

Elymus in South America – An Overview

Elymus i Sydamerika – en översikt

Jonatan Leo



Elymus in South America – An Overview

Elymus i Sydamerika – en översikt

Jonatan Leo

Swedish University of Agricultural Sciences, Department of
Plant Breeding, jonatan.leo@slu.se

Place of publication: Epsilon, SLU

Year of publication: 2020

Title of series: Introductory paper at the Faculty of Landscape Architecture,
Horticulture and Crop Production Science

Part number: 2020:1

Online publication: <https://pub.epsilon.slu.se>

Bibliografic reference: Leo, J. (2020). *Elymus in South America - An Overview*. Epsilon, SLU: Sveriges lantbruksuniversitet. (Introductory paper at the Faculty of Landscape Architecture, Horticulture and Crop Production Science, 2020:1).

Keywords: Elymus, Triticeae, Poaceae, South America

Swedish University of Agricultural Sciences

Faculty of Landscape Architecture, Horticulture and Crop Production Science

Department of Plant Breeding

Abstract

The tribe Triticeae (in Poaceae, the grass family) contains some of the economically most important crop species in the world such as wheat, barley and rye, as well as several more or less locally important forage crops, especially in Asia and North America. The wild species of the tribe constitutes an underutilized genetic resource for crop improvement through selection and breeding. Species within the tribe could potentially be used directly as forage crops, after initial selection from wild material, or as a resource in future forage or crop improvement. In South America, the two major genera of Triticeae are *Hordeum* and *Elymus*. *Hordeum* has been well collected in South America and the taxonomy and phylogeny have been studied, but there is less knowledge about *Elymus* from this continent and far less material has been collected. Fundamental knowledge of taxonomy, nomenclature, phylogeny, genetic variation, population structures and gene flow needs to be investigated. Further information about the ecology, agricultural qualities and nutritional content is needed for optimal utilization and conservation. This paper gives an overview of the characteristics of Triticeae in general, and *Elymus* in South America in particular. The purpose is to map the state of knowledge and identify gaps for future research.

Keywords: Triticeae, Elymus, genetic resources, forage crops

Sammanfattning

Triticeae (i Poaceae, gräsfamiljen) innehåller några av de ekonomiskt viktigaste grödorna i världen, som vete, korn och råg, samt flera lokalt viktiga fodergrödor i Asien och Nordamerika. Vilda arter inom Triticeae utgör en underutnyttjad genetisk resurs för utveckling och förbättring av nya grödor genom urval och förädling. Arter kan användas direkt som fodergrödor, men också som en resurs för förädling av existerande grödor. Triticeae i Sydamerika är framför allt representerade av släktena *Hordeum* och *Elymus*. Arter av *Hordeum* har samlats in i Sydamerika och det finns en god kunskap om deras släktskap och taxonomi, men det finns inte mycket studier om *Elymus*. Grundläggande kunskaper om taxonomi, nomenklatur, fylogeni, genetisk variation, populationsstrukturer och genflöde behövs för att uppskatta den potentiella användningen av de inhemska arterna. Information om ekologi, jordbruksegenskaper och näringsinnehåll är också önskvärt. Denna artikel ger en översikt över egenskaperna hos Triticeae i allmänhet, och *Elymus* i Sydamerika i synnerhet, som genetiska resurser. Syftet är att kartlägga kunskapsståndet och identifiera luckor för framtida forskning.

Keywords: Triticeae, Elymus, genetiska resurser, foderväxter

Table of contents

1	Introduction	4
2	Triticeae	5
2.1	Classification of the tribe	6
2.2	Triticeae as a genetic resource	7
3	Elymus	8
3.1	Classification of the genus	8
3.2	Polypoidy and Genome constitution	9
3.3	Elymus as a genetic resource	12
4	Elymus in South America	13
4.1	Description of Elymus species in South America	15
4.2	Species related to Elymus in South America	17
4.3	Elymus in South America as a genetic resource	19
5	Elymus in Chile	20
	References	21

1 Introduction

At the same time as the global climate is changing, affecting agricultural environments, the human population is not only growing but demands more, better and cheaper food. This poses major challenges in terms of crop adaptation, improvement and diversification to create global resilient food systems, to not only survive and stay healthy, but also to meet higher market demands and competing land use. An intensified breeding of established crops, as well as domestication of new crops, are necessary to meet these challenges.

Grasses were among the first domesticated crops and they are still the main staple food of the world (Lu & Ellstrand, 2014). The tribe Triticeae (in Poaceae, the grass family) contains some of the economically most important species, such as wheat, barley and rye. Several members of the tribe are also important forage crops, especially in Asia and North America. The wild species of the tribe constitute underutilized genetic resources for crop improvement through selection and breeding and new domestication. Much research has been done to increase the knowledge and utilization of wild species, but there are still knowledge gaps that need to be filled. In South America, the two major genera of Triticeae are *Hordeum* and *Elymus*. The taxonomy and phylogeny of *Hordeum* in South America have been closely studied (von Bothmer *et al.*, 1995; Brassac & Blattner, 2015), but there is much less known about *Elymus* from this continent. The main research of *Elymus* has been conducted in North America and Eurasia and focused primarily on taxonomy, genetic diversity and phylogeny. Fundamental knowledge of taxonomy, nomenclature, phylogeny, genetic variation, population structures and gene flow are needed to estimate the potential usefulness of the native species and to build efficient and sustainable breeding programs and conservation strategies. Solid information about the ecology, agricultural qualities and nutritional content is also desirable.

This paper gives an overview of Triticeae in general, and *Elymus* in South America in particular. The purpose is to map the state of knowledge, identify gaps for future research and outline research areas.

2 Triticeae

The tribus Triticeae Dumort. in the grass family (Poaceae) comprises some of the oldest and most economically important crops such as *Triticum aestivum* L. (bread wheat), *T. turgidum* subsp. *durum* Desf. MacKey (durum wheat), *Secale cereal* L. (rye) and *Hordeum vulgare* L. (barley), as well as many perennial forage grasses, weeds, sand binders and even ornamentals (Barkworth & von Bothmer, 2009). The actual number of species in the tribe is imperfectly known which is partly due to the fact that there are no generally accepted principles for species delimitation in the tribe. The reported number by different authors varies between 350–500 annual and perennial species (Dewey, 1984; Löve, 1984; West *et al.*, 1988; Tzvelev, 1989), distributed in almost all temperate regions of the world. Triticeae constitutes a vast gene pool for actual or potential cereal improvement, with traits such as pathogen and pest resistance, stress adaptation, salt tolerance, cold hardiness, nutrient content, apomixis and perennial life form (von Bothmer, 1992; Lu, 1993; Diaz, 1999). The rather weak hybridization barriers between genera makes it possible to induce new natural and domesticated variation by combination breeding. The breeding efforts involving wild material from Triticeae have mainly focused on improving wheat, rye and forage grasses, but there is also a great potential for producing new food and forage crops (Lu, 1993).

All species in Triticeae are characterized by a simple spike with one or two, rarely more, sessile spikelets per node. Open leaf sheaths, membranous ligules and ovaries with a hairy top differentiate Triticeae from other grasses (Barkworth & von Bothmer, 2009). Members of Triticeae are distributed in almost all temperate regions with a center of diversity, defined as the highest number of species, in China (Barkworth, 2005).

The taxonomic treatment of Triticeae has changed over time mainly based on access to newly collected material and to new data achieved by new technological advancements. New species and generic concepts have been developed as a consequence of differences in evaluation methods and priorities of taxonomic characters. Several taxonomic treatments within Triticeae are still under dispute (Wang *et al.*,

1994; Yen *et al.*, 2005; Baum *et al.*, 2011). A large number of species, together with the vast distribution area, makes it difficult to establish a comprehensive and easily used system, which also represents relationships and phylogenetic patterns.

Linnaeus (1753) was the first to describe the five genera *Elymus*, *Triticum*, *Aegilops*, *Secale* and *Hordeum*, which are included in Triticeae today. Linnaeus' classification is artificial with an emphasis on easily identified morphological traits, thus not mirroring phylogenetic relationships. His classification is considered outdated, but the taxonomic names are still valid. Several other pre-Darwinian taxonomists based their classification of Triticeae on primarily morphological traits, mainly comprising a few inflorescence characters. Nevski (1934) was the first author who suggested a generic taxonomy of the tribe reflecting evolutionary relationship and his treatment included 25 genera. The ease with which species in Triticeae hybridize led to the suggestion to lump all species in Triticeae into a single genus (Stebbins, 1956; Stebbins & Snyder, 1956). Löve (1982) disagrees on this broad generic circumscription on both taxonomical and practical grounds and claims that crossability is considerably restricted between species in the tribe. Morphological data is, however, inadequate for phylogenetic reconstruction in Triticeae due to instability and homoplasy (Kellogg, 1989).

In the beginning of the 20th century, the taxonomical treatment of the tribe differed between geographical regions and there was a need for an international agreement on generic boundaries (Barkworth, 2005). The accumulation of cytogenetic data in the 1960s and 1970s led to two independent works by Löve (1984) and Dewey (1984) suggesting genomic constitutions as the base for generic circumscription. A genus is circumscribed as monogenomic if all species have the same haplome or haplome combinations. A haplome is here defined as the basic or monoploid set of chromosomes. Triticeae constitutes both diploid and polyploid species with the basic chromosome number seven ($x=7$). Monogenomic delimitation is accepted today by most authors in the world as the fundament in Triticeae classification. Examples of generic haplome designations are presented in Table 1. Most described genera are diploids or sometimes autopolyploids and with one type of haplome, like *Agropyron* (**P**), *Pseudoroegneria* (**St**) and *Secale* (**R**). Other genera are allopolyploids and defined as a specific combination of two or more parental haplomes, such as *Anthosachne* (**StHW**) with hexaploid species derived from *Pseudoroegneria* (**St**), *Hordeum* (**H**) and *Australopyrum* (**W**). Bread wheat, *Triticum aestivum* (**ABD**), is an allohexaploid with haplomes from *Triticum turgidum* (**AB** genome) and *Aegilops tauschii* (**D** genome) (Chalupska *et al.*, 2008). Genera such as *Aegilops* (**B**, **C**, **D**, **M**, **N**, **U** or **X**) and *Hordeum* (**H**, **Xa**, **Xu**, **I**) have several haplomes. *Thinopyrum* has one unifying haplome (**E**) without or together with additional one or several haplomes (**P**, **St** or **L**), and *Elymus* has one unifying haplome

(**St**) together with additional one or several haplomes (**H**, **Y** or **W**). Sometimes variation within haplomes is noted, as in *Psathyrostachys* (**N**^{*j, f or h*}).

Table 1. Example of genera in Triticeae with haplome constitution. Based on Barkworth and von Bothmer (2009) and Wang *et al.* (1994).

Genus	Genomic composition
<i>Aegilops</i>	B, C, D, M, N, U or X
<i>Agropyron</i>	P
<i>Anthosachne</i>	StHW
<i>Australopyrum</i>	W
<i>Douglasdeweya</i>	StP
<i>Elymus</i> ¹	St plus at least one of H , Y or W
<i>Festucopsis</i>	L
<i>Hordeum</i>	H, Xa, Xu or I
<i>Leymus</i>	NX
<i>Psathyrostachys</i>	N ^{<i>j, f or h</i>}
<i>Pseudoroegneria</i>	St
<i>Secale</i>	R
<i>Thinopyrum</i>	E , sometimes with P , St , or L
<i>Triticum</i> ¹	A, AB, AAB, ABD
Unknown ancestor	Y

¹Most commonly accepted

The genome-based classification has been criticized, especially the years following the first proposal by Löve (1984) and Dewey (1984). The arguments are based on “maximum information” vs. “single character” in classification, possible polyphyletic origins of genome combinations and a general concern for problems connected to name changes (Gupta & Baum, 1989; Seberg & Frederiksen, 2001). Baum *et al.* (1987) and Seberg (1989) argue that genome analysis are useful in phylogenetic work but should not be considered as an ascertainment of generic delimitations since a monophyletic relationship among combination of genomes cannot be ascertained without additional knowledge about relationships. Haplomes should be used rather as a character among others. They claim that a sound taxonomy should be based on conclusive evolutionary relationships and not restricted to a single defining character. Petersen *et al.* (2011) also criticize the genome-based classification and argue that the lack of chromosome pairing in meiosis is most likely a consequence of mutations in the mechanism controlling meiosis and not to general sequence differences. It is hence not a satisfactory character for phylogenetic conclusions due to the risk of potential homoplasies. Even if the new criteria of generic delimitation was criticized when first suggested (Baum *et al.*, 1987), most circumscriptions of today take genome combinations into consideration. Cytogenetic data cannot be

used as a theoretical base for hierarchic phylogenetic inferences due to the possibility of homoplasy. In addition, the character is not universal and cannot be used in all plant groups on all taxonomical levels. However, the character is suitable for understanding the current segregation of taxa as an important evolutionary mechanism. As shown above in Table 1, the system is not consistent and some genera have several haplomes with variations within one genus (i.e. *Hordeum*, *Aegilops* and *Elymus*). For a discussion on *Elymus* haplome combinations, see below. The generic delimitation should be seen as a convention and has served Triticeae research well. Today, most articles follow the genome designation of diploid genera in Triticeae suggested by Wang *et al.* (1994). A comprehensive review of the historical taxonomy of Triticeae can be found in *Taxonomy of the Triticeae: a historical perspective* by Barkworth (1992).

Most treatments of Triticeae are incomplete (Barkworth & von Bothmer, 2009). Some studies only have regional scopes, others are based on one or a few genera, or a specific group of species not representing the whole genus. Broader publications usually only include generic circumscription without treatments of individual species. Löve's (1982) work is the only comprehensive treatment of the whole tribe and includes a checklist with genera as well as species (Barkworth & von Bothmer, 2009). Dewey (1984) limited his paper only to include perennial genera.

Molecular techniques based on sequencing data have contributed to new insights into the evolution of Triticeae (Bernhardt *et al.*, 2017; Edet *et al.*, 2018). It is, however, hard to define cladistic monophyletic groups also with the new techniques. Multiple polyploidization and reticulate evolution makes several genera of Triticeae paraphyletic (Figures 1 and 2) (Barkworth, 1992; Dvorak & Zhang, 1992; Brassac & Blattner, 2015). Baum *et al.* (2015) argue that molecular markers should be used to circumscribe species within genome combinations due to the ambiguity and impreciseness of morphological characters.

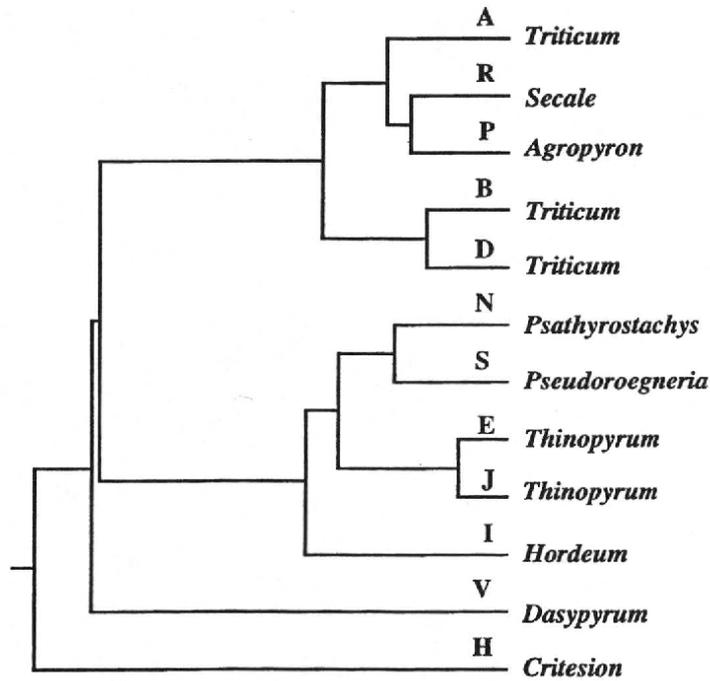


Figure 1. Relationships of some of the haplotypes within Triticeae (von Bothmer & Salomon, 1994) based on Monte *et al.* (1993). *Critesion* is usually included in *Hordeum*.

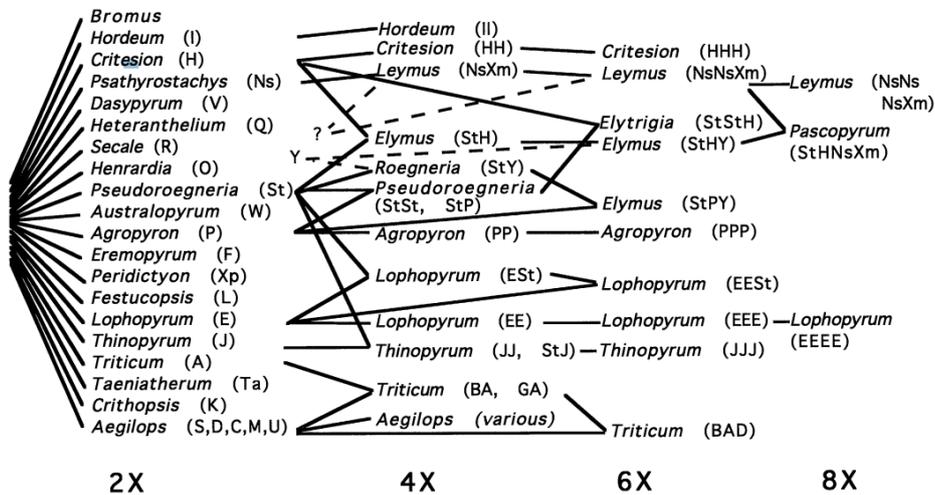


Figure 2. Relationships between diploids and polyploids from Kellogg *et al.* (1996).

3 *Elymus*

Elymus L. (wheatgrasses) is the largest genus in Triticeae with approximately 150 species according to the generic delimitation used here (Löve, 1984). The species are perennials, densely to loosely caespitose (occasionally rhizomatous) and presumably most self-pollinating with short anthers (1–5 mm) (Löve, 1984; Diaz, 1999; Sun & Salomon, 2009). Spikelets are 1–2, occasionally up to five, per spike node and with internodes less than half as long as the spikelets (Barkworth & von Bothmer, 2009). The genus is distributed mostly in temperate areas in the world in both the northern and southern hemispheres with a main diversity center in central Asia. It inhabits grasslands, semi-deserts, mountain slopes and valleys, and grows among bushes, in forests and forest margins (Lu, 1993; Salomon *et al.*, 1997). The basic chromosome number is $x = 7$ and all species are tetra-, hexa- or octaploids. The taxonomy and evolutionary relationships are complex due to the morphological variation and the polyphyletic origin of the group, and there are still disagreements on generic and species delimitations (Lu, 1993). The genus is morphologically diverse with huge variation both within and between species (Sun & Salomon, 2009). Morphology is also affected by the environment due to a high degree of phenotypic plasticity.

3.1 Classification of the genus

Baum *et al.* (2015) describe *Elymus* as a “dustbin” genus in which species were assigned to if they did not belong to another Triticeae genus. They describe the history of *Elymus* classification as a process with different phases where new progressive approaches emerged as a consequence of the development of new research techniques. Conventions of how genera should be defined have changed, and still, no classification relies exclusively on an evolutionary approach based on phylogenetic relationships. The number of recognized species in the genus varies immensely

between authors depending on the adopted generic delimitation and species recognition.

The genus *Elymus* was first described by Linnaeus (1753) and the classification has traditionally been based on morphological traits. However, a phylogenetic classification based solely on morphological characters is not possible because of the large number of taxa and the low number of comparable morphological characters (Petersen *et al.*, 2011). It is often difficult to delimit species based on morphological characters due to high variation and phenotypic plasticity (McMillan & Sun, 2004).

The main morphological character used to differentiate *Elymus* from close related genera have primarily comprised the inflorescence with single versus multiple spikelets per rachis node. Bentham (1881), Hitchcock (1951), Baum (1983) and Keng (1989) all have a this narrow circumscription of *Elymus* and restrict it to species with multiple spikelets per rachis node. The species with single spikelets are considered to belong to other genera such as *Agropyron* and *Roegneria*. Tzvelev (1976), Meledris (1980) and Löve (1984) on the other hand have a wider circumscription and consider the number of spikelets as an insignificant character. The separation between species with single and multiple spikelets per rachis node has no support in phylogenetic studies (McMillan & Sun, 2004). Different taxonomic classifications have traditionally been followed in different geographical areas; Hitchcock in North America, Meledris and Tzvelev in Europe and Russia, and Keng in China (Barkworth, 1992; Lu, 1993; Sun, 2014).

The proposal to determine generic delimitation in Triticeae based on cytogenetics (karyology and chromosome pairing in interspecific hybrids) made by Löve (1984) and Dewey (1984), contributed to a change in the *Elymus* research community for approaching a stabilization of taxonomy and for a standardized nomenclature. All species with the same haplome or combination of haplomes are considered to belong to the same genus. In the 1990's and onwards, molecular data from DNA sequences have been introduced, but the generic delimitations are still genomically based in most contemporary studies (Baum *et al.*, 2015). Petersen *et al.* (2011) argue that a combination of morphology, cytology and molecular data should be used to establish a classification of *Elymus*. The major issue is still how narrow *Elymus* should be circumscribed since the genus holds several different combinations of genomes.

3.2 Polyploidy and genome constitutions

All species in *Elymus* are allopolyploids and originating from multiple intergeneric polyploidization events (Svitashev *et al.*, 1996). There is a variation in polyploid

levels where the majority (75%) are tetraploids with two non-homologous chromosome sets ($2n = 4x = 28$), some (20%) are hexaploids ($2n = 6x = 42$) and a few (5%) are octaploid ($2n = 8x = 56$) (Dewey, 1984; Löve, 1984; Diaz, 1999). The genome relationships have been studied for decades with mainly traditional cytogenetic methods and are generally well documented.

Elymus is a heterogenomic group and five different basic haplomes from closely related genera have so far been identified, following Wang *et al.* (1994): **St** (*Pseudoroegneria*: mostly diploids in Asia and N America), **H** (*Hordeum*: diploids, tetraploids and some hexaploids widespread in most temperate areas in the world), **P** (*Agropyron*: Central Asiatic diploids, tetraploids and hexaploids), **W** (*Australopyron*: only in one hexaploid Australasian *Elymus* species), **Y** (unknown origin: found in Asiatic tetraploids and hexaploids in combination with other genomes) (Dewey, 1984; Lu, 1993; Svitashv *et al.*, 1996; Sun *et al.*, 1997; Liu *et al.*, 2006; Sun *et al.*, 2008; Petersen *et al.*, 2011). Each species contains two or three different combinations of haplomes with only the **St**-genome represented in all species. The tetraploids exhibit **StH** and **StY** combinations, and the other haplomes are included in the hexaploid and octaploid combinations: **StH**, **StHH**, **StStH**, **StStHH**, **StY**, **StHY**, **StStY**, **StPY** and **StWY** (Lu, 1993; Diaz, 1999). Yen *et al.* (2005) fulfilled the strict generic classification based on genomic constitution and separated *Roegneria* (**StY**), *Kengyilia* (**StYP**), *Australopyrum* (**W**) and *Stenostachys* (**HW**) from *Elymus* (**StH**). Several names are considered as sections rather than having generic status (Salomon & Lu, 1992). The combination of **StH**, **StY**, and **StW** with hexa- and octaploids are considered by some authors as a broad circumscription of the genus (*Elymus* s.l.), while only including **StH** is considered to be the narrow sense (*Elymus* s.s.) (Barkworth & von Bothmer, 2009).

The **StY** genome species are restricted to Central and East Asia while the **StH** genome species are distributed all over the world, in subtropical to arctic habitats (Sun & Ma, 2009). *Pseudoroegneria* is the most likely female genome donor of the **St** haplome for both combinations (McMillan & Sun, 2004; Mason-Gamer *et al.*, 2010; Petersen *et al.*, 2011). Both *P. spicata* and *P. stipifolia* have been suggested as potential **St** donors, but it is still unclear if the **St** genome derives from one or several *Pseudoroegneria* species (Sun, 2014). Only two characters correlate with genome combination – palea apex shape and size of cilia of palea. Characters such as spike orientation, number of spikelets per rachis node and shape and length of the lemma awn do not correlate with genome combination (Salomon & Lu, 1992).



Figure 3. Morphological characters, palea apex shape and size of cilia of palea, that correlate with genome combination – **StH** (left; *E. caninus*) and **StY** (right, *E. gmelinii*). From Salomon and Lu (1992).

The analyses of genome constitution have been inferred by several methods such as; studying meiotic chromosome pairing in intergeneric and interspecific hybrids (Seberg & von Bothmer, 1991; Jensen, 1993); comparison of karyotypes by Giemsa C- and N-banding (Linde-Laursen *et al.*, 1994; Linde-Laursen & Seberg, 1999); studying variation in repeated nucleotide sequences (Dubcovsky *et al.*, 1997); using molecular cytogenetics and *in situ* hybridization (FISH-GISH) (Tomas *et al.*, 2012). Molecular markers can also be used to differentiate between the genome combinations. Baum *et al.* (2015) used 5S NTS as a marker to identify genome (haplome) compositions. Svitashv *et al.* (1998) show that genome-specific molecular markers (RFLP and RAPD) may be used to differentiate between different genome constitutions. The evolutionary value of genome combination is shown from crossing experiments with no inter-fertility between species in different genome combinations (Salomon & Lu, 1992), whereas there is a rather high crossability of species with the same genomic combinations.

The phylogenetic framework is based on a presumption of divergent evolution, which makes reticulate evolution with hybridizations between independent evolutionary lines difficult to handle. Reticulate evolution through frequent interspecific hybridization and introgression is common and karyotype rearrangements by inter-genomic translocations have been documented in Triticeae (Devos & Gale, 2000; Wang *et al.*, 2010), including *Elymus scabrifolius* (Tomas *et al.*, 2012). All these factors make it difficult to resolve the phylogeny even within smaller species groups of the genus, though attempts have been made (Sun, 2014). The genus is considered polyphyletic also within a particular genome combination and may have arisen more

than once (Soltis & Soltis, 1993). Multiple origins of morphologic similar species have also been reported (Yan & Sun, 2012).

Species with the **StH** genome combination occur all over the world from sea level up to 5000 m in altitude (Dewey, 1984; Löve, 1984). The group contains approximately 50 species and is very diverse in both habitat preference and morphology, with species reaching between 5 cm and 2 m (Sun & Salomon, 2009). The variation makes them interesting from a genetic resource perspective. The main diversity, defined as the number of species, occurs in the northern hemisphere, but a high diversity can also be found in the southern hemisphere, especially in Chile and Argentina. Only the **StH** combination occurs in South America (Seberg & Petersen, 1998).

Species in America and Eurasia originate most likely from different, independent *Pseudoroegneria* × *Hordeum* hybridization events showing different **H**-genome donors, and **StH** hence constitutes a polyphyletic group (Jaaska, 1992; Linde-Laursen *et al.*, 1994; Sun *et al.*, 2008). Dubcovsky *et al.* (1997) found specific restriction fragments in *Hordeum* and *Elymus* from the New World which were absent in *Hordeum* and *Elymus* from the Old World (*E. tilcarensis* from South America was an exception). The **St** genome in *E. trachycaulus* in North America originates maternally most likely from North American *P. strigosa*, *P. stipifolia*, *P. spicata* or *P. geniculata* (Zuo *et al.*, 2015). However, reciprocal hybrids cannot be excluded, and polymorphic **H** genomes indicate a polyphyletic origin either from multiple independent hybridization events or introgression by subsequent backcrossing (Zuo *et al.*, 2015). It is still not clear if morphologically similar species are genetically closely related to each other.

4 *Elymus* in South America

Only three genera in Triticeae are today recognized as native in South America; *Hordeum*, *Elymus* s.l. and *Leymus* according to the Catalogue of New World Grasses (Campbell & Soreng, 2003). Seberg and Linde-Laursen (1996) and Seberg and Petersen (1998) also include the monotypic genus *Eremium* (syn. *Elymus erianthum*). All *Elymus* species in South America are endemic except a few introduced taxa. The major diversity is in the southern cold temperate parts of Chile and Argentina (Seberg & Petersen, 1998). Southern South America is considered one of the major center of Triticeae diversity worldwide, i.e. an area where the highest number of species are distributed (von Bothmer & Salomon, 1994). Apart from the native species, there are also some introduced weedy taxa, such as wild barley (*Hordeum murinum*), couch grass (*Elymus repens* or *Elytrigia repens*) and lyme grass (*Leymus arenarius*), the latter as a sand binder in coastal areas.

Based on the number of spikelets per node, *Elymus* s.l. has traditionally been divided into *Agropyron*, with one spikelet per node, and *Elymus* s.s., with two or more spikelets per node. However, the inclusion of South American *Agropyron* species in *Elymus* is supported by morphological and cytological evidence (Runemark & Heneen, 1968) as well as genome relationships (Dewey, 1984; Löve, 1984). Variation of spikelet number has, for example, been documented in some species, e.g. *E. angulatus* and *E. scabriglumis* (Seberg & Petersen, 1998). *Agropyron* is now restricted to a few species, called crested wheatgrasses, naturally occurring in Asia containing only the **P**-genome and used as forage grasses. The traditional separation of *Elymus* s.s. and *Agropyron* s.l. is, however, used in all floras of Triticeae in South America prior to the revision by Seberg and Petersen (Parodi, 1940; Nicora, 1978; Moore, 1983; Seberg & Petersen, 1998).

Parodi (1940) revised the genus *Agropyron* in South American, now included in *Elymus*, and recognized 12 species (Table 2). Today, ten of them are considered as naturally occurring species, one as an intergeneric hybrid (*E. elymoides*, syn. \times *Elyhordeum elymoides* (Hack.) J.H. Hunz. & Xifreda), and one as an introduced

species (*E. repens* (L.) Gould, syn. *Elytrigia repens* (L.) Desv. ex Nevski). The latest revision of *Elymus* in South America was made by Seberg and Petersen (1998), which place the species of *Agropyron* in *Elymus* s.l. (Table 2.). They base their taxonomy on morphological measurements from herbarium and living material and recognize seven naturally occurring species and one common hybrid. Löve (1984) lists 30 taxa (29 species and one variety) from South America but most of them are considered as synonyms today. Flora of Argentina published Monocotyledoneae, Poaceae: Pooideae, including *Elymus*, in 2012 and recognizes six species (Seberg & Petersen, 2012) (Table 2).

Additionally, two local treatments of *Agropyron* should be acknowledged; Flora of Patagonia by Nicora (1978) and Flora of Tierra del Fuego by Moore (1983) (Table 2). Both points out the difficulty in species delimitations in the Patagonian region due to a high diversity and intermediate types. Nicora (1978) recognized seven species in the Patagonian region. Moore (1983) recognized four naturally occurring species on Tierra del Fuego, but he also comments that his treatment most likely simplifies the variation in the region. In total, 25 epithets on South American *Elymus* species have been validly published, most of them by Philippi (Seberg & Petersen, 1998).

This paper follow Campbell and Soreng (2003) and the Catalogue of New World Grasses which recognizes eight *Elymus* species in South America. All tetraploids have been identified with the genome combination **StH** and all hexaploids as **StHH**, thus the same combinations of basic genomes as the North American *Elymus* species (Dubcovsky *et al.*, 1989; Seberg & von Bothmer, 1991; Dubcovsky *et al.*, 1992; Linde-Laursen *et al.*, 1994; Lewis *et al.*, 1996; Dubcovsky *et al.*, 1997). Phylogenetic analysis based on the *rbcL* gene suggests that all *Elymus* in America share a common ancestor in *Pseudoroegneria*, probably *P. spicata* or a closely related species, as the **St** genome donor (Seberg & Linde-Laursen, 1996). The **St** genome is more closely related to North American *Pseudoroegneria spicata* and *Agropyron dasystachyum* than to Asian *P. libanoticum* and *A. angustiglume*, and since no *Pseudoroegneria* species is native to South America, it is most likely that all *Elymus* in South America have a North American origin (Linde-Laursen *et al.*, 1994). However, a historical occurrence of *Pseudoroegneria* cannot be excluded.

Table 2. List of recognized *Elymus* and *Agropyron* taxa in South America from comprehensive publications. All South American *Agropyron* species are now included in *Elymus*.

Parodi (1940)	Nicora (1978)	Moore (1983)	Löve (1984)	Seberg and Petersen (1998)	Campbell and Soreng (2003)	Seberg and Petersen (2012)
South America	Patagonia	Tierra del Fuego	South America	South America	South America	Argentina
<i>A. mendocinum</i>	<i>E. erianthus</i>	<i>E. agropyroides</i>	<i>E. agropyroides</i>	<i>E. angulatus</i>	<i>E. angulatus</i>	<i>E. angulatus</i>
<i>A. elymoides</i>	<i>E. arenarius</i>	<i>A. pubiflorum</i>	<i>E. andinus</i>	<i>E. cordilleranus</i>	<i>E. cordilleranus</i>	<i>E. magellanicus</i>
<i>A. remotiflorum</i>	<i>E. antarcticus</i>	<i>A. fuegianum</i>	<i>E. antarcticus</i>	<i>E. glaucescens</i>	<i>E. magellanicus</i>	<i>E. mendocinus</i>
var. <i>macrochaetum</i>	<i>E. agropyroides</i>	<i>A. elymoides</i>	<i>E. araucanus</i>	<i>E. mendocinus</i>	<i>E. mendocinus</i>	<i>E. patagonicus</i>
<i>A. patagonicum</i>	<i>E. patagonicus</i>		<i>E. asper</i>	<i>E. parodi</i>	<i>E. patagonicus</i>	<i>E. scabrifolius</i>
var. <i>festucoides</i>	<i>E. rigescens</i>		<i>E. barbatus</i>	<i>E. patagonicus</i>	<i>E. scabrifolius</i>	<i>E. scabrifolius</i>
var. <i>austral</i>	<i>E. gayanus</i>		<i>E. bolivianus</i>	<i>E. scabrifolius</i>	<i>E. scabrifolius</i>	
<i>A. scabrifolium</i>	<i>E. andinus</i>		<i>E. breviaristatus</i>		<i>E. tilcarensis</i>	
<i>A. attenuatum</i>			var. <i>scabrifolius</i>			
var. <i>platense</i>			<i>E. chonoticus</i>			
var. <i>nitzianum</i>			<i>E. corallensis</i>			
var. <i>araucanum</i>			<i>E. erianthus</i>			
<i>A. pubiflorum</i>			<i>E. fuegianus</i>			
var. <i>fragile</i>			<i>E. magellanicus</i>			
<i>A. repens</i>			<i>E. mendocinus</i>			
var. <i>scabriflorum</i>			<i>E. muticus</i>			
var. <i>vallanicum</i>			<i>E. notius</i>			
<i>A. pungens</i>			<i>E. preophilius</i>			
<i>A. antarcticum</i>			<i>E. palenae</i>			
<i>A. magellanicum</i>			<i>E. paposanus</i>			
<i>A. fuegianum</i>			<i>E. patagonicus</i>			
var. <i>brachyatherum</i>			<i>E. pilisus</i>			
var. <i>chaetophorum</i>			<i>E. pratensis</i>			
var. <i>polystachyum</i>			<i>E. remotiflorus</i>			
			<i>E. rigescens</i>			
			<i>E. scabrifolius</i>			
			<i>E. tenuatus</i>			
			<i>E. tilcarensis</i>			
			<i>E. uniflorus</i>			
			<i>E. vaginatus</i>			

The karyotype characteristics in all tetraploid species show a high uniformity. The two hexaploid species, *E. patagonicus* and *E. scabriglumis*, are assumed to share the **StHH** composition but are significantly differentiated in morphology. This indicates independent origins of the two hexaploid species from at least two hybridization events between a tetraploid *Elymus* species and a diploid *Hordeum* species (Dubcovsky *et al.*, 1989; Lewis *et al.*, 1996). Hybrids between *Elymus* and *Hordeum* are regularly found in nature, although, mainly seed sterile and yielding no offspring indicating rather strong crossing barriers (Seberg & von Bothmer, 1991). Hybridization studies suggest that gene transfer is possible between tetraploid *Elymus* species from South and North America if grown sympatrically (Hunziker, 1955; Dewey, 1972; Dewey, 1977; Jensen, 1993).

Research of genome constitution concerning South American *Elymus* have been dominated by karyotype analysis and studies of meiosis in interspecific hybrids, but the relationships are poorly known (Dubcovsky *et al.*, 1989; Seberg & von Bothmer, 1991; Dubcovsky *et al.*, 1992; Linde-Laursen *et al.*, 1994; Lewis *et al.*, 1996; Dubcovsky *et al.*, 1997). Jensen (1993) compared *E. magellanicus* to North American species and concluded that it is genomically more closely related to *E. lanceolatus* than to *E. trachycaulus* and *E. glaucus*. On the other hand, Dewey (1977) concluded that *E. tilcarensis* is genomically more closely related to *E. trachycaulus* than *E. lanceolatus*. Together, this suggests that *Elymus* in South America has not diversified from a single migration event and several hybridization events, but have rather migrated several times from North to South America, but more information is needed to draw any final conclusions. No comprehensive phylogenetic study has been conducted on American *Elymus*.

4.1 *Elymus* species in South America

The delimitation of species has been made according to the Catalogue of New World Grasses: IV (Campbell & Soreng, 2003).

***E. angulatus* J. Presl**

The names *E. andinus* Poepp. ex Trin., *E. rigescens* Trin., *E. agropyroides* J. Presl., *E. gayanus* E. Desv. and *E. antarcticus* Hook. f. occur in the literature and floras, but are all considered as synonyms to *E. angulatus* J. Presl by Seberg and Petersen (1998) and Campbell and Soreng (2003). In total, Tropicos.org (2019) lists 33 synonyms. The genome combination **StH** has been documented in *E. agropyroides* by Dewey (1970), in *E. andinus* and *E. antarcticus* by Dubcovsky *et al.* (1989) and in

E. agropyroides, *E. angulatus*, *E. gayanus*, *E. rigescens* by Lewis *et al.* (1996). However, Seberg and von Bothmer (1991) ascribe *E. angulatus* as a hexaploid with a **StHH** genome combination. The two homologous *Hordeum* chromosomes were not identical and Seberg and von Bothmer (1991) denotes them **SH₁H₂**, just like for *E. patagonicus*. Variation in chromosome number within a species is not common in *Elymus*. The determination of Seberg and von Bothmer (1991) could be wrong due to the complexity in taxonomy. However, if the determination is correct, it suggests that the species is rather a complex with closely related taxa (or crypto species) with a wide range of morphological variation and several intermediates. *Elymus angulatus* has usually two spikelets per rachis node, but occasionally shows only one (Seberg & Petersen, 1998), and some populations show more than two (per. obs.). The number of spikelets might partially depend on the interaction between genotype and the environment. Awn length vary within populations and should not be a reliable character for species separation. The morphological plasticity makes it difficult to do taxonomical comparisons with wild collected material. The species is the most widespread of all *Elymus* species in South America and occurs mainly in Chile, Argentina, Peru and Bolivia (IICA, 1970; Seberg & Petersen, 1998; Jörgensen *et al.*, 2014). In southern Chile, the species grows in areas with high rainfall or close to water, among bushes, in meadows or forests. Populations are often vast in open habitats. The large geographical distribution and heterogeneity in environmental conditions make it likely for a clinal variation due to local selection and gene flow, but no studies have been conducted to investigate this issue.

E. cordilleranus Davidse & Pohl

When Löve (1984) transferred all South American *Agropyron* species to *Elymus*, he accidentally created the illegitimate homonym *E. attenuatus* (the legitimate homonym is a synonym for *Leymus racemosus* according to World Checklist of Selected Plant Families), and was replaced by Davidse and Pohl (1992) with the new name *E. cordilleranus*. *E. attenuatus* was ascribed **StH** by Lewis *et al.* (1996). The species is distributed only in northern South America; in Bolivia, Peru, Colombia, Venezuela and Panama (Seberg & Petersen, 1998; Jörgensen *et al.*, 2014). The species could be a link between North American species and more southern *Elymus* species.

E. magellanicus (E. Desv.) Á. Löve

Elymus magellanicus is an allotetraploid with a **StH** genome combination (Jensen, 1993). The southernmost parts of South America is a hot spot for *Elymus* with a large variation, and several species have been described from this area. Seberg (1989) used biometrical data from living plants and herbarium specimens to study the species delimitation in Patagonia, Tierra del Fuego and the Falkland Islands. He

concluded that *Agropyrum patagonicum*, *E. notius* (syn *E. antarcticus*), *E. fuegianus*, *E. remotiflorus*, *E. magellanicus* is a clinal variation, with *A. patagonicum* at one end and *E. magellanicus* at the other end, and treated all as one variable species: *E. glaucescens*. He argues that no morphological character or combination of characters are able to sufficiently differentiate between the taxa. Seberg and Petersen (1998) recognize *E. glaucescens* in the latest revision of *Elymus* in South America, but this broad circumscription is not accepted by Campbell and Soreng (2003) who recognizes *E. magellanicus*. Genetic evidence is needed to solve the complexity of variation seen in *Elymus* in southern Patagonia. Jensen (1993) studied chromosome pairing in interspecific hybrids between *E. magellanicus* and three North American species, all with **StH** genomes. He concluded that *E. magellanicus* is more closely related to *E. lanceolatus* than to *E. trachycaulus* and *E. glaucus*.

E. mendocinus (Parodi) Å. Löve

Elymus mendocinus is the only octaploid *Elymus* species in South America (Lewis *et al.*, 1996; Linde-Laursen & Seberg, 1999), but the origin and classification is not fully solved. As with *Eremium erianthus* (see below), *E. mendocinus* does not hybridize with an **H**-genome specific repetitive sequence, indicating an origin not involving *Hordeum* as a progenitor (Lewis *et al.*, 1996). Instead, the variation in the repeated nucleotide sequence resembled the sequence found in species carrying the **N** genome, in the study represented by diploid *Psathyrostachys juncea*, the two polyploids *Leymus alaicus* ssp. *karataviensis* and *L. multicaulis* (Dubcovsky *et al.*, 1997; Linde-Laursen & Seberg, 1999). The marker bands indicated a closer relationship to the *Leymus* species than to *Psathyrostachys juncea*. Also, *E. mendocinus* differentiates from Asiatic *Elymus* species with no **H** genome (**StPY**, **StY**, **StStY**), which indicates the absence of the **St**-genome. Based on these findings, Dubcovsky *et al.* (1997) transferred *E. mendocinus* to *Leymus* Hochst. Linde-Laursen and Seberg (1999), used Giemsa C-banding and N-banding to analyze the genome of *E. mendocinus* and confirmed the absence of the **H** genome and the presence of the **N**-genome. Their analysis also suggested the absence of the **St** genome, and if so, following the genome-based classification by Löve (1984), *E. mendocinus* should be excluded from the genus. However, Linde-Laursen and Seberg (1999) hesitated to do so until further investigations could confirm the findings. They argue that the species is still within the morphological variation of *Elymus* in South America and not distinct enough to be recognized as an own genus. Drastic modification from a **St** and **H**-based genome cannot be excluded. Seberg and Petersen (1998) also argue that no morphological synapomorphies are supporting the classification of *E. mendocinus* in *Leymus*. The taxon is still recognized as *E. mendocinus* by Campbell and Soreng (2003) in the Catalogue of New World Grasses. The species reproduces, at least partly, through outbreeding (Linde-Laursen & Seberg, 1999). The species has

only been documented from a few locations in western Argentina. Thus studies of the origin and evolutionary history are needed.

E. patagonicus Speg.

Elymus patagonicus is hexaploid with a **StStHHHH** genome (Hunziker, 1955; Dewey, 1972; Seberg & von Bothmer, 1991; Seberg & Petersen, 1998). The two homologous *Hordeum* chromosomes are not identical and Seberg and von Bothmer (1991) denote them as **StStH₁H₁H₂H₂**. Hunziker (1953) crossed *E. patagonicus* with hexaploid *E. scabriglumis* (= *Agropyron agroelymoides*) and got only sterile hybrids, which indicates that the two species have either been formed independently or diverged early. The species is distributed in southern Argentina and could originate from a hybridization between *E. angulatus* or *E. magellanicus* and an unknown *Hordeum* species.

E. scabrifolius (Döll) J. H. Hunz.

Elymus scabrifolius (syn. *E. parodii* Seberg & G. Petersen, *Elymus breviaristatus* subsp. *scabrifolius* (Döll) Å. Löve) is tetraploid with an uncertain genome composition **HH(StSt?)**. The **H**-genome has been documented (Tomas *et al.*, 2012), but the **St**-genome has only been deduced based on morphology and has not been confirmed by other methods (Linde-Laursen & Seberg, 2001; Tomas *et al.*, 2012). The species is not recognized by Seberg and Petersen (1998) but included in *E. parodii*. It is distributed in southern Brazil, Uruguay and Argentina (Seberg & Petersen, 2012). The taxonomical status of the species needs to be confirmed by genetic data.

E. scabriglumis (Hack.) Å. Löve

Both tetra- and hexaploid cytotypes have been documented for *E. scabriglumis* (Hunziker, 1955; Lee *et al.*, 1993; Seberg & Petersen, 1998; Tomas *et al.*, 2012): **StStHH**, **StStHHHH**. However, these findings could be questioned due to the taxonomical complexity of the species. The **Y** genome was first ascribed to *E. scabriglumis* by Gupta *et al.* (1988), but later disproved by Lee *et al.* (1993) who found a high level of meiotic pairing and multivalent chromosome formation in hybrids with hexaploid *Hordeum parodii*, indicating the involvement of the **H** genome in *E. scabriglumis*. Also, *E. scabriglumis* differs in morphology compared to species with **StStYY** genome composition (Seberg & Petersen, 1998), which are restricted to Asia (Salomon & Lu, 1992). *Elymus scabriglumis* shows occasionally two spikelets per rachis node (Seberg & Petersen, 1998). The species occurs sporadically in Argentina and Chile and need further investigations to resolve the taxonomical species delimitations. The difference in genome combination suggests that the species should be considered as a complex with two or several crypto species (also see below for *E. tilcarensis*).

***E. tilcareense* (J. H. Hunz.) Å. Löve**

The species is recognized in Catalogue of New World Grasses with a notation that this taxon may be better placed in *E. scabriglumis* (Campbell & Soreng, 2003). Seberg and Petersen (1998) include it in *E. scabriglumis*. Dewey (1977) ascribe **StStHH** to *E. tilcareense* and concluded that the species is more closely related to *E. trachycaulus* than to *E. lanceolatus*. The distribution of the species is not known.

Excluded species and hybrids

The earlier *Elymus erianthus* Phil. was transferred to the monotypic genus *Eremium* as *E. eranthium* (Phil.) Seberg & Linde-Laursen by Seberg and Linde-Laursen (1996) but is now included in *Leymus* as *L. erianthus* (Campbell & Soreng, 2003). It is a hexaploid ($2n = 6x = 42$) (Dubcovsky *et al.*, 1992; Seberg & Linde-Laursen, 1996) however, the genome composition is not known (Seberg & Petersen, 1998). Karyotype parameters, morphology and genetic characters differentiate *L. erianthus* from all South American *Elymus* species (Nicora, 1978; Dubcovsky *et al.*, 1992; Lewis *et al.*, 1996; Seberg & Linde-Laursen, 1996; Dubcovsky *et al.*, 1997). It has unique restriction sites in the rDNA repeat unit (Dubcovsky *et al.*, 1992) and sequence variations in the chloroplast gene *rbcL* in phylogenetic comparisons (Seberg & Linde-Laursen, 1996). Like *E. mendocinus*, *L. erianthus* lack genome-specific (genotype) characters seen in *Hordeum* and all South American *Elymus*. The species does not hybridize with a **H**-genome specific repetitive sequence, as seen with species with a **StStYY**-genome which indicates the absence of the **H**-genome in *L. erianthus* (Lewis *et al.*, 1996). This has been confirmed by Dubcovsky *et al.* (1997) who documented an absence of the repeated nucleotide sequence (RNS) clone pHch2 in *E. erianthus*, which is readily amplified in *Hordeum*, and all *Elymus* species with **StH**, **StHH** and **StHY** genome compositions. It has also been confirmed by Pedersen *et al.* (1996) who found a lack of fluorescent *in situ* hybridization (FISH) with a GAA satellite sequence abundant in the **H** genome. The presence of a **N**-genome has been suggested by Seberg and Linde-Laursen (1996) who documented a failure to produce **St** specific bands with chromosome N-banding. These findings were confirmed by Dubcovsky *et al.* (1997) who transferred the species into *Leymus*. The taxon also shares similar ecological and morphological characters with other *Leymus* species (Dubcovsky *et al.*, 1997). However, Seberg and Linde-Laursen (1996) opposed to the inclusion of *E. erianthus* in *Leymus* and argue that it only makes *Leymus* more morphologically heterogeneous, but they cannot exclude a phylogenetic relationship to *Leymus*. Seberg and Petersen (1998) argue that no morphological synapomorphies are supporting this classification. Also, *E. erianthus*

shows only distant phylogenetic relationship with Eurasian *Leymus* and *Psathyrostachys* and the parental species have not been identified (Zhou *et al.*, 2010). *L. erianthus* is normally self-fertilizing (Seberg & Linde-Laursen, 1996).

Also, hybrids between genera do occur. \times *Elyhordeum elymoides* (Hack.) J.H. Hunz. & Xifreda (syn. *Elymus* \times *lineariglumis* Seberg & G. Petersen) is supposed to be an intergeneric hybrid between *Elymus* and *Hordeum* (Hunziker & C.D., 1980), probably between *E. magellanicus* (syn. *E. glaucescens*) and *Hordeum tetraploidum* (Seberg & Petersen, 1998). The hybrid is quite common in southern Patagonia.

5 Future research of *Elymus* in South America

Triticeae has been studied not only for valuable traits and breeding potentials but also because of the combinations of several biological mechanisms and genetic systems shaping complex evolutionary processes (von Bothmer & Salomon, 1994). The variation in morphology, polyploidy levels, intergeneric and interspecific hybridization, life cycles, phenotypic plasticity and reproduction systems makes the tribus particularly interesting as a model group for studies of plant speciation and genetic diversity (allele number and frequencies). It is also an interesting model group for studying the advantageous evolutionary success of polyploids compared to diploids and levels and distribution of genetic variation in space and time on multiple taxonomical levels and geographical scales (non-random variation).

There is still much research to be done in South America on *Elymus* and Triticeae. We still lack a comprehensive phylogeny and a clear picture of the origin of the South American species. The hitherto low number of accessions in phylogenetic studies of *Elymus* may be misleading. No species of *Pseudoroegneria* currently grows in South America today, which makes it likely that the allopolyploid South American *Elymus* have originated in North America and migrated south. However, we cannot exclude that one or several now extinct species of *Pseudoroegneria* have contributed to the origin of the South American species. There could potentially also be multiple migrations from North to South America (Dewey, 1977; Jensen, 1993), making *Elymus* in South America a polyphyletic group. Blattner (2006) showed that several long-distance dispersal between North and South America has occurred in *Hordeum* acting as an important colonization mechanism. Migrating birds are most likely the dispersal vector for the seeds (Pleines & Blattner, 2008). The relationship with North American species need to be settled before drawing any final conclusions about the phylogeny and taxonomy of *Elymus* in South America.

The particular biogeographical and evolutionary history of the genus makes it possible to study the connection between polyploid diversification and polyploid speciation (Kellogg, 2016). The large genetic diversity in *Elymus* species may derive from multiple formation events, diversification of polyploid lineages and/or introgressive hybridization between closely related species. It is still unclear which the dominant factor is. We know that the tetraploid South American *Elymus* species share the **StH**, and hexaploids the **StHH**, genome combination, but we still do not know the full derivation history, the involved parental species, time for polyploidization events, or if it is an ongoing process.

At the species and population levels, several taxa need to be investigated in more detail. Diverse species such as *E. angulatus* and *E. magellanicus* (*E. glaucescens*) require additional genetic data in order to resolve the population relationships, clinal variation and species delimitations. Taxonomy at the species level is not only name tags but a system to describe the variation between living entities. An adequate taxonomy is essential for successful conservation management and efficient exploitation of genetic resources. Gene flow is an important factor to understand speciation and is another aspect that needs to be studied, not only between species and populations within the genus but also intergeneric gene transfer. Asymmetric introgression among species within *Elymus* has been shown in Northern European species (Wu *et al.*, 2016). Hybrids between *Elymus* and *Hordeum* do exist in nature, but it is not known how this affects genetic diversity and population structure of the involved species. The generic hybrid \times *Elyhordeum elymoides* is rather unusual in Southern Chile and is supposed to be sterile (Hunziker & C.D., 1980). The species usually occurs as single individuals or in groups with few individuals at dispersed locations (pers. obs.).

5.1 *Elymus* in South America as a genetic resource

Elymus belongs to the tertiary gene pool of wheat and the primary and secondary gene pool of forage grasses (von Bothmer, 1992), following the definitions of gene pools made by Harlan (1971). Gene transfer from *Elymus* to *Triticum* is difficult but possible with artificial methods (Franke *et al.*, 1992; Newell *et al.*, 2015). *Elymus* belongs to the tertiary gene pool of *Hordeum* (barley) according to von Bothmer (1992), but successful crosses have been made between *Hordeum* species, including *H. vulgare*, and several *Elymus* species (Salomon *et al.*, 1991; Dahleen, 1999; Kim *et al.*, 2008). Stress tolerance, disease resistance and perenniality are the main target traits breeders aiming to incorporate into the domesticated crops. Several species of *Elymus* are used or have the potential to be used as forage crops directly, or as a

genetic resource in forage breeding. The genus holds several benefits such as tolerance to environmental stresses, for example, drought, cold and soil impoverishment and resistance to pest and diseases which is beneficial for forage crops, especially in areas not appropriate for other food production (Schellenberg *et al.*, 2012; Ding *et al.*, 2019; Xiong *et al.*, 2019). Hybridization between species within *Elymus* is usually easy to perform under suitable conditions. However, the hybrids between different genome combinations are sterile with poor pollen development and no seed set, while hybrids within genome combinations are fertile (Salomon & Lu, 1992). Hybrids have been found in nature, but it is still not clear to which extent hybridization and introgression occurs in *Elymus*.

In breeding programs aiming for efficient and sustainable crop production, native ecotypes are valuable sources of attractive agricultural traits because of their local adaptation. Traits connected to growing conditions, land use or land management might be unique and necessary to incorporate in cultivars to maximize future utilization of the land for food production. Many native grass species, including *Elymus*, may be used as a low input forage crop on soils otherwise inadequate for high output plant cropping systems. However, a lot of research needs to be done in order to fully exploit the natural resources. Investigations of species distribution and collecting wild material is the first step, creating programs for seed propagation and regeneration *in situ* is the next, and finally, there needs to be a system for distribution of the material to scientists and breeders. However, plant material is not easy to distribute between countries in South America. National organizations need to be established and local populations of *Elymus* in several countries need to be investigated.

In Chile, there is a demand for indigenous forage crop species (Ortega. pers. comm.). Most of the cultivated grass species come from Europe and the cultivars are usually bred in New Zealand. *Bromus valdivianus*, a native species for Chile, has been successfully developed as a forage crop through the utilization of wild material and population selections. Phenotype characterization with whole-plant assessment and physiological analysis is necessary as well as evaluations of agricultural qualities. It is important to compare several sites with a variation in growing conditions, as well as nutritional content and variation in nutritional content depending on environmental factors for cultivar development, winter hardiness, production capacity, regrowth capacity, forage nutritional qualities, seed characters, disease resistance and longevity are all important traits. Climate change may affect precipitation and temperature, but not photoperiodism and light conditions. In addition, a change in climate might affect winter hardening and winter survival, carbohydrate accumulation and growth cessation. The use of the new crops, for grazing or ensilage, also sets the standard for developmental goals.

Great effort is needed in order to fully explore the agricultural qualities of the indigenous species. Ecotypes of *E. angulatus* have been found growing naturally in pastures in southern Chile and more knowledge about pasture ecology would be desirable, especially in low input forage crop systems. Test plots are needed on several sites, depending on the intended market, to investigate biomass production and nutritional values. Other species such as *E. magellanicus* produce less biomass when growing in natural habitats but have a high tolerance to dry and salty environments, which could make it suitable for gene introgression into other species.

6 Conclusion

Like other crops, the domesticated cereals need continuous improvement and release of new cultivars to meet present and future challenges to feed a growing human population which requires sustainable production. Breeders continuously search for new sources of genes transferable to the cultivated forms. Most research in Triticeae concerning genetic resources and breeding potential has focused on the economically important cereals and their closest relatives. There is, however, an immense genetic resource in the diverse and species-rich tribe that is not fully used today with the potential to develop new crops. Information about gene content and the genetic variation in the breeding material and exotic gene sources is crucial when planning efficient breeding programs. A survey of variation patterns in *Elymus* in South America would support both pre-breeding and breeding programs. In addition, collecting plant material is essential, as well as the subsequent conservation, like germplasm banks, and the distribution of the material to breeders and scientists. It is desirable to have as much information as possible about the phenotype, population structure and phytogeography of the collected accessions. In order to optimize the potential use of the genetic material, information, such as ecology, exact collecting location, population size, growing conditions, land use and land management, is desirable. It is not only important to preserve species and populations containing traits valued today, but also characters that might be useful in an unforeseeable future. The research of systematics, phylogeny and evolution is still needed, as well as studies concerning ecology and genetic diversity.

Glossary

Allopolyploid – individual with multiple chromosome sets derived from two or several different taxa. Compare *Autopolyploid*.

Apomixis – clonal reproduction by seed.

Asymmetric introgression – an asymmetric flow of genes between taxa. Compare *Introgression*.

Autopolyploid – individual with multiple chromosome sets derived from a single taxon. Compare *Allopolyploid*.

Caespitose – growing in tight groups, tufted or clumped.

Crypto species – species that are hard to differentiate due to high morphological similarity.

Cytotype - An individual of a species that has a different chromosomal number to another.

Haplome - the basic or monoploid set of chromosomes. Sometimes referred to as the genome.

Heterogenomic group – group of plants that differ in haplome combination within the group.

Homoplasy - when a trait has been gained or lost independently in separate lineages because of similar selection or genetic drift.

Intergeneric hybridization – hybridization between two species from different genera. Compare *Interspecific hybridization*.

Interspecific hybridization – hybridization between two species. Compare *Intergeneric hybridization*.

Introgression – incorporation of a gene (gene flow) from one taxon to another by hybridization and repeated backcrossing. Compare *Asymmetric introgression*.

Monogenomic – relating to a single genome. Group of species with the same haplome or haplome combination. Compare *Haplome*.

Monophyletic - a group of organisms that are classified in the same taxa and share a most common recent ancestor and all of the descendants. Compare *Paraphyletic* and *Polyphyletic*.

Monotypic – a taxa that only includes one taxa.

Paraphyletic - a group of organisms that are classified in the same taxa and share a most common recent ancestor but not all of the descendants. Compare *Monophyletic* and *Polyphyletic*.

Polyphyletic – a group of organisms that are classified in the same taxa but does not share a most common recent ancestor. Compare *Paraphyletic* and *Monophyletic*.

RAPD – stands for “Random Amplification of Polymorphic DNA”.

RFLP – stands for “Restriction Fragment Length Polymorphism”.

Rhizomatous – growing and spreading with an underground stem.

Sympatric distribution – when two or more related species or populations exist in the same geographical area.

Synapomorphy – shared derived character of a clade.

References

- Barkworth, M.E. (1992). Taxonomy of the Triticeae - a historical perspective. *Hereditas*, 116(1-2), pp. 1-14.
- Barkworth, M.E. & von Bothmer, R. (2009). *Scientific names in the Triticeae*. (Genetics and Genomics of the Triticeae, 7). New York: Springer.
- Barkworth, M.E.v.B., R. (2005). Twenty-one years later: the impact of Löve and Deweys genomic classification proposal. *Czech Journal of Genetics and Plant Breeding*, 41, pp. 3-9.
- Baum, B.R. (1983). A phylogenetic analysis of the tribe Triticeae (Poaceae) based on morphological characters of the genera. *Canadian Journal of Botany-Revue Canadienne De Botanique*, 61(2), pp. 518-535.
- Baum, B.R., Edwards, T. & Johnson, D.A. (2015). Diversity within the genus *Elymus* (Poaceae: Triticeae) as investigated by the analysis of the nr5S rDNA variation in species with St and H haplomes. *Molecular Genetics and Genomics*, 290(1), pp. 329-342.
- Baum, B.R., Estes, J.R. & Gupta, P.K. (1987). Assessment of the genomic system of classification in the Triticeae. *American Journal of Botany*, 74(9), pp. 1388-1395.
- Baum, B.R., Yang, J.L., Yen, C. & Agafonov, A.V. (2011). A taxonomic synopsis of the genus *Campeiosachys* Drobov. *Journal of Systematics and Evolution*, 49(2), pp. 146-159.
- Bentham, G. (1881). Notes on Gramineæ. *Botanical Journal of the Linnean Society*, 19(115-1160), pp. 14-134.
- Bernhardt, N., Brassac, J., Kilian, B. & Blattner, F.R. (2017). Dated tribe-wide whole chloroplast genome phylogeny indicates recurrent hybridizations within Triticeae. *Bmc Evolutionary Biology*, 17.
- Blattner, F.R. (2006). Multiple intercontinental dispersals shaped the distribution area of *Hordeum* (Poaceae). *New Phytologist*, 169(3), pp. 603-614.
- Brassac, J. & Blattner, F.R. (2015). Species-level phylogeny and polyploid relationships in *Hordeum* (Poaceae) inferred by Next-Generation Sequencing and In Silico Cloning of multiple nuclear loci. *Systematic Biology*, 64(5), pp. 792-808.
- Campbell, J.J.N. & Soreng, R.J. (2003). *Elymus*. In Catalogue of New World Grasses (Poaceae): IV. Subfamily Pooideae. *Contributions from the United States National Herbarium*, 48, pp. 279-307.
- Chalupska, D., Lee, H.Y., Faris, J.D., Evrard, A., Chalhoub, B., Haselkorn, R. & Gornicki, P. (2008). Acc homoeoloci and the evolution of wheat genomes. *Proceedings of the National Academy of Sciences of the United States of America*, 105(28), pp. 9691-9696.
- Dahleen, L.S. (1999). Tissue culture increases meiotic pairing of regenerants from barley x Canada wild rye hybrids. *Journal of Heredity*, 90(2), pp. 265-269.

- Davidse, G. & Pohl, R.W. (1992). New taxa and nomenclatural combinations of Mesoamerican grasses (Poaceae). *Novon*, 2(2), pp. 81-110.
- Dewey, D.R. (1970). Hybrids of South American *Elymus agropyroides* with *Agropyron caespitosum*, *Agropyron subsecundum* and *Sitanion hystrix*. *Botanical Gazette*, 131(3), pp. 210-&.
- Dewey, D.R. (1972). Genome analysis of South American *Elymus patagonicus* and its hybrids with two North American and two Asian *Agropyron* species. *Botanical Gazette*, 133(4), pp. 436-443.
- Dewey, D.R. (1977). Genome relations of South American *Agropyron tilcarensis* with North American and Asian *Agropyron* species. *Botanical Gazette*, 138(3), pp. 369-375.
- Dewey, D.R. (1984). The genomic system of classification as a guide to intergeneric hybridization with the perennial Triticeae. *Gene manipulation in plant improvement*, pp. 209-279.
- Devos, K.M. & Gale, M.D. (2000). Genome relationships: The grass model in current research. *Plant Cell*, 12(5), pp. 637-646.
- Diaz, O. (1999). *Genetic diversity in Elymus species (Triticeae) with emphasis on the Nordic region (Doctoral thesis)*. Diss.: Swedish University of Agricultural Sciences.
- Ding, C.X., Dong, Q.M., Yang, X.X., Zhang, C.P. & Chu, H. (2019). Characterization of the complete chloroplast genome of *Elymus sibiricus* Linn (Gramineae). *Mitochondrial DNA Part B-Resources*, 4(1), pp. 478-479.
- Dubcovsky, J., Lewis, S.M. & Hopp, E.H. (1992). Variation in the restriction fragments of 18S-26S ribosomal RNA loci in South American *Elymus* (Triticeae). *Genome*, 35(5), pp. 881-885.
- Dubcovsky, J., Schlatter, A.R. & Echaide, M. (1997). Genome analysis of South American *Elymus* (Triticeae) and *Leymus* (Triticeae) species based on variation in repeated nucleotide sequences. *Genome*, 40(4), pp. 505-520.
- Dubcovsky, J., Soria, M.A. & Martinez, A. (1989). Karyotype analysis of the Patagonian *Elymus*. *Botanical Gazette*, 150(4), pp. 462-468.
- Dvorak, J. & Zhang, H.B. (1992). Application of molecular tools for study of the phylogeny of diploid and polyploid taxa in Triticeae. *Hereditas*, 116(1-2), pp. 37-42.
- Edet, O.U., Gorafi, Y.S.A., Nasuda, S. & Tsujimoto, H. (2018). DArTseq-based analysis of genomic relationships among species of tribe Triticeae. *Scientific Reports*, 8, p. 11.
- Franke, R., Nestrowicz, R., Senula, A. & Staat, B. (1992). Intergeneric hybrids between *Triticum aestivum* and wild Triticeae. *Hereditas*, 116(3), pp. 225-231.
- Gupta, P.K., Balyan, H.S. & Fedak, G. (1988). A study on genomic relationships of *Agropyron trachycaulum* with *Elymus scabriglumis*, *Elymus innovatus* and *Hordeum procerum*. *Genome*, 30(4), pp. 525-528.
- Gupta, P.K. & Baum, B.R. (1989). Stable classification and nomenclature in the Triticeae - desirability, limitations and prospects. *Euphytica*, 41(3), pp. 191-197.
- Harlan, J.R.d.W., J. M. J. (1971). Toward a rational classification of cultivated plants. *Taxon*, 20(4), pp. 509-517.
- Hitchcock, A.S. (1951). Tribe 3. Hordeae. In: *Manual of the Grasses of the United States*. Washington, D.C.: U.S. Government Printing Office, pp. 230-274.
- Hunziker, J.H. (1953). Estudio citogenético de un híbrido entre *Elymus patagonicus* y *Agropyron agroelymoides*. *Rev. Invest. Agr.*, 7, pp. 73-79.
- Hunziker, J.H. (1955). Artificial and natural hybrids in the Gramineae, tribe Hordeae, hybrids of *Elymus* and *Agropyron*. *American Journal of Botany*, 42(5), pp. 459-467.
- Hunziker, J.H. & C.D., I. (1980). Hibridación natural entre *Agropyron* y *Hordeum* en Tierra del Fuego. *Boletín de la Sociedad Argentina de Botánica*, 19, pp. 91-102.
- IICA (1970). *Programa nacional de pastos y forrajes de Bolivia*1): Bib. Orton IICA / CATIE. Available from: <https://books.google.se/books?id=ydYOAQAIAAJ>.

- Jaaska, V. (1992). Isoenzyme variation in the grass genus *Elymus* (Poaceae). *Hereditas*, 117(1), pp. 11-22.
- Jensen, K.B. (1993). Cytogenetics of *Elymus magellanicus* and its intrageneric and intergeneric hybrids with *Pseudoroegneria spicata*, *Hordeum violaceum*, *Elymus trachycaulus*, *E. lanceolatus* and *E. glaucus* (Poaceae, Triticeae). *Genome*, 36(1), pp. 72-76.
- Jørgensen, P.M., Nee, M.H. & Beck, S.G. (2014). Catálogo de las plantas vasculares de Bolivia. *Monographs in systematic botany from the Missouri Botanical Garden*.
- Kellogg, E.A. (1989). Comments on genomic genera in the Triticeae (Poaceae). *American Journal of Botany*, 76(6), pp. 796-805.
- Kellogg, E.A. (2016). Has the connection between polyploidy and diversification actually been tested? *Current Opinion in Plant Biology*, 30, pp. 25-32.
- Kellogg, E.A., Appels, R. & Mason-Gamer, R.J. (1996). When genes tell different stories: The diploid genera of Triticeae (Gramineae). *Systematic Botany*, 21(3), pp. 321-347.
- Keng, Y.L. (1989). Tribe Hordeae. In: Keng, Y.L. (ed. *Flora Illustralis Plantarum Primarum Sinicarum (Gramineae)*). Beijing: Science Press, pp. 340-451.
- Kim, N.S., Fedak, G., Han, F. & Cao, W. (2008). Cytogenetic analyses of intergeneric hybrids between barley and nine species of *Elymus*. *Genome*, 51(11), pp. 897-904.
- Lee, Y.H., Balyan, H.S., Wang, B.J. & Fedak, G. (1993). Cytogenetic analysis of three *Hordeum* x *Elymus* hybrids. *Euphytica*, 72(1-2), pp. 115-119.
- Lewis, S.M., Martinez, A.J. & Dubcovsky, J. (1996). Karyotype variation in South American *Elymus* (Triticeae). *International Journal of Plant Sciences*, 157(1), pp. 142-150.
- Linde-Laursen, I.B. & Seberg, O. (1999). The karyotype of *Elymus mendocinus* (Poaceae; Triticeae) from Argentina studied by banding techniques. *Hereditas*, 131(3), pp. 247-252.
- Linde-Laursen, I.B. & Seberg, O. (2001). Karyotypes of *Elymus scabrifolius* (Poaceae : Triticeae) from South America studied by banding techniques and in situ hybridization. *Hereditas*, 135(1), pp. 41-50.
- Linde-Laursen, I.B., Seberg, O. & Salomon, B. (1994). Comparison of the Giemsa C-banded and N-banded karyotypes of two *Elymus* species, *E. dentatus* and *E. glaucescens* (Poaceae, Triticeae). *Plant Systematics and Evolution*, 192(3-4), pp. 165-176.
- Liu, Q., Ge, S., Tang, H., Zhang, X., Zhu, G. & Lu, B.R. (2006). Phylogenetic relationships in *Elymus* (Poaceae: Triticeae) based on the nuclear ribosomal internal transcribed spacer and chloroplast trnL-F sequences. *New Phytol*, 170(2), pp. 411-20.
- Lu, B.R. (1993). *Biosystematic Investigations of Asiatic Wheatgrasses - Elymus L. (Triticeae: Poaceae)* (Doctoral thesis). Diss.: Swedish University of Agricultural Sciences.
- Lu, B.R. & Ellstrand, N. (2014). World food security and the tribe Triticeae (Poaceae): Genetic resources of cultivated, wild, and weedy taxa for crop improvement. *Journal of Systematics and Evolution*, 52(6), pp. 661-666.
- Löve, A. (1982). Generic evolution of the wheatgrasses. *Biologisches Zentralblatt*, 101(2), pp. 199-212.
- Löve, A. (1984). Conspectus of the Triticeae. *Feddes Repertorium*, 95(7/8), pp. 425-521.
- Mason-Gamer, R.J., Burns, M.M. & Naum, M. (2010). Phylogenetic relationships and reticulation among Asian *Elymus* (Poaceae) allotetraploids: analyses of three nuclear gene trees. *Mol Phylogenet Evol*, 54(1), pp. 10-22.
- McMillan, E. & Sun, G. (2004). Genetic relationships of tetraploid *Elymus* species and their genomic donor species inferred from polymerase chain reaction-restriction length polymorphism analysis of chloroplast gene regions. *Theor Appl Genet*, 108(3), pp. 535-42.

- Meledris, A. (1980). *Elymus* L. In: Tutin, T.G.H., V. H.; Burges, N. A.; Moore, D. M.; Valentine, D. H., Walters, S. M.; Webb D. A. (ed. *Flora Europea vol. 5*. Cambridge, New York, Port Chester, Melbourne, Sydney: University Press, pp. 192-198.
- Monte, J.V., McIntyre, C.L. & Gustafson, J.P. (1993). Analysis of phylogenetic relationships in the Triticeae tribe using RFLPs *Theoretical and Applied Genetics*, 86(5), pp. 649-655.
- Moore, D.M. (1983). *Flora of Tierra del Fuego*: Oswestry & St. Louis.
- Newell, M.T., Hayes, R.C., Virgona, J.M. & Larkin, P.J. (2015). Summer dormancy in *Elymus* scaber and its hybridity with wheat. *Euphytica*, 204(3), pp. 535-556.
- Nevski, S.A. (1934). Agrostological studies IV. The systematics of the tribe Hordeae. *Benth. Akad Nauk SSSR Bot Inst Trudy*, 1, pp. 9-32.
- Nicora, E.G. (1978). Gramineae. Triticeae. In: Correa, M.N. (ed. *Flora Patagonica*8, 3). Buenos Aires.
- Parodi, L.R. (1940). Estudio crítico de las gramíneas Austral-Americanas del género *Agropyron*. *Revista del Museo de La Plata. Seccion Botanica.*, 3, pp. 1-63.
- Pedersen, C., Rasmussen, S.K. & LindeLaursen, I. (1996). Genome and chromosome identification in cultivated barley and related species of the Triticeae (Poaceae) by in situ hybridization with the GAA-satellite sequence. *Genome*, 39(1), pp. 93-104.
- Petersen, G., Seberg, O. & Salomon, B. (2011). The origin of the H, St, W, and Y genomes in allotetraploid species of *Elymus* L. and *Stenostachys* Turcz. (Poaceae: Triticeae). *Plant Systematics and Evolution*, 291(3-4), pp. 197-210.
- Pleines, T. & Blattner, F.R. (2008). Phylogeographic implications of an AFLP phylogeny of the American diploid *Hordeum* species (Poaceae : Triticeae). *Taxon*, 57(3), pp. 875-881.
- Runemark, H. & Heneen, W.K. (1968). *Elymus* and *Agropyron* a problem of generic delimitation. *Botaniska Notiser*, 121(1), pp. 51-&.
- Salomon, B. & Lu, B.R. (1992). Genomic groups, morphology and sectional delimitation in Eurasian *Elymus* (Poaceae, Triticeae). *Plant Systematics and Evolution*, 180(1-2), pp. 1-13.
- Salomon, B., von Bothmer, R. & Jacobsen, N. (1991). Intergeneric crosses between *Hordeum* and North American *Elymus* (Poaceae, Triticeae) *Hereditas*, 114(1), pp. 35-39.
- Salomon, B., von Bothmer, R. & Seberg, O. (1997). A proposal for an *Elymus* core collection. *Plant Genetic Resources Newsletter (IPGRI/FAO)*, 111, pp. 77-81.
- Schellenberg, M.P., Biligetu, B. & Iwaasa, A.D. (2012). Species dynamic, forage yield, and nutritive value of seeded native plant mixtures following grazing. *Canadian Journal of Plant Science*, 92(4), pp. 699-706.
- Seberg, O. (1989). A biometrical analysis of the South American *Elymus glaucescens* complex (Poaceae, Triticeae). *Plant Systematics and Evolution*, 166(1-2), pp. 91-104.
- Seberg, O. & Frederiksen, S. (2001). A phylogenetic analysis of the monogenomic Triticeae (Poaceae) based on morphology. *Botanical Journal of the Linnean Society*, 136(1), pp. 75-97.
- Seberg, O. & Linde-Laursen, I.B. (1996). *Eremium*, a new genus of the Triticeae (Poaceae) from Argentina. *Systematic Botany*, 21(1), pp. 3-15.
- Seberg, O. & Petersen, G. (1998). A taxonomic revision of the genus *Elymus* L. s. l. (Poaceae, triticeae) in South America. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*, 120(4), pp. 503-543.
- Seberg, O. & Petersen, G. (2012). *Elymus*; *Monocotyledoneae, Poaceae: Pooideae, Flora of Argentina* Volume 3 Tomo II).
- Seberg, O. & von Bothmer, R. (1991). Genome analysis of *Elymus angulatus* and *E. patagonicus* (Poaceae) and their hybrids with North American and South American *Hordeum* spp. *Plant Systematics and Evolution*, 174(1-2), pp. 75-82.

- Soltis, D.E. & Soltis, P.S. (1993). Molecular data and the dynamic nature of polyploidy. *Critical Reviews in Plant Sciences*, 12(3), pp. 243-273.
- Stebbins, G.L. (1956). TAXONOMY AND THE EVOLUTION OF GENERA, WITH SPECIAL REFERENCE TO THE FAMILY GRAMINEAE. *Evolution*, 10(3), pp. 235-245.
- Stebbins, G.L. & Snyder, L.A. (1956). Artificial and natural hybrids in the Gramineae, tribe Hordeae, hybrids between western and eastern North American species. *American Journal of Botany*, 43(4), pp. 305-312.
- Sun, G. (2014). Molecular phylogeny revealed complex evolutionary process in *Elymus* species. *Journal of Systematics and Evolution*, 52(6), pp. 706-711.
- Sun, G., Ni, Y. & Daley, T. (2008). Molecular phylogeny of RPB2 gene reveals multiple origin, geographic differentiation of H genome, and the relationship of the Y genome to other genomes in *Elymus* species. *Molecular Phylogenetics and Evolution*, 46(3), pp. 897-907.
- Sun, G. & Salomon, B. (2009). Molecular evolution and origin of tetraploid *Elymus* species. *Breeding Science*, 59(5), pp. 487-491.
- Sun, G.L. & Ma, X.Z. (2009). Nucleotide diversity and minisatellite in chloroplast Asp(GUC)-Thr(GGU) region in *Elymus trachycaulus* complex, *Elymus alaskanus* and *Elymus caninus*. *Biochemical Systematics and Ecology*, 37(2), pp. 67-75.
- Sun, G.L., Salomon, B. & von Bothmer, R. (1997). Analysis of tetraploid *Elymus* species using wheat microsatellite markers and RAPD markers. *Genome*, 40(6), pp. 806-814.
- Svitashev, S., Bryngelsson, T., Li, X.M. & Wang, R.R.C. (1998). Genome-specific repetitive DNA and RAPD markers for genome identification in *Elymus* and *Hordelymus*. *Genome*, 41(1), pp. 120-128.
- Svitashev, S., Salomon, B., Bryngelsson, T. & von Bothmer, R. (1996). A study of 28 *Elymus* species using repetitive DNA sequences. *Genome*, 39(6), pp. 1093-1101.
- Tomas, P.A., Gonzalez, G.E., Schrauf, G.E. & Poggio, L. (2012). Chromosomal characterization in native populations of *Elymus scabrifolius* from Argentina through classical and molecular cytogenetics (FISH-GISH). *Genome*, 55(8), pp. 591-598.
- Tropicos.org *Triticeae*. Available at: <http://www.tropicos.org/Name/100409000>.
- Tzvelev, N.N. (1976). Tribe 3: Triticeae Dum. In: *Poaceae U.R.S.S.* Leningrad: Nacka Publishing House, pp. 146-298.
- Tzvelev, N.N. (1989). The system of grasses (Poaceae) and their evolution. *Botanical Review*, 55(3), pp. 141-204.
- Wang, Q.X., Xiang, J.S., Gao, A.N., Yang, X.M., Liu, W.H., Li, X.Q. & Li, L.H. (2010). Analysis of chromosomal structural polymorphisms in the St, P, and Y genomes of Triticeae (Poaceae). *Genome*, 53(3), pp. 241-249.
- Wang, R.-C., von Bothmer, R., Dvorak, J., Fedak, G., Linde-Laursen, I.B. & Muramatsu, M. (1994). Genome Symbols in Triticeae. In: Wang, R.R.C., Jensen, K.B. & Jaussi, C. (eds) *Proceedings of the 2nd International Triticeae Symposium*. Logan: Utha state University Press, pp. 29-34.
- West, J.G., McIntyre, C.L. & Appels, R. (1988). Evolution and systematic relationships in the Triticeae (Poaceae). *Plant Systematics and Evolution*, 160(1-2), pp. 1-28.
- von Bothmer, R., Jacobsen, N., Baden, C., Jorgensen, R.B. & Linde-Laursen, I. (1995). An ecogeographical study of the genus *Hordeum*. *Systematic and Ecogeographic Studies on Crop Gene-pools*, 7.
- von Bothmer, R. & Salomon, B. (1994). Triticeae: a tribe for food, feed and fun. In: Wang, R.R.C., Jensen, K.B. & Jaussi, C. (eds) *Proceedings of the 2nd International Triticeae Symposium*. Logan: Utha state University Press, pp. 1-12.
- von Bothmer, R.S., O.; Jacobsen, N. (1992). Genetic resources in the Triticeae. *Hereditas*, 116, pp. 141-150.

- Wu, P.P., Zuo, H.W., Sun, G.L., Wu, D.X., Salomon, B., Hu, Q.W. & Dong, Z.R. (2016). Comparison of gene flow among species that occur within the same geographic locations versus gene flow among populations within species reveals introgression among several *Elymus* species. *Journal of Systematics and Evolution*, 54(2), pp. 152-161.
- Xiong, Y.L., Liu, W.H., Xiong, Y., Yu, Q.Q., Ma, X., Lei, X., Zhang, X.Q. & Li, D.X. (2019). Revelation of genetic diversity and structure of wild *Elymus excelsus* (Poaceae: Triticeae) collection from western China by SSR markers. *Peerj*, 7, p. 18.
- Yan, C. & Sun, G.L. (2012). Multiple origins of allopolyploid wheatgrass *Elymus caninus* revealed by RPB2, PepC and TrnD/T genes. *Molecular Phylogenetics and Evolution*, 64(3), pp. 441-451.
- Yen, C., Yang, J.L. & Yen, Y. (2005). Hitoshi Kihara, Askeell Dive and the modern genetic concept of the genera in the tribe Triticeae (Poaceae). *Acta Phytotaxonomica Sinica*, 43(1), pp. 82-93.
- Zhou, X.C., Yang, X.M., Li, X.Q. & Li, L.H. (2010). Genome origins in *Leymus* (Poaceae: Triticeae): evidence of maternal and paternal progenitors and implications for reticulate evolution. *Plant Systematics and Evolution*, 289(3-4), pp. 165-179.
- Zuo, H., Wu, P., Wu, D. & Sun, G. (2015). Origin and Reticulate Evolutionary Process of Wheatgrass *Elymus trachycaulus* (Triticeae: Poaceae). *Plos One*, 10(5), p. e0125417.