptoe'/'Morex', 'Harrington'/TR306, 'Harrington'/'Morex' and some other populations. European researchers have studied the 'Blenheim'/E224/ 3 population and Australian researchers have concentrated on the 'Chebec'/'Harrington', 'Clipper'/'Sahara' and 'Galleon'/'Haruna Nijo' mapping populations (Zale *et al*., 2000). More than 750 QTLs are identified (Hayes *at al*., 2003).

An important and practical question is whether QTLs are conserved among genotypes of the same species. This question is especially important for MAS (Clancy *et al.*, 2003). Traditionally, researchers have looked at single genes and QTLs for disease resistance, morphological markers and many agronomic traits. Indirect comparison of QTL effects is possible by means of the current 'Steptoe' x 'Morex' map, published by Kleinhofs (2001). Ultimately, with micro-array technology and knowledge about genetics of parents, MAS should become accurate and precise. The better knowledge breeders have about genes controlling economically important traits, especially quantitatively inherited traits, the more direct crop improvement efforts can be (Clancy *et al.*, 2003). MAS using

inaccurate QTL estimates still in most cases gives better results than phenotypic selection (Liu *et al*., 2004). Plant breeding programs should effectively use the wealth of information derived from QTL mapping studies to develop new cultivars. To date, QTL information has been used primarily in marker-assisted introgression of one or more desirable alleles into an elite background or through marker-based recurrent selection (Wingbermuehle *et al.*, 2004). A breeder using phenotypic selection must test 1.0-16.7 times more progeny than a breeder using MAS to be assured of selecting one or more superior genotypes (Knapp, 1998). MAS gives not only larger responses but also dramatically increases the frequencies of superior genotypes compared with phenotypic selection (Liu *et al.,* 2004). However, the advantages of MAS over phenotypic selection are considerably reduced when conducting selection in later generations. Liu *et al.* (2004) proposed a modification by combining MAS in early generations with phenotypic selection in later generations as the most efficient procedure.

The rapid development of molecular techniques and intensification of plant breeding makes it possible to change the crop faster and there is an increase in the breeding pressure on the crop. This leads to an even greater interest in questions such as: How does plant breeding affect the crop? In what way and how much has barley already changed? What changes might be expected in the future? Are there negative consequences of plant breeding and its intensification? Does breeding affect the genetic diversity of the crop? Does it pose a threat to genetic plasticity of the crop, leading to restrictions in the ability to adapt?

Genetic diversity and genetic erosion

More than 30 years have passed since the scientific community raised the alarm about genetic erosion. Jack Harlan (1975) used this term in the early 1970s to describe a potentially disastrous narrowing of the germplasm base employed in improving food crops. A dramatic decrease in diversity in a cultivated crop could bring serious consequences, since genetically uniform cultivars grown over vast areas are susceptible to devastating epidemics (Baker *et al.*, 1997). The classic example of this is the Irish potato famine of the mid 19th century or the coffee rust epidemic in Ceylon in the 1870s. More recent examples include the southern corn leaf blight epidemic in the USA in 1970 (Browning, 1988) and the mould epidemic on tobacco in the USA and Europe in the 1960s (Marshall, 1977). The variation is essential for the future breeding material, since a decrease in genetic variability in general might result in a reduction in the plasticity of the crop to respond to any environmental changes and agricultural practices (Manifesto *et al*., 2001). For example, climate changes in the future could bring new challenges for adaptation of the crop (Arnell, 1999).

During recent decades, extensive progress has been made in Nordic and Baltic barley breeding with respect to yield, disease resistance, etc. (Ortiz *et al*, 2002; Öfversten *et al*., 2004), mainly due to the efficient exploitation of the genetic diversity. To ensure that this progress is maintained it is important to sustain the level of genetic diversity within the breeding material used. A reliable knowledge of the genetic diversity of the breeding material is also important in order to select parents for a new breeding cycle (Pillen *et al.*, 2000).

Some studies done show evidences of a decrease in genetic diversity during the process of barley domestication (Clegg *et al*., 1984; Provan *et al*., 1999;). The replacement of landraces by modern cultivars was also an important factor contributing to genetic erosion (Hammer *et al*., 1996). There is a concern about a continuous decrease in genetic diversity due to the narrow genetic base of the European barley germplasm (Melchinger *et al*., 1994). Fishbeck (1992) mentioned several reasons for this presumed restricted genetic base:

1. Only a few landraces from the major barley growing regions have been successfully exploited for selection of superior genotypes in the initial phase of barley breeding.
2. A small number of outstanding cultivars have been extensively used as progenitors for the development of new cultivars in recycling breeding programmes.
3. Introgression of exotic germplasm has been practised only on a limited scale.

To estimate diversity within modern cultivars using only the pedigrees is insufficient, since the breeding history does not account for the effects of selection, mutation and random genetic drift (Melchinger *et al.*, 1994). In some cases the pedigree is not even known. Methods used to evaluate genetic variation in barley include comparison of differences in morphology, agronomic traits, isozymes and hordeins (Ortiz, 2001). Nowadays they are complemented by DNA marker analysis (Karp *et al*., 1997;Wolko & Kruszka, 1997; Koebner *et al*., 2001), which allows the observation of changes that have occurred in the cultivated barley gene pool at the genotypic level, and to compare these changes with observed phenotypic differences (Swanston & Ellis, 2002). DNA analysis shows a closer relationship for the cultivars than that estimated by the pedigree analysis, which may overestimate divergence, particularly when one parent has an 'exotic' genotype in its own lineage (Ellis *et al.,* 1997).

The knowledge about marker location on chromosomes and association with gene-rich regions of barley will also give better understanding about diversity structure in the evaluated material.

To date, a number of studies have been performed to evaluate the changes in genetic diversity in barley due to plant breeding. However, these show different results depending on the country or region origin of analysed material. In some cases differences are also shown when different methods for evaluation were used. For example, Reeves *et al*. (2004) in their European barley study found just a temporal flux of genetic diversity without detecting genetic erosion, similar to the results of Koebner *et al.* (2003) studying UK barley. Matus & Hayes (2002), on the other hand, in material from Busch agricultural Resources barley improvement programme and Russel *et al*. (2000) in European spring barley detected a lower diversity level within modern material.

The Nordic and Baltic region is particularly interesting for evaluation of diversity changes. One of the reasons is the specific growing conditions, mainly related to the climate, and how this has affected the material in the breeding process. The second reason is that plant breeding has been performed over a long

period of time and implications of whether genetic erosion has taken place should be detectable.

Objectives

The general aim of this thesis was to visualise the changes in genetic diversity and relationships in Nordic and Baltic barley over the 20th century. Specific objectives of the studies included are to:

- Determine the degree of putative genetic erosion in Nordic and Baltic barley
- Determine the relationships between Nordic and Baltic barley
- Determine the genetic and phenotypic relationships between old cultivars and landraces versus modern material
- Detect the genetic diversity changes over time in material with different countries of origin
- Compare the changes in genetic diversity and relationships in two-rowed and six-rowed barley

Diversity in Nordic and Baltic barley

Nordic (Denmark, Finland, Norway and Sweden) and Baltic (Estonia, Latvia and Lithuania) barley material representing landraces and cultivars from the end of the 19th century up to the modern cultivars and breeding lines were investigated. In this study, a number of molecular diversity evaluation methods were chosen in order to increase the reliability of the results: isozymes (paper I), ISSRs (inter-simple sequence repeats) (paper II) and SSRs (simple sequence repeats) (paper III. Study of agronomic traits was also included (paper IV). These traits represent the variation in adaptation that most probably has been affected by conscious selection. Isozymes are biochemical markers that have been successfully utilized in barley diversity studies (Linde-Laursen *et al*., 1987; Parzies *et al*., 2000). ISSRs and SSRs are DNA markers used for DNA fingerprinting and assessing genetic diversity in closely related germplasm (Röder *et al.*, 1995; Liu *et al.*, 1996; Martín & Sánchez-Yélamo, 2000). SSR markers are also widely used for assessing QTLs (Mesfin *et al.*, 2003; Pillen *et al.*, 2003).

Relationships

In our study we found a distinct differentiation of two-rowed and six-rowed barley based not only on field experiments (Fig. 9), but also on the DNA analysis using ISSRs and SSRs (Fig. 10). Only the isozyme data did not demonstrate this, which was probably due to the low number of polymorphic loci.

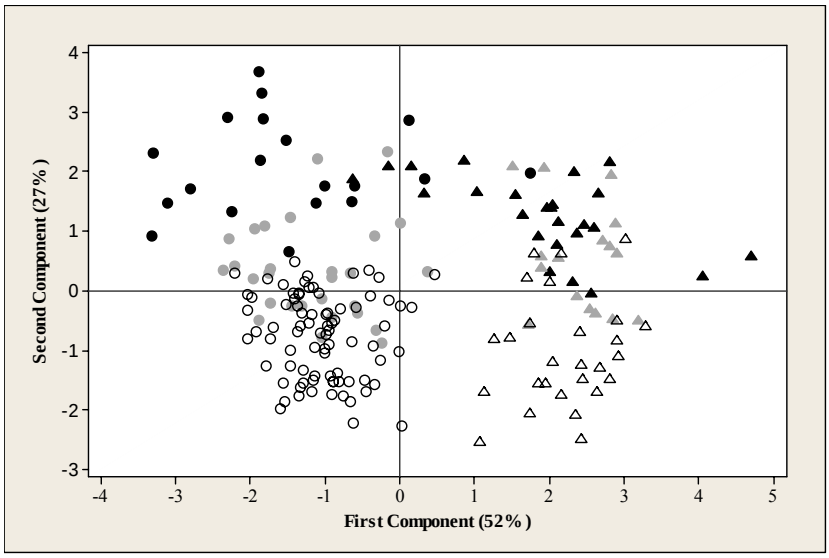

Fig. 9. Bi-plots of first two principal components for PCA based on the agronomical data ('days to heading', 'days to maturing', 'plant height', 'harvest index', 'volumetric weight' and 'thousand kernel weight') from a trial in Landskrona (Sweden) 2002, Symbols for accessions are ● – two-rowed landraces and cultivars before 1930; ● – two-rowed cultivars 1931-1970; ○ – two-rowed cultivars after 1971 and breeding lines; ▲ – six-rowed landraces and cultivars before 1930; ▲ – six-rowed cultivars 1931-1970; Δ – six-rowed cultivars after 1971 and breeding lines.

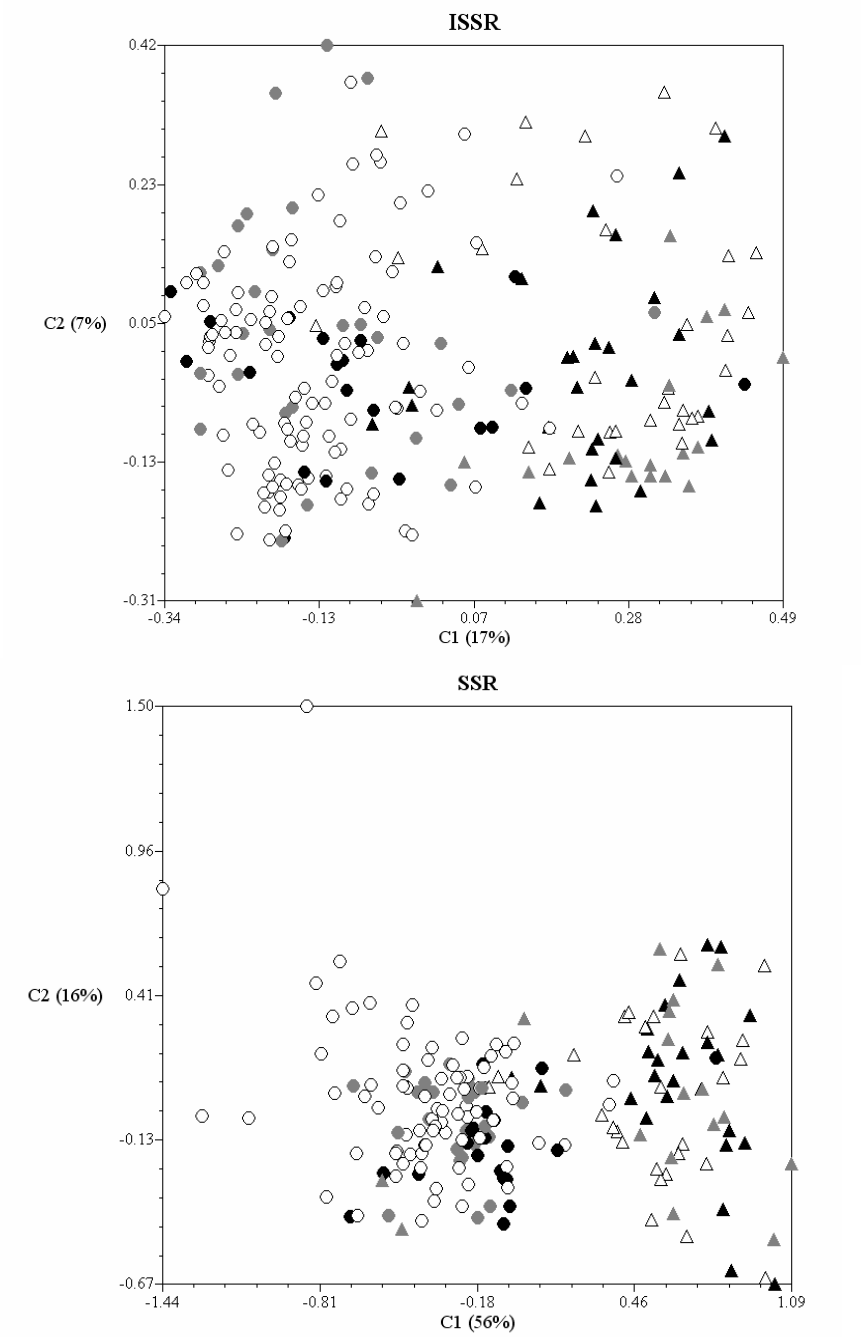

Fig. 10. Principal coordinate analysis on ISSR (based on similarity matrix) and SSR (based on Nei 78 genetic distance matrix) data in Nordic and Baltic material. Symbols for accessions are ● – two-rowed landraces and cultivars before 1930; ● – two-rowed cultivars 1931-1970; ○ – two-rowed cultivars after 1971 and breeding lines; ▲ – six-rowed landraces and cultivars before 1930; ▲ – six-rowed cultivars 1931-1970; Δ – six-rowed cultivars after 1971 and breeding lines.

The differentiation of accessions according to the row type (Principal component analysis of agronomic data) was mainly affected by factors like 'days to heading', 'days to maturing', 'volumetric weight' and 'thousand kernel weight'. This could be expected, since the six-rowed types commonly are earlier-maturing cultivars, whereas the differences in 'volumetric weight' and 'thousand kernel weight' are associated with the spike type (Marquez-Cedillo *et al.*, 2001). These two germplasm groups carries, according to the SSR data, also different alleles at other loci in addition to those determining lateral floret fertility. Similar results were reported by Ordon *et al.* (2004) in a study of German winter barley, where a clear separation and non-homogeneous allele distribution between six-rowed and two-rowed cultivars was found for most SSRs. Thus, crosses between the two germplasm groups could be expected to produce positive transgressive segregants for economically important phenotypes. However, generally two-rowed x six-rowed crosses are less successful for cultivar development (Kjær & Jensen, 1999). This might be due to different ideotypes for two-rowed and six-rowed barley. The traits determining the ideotype are quantitative and they are distributed throughout the genome. In two-rowed cultivars there is a significant influence on yield by 'number of ears' but for six-rowed barley, the most significant factor is 'number of grains per ear' (Äyräväinen, 1976). Since the selection of these traits has been carried out probably even before commercial plant breeding started and these are quantitatively inherited traits, the difficulty in obtaining successful cultivars from direct crosses of two-rowed and six-rowed types of barley is not surprising.

The data on agronomic traits differentiated effectively the cultivars according to the breeding period (Fig. 9). The main effects on this differentiation are 'plant height' and 'harvest index'. Obviously differentiation of the old and modern cultivars is due to increase in 'harvest index' and decrease in 'plant height' over time (Ortiz *et al*., 2002; Öfversten *et al*., 2004).

It was not possible to separate by molecular markers cultivars according to the breeding period in the entire data set (Fig. 10). However, the differentiation could be detected by ISSR data, and for some countries by SSR data, when gentypes from different countries were analysed separately. The differentiation between modern and old cultivars in Sweden was the most pronounced based on the SSR data (Figure 11). The variation in SSRs that accounts for differentiation between breeding periods was higher in the Swedish and Danish material than that from Finland and Norway. These differences between modern and old material in the north and south of the region might illustrate the specific objectives of the breeding programmes. In the northern part, the adaptation to the marginal growing conditions is very important and requires that locally adapted material be included in the crosses. This reliance on an adapted gene pool might explain why plant breeding in this part of the region results in fewer changes in the SSRs. The inconsistency in the marker data is probably due to the fact that different markers represent different genome regions. Most ISSRs are presumably noncoding loci dispersed throughout the genome (Wolfe & Liston, 1998), but a number of SSRs included in this study have known associations with agronomic and adaptive traits, i.e. 'days to heading', 'ears per m^2', 'grain yield' etc. (Turpeinen *et al*., 2001; Baek *et al.*, 2003; Long *et al.*, 2003; Pillen *et al.* 2003; Korff *et al*., 2004).

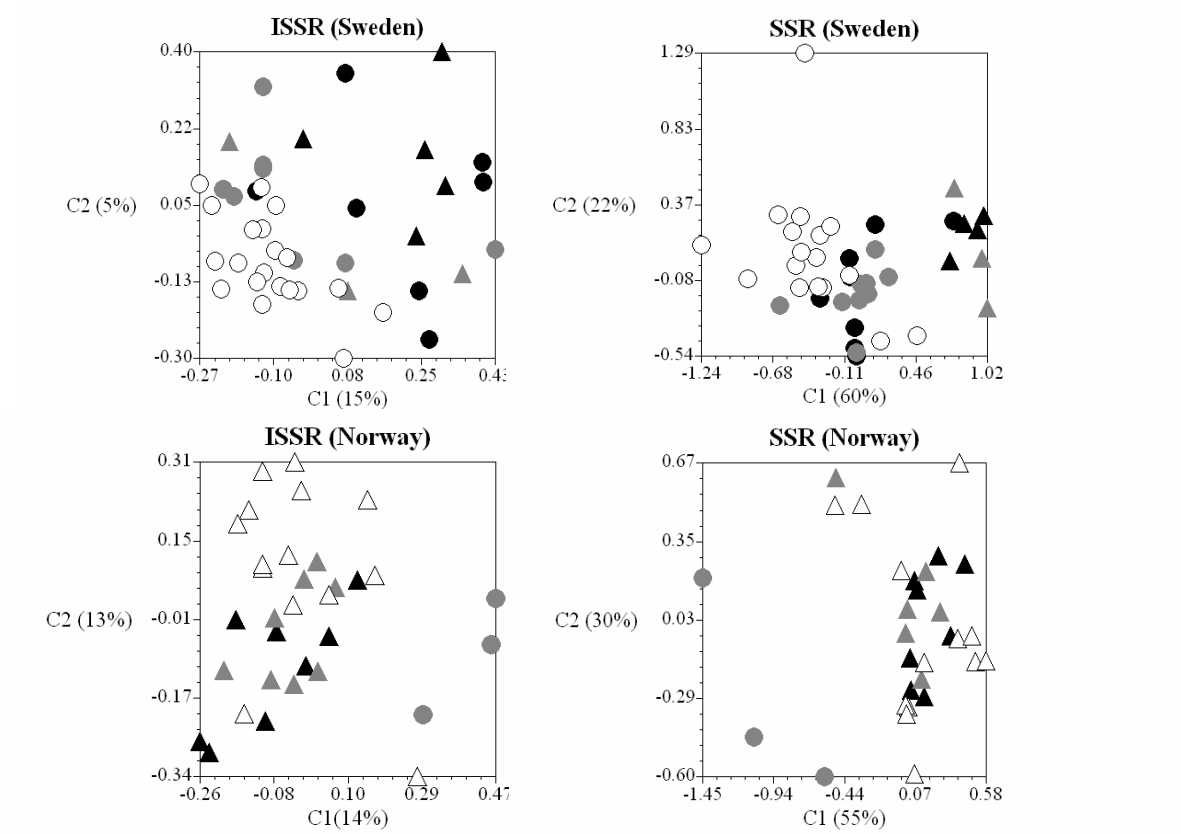

Fig. 11. Principal coordinate analysis on ISSR (based on similarity matrix) and SSR (based on Nei 1978 genetic distance matrix) data in material of Swedish and Norwegian origin.

Symbols for accessions are ● – two-rowed landraces and cultivars before 1930; ● – two-rowed cultivars 1931-1970; ○ – two-rowed cultivars after 1971 and breeding lines; ▲ – six-rowed landraces and cultivars before 1930; ▲ – six-rowed cultivars 1931-1970; Δ – six-rowed cultivars after 1971 and breeding lines.

Genetic erosion?

In the Nordic and Baltic material, the diversity changes were detected by the analysis of agronomic traits. As expected, the highest diversity was detected in landraces and old cultivars (based on Euclidean distances and coefficient of variation). This was also observed when molecular markers were analyzed (based on Nei and Shnannon-Weaver diversity indexes). However, the overall significance of this decrease could not be proven. In the marker studies (isozymes, ISSRs and SSRs), unique alleles were found in landraces and cultivars from before 1930 that could not be found in material from later periods. In modern material, however, other unique alleles not found in earlier cultivars were detected. This result is similar to that found by Donini *et al.* (2001) in UK barley and Cristiansen *et al.* (2002) in Nordic wheat.

Significant changes in genetic diversity were detected in material from the southern part of the region, but not in that from the north. ISSR and SSR markers both demonstrated a decrease in diversity in the south (Fig. 12).

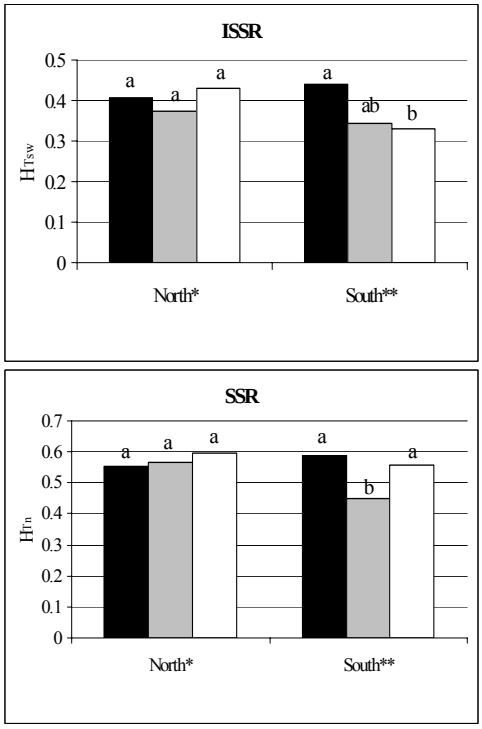

Fig. 12. Comparison of diversity values in cultivars from different breeding periods in the northern and southern parts of the region (ISSR and SSR data)
H_{TN} Nei 1987 diversity index, H_{TSW}- Shannon-Weaver diversity index, ■ – landraces and cultivars befor 1930; ■ – cultivars 1931-1970; □ – cultivars after 1971 and breeding lines
* north of 58ºN (Estonia, Finland, Norway and northern Sweden), ** south of 58ºN (Denmark, Latvia, Lithuania and southern Sweden).

These differences in diversity changes could be explained by the fact that cultivars from the north have a broader genetic base, due to adaptation breeding. SSR markers demonstrated an increase in diversity in the south after 1970, whereas other markers did not. Since at least half the SSR markers showing significant changes in the south of the region are associated with agronomic traits and probably located near gene-rich regions, the increase in diversity in modern material could visualize the accumulation of different genes. This may be based on introductions of non-Nordic material and use of exotic gene sources in later breeding periods.

The diversity changes over time were also dependent on the country of origin. For example, a significant decrease in diversity was found in the middle of the 20th century in Danish material both by ISSR and SSR markers, whereas in Norwegian material no significant changes were observed, although there was a tendency for

a slight increase. In two-rowed and six-rowed cultivars, there was an indication of a decrease in diversity in several agronomic traits. Molecular markers showed the same tendency, although the decrease was not significant. The only exception was in six-rowed cultivars, where ISSR data showed a significant decrease in the middle of the century, but modern cultivars appeared to be as variable as the old ones. The drop in diversity detected by ISSR might be explained by the fact that after 1930 the use of six-rowed barley decreased dramatically in the south and only two cultivars from this part were included in the study ('Priekuļu 1' and 'Agra' from Latvia). However, both these cultivars are derived from Norwegian and Finnish material. The increase in diversity after 1970 in six-rowed material, as shown by ISSR, could be explained by the fact that two-rowed cultivars from the south part and non-Nordic introductions were used in the breeding of Norwegian and Finnish six-rowed cultivars.

Conclusions

Based on the molecular and agronomic studies of Nordic and Baltic barley material from the 20th century described in this thesis, the following conclusions can be drawn:

- There has been a distinct decrease in genetic variability of agronomic traits
- The decrease in variation shown by molecular markers was not significant throughout the whole data set
- In the southern parts of the region, it was possible to detect a significant decrease in diversity using ISSR markers
- The SSR data showed a decrease in diversity in material from southern parts in the middle of the last century, but in modern cultivars it appeared to increase again
- Diversity changes were different between the investigated countries
- Two-rowed and six-rowed barley cultivars were clearly differentiated by agronomic and DNA data, but not by isozymes
- The differentiation between two-rowed and six-rowed cultivars were also determined by loci different from the inflorescence-determining genes
- In general, modern and old material were separated by agronomic data and not by marker data
- The differentiation between old versus modern material could be detected by ISSR markers when material was analysed separately by country
- The differentiation between old versus modern material by SSR markers was more pronounced in the material from the southern parts of region than in that from northern parts

This study in general indicated a decrease in genetic diversity during breeding. The significance of this overall decrease could not be proven, although it was significant for some geographical regions and traits. Some losses of alleles were also detected. This shows that conservation of Nordic and Baltic landraces and old cultivars is important, because they are sources of genetic diversity that might become import for future breeding. The significant decrease in genetic diversity in some of the barley groups and traits also reveals the importance of monitoring diversity changes in the regions in order to improve breeding strategies and to maintain prosperous barley cultivation in the future.

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