

Chapter 2

Agropyron and Psathyrostachys

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2.1 Introduction

Wheatgrass and wildrye grasses are some of the most important grasses in the temperate regions of the world (Asay and Jensen 1996a, b). These drought-resistant grasses are excellent sources of forage and habitat for livestock and wildlife; and they are valued for weed control, habitat use, soil stabilization, and watershed management. Many of these grasses are related to and have been hybridized with cultivated cereal crops including wheat (*Triticum aestivum* L. and *T. durum* Desf.), barley (*Hordeum vulgare* L.), and rye (*Secale cereale* L.) as genetic sources for disease resistance, salinity tolerance, and other traits. These hybrids were summarized in several early review articles (Sharma and Gill 1983; Dewey 1984; Wang 1989a). Since then, certain specific subjects of alien gene transfer from wild Triticeae into wheat have been extensively reviewed and discussed (Knott 1989; Pienaar 1990; Jiang et al. 1994b; Friebe et al. 1996; Fedak 1999; Jauhar and Chibbar 1999; Repellin et al. 2001; Sahrawat et al. 2003; Jauhar 2006; Qi et al. 2007; Trethowan and Mujeeb-Kazi 2008).

The taxonomy of the wheatgrass and wildrye grasses has been the object of considerable controversy. Even with the advent of molecular phylogenetics, Kellogg (2006) stated that “generic relationships within Triticeae have always been and remain problematic.” In North America, the wheatgrasses traditionally have

been included in the genus *Agropyron*, and the wildryes have largely been treated as species in the genus *Elymus* (Bowden 1965; Hitchcock 1971). Depending on how the genus *Agropyron* was treated, the number of species in this genus varied. Benthams (1882) included about 20 species in *Agropyron*, whereas Hackel (1887) listed 32 species. More recently, however, taxonomic realignments have been proposed that are based on genomic or biological relationships as well as plant morphology (Tsvelev 1976; Dewey 1984; Yen et al. 2005b). Dewey (1984) proposed that *Agropyron* be restricted to species of the crested wheatgrass complex, a polyploid series based on the **P**-genome. Thus, bluebunch wheatgrass, previously *A. spicatum* (Pursh) Scribner & Smith, and related species based on the **St**-genome are now included in the genus *Pseudoroegneria* A. Löve. Tall wheatgrass and intermediate wheatgrass are now included in the genus *Thinopyrum* A. Löve as *Th. ponticum* (Podp.) Barkworth & D.R. Dewey and *Th. intermedium* (Host) Barkworth & D.R. Dewey, respectively. Species in this genus possess the **J**- or **E**-genome, which Dewey (1984) designated as “**J** = **E**,” and sometimes also contains the **St**-genome (Liu and Wang 1993; Kishii et al. 2005). Slender wheatgrass, previously *A. trachycaulum* (Link) Malte ex H.F. Lewis, and its self-fertile caespitose relatives are in the genus *Elymus* along with several wildryes. This genus is based on the **St**-genome, in combination with one or more of **H**-, **Y**-, **W**-, or **P**-genomes (Wang et al. 1995).

Depending on the taxonomic treatment, between 200 and 250 wheatgrass and wildrye species have been described worldwide (Asay and Jensen 1996a, b). More than two-thirds are native to Eurasia and about 22 to 30 are considered native to North America.

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Relatively few species are found in South America, New Zealand, Australia, and Africa. The wheatgrass and wildrye grasses are generally adapted to subhumid to arid climatic conditions in steppe or desert regions. In North America, the wheatgrass and wildrye grasses are most prevalent in the northern Great Plains, as well as on the semi-arid to arid rangelands of the Intermountain and Great Basin Regions. In their natural setting, wheatgrass and wildrye grasses are most often found in association with other grasses, sedges, forbs, and shrubs.

The genus *Agropyron* Gaertner belongs to the tribe Triticeae, which is composed of about 20 genera and 400–500 species (Löve 1884). Although it is now agreed by taxonomists that *Agropyron* should be restricted to *A. cristatum* and its close relatives, for this review, *Agropyron* will be used to include species in the genera *Australopyrum* (Tzvelev) A. Löve, *Dasyphyrum* (Coss. & Durieu) T. Durand, *Elymus* Linnaeus, *Leymus* Hochstetter, *Pascopyrum* A. Löve, *Pseudoroegneria* (Nevski) A. Löve, and *Thinopyrum* A. Löve, etc. Some of these genera are not widely accepted by taxonomists. There is even less agreement on how their members should be treated. As a result, most Triticeae species had one or more synonyms, indicating that they were placed in the past by taxonomists in the genus *Agropyron* (Table 2.1). On the other hand, *Psathyrostachys* Nevski is a small genus with about 10 species that were formerly treated in genera *Elymus* and *Hordeum* (Quattrocchi 2006; Table 2.2).

Wheatgrasses and wildryes have been mainly used as forage crops (Wang and Jensen 2009). They are also served as the tertiary gene pool for wheat improvement (Dewey 1984; Mujeeb-Kazi and Wang 1995). Because species of various known genome constitutions in the perennial Triticeae (i.e., P, St, Ns, E, ESt, StH, StY, StHY, StWY, and NsXm, etc. as designated by Wang et al. 1995) have been successfully crossed with wheat (Jiang et al. 1994b), all species in the genera *Agropyron*, *Pseudoroegneria*, *Psathyrostachys*, *Thinopyrum*, *Elymus*, and *Leymus* are theoretically capable of being hybridized with wheat. Hybrids, natural or man-made, between wheat and these species had been generally called *Agrotricum*. The use of wheatgrasses and wildryes as forage crops had been recently reviewed (Wang and Jensen 2009). Thus, only the contribution of specific wheatgrass and wildrye species to wheat improvement will be reviewed in this chapter.

2.2 Basic Botany

2.2.1 Morphology

Wheatgrass encompasses five genera of Triticeae and wildrye species belong to three genera (Table 2.1); thus their morphological features are highly variable. Brief descriptions of morphology for some important wheatgrass and wildrye grasses were provided in the previous reviews (Asay and Jensen 1996a, b). More detailed morphological descriptions for *Agropyron*, *Pseudoroegneria*, *Psathyrostachys*, *Elymus*, *Leymus*, *Thinopyrum*, and *Pascopyrum* can be found in the *Flora of North America, Volume 24* (Barkworth et al. 2007). With the advent of internet, people can now find the required information on these grasses or crops by visiting the websites housing the “Catalogue of New World Grasses (Poaceae)” (Soreng et al. 2000 onwards), “Flora of China, Volume 22” (Wu and Raven 2004), and the “GrassBase – The Online World Grass Flora” (Clayton et al. 2006 onwards). These interactive electronic databases are valuable resources for taxonomic nomenclature, geographical distributions, and other pertinent information of any species of interest to the visitors.

2.2.2 Distribution

Based on “Flora of North America, Volume 24” (Barkworth et al. 2007) and “Flora of China, Volume 22” (Wu and Raven 2004), geographic distributions of perennial Triticeae species are presented in Tables 2.3 and 2.5.

2.2.2.1 *Agropyron* *Senso Stricta*

Crested wheatgrass is indigenous to the Steppe region of European Russia and southwestern Siberia, and it was apparently cultivated initially in the Volga district east of Saratov (Kirk 1932). This genus comprises 10 to 15 species, of which *A. cristatum* and *A. fragilie* have been introduced and widely cultivated in North America and five species (one endemic) are found in China.

The tetraploid form of crested wheatgrass is the most common of the three crested wheatgrass ploidy

Table 2.1 Examples of Triticeae species that had ever been included in the genus *Agropyron* or other genera. Species that had been hybridized with wheat are in bold-face

Current scientific name	Synonym
<i>Agropyron badamense</i> Drob.	<i>Agropyron desertorum</i> aucto., non Schultes & Schultes
<i>Agropyron cimmericum</i> Nevski	<i>Agropyron dasyanthum</i> subsp. <i>birjutczenae</i> (Lavr.) Lavr.
<i>Agropyron cristatum</i> (L.) Beauv.	<i>Bromus cristatus</i> L.; <i>B. distichus</i> Georgi; <i>Triticum pumilum</i> L.f.
<i>Agropyron dasyanthum</i> Ledeb.	<i>Triticum dasyanthum</i> (Ledeb.) Sprengel
<i>Agropyron desertorum</i> (Fischer ex Link) Schultes	<i>Triticum desertorum</i> Fischer ex Link
<i>Agropyron fragile</i> (Roth) Candargy	<i>Agropyron sibiricum</i> (Willd.) Beauv.; <i>Triticum fragile</i> Roth; <i>T. sibiricum</i> Willd.
<i>Agropyron krylovianum</i> Schischk.	<i>Elytrigia kryloviana</i> (Schischk.) Nevski
<i>Agropyron michnoi</i> Roshevitz	–
<i>Agropyron mongolicum</i> Keng	–
<i>Agropyron pumilum</i> Candargy	<i>Triticum pumilum</i> Steudel, non L.
<i>Agropyron tanaiticum</i> Nevski	–
<i>Australopyrum pectinatum</i> (Labillardiere) A. Löve	<i>Agropyron pectinatum</i> (Labillardiere) P. Beauv.; <i>A. brownei</i> (Kundt) Tzvelev
<i>Dasyphyrum villosum</i> (L.) Candargy	<i>Agropyron villosum</i> (L.) Link; <i>Haynaldia villosa</i> (L.) Schur
<i>Elymus alaskanus</i> (Scribner & Merr.) A. Löve subsp. <i>alaskanus</i>	<i>Agropyron boreale</i> (Turcz.) Drobov
<i>Elymus alaskanus</i> subsp. <i>latiglumis</i> (Scribner & J.G. Sm.) A. Löve	<i>Agropyron latiglume</i> (Scribner & J.G. Sm.) Rydb
<i>Elymus alatavicus</i> (Drobov) A. Löve	<i>Agropyron alatavicum</i> Drobov
<i>Elymus angulatus</i> J. Presl in C. Presl	<i>Agropyron brevistaristatus</i> Hitchc.
<i>Elymus antiquus</i> (Nevski) Tzvelev	<i>Agropyron antiquus</i> Nevski; <i>A. microlepis</i> Bor
<i>Elymus arizonicus</i> (Scribn. & J.G. Smith) Gould	<i>Agropyron arizonicum</i> Scribner & Smith
<i>Elymus batalinii</i> (Krasn.) A. Löve	<i>Agropyron batalinii</i> (Krasn.) Roshev.
<i>Elymus burchan-buddae</i> (Nevski) Tzvelev	<i>Agropyron burchan-buddae</i> Nevski
<i>Elymus canaliculatus</i> (Nevski) Tzvelev	<i>Agropyron canaliculatum</i> Nevski
<i>Elymus caninus</i> (L.) L.	<i>Agropyron caninum</i> (L.) P. Beauv.; <i>A. alpinum</i> Schur.; <i>A. pauciflorum</i> Schur.
<i>Elymus caucasicus</i> (C. Koch) Tzvelev	<i>Agropyron caucasicum</i> (C. Koch) Grossh.; <i>A. roegneri</i> (Griseb.) Boissier
<i>Elymus ciliaris</i> (Trin.) Tzvelev	<i>Agropyron ciliare</i> (Trin.) Franch.
<i>Elymus dolichatherus</i> (Keng) A. Löve	<i>Roegneria dolichatera</i> Keng
<i>Elymus drobovii</i> (Nevski) Tzvelev	<i>Agropyron drobovii</i> Nevski; <i>A. turkestanum</i> Drobov
<i>Elymus ensyii</i> (Kirk) A. Löve & Connor	<i>Agropyron ensyii</i> Kirk; <i>A. aristatum</i> Cheeseman
<i>Elymus fibrosus</i> (Schrenk) Tzvelev	<i>Agropyron fibrosum</i> (Schrenk) Candargy
<i>Elymus formosanus</i> (Honda) A. Löve	<i>Agropyron formosanum</i> Honda
<i>Elymus glaucescens</i> Seberg	<i>Agropyron pubiflorum</i> (Steudel) Parodi; <i>A. antarcticum</i> Parodi
<i>Elymus gmelinii</i> (Ledeb.) Tzvelev	<i>Agropyron turczaninovii</i> Drobov
<i>Elymus grandiglumis</i> (Keng) A. Löve	<i>Agropyron grandiglume</i> (Keng) Tzvelev
<i>Elymus hyperarcticus</i> (Polunin) Tzvelev	<i>Agropyron boreale</i> var. <i>hyperarcticum</i> (Polunin) A. Löve & D. Löve
<i>Elymus jacquemontii</i> (Hooker f.) Tzvelev	<i>Agropyron jacquemontii</i> Hooker f
<i>Elymus kengii</i> Tzvelev	<i>Agropyron kengii</i> Tzvelev
<i>Elymus lanceolatus</i> (Scribner & Smith) Gould	<i>Agropyron lanceolatum</i> Scribner & Smith; <i>A. dasystachyum</i> (Hook.) Scribner
<i>Elymus longearistatus</i> (Boiss.) Tzvelev	<i>Agropyron longearistatum</i> (Boiss.) Boiss.
<i>Elymus mendocinus</i> (Parodi) A. Löve	<i>Agropyron mendocinum</i> Parodi
<i>Elymus multiflorus</i> (Banks & Solander ex Hook. f.) A. Löve & Connor	<i>Agropyron multiflorum</i> (Banks & Solander ex Hook. f.) Kirk ex Cheeseman
<i>Elymus mutabilis</i> (Drobov) Tzvelev	<i>Agropyron mutabilis</i> Drobov
<i>Elymus nipponicus</i> Jaaska	<i>Agropyron yezoense</i> Honda
<i>Elymus parodii</i> Seberg & G. Petersen	<i>Agropyron condensatum</i> J. Presl
<i>Elymus rectisetus</i> (Nees in Lehm.) A. Löve & Connor	<i>Agropyron youngii</i> (Hook. f.) Candargy

(continued)

Table 2.1 (continued)

Current scientific name	Synonym
<i>Elymus repens</i> (L.) Gould	<i>Agropyron repens</i> (L.) P. Beauv.
<i>Elymus scabriglumis</i> (Hackel) A. Löve	<i>Agropyron scabriglume</i> (Hackel) Parodi
<i>Elymus scabrus</i> (R. Br.) A. Löve	<i>Agropyron scabrum</i> (R. Br.) P. Beauv.
<i>Elymus semicostatus</i> (Nees ex Steud.) A. Löve	<i>Agropyron semicostatum</i> Nees ex Steud.
<i>Elymus stebbinsii</i> Gould	<i>Agropyron parishii</i> Scribner J.G. Smith
<i>Elymus subsecundus</i> (Link.) A. Löve & D. Löve	<i>Agropyron subsecundum</i> (Link) Hitchc.
<i>Elymus tianschanicus</i> (Drobov) Nevski	<i>Agropyron tianschanicum</i> Drobov; <i>Elymus tianschanigenus</i> Czerepanov;
<i>Elymus tibeticus</i> (Melderis) G. Singh	<i>Agropyron tibeticum</i> Melderis; <i>Roegneria tibetica</i> (Melderis) H. L. Yang
<i>Elymus trachycaulus</i> (Link) Gould ex Shinners	<i>Agropyron tenerum</i> Vasey; <i>A. violaceum</i> (Hornem.) Lange
<i>Elymus transhyrcanus</i> (Nevski) Tzvelev	<i>Agropyron transhyranicum</i> (Nevski) Bondartseva
<i>Elymus tsukushiensis</i> Honda	<i>Agropyron tsukushiensis</i> (Honda) Ohwi
<i>Festucopsis festucoides</i> (Maire) A. Löve	<i>Agropyron festucoides</i> Maire; <i>A. pseudofestucoides</i> Emb
<i>Festucopsis serpentini</i> (C.E. Hubbard) Melderis	<i>Agropyron kosanii</i> Cernjav. & Soska in Cernjav.
<i>Leymus chinensis</i> (Trin.) Tzvelev	<i>Agropyron chinense</i> (Trin.) Ohwi
<i>Leymus racemosus</i> (Lam.) Tzvelev	<i>Elymus giganteus</i> Vahl; <i>Leymus giganteus</i> (Vahl) Pilger
<i>Leymus ramosus</i> (Trin.) Tzvelev	<i>Agropyron ramosum</i> (Trin.) K. Richter
<i>Leymus secalinus</i> (Georgi) Tzvelev	<i>Agropyron chinorossicum</i> Ohwi; <i>A. berezovcanum</i> Prodan
<i>Pascopyrum smithii</i> (Rydb.) A. Löve	<i>Agropyron smithii</i> Rydberg; <i>A. occidentalis</i> (Scribner) Scribner
<i>Peridictyon sanctum</i> (Janka) O. Seberg, S. Frederiksen, & C. Baden	<i>Agropyron sanctum</i> (Janka) Hackel ex Formanek
<i>Pseudoroegneria cognata</i> (Hackel) A. Löve	<i>Agropyron cognatum</i> Hackel; <i>A. ferganense</i> Drobov; <i>A. dsungaricum</i> Nevski
<i>Pseudoroegneria geniculata</i> (Trin.) A. Löve	<i>Agropyron geniculatum</i> (Trin.) C. Koch
<i>Pseudoroegneria pertenuis</i> (C.A May.) A. Löve	<i>Agropyron pertenuis</i> (C.A May.) Nevsski
<i>Pseudoroegneria spicata</i> (Pursh) A. Löve	<i>Agropyron spicatum</i> (Pursh) Scribner & Smith; <i>A. divergens</i> (nees) Vasey;
<i>Pseudoroegneria stipifolia</i> (Czern. Ex Nevski) A. Löve	<i>Agropyron stipifolium</i> Czern. Ex Nevski
<i>Pseudoroegneria strigosa</i> (M. Bieb.) A. Löve	<i>Agropyron strigosum</i> (M. Bieb.) Boiss; <i>A. microcalyx</i> (Regel) Candargy
<i>Pseudoroegneria tauri</i> (Boiss. & Bal.) A. Löve	<i>Agropyron tauri</i> Boiss. & Bal.
<i>Thinopyrum bessarabicum</i> (Savul. & Rayss) A. Löve	<i>Agropyron bessarabicum</i> Savul. & Rayss
<i>Thinopyrum caespitosum</i> (C. Koch) Z.-W. Liu & R.-C. Wang	<i>Agropyron caespitosum</i> C. Koch; <i>Lophopyrum caespitosum</i> (c. Koch) A. Löve
<i>Thinopyrum elongatum</i> (Host) D.R. Dewey	<i>Agropyron elongatum</i> (Host) P. Beauv; <i>Triticum elongatum</i> Host; <i>Lophopyrum elongatum</i> (Host) A. Löve
<i>Thinopyrum intermedium</i> (Host) Barkworth & D.R. Dewey	<i>Agropyron intermedium</i> (Host) P. Beauv; <i>Elytrigia intermedia</i> (Host) Nevski
<i>Thinopyrum junceiforme</i> (A. Löve & D. Löve) A. Löve	<i>Agropyron junceum</i> ssp. <i>boreoatlanticum</i> Simonet & Guinochet
<i>Thinopyrum junceum</i> (L.) A. Löve	<i>Agropyron junceum</i> (L.) P. Beauv.
<i>Thinopyrum nodosum</i> (Nevski) D.R. Dewey	<i>Agropyron nodosum</i> Nevski; <i>Lophopyrum nodosum</i> (Nevski) A. Löve
<i>Thinopyrum ponticum</i> (Podp.) Barkworth & D.R. Dewey	<i>Agropyron elongatum</i> (Host) P. Beauv.; <i>Elytrigia pontica</i> (Podp.) Holub; <i>Lophopyrum ponticum</i> (Podp.) A. Löve
<i>Thinopyrum scirpeum</i> (K. Presl) D.R. Dewey	<i>Agropyron scirpeum</i> K. Presl; <i>Lophopyrum scirpeum</i> (K. Presl) A. Löve

levels, spanning the natural distribution range of the complex from central Europe and the Middle East across Central Asia to Siberia, China, and Mongolia (Tsvelev 1976; Dewey 1986). The diploids are distributed across the same range; however, they occur

much more sporadically. Although the hexaploids are rare, they are known to occur in Turkey, Iran, and Kazakhstan (Dewey and Asay 1975). Diploid, tetraploid, and hexaploid species in this genus are all based on the basic genome-**P**, thus forming a common gene

Table 2.2 Species in the genus *Psathyrostachys*. Species that had been hybridized with wheat are in bold-face

Current scientific name	Synonym	Agricultural status
<i>P. caduca</i> (Boiss.) Melderis	<i>Elymus caducus</i> Boiss.	—
<i>P. daghestanica</i> (Alexeenko) Nevski	<i>Elymus daghestanicus</i> Alexeenko; <i>Hordeum daghestanicum</i> (Alexeenko) Alexeenko	—
<i>P. fragilis</i> (Boiss.) Nevski subsp. <i>fragilis</i>	<i>Hordeum fragile</i> Boiss.; <i>Elymus fragilis</i> (Boiss.) Griseb.	—
<i>P. fragilis</i> subsp. <i>secaliformis</i> Tzvelev	<i>Elymus secaliformis</i> Trin. ex Steud.	—
<i>P. fragilis</i> subsp. <i>villosus</i> C. Baden	<i>Elymus junceus</i> var. <i>villosus</i> Drobov	—
<i>P. huashanica</i> Keng	—	Model plant
<i>P. juncea</i> (Fisch.) Nevski	<i>Elymus junceus</i> Fischer; <i>E. altaicus</i> Sprengel; <i>E. desertorum</i> Kar. & Kir.; <i>E. albertii</i> Regel	Forage
<i>P. juncea</i> var. <i>hyalanthus</i> (Rupr.) S.L. Chen	<i>Elymus hyalanthus</i> Rupr.	—
<i>P. kronenburgii</i> (Hack.) Nevski	<i>Hordeum kronenburgii</i> Hackel; <i>Elymus kronenburgii</i> (Hackel) Nikif.	—
<i>P. lanuginosa</i> (Trin.) Nevski	<i>Elymus lanuginosus</i> Trin.; <i>Hordeum lanuginosum</i> (Trin.) Schenk	Model plant
<i>P. perennis</i> Keng	—	—
<i>P. rupestris</i> (Alexeenko) Nevski	<i>Hordeum rupestre</i> Alexeenko	—
<i>P. stoloniformis</i> C. Baden	—	—

Table 2.3 Geographic distribution of some perennial Triticeae species. Species that had been hybridized with wheat are in bold-face

Current scientific name	Distribution	Agricultural status
<i>Agropyron badamense</i> Drob.	Central Asia	—
<i>Agropyron cimmericum</i> Nevski	Endemic to the Black Sea and Caucasus regions	—
<i>Agropyron cristatum</i> (L.) Beauv.	Eastern Europe, western Siberia, eastern Siberia, Far East, Mongolia, China	Forage
<i>Agropyron dasyanthum</i> Ledeb.	Eastern Europe, along the Dniepr and Molochnaya Rivers	—
<i>Agropyron desertorum</i> (Fischer ex Link) Schultes	Eastern Europe, Caucasus, western Siberia, Central Asia, Mongolia, China	Forage
<i>Agropyron fragile</i> (Roth) Candargy	Eastern Europe, Caucasus; western Siberia, Central Asia, Mongolia, China	Forage
<i>Agropyron krylovianum</i> Schischk.	Western Siberia, eastern Siberia, Central Asia	—
<i>Agropyron michnoi</i> Roshevitz	Eastern Siberia, Mongolia, China	—
<i>Agropyron mongolicum</i> Keng	China (Gansu, Nei Mongol, Ningxia, Shaanxi, Shanxi, Xinjiang)	Forage
<i>Agropyron pumilum</i> Candargy	Endemic to the banks of the Enisei River, eastern Siberia	—
<i>Agropyron tanaiticum</i> Nevski	Eastern Europe, endemic to the Volga and Don river basins	—
<i>Australopyrum pectinatum</i> (Labillardiere) A. Löve	Australia, New Zealand	—
<i>Dasyphyrum villosum</i> (L.) Candargy	Southern Europe to Turkey, the Crimea, Caucasus	Model plant
<i>Elymus alaskanus</i> (Scribner & Merr.) A. Löve subsp. <i>alaskanus</i>	Alaska, Canada (Yukon, Northwest Territories)	—
<i>Elymus alaskanus</i> subsp. <i>latiglumis</i> (Scribner & J.G. Sm.) A. Löve	Canada (Alberta, BC) USA (Alaska, Idaho, Washington, Montana, Wyoming)	—
<i>Elymus alatavicus</i> (Drobov) A. Löve	Kazakhstan, Kyrgyzstan, Tajikistan, Mongolia, China (Gansu, Xinjiang, Tibet)	—
<i>Elymus angulatus</i> J. Presl in C. Presl	Peru south to Tierra del Fuego, east to western Argentina and Bolivia	—
<i>Elymus antiquus</i> (Nevski) Tzvelev	Western and northwestern China, Nepal	—
<i>Elymus arizonicus</i> (Scribn. & J.G. Smith) Gould	USA (AZ, CA, NM, TX), Mexico	—
<i>Elymus batalinii</i> (Krasn.) A. Löve	China (Xinjiang, Tibet), Mongolia, Russia	Model plant

(continued)

Table 2.3 (continued)

Current scientific name	Distribution	Agricultural status
<i>Elymus burchan-buddae</i> (Nevski) Tzvelev	China, India, maybe in Nepal	—
<i>Elymus canaliculatus</i> (Nevski) Tzvelev	Alai, Iran, Kashmir, Pakistan, Pamir, Tadjikistan, Tibet	—
<i>Elymus caninus</i> (L.) L.	China, Kazakhstan, Kyrgyzstan, Russia, Turkmenistan, Uzbekistan; SW Asia, Europe	—
<i>Elymus caucasicus</i> (C. Koch) Tzvelev	Daghestan, Turkmenia, northern Iran	—
<i>Elymus ciliaris</i> (Trin.) Tzvelev	China, Japan, Korea, Mongolia, Russia	Model plant
<i>Elymus dolichatherus</i> (Keng) A. Löve	Southwestern China	—
<i>Elymus drobovii</i> (Nevski) Tzvelev	Asia-temperate: Soviet Middle Asia	—
<i>Elymus enysii</i> (Kirk) A. Löve & Connor	New Zealand	—
<i>Elymus fibrosus</i> (Schrenk) Tzvelev	Finland, Russian Federation	—
<i>Elymus formosanus</i> (Honda) A. Löve	Taiwan	—
<i>Elymus glaucescens</i> Seberg	Southern Chile and Argentina	—
<i>Elymus gmelinii</i> (Ledeb.) Tzvelev	China, Japan, Kazakhstan, Korea, Kyrgyzstan, Mongolia, Russia, Turkmenistan, Uzbekistan	—
<i>Elymus grandiglumis</i> (Keng) A. Löve	China (Qinghai)	—
<i>Elymus hyperarcticus</i> (Polunin) Tzvelev	USA (Alaska); Russia (Arctic)	—
<i>Elymus jacquemontii</i> (Hooker f.) Tzvelev	Western Tibet and the Himalayas, above 3,900 m	—
<i>Elymus kengii</i> Tzvelev	China	—
<i>Elymus lanceolatus</i> (Scribner & Smith) Gould	USA, Canada	—
<i>Elymus longearistatus</i> (Boiss.) Tzvelev	Gissar-Darvaz, Iran, Tadjikistan	Model plant
<i>Elymus mendocinus</i> (Parodi) A. Löve	Argentina (endemic around Mendoza)	—
<i>Elymus multiflorus</i> (Banks & Solander ex Hook. f.) A. Löve & Connor	New Zealand	—
<i>Elymus mutabilis</i> (Drobov) Tzvelev	Mongolia, Russia; C and SW Asia, Europe, China	—
<i>Elymus nipponicus</i> Jaaska	North and Northeast Asia	—
<i>Elymus parodii</i> Seberg & G. Petersen	Southern Brazil, Uruguay, and northern Argentina	—
<i>Elymus rectisetus</i> (Nees in Lehm.) A. Löve & Connor	Australia	Model plant
<i>Elymus repens</i> (L.) Gould	China, India, Japan, Korea, Mongolia, Russia; C and SW Asia, Europe	Weed
<i>Elymus scabriglumis</i> (Hackel) A. Löve	Argentina	—
<i>Elymus scabrus</i> (R. Br.) A. Löve	Australia	Model plant
<i>Elymus semicostatus</i> (Nees ex Steud.) A. Löve	Afghanistan, India, Nepal, Pakistan	—
<i>Elymus stebbinsii</i> Gould	California	—
<i>Elymus subsecundus</i> (Link.) A. Löve & D. Löve	USA, Canada	—
<i>Elymus tianschanicus</i> (Drobov) Nevski	China, Kazakhstan, Kyrgyzstan, Turkmenistan, Uzbekistan	—
<i>Elymus tibeticus</i> (Melderis) G. Singh	China (Tibet, Yunnan), Bhutan	—
<i>Elymus trachycaulus</i> (Link) Gould ex Shinnars	North America (USA, Canada, Mexico)	—
<i>Elymus transhyrcanus</i> (Nevski) Tzvelev	Iran and Central Asia	—
<i>Elymus tsukushiensis</i> Honda	China, Korea, Japan	—
<i>Festucopsis festucoides</i> (Maire) A. Löve	Morocco (High Atlas)	—
<i>Festucopsis serpentini</i> (C.E. Hubbard) Melderis	Albania	—
<i>Leymus chinensis</i> (Trin.) Tzvelev	China, Korea, Mongolia, Russia	Forage
<i>Leymus racemosus</i> (Lam.) Tzvelev	China (Xinjiang), Kazakhstan, Kyrgyzstan, Mongolia, Russia, Turkmenistan, Uzbekistan	Forage
<i>Leymus ramosus</i> (Trin.) Tzvelev	China (Xinjiang), Mongolia, Russia (W Siberia); Europe	—
<i>Leymus secalinus</i> (Georgi) Tzvelev	China, India, Japan, Korea, Kazakhstan, Kyrgyzstan, Mongolia, Russia, Turkmenistan, Uzbekistan	—

(continued)

Table 2.3 (continued)

Current scientific name	Distribution	Agricultural status
<i>Pascopyrum smithii</i> (Rydb.) A. Löve	USA	Forage
<i>Peridictyon sanctum</i> (Janka) O. Seberg, S. Frederiksen, & C. Baden	Eastern Greece and southern Bulgaria	–
<i>Pseudoroegneria cognata</i> (Hackel) A. Löve	Russia, Jungaria-Kashgaria, Kashmir, China (Xinjiang, Tibet)	–
<i>Pseudoroegneria geniculata</i> (Trin.) A. Löve	Western Siberia (Altai), eastern Siberia (Agara-Sayan, Mongolia)	–
<i>Pseudoroegneria pertenuis</i> (C.A May.) A. Löve	Northwest Iran and Caucasus	Model plant
<i>Pseudoroegneria spicata</i> (Pursh) A. Löve	Western North America	Forage
<i>Pseudoroegneria stipifolia</i> (Czern. Ex Nevski) A. Löve	Russia, Ukraine, Caucasus	Model plant
<i>Pseudoroegneria strigosa</i> (M. Bieb.) A. Löve	Russia Crimea	Model plant
<i>Pseudoroegneria tauri</i> (Boiss. & Bal.) A. Löve	Turkey, Iraq, Iran, Syria	Model plant
<i>Thinopyrum bessarabicum</i> (Savul. & Rayss) A. Löve	Turkey, Moldova, Ukraine, Bulgaria, Romania [Black Sea shores]	Model plant
<i>Thinopyrum caespitosum</i> (C. Koch) Z.-W. Liu & R.-C. Wang	Iran, Iraq, Syria, Turkey, Armenia; Azerbaijan, Turkmenistan, Pakistan, Ukraine, France	Model plant
<i>Thinopyrum elongatum</i> (Host) D.R. Dewey	Eastern and southern Europe, Caucasus, western Asia, northern Africa	Model plant
<i>Thinopyrum intermedium</i> (Host) Barkworth & D.R. Dewey	Iran, Iraq, Syria, Turkey, Caucasus, Soviet Middle Asia, Pakistan, Europe	Forage
<i>Thinopyrum junceiforme</i> (A. Löve & D. Löve) A. Löve	Europe	Model plant
<i>Thinopyrum junceum</i> (L.) A. Löve	Southern Europe, western Asia, northern Africa, naturalized in North America	–
<i>Thinopyrum nodosum</i> (Nevski) D.R. Dewey	Ukraine	Model plant
<i>Thinopyrum ponticum</i> (Podp.) Barkworth & D.R. Dewey	Eastern and southern Europe, Caucasus, western Asia, northern Africa	Forage
<i>Thinopyrum scirpeum</i> (K. Presl) D.R. Dewey	Southern Europe (Albania; Greece [incl. Crete]; Italy – Sicily; Yugoslavia, Spain), Algeria, Turkey	Model plant

pool in which gene flows occur between the three ploidy levels (Asay and Dewey 1979).

2.2.2.2 *Pseudoroegneria*

This genus consists of about 15 species that are distributed throughout the Northern hemisphere; *Pseudoroegneria spicata* is the only North American species with the remainder indigenous to Eurasia. The genus consists of diploid ($2n = 2x = 14$) and tetraploid ($2n = 4x = 28$) taxa, all of which contain the **St**-genome or some variation of it. The polyploid races of *Pseudoroegneria* are autopolyploids (**StSt**) or near-autopolyploids (**St₁St₂**). Some tetraploid *Pseudoroegneria* species such as *P. tauri* (Boiss. & Bal.) A. Löve (Wang et al. 1986) and *P. deweyi* K.B. Jensen, S.L. Hatch, & J.K. Wipff (Jensen et al. 1992) contain **St**- and **P**-genomes.

These species have subsequently been treated in a newly erected genus *Douglasdeweya* as *D. wangyii* C. Yen, J.L. Yang & B.R. Baum and *D. deweyi* (K. B. Jensen, S.L. Hatch & J.K. Wipff) C. Yen, J.L. Yang & B.R. Baum, respectively (Yen et al. 2005a). Relationships among *Douglasdeweya*, *Pseudoroegneria*, and *Agropyron* have been clearly shown in a study of their 5S ribosome DNA sequences (Baum et al. 2008).

2.2.2.3 *Psathyrostachys*

Species in this genus are indigenous to the steppes and semi-desert regions from western Russia and Turkey eastward to Siberia and China; all *Psathyrostachys* species contain the basic **Ns**-genome. Among 10 *Psathyrostachys* species listed (Table 2.5), only *P. juncea* (Fisch.) Nevski (Russian wildrye) is

cultivated in North America; and six species, of which three are endemic, are found in China. Species of *Psathyrostachys* are predominately diploids with tetraploids reported in the former Soviet Union.

2.2.2.4 *Elymus*

Elymus is by far the largest genus of the Triticeae when defined according to genome content (Dewey 1984). It contains approximately 150 species that have the pivotal **St**-genome in combination with one or more of **H**-, **Y**-, **W**-, or **P**-genomes (Wang et al. 1995). Geographically, these grasses occur in the temperate regions of both hemispheres, mainly in Asia; of these, 88 species (62 endemic) are in China, while 32 species are native and seven are non-native to North America. Yen et al. (2005b) divided *Elymus* into six genera strictly based on genome compositions – *Douglasdeweya* C. Yen, J.L. Yang & B.R. Baum (**PPStSt**), *Roegneria* C. Koch (**StStYY**), *Anthosachne* Steudel (**StStWWYY**), *Kengyia* C. Yen & J.L. Yang (**PPStStYY**), *Campeios-tachys* Drob. (**HHStStYY**), and *Elymus* L. (**StStHH**, **StStStHH**, and **StStHHHH**). The **Y**-genome has not been traced to any existing diploid species. However, recent reports suggest that **Y**- and **St**-genomes shared a common ancestral genome (Liu et al. 2006; Okito et al. 2009).

2.2.2.5 *Leymus*

Leymus is a polyploid genus of about 50 species that are found in temperate regions of the northern hemisphere; 24 species (11 endemic) occur in China and 17 species (11 native, four introduced, and two natural hybrids) are present in North America. All *Leymus* species are based on the **Ns**-genome of *Psathyrostachys* and the **Xm**-genome of an unknown origin (Wang and Jensen 1994; Jensen and Wang 1997; Zhang et al. 2006; Liu et al. 2008). Although several reports suggested that tetraploid *Leymus* species are near autopolyploids having the **Ns₁Ns₂**-genome formula (Zhang and Dvořák 1991; Anamthawat-Jónsson and Bödvarsdóttir 2001; Bödvarsdóttir and Anamthawat-Jónsson 2003), more recent studies support the conclusion that the genomic constitution of tetraploid

Leymus species is **NsXm** (Zhang et al. 2006; Liu et al. 2008; Fan et al. 2009; Larson et al. 2009). Still further, data obtained by Fan et al. (2009) suggest that the **Xm**-genome might have derived ancestrally from the **P** of *Agropyron* and **F** of *Eremopyrum triticeum* (Gaertn.) Nevski. Because adaptive radiation might have occurred in *Leymus* species (Fan et al. 2009), the rich diversity and ecological adaptation of *Leymus* species observed by Yang et al. (2008) could be accounted for.

2.2.2.6 *Thinopyrum*

Contained within this genus are about 20 species (Dewey 1984). These species are indigenous to Europe, particularly in the Mediterranean region, western Asia, and northern Africa. The most common introduced grasses are intermediate and tall wheatgrass in North America. *Thinopyrum* as treated herein consists of three species complexes: *Th. junceum* (L.) A. Löve, *Th. elongatum* (Host) D.R. Dewey; and *Th. intermedium*. Species in this genus possess the **J**- (or **E**)-genome, which Dewey (1984) designated as “**J** = **E**,” and sometimes contains the **St**-genome (Liu and Wang 1993a, b; Kishii et al. 2005). This genus consists of diploids, segmental allotetraploids, segmental allohexaploids, and genomically complex octaploids and decaploids.

2.2.3 Genome Size

The Triticeae tribe is characterized with large chromosomes in groups of seven, i.e., diploid is $2n = 2x = 14$ and decaploid is $2n = 10x = 70$. Each group of seven chromosomes is represented by a genome symbol so that the haplome of a diploid *Agropyron* species is shown as **P** and that of a tetraploid species is **PP**. Genome symbols follow the designations by the International Triticeae Consortium (Wang et al. 1995). The nuclear DNA content of various species (included in Tables 2.4 and 2.5) was reported by Vogel et al. (1999). The mean nuclear DNA content on a diploid basis (DNA pg/2C) were as follows: *Agropyron* (**P**) 13.9 pg, *Pseudoroegneria* (**St**) 8.8 pg, *Psathyrostachys* (**Ns**) 16.7 pg, and *Thinopyrum* genomes (**E^b**) 14.9 pg

Table 2.4 Chromosome number, genome constitution and DNA content of important perennial Triticeae species including those (in bold) that had been hybridized with wheat

Current scientific name	2n	Haplome ^a	DNA (pg/2C) ^b
Agropyron cristatum (L.) Beauv.	14–42	P to PPP	13.63
<i>Agropyron dasyanthum</i> Ledeb.	28	PP	–
Agropyron desertorum (Fischer ex Link) Schultes	28	PP	25.92
<i>Agropyron fragile</i> (Roth) Candargy	14, 28	P, PP	–
Agropyron michnoi Roshevitz	28	PP	–
Agropyron mongolicum Keng	14	P	15.37
<i>Agropyron tanaiticum</i> Nevski	28	PP	–
<i>Australopyrum pectinatum</i> (Labillardiere) A. Löve	14	W	–
Dasypyrum villosum (L.) Candargy	14	V	–
<i>Elymus abolinii</i> (Drob.) Tzvelev	28	StY	18.7
<i>Elymus alaskanus</i> (Scribner & Merr.) A. Löve subsp. <i>alaskanus</i>	28	StH	–
<i>Elymus alaskanus</i> subsp. <i>latiglumis</i> (Scribner & J.G. Sm.) A. Löve	28	StH	–
<i>Elymus alatavicus</i> (Drobov) A. Löve	42	StPY	30.31
Elymus altissimus (Keng) A. Löve	28	StY	–
Elymus anthosachnoides (Keng) A. Löve	28	StY	–
<i>Elymus antiquus</i> (Nevski) Tzvelev	28	StY	–
<i>Elymus arizonicus</i> (Scribn. & J.G. Smith) Gould	28	StH	–
<i>Elymus batalinii</i> (Krasn.) A. Löve	42	StPY	–
<i>Elymus burchan-buddae</i> (Nevski) Tzvelev	28	StY	–
Elymus canadensis L.	28	StH	21.11
<i>Elymus canaliculatus</i> (Nevski) Tzvelev	28	StY	–
Elymus caninus (L.) L.	28	StH	17.87
Elymus caucasicus (C. Koch) Tzvelev	28	StY	–
Elymus ciliaris (Trin.) Tzvelev	28	StY	17.33
Elymus cylindricus (Franch.) Honda	42	StHY	–
Elymus dahuricus Turez ex Griseb	42	StHY	25.79
Elymus dolichatherus (Keng) A. Löve	28	StY	–
<i>Elymus drobovii</i> (Nevski) Tzvelev	42	StHY	–
<i>Elymus enysii</i> (Kirk) A. Löve & Connor	28	HW	–
Elymus fibrosus (Schrenk) Tzvelev	28	StH	–
<i>Elymus glaucus</i> Buckl.	28	StH	18.48
<i>Elymus gmelinii</i> (Ledeb.) Tzvelev	28	StY	–
<i>Elymus grandiglumis</i> (Keng) A. Löve	42	StPY	–
<i>Elymus jacquemontii</i> (Hooker f.) Tzvelev	28	StY	–
Elymus kamoji (Ohwi) S. L. Chen	42	StHY	–
<i>Elymus kengii</i> Tzvelev	42	StPY	–
<i>Elymus lanceolatus</i> (Scribner & Smith) Gould	28	StH	16.71
<i>Elymus longearistatus</i> (Boiss.) Tzvelev	28	StY	–
<i>Elymus multiflorus</i> (Banks & Solander ex Hook. f.) A. Löve & Connor	42	StWY	–
<i>Elymus mutabilis</i> (Drobov) Tzvelev	28	StH	16.96
Elymus nipponicus Jaaska	28	StY	–
Elymus parviglumis (Keng) A. Löve	28	StY	–
Elymus pendulinus (Nevski) Tzvelev	28	StY	–
Elymus rectisetus (Nees in Lehm.) A. Löve & Connor	42	StWY	–
Elymus repens (L.) Gould	42	StStH	–
<i>Elymus scabriglumis</i> (Hackel) A. Löve	42	StStH	–
Elymus scabrus (R. Br.) A. Löve	42	StWY	–
Elymus semicostatus (Nees ex Steud.) A. Löve	28	StY	–
Elymus shandongensis B. Salomon	28	StY	–
<i>Elymus sibiricus</i> L.	28	StH	16.61
<i>Elymus stebbinsii</i> Gould	28	StH	–
<i>Elymus subsecundus</i> (Link.) A. Löve & D. Löve	28	StH	–

(continued)

Table 2.4 (continued)

Current scientific name	2n	Haplome ^a	DNA (pg/2C) ^b
<i>Elymus tianschanicus</i> (Drobov) Nevski	28	StY	—
<i>Elymus tibeticus</i> (Melderis) G. Singh	28	StY	—
<i>Elymus trachycaulus</i> (Link) Gould ex Shinnars	28	StH	18.14
<i>Elymus transhyrcanus</i> (Nevski) Tzvelev	42	StStH	—
<i>Elymus tschimganicus</i> (Drobov) Tzvelev	42	StStY	—
<i>Elymus tsukushiensis</i> Honda	42	StHY	—
<i>Elytrigia acutum</i>	42	—	—
<i>Elytrigia varnense</i> (Velen.) Holub	42	—	—
<i>Elytrigia pungens</i> (Pers.) Tutin	56	ESTStP or ESTLP	—
<i>Festucopsis festucoides</i> (Maire) A. Löve	14	L	—
<i>Festucopsis serpentini</i> (C.E. Hubbard) Melderis	14	L	—
<i>Leymus angustus</i> (Trin.) Pilger	56, 84	NsNsXmXm	—
<i>Leymus chinensis</i> (Trin.) Tzvelev	28	NsXm	19.56
<i>Leymus cinereus</i> (Scribn. & Merr.) A. Löve	28	NsXm	—
<i>Leymus innovatus</i> (Beal) Pilger	28	NsXm	—
<i>Leymus mollis</i> (Trin.) Pilger	28	NsXm	—
<i>Leymus multicaulis</i> (Kar. & Kir.) Tzvelev	28	NsXm	—
<i>Leymus racemosus</i> (Lam.) Tzvelev	28	NsXm	22.36
<i>Leymus ramosus</i> (Trin.) Tzvelev	28	NsXm	20.31
<i>Leymus sabulosus</i> (M. Bieb.) Tzvelev	28	NsXm	22.85
<i>Leymus secalinus</i> (Georgi) Tzvelev	28	NsXm	21.47
<i>Leymus triticoides</i> (Buckl.) Pilger	28	NsXm	21.87
<i>Pascopyrum smithii</i> (Rydb.) A. Löve	56	StHNsXm	34.33
<i>Peridictyon sanctum</i> (Janka) O. Seberg, S. Frederiksen, & C. Baden	14	Xp	—
<i>Pseudoroegneria cognata</i> (Hackel) A. Löve	14	St	—
<i>Pseudoroegneria geniculata</i> (Trin.) A. Löve	28	StSt	17.22
<i>Pseudoroegneria libanotica</i> (Hackel D.R. Dewey)	14	St	7.91
<i>Pseudoroegneria pertenuis</i> (C.A. May.) A. Löve	28	StP	—
<i>Pseudoroegneria spicata</i> (Pursh) A. Löve	14	St	9.26
<i>Pseudoroegneria stipifolia</i> (Czern. Ex Nevski) A. Löve	14	St	8
<i>Pseudoroegneria strigosa</i> (M. Bieb.) A. Löve	14	St	9.59
<i>Pseudoroegneria tauri</i> (Boiss. & Bal.) A. Löve	14	St	—
<i>Thinopyrum bessarabicum</i> (Savul. & Rayss) A. Löve	14	J or E ^b	14.92
<i>Thinopyrum caespitosum</i> (C. Koch) Z.-W. Liu & R.-C. Wang	28	EST	19.88
<i>Thinopyrum curvifolium</i> (Lange) D.R. Dewey	28	EE or J ^e J ^e	—
<i>Thinopyrum distichum</i> (Thunb.) A. Löve	28	JE or E ^b E ^e	—
<i>Thinopyrum elongatum</i> (Host) D.R. Dewey	14	E or J ^e	11.97
<i>Thinopyrum gentryi</i> (Melderis) D.R. Dewey	42	EE st St or EST(V-J-R)	—
<i>Thinopyrum intermedium</i> (Host) Barkworth & D.R. Dewey	42	EE st St or EST(V-J-R)	26.09
<i>Thinopyrum junceiforme</i> (A. Löve & D. Löve) A. Löve	28	JE or E ^b E ^e	24.79
<i>Thinopyrum junceum</i> (L.) A. Löve	42	JJE or E ^b E ^b E ^e	—
<i>Thinopyrum nodosum</i> (Nevski) D.R. Dewey	28	EST	—
<i>Thinopyrum ponticum</i> (Podp.) Barkworth & D.R. Dewey	70	EEEE st Est or EEEStSt	45.26
<i>Thinopyrum sartorii</i> (Boiss. & Heldr.) A. Löve	28	JE or E ^b E ^e	—
<i>Thinopyrum scirpeum</i> (K. Presl) D.R. Dewey	28	EE or J ^e J ^e	—
<i>Elymus repens</i> /Agropyron desertorum amphiploid	70	StStHPP	—

^aWang et al. (1995)^bVogel et al. (1999)

and (E^e) 12.0 pg (Vogel et al. 1999). Based on the difference, the Y-genome size was determined to be 9.3 pg. Thus, Vogel et al. (1999) concluded that gain

or loss of nuclear DNA has occurred during the evolution of the perennial Triticeae and was probably part of speciation.

Table 2.5 Geographic distribution, chromosome number, genome constitution and DNA content of *Psathyrostachys* species. Species that had been hybridized with wheat are in bold-face

Current scientific name	Distribution	2n	Haplome ^a	DNA (pg/2C) ^b
<i>P. caduca</i> (Boiss.) Melderis	Afghanistan, Asia, Europe	—	—	—
<i>P. daghestanica</i> (Alexeenko) Nevski	Dagestan	14, 28	Ns, NsNs	—
<i>P. fragilis</i> (Boiss.) Nevski subsp. <i>fragilis</i>	Iran, Russia	14	Ns	16.79
<i>P. fragilis</i> subsp. <i>secaliformis</i> Tzvelev	Caucasus, Iran, Iraq, Turkey, Russia	28	Ns,Ns	—
<i>P. fragilis</i> subsp. <i>villosus</i> C. Baden	Turkey, Russia	14	Ns	—
<i>P. huashanica</i> Keng	China (Shaanxi)	14	Ns	—
<i>P. juncea</i> (Fisch.) Nevski	Afghanistan, Russia, C. Asia, China	14	Ns	15.57
<i>P. juncea</i> var. <i>hyalanthia</i> (Rupr.) S.L. Chen	China (Xinjiang), C. Asia, Russia	—	—	—
<i>P. kronenburgii</i> (Hack.) Nevski	Russia, China (Xinjiang), Kazakhstan, Kyrgyzstan, Tadjikistan, C. Asia	14	Ns	—
<i>P. lanuginosa</i> (Trin.) Nevski	Afghanistan, China (Xinjiang), Kazakhstan, Kyrgyzstan, C. Asia, W. Siberia	14, 28	Ns, NsNs	—
<i>P. perennis</i> Keng	China	14	Ns	—
<i>P. rupestris</i> (Alexeenko) Nevski	Dagestan, Russia	14, 42	Ns	—
<i>P. stoloniformis</i> C. Baden	China (Gansu, Qinghai)	14	Ns	17.88

^aWang et al. (1995)^bVogel et al. (1999)

2.2.4 Cytology and Karyotype

Karyotypes in 22 diploid species of perennial Triticeae, representing **P**-, **St**-, **J** (=E)-, **H**-, **I**-, **Ns**-, **W**-, and **R**-genomes, had been studied (Hsiao et al. 1986). Each basic genome manifests a unique karyotypic pattern for its seven chromosomes. Prior to this, C-banding patterns were studied in 10 diploid species encompassing five basic genomes – **P**, **Ns**-, **J** (=E)-, **St**-, and **W**- (designated as C, Ju, J = E, S, and V, respectively, in Endo and Gill 1984). Based on differences in C-banding patterns, Endo and Gill (1984) questioned the equivalence of **J**- and **E**-, which was a viewpoint at that time shared by Dewey (1984) and Dvořák et al. (1984) based on extensive evidence from karyotype and genome analyses (Cauderon and Saigne 1961; Heneen and Runemark 1972; Dvořák 1981; McGuire 1984).

Since then, the close relationship between **J**- and **E**-genome in *Th. bessarabicum* (Savul. and Rayss) A Löve and *Th. elongatum* (Host) D.R. Dewey (= *Lophopyrum elongatum* (Host) A. Löve), respectively, had been revealed by studies using different methodologies, including chromosome pairing (Wang 1985; Pienaar 1988; Forster and Miller 1989; Wang and Hsiao 1989), random amplified polymorphic DNA (RAPD) and sequence tagged site (STS) markers (Wei and Wang 1995; Li et al. 2007), genomic in situ hybridization (GISH) technique (Kosina and

Heslop-Harrison 1996; Chen et al. 1998, 2003), chloroplast DNA sequences (Mason-Gamer et al. 2002; Liu et al. 2008), sequences of a gene encoding plastid acetyl-CoA carboxylase (Fan et al. 2007), and nuclear rDNA internal transcribed spacer (ITS) sequences (Hsiao et al. 1995; Liu et al. 2008; Yu et al. 2008). But the use of one basic genome symbol for these two species and/or the merge of them into the same genus were rejected by some researchers (Jauhar 1988, 1990a, b; Jarvie and Barkworth 1992; Hsiao et al. 1995; Jauhar et al. 2004). Only Fan et al. (2009) used the same basic genome symbol while keeping the two genera delimitation.

Forster and Miller (1989) pointed out that the relationship between **J**- and **E**-genomes is similar to that between **R^c** and **R^m** (genomes of *S. cereale* L. and *S. montanum* Guss., respectively); and they concluded that, on the basis of chromosome pairing in the diploid hybrids reported by Wang (1985), the **J**-genome in *Th. bessarabicum* should be designated **E^b**, as proposed by Dvořák (1981) and McGuire (1984). At the second International Triticeae Symposium, the Genome Designation Committee (Wang et al. 1995) adopted the symbols **E^c** and **E^b** for the genome in *Th. elongatum* and *Th. bessarabicum*, respectively. However, some Triticeae workers preferred to use **J^e** and **J^b** for genomes in these two species (Chen et al. 1998, 2003; Li et al. 2003) while others transferred *Th. bessarabicum* to the genus *Lophopyrum* so that it could have the

symbol E^b along with E^e for *L. elongatum* (Yen et al. 2005b; Yu et al. 2008).

2.3 Role in Elucidation of Origin and Evolution of Allied Crop Plants

Perennial Triticeae species are related to important cereal crops, including wheat, barley, rye, and man-made triticale (\times *Triticosecale* Wittm. Ex A. Camus). Studies on evolution of these annual crop species often included perennial Triticeae species, or vice versa; thus, the literature, such as the report by Petersen et al. (2006), was useful in understanding the evolution of both groups of species.

The *Thinopyrum bessarabicum*/*Th. elongatum* amphidiploid was originally synthesized by Wang (Wang and Hsiao 1989; Wang 2006). Based on his analysis on some of these amphidiploid plants, Jauhar (1988) disputed Wang's (1985) conclusion on the close relationship between the two diploid *Thinopyrum* species. Jauhar et al. (2004) further studied the trigeneric hybrids, with and without *Ph1*, of durum wheat with the amphidiploid of *Th. bessarabicum*/*Th. elongatum*. Their data revealed that without the *Ph1* in the ABE^bE^e hybrid, there were 3.97 chiasmata between (and among) E^b - and E^e -genome chromosomes, compared to 2.29 chiasmata between (and among) A- and B-genome chromosomes. Thus, the two E-genomes are more closely related to each other than A and B are to each other. Interestingly, the average *c* value (mean arm-pairing frequency; Alonso and Kimber 1981) for the diploid AB hybrids was 0.319 (cited in Wang 1990), so that for E^bE^e hybrids should be 0.553 ($= 0.319 \times 3.97 \div 2.29$). The observed *c* value for E^bE^e hybrids was 0.552 (Wang 1985) to 0.597 (Jauhar 1988). As demonstrated in many studies, chromosome pairing in diploid hybrids does reveal the true genome relationships (Forster and Miller 1989; Wang 1989b, 1992).

Using genomic hybridization (both Southern and in situ hybridization), Liu et al. (2007) demonstrated that the St and E-genomes are closely related and also that the two are more closely related to the D-genome than to the A- and B-genomes. Among the three wheat genomes, A- and D-genomes are closer with each other than either one is to B-genome. These

conclusions are in agreement with those based on chromosome pairing data obtained from intergenomic diploid hybrids and their derivatives (Wang 1990, 1992, 1993). The closeness between St and E was also supported by the study based on the sequences of a gene encoding plastid acetyl-CoA carboxylase (Fan et al. 2007) and 5S rDNA (Shang et al. 2007). The St and J ($=E$) were also more closely related to the R-genome of *Secale* than to the V-genome of *Dasypyrum* (Shang et al. 2007). Based on ITS of the nuclear rDNA sequences, Hsiao et al. (1995) reported that $E (=E^e)$ and $J (=E^b)$ jointly clustered with A, B, and D; but genomes B- and D- were grouped more closely together than were A- and D-genomes.

Because of these genome relationships among St-, E-, and A-, B-, and D-genomes, more cross-hybridization occurred on wheat chromosomes when DNA from the E-genome (either E^b or E^e) was used as the probe in genomic or fluorescence in situ hybridization (GISH or FISH) of wheat-*Thinopyrum* hybrid derivatives. These cross-hybridization signals were often misinterpreted as translocated alien segments in wheat chromosomes. To avoid such interpretation, an adequate probe/block DNA ratio must be selected based on a preliminary test of the negative control using the same wheat line used for alien gene transfer. Using the total genomic DNA of *Th. intermedium* [$2n = 6x = 42$; E^bE^eSt (Liu and Wang 1993a); or $E^eSt(V-J-R)$ (Kishii et al. 2005)] or *Th. ponticum* [$2n = 10x = 70$; $EEEE^{st}E^{st}$ (Chen et al. 1998); or $E^bE^eE^{st}StSt$ (Liu et al. 2007)] as probes for GISH or FISH would often lead to false-positives from cross-hybridizations between E-genome probing DNA and D- or A-genome chromosomes. Therefore, it is advised to use St genomic DNA as the probe in GISH or FISH so that only the St- and E-genome chromosomes or chromosomal segments will be showing hybridization signals (Wang and Zhang 1996; Zhang et al. 1996).

2.4 Role in Development of Cytogenetic Stocks and Their Utility

To utilize alien genes for wheat improvement, the first step is crossing wheat with the alien species followed by the production of amphidiploids through chromosome doubling. Partial amphidiploids usually contain a varying combination of chromosomes originating

Table 2.6 Depositories of wheat alien addition, substitution, and translocation lines

Location and contact	Alien species	Amphiploids	Addition lines	Substitution lines	Translocation lines
Wheat Genetic Resources Center, Kansas State University, Manhattan, Kansas, USA; wgrc@k-state.edu	<i>Thinopyrum elongatum</i>	cv. Chinese Spring/ <i>Th. elongatum</i>	Chinese Spring disomic addition lines (CS-DA): 7 (1E ^c – 7E ^c); Chinese Spring ditelosomic addition lines (CS-DtA): 5 (1E ^c S, 3E ^c S, 3E ^c L, 6E ^c S, 6E ^c L); miscellaneous addition lines: 1	Miscellaneous substitution lines: 3 (7E/AD)	–
	<i>Thinopyrum scirpeum</i>	cv. Chinese Spring/ <i>Th. scirpeum</i>	–	–	–
	<i>Thinopyrum ponticum</i>	cv. PWM206/ <i>Th. ponticum</i> Partial Amphiploid; cv. PWM206/ <i>Th. ponticum</i> Partial Amphiploid; cv. PWMIII/ <i>Th. ponticum</i> Partial Amphiploid; cv. PWM706/ <i>Th. ponticum</i> Partial Amphiploid; cv. OK7211542/ <i>Th. ponticum</i> Partial Amphiploid; Triticum aestivum subsp. aestivum/ <i>Th. ponticum</i> Partial Amphiploid.	–	–	Disomic substitutions in Chinese Spring = 37 (3B/3Ag, 3D/3Ag, and 7D/7Ag translocations from 21 different <i>Th. elongatum</i> accessions, two interstitial translocations Ti3D-3Ag; all produced by ER Sears); disomic substitutions in other cultivars = 2 (OK65C77-6 resistant to WSMV, T4B-4E)
	<i>Thinopyrum bessarabicum</i>	Triticum aestivum subsp. aestivum/ <i>Th. bessarabicum</i>	–	–	–
	<i>Thinopyrum distichum</i>	Triticum aestivum subsp. aestivum/ <i>Th. distichum</i>	–	–	–
	<i>Thinopyrum intermedium</i>	cv. Vilmorin 27/ <i>Th. intermedium</i> #1; cv. Zhong/Agropyron <i>intermedium</i> : 9 lines; cv. Summer/ <i>Th. intermedium</i> : 2 lines; cv. OK7211542/ <i>Th. intermedium</i> ; cv. Otrastajusca 38/ <i>Th. intermedium</i> ; cv. Otrastajusca 38/ <i>Th. intermedium</i> ; cv. Zhong 8423 disomic <i>Th. intermedium</i> Partial Amphiploid; Triticum turdigum subsp. durum cv. Nodak/ <i>Th. intermedium</i> Partial Amphiploid; MT1, MT2; Triticum turdigum subsp. durum cv. Nodak/ <i>Th. intermedium</i> Partial Amphiploid.	CS-DA: 4 (unknown); Vilmorin 27 disomic addition lines (V27-DA): 6 (1Ai, 3Ai – 7Ai) V27-DtA: 1 (7AiS); Zhong 8423 disomic addition lines (Z8423-DA): 7 (unknown); miscellaneous addition lines: 4	Miscellaneous substitution lines: 6	Disomic substitutions in Sunstar = 7 (1BS/7Ai#1S-7Ai#1L, T7DS-7DL-7Ai#1L, 7DS/7Ai#1S-7Ai#1L (5 lines)); disomic substitutions in Heine IV = 6 (T1DS-1DL-7Ai#2L, T2AS-2AL-7Ai#2L (2 lines), T6DS-6DL-7Ai#2L, T7Ai#2L-3DS-3DL, T7Ai#2L-5AS-5AL); disomic substitutions in other cultivars = 4 (T7DS-7Ai#1L-7Ai#1S and one unknown in Chinese Spring); 6AL-4Ai#2S, T6AS-4Ai#2L, T4DL-4Ai#2S, T7AS-7St#1S-7St#1L in Centurk.

(continued)

Table 2.6 (continued)

Location and contact	Alien species	Amphiploids	Addition lines	Substitution lines	Translocation lines
	<i>Elymus ciliaris</i>	<i>Elymus ciliaris</i> / <i>Triticum aestivum</i> subsp. <i>aestivum</i> cv. Inayama-komugi	CS-D4: 9 (1St, 1Y, 2St, 3St, 5Y, 7St; 1St + 5Y = dDA; 1 unknown); CS-D4A: 2 (1YS, 2StL) CS-D4A: 7 (1H, 1St, 5H-7H; 1H + 4H = dMA; 5St = MA); CS-D4A: 9 (1HS, 1HL, 1StL, 5HS, 5HL, 7HS, 7HL; 5StS, 5StL = MA)	-	<i>Elymus ciliaris</i> disomic substitution/addition in Chinese Spring = 2 (1Y ^c S)
	<i>Elymus trachycaulus</i>	-			<i>Elymus trachycaulus</i> -E. <i>trachycaulus</i> disomic additions in Chinese Spring = 6 (1H ¹ S-2H ¹ S, 1H ¹ S-5H ¹ L, 1H ¹ S-6H ¹ L, 1H ¹ S-7H ¹ L, 1St ¹ L-7St ¹ L, 2H ¹ S-7H ¹ S); E. <i>trachycaulus</i> -E. <i>trachycaulus</i> monosomic additions in Chinese Spring = 1 (1H ¹ L-3St ¹ L); E. <i>trachycaulus</i> disomic substitutions in Chinese Spring = 3 (1H ¹ S, 1St ¹ S, zebra chromosome (25A)); E. <i>trachycaulus</i> isosomic translocations in Chinese Spring = 3 (1H ¹ S-1H ¹ S, 5H ¹ L-5H ¹ L)
	<i>Elymus tsukushiense</i>	-	Miscellaneous addition lines: 3	Miscellaneous substitution lines: 1	-
	<i>Leymus racemosus</i>	-	CS-D4A: 7 (2Lr, 5Lr-7Lr; 1Lr 5Lr, 3Lr 7Lr = dDA); CS-D4A: 2 (2LrS, 7LrS)	Miscellaneous substitution lines: 1	-
	<i>Leymus arenarius</i>	<i>Triticum</i> sp./ <i>Leymus arenarius</i>	-	-	-
	<i>Criteston bogdani</i>	<i>Triticum timopheevii</i> subsp. <i>timopheevii</i> / <i>Criteston bogdani</i>	-	-	-
	<i>Criteston californicum</i>	<i>Criteston californicum</i> /cv. Chinese Spring	-	-	-
	<i>Dasyphyrum villosum</i>	<i>Triticum aestivum</i> /D. <i>villosum</i>	CS-D4A: 16 (#1: 1V, 2V, 4V - 7V; #2: 3V - 5V; #3: 1V - 7V) 15 (A, C, E, F, H, I, J, K, L, N, 2Lr, 5Lr, 7Lr, ?) 3 (A, G, H) D4A: 6 (1H, 1H + 4H, 1St, 5H, 5St, 6H); D4A: 8 (1HS, 1HL, 1StL, 5HS, 5HL, 5StS, 7HS, 7StL); 10 (complex translocation additions)	-	-
Tottori Alien Chromosome Bank of Wheat (TACBOW), University of Tottori, 4-101 Koyama-Minami, Tottori 680-8550 Japan; PHONE: 0857-31-5352; FAX: 0857-31-5347	<i>Leymus racemosus</i>	-		2 (H, 2Lr)	-
	<i>Leymus mollis</i>	-		-	-
	<i>Elymus trachycaulus</i>	-		1 (20" + T7AL 1AS-1StS); 1 (19" + 1" [T7AL 1AS-1StS] + 1" [T5DL 7AS (5D)])	1 (20" + 1" 1HS.1BL)

Forage & Range Research Laboratory (FRR), USDA- ARS, Logan, Utah, USA; Richard. Wang@ars.usda.gov	<i>Elymus ciliaris</i>	–	–	7 (1St, 1Y, 1YS, 2St, 3St, 1St + 5Y, ?Y)	–
	<i>Psathyrostachys huashanica</i>	–	–	5 (A, B, C, D, E)	–
	<i>Thinopyrum elongatum</i>	<i>Triticum durum</i> / <i>Th. elongatum</i>	–	DA: 7 (1E ^c –7E ^c); DtA: 6 (1E ^c S, 3E ^c S, 3E ^c L, 6E ^c S, 6E ^c L, 7E ^c L)	–
	<i>Thinopyrum intermedium</i>	<i>Triticum durum</i> / <i>Th. intermedium</i> ;	–	12 (1Ai, 3Ai, 4Ai, 5Ai, 6Ai, 7Ai, B, C, D, E, F, G)	–
	<i>Dasyphyrum villosum</i>	<i>Triticum aestivum</i> / <i>Th. intermedium</i>	–	7 (1V–7V)	–
	<i>Hordeum chilense</i>	<i>Triticum durum</i> / <i>D. villosum</i>	–	5 (2H, 4H, 5H, 6H, 7H)	1 (IH)
	<i>Thinopyrum junceum</i>	<i>Triticum aestivum</i> cv. CS/ <i>Th. junceum</i> partial amphiploids: 9 (2n = 56 = 21'' + 7'')	–	CS-DA: 13 (1E ^b , 1E ^c , 2E ^b , 2E ^c , 5E ^b –5E ^c , 6E ^b –6E ^c , 7E ^b –7E ^c , and complex translocations)	–
	<i>Thinopyrum bessarabicum</i>	–	–	CS-DA: 7 (1E ^b –7E ^b)	–
	<i>Thinopyrum elongatum</i>	cv. Chinese Spring/ <i>Th. elongatum</i>	–	Chinese Spring disomic addition lines (CS-DA): 7 (1E ^c –7E ^c)	–
	<i>Elymus rectisetus</i>	–	–	<i>Triticum aestivum</i> cv. Fukuhokomugi DA: 9 (?) W, ?W, 18''ABD + 1''? St + 1''?St + 1''? W + 1''?X, etc.)	Miscellaneous substitution lines: 6 [18''ABD + ''?St + 1''? St + 1''?W
	<i>Dasyphyrum villosum</i>	–	–	–	–
	<i>Triticum aestivum</i> / <i>D. villosum</i>	CS-DA: 7 (1V–7V)	–	–	–

(2D + 3B + ?A), unknown etc.]

from the alien species (Banks et al. 1993; Fedak et al. 2001). Therefore, crossing different partial amphiploids is not advised. Then through a series of backcrosses with wheat, addition, substitution, or translocation lines are developed and subsequently phenotyped for the desired traits. These cytogenetic stocks (Table 2.6) provide essential tools for chromosome engineering in wheat.

Chromosome translocations can result from either spontaneous or induced recombination. Various methods have been used to induce chromosomal recombination: irradiation (Sears 1956), tissue culture (Banks et al. 1995), and homeologous pairing (Wang et al. 1977, 1980, 2003b; Kibirige-Sebunya and Knott 1983; Koebner and Shepherd 1985; Islam and Shepherd 1992; Aghaee-Sarbarzeh et al. 2002). The last method involves the use of N5BT5D (Sears 1966), *Ph1b* deletion mutant (Sears 1977), or *Ph* inhibitor (*Ph*¹) line (Chen et al. 1994) to promote homeologous recombination by removing or suppressing the effect of *Ph1* gene on the long arm of chromosome 5B. The latter two wheat lines are more advantageous than the 5B nullisomy in producing translocation lines (Qi et al. 2007).

Wheat translocation lines involving “*Agropyron*” have been characterized and listed for their utilization in agriculture (WGGRC, http://www.k-state.edu/wgrc/Germplasm/Stocks/Agropyron_translocations.html; accessed on 29 Oct 2009, 16:19 GMT). Due to deleterious traits associated with transferred alien chromosome segments, i.e., linkage drags, most alien transfers had not led to acceptable wheat cultivars. The majority of alien genes transferred and utilized in wheat cultivars are single genes for disease resistance, especially those to the rusts and viruses.

Marais et al. (2001) used Sears’ *ph1b* mutant to induce allosyndetic recombination for further shortening of the *Lr19* translocation segment in line *Lr19*-149, which lacked the deleterious yellow endosperm pigmentation gene. The shortest alien chromosome segment was obtained in the recombinant line *Lr19*-149-299 but still retained the segregation distortion gene *Sd2*.

Dundas et al. (2007) reported the advancements made over the past two decades on improving the usefulness of translocation lines with alien genes for stem rust resistance by eliminating linkage drags. Using *ph1bph1b*-induced homeologous recombination between the alien chromosome segments and normal

wheat chromosomes, lines with shortened alien chromatin were identified by dissociation patterns of molecular-based markers. New lines of bread wheat were developed containing 1RS segment with rust resistance gene *SrR* (*S. cereale* L.), 6Ae#1L chromosome segments with *Sr26* (*Th. ponticum*), 2S#1 chromosome segments with *Sr32* and a previously unnamed gene, 2S#2 chromosome segment with *Sr39* (*Triticum speltoides*), 4G#1 chromosome segments with *Sr37*, and 2G#2 chromosome segments with *Sr40* (*T. timopheevii*).

Recently, a disomic addition line ($2n = 44$) derived from *T. aestivum* cv. Fukuhokomugi \times *Elymus rectisetus* (Nees in Lehm.) A. Löve & Connor hybrids, which were made aiming to transfer apomixis (see under Sect. 2.6 later), had been identified to have resistance to both tan spot (caused by *Pyrenophora tritici-repentis*) and *Stagonospora nodorum* blotch (SNB; caused by *S. nodorum* Castellani and Germano) (Oliver et al. 2008). Furthermore, Xu et al. (2009) identified seven wheat–*Th. intermedium* amphiploids, one wheat–*Th. ponticum* amphiploid, six durum–*Aegilops speltoides* amphiploids, one wheat–*Th. junceum* disomic addition line, two wheat–*Ae. caudata* disomic addition lines, and a wheat–*Th. bessarabicum* 7J disomic addition line that might carry novel genes for resistance to the stem rust race TTKSK (commonly known as Ug99 or TTKS).

Resistance to barley yellow dwarf virus (BYDV) in *Th. intermedium* is located on two group-7 chromosomes (7St and 7E) and one group-2 chromosome 2Ai-2 (an E-St translocation) in addition lines L1, P107, and Z6, respectively (Banks et al. 1995; Sharma et al. 1995; Wang and Zhang 1996; Lin et al. 2007). Subsequently, genes for BYDV resistance *Bdv2* and *Bdv3* were identified based on translocation lines derived from L1 and P107, respectively (see Table 2.7 in Sect. 2.6 later; Banks et al. 1995; Hohmann et al. 1996; Francki et al. 1997; Crasta et al. 2000; Zhang et al. 2000, 2009; Ayala et al. 2001; Xin et al. 2001; Larkin et al. 2002; Ohm et al. 2005). In addition, BYDV resistance was reported in the disomic addition line Tai-27 (Jiang et al. 2009), which appears to be similar to lines Z1 and Z6 (Larkin et al. 1995; Barloy et al. 2003; Han et al. 2003; Lin et al. 2006), all of which contain the group-2 St chromosome in the wheat background. Although BYDV resistance gene *Bdv4* on the group-2 St chromosome has not yet been transferred to a wheat chromosome, expressed

Table 2.7 Alien resistance genes for biotic stress transferred to wheat

Diseases or pests	Gene symbol	Alien species	Alien chromosome	Wheat chromosome	Germplasm or cultivars	Molecular markers	References
Leaf rust (<i>Puccinia recondita</i> f.sp. <i>tritici</i>)	<i>Lr19</i>	<i>Thinopyrum ponticum</i> and <i>Th. distichum</i>	7Ae#1L	7DL = T7DS, 7DL-7Ae#1L in Agatha and Sears transfer 7D-7Ag no.1; 7DL = T7DS, 7DL-7Ae#1-7DL in Mutant 235; 7AL = T7A-7Ae#1 in Sears' 7A-7Ag No.12	Agatha; Indis; L503; L513; Mutant 28; Mutant 235; Sunnan; Oasis 86; Lr19-149-299; I-22; I-23; I-96	The gene order: Sd-1-Xpsr105-7D-Xpsr129-7D-Lr19-Wsp-D1-Sr25-Y; Cent-Sd1-Xpsr165-7D-Xpsr105-7D-Xpsr129-7D-XcslH81-1-Xwg380-7D-Xmwg2062-7D-Lr19-Wsp-D1-Sr25/Y; RAPD, SCAR and SSR markers co-occurring with, or flanking, Lr19 in a derivative of Knott's Agatha Mutant 28 (C80.1) were reported; An STS marker closely linked and distal to Lr19 was developed from an AFLP	Eizenga (1987); Friebe et al. (1994); Aurique et al. (1995); Prins and Marais (1998); Prins et al. (1996, 2001); Zhang et al. (2005); Gupta et al. (2006)
	<i>Lr24</i>	<i>Thinopyrum ponticum</i>	3Ae#1L	3DL in Agent, Cody, Osage, Payne; 1BL = T1BL, 1BS-3Ae#1L in Amigo, Teewon	Cody; Osage; Payne; SST 23; SST 44 = T4R; Timpaw; Torres; Wanken; Australian genotypes; Blueboy II; Fox; Lockett; Parker 76; Siouxland	Always present with Sr24; cosegregation with RAPD marker that was converted to a SCAR; Linked with SCAR marker SCS73719 earlier thought to tag Lr19; A PCR marker, Sr24#12, was confirmed across all sources of Lr24	McIntosh et al. (1977); Jiang et al. (1994a); Aurique et al. (1995); Dedryver et al. (1996); Prabhu et al. (2004); Mago et al. (2005)
	<i>Lr29</i>	<i>Thinopyrum ponticum</i>	7Ae#1	7DS = 7DL-7Ae#1L, 7Ae#1S.	Sears' CS 7D/Ag#11; RL6080 = Thatcher*6/ Sears' 7D/Ag#11	Cosegregation with two RAPDs	Procnier et al. (1995); Friebe et al. (1996)
	<i>Lr38</i>	<i>Th. intermedium</i>	7Ai#2L	1DL = T1DS, 1DL-7Ai#2L, v: T25; 2AL = 2AS, 2AL-7Ai#2L, v: W49 = T33; 3DS = 3DL, 3DS-7Ai#2L, v: T4; 5AS = 5AL, 5AS-7Ai#2L, v: T24; 6DL = 6DS, 6DL-7Ai#2L, v: T7	T25; W49 = T33; T4; T24; T7; RL6097 = Thatcher*6/ T7		Friebe et al. (1992, 1993, 1996)

(continued)

Table 2.7 (continued)

Diseases or pests	Gene symbol	Alien species	Alien chromosome	Wheat chromosome	Germplasm or cultivars	Molecular markers	References
	<i>Lr55</i>	<i>Elymus trachycaulis</i>	IHS	1B = 1BL, 1H'S	KS04WGRC45 = Heyne*3/TA5586		Friebe et al. (2005)
Stem rust (<i>Puccinia graminis</i>)	<i>Sr24</i>	<i>Thinopyrum ponticum</i>	3Ae#1L	3DL = T3DS, 3DL-3Ae#1L in Sears' 3D/Ag translocations; T1BL = IBS-3Ae#1L in Amigo	Agent; Blueboy II; Collin; Cloud; Cody; Fox; Gamka; Karee; Kinko; Palmiet; Sage; SST 23; SST 25; SST 44 = T4R; SST 102; Torres; Wilga; Siouland; Australian genotypes; T1BL = IBS-3Ae#1L Amigo; Teewon	Sr24 is completely linked in coupling with Lr24 and often with red grain color	Sears (1973); McIntosh et al. (1977); The et al. (1992); Jiang et al. (1994a); Autrique et al. (1995); Friebe et al. (1996)
	<i>Sr25</i>	<i>Thinopyrum ponticum</i>	7Ae#1L	7DL = T7DS, 7DL-7Ae#1L in Sears' CS 7D/7Ag translocations; 7AL = T7A-7Ae#1L in Sears' 7A/7Ae#1L No. 12	Sears' CS 7D/7Ag translocations except #11; Agatha = T4; Mutant 28; Sears' 7A/7Ae#1L No. 12; Indis	Sr25/Lr19 often show complete linkage; Sears' 7D/7Ag#11 carries neither Sr25 nor Lr19	McIntosh et al. (1977); Eizenga (1987); Kim et al. (1993); Friebe et al. (1994)
	<i>Sr26</i>	<i>Thinopyrum ponticum</i>	6Ae#1L	6AL = T6AS, 6AL-6Ae#1L	Avocet; Flinders; Harrier; Jabiru; King; Kite; Knott's 6A-6Ae#1L translocation to Thatcher; Takari; Bass; Eagle	A PCR marker, Sr26#43 was reported	Friebe et al. (1994, 1996); Mago et al. (2005)
	<i>Sr43</i>	<i>Thinopyrum ponticum</i>	7Ae#2L	T7DL-7Ae#2L, 7Ae#2S or T7DS, 7Ae#2L	KS10-2; KS23-9; KS24-1; KS24-2		Kim et al. (1993); Friebe et al. (1996)
	<i>Sr44</i>	<i>Thinopyrum intermedium</i>	7Ai#1L	T7DS-7Ai#1L, 7Ai#S; Several 7A-7Ai#1L translocations	Line 86,187; Several 7A-7Ai#1L translocations		Friebe et al. (1996); Khan (2000)
Colonization by curl mites (<i>Eriophyes tulipa</i>)	<i>Cmc2</i>	<i>Thinopyrum ponticum</i>	6Ae#2S	T6AS, 6Ae#2S; T5BL, 6Ae#2S; 6D = T6DL, 6Ae#2S	875-94-2; Rescue derivative		Whelan (1988); Whelan and Hart (1988); Friebe et al. (1996)
Wheat Streak Mosaic Virus (WSMV)	<i>Wsm1</i>	<i>Thinopyrum intermedium</i>	4ES = 4Ai#2S in CI 15092 (2n = 42)	4A = T4AL, 4Ai#2S; 4D = T4DL, 4Ai#2S; T6AS, 4Ai#2L + T6AL-4Ai#2S	CI 17766 = B-6-37-1; CI 17884; KS90H445; KS90H450; CI 17883	Wsm1 cosegregated with a STS amplified by the primer set STS115	Liang et al. (1979); Wang et al. (1980); Friebe et al. (1991); Talbert et al. (1996)

Barley yellow dwarf virus (BYDV)	<i>BdV2</i>	<i>Thinopyrum intermedium</i>	7St = 7Ai#1L in L1 ($2n = 44$)	T7DS, 7DL-7Ai#1L in TC14 (Distal 10% of 7DL), translocation point between RFLP markers Xpsr680 and Xpsr965; T7DS-7Ai#1S, 7Ai#1L in TC5, TC6, TC8, TC9, TC10; 1B = T1BS-7A#1S, 7Ai#1L in TC7	Glover (with TC6); Mackellar = LH64C (from tissue culture); TC14*2/Hartog; TC14*2/Spear; TC14*2/Tatiara; Yw243, Yw443, Yw642 and Yw1029 (derived by ph1 induced recombination)	Complete association with Xpsr129-7D, Xpsr548-7D, Xksu2-7D, XcsH81-7D, and Xgwm37-7D selected as a diagnostic marker; Two RGAP and 1 RAPD markers developed for the Yw series also effective for at least TC14	Banks et al. (1995); Larkin et al. (1995); Hohmann et al. (1996); Wang and Zhang (1996); Zhang et al. (2000, 2004)
	<i>BdV3</i>	<i>Thinopyrum intermedium</i> cv. <i>Ohake</i>	7E in P107 ($2n = 44$) and P29 ($2n = 42$)	7DS, 7DL-7EL	PI 634825 = P961341	RFLP and GISH; Three SSRs (gdm67, wmc121, and gdm46) and two STSs (BE44572, S253737) for bin 3; one SSR (barcl72) and two STSs (BF293181, BE442755) for bin 4	Sharma et al. (1995); Francki et al. (1997); Crasta et al. (2000); Ohm et al. (2005); Ayala-Navarrete et al. (2009)
	<i>BdV4</i>	<i>Thinopyrum intermedium</i>	2Ai#2	2Ai#2(2D); 2Ai#2(2B)	Addition lines TAI-27, DH549 and DH554 ($2n = 44$); substitution in N431, N452, HG295, and Yi4212; substitution in N420 and N439; translocation line Y5579	EST-based PCR marker BF145935	Lin et al. (2006, 2007); Ayala-Navarrete et al. (2007); Zhang et al. (2009)
Scab, Head blight (<i>Fusarium graminearum</i>)	<i>Fhb3</i> confers type 2 resistance similar to Sumai 3	<i>Leymus racemosus</i>	7Lr#1S	7A = T7AL, 7Lr#1S in T09; T4BS-4BL-7Lr#1S + T4BL-7Lr#1S-5Lr#1S in T01; T6BS-6BL-7Lr#1S + T6BL-5Lr#1S in T14	NAU502 DA7Lr#1 ($2n = 44$); NAU601 T4BS-4BL-7Lr#1S ($2n = 42$); NAU615 T4BS-4BL-7Lr#1S-1 ($2n = n = 42$); NAU617 T6AL-7Lr#1S ($2n = 42$); NAU635 T1BL-7Lr#1S ($2n = 42$); T09 ($2n = 42$); T01 ($2n = 44$); T14 ($2n = 44$)	Three PCR-based markers, BE586744-STS, BE404728-STS, and BE586111-STS, specific for 7Lr#1S were developed	Cai et al. (2005); Chen et al. (2005); Qi et al. (1997, 2008)
Powdery mildew (<i>Blumeria graminis</i> DC)	<i>PmP</i>	<i>Agropyron cristatum</i>	Unknown	Unknown	Xiaobing	Two AFLP marker loci, XM55P66 and XM55P37, flanked the locus with a distance of 0.8 cM and 2.4 cM, respectively, from the locus	Zhou et al. (2005)

sequence tag (EST) sequences for the resistance had been isolated (Jiang et al. 2004, 2005, 2009). These DNA sequences will be useful in furthering our understanding of the BYDV resistance genes.

Thinopyrum species, especially *Th. ponticum*, are highly tolerant to salinity (Zhang et al. 2005; Colmer et al. 2006). Tolerance to abiotic stresses, such as drought, cold, or salinity, is usually controlled by complex physiological processes that involve the action of many independent genes. Thus, these traits are generally quantitatively inherited, e.g., salinity tolerance of *Th. elongatum* is governed by several genes located on different chromosomes of the E^c -genome (Dvořák et al. 1988; Dubcovsky et al. 1994; Zhong and Dvořák 1995). As a result, the single-chromosome disomic addition lines are always less tolerant to abiotic stresses or certain diseases than the amphidiploid or partial amphidiploid, exemplified by the salinity tolerance in the wheat–*Thinopyrum junceum* derivatives (Wang et al. 2003b) and the wheat scab (or Fusarium head blight, FHB) resistance in wheat \times *Leymus racemosus* (Lam.) Tzvelev derivatives (Cai et al. 2005; Chen et al. 2005). In these cases, gene(s) from each disomic addition line carrying a different alien chromosome must be independently transferred to a homeologous wheat chromosome before separate translocation lines are subsequently crossed to achieve gene pyramiding. Despite this, partial salt tolerance of *Th. junceum* and *Th. ponticum* have been transferred into wheat giving their hybrid derivatives increased salt tolerance over the recipient wheat lines (Wang et al. 2003b; Chen et al. 2004).

2.5 Role in Classical and Molecular Genetic Studies

After the salt tolerance genes from AJDAj5 (a wheat–*Th. junceum* disomic addition line; Charpentier 1992) and Ph^1 (the line carrying Ph^1 gene allele from *Ae. speloides*; Chen et al. 1994) were transferred into two translocation lines W4909 and W4910 (Wang et al. 2003a), a microarray study was carried out to trace transcriptome changes (or gene actions) to the two parents (Mott and Wang 2007). Because Chinese Spring (CS) wheat was the common background of the two parental lines, CS was included in the microarray study. By comparing the gene expression in the five

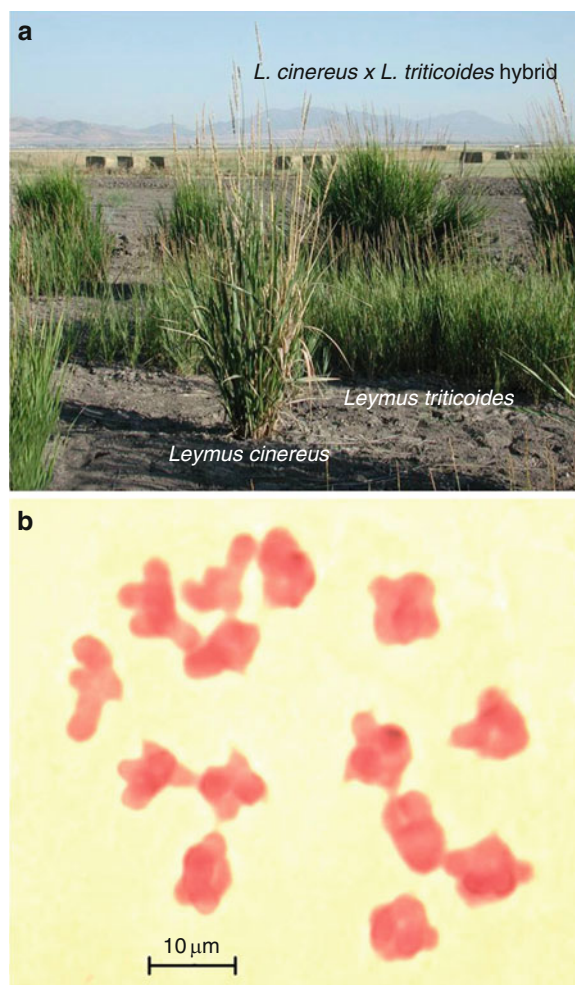


Fig. 2.1 *Leymus* hybrid derivatives used as mapping populations for the $NsXm$ -genome. (a) Plants of *Leymus cinereus* (front), *L. triticoides* (middle), and their F_1 hybrid (back). (b) Chromosome pairing at meiotic metaphase I in the *L. cinereus* \times *L. triticoides* F_1 hybrid. Photo 1A is provided by Steve R. Larson, USDA-ARS FRRL

lines, Mott and Wang (2007) were able to demonstrate that the combination of genes from AJDAj5 and Ph^1 resulted in a higher salinity tolerance in W4909 and W4910 than the two parental lines, which were more salt-tolerant than CS. It is also clear that W4909 and W4910 inherited from Ph^1 the mechanism that allowed the plants to tolerate high Na^+ concentrations in their leaves. While many other genes might be involved to account for their salt tolerance, a gene for tonoplast aquaporin from Ph^1 and a gene for putative potassium channel protein attributable to AJDAj5 were identified

as candidate genes for the tissue salt tolerance in W4909 and W4910.

Efforts to map important agronomic traits have been conducted with mapping populations derived from the hybrid between *Leymus cinereus* (Scribn. & Merr.) A. Löve and *L. triticoides* (Buckl.) Pilger (Wu et al. 2003; Hu et al. 2005; Larson et al. 2006; Larson and Mayland 2007). *L. cinereus* and *L. triticoides* are tall caespitose and short rhizomatous perennial Triticeae grasses, respectively (Fig. 2.1a); but the interspecific hybrid had complete chromosome pairing (Fig. 2.1b) and was highly fertile to produce progenies that are suitable for mapping molecular markers of many contrasting characteristics in the two species. Quantitative trait loci (QTLs) for circumference of rhizome spreading, proportion of bolting culms, anthesis date, and plant height were mapped in one study (Larson et al. 2006) and those for neutral detergent fiber, acid detergent fiber, crude protein, and 14 minerals content in another (Larson and Mayland 2007). These studies contribute valuable data benefiting the comparative genomics of monocotyledon grasses that include rice, maize, wheat, barley, rye, and sorghum.

2.6 Role in Crop Improvement Through Traditional and Advanced Tools

Table 2.7 lists the transferred genes for resistance to disease and insect pests that originated from perennial Triticeae species. These genes were introgressed into wheat through chromosome engineering by aforementioned methods in Sect. 2.4. All except three cases (those for *Lr55*, *Fhb3*, and *PmP*) originated from *Thinopyrum* species. This can be attributed to the fact that among the genomes of the perennial Triticeae, the **E**-genome in *Thinopyrum* species is most closely related to the **ABD**-genome of wheat (Hsiao et al. 1995; Liu et al. 2007).

The short arm of chromosome 1H carrying *Lr55* for leaf rust resistance in *Elymus trachycaulis* was fused by centromere to 1B long arm of wheat in the germplasm KS04WGRC45 (Friebe et al. 2005). Scab resistance gene *Fhb3* from *L. racemosus* was transferred to wheat by recombinations involving 4BL, 6AL, and 1BL with 7Lr#1S (=either 7NsS or 7XmS) in several germplasm lines (Chen et al. 2005; Qi et al. 1997, 2008). According to Zhou et al. (2005), the Chinese

wheat “Xiaobing” is a derivative of *T. aestivum*/Agropyron *cristatum* that carries a dominant powdery mildew resistance gene, temporarily named *PmP*. These three genes are the only transferred alien genes that originated from a genome other than **E** of the perennial Triticeae.

Ahmad and Comeau (1991) aimed to transfer apomixes into wheat by producing interspecific hybrids between *T. aestivum* and *E. scabrus* (R. Br.) A. Löve. Unfortunately, *E. scabrus* is not apomictic and they were unsuccessful in obtaining backcross progeny from hybrid plants. Later, transferring apomixis into wheat was attempted with the synthesis of interspecific hybrids between *T. aestivum* and apomictic *E. rectisetus* (Carman and Wang 1992; Wang et al. 1993; Liu et al. 1994; Peel et al. 1997). However, the trait was not fully expressed in the hybrids probably due to the suppressive action of genes for sexual reproduction in wheat. Thus, all addition lines derived from the backcross progenies of original hybrids of this combination (Xue and Wang 1999) exhibited no sign of apomixis, except in one 46-chromosome addition line that was able to repeatedly produce a 23-chromosome offspring, through a very low frequency of parthenogenesis, among other sexual progenies (Fig. 2.2; Wang unpublished). This suggests that even the expression of parthenogenesis, one of processes for apomictic reproduction, requires more than two *E. rectisetus* chromosomes, let alone the

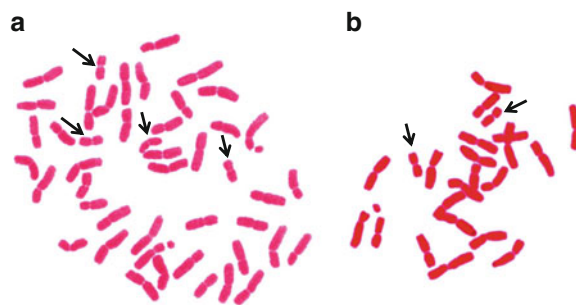


Fig. 2.2 A backcross derivative of *Triticum aestivum* cv. Fukuhokomugi \times *Elymus rectisetus* had the capability of producing seed through parthenogenesis, even though at a very low frequency. The 46-chromosome addition line (a), which had two pairs of alien chromosomes (arrowed) in the wheat genome, produced a 23-chromosome offspring (b) apparently through parthenogenesis, i.e., a $n = 23$ female gamete in the 46-chromosome plant developed into the functional embryo, without being fertilized by a male gamete in the pollen grain, in a seed resulting in the 23-chromosome offspring

more complex apomixis. Today, apomictic wheat remains a dream for wheat researchers.

The most successful utilization of alien genetic resources for wheat cultivar development is exemplified by the Chinese cultivar “Xiaoyan 6” that has been grown on more than 10 million ha. in China since 1980 (Xueyong Zhang personal communication). Xiaoyan 6, a derivative of hybrids between wheat and *Thinopyrum ponticum*, has also been used as a core parent for wheat breeding in China in the past 20 years. Pedigree analysis of the Chinese wheat cultivars showed that there are more than 50 wheat varieties derived from crosses involving Xiaoyan 6. These derivative varieties have been grown on more than 20 million ha. and increased the total wheat grain production by 7.5 billion kg. Xiaoyan 6 has set an unparalleled example in the development and application of wheat varieties through wide hybridization and chromosomal engineering in China. The positive contribution of Xiaoyan 6 to wheat production and breeding in China is possibly due to the possession of three valuable characteristics (1) wide spectrum and durable resistance to stripe rust; (2) tolerance to high temperature, strong light, and hot-dry wind; and (3) superior grain quality suitable for making traditional Chinese wheat food products. For the enormous contribution of Xiaoyan 6 in food production, Chinese Government granted its State Scientific and Technological Award for 2006 to scientist Prof. Li Zhensheng, who developed the cultivar in 1979 and is the tenth Chinese scientist to win this top award. Prof. Li has also introduced chromosome engineering to the breeding of wheat strains with a “nullisomic backcross method,” which has reduced the duration of wheat breeding through distant hybridization to 3.5 years, whereas the previous breeding of “Xiaoyan” took 20 years.

2.7 Development of Genomics Resources

Molecular markers had been developed for chromosomes of diploid *Thinopyrum bessarabicum* and *Th. elongatum*. William and Mujeeb-Kazi (1995) found six diagnostic protein isozymes for the **J** (= **E^b**)-genome chromosomes in the wheat background. Then, Zhang et al. (2002) identified amplified fragment length polymorphism (AFLP) and RAPD markers for five of the

seven **E^b**-genome chromosomes. Markers that were present in the wheat × *Th. bessarabicum* amphidiploid but absent in the five disomic addition lines would be markers for the two missing chromosomes 3**E^b** and 6**E^b**. You et al. (2004) developed specific simple sequence repeat (SSR) marker for **E^c**-genome of *Thinopyrum* spp. using wheat microsatellites.

Collections of annual Triticeae ESTs were available for *Hordeum vulgare*, *S. cereale*, *T. aestivum*, and *Triticum monococcum* (<http://www.plantgdb.org/prj/ESTCluster/progress.php>; accessed on 29 Oct 2009, 16:21 GMT). Barley EST primer sets had been used to find polymorphic markers for identifying alien Triticeae chromosomes in wheat addition lines (Hagras et al. 2005). The number of polymorphic markers distinguishing wheat from some perennial Triticeae ranged from 78 to 572. Again, the **E**-genome in *Th. elongatum* was grouped with **ABD** of wheat by having the lowest number of polymorphic markers between their genomes. The dendrogram from their data did not largely deviate from those based on other molecular phylogenies (Hsiao et al. 1995; Peterson and Seberg 2002; Peterson et al. 2006).

Only recently, EST libraries of *L. cinereus*/*L. triticoide*s hybrid, a mixture of *Elymus wawawaiensis* J.R. Carlson & Barkworth and *E. lanceolatus* (Scribn. & J. G. Sm.) Gould, and *Pseudoroegneria spicata* (Pursh) A. Löve had become available (Bushman et al. 2008). Sequences were obtained in both directions for 16,128 clones of the *Pseudoroegneria* library, 15,360 clones of the *Leymus* library, and 10,368 clones of the *Elymus* library. The EST sequences were assembled into 8,780 unigenes for *P. spicata*, 11,281 unigenes for *Leymus*, and 7,212 unigenes for *Elymus*. The three library databases are available for searching on the ESTIMA Web site (<http://titan.biotech.uiuc.edu/triticeae/>).

For the *Leymus* interspecific hybrid, a bacterial artificial chromosome (BAC) library consisting of over 400,000 clones, resulted from independent digestions of genomic DNA by two restriction enzymes *Bam*HI and *Mbo*I, had been constructed (Larson et al. 2007). This library is being utilized to map agronomically important traits for gene discovery (Larson et al. 2009).

ESTs have also been obtained from wheat alien addition lines using chromosome microdissection techniques in combination with several molecular methods (Jiang et al. 2004, 2005, 2009; Zhou et al. 2008). The alien chromosomes in these addition lines, which had been either treated (e.g., infected by a

pathogen) or untreated (used as the control), were first dissected under an inverted microscope and collected into microcentrifuge tubes for molecular manipulations to clone desired genes. ESTs for disease resistance genes, especially those for BYDV, have been isolated from chromosomes of *Th. intermedium* and then sequenced (Jiang et al. 2004, 2005, 2009). These genomic resources will be useful to develop molecular markers for the application of marker-assisted selection (MAS) by breeders.

2.8 Scope for Domestication and Commercialization

2.8.1 Perennial Wheat

Perennial wheat was another dreamed goal for wheat scientists because it would save money for wheat farmers and reduce soil erosion due to tillage, wind, and water runoff, a concern for soil conservationists. Again, introducing genes for perenniality into wheat by chromosome engineering would be as difficult as making apomictic wheat because these traits are believed to be controlled by many genes present on different chromosomes. This belief was the result of numerous observations that some partial amphidiploids between wheat and perennial Triticeae, especially *Thinopyrum* species, exhibited perenniality (Lyubimova 1991; Cai et al. 2001; Scheinost et al. 2001). After many years of cessation of perennial wheat research in the former Soviet Union as well as United States (Tsitsin 1960; Suneson et al. 1963), the hope was rekindled by the report that gene or genes on a single-chromosome 4E of *Th. elongatum* confers a polycarpic perennial habit to annual wheat (Lammer et al. 2004). Research on perennial wheat is being actively carried on by Prof. Stephen S. Jones and his colleagues at the Washington State University (Cox et al. 2002a, b; Murphy et al. 2007).

2.8.2 Domestication of Perennial Triticeae Species for Bread Making

Because perennial wheat is not yet a reality, several perennial Triticeae species have been exploited and/or improved for using their grains to make bread (Cox et al. 2002a, b). Rodale Institute Research Center (a

division of Rodale Press, Inc.) in Kutztown, PA, had devoted many years of effort to perennial grain development by adapting *Th. intermedium* as a new grain crop called Wild Triga (Wagoner 1990, 1995). Having higher levels of protein (20.8%), fat (3.21%), and ash (2.64%) than wheat, seeds of Wild Triga are used for human consumption. Wild Triga has higher levels than wheat of all essential amino acids except lysine. Naked grain that lost its hulls can be ground into flour to make baked product or cooked whole like rice. Because of their good seed yield and quality and the fact that they lose their hulls somewhat easily as compared to some of the other cultivars, “Oahe” and “Luna” intermediate wheatgrass are the cultivars most suitable for perennial grain production.

The Land Institute in Kansas has evaluated almost 1,500 accessions representing 85 species of *Agropyron*, *Thinopyrum*, *Elymus*, and *Leymus*, along with 2,630 accessions of other species, between 1979 and 1987 (Jackson and Jackson 1999). The species having the greatest potential for domestication was *L. racemosus* (giant or mammoth wildrye). However, among 16 accessions evaluated over 2 years, yields did not exceed 830 kg/ha (Piper 1993), and yield declined rapidly in the following generations. Thus, there is no current breeding program for grain yield in *L. racemosus* and, until selection is undertaken, no conclusions can be drawn regarding its potential for direct domestication as a perennial grain crop.

Leymus arenarius (L.) Hochst. (Lyme grass or beach wildrye) has been used as a food grain since the time of the Vikings (Griffin and Rowlett 1981). Lately, it has been studied as a potential grain crop in Iceland (Anamthawat-Jónsson 1996). This northern European species ($2n = 8x = 56$) is more closely related to *L. racemosus* ($2n = 4x = 28$, southeastern European and central Asian) than to *L. mollis* (Trin.) Pilger (tetraploid, $2n = 4x = 28$, northern American/Pacific) (Anamthawat-Jónsson and Bödvarsdóttir 2001). These three *Leymus* species had been hybridized with wheat to produce amphidiploids (Anamthawat-Jónsson et al. 1997; Anamthawat-Jónsson 1999). But these three perennial Triticeae species have not been fully domesticated to have a significant impact on production of perennial grain crops. It is partly due to “relatively small efforts at domestication, which are within the capabilities of non-profit organizations such as the Rodale Institute or Land Institute, must be expanded to a much larger scale by university, government, or corporate breeding programs if wholly

new perennial grain crops are to be developed” (Cox et al. 2002b).

2.9 Some Dark Sides and Their Addressing

Elymus repens (L.) Gould, commonly named quackgrass, is an introduced noxious weed with aggressively strong rhizomatous growth and complex genomic origins (Fahleson et al. 2008). This weed grass has an almost worldwide distribution and is easily hybridized with species in many genera of Triticeae in nature (Dewey 1984). Thus, it is subjected to strict regulations on seed certification and movements. The cultivar Newhy (Asay et al. 1991), which was developed from derivatives of the cross between hexaploid quackgrass (*E. repens*; **StStStStHH**) and tetraploid bluebunch wheatgrass (*Pseudoroegneria spicata*; **StStStSt**), has seeds so similar to those of quackgrass that growers of this cultivar often had difficulty to get their seed certified on the seed purity.

Although *E. repens* does not pose a great threat of genetic contamination to wheat, barley, and rye, many perennial Triticeae species are capable of producing unreduced gametes and hybridizing with other species naturally. The best example is that of *Pascopyrum smithii* (Rydb.) A. Löve ($2n = 8x = 56$; **StStHHNsNsXmXm**), which originated from the natural hybridization between an *Elymus* species (**StStHH**) and a *Leymus* species (**NsNsXmXm**). The *Elymus* species arose from a hybrid between *Pseudoroegneria* (**StSt**) and *Hordeum* (**HH**), whereas *Leymus* arose from that between *Psathyrostachys* (**NsNs**) and an unknown (**XmXm**) species (Jones et al. 2000; Redinbaugh et al. 2000). Therefore, transgenics for herbicide resistance in perennial Triticeae species should not be pursued due to the concern of gene flow from wild Triticeae to annual cereals (Wang and Jensen 2009).

2.10 Conservation Initiatives

Loss of wilderness from human activities (such as home building, road construction, and recreation, etc.) had led to extinction of many species including

plants and animals. For example, China has put *Psathyrostachys huashanica* Keng on the list of endangered species. Seed of this species are either not available in gene banks or have lost germinability. Because this species has a unique karyotype (Hsiao et al. 1986) for the **Ns**-genome, preserving it both in situ and ex situ shall be a very important conservation issue in China.

Wheatgrasses and wildryes are being preserved as seed in many Gene Banks, with the US National Plant Germplasm System (NPGS) located in Pullman, Washington, holding the largest number of accessions (Wang and Jensen 2009). NPGS lists approximately 610 accessions of *Agropyron* (3 species), 1,000 *Elymus* accessions (over 300 species/hybrids), 229 accessions of *Pseudoroegneria* (8 species), 534 accessions of *Thinopyrum* (12 species), 17 accessions (3 species) of *Elytrigia*, 450 accessions of *Leymus* (28 species), 31 accessions of *Pascopyrum* (1 species), and 86 accessions of *Psathyrostachys* (4 species).

From this review, it is obvious that *Th. intermedium* and *Th. ponticum* had been the two most valuable wild relatives contributing a wide range of desirable traits to wheat cultivar development (Table 2.7). Firstly, it is due to the fact that these two species have genes for resistance to many diseases and pests including leaf rust, stem rust, stripe rust, common root rot, wheat scab, wheat streak mosaic virus (WSMV), BYDV, greenbug, and wheat curl mite (Friebe et al. 1991, 1992; Chen et al. 2003; Li et al. 2003, 2004, 2005; Shen and Ohm 2007; Jiang et al. 2009; Xu et al. 2009), tolerance to abiotic stresses such as drought, high temperature, and salinity (Chen et al. 2004; Trethowan and Mujeeb-Kazi 2008), perennial growth habit (Cai et al. 2001), and grain quality traits such as high protein content (Feng et al. 2004; Chen et al. 2007). Secondly, it can be attributed to the fact that these two species contain the basic genomes **E**- (or **J**-) and **St**- that are closely related to **A** and **D** of bread wheat (see Sect. 2.3). *Th. intermedium* is rhizomatous, whereas *Th. ponticum* is caespitose. Both of them are native to Europe and western Asia but were introduced and well established in North America. Because of their polyploidy nature, these two species could have multiple origins involving different progenitor species in different geographic areas at different time scales. Therefore, there should be a great wealth of genetic variability and molecular polymorphism (García et al. 2002) worthy of being exploited by breeders and

biologists, respectively. Collection, characterization, and preservation of these and other *Thinopyrum* species should be emphasized by government and non-government organizations that are concerned about genetic diversity and natural heritage.

2.11 Recommendations for Future Actions

Perennial Triticeae species such as wheatgrasses (*Agropyron*) and wildryes (*Psathyrostachys*) are important grasses that serve not only as forage crops but also as tertiary gene pools for wheat improvement. Many desirable genes that are absent in wheat, particularly those for resistance or tolerance to biotic and abiotic stresses, could be found in these wild grasses. As the environmental conditions deteriorate, shortage of clean fresh water will make drought- and salt-tolerant wheat cultivars necessities for keeping mankind from hunger. Similarly, the appearance of new races or biotypes of wheat pests requires the continuing search and incorporation of new disease/insect resistance genes into wheat cultivars. These genes are oftentimes present in wild grasses related to wheat and can be introgressed into wheat through chromosome engineering and new molecular tools. Furthermore, some perennial Triticeae grasses also carry desirable genes for wheat grain quality that may improve bread-making or nutritional values (Feng et al 2004; Chen et al. 2007). This prospect needs more future attention to fully exploit the potential of the tertiary gene pool.

With climate change and energy shortage becoming hard-pressing problems for the whole world, perennial wheat and biomass production from perennial wheatgrasses and wildryes are two prospects that may contribute to the solution of these problems. The former can reduce the use of energy by eliminating the tillage and seeding operations. The latter can produce alternative biofuels to supplement the fossil fuel. These two areas of research certainly will receive more emphasis from this moment on.

Conservation of these wheat-relative grasses is pivotal to ensure continuing success in wheat improvement for sustainable food production. Both in situ and ex situ conservation of the wild germplasm are needed. As ex situ conservation effort intensified, cryopreservation of DNA samples representing each

species should be undertaken to supplement the seed storage method. Planning collecting expeditions of new accessions or species should take into consideration targeted traits and the favorable environmental conditions for such traits to select likely geographic regions to find plants carrying desirable genes. For example, resistance to Fusarium head blight (wheat scab, a destructive disease in the warm and humid wheat-growing areas of the world) was found in many perennial Triticeae species including *L. racemosus* (syn. *Elymus giganteus* Vahl.), *Roegneria kamoji* (Ohwi) Ohwi ex Keng (syn. *E. tsukushiensis* Honda), *R. ciliaris* (Trin.) Nevski [syn. *E. ciliaris* (Trin.) Tzvelev], and *Dasypyrum villosa* L. (Oliver et al. 2005) that are all growing in humid regions (Cai et al. 2005). Characterization of wild Triticeae grasses for desirable traits still needs to be strengthened. A global network of regional gene banks holding seed and/or DNA samples of these wheat relatives must also encourage the exchanges of materials and information by making them freely available to bona fide scientists to use in wheat germplasm enhancement projects.

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