It is well known that *Elymus* arose through hybridization between representatives of different genera and several different polyploidy genomes have been described. Cytogenetically, five basic genomes (St, H, Y, P and W) in different combinations have been found in the genus. The vast majority of species are tetraploids and they are characterized by having the StY genome or the StH genome. It is not known where the Y genome originated, although it is a common in *Elymus* from Central and East Asia. It has been hypothesized from isozymic and cytological studies of *Elymus* species that the Old and New World taxa may be of separate origin of the H genome in the StH genome species. Data from single copy of nuclear gene RPB2 indicated that the Eurasian and American StH genome species have independent alloplid origins with different H-genome donors. This hypothesis is needed to be tested by using more molecular data. Sequences from single copy of nuclear genes (*RPB*, *β*-amylase gene and *EF-G*) indicated that StY genome species is allopolyploid origin. This paper presents a briefly review on current status of molecular evolution and origin of tetraploid *Elymus* species.

**Key Words:** *Elymus*, Polyploidy, Origin, nuclear genes.

The Triticeae tribe contains the world’s most important crops such as wheat and barley, also included in this tribe are other species valuable for crop and forage breeding. The tribe combines a wide variety of biological mechanisms and genetic systems which makes it an excellent group for research in evolution, genetic diversity, taxonomy, and speciation in plants (Bothmer and Salomon 1994). Cytogenetic analyses have extensively been used to illustrate systematic relationships of the tribe and to clarify the origin of polyploid species (Dewey 1984, Løve 1984, Lu 1993). The most challenging problems within the Triticeae are the delimitation of the *Elymus* genus and its phylogenetic relationships.

The *Elymus* genus—current status of taxonomy

*Elymus* L., as circumscribed by Dewey (1984) and Løve (1984) and adopted throughout this paper, is the largest and most widely distributed genus in the tribe Triticeae. *Elymus* comprises relatively short-lived perennial and exclusively polyploidy grass species. Most of the species are densely to loosely caespitose, or rarely rhizomatous, small anthered, and self-pollinating. The genus encompasses approximately 150 species occurring worldwide. Although predominately a northern temperate genus, *Elymus* species occur from the Arctic and temperate to subtropical regions. These species inhabit various ecological niches, including grasslands, semi-desert, mountain slopes and valleys among bushes, and inside or along the edge of forests.

Taxonomy of *Elymus* is extremely complex because of the huge morphological variation within and between species (both environment and developmental stage could affect morphometric markers), the polyploid origin of the genus, and the frequent spontaneous hybridizations between species. Adding to the complexity is that wide divergence of classification concepts among taxonomists were used in different geographical regions. The major argument on the circumscription of *Elymus* proposed by various authors is whether single versus multiple spikelets per rachis node can be used as a key characteristic in the taxonomic circumscription. Some taxonomists used rather narrow circumscription for *Elymus*, which only contained few species. They included all species with multiple spikelets per rachis node in *Elymus*, and thus placed those species with single spikelets per node into other genera, such as *Agropyron* or *Roegneria*; the treatments for example by Hitchcock (1951), Keng (1959) and Baum (1983). However, other taxonomists did not consider single versus multiple spikelets per rachis node as significant feature in generic circumscription (Tzvelev 1976, Melderis et al. 1980, Løve 1984). They used much wider circumscription for *Elymus*, and put the species in *Elymus* regardless of the number of spikelets per rachis node. Still today, there is no worldwide acceptable circumscription.
of the genus. The various taxonomic classifications were followed and used in different geographic regions, such as, today, in North America, taxonomists still tend to follow Hitchcock’s (1951) definition of Elymus; Keng’s (1959) treatment of the Triticeae is widely accepted and used by Chinese agrostologists; whereas in Russia and Europe classification systems of Tzvelev’s (1976) and Melderis et al. (1980) are followed, respectively (Lu 1994).

Genomic constitution of Elymus species

All Elymus species are allopolyploids with 2n=28, 42 or 56. It is well known that Elymus arose through hybridization between representatives of different genera and several different polyhaplomeric genomes have been described (Dewey 1971, Jensen 1990a, 1990b, Torabinejad and Mueller 1993). Analysis of meiotic chromosome pairing has been widely applied in interspecific and intergeneric hybrids to elucidate homology or homoeology between the parental genomes in Elymus (e.g., Dewey 1968, 1984, Lu and Salomon 1992). Cytologically, five basic genomes, namely, St, H, Y, P and W in different combinations, have so far been found in the genus. The St genome derived from Pseudoroegneria (Nevski) Á. Löve is the most important composition of the genus, and can be found in allopolyploid combinations with H (from Hordeum L.), Y (from an unknown donor), P (from Agropyron Gaertn.), and W (from Australopyrum (Tzvelev) Á. Löve) or with a combination of these genomes in various tetraploid, hexaploid, and (rarely) octoploid configurations (e.g., Dewey 1984, Løve 1984, Jensen 1990a, 1990b, Lu 1993). (Genome symbols follows Wang et al. 1994). The vast majority of species are tetraploids and they are characterized by having the StY genome or the StH genome. The StY genome species are essentially limited to Central and East Asia.

The tetraploid Elymus species with StH genome

The StH genome species are distributed throughout the world in non-tropical areas, from northern Greenland in the north to Tierra del Fuego in southernmost South America. They are found from the arctic to the subtropics, from the seacoast to above 5000 m in the Himalayas, and their morphology is also very diverse and they can, for instance, vary from 5 cm to more than 2 meters in height. Hence, the StH genome Elymus species display an enormously wide range of adaptation to various climates and habitats, making them of utmost interest for plant breeding as well as basic research. This group of Elymus consists of approximately 50 species. Cytogenetic analysis revealed that this group of Elymus species has genome containing two basic haplotypes. The St haplome originates from the genus Pseudoroegneria which was erected by Löve (1980) on cytological grounds, and contain approximately 15 diploid or tetraploid species distributed in Middle east, central Asia, northern China and western North America (Watson and Dallwitz 1992). A very high homology between the St genomes in the Elymus and Pseudoroegneria was revealed by meiotic pairing data, although with slight modifications in some species (Dewey 1982, Løve and Connor 1982, Jensen 1990a, 1990b). Chloroplast DNA data suggested Pseudoroegneria as the maternal genome donor to Elymus species (tetraploids and hexaploids) (Jones et al. 2000, Redinbaugh et al. 2000, Mason-Gamer et al. 2002, McMillan and Sun 2004, Xu and Ban 2004, Liu et al. 2006). Cytological data suggested that there exists genome differentiation among the Pseudoroegneria species (Wang et al. 1994). A study based on the waxy gene indicated that St sequences formed two distinct clades which did not correspond to geographical differentiation (Mason-Gamer and Kellogg 2000). RP2 sequence data showed that the St genome in P. libanotica is differentiated from the St genome in P. spicata and P. stipifolia, and did not contradict the idea of paraphyly in Pseudoroegneria (Sun et al. 2008). RP2 results also suggest that P. spicata and P. stipifolia may be the St genome donor for Elymus species, P. libanotica may therefore not be the St genome donor of the Elymus species studied (Sun et al. 2008).

The H haplome donor, Hordeum, which is distributed in temperate areas in both the northern and southern hemispheres, is known to be extremely variable (Bothmer et al. 1995). Cytogenetic and molecular data indicated differentiation of the New World H genome Hordeum species from the Old World diploid species (Dubcovsky et al. 1997). Several studies suggested that the H haplome in Elymus could be from different sources. Isoenzyme analyses suggested that Eurasian and American StH-genome species may have independently originated from different H-genome donors (Jaaska 1992). Genome (Wang and Hsiao 1986) and karyotype analyses (Linde-Laursen et al. 1994) suggested that the H genome in Old and New World Elymus taxa may be of separate origin. WMS-PCR (wheat microsatellite-PCR) and RAPD analyses of tetraploid Elymus species seems to favor the independent allopolyploid origins for the Eurasian and American StH-genome species (Sun et al. 1997). The β-amylase sequences from H genome indicated that the two of the three North American Elymus tetraploid form a clade, while the remaining North American and Eurasian species are only slightly differentiated from one another (Mason-Gamer et al. 2005). The starch synthase sequence from H genome revealed that the relationships among the StH species are not clear-cut, but the weak basal split within the clade is relatively consistent with a North American-Eurasian distinct. The polyphyly of the H-genome sequences from Eurasian Elymus is consistent with multiple origins of StH Elymus in Eurasia, involving different Hordeum genome donors (Mason-Gamer et al. 2005). The RP2 sequence data showed a good separation of the H genomes in Elymus species which is in good agreement with their geographical origins—Eurasian and North/South American distinction with relative high bootstrap support (81% and 86%) (Fig. 1, Sun et al. 2008). RP2 data indicated that the H genome in Elymus species is highly differentiated reflecting its geographical origin. The
Fig. 1. Strict consensus tree of 529 most parsimonious trees derived from rpb2 sequence data, redrawn from Sun et al. (2008). Numbers above branches are bootstrap values. *Leymus coreanus* was used as an outgroup. Consistency Index (CI) = 0.714, retention index (RI) = 0.907, rescale consistency index (RCI) = 0.648.
Eurasian and American StH genome species thus have independent allopolyploid origins with different H-genome donors.

The tetraploid *Elymus* species with StY genome

The most common *Elymus* genome combination in Asia is StY, which is present in more than 75% of the known Asiatic tetraploid, and almost all known Asiatic hexaploids in which the Y genome is derived from an unknown donor. A low affinity between the St and Y genomes was indicated by chromosome pairing analysis (Sakamoto 1964, Lu and Bothmer 1989). Phylogeny of ITS sequences put all StY species in the St clade, and found only one genomic type of ITS sequence for each tetraploid StY genome *Elymus* species (Liu et al. 2006). Based on this result, the authors speculated that the St and Y genomes may have the same origin, and that allopolyploid StY genome species may have an origin from autoployploids (StSt) and the same genomes differentiated gradually within the polyploidy species resulting in today’s StY genome allotetraploid *Elymus* (Lu and Liu 2005, Liu et al. 2006). However, analysis of *Elymus* StY species based on β-amylase gene sequences yielded distinct, presumed Y-genome sequences (Mason-Gamer et al. 2005). RP2B data generated an obvious Y genome specific clade which is distinct from the St clade. Phylogenetic analysis of Y genome sequences with other genome donors (St, H, P, W) of *Elymus* revealed W and P genomes are sisters to Y genome (Sun et al. 2008). It is worth mentioning that the obvious Y genome specific clade is distinct from the St clade (Fig. 1). In an analysis of StH and StY species with EF-G sequences, two distinct copies of sequences were obtained from each species analyzed. Phylogenetic analysis yielded two distinct groups, one with St genome, another with Y genome (unpublished data). Single copy of nuclear sequence data (RP2B, β-amylase gene and EF-G) suggested that Y genome was originated from a distinct diploid species, and support an allopolyploid origin of StY species.

Conclusion

Huge morphological variation, the polyploid origin of the genus, and the frequent spontaneous hybridizations between species made the taxonomy treatment of *Elymus* extremely complex. Various taxonomists dealt with *Elymus* species from different geographical and historical perspectives. So far, no complete agreement on the circumscription of the genus has been reached. Cytological and molecular data proved that the St genome is pivotal genome and present in all *Elymus* species which combines with one or two of other four basic genomes (H, P, W and Y) in different combinations in *Elymus* species. Two genomic combinations have been identified in tetraploid *Elymus*, StH and StY genomic combinations. Systematic relationships among some *Elymus* species have been established based on cytological and taxonomic data. DNA sequence data have been used to study the phylogeny of some tetraploid species in *Elymus* which adds to our understanding of the phyloney and origin of *Elymus* species. However, phylogeny and origin of tetraploid *Elymus* is far from clear, and these studies do not test the hypothesis of whether the species with similar morphology are genetically related to each other. The chloroplast DNA data indicated that *Pseudoroegneria* is the maternal genome donor to *Elymus* species as above mentioned, but little more is known their origin. The specific progenitor species involved remain a mystery. The significant question remains unanswered: which diploid species best represent the parental species? Different hypotheses regarding the origin of Y genome were suggested, and still under debate. In future, by using several unlinked biparentally inherited DNA regions, we can test the mode of origin (i.e., auto- or allopolyploids) and hypotheses of the closest relatives of polyploids in a phylogenetic perspective. We can find out which parts of the genome have similar histories and which have different histories. This will help us to better understand phylogeny of evolution of this genus.

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Literature Cited


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