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Wide-hybrids between wheat and lymegrass: breeding and agricultural potential

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SUMMARY

Wide-hybrids between wheat (*Triticum aestivum*; *T. carthlicum*) and lymegrass (*Leymus arenarius*; *L. mollis*) can serve as a bridge to increase genetic diversity both of wheat (with respect to biotic and abiotic stress tolerance) and of lymegrass (with respect to end-use quality). The hybrids have been made and they are being developed further by (1) direct back-crossing with the parental species and (2) chromosome doubling to produce fertile amphiploids. The back-cross strategy allows introgression of desirable characters from one species into the other, whereas amphiploids can be exploited directly as a new synthesized species. The genetic resources of wheat are used for improving lymegrass, via the wide-hybrids, with a long-term aim to convert lymegrass into a viable grain and/or fodder crop suitable for marginal habitats. Simultaneously, lymegrass characters such as stress tolerance and disease resistance can be introgressed into wheat, making the cultivation more reliable in many different production regions. The present review describes the study of genetic diversity of lymegrass, the wide-hybridization as a breeding strategy, the wide-hybrids and their agricultural potential.

Key words: cereal breeding, genetic diversity, *Leymus*, marginal farming, wheat, wide-hybridization.

YFIRLIT

Tegundablendingar milli hveitis og mels og nýting þeirra í landbúnaði

Melur er mjög harðgerð og veðurþolin planta sem þrífst vel við norðlægar breiddargráður. Nafnið melur (lymegrass) er notað í þessu tilfelli sem samheiti yfir tvær náskyldar tegundir: melgresi (*Leymus arenarius* (L.) Hochst.), sem hefur megin útbreiðslu í Norður-Evrópu, og dúnmel (*L. mollis* (Trin.) Pilger), sem er útbreiddur í Norður-Ameríku. Áður fyrr var melkorn nýtt í brauðgerð og til fóðrunar en það tíðkast ekki nú á dögum þar sem mun gæðabetra korn er á markaðnum. Með því að kynbæta melinn er talið að hægt sé að nýta harðgerða eiginleika hans til kornræktar. Þessir eiginleikar eru til dæmis veðurþol, fjölærni, örugg fræmyndun og þol gegn plöntusjúkdómum. Í þessu sambandi hefur mel (*L. arenarius*; *L. mollis*) verið æxlað saman við hveitiplöntur (*Triticum aestivum* L. em. Thell.; *T. carthlicum* Nevski) og er framtíðarmarkmiðið að melurinn öðlist þannig góða korneiginleika hveitis, svo sem kornstærð, brauðgæði, fóðurgildi og ræktunareiginleika.

Tegundablöndun er vel þekkt kynbótaaðferð sem hefur þróast með áratuga rannsóknum og er notuð hér til að kynbæta mel og hveiti eða til að fá út nýja blendingstegund, melhveiti. Mörg gen sem stjórna víxlunum milli tegunda, litningapörunum og litningatilfærslum hafa verið kortlögð á litningum. Víxlunartilraunir hafa tekist vel þar sem notaður er hveitistofn sem inniheldur þessi gen. Í dag er auðveldara að fylgjast nákvæmlega með erfðabreytingum í kynbótatilraunum með sameinda- og frumuerfðafræðilegum aðferðum. Rannsóknir í erfðatækni og kynbótum kornjurta eru mjög langt á veg komnar, þannig að góður möguleiki er að flytja eiginleika á milli tegunda.

Nú hafa fengist hér á landi um 200 tegundablendingar milli hveitis og mels en þeir eru mikilvægur grunnur fyrir áframhaldandi þróun og rannsóknir. Í fyrsta lagi er verið að þróa melhveiti sem nýja blendingstegund. En þar sem fyrsta kynslóð tegundablendinganna er einlitna (haploid), og því ófrjó, er efnafræðilegum aðferðum beitt til að fá erfðamengið tvílitna (amphidiploid), þannig að plönturnar verði frjóar. Því næst eru plönturnar prófaðar og eiginleikar þeirra mældir með tilliti til ræktunar. Í öðru lagi er tegundablendingunum bakvíxlað við mel til að kynbæta melinn með korngæðum hveitisins, en þó þannig að harðgerðir eiginleikar melsins haldist ríkjandi í plöntunum. Mikið verk er því enn óunnið þangað til við getum átt von á að hægt verði að rækta mel til kornnytja eða sem fóður.

Í greininni verður nánar skýrt frá erfðafræðirannsóknum meltegunda og helstu kynbóta- og líftækniaðferðum. Gerð verður grein fyrir núverandi stöðu rannsókna á melhveiti og frá samstarfsrannsóknum sem tengjast þeim.

INTRODUCTION

Lymegrass is a common name used in this study to refer to two taxonomically related species: the octoploid, North-European *Leymus arenarius* (L.) Hochst. and the tetraploid, North-American *L. mollis* (Trin.) Pilger. The species belong to the tribe *Triticeae* (family *Poaceae*) which includes major cereal species as wheat, rye and barley.

Leymus was first recognized by Hochstetter (1848) as a distinct genus from *Elymus* L. *Leymus* (Melderis *et al.*, 1980; Barkworth and Atkins, 1984; Dewey, 1984; Löve, 1984) is a genus of about 30 species of perennials. Most species are rhizomatous, leaf blades strongly ribbed, spike (inflorescence) not disarticulating at maturity, spikelets one to many at a node, glumes unawned and usually lanceolate, florets 2–7 per spikelet, anthers 2.5–7 cm long, all species polyploids. Lymegrass (*L. arenarius*; *L. mollis*) is a perennial with long rhizomes, thick culms 0.5–2 m tall, spikes 12–35 cm long with 12–30 nodes, spikelets usually two per node, seeds numerous. Lymegrass seeds are considered large compared to those of other *Leymus* species: average naked seed is 10–17 mg in *L. arenarius* and 6–11 mg in *L. mollis*. The two lymegrass species are morphologically similar that it is often difficult to differentiate them. Whereas *L. arenarius* has strongly glaucous culms and leaves (covered with waxy or powdery bloom; bluish-green), *L. mollis* is usually green. *L. arenarius* has culms glabrous below the spike, occasionally with a small patch of short pubescence, whereas those of *L. mollis* are usually densely pubescent. However, the reliable differences are in the chromosome number (56 in *L. arenarius* and 28 in *L. mollis*; Löve and Löve, 1975), endospermal protein prolamins (Ahokas and Fredskild, 1991) and several molecular markers (Kesara Anamthawat-Jónsson, unpublished).

Natural habitats of lymegrass are diverse, occurring in coastal and inland areas, and including a wide range of soil types and climatic conditions. Lymegrass is particularly adapted to cold climates as reflected by its wide distribution in the Arctic-temperate regions (Bowden, 1957; Hultén and Fries, 1986). It has been used extensively for land reclamation purposes, especially to combat soil erosion (reviewed in Greipsson and Davy, 1994). This soil binding quality, together with its perennial habit, large seeds and tolerance to diverse environmental conditions, have made lymegrass attractive as a potential crop for farming in marginal habitats.

Although lymegrass has a long history of food and non-food uses, i.e. as grains for baking and hay for animal feed (Sigurbjörnsson, 1960; Griffin and Rowlett, 1981; Klebesadel, 1985), its present cultivation would not be practical or economically justifiable. The aim of our research is therefore to improve lymegrass, using the genetic resources of wheat to address the shortcomings by means of chromosome transfer via wide-hybridization between wheat and lymegrass. The hybrids are being used in the back-crossing programme designed to fix certain crop characters such as grain and fodder quality, yield, characters manageable by mechanical harvest, and genetic stability. The long-term aim is to convert lymegrass into a viable grain and/or fodder crop in habitats which are not suitable for conventional cereals. The wide-hybrids are also valuable as a means to incorporate new genes into wheat making the crops more adaptable and reliable in diverse environments.

GENETIC DIVERSITY OF LYMEGRASS

In order to make full and effective use of the potential of lymegrass, it is essential to assess the extent of genetic resources and the level of genetic variation between and within the different lymegrass populations.

Lymegrass is a valuable genetic resource of the Arctic-temperate regions and can serve as a gene pool for cereal crop improvement. Several collections have therefore been made in the past, including 35 accessions maintained by the Icelandic Agricultural Research Institute, 7 accessions in the US Germplasm collection at Logan, Utah, and a number of further accessions maintained in Europe. Some evaluation of the materials has been made, especially with respect to cultivation and adaptation of lymegrass (Helgadóttir, 1993), disease resistance and other characters for wheat improvement (Merker, 1992a).

Using the existing Icelandic *L. arenarius* accessions, we are examining the genetic diversity at molecular level, using DNA profiling techniques, in particular PCR-based methods and micro-satellite analysis. DNA has been isolated from individual seeds collected from open-pollinated populations. Random oligo-primers have been used to amplify the seed genomic DNA, following the standard method of Williams *et al.* (1990), and we now have established about ten primers that detect polymorphisms within and between lymegrass populations (Birkir Þór Bragason and Kesara Anamthawat-Jónsson, unpublished). The molecular markers will be analyzed statistically to get an estimation of genetic distance within and between accessions, in a form of a dendrogram where “diversity” and “relatedness” are quantified using cluster analysis of similarity coefficients and principal component analysis. The method would be similar to those used to estimate genetic diversity based on RFLP (Restriction Fragment Length Polymorphism) data in wheat (Siedler *et al.*, 1994) and oilseed rape (Diers and Osborn, 1994). The molecular diversity data are also useful for breeding because the markers can be mapped, allowing identification of important genes.

At the interspecific level, the diversity can also be examined by cytogenetic methods. Large seed *Leymus* includes three main species: the northern European lymegrass (*L. arenarius*), the northern American lymegrass (*L. mollis*) and the central Eurasian *L. racemosus*. Although these species have distinct centres of diversity (Hultén and Fries, 1986), their geographical distributions are wide spread and the species boundaries overlap. For example, some populations of *L. arenarius* reach central Europe, and the species is further extended to southern Europe by introduction. In these margins, *L. arenarius* populations are likely to come into contact with those of *L. racemosus* and exchanges of genetic material can occur. On the north-western boundary of *L. arenarius*, the populations overlap with those of *L. mollis* in Greenland, where *L. arenarius* was probably introduced for cereal growing purpose during the Norse period (Ahokas and Fredskild, 1991). There, the hexaploid lymegrass, having the chromosome number of interspecific hybrid between *L. arenarius* and *L. mollis*, has often been identified. Such hybrids are carriers for gene transfer between species, and therefore cytogenetic and molecular studies of these natural *Leymus* hybrids will give insights into the level of gene flow in association with the environments.

Lymegrass species are allopolyploids consisting of genomes presumably deriving from two different ancestral species, one of which is a related perennial grass in the genus *Psathyrostachys*, but the other is of an unknown origin (Wang and Jensen, 1994; Sun *et al.*, 1994; Wang *et al.*, 1995). The work is now concentrated on isolating genome-specific

DNA probes (Anamthawat-Jónsson and Heslop-Harrison, 1993) and using them to characterize different lymegrass species and hybrids. A recent study by Ørgaard and Heslop-Harrison (1994) indicated many chromosomal regions where the DNA sequences of *Leymus* and *Psathyrostachys* have been evolutionarily diverged. Such sequences, when isolated, will be useful for detecting changes that have occurred between the different *Leymus* genomes and between closely related species. The understanding of genomic relationships will help reveal mechanisms underlying the lymegrass diversity.

WIDE-HYBRIDIZATION AS A BREEDING STRATEGY

The use of wide- (interspecific and intergeneric) hybridization as a method for crop improvement is long-established and widely practised. Its significance was emphasized for the first time in Denmark by Winge (1917) and was later realized by the successful artificial synthesis of tobacco *Nicotiana digluta* (Clausen and Goodspeed, 1925) and a few other dicoteledonous species. With the discovery of the colchicine technique (Blakeslee and Avery, 1937; Nebel and Ruttle, 1938), it became possible for plant breeders to repeat nature's process of wide-hybridization and chromosome doubling. In the cereal group, triticale (× *Triticosecale* Wittmack), deriving from crosses between wheat and rye (reviewed in Gupta and Priyadarshan, 1982), has been the most successful synthesized "amphiploid" (amphidiploid, wide-hybrid after chromosome doubling). A collection of over 1000 accessions and cultivars of triticale is maintained world-wide. Triticale is a common cereal crop and some of the new cultivars yield more than wheat.

Apart from triticale, wide-hybrids have not found a direct use in agriculture, but they are the foundation material for the many introgression lines used in wheat improvement (Sharma and Gill, 1983; Gale and Miller, 1987; Jiang *et al.*, 1994). The 1B/1R translocation (Zeller, 1973; Mettin *et al.*, 1973), a centric fusion of the long arm of wheat chromosome 1B and the short arm of rye chromosome 1R, has been exploited in wheat. These cultivars are known for their high yield and good disease resistance (Merker, 1982). Many wheat breeding lines have been developed from wide-hybrids between wheat and a great number of its wild relatives. Desirable characters from the wild species have been integrated into wheat, especially disease resistance, for example leaf rust resistant gene from *Agropyron intermedium* chromosome 7A (Friebe *et al.*, 1993) or nematode resistance from *Hordeum chilense* (Person-Dedryver *et al.*, 1990). Quality characters are also targeted, such as an exceptionally high molecular weight glutenin present in *Aegilops umbellulata* which should be useful for improving wheat bread-making quality (Law and Payne, 1983).

Wide-hybridization is the first step in the long process of production of breeding lines with alien gene or chromosome transfers. The hybrids are either made amphiploids before back-crossing them with wheat (standard method, O'Mara, 1940) or the F1 hybrids enter the back-crossing directly which is much less time-consuming (Islam *et al.*, 1978). From the back-crossed progeny, sets of chromosome addition and substitution lines are produced, and these are used as bridge materials to generate chromosome translocation lines (Gale and Miller, 1987; Lukaszewski, 1988; Jiang *et al.*, 1994). As this breeding strategy is used widely to transfer alien characters into crops, it is also promising for the transfer of crop characters into the wild species. The wide-crossing strategy has already been used to domesticate wild oat species by transferring from common oat the crop characters of non-shedding spikelets (Ladizinsky, 1995). The present collaborative research involves wide-hybridization between wheat and lymegrass with the aim of using the wide-hybrids to improve both parental species. Here at the Icelandic Agricultural Research Institute, the wide-hybrids are made as the first step to improve lymegrass for agricultural uses, while at the Swedish Agricultural University, similar wide-hybrids are used for wheat improvement.

The wide-hybridization strategy is seen as a realistic method for wheat and lymegrass breeding. The procedure is well-established with strong research background and the results are predictable. Genes underlying the success of the process have been identified and most can be cytogenetically manipulated. The bread wheat parent used in the present study, for example, is a specific cytogenetic stock in which chromosome 5B from cv. Chinese Spring has been substituted into a good quality spring wheat cv. Sicco (Snape *et al.*, 1986). This added chromosome carries the crossability promoting gene *kr1* (Riley and Chapman, 1967). Genes involved in the production of successful chromosome transfers such as homoeologous chromosome pairing genes (Riley *et al.*, 1968), gametocidal genes (Endo, 1990) and preferentially transmitted "cookoo" quality genes (Miller *et al.*, 1982) have been studied. Major determinants of high bread-making quality in bread wheat, glutenin and gliadin genes, are located on wheat chromosome homoeologous groups 1 and 6 and especially on 1D, 1B, 6A (Rogers *et al.*, 1990), and therefore these chromosomes are targeted in our lymegrass breeding plan. Methods for detection of chromosome transfers have also been developed and are routinely applicable (Anamthawat-Jónsson *et al.*, 1990; Schwarzacher *et al.*, 1992; Anamthawat-Jónsson and Reader, 1995). The laboratory and field experiments are standard and pose no adverse environmental or social impacts.

The direct gene transfer technology, on the other hand, is not ready for use in the breeding application described here. Although transformation protocols for cereal species have been reached and fertile transgenic plants have finally been made (wheat: Bialy, 1992; Vasil *et al.*, 1992, 1993; barley: Funatsuki *et al.*, 1995), we still face considerable difficulties in transferring agronomically important traits. Because wheat and lymegrass, unlike rice, have large genomes with many repetitive sequences, the plants are often recalcitant to tissue culture and can not be routinely transformed or regenerated. The fundamental problems with these species are not so much in the delivery or in the integration of the introduced DNA, but rather in the establishment of long-term cultures from which transgenic plants can be recovered efficiently. A rapidly growing long-term wheat suspension culture, probably not regenerable, has been found to be highly unstable karyotypically (Leitch *et al.*, 1993), i.e. high incidence of chromosome rearrangements and loss of DNA, and this is likely to be associated with its large genome size.

Furthermore, the gene isolation for cereal species is still in an infant stage. Most genes controlling morphological adaptive or disease resistance traits are likely to be complex – the characters are the cumulative result of one or more biochemical pathways, each with several steps controlled by independent single genes. Research on comparative genome mapping has shown that such genes, unlike RFLP markers (Gale *et al.*, 1995), may not exhibit strict conservation and colinearity between species, meaning that gene isolation requires the development of gene tagging strategies to isolate species-specific alleles (Moore *et al.*, 1993). No endogenous transposable element system, like that used in gene tagging in *Arabidopsis* or maize, has yet been discovered. Clearly this direct gene technology approach is unlikely to be applicable to the breeding of a wild species with such little economic importance as lymegrass.

WHEAT × LYMEGRASS HYBRIDS

Over 200 wheat × lymegrass F1 hybrids have been produced (Anamthawat-Jónsson *et al.*, 1996). Most of the hybrids (93%) were made in 1994 from crosses conducted in a growth room using a temperature regime of 15°C/13°C (16 h day/8 h night). Two wheat species were used as female parent in the crosses with two lymegrass species. The wheat parents were (1) a cytogenetic stock of bread wheat (*Triticum aestivum*, hexaploid, 2n=6x=42), spring variety Sicco (CS 5B) containing the crossability gene *kr1* and (2) *T. carthlicum* (tetraploid Persian wheat, 2n=4x=28) which has been reported to produce spontaneous chromosome doubling in wide-crosses (Fukuda and Sakamoto, 1992). The lymegrass pollen donors were *L. arenarius* (octoploid, 2n=8x=56, from a wild stand in Seltjarnarnes, Iceland) and *L. mollis* (tetraploid, 2n=4x=28, plants collected in Alaska by Óli Valur Hansson in 1985).

The crossing procedure followed that of Laurie and Bennett (1986), with the help of plant hormones gibberellic acid (50 ppm spray) before and after pollination, and 2,4-D (2,4-dichloro-phenoxyacetic acid, 20 mg l^{-1} injection) to facilitate fertilization and ovary development. The embryos were rescued onto tissue culture medium (Murashige & Skoog with Gamborg's vitamins, 2% sucrose, 0.9% agar). The seedlings (Figure 1) were transferred to soil (Figure 2). When the plants were well established, they were treated with colchicine (5 h root immersion in 0.05% colchicine, 1.5% DMSO, 1 drop/100 ml Tween 20) in an attempt to double the chromosome complement.

The overall frequency of embryo formation from these wheat × lymegrass crosses is considered very high (20% of the ovaries), and furthermore, almost all (96%) of the embryos have developed into hybrid plants. Similar crosses between species of *Triticum* and *Leymus* have been less successful, generally less than 1% (Ahokas, 1970; Mujeeb-Kazi *et al.*, 1984; Plourde *et al.*, 1989), while in a few cases the seed set was close to 10% (Thomas *et al.*, 1981; Comeau *et al.*, 1985)

Figure 1. The embryo culture. From right to left: newly excised hybrid embryo on a culture medium at 14 days after pollination (arrowed), germinating embryo, embryo becoming a hybrid plant, and a developed hybrid with shoot and root at about two months after embryo rescue.

1. mynd. Kímrækt. Lengst til hægri er nýmyndað tegundablendingskím í vefjarækt, aðeins um 14 dögum eftir frævun (ör). Þar við hliðina er spírandi kím, því næst er spírandi kím orðið að plöntu og lengst til vinstri er blendingurinn kominn með stöngul og rætur eftir um tvo mánuði frá kímbjörgun.

Figure 2. The hybrids transferred from embryo culture medium to soil and maintained in a growth room with a temperature regime of 15°C/13°C (16 h/day).

2. mynd. Búið er að flytja tegundablendingana úr kímræktinni yfir í gróðurmold og þeir ræktaðir í klefa við 15°C/13°C dags-/næturhita með 16 klst. lýsingu á sólarhring.

Figure 3. A hybrid plant from *T. aestivum* × *L. mollis* cross, showing vigorous vegetative growth with many tillers.

3. mynd. Tegundablendingur af víxlunum T. aestivum × L. mollis *með marga sterklega og vel vaxna sprota.*

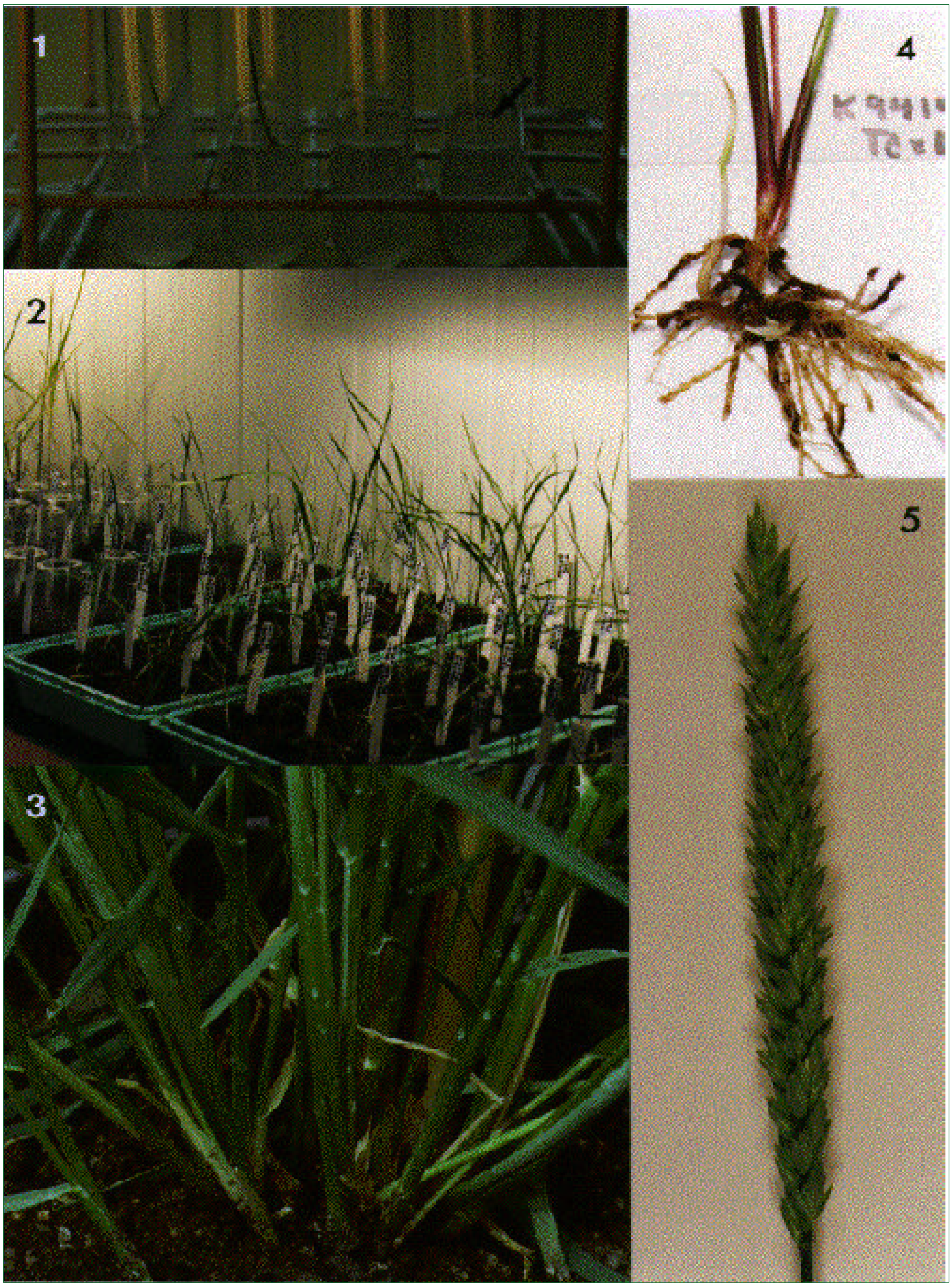
Figure 4. A hybrid from *T. carthlicum* × *L. arenarius* cross, showing rhizomatous habit with new shoots and roots.

4. mynd. Tegundablendingur af víxlunum T. carthlicum × L. mollis *með jarðstöngul (rhizome) sem leiðir af sér nýja stöngla og nýjar rætur.*

Figure 5. A spike of *T. aestivum* × *L. mollis* hybrid, about half the actual size. Several florets are open for pollination and there the ovaries and anthers can be seen.

5. mynd. Kornax blendinga T. aestivum × L. mollis *er um helmingur af raunverulegri stærð. Nokkur blóm eru opin til frævunar og þar er hægt að sjá frævur og fræfla.*

and there the wheat parents were known to have good crossability. The success of the present crosses is due to a combination of the following factors: the choice of wheat parents, the environmental conditions during crossing and the crossing method.



The wheat × lymegrass hybrids grew vigorously and tillered profusely (Figure 3). On fertilized soil in the field at Keldnaholt, a hybrid produced as many as 40 tillers and about half of them produced spikes. The hybrids appeared to be intermediates between the parental species in many morphological characters including shape, colour and stiffness of the leaves, spike architecture and growth habit. The plants had large, green leaves which were much less stiff than the lymegrass leaves. The culms were robust and thick, and the plants reached about 1–1.5 m in height at flowering in the field. The hybrids showed rhizomatous growth (Figure 4) and appeared to have a perennial habit. Unlike the parents, however, the hybrids showed indeterminate growth, allowing extensive propagation by layering or node-cloning (Koebner *et al.*, 1995). The hybrids deriving from the bread wheat reached flowering 6–10 months after embryo rescue, while those from the tetraploid wheat parent have not yet flowered after 16 months. The spikes were 10–25 cm long, having 25–30 nodes, 1–2 spikelets per node, and each spikelet normally had 2–6 florets (Figure 5). The ovaries and stigmas appeared to be well-developed, anthers were non-dehiscent but contained a few normal pollen. Indeed self-pollinated seeds have already been produced. Initial back-crossing of the hybrids with lymegrass pollen produced well-developed caryopses which is a good sign of normal ovary development. Although no embryo has been rescued from these few spikes, the success of further back-crossing is promising as a large number of hybrid plants are available.

F1 wide-hybrids are universally sterile because they carry an unbalanced chromosome set. However, a very small frequency of unreduced gametes exists, and this is valuable for the direct back-crossing as normal embryo formation can occur. Tsitsin (1965), Mujeeb-Kazi and Rodriguez (1981) and Plourde *et al.* (1989) obtained a few back-crossed progeny with wheat following embryo rescue, presumably from unreduced female gametes in the F1 wheat and Asian *Leymus* hybrids. Some hybrids between bread wheat and *Thinopyrum* species showed unusually high pollen (18–42%) and seed (3–29%) fertility (Jauhar, 1995), possibly because the *Thinopyrum* genotypes or the interaction between the parental genotypes in the hybrids inactivated the major homeologous pairing suppressor (*Ph1* allele) in wheat. The study of meiotic chromosome pairing in the present wheat and lymegrass hybrids is required to estimate the level of fertility. A further manipulation may be necessary, for example using specific wheat genotypes lacking chromosome pairing suppressor genes (Merker, 1992b), or using irradiation treatments.

The more common method of restoring fertility is by treating the F1 hybrids with the chromosome doubling agent colchicine, converting the hybrids into amphiploids with self-fertility. The present hybrid plants have been treated with colchicine and chromosome analysis reveals chromosome mosaics in the root meristem cells – for example, the *T. aestivum* × *L. mollis* hybrids has both haploid (35 chromosomes: 21 wheat + 14 lymegrass) and diploid (70 chromosomes) cells. Such sectors of diploid cells when occurring in the germ lines would be sufficient to start the F2 generation, after which the self-fertility will increase and eventually lead to the production of fertile hybrids suitable for cultivation like the triticale. Alternatively, these amphiploids can be used for back-crossing. Here an old partial amphiploid containing 30 wheat and 12 lymegrass chromosomes (obtained from B.S. Gill, Wheat Genetics Center, Kansas State University, USA) has already been back-crossed successfully with *L. mollis* pollen (Kesara Anamthawat-Jónsson, unpublished). The back-crossed progeny are very strong with vigorous vegetative growth and long rhizomes. Most interestingly, spontaneous chromosome doubling has been observed in these plants, meaning that fertility can be expected and the prospect of transferring characters between species is indeed realistic.

THE AGRICULTURAL POTENTIAL

The potential applications of wheat × lymegrass wide-hybrids are three-fold: (1) development of lymegrass as a grain and/or fodder crop for northern latitudes, (2) exploitation of the hybrids as a new perennial fodder and biomass crop adapted to cold environments, and (3) transfer of disease resistance and stress tolerance genes from lymegrass to wheat. This has been initiated as a collaborative project, with A. Merker (Swedish Agricultural University), R.M.D. Koebner (John Innes Centre, UK) and D.G. Christian (Rothamsted Experimental Station, UK).

(1) Lymegrass (*L. arenarius*; *L. mollis*) is suitable for cultivation in the northern latitudes where climatic conditions do not allow conventional cereal crops. Field trials in Iceland, for example, confirm that even winter-hardy wheat and triticale do not mature to grain-harvesting stage (Sveinsson, 1993), whereas barley can be grown in certain regions (Hermannsson, 1993). Lymegrass, on the other hand, is highly adapted to marginal habitats such as eroded, low fertility, saline and alkaline soils, but at present lymegrass is not domesticated. The semi-cultivation in Iceland is primarily aimed for seed production for land reclamation. Given improvement, through back-crossing of wheat × lymegrass hybrids with the wild parent as described above, lymegrass has a potential as a low input, environmentally sensible crop. The characters which need attention include (a) perennial growth, (b) production of high quality grain, (c) easily threshed grain, (d) manageable grain size (2 mg and more), (e) synchronous seed maturity, (f) shatter resistance, (g) strong and non-lodging seed stalks, (h) high potential for mechanical harvest, (i) acceptable yield, (j) sufficient genetic variability to facilitate selection of desirable types and (k) meiotic stability.

(2) The wheat × lymegrass hybrids are perennial, winter-hardy and vigorous, but to date sterile plants. In certain circumstances, this sterility is desirable as the plant continues to produce vegetative tissue. This has advantages for both fodder production and biomass crops. As for fodder, the hybrids will be analyzed for its quality, nutritional values and digestibility, using laboratory measurements (Brown *et al.*, 1990) and feeding experiments (Guðmundsson, 1993). As for biomass option, the hybrids will be assessed for the suitability of gasification by chemical analyses and combustion tests, in comparison to other conventional (coal, peat) and biomass (*Phalaris*, *Miscanthus*, *Salix*) materials. Although bioenergy accounts for 15% of primary world energy usage, the equivalent usage in Europe is only 4% (Scurlock *et al.*, 1993). Various candidate plant species are being considered, both woody and herbaceous, but their cultivation seems to be limited by high investment and operation cost, poor adaptability, or it requires specialized equipment. There is thus a place for the development of a cold tolerant, perennial, non-woody biomass crop, as wheat × lymegrass hybrids should be able to offer.

(3) The wheat × lymegrass hybrids can be used to widen the genetic base of the wheat crop. The hybrids produced to date have shown a good level of genetic resistance to wheat pathogens, and therefore represent a novel source of genes for disease resistance. New genes are in constant demand, since the pathogens have the ability to create virulent races through recombination or mutation. The *Leymus* gene pool is rich in desirable characters for crop improvement. Asian *Leymus* species such as *L. racemosus*, *L. multicaulis* and *L. angustus* have been targeted, on account of their tolerance to high salinity and drought (McGuire and Dvôrák, 1981; Gorham *et al.*, 1984; Dewey, 1984) and resistance to virus diseases (Plourde *et al.*, 1989, 1992). Some wheat lines containing these *Leymus* chromosomes have been identified (Mujeeb-Kazi

et al., 1983; Dong *et al.*, 1986). In this context, lymegrass (*L. arenarius*; *L. mollis*) has been exploited to a very limited extent in wheat breeding. Lymegrass carries resistance against wheat diseases such as mildew and rusts (Fatih, 1983; Merker, 1992a). Furthermore, the spike architecture of lymegrass, with big spikes having numerous florets per node, is an interesting character to transfer to wheat because it gives an opportunity to influence yield. The wheat × lymegrass hybrids would allow transfers of such traits to crops, via back-crossing with wheat, making wheat more adapted to systems with low input of chemicals. A large population of back-crossed progeny has already been produced (Arnulf Merker, unpublished), from an old partial amphiploid line derived from crosses by Tsitsin (1965). These plants will be tested for the presence of resistance and other desirable lymegrass characters, and the offspring will be used for future production of homozygous lines and cultivars.

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