

ALLOPOLYPLOIDS OF THE GENUS *ELYMUS* (TRITICEAE, POACEAE):
A PHYLOGENETIC PERSPECTIVE

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ABSTRACT

The wheat tribe, Triticeae, includes many genomically distinct polyploid taxa. *Elymus* is an entirely allopolyploid genus, with all species containing the **St** genome of *Pseudoroegneria*. The **St** genome may be combined with one or more distinct genomes representing multiple, diverse diploid donors from throughout the tribe. This study includes a simultaneous phylogenetic analysis of new and previously published data from several distinct *Elymus* groups, including North American and Eurasian **StStHH** tetraploids, in which the **H** genome is derived from *Hordeum*, Eurasian **StStYY** tetraploids, in which the **Y** genome is derived from an unknown donor, and a putative **StStStStHH** hexaploid. *Elymus* species were analyzed with a broad sample of diploid genera from within the tribe using a combination of molecular data from the chloroplast and the nuclear genomes. The data confirm the genomic constitution of the **StStHH** and **StStYY** tetraploids, but do not provide additional information on the identity of the **Y**-genome donor. The genomic diversity in the hexaploid is greater than expected, inconsistent with the hypothesis of an **StStStStHH** genome complement.

Key words: *Elymus*, Poaceae, polyploidy, reticulation, Triticeae, wheat tribe.

INTRODUCTION

The wheat tribe, Triticeae (Pooideae, Poaceae), is widely known for its economic importance. This monophyletic tribe includes three major grain crops—wheat, barley, and rye—along with several important forage grasses and numerous weedy, invasive species. From an evolutionary standpoint, the tribe's complex reticulate history has been of interest for many years. At the diploid level, conflict among gene trees, especially between those based on chloroplast and nuclear DNA data (Mason-Gamer and Kellogg 1996a), suggests a history of gene exchange, lineage sorting, or a combination of both (Kellogg et al. 1996). Furthermore, polyploidy is common in the tribe; about 75% of the species with known chromosome numbers are polyploid (Löve 1984).

Allopolyploidy represents a reticulate process by which distinct genomes are united in a single nucleus. While there are problems with placing reticulate taxa within the bifurcating trees that are obtained using many methods of analysis (e.g., Hull 1979; Cronquist 1987; McDade 1992, 1998), studies of individual gene trees often allow these problems to be circumvented. Thus, molecular phylogenetic data have recently revealed the reticulate histories of several polyploid species or groups, for example: *Gossypium* L. (e.g., Cronn et al. 1996, 2003; Seelanan et al. 1997; Small and Wendel 2000), *Geum* L. (Smedmark et al. 2003), *Glycine* Willd. (e.g., Doyle et al. 2002; Rauscher et al. 2002), *Oxalis* L. (Emshwiller and Doyle 1998, 2002), *Oryza* L. (Ge et al. 1999), and *Paeonia* L. (e.g., Sang and Zhang 1999).

Within Triticeae, *Elymus* L. is a genomically heterogeneous polyploid group of about 140 species (Löve 1984). According to its genomic definition, *Elymus* comprises allopolyploid species with at least one set of chromosomes derived from *Pseudoroegneria* (Nevski) Á. Löve (genome designation **St**). The **St** genome can also be found in both

diploid and autotetraploid species, which are classified as *Pseudoroegneria* (Dewey 1984). In *Elymus*, the **St** genome can be combined with genomes from one or more Triticeae genera, including *Hordeum* L. (genome designation **H**), *Agropyron* Gaertn. (**P**), *Australopyrum* (Tzvelev) Á. Löve (**W**), and an unknown donor (**Y**), in various allopolyploid combinations including **StStHH**, **StStYY**, **StStHHHH**, **StStStStHH**, **StStStYY**, **StStYYYY**, **StStHHYY**, **StStYYWW**, and **StStYYPP** (e.g., Dewey 1967, 1968, 1970b, 1974, 1984; Jensen 1990, 1993, 1996; Salomon and Lu 1992, 1994; Lu and von Bothmer 1993; Lu et al. 1995). Other **St**-containing allopolyploids include *Pascopyrum smithii* (Rydb.) Barkworth & D. R. Dewey, which combines the *Pseudoroegneria* and *Hordeum* genomes with the **Ns** genome of *Psathyrostachys* Nevski in an **StStHHNsNsNsNs** octoploid configuration (Dewey 1975), and *Thinopyrum* Á. Löve, some species of which are hypothesized to combine the **St** genome with the **E** and/or **J** genomes usually considered characteristic of *Thinopyrum* (e.g., Liu and Wang 1993; Zhang et al. 1996; Chen et al. 1998). Thus, the **St** genome, probably more than any other in Triticeae, plays an important role in the complex reticulate allopolyploid patterns that characterize the tribe.

This overview focuses on a subset of species from the genomically heterogeneous *Elymus*, and presents molecular phylogenetic data that address their relationships to the diploid members of the tribe. These species include (1) North American tetraploid species with presumed **StStHH** genome configurations (e.g., Dewey 1982, 1983a, b, 1984; Mason-Gamer 2001; Mason-Gamer et al. 2002; Helfgott and Mason-Gamer 2004), (2) Eurasian tetraploid species, with presumed **StStHH** or **StStYY** genome configurations (e.g., Lu and von Bothmer 1990, 1993; Salomon and Lu 1992, 1994; Lu 1993; Lu et al. 1995), and (3) a Eurasian hexaploid spe-