

6-24-1994

## TRITICEAE: a tribe for food, feed and fun

Roland von Bothmer  
*Swedish University of Agricultural Sciences*

Björn Salomon  
*Swedish University of Agricultural Sciences*

Follow this and additional works at: [https://digitalcommons.usu.edu/herbarium\\_pubs](https://digitalcommons.usu.edu/herbarium_pubs)



Part of the [Plant Sciences Commons](#)

---

### Recommended Citation

von Bothmer, Roland and Salomon, Björn, "TRITICEAE: a tribe for food, feed and fun" (1994). *Herbarium Publications*. Paper 24.

[https://digitalcommons.usu.edu/herbarium\\_pubs/24](https://digitalcommons.usu.edu/herbarium_pubs/24)

This Conference Paper is brought to you for free and open access by the Intermountain Herbarium of Utah State University at DigitalCommons@USU. It has been accepted for inclusion in Herbarium Publications by an authorized administrator of DigitalCommons@USU. For more information, please contact [digitalcommons@usu.edu](mailto:digitalcommons@usu.edu).

# TRITICEAE: a tribe for food, feed and fun

Roland von Bothmer and Björn Salomon

Department of Plant Breeding Research

Swedish University of Agricultural Sciences

S-265 31 Svalöv, Sweden

## INTRODUCTION

Triticeae is an important tribe in the grass family, Poaceae. It contains the cereals wheat, rye, triticale, and barley as well as a large number of wild species, some of which are utilized as forage grasses. The tribe combines all kind of biological mechanisms and genetic systems: diploids and polyploids; annuals and perennials, inbreeders and outbreeders, and even apomicts. Due to this large variation Triticeae is an excellent model group for research in genetics, plant breeding, genetic diversity, taxonomy, and speciation in plants.

Triticeae is distributed in almost all temperate areas of the world and consists of some 350-450 species (Dewey

1984, West *et al.* 1988, Tzvelev 1989). Most genera as defined today are exclusively either annuals or perennials, except the genera *Hordeum*, *Dasypyrum* and *Secale* that include annual as well as perennial species. Of the perennial genera, some are very large like *Elymus* with ca. 150 species down to the monotypic genera *Hordelymus*, *Peridictyon*, and *Pascopyrum* (Fig. 1). Apart from the *Triticum/Aegilops* group, which contains around 30 species, the other annual genera are small with 1-4 species.

There have been important contributions by many great scientists for research in Triticeae. Three persons should be mentioned who have had a great impact on the research in the tribe, but in different areas.

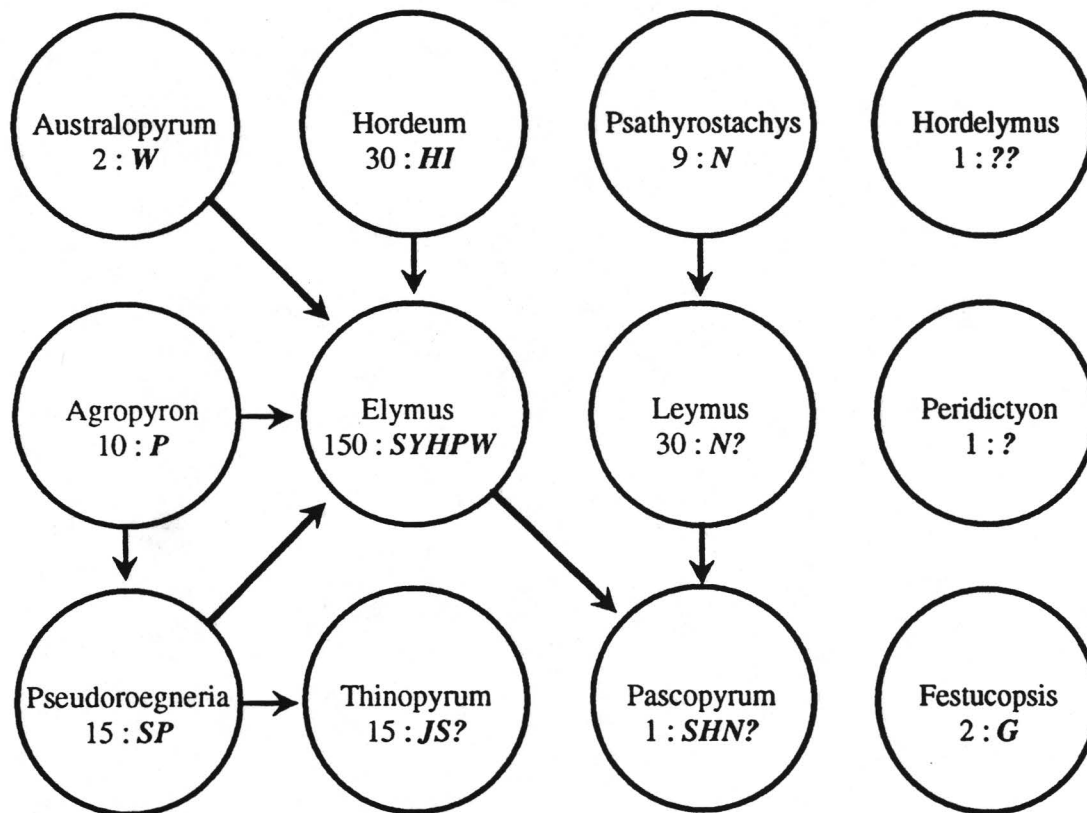
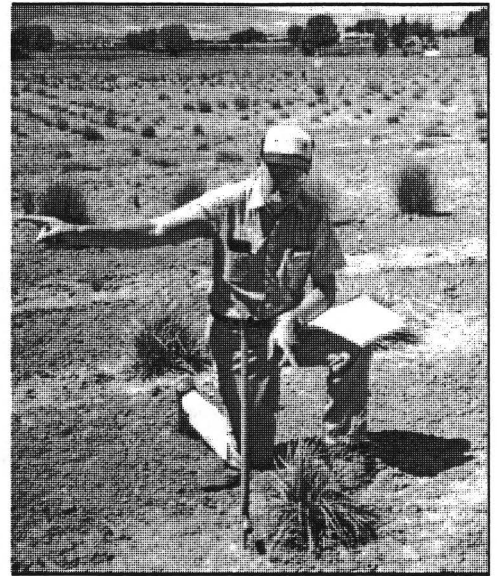


Figure 1 Perennial genera in the Triticeae with approximate number of species and genomes occurring within each genus.



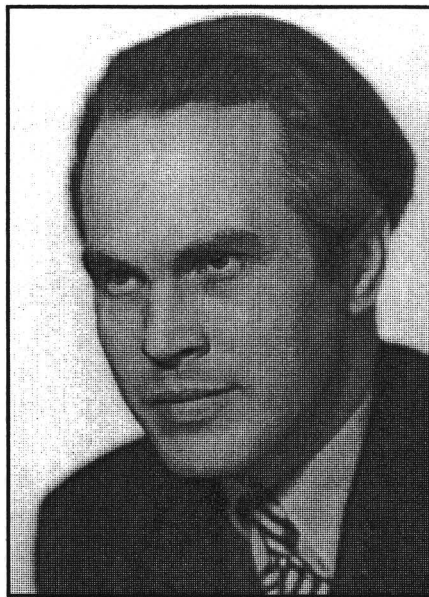
S. A. Nevski (Fig. 2).

The excellent Russian botanist S.A. Nevski died in his early 30s after some outstanding achievements. He had a remarkably good eye for biological variation and good judgements in taxonomic delimitations. Nevski made a comprehensive monograph of *Hordeum*, he treated the whole tribe for the Russian flora and made several taxonomic contributions (Nevski 1934, 1941).



D. R. Dewey (1929-1993, Fig. 3)

A pioneer contribution to the broadened investigation on Triticeae was made in Logan by Doug Dewey. Patiently he collected material, produced interspecific and intergeneric hybrids and studied their meiosis over a period of more than 25 years. Thanks to his work there is now a basic knowledge on the genome content in most perennial groups of the tribe (Dewey 1982, 1984).



Á. Löve (1919 - 1994, Fig. 4)

The third person is more controversial, namely Áskell Löve. His very consequential treatment of the genomes (haplomes) as a basis for generic delimitation caused a very intense debate and his work encouraged people to work in Triticeae (cf. Löve 1982, 1984).

In this presentation four major areas of research and development and the current problems will be reviewed: (i) germplasm; (ii) taxonomy; (iii) phylogeny and relationships; and (iv) breeding aspects.

## GERMPLASM

### Collecting

Collecting of Triticeae germplasm has over the last decade been rather intense and a major undertaking for several national and international organizations and research groups. The target areas for collecting have primarily been the centers of diversity. For the crop species and their closest wild relatives this center is defined as the area with maximal genetic diversity, which, for the Triticeae, occurs in SW Asia (Fig. 5). For the other Triticeae species diversity centers are defined as areas where the highest number of species are distributed, namely in southern South America, western North America and particularly in Central Asia (Fig. 5).

The most intense collecting efforts have concerned wheat and barley, especially in the Fertile Crescent in SW Asia- The major part of these collections are landraces, weedy and primitive material, introgressional forms and wild taxa of the primary gene pools. Large holdings of *Hordeum vulgare* ssp. *spontaneum* (C. Koch) Thell. and *Triticum/Aegilops* spp. have successively been built up at

several genebanks, e.g. USDA, ICARDA, CIMMYT, John Innes Center, the Ethiopian Genebank and others. There are, however, still underrepresented areas, where further collecting should be encouraged. For the genus *Aegilops* areas to consider include parts of northern Iraq, eastern Iran and the Caucasus.

The genus *Secale*, including wild and primitive material of rye, is quite underrepresented in the world holdings. There have been no large scale missions for collecting of landraces, wild and weedy forms of *Secale*. The target areas for the rye group would be central Anatolia, the Caucasus area, and the region north of the Black Sea.

For the species more distantly related to the crops, the situation is somewhat different. Central Asia, parts of southwest Asia, South and North America are the most well collected areas, but there are still many regions from which living material is lacking. The more species rich areas where collecting should be made include parts of China, Afghanistan, Mongolia, Central Siberia, the Caucasus area, SW Asia, and parts of South America (Fig. 5). Some marginal areas like parts of SE Europe, New Zealand, North Africa, South Africa, and Erithrea need to be further explored. Some groups are underrepresented in the collections, like species of *Pseudoroegneria*, *Leymus*, and many of the annual genera.

The problems for earlier collectors were mainly of political nature due to wars and conflicts. The difficulty to

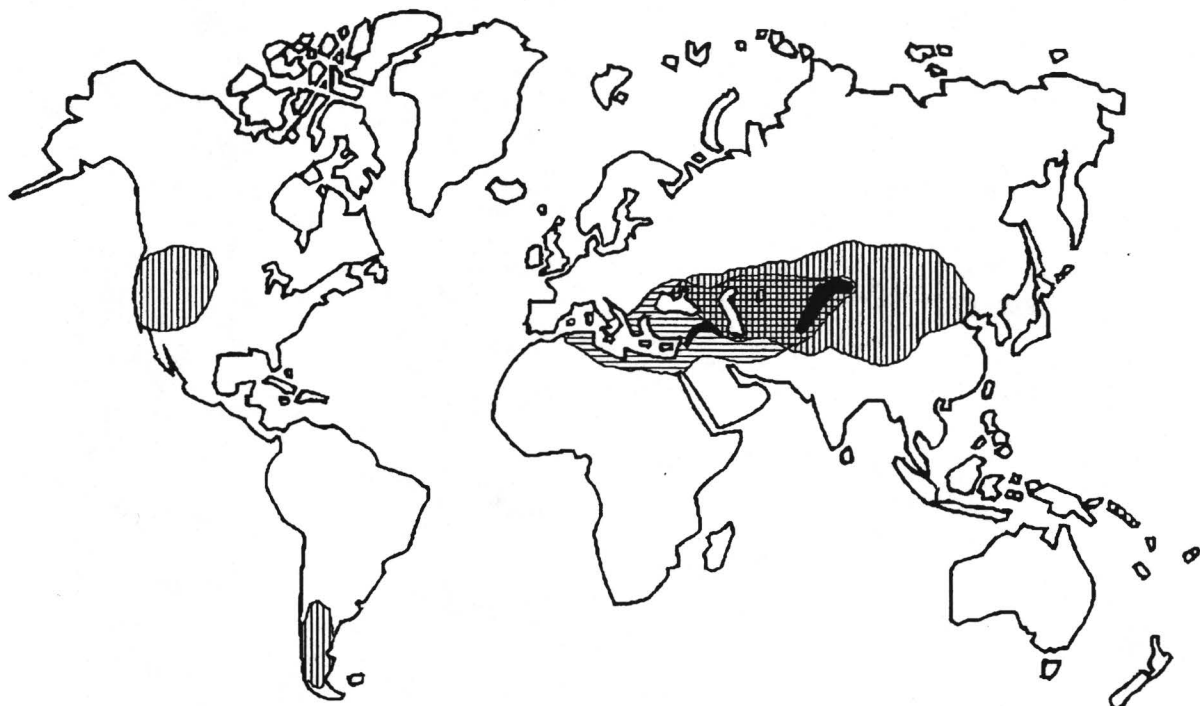


Figure 5 Diversity centers for the Triticeae; for the cereal crops and their closest allies, the center of diversity lies in the Middle East, and for the perennial genera, in Central Asia.

get access to material is now added with the possible problems arising with restrictions of collecting and free distribution of material. This is a result of the Rio convention which decided on the national ownership of genetic resources. Negotiations at FAO between member countries are going on and may hopefully lead to multilateral agreements about collecting and access to genetic resources. If this is not the case it will severely affect the possibilities to organize collecting missions and the access to germ plasm in the future.

### **Conservation and Genebank Problems**

Material of wild species is invaluable for basic research and hopefully also for prebreeding programs and the need for collecting is obvious. It is, however, not self-evident that all material should be included in the gene banks. The importance of preservation of gene resources of primary and secondary gene pools for breeding purposes is well documented, but the value for preservation of other species of no immediate importance for breeding is not simple. Beside the general question of the value for preservation of the secondary and tertiary gene pools there are also several practical aspects which must be solved for the preservation of wild material.

**Contamination.** During multiplication and rejuvenation contamination through seed and pollen is common and difficult to avoid. It is a general problem for everyone dealing with wild species. The measure would be to develop effective isolation between plots either spatially or mechanically for keeping each accession as clean as possible. For each cycle of multiplication or rejuvenation the identity of each accession must also be carefully checked.

**Loss of viability.** The knowledge about the longevity of seeds is still fragmentary concerning wild species. Some species can survive in room temperature for decades, while others may lose their viability despite that careful precautions have been taken. The measure here is that more studies on seed storage conditions and seed physiology must be undertaken in a systematic way.

**Labor intensive work.** The keeping of seeds of many wild species means that most seed handling must be done by hand, which is time consuming, ineffective and costly. Development of new technology is highly desired. Due to the above mentioned practical problems it is out of question trying to preserve all wild material that has been collected. One fundamental problem concerning the wild species is the strategy about which material is prioritized for preservation. Unfortunately, no real strategy has been developed. As it is now the gene banks simply include whatever comes in. The aim for the preservation must be that the material in gene banks should optimally represent the entire variation amplitude of each species. Two major parameters can be used concerning what material to

preserve, namely ecogeographic data on genetic diversity.

Ecogeographic data starts to be available for the primary gene pool of the cereals. In *Aegilops* information about geographical origin, altitude, soil conditions etc. for some of the about 30,000 accessions is available in databases (Hodgkin *et al.* 1992), but for other genera this information is fragmentary. When better facilities are obtained studies of *genetic diversity* with biochemical, molecular or adaptive characters must be applied.

If little material of wild species has been included in the gene bank the situation for the crops and the primary gene pool is quite the reverse. Of wheat, the global holding constitute 570 000 accessions and of barley 320 000 accessions (Hintum 1994). These are very high numbers, but what the accessions represent in terms of genetic diversity is not known. There are also many types of duplicates among the total number of gene bank accessions (Hintum and Knüpffer 1994). The high number of accessions together with the unknown number of duplicates among them makes the access to the gene bank material rather difficult. One solution out of this problem is the set up of *core collections* (Brown 1989). The core collection is "a selected and limited set of accessions optimally representing the genetic diversity of a crop and its wild relatives". That is where the ordinary germ plasm collection in a gene bank has an uneven distribution of accessions regarding ecogeographic or genetic diversity parameters the core collection should have an even distribution (Fig. 6). The Core Collection will not replace the regular gene bank holdings but, on the contrary, make an easier access to them. The first core collection to be realized concerns barley (the BCC). The number of accessions is decided to be about 2 000 representing about 1 % of the available gene bank accessions. The BCC is now under multiplication and the objective is that it will be completed and fully operating until the next Barley Genetics Symposium (1996 in Canada). Based on the BCC a number of investigations will be set up to actually test how much of genetic diversity the chosen set represents.

The creation of a "Triticeae Core Collection" (TCC) with a fixed set of accessions for each species which could serve as standards in basic investigations and for preliminary pre-breeding efforts should be discussed and decided upon. Two accessions from each taxon or cytotype could be included, which results in a TCC consisting of 700 to 800 accessions, which is fully feasible.

### **Utilization**

The collected and preserved material should naturally be widely utilized in research and breeding. The more an accession is used the more information will be available and the more will it be justified to preserve. There is a gap between the collection and preservation on one side and utilization on the other. The major problem, especially in

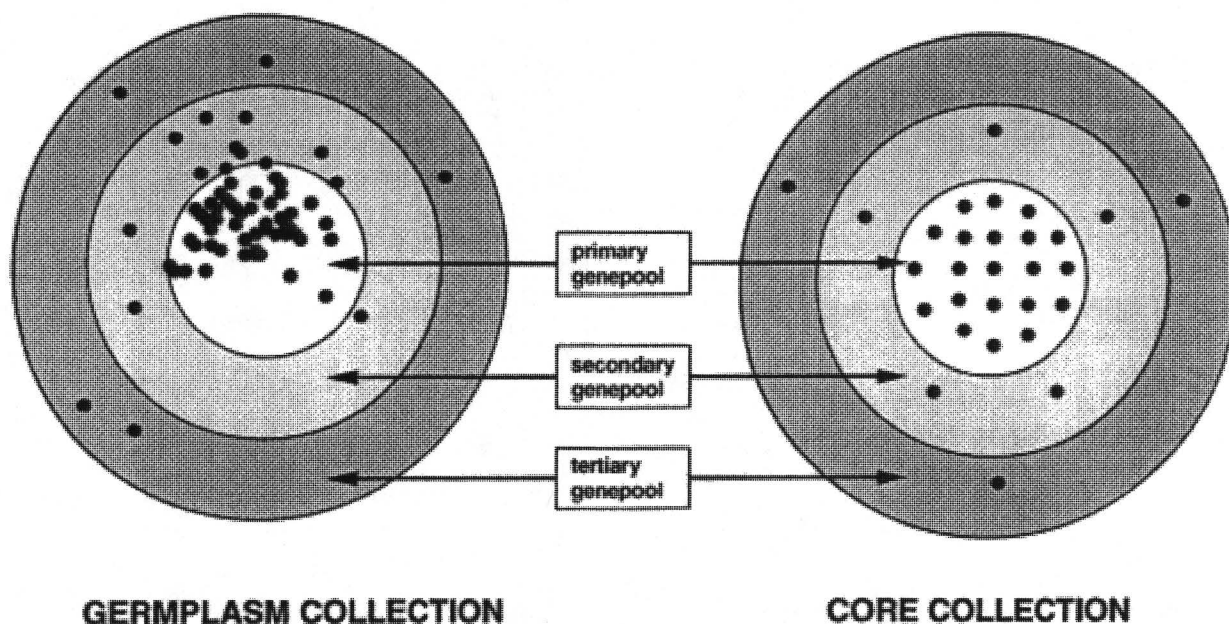


Figure 6 The core collection concept. A regular germ plasm collection has an uneven distribution of accessions whereas the core collection has an even distribution. (Modified from Hintum 1994).

research, is that the accuracy and the source of the material used often is neglected. If scientists were as careful about their material as they are about their methodology our knowledge about the Triticeae species would be far better. The use of unidentified or not verified material should not be allowed in publications. Accurate citations of the seed source with passport data or at least a number referring to a particular genebank accession should be obligatory, but it is sadly far from common. Documentation by voucher specimens for later verification of the identity is also desirable.

### Taxonomy

The basis for our understanding of relationships and phylogeny is the species. If we know how the individual species look, how they vary and how they are distributed, there are better possibilities to choose material for phylogenetic studies and breeding. Classical taxonomic studies based on herbarium specimens are urgent and should have a high priority. Efforts should also be invested to gather data on habitat requirements which are lacking for many species. The taxonomic data at the species level will also throw light on the delicate and controversial discussion on generic delimitations.

Over the years many taxonomic studies of genera or groups of species have been made. One could thus get an

impression that further basic taxonomic work is superfluous. Nothing could be more wrong! During the last two decades there have been surprisingly few taxonomic studies and there are still several complicated groups which have not been thoroughly investigated.

Some groups have been the subject for recent taxonomic treatments, for example, the annuals: *Dasypyrum*, *Eremopyrum*, *Henrardia*, *Amblyopyrum*, *Heterantheium*, and *Taeniatherum* (Frederiksen 1986, 1990, 1991, 1993). The genera *Aegilops* and *Triticum* are at present under revision, where *Aegilops* and some of the *Triticum* species are ready for publication (Van Slageren, ICARDA, personal comm.). Among the perennials, which have been treated recently, are *Psathyrostachys* (Baden 1991), *Hordeum* (Bothmer et al. 1991), *Leymus* in North America (Barkworth & Atkins 1984), and some groups in *Elymus* (Salomon 1994, Lu 1995) and *Thinopyrum* (Jarvie 1992, Assadi 1994). Cladistic and numerical approaches based on morphological characters have also been carried out in the tribe (cf. Baum 1982, Kellogg 1989, (Frederiksen & Seberg 1992).

There are still several groups which are poorly known, for example *Leymus* and *Pseudoroegneria* in Asia, and the major parts of *Elymus* and *Thinopyrum*. Joint international efforts could solve some of these taxonomic problems. One such proposal is a Scandinavian initiative for an *Elymus* network with the aim to study the genus from different

angles and hopefully ultimately lead to a monographic treatment of this huge genus. National and regional initiatives for taxonomic treatments, especially in the diversity centers, should be greatly encouraged and financially supported.

## PHYLOGENY AND RELATIONSHIPS

### Cytogenetic Methods

Based on chromosomal pairing in the meiosis of interspecific and intergeneric hybrids classical cytogenetics has gradually built up the knowledge on genome relationships in the Triticeae (cf. Dewey 1984, Love 1984). There is now a framework done, and the genomic content is partly known for some genera with some genomes occurring in more than one genus (Fig. 1). The **H** genome occurs in the genera *Hordeum*, *Elymus* and *Pascopyrum*. The **S** genome occurs in species of *Elymus*, *Pseudoroegneria*, *Thinopyrum* and *Pascopyrum*. The **N** genome occurs in *Psathyrostachys*, *Leymus*, and *Pascopyrum*. The **J** genome occurs only in *Thinopyrum* in a broad sense and not in *Leymus* as formerly postulated (Zhang & Dvorak 1991, Wang & Jensen 1994).

There are still several species which are not studied at all. Including in particular species of *Elymus* and *Leymus* in Asia. Still unknown genomes occur in *Hordelymus*, *Peridictyon*, *Leymus*, *Pascopyrum* and *Thinopyrum*. Several of the studied genomes have no obvious connections to

others, e.g. the **G** genome of *Festucopsis*.

The problems included in genome analysis should not be ignored. This encounters especially the genetic pairing regulation like the Ph genes in wheat and other species (McGuire & Dvorak 1982, Petersen 1991). The operation of these pairing promoting or pairing reducing genes disrupt the regular pairing patterns which may result in wrong conclusions on genome affinities. However, by the analysis of a large number of hybrid combinations this risk is reduced. Information on genome relationships will also in the future contribute to the understanding of species relationships in the Triticeae.

### Molecular Methods

Much effort has been invested in development of new techniques for studies of phylogenetic relationships, which also have been applied in the Triticeae. These methods include biochemical techniques like electrophoresis of isoenzymes and storage proteins (cf. Jorgensen 1986, Jaaska 1992). Molecular biology has added to the richness of new, powerful, and sophisticated techniques, like RFLPs, and RAPDs both of nuclear and organellar DNA (cf. Talbert *et al.* 1991, Doebley *et al.* 1992, Dvorak & Zhang 1992, Kellogg 1992, Molinar *et al.* 1992, Terachi & Tsunewaki 1992).

Over the last years there are mainly two types of molecular investigations that have been done. (1) This group includes studies that are concentrated on a genus or

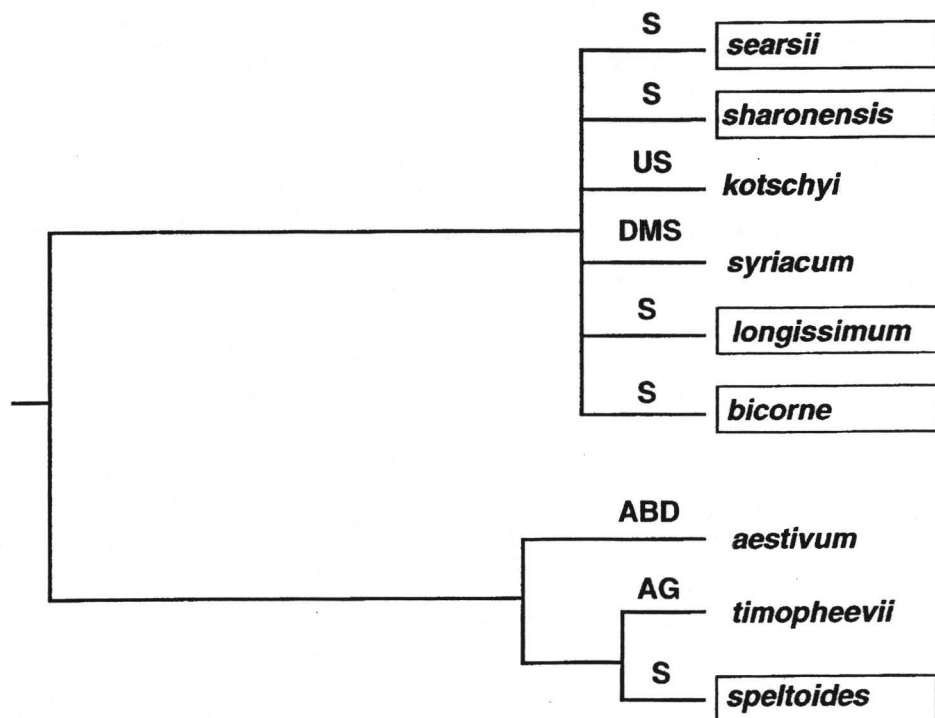


Figure 7 Variation in repetitive DNA sequences in the *Triticum/Aegilops* group. The letters represent genome designations. (Modified from Talbert *et al.* 1991).

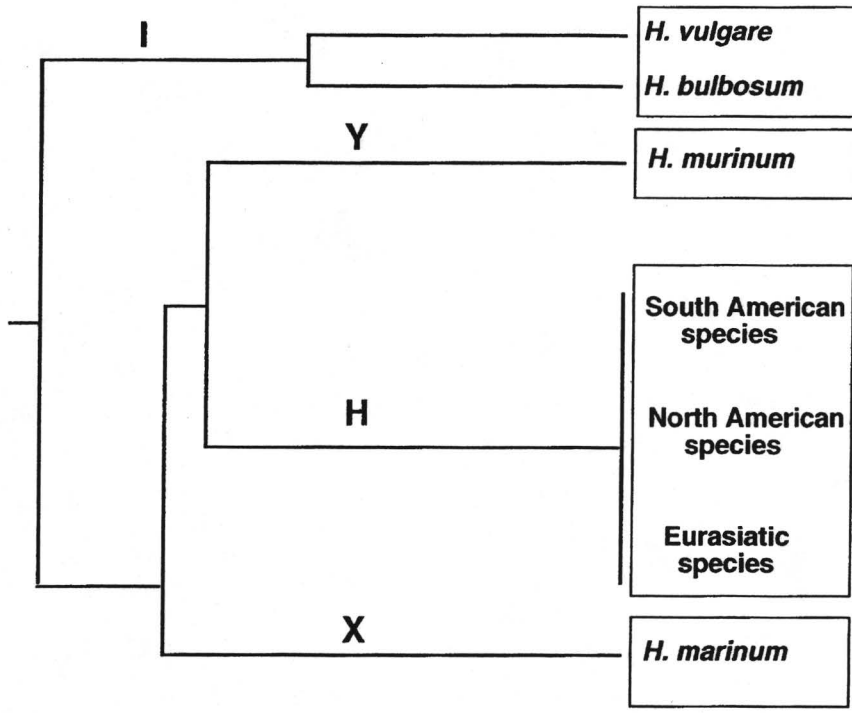


Figure 8 Variation in repetitive DNA sequences in *Hordeum*. The letters represent genome designations. (Modified from Svitashev et al. 1994).

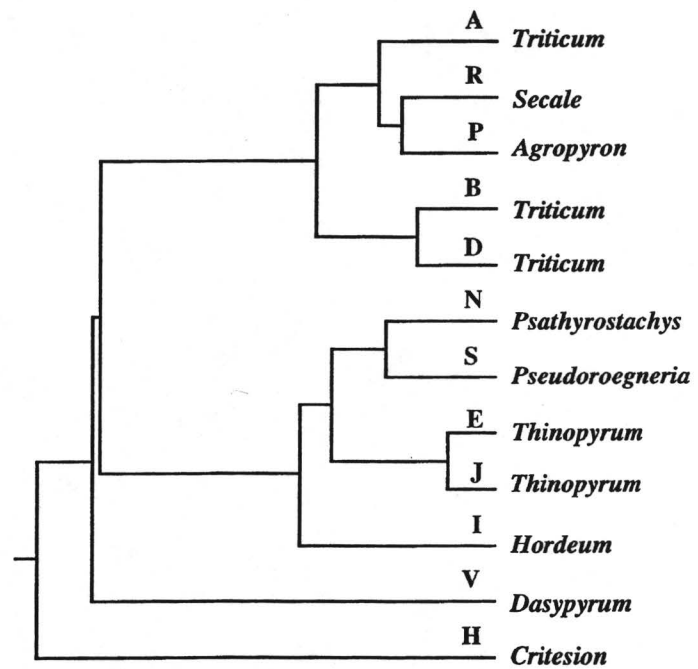


Figure 9 RFLP variation between different genera of the Triticeae. The letters represent genome designations. (Modified from Monte et al. 1993).

a restricted group of species. Here several more or less closely related species or populations are selected. In the *Triticum/Aegilops* group Talbert et al. (1991) studied the repetitive DNA sequences primarily characteristic for the S genome and how the diploid and the polyploid species are

related. *T. speltoides* (Tausch) Gren. is distinct from the other diploid S-genome species. The tetraploid *T. timopheevi* (Zhuk.) Zhuk. is shown to be 98 % identical showing close affinity between the S and the G genomes (Fig. 7).



In *Hordeum* several studies with different techniques have been applied, like a cpDNA study by Doebley *et al.* (1992) showing differentiation between the four basic genomes in the group. This pattern is also evident in the study of repetitive sequences of the nuclear DNA by Svitashv *et al.* (1994, Fig. 8).

In this kind of studies it is often so that a too narrow group is chosen. Further representatives outside the group should be included. It is, for example, usually not meaningful to compare just the cereals and include none of the wild species. (2) The other approach includes usually the whole tribe. The species are chosen to represent an entire group or genus. For example, Monte *et al.* (1993) studied the RFLP variation of 21 cDNA probes from hexaploid wheat in 16 species of the Triticeae (Fig. 9). They found a good correlation between the phylogenetic tree produced by this approach and by earlier investigations.

In this type of investigations the chosen species may not at all be representative for the group or the variation within the group is not covered sufficiently. More careful considerations and planning about the material should be done before the costly techniques are applied.

### ***In Situ Hybridization***

One particular molecular technique is *in situ* hybridization or molecular cytogenetics where a probe is hybridized with chromosomes - usually in the metaphase plates. *In situ* hybridization has contributed quite a new tool to study the organization of the DNA structures in the chromosomes and affinities between species (Lapitan *et al.* 1987, Anathawast-Jónsson, K. *et al.* 1990, Heslop-Harrison 1992, Ørgaard & Heslop-Harrison 1994 a,b). It refines our tools for genome analysis and for breeding purposes.

The probes can detect: cloned sequences, chromosomal segments, whole chromosomes, and entire genomes. A special aspect is the possibility to study the meiosis and distinguish between auto- and allozyndetic pairing.

All the new techniques have added immensely to the knowledge of relationships in the Triticeae. In the future we will get new and exciting results. There are two major areas where the knowledge of relationships and phylogeny is particularly weak. (1) Many of the annual species of the Triticeae belong to small or even monotypic genera. The morphology is in most cases quite distinct. Crossing experiments and genome analysis have not added much to our understanding of the affinity to perennial groups or genomes. How are these annuals differentiated, which are their respective closest relatives and are they old or new taxa? Do the annuals have particular genetic systems which promote rapid differentiations? (2) Several of the perennials have been poorly studied mainly due to lack of material. These include several species of Asiatic *Leymus* and *Elymus*.

With various methods one should study which groups of species are monophyletic and perhaps ultimately to get a better generic delimitation.

## **BREEDING**

The breeding aspects in the Triticeae are naturally dominated by the big cereal crops, wheat, barley, and rye. In this context the elite breeding in cereals will not be discussed, but merely the utilization of a wider genepool in pre-breeding programs. The entire tribe constitute a vast genepool. Many species belong to the primary and secondary genepools of bread and durum wheats, and due to the polyploidy several species from the tertiary genepool are also used. The efforts in pre-breeding is dominated by screening for disease resistance in wild *Aegilops* and *Triticum*. Over the last decade resistance to at least 15 pathogens have been investigated and some of the sources are now included in conventional breeding programs (cf. Tosa & Sakai 1991, Eastwood *et al.* 1994, Siedler *et al.* 1994). Some work has also been devoted

to stress tolerance, mainly for salt and drought (cf. Nevo *et al.* 1993, Taeb *et al.* 1993, Dubcovsky *et al.* 1994). Among other genera of interest for wheat improvement include the annual *Dasyphyrum villosum* (L.) Candargy and some perennial species like *Thinopyrum elongatum* (Host.) D.R. Dewey, *Th. bessarabicum* (Savul. & Rayss) A. Löve and *Th. intermedium* (Host) Barkworth & D.R. Dewey (cf. Blanco *et al.* 1988, Jiang *et al.* 1993, William & Mujeeb-Kazi 1993, Zhong & Qualset 1993).

Contrary to wheat, barley is a diploid organism which makes gene transfer more problematic. Only the progenitor of the crop, *Hordeum vulgare* ssp. *spontaneum* belongs to the primary genepool. It has been studied particularly for resistance to BYDV, powdery mildew and rust (cf. Jana & Nevo 1991, Jahor & Fischbeck 1993). Ssp. *spontaneum* material is at present included in at least three major pre-breeding programs (cf. Lehmann & Bothmer 1988).

*Hordeum bulbosum* L., which is the single species in the secondary genepool of barley (Bothmer *et al.* 1991), has since long been used in production of doubled haploids through chromosome elimination (cf. Lange 1988). Now there are also promising results with the use of *H. bulbosum* for transferring genes to barley (Pickering 1992, Xu & Kasha 1992). The first successful transfer was with a resistance gene for powdery mildew. The other wild species of *Hordeum* are more inaccessible for breeding (Bothmer *et al.* 1991).

Rye has been extensively used as a gene source for transfer of resistance genes to wheat. For breeding of rye the very closely related wild species could be utilized but so far very little efforts have been invested (Singh & Seti 1991, Izdebski 1992).

## New Crops

The intergeneric hybrid between wheat and rye, triticale, is now at last established as an important cereal in some countries. It took about a century to develop triticale from the time of the first crosses. It is thus not an easy task to introduce new crops. One very interesting attempt to develop another amphiploid, putative new crop is tritordeum, i.e. the intergeneric hybrid between *Hordeum chilense* Roem. & Schult. and *Triticum*, especially durum-wheat. The first crosses were made at PBI in Cambridge some 20 years ago (Martin & Chapman 1977). The first papers included mainly hybridization, cytogenetics, and molecular studies (cf. Martin & Sanchez-Monge Laguna 1980, Padilla & Martin 1983, Schwarzacher *et al.* 1989). Later more applied approaches were performed, for example, on resistance to rust, powdery mildew and nematodes as well as on field trials (cf. Milan *et al.* 1988, Alvarez *et al.* 1992, Rubiales *et al.* 1992, 1993). Another interesting new combination is wheat X *Leymus spp.* (cf. Plourde *et al.* 1993). Even if the task to

establish a new crop seems frustrating further initiatives should be encouraged.

## Forages

Triticeae comprises also several range and forage grasses, which are important for grazing in natural conditions in Central Asia as well as under domesticated conditions in North America. The most important species are the crested wheatgrasses (*Agropyron cristatum* (L.) Gaertn.), intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey), and Russian wildrye (*Psathyrostachys juncea* (Fisch.) Nevski). Much work is in progress concerning disease resistance, stress tolerance and yield potentials in these and other species (cf. Berdahl & Krupinsky 1987, Johnson 1991, Asay 1992, Dong *et al.* 1992, Vogel *et al.* 1993, Xu & Conner 1994, Wang 1994). Similar studies should be encouraged in other parts of the world, e.g. in Central Europe, SW Asia, and South America (cf. Salomon *et al.* 1992, Esteban *et al.* 1993).

## CONCLUSIONS

There is a huge task lying in front of us for research and development in the Triticeae. To summarize some of the major topics:

### Germplasm :

- enlarge collecting
- improve preservation
- increase utilization

### Taxonomy:

- more monographic studies
- improve the generic delimitation

### Relationships and phylogeny.

- consensus of genome designation
- study the relationships with the annuals

- study the relationships with the perennials

### Breeding:

- improved technique for gene transfer
- more studies of agronomic traits

The Triticeae symposia need to get a formalized continuation. It is important that breeders and researchers meet at regular intervals to discuss this fascinating plant group. Further international cooperation in Triticeae research is also required.

**Acknowledgements** - We wish to thank several of colleagues to let us use their results and material. We will particularly mention: Michiel van Slageren, ICARDA, Aleppo, Syria, Marian Ørgaard, Copenhagen, Denmark and Sergei Svitashv, Svalöv, Sweden.

## LITERATURE CITED

- Alvarez, J.B., Ballesteros, J., Sillero, J.A. & Martin, L.M. 1992. Tritordeum: a new crop of potential importance in the food industry. - *Hereditas* 116: 193-197.
- Anamthawat-Jonsson, K., Schwarzacher, T., Leitch, A.R., Bennett, M.D. & Heslop-Harrison, J.S. 1990. Discrimination between closely related Triticeae species using DNA as a probe. - *Theor. Appl. Genet.* 79: 721-728.
- Asay, K.H. 1992. Breeding potentials in perennial Triticeae grasses. - *Hereditas* 116: 167-173.
- Assadi, M. 1994. The genus *Elymus* L. (Poaceae) in Iran: Biosystematic studies and generic delimitation. - Doctoral dissertation, Lund University, Lund
- Baden, C. 1991. A taxonomic revision of *Psathyrostachys* (Poaceae). - *Nord. J. Bot.* 11: 3-26.
- Barkworth, M.E. & Atkins, R.J. 1984. *Leymus* in North America, taxonomy and distribution. - *Am. J. Bot.* 71: 609-625.
- Baum, B. R. 1982. Cladistic analysis of Triticeae by means of Farri's "distance Wagner procedure". *Can. J. Bot.* 60: 1194-1199.
- Berdahl, J.D. & Krupinsky, J.M. 1987. Heritability of resistance to leaf spot diseases in intermediate wheatgrass. - *Crop Sci.* 27: 58.
- Blanco, A., Perrone, V. & Simeone, R. 1988- Chromosome pairing variation in *Triticum turgidum* L. X *Dasypyrum villosum* (L.) Candargy hybrids and genome affinities. - *Proc. 7th Int. Wheat Genet. Symp.*, Cambridge, pp. 63-67.
- Bothmer, R. von, Jacobsen, N., Baden, C., Jorgensen, R.B. & Linde-Laursen, I. 1991. An ecogeographic study of the genus *Hordeum*. - *Systematic and Ecogeographic Studies of Crop Gene pools 6*, IBPGR, Rome.
- Brown, A.H.D. 1989. Core collections: a practical approach to genetic resources management. *Genome* 31: 818-824.
- Dewey, D.R. 1982. Genomic and phylogenetic relationships among North American perennial Triticeae. - In: *Grasses and Grasslands*, pp. 51-88.
- Dewey, D.-R. 1984. The genomic system of classification as a guide to intergeneric hybridization with perennial Triticeae. - In: *Gene Manipulation in Plant Improvement*, pp. 209-279.
- Doebley, J., Bothmer, R. von & Larson, S. 1992. Chloroplast DNA variation and the phylogeny of *Hordeum* (Poaceae). - *Am. J. Bot.* 79: 576-584.
- Dong, Y.S., Zhou, R.H., Xu, S.J., Li, L.H., Caudeyron, Y. & Wang, R. R.-C. 1992. Desirable characteristics in perennial Triticeae collected in China for wheat improvement. - *Hereditas* 116: 175-178.
- Dubcovsky, J., Galvez, A.F. & Dvorak, J. 1994. Comparisons of the genetic organization of the early salt-stress-response gene system in salt-tolerant *Lophopyrum elongatum* and salt-sensitive wheat. - *Theor. Appl. Genet.* 87: 957-964.
- Dvorak, J. & Zhang, H.-B. 1992. Reconstruction of the genus *Triticum* from variation in repeated nucleotide sequences. - *Theor. Appl. Genet.* 84: 419-429.
- Eastwood, R.F., Lagudah, E.S. & Appels, R. 1994. A direct search for DNA sequences tightly linked to cereal cyst nematode resistance in *Triticum tauschii*. - *Genome* 37: 311-319.
- Frederiksen, S. 1986. Revision of *Taeniatherum*. - *Nord. J. Bot.* 6: 389-397.
- Esteban Oliva, G., Montes, L. & de las Mercedes Masco, E. 1993. Collecting native forage germplasm in Patagonia. - *FAO/IBPGR Plant Genet. Res. Newsl.* 93: 34-37.
- Frederiksen, S. 1990. Taxonomic studies in *Dasypyrum* (Poaceae). - *Nord. J. Bot.* 11: 135-142.
- Frederiksen, S. 1991. Taxonomic studies in *Eremopyrum* (Poaceae). - *Nord. J. Bot.* 11: 217-285.
- Frederiksen, S. 1993. Taxonomic studies in some annual genera of the Triticeae. - *Nord. J. Bot.* 13: 481-493
- Frederiksen, S. & Seberg, O. 1992. Phylogenetic analysis of the Triticeae (Poaceae). - *Hereditas* 116: 15-19.
- Heslop-Harrison, J.S. 1992. Molecular cytogenetics, cytology and genomic comparisons in the Triticeae. - *Hereditas* 116: 93-99.
- Hintum, T. van, 1994. Drowning in the gene pool: Managing genetic diversity in genebank collections. - Thesis at the Swedish Univ. Agric. Sci.
- Hintum, T. van & Knupffer, H. 1994. Duplication within and between germ plasm collections. I. Tracing duplication on the basis of passport data. - *Genet. Res. Crop Evol.* (in press)
- Hodgkin, T., Adham, Y. J. & Powell, K.S. 1992. A preliminary survey of wild *Triticum* and *Aegilops* species in the world's genebanks. - *Hereditas* 116: 155-162.

- Izdebski, R. 1992. Utilization of rye genetic resources initial material selection. - *Hereditas* 116:179-185.
- Jaaska, V. 1992. Isoenzyme variation in the genus *Elymus* (Poaceae). - *Hereditas* 117:11-22.
- Jahor, A. & Fischbeck, G. 1993. Identification of new genes for mildew resistance to barley at the *Mla* locus in lines derived from *Hordeum spontaneum*. - *Plant Breeding* 110:116-122.
- Jana, S. & Nevo, E. 1991. Variation in response to infection with *Erysiphe graminis hordei* and *Puccinia hordei* in some wild barley populations in a center of diversity. - *Euphytica* 57: 133-140.
- Jarvie, J.K. 1992. Taxonomy of *Elytrigia* sect. *Caespitosae* and sect. *Junceae* (Gramineae: Triticeae).- *Nordic J. Bot.* 12: 155-169.
- Jiang, J., Friebe, B., Dhaliwal, H.S., Martin, T J. & Gill, B.S. 1993. Molecular cytogenetic analysis of *Agropyron elongatum* chromatin in wheat germplasm specifying resistance to wheat-streak mosaic virus. - *Theor. Appl. Genet.* 86: 41-48
- Johnson, R.C. 1991. Salinity resistance, water relations, and salt content of crested and tall wheatgrass accessions. - *Crop Sci.* 31: 730-734.
- Jorgensen, R.B. Relationships in the barley genus (*Hordeum*): An electrophoretic examination of proteins- - *Hereditas* 104: 273-291.
- Kellogg, E.A. 1989. Comments on genomic genera in the Triticeae (Poaceae). - *Am. J. Bot.* 76: 796-805.
- Kellogg, E.A. 1992. Restriction site variation in the chloroplast genomes of the monogenomic Triticeae. - *Hereditas* 116: 43-47.
- Lange, W. 1988. Cereal cytogenetics in retrospect. What came true of some cereal cytogeneticists' pipe dreams? - *Euphytica Supplement* 1988: 7-25.
- Lapitan, N.L.V., Gill, B.S. & Sears, R.G. 1987. Genomic and phylogenetic relationships among rye and perennial species in the Triticeae. - *Crop Sci.* 27: 682-687.
- Lehmann, L. & Bothmer, R. von, 1988. *Hordeum spontaneum* and landraces as a gene resource for barley breeding. - In: *Cereal Breeding Related to Integrated Cereal Production*, Pudoc, Wageningen, pp- 190-194.
- Löve, A. 1982. Generic evolution of the wheatgrasses. - *Biol. Zbl.* 101: 199-212.
- Löve, A. 1984. Conspectus of the Triticeae. - *Feddes rep.* 95: 425-521.
- Lu, B.R. 1995. Taxonomy and morphology of the *Elymus parviglumis* group (Poaceae). - *Nordic J. Bot.* (in press)
- Martin, A. & Chapman, V. 1977. A hybrid between *Hordeum chilense* and *Triticum aestivum*. *Cereal Res. Comm.* 5: 365-368.
- Martin, A. & Sanchez-Monge Laguna, E. 1980. Effects on the 5B system on control of pairing in *Hordeum chilense* X *Triticum aestivum*. - *Z. Pflanzenzuchtg.* 85: 122-127.
- McGuire, P.E. & Dvorak, J. 1982. Genetic regulation of heterogenetic chromosome pairing in polyploid species of the genus *Triticum sensu lato*. - *Can. J. Genet. Cytol.* 24: 57-82.
- Milan, T, Martin, A. & de Haro, A. 1988. Field trial of Tritordeum. - *Cereal Res. Comm.* 16: 31-38.
- Molinar, S.J., Wheatcroft, R. & Fedak, G. 1992. RFLP analysis of *Hordeum* species relationships. *Hereditas* 116: 87-91.
- Monte, J.V., McIntyre, C.L. & Gustafson, J.P. 1993. Analysis of phylogenetic relationships in the Triticeae tribe using RFLPs. - *Theor. Appl. Genet.* 86: 649-655.
- Nevo, E., Krugman, T. & Beiles, A. 1993. Genetic resources for salt tolerance in the wild progenitors of wheat (*Triticum dicoccoides*) and barley (*Hordeum spontaneum*). - *Plant Breeding* 110: 338-341.
- Nevski, S.A. 1934. Tribe XIV. Hordeae Benth. - In: Komarov, V L. (ed.) *Flora of the USSR*, vol. 2, pp. 590-728.
- Nevski, S.A. 1941. Beitrage zur Kenntnis der wildwachsenden Gersten in Zusammenhang mit der Frage über den Ursprung von *Hordeum vulgare* L. und *Hordeum distichon* L. (Versuch einer Monographie der Gattung *Hordeum*). - *Trudy Bot Inst. Akad. Nauk. SSSR*, ser. 1, 5: 64-255.
- Ørgaard, M. & Heslop-Harrison, J.S. 1994a. Investigation of genome relationships between *Leymus*, *Psathyrostachys* and *Hordeum* inferred by genomic DNA:DNA *in situ* hybridization. - *Ann. Bot.* 73: 195-203.
- Ørgaard, M. & Heslop-Harrison, J.S. 1994b. Relationships between species of *Leymus*, *Psathyrostachys* and *Hordeum* (Poaceae, Triticeae) inferred from Southern hybridization of genomic and cloned DNA probes. - *Pl. Syst. Evol.* 189: 217-231.

- Padilla, J.A. & Martin, A. 1983. New hybrids between *Hordeum chilense* and tetraploid wheat. *Cereal Res. Comm.* 11: 5-7.
- Petersen, G. 1991. Intergeneric hybridization between *Hordeum* and *Secale* II. Analysis of meiosis in hybrids. - *Hereditas* 114: 141-159.
- Pickering, R.A. 1992. Monosomic and double monosomic substitutions of *Hordeum bulbosum* into *H. vulgare* L. - *Theor. Appl. Genet.* 84: 466-472.
- Plourde, A., Comeau, A. & St. Pierre, C.A. 1992. Barley Yellow Dwarf Virus resistance in *Triticum aestivum* X *Leymus angustus* hybrids. - *Plant Breeding* 108: 97-103.
- Rubiales, D., Brown, J.K.M. & Martin, A. 1993. *Hordeum chilense* resistance to powdery mildew and its potential use in cereal breeding. - *Euphytica* 67: 215-220.
- Rubiales, D., Ramirez, M.C. & Niks, R.E. 1992. The contribution of *Hordeum chilense* to wheat brown rust. - *Euphytica* 59: 129-133.
- Salomon, B. 1994. Taxonomy and morphology of the *Elymus semicostatus* group (Poaceae). - *Nordic J. Bot.* 14: 7-14.
- Salomon, B., Lu, B.R., Bothmer, R. von & Jonsson, H.A. 1992. Assessment of agronomic performance of Asiatic wheatgrasses cultivated at Landskrona, Sweden. - *J. Swed. Seed Assoc.* 102: 119-125.
- Schwarzacher, T., Leitch, A.R., Bennett, M.D. & Heslop-Harrison, J.S. 1989. *In situ* localization of parental genomes in a wide hybrid. - *Ann. Bot.* 64: 315-324.
- Siedler, H., Obst, A., Hasam, S.L.K. & Zeller, F.J. 1994. Evaluation for resistance to *Pyrenophora tritici-repentis* in *Aegilops tauschii* Coss. and synthetic hexaploid wheat amphiploids- *Genet. res. Crop Evol.* 41: 27-34.
- Singh, S. & Seti, S. 1991. Crossability of some bread wheat landraces and improved cultivars from western Himalayas with rye. - *Euphytica* 53: 137-141.
- Svitashev, S., Bryngelsson, T., Vershinin, A., Pedersen, C., Säll, T. & Bothmer, R. von, 1994. Phylogenetic analysis of the genus *Hordeum* using repetitive DNA sequences. - *Theor. Appl. Genet.* (in press).
- Taeb, M., Koebner, R.M.O. & Forster, B-P. 1993. Genetic variation for water logging tolerance in the Triticeae and the chromosomal location of genes conferring waterlogging tolerance in *Thinopyrum elongatum*. - *Genome* 36: 825-830.
- Talbert, L.E., Magyar, G.M., Lavin, M., Blake, T.K. & Moylan, S.L. 1991. Molecular evidence for the origin of the S-derived genomes of polyploid *Triticum* species. - *Amer. J. Bot.* 78: 340-349.
- Terachi, T. & Tsunewaki, K. 1992. The molecular basis of genetic diversity among cytoplasm of *Triticum* and *Aegilops*. VIII. Mitochondrial RFLP analyses using cloned genes as probes.- *Mol. Biol. Evol.* 9: 917-931.
- Tosa, Y & Sakai, K. 1991. Analysis of the resistance of *Aegilops squarrosa* to the wheatgrass mildew fungus by using the gene-for-gene relationship. - *Theor. Appl. Genet.* 81: 735-759.
- Tzvelev, N.N. 1989. The systems of grasses (Poaceae) and their evolution. - *Bot. Rev.* 55: 141-204.
- Vershinin, A., Svitashev, S., Gummesson, P.-O., Salomon, B., Bothmer, R von & Bryngelsson, T. 1994. Characterization of a family of tandemly repeated DNA sequences in Triticeae. - *Theor. Appl. Genet.* (in press).
- Vogel, K.P., Reece, P.E. & Nichols, J.T. 1993. Genotypes and genotypes X environment interaction effects on forage yields and quality in swards. - *Crop Sci.* 33: 37-41.
- Wang, R. R.-C. 1994. Germplasm enhancement of range forage grasses in the tribe Triticeae. - 1993 Progress Report USDA-ARS, Utah State Univ., pp. 81-82.
- Wang, R. R.-C. and K. B. Jensen, 1994. Absence of the J genome in *Leymus* species (Poaceae: Triticeae): evidence from DNA hybridization and meiotic pairing. *Genome* 37: 231-235.
- West, J.G., McIntyre, C.L. & Appels, R. 1988. Evolution and systematic relationships in the Triticeae (Poaceae). - *Pl. Syst. Evol.* 160: 1-28.
- William, M.D.H.M. & Mujeeb-Kazi, A. 1993. *Thinopyrum bessarabicum*: biochemical and cytological markers for the detection of genetic introgression in its hybrid derivatives with *Triticum aestivum* L. - *Theor. Appl. Genet.* 86: 365-370.
- Xu, J. & Conner, R.L. 1994. Intervarietal variation in satellites and C-banded chromosomes of *Agropyron intermedium* ssp. *trichophorum* cv. Greenleaf. - *Genome* 37: 305-310.
- Xu, J. & Kasha, K.J. 1992. Transfer of a dominant gene for powdery mildew resistance and DNA from *Hordeum bulbosum* into cultivated barley (*H. vulgare*). - *Theor. Appl. Genet.* 84: 771-777.
- Zhang, H. B. and J. Dvorak. 1991. The genome origin of tetraploid species of *Leymus* (Poaceae: Triticeae) inferred from variation in repeated nucleotide sequences. *Am. J. Bot.* 78: 871-884.
- Zhong, G.-Y. & Qualset, C.O. 1993. Allelic diversity of high molecular-weight glutenin protein subunits in natural populations of *Dasyphyrum villosum* (L.) Candargy. - *Theor. Appl. Genet.* 86: 851-858.