Review

Molecular phylogeny among *Triticum-Aegilops* species and of the tribe *Triticeae*

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The tribe *Triticeae* includes some of the world's most important cereal crops, such as wheat, barley, and rye. It also includes important, mostly perennial, fodder grasses such as *Agropyron*, *Elymus*, *Leymus*, *Psathyrostachys*, and others. Many wild annual grasses of the tribe *Triticeae* belong to a highly valuable gene pool for cereal breeding—*Triticum*, *Aegilops*, *Secale*, *Hordeum*, *Dasypyrum*, etc., and some are interesting ephemeral plants of deserts, including *Eremopyrum*, *Crithopsis*, and *Heteranthelium*. Another group is interesting taxonomically, because they are on the border or just beyond the limit of the tribe, such as *Brachypodium* and *Henrardia*. *Triticeae* is a taxonomically controversial group at both the species and generic level. One extreme is considering *Triticum* to be the only genus of *Triticeae*, and an opposite extreme is accepting of a huge amount of often monotypic genera. Therefore, it seemed appropriate to review here several issues of the taxonomy and phylogeny of the tribe *Triticeae*.

Key Words: Molecular phylogeny, *Triticum-Aegilops* complex, *Triticeae*, monophyly.

Introduction

This special issue of Breeding Science, Japanese Society of Breeding, constitutes the proceeding of the 6th International Triticeae Symposium, which was held in Kyoto, Japan, from 31 May to 5 June 2009. The previous symposia were held in Helsingborg, Sweden (1991), Logan, Utah, U.S.A. (1994), Aleppo, Syria (1997), Cordoba, Spain (2001), and Prague, Czech Republic (2005). Like its predecessors, the Sixth Symposium brought together individuals in many different disciplines who have in common their interest in one group of grasses, the *Triticeae* (Kawahara 2009).

The tribe *Triticeae* includes several of the world's most important cereal crops, such as wheat, barley, triticale, and rye. It also includes important, mostly perennial, fodder grasses such as *Agropyron*, *Elymus*, *Leymus*, *Psathyrostachys*, and others. Many wild annual grasses of the tribe *Triticeae* belong to a highly valuable gene pool for cereal breeding, including *Triticum*, *Aegilops*, *Secale*, *Hordeum*, *Dasypyrum*, etc., and some are interesting ephemeral plants from desert environments, such as *Eremopyrum*, *Crithopsis*, and *Heteranthelium*. Another group is interesting taxonomically, because they are on the border or just beyond the limit of the tribe, namely *Brachypodium* and *Henrardia*. *Triticeae* grasses are distributed worldwide; however, their center of diversity is in the temperate belt of Eurasia, North America, and South America. They are important, dominant, or the

only plants in several habitats and accompany humans as weeds. They all possess a tremendous richness of genes and gene complexes useful in agricultural research and breeding. The tribe *Triticeae* is a taxonomically controversial group at both the species and generic level. One extreme is considering *Triticum* to be the only genus of the *Triticeae* (Stebbins 1956), and an opposite extreme is accepting of a huge amount of often monotypic genera (Dewey 1984, Löve 1984). On the other hand, common wheat, *Triticum aestivum* L., has been the textbook example of evolution by allopolyploid formation (Kihara 1954). Hence, recent studies on molecular phylogeny of the tribe *Triticeae* are reviewed here with special emphasis on the *Triticum-Aegilops* complex, which has a very long history of evolutionary studies.

Current taxonomic status of *Triticum-Aegilops* complex and the tribe *Triticeae*

The tribe *Triticeae* is a fairly big group of grasses with 330 (Clayton and Renvoize 1986) to 360 (Watson and Dallwitz 1994) species, in which the genus *Elymus* (ca. 150 species) is the largest and most widely distributed. After the finding of a polyploid series in wheat by Sakamura (1918), Kihara started genome analysis in wheat and its wild relative *Aegilops* (Kihara 1954, Lilienfeld 1951). Genome analysis has proved its effectiveness in unraveling genomic and phylogenetic relationships in the *Triticum-Aegilops* complex and was applied to other genera of the *Triticeae* (von Bothmer 1995, Wang *et al.* 1994). These methods were employed first to examine the phylogenetic relationships of *Hordeum* and *Secale*, two important crops of the *Triticeae*, and then other

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perennial genuses, such as *Elymus*. Based on the accumulated information on these genomes, Dewey and Löve independently proposed that generic classification in the *Triticeae* should be based on the genomic constitution of each species just a quarter century ago (Dewey 1984, Löve 1984). Their proposal has been widely accepted by many researchers, especially those who deal with perennial species such as *Elymus* (e.g. Mason-Gamer *et al.* 2005, Sun and Salomon 2009) as well as most taxonomists (for reviews, Barkworth and von Bothmer 2005, 2009, Yen and Yang 2009, see also Table 1).

On the other hand, support for the proposals of Dewey and Löve has not forthcoming from those who deal with annual group. Löve's idea to split *Aegilops* by their genomic constitution was generally rejected and the genus retained its previous status as treated by Linnaeus. The opposite proposal to merge *Aegilops* into *Triticum* (Bowden 1959, Yen and Yang 2009) also failed to receive widespread acceptance. The *Triticum-Aegilops* complex is a small group in the *Triticeae* with ca. 28 species, but its economic importance is very large and most wheat geneticists and breeders prefer to retain the familiar names of *Aegilops* and *Triticum*. In this context, Clayton and Renvoize (1986) wrote, "Bearing in mind the genetic constitution of *T. aestivum*, its separation from *Aegilops* is a matter of some contention." Similarly, Löve's separation of *Critesion* Raffin. with the H genome from *Hordeum* L. with the I genome also failed to find acceptance, and many researchers (e.g. Kakeda *et al.* 2009, Peterson and Seberg 2009, Taketa *et al.* 2009) continue to use *Hordeum s.l.* Yen and Yang (2009) proposed retaining *Hordeum* but used genomic constitutions to separate sections within the genus. Clear morphological uniformity of *Hordeum* with triads of one central spikelet and two laterals in fragile rachis may help to retain this familiar name.

Molecular phylogeny of diploid *Triticeae*

In the past 15 years, the tribe *Triticeae* has been the focus of numerous molecular phylogenetic studies based on data from chloroplast DNA markers, high-copy nuclear genes, and low or single-copy nuclear genes. Some of the earlier studies showed conflict with one another due to past hybridization among genera, possible introgression, limited taxon sampling, or a combination of these. For example, although some molecular studies showed that *Aegilops* and *Triticum* form a monophyletic clade (Hsiao *et al.* 1995, Huang *et al.* 2002a, 2002b, Kellog and Appels 1995, Kellog *et al.* 1996, Mason-Gamer *et al.* 1998, 2002), many other molecular and morphological studies revealed polyphyly of the *Triticum-Aegilops* complex (Mason-Gamer 2001, 2004, 2005, Peterson and Seberg 1997, Sallares and Brown 2004, Seberg and Frederikson 2001). To reduce the effect of past hybridization among genera, it is necessary to construct a robust phylogeny among diploid genomes first, as well as clarifying species relationships among diploids and polyploids. Yamane and Kawahara (2005) analyzing base-pair substitutions,

Table 1. Genera included in tribe *Triticeae* in recent monographs on Grasses

Clayton and Renvoize (1986)
<i>Aegilops</i> , <i>Agropyron</i> , <i>Brachypodium</i> , <i>Crithopsis</i> , <i>Dasyphyrum</i> , <i>Eremopyrum</i> , <i>Elymus</i> , <i>Henrardia</i> , <i>Heteranthelium</i> , <i>Hordelymus</i> , <i>Hordeum</i> , <i>Hystrix</i> , <i>Leymus</i> , <i>Psathyrostachys</i> , <i>Secale</i> , <i>Sitanion</i> , <i>Taeniatherum</i> , <i>Triticum</i>
Watson and Dallwitz (1994) ^a
<i>Aegilops</i> , <i>Agropyron</i> , <i>Amblyopyrum</i> , <i>Australopyrum</i> , <i>Cockaynea</i> , <i>Crithopsis</i> , <i>Dasyphyrum</i> , <i>Elymus</i> , <i>Elytrigia</i> , <i>Eremopyrum</i> , <i>Festucopsis</i> , <i>Henrardia</i> , <i>Heteranthelium</i> , <i>Hordelymus</i> , <i>Hordeum</i> , <i>Hystrix</i> , <i>Kengyilia</i> , <i>Leymus</i> , <i>Lophopyrum</i> , <i>Malacurus</i> , <i>Pascopyrum</i> , <i>Peridictyon</i> , <i>Psathyrostachys</i> , <i>Pseudoroegneria</i> , <i>Secale</i> , <i>Sitanion</i> , <i>Taeniatherum</i> , <i>Thinopyrum</i> , <i>Triticum</i>

^a *Brachypodium* is placed in the separate monogeneric tribe *Brachypodieae*.

indels, and microsatellites in chloroplast noncoding regions in all diploid *Triticum-Aegilops* species, revealed the polyphyletic nature of the *Triticum-Aegilops* clade. Their data showed that *Aegilops speltoides* Tausch is the sister group to the remaining species of the *Triticum-Aegilops* complex, including *Ae. mutica* Boiss. (*Amblyopyrum muticum*), and the latter included the *Secale* branch containing cross-fertilizing *Secale cereale* L. and self-fertilizing *S. sylvestre* Host.

Peterson *et al.* (2006) also confirmed this basal position of *Ae. speltoides* based on the sequence data of two nuclear genes, DMC1 and EF-G, and a plastid gene, *ndhF*. They further revealed that as many as 14 other *Triticeae* genera formed a clade together with *Triticum-Aegilops* that is the sister to *Ae. speltoides* and the B genome of polyploid wheat. The 14 *Triticeae* genera were *Agropyron*, *Australopyrum*, *Crithopsis*, *Dasyphyrum*, *Eremopyrum*, *Festucopsis*, *Heteranthelium*, *Hordeum*, *Lophopyrum*, *Peridictyon*, *Psathyrostachys*, *Secale*, *Taeniatherum*, and *Thinopyrum* (Peterson *et al.* 2006). Another sister clade contained only two genera, *Henrardia* and *Pseudoroegneria*. Because they selected representatives of all the genomes traditionally recognized in diploid *Triticeae*, there is no problem in taxon sampling. On the other hand, the possible effect of past hybridization among genera and/or possible introgression cannot be ruled out because they used two nuclear genes. Their phylogenetic tree based on the plastid gene *ndhF* showed that only three genera, *Crithopsis*, *Secale*, and *Taeniatherum*, has the possibility to be included within *Ae. speltoides* plus the other *Triticum-Aegilops* clade (Peterson *et al.* 2006). *Crithopsis*, *Secale*, and *Taeniatherum* again formed a cluster together with *Aegilops* (and *Ambryopyrum*) and *Triticum* in the phylogenetic tree based on plastid *RbcL* and *ndhF* in a recent study (Peterson and Seberg 2008). These studies apparently showed polyphyly of the *Triticum-Aegilops* complex where *Ae. speltoides* formed a distinct clade. They further suggested that several *Triticeae* genera, at least *Secale*, will be included in between

Ae. speltoides and the *Triticum-Aegilops* clade.

The genus *Hordeum* is another group with abundant information on its molecular phylogeny, but such a polyphyletic relationship has not yet been reported (Baum and Johnson 2007, Blattner 2004, Kakeda *et al.* 2009, Komatsuda *et al.* 2001, Nishikawa *et al.* 2002, Sun *et al.* 2009, Peterson and Seberg 2003, 2009, Taketa *et al.* 2009). Because most of these studies focused on the phylogenetic relationships among diploid, tetraploid, and hexaploid species, only one or two accessions belonging to other *Triticeae* genera were employed as outgroups. All four phylogenetic trees constructed by Peterson *et al.* (2006) strongly suggested a monophyletic status of *Hordeum*, but more studies will be necessary to confirm this.

Genetic background that control spike morphology

Yamane and Kawahara (2005) also pointed out the terminal position of *Ae. mutica* together with *Ae. umbellulata* Zhuk. within the *Triticum-Aegilops* clade. Some molecular analyses also suggested that *Ae. mutica* is close to *Ae. umbellulata* (Terachi *et al.* 1984, Murai *et al.* 1989) as well as to *Ae. caudata* L., *Ae. comosa* Sm. in Sibth. & Sm., *Ae. umbellulata*, *Ae. uniaristata* Vis. (Dvořák and Zhang 1992), and *Ae. tauschii* Coss. (Terachi and Tsunewaki 1992). This poses a discrepancy between molecular phylogeny and classification based on morphology. Based on several morphological characters (e.g., awnless linear spikes) that differentiate *Ae. mutica* from other *Aegilops* species, van Slageren (1994) claimed that *Ae. mutica* should belong to genus *Amblyopyrum* instead of genus *Aegilops*. *Ae. mutica* and *Ae. speltoides* are the only predominantly cross-pollinating diploid species in the genus. Because most perennial relatives in the tribe *Triticeae* are allogamous, allogamy is generally accepted as an ancestral character. In addition, *Ae. mutica* bears a close resemblance to the perennial relatives, especially *Agropyron*, so it has been considered an ancestral species based on morphological and cytogenetic analyses (reviewed by Ohta 1991). *Ae. mutica* and *Ae. umbellulata* have quite different morphological characteristics, as shown in Table 2. If the two species differentiated rather recently, it is highly possible that few genes or a few tightly linked clusters of genes control these characteristics. A similar situation is also

found in *Secale*. *Secale* has linear membranous glumes but *Aegilops* and *Triticum* (and also other genus such as *Elymus*) has oblong to ovate glumes.

Zohary and Imber (1963) and Wains *et al.* (1979) pointed out that drastic morphological change in spike shape could be caused by a block of closely linked genes. *Ae. speltoides* has two varieties, var. *speltoides* with narrow cylindrical, 7–15 (–20) cm long spikes, awnless lateral spikelets, disarticulating usually at the bottom of the spike and var. *ligustica* with distichous, narrow cylindrical, 7–10 cm long spikes, awned lateral spikelets disarticulating wedge-type (spike axis attaching to below spikelets) at maturity, with the *ligustica* characters dominant over the *speltoides* ones. Similarly, when hybrids were made between *Ae. longissima* Scwinf. et Muschl. without lateral awn and disarticulation at the bottom of the spike and *Ae. bicornis* (Forsk.) Jaub. et Sp. with lateral awns and wedge-type disarticulation, the *Ae. bicornis* disarticulation character was dominant over the intact rachis of *Ae. longissima* (Wains *et al.* 1979). In the F₂ generation of hybrids between *Ae. longissima* and *Ae. bicornis*, a 3:1 segregation for spike shattering was observed, suggesting that the *Ae. bicornis* wedge-type disarticulation character is controlled by one gene or one block of linked genes. Such a drastic morphological change in spike character caused by one mutation was also reported in *Hordeum*. It is well known that six-rowed cultivated barley with the *vrs1* gene originated with a mutation from two-rowed barley with *Vrs1*. This *Vrs1* gene was recently characterized and loss of function leads to conversion of the rudimentary spikelets of two-rowed barley into the fertile spikelets of six-rowed barley (Komatsuda *et al.* 2007). Because the genus *Hordeum* has three spikelets at each rachis node, *Vrs1* is apparently one of the genes that regulate the development of lateral spikelets and cause morphological changes in the spikes. The number of spikelets at each rachis node is sometimes considered significant in generic circumscription in *Triticeae*, but one or a few genes may control this. If linear membranous glumes of *Secale* can change to oblong to ovate glumes of *Triticum-Aegilops* complex or *vice versa* by a single mutation, inclusion of *Secale* in between the *Ae. speltoides* clade and the other *Triticum-Aegilops* clade will be explained by this single mutation. Similarly, drastic morphological differences between *Ae. umbellulata* and

Table 2. Differences in morphological characteristics between *Aegilops mutica* and *Ae. umbellulata*

Character	<i>Ae. mutica</i>	<i>Ae. umbellulata</i>
Shape of spike	Very long, linear	Short, ovate, the upper markedly smaller
No. of spikelets	Many	Few, usually only 1–2 well developed
No. of fertile florets	3–4, rarely 5	Usually 2
Glume awn	No	3–5 awned
Lemma awn	No	2–3 awned
Pollination	Predominantly cross-pollination	Self-pollination possible
Seed set by bagging	No	Yes
Disarticulation	At the base of spikelets or florets, when rachis disarticulate usually upper half of spike only	At the base of spike, spike intact

Ae. mutica (Table 2) in spite of their supposed close phylogenetic relationship may be explained by a single gene or a closely linked block of genes.

Outlook and conclusions

The papers by Dewey and Löve have encouraged genomic studies and discussions on generic definitions within the tribe *Triticeae*. Although their proposal to define genera by their genomic constitution has not been accepted in several genera, many research paper have provided information on the genomic constitution of the species involved. Genome analysis based on morphological, cytological, and molecular information has been a very powerful tool in phylogenetic studies, including tetraploid and hexaploid species. Ellneshog-Staam *et al.* (2007) proposed to place *Leymus*-like species of *Hystrix* into *Leymus* and *Elymus*-like ones into *Elymus*, respectively, based on genomic analysis by GISH (genomic *in situ* hybridization) and Southern genomic hybridization. Although such taxonomic rearrangements will continue, we need to clarify the phylogenetic relationships of this tribe as a whole to integrate information on the individual genomes at the same time. The first step will be to construct a robust phylogenetic tree of all the diploid genomes in the tribe *Triticeae*.

Through advances in *Triticeae* genomics (e.g. Stein 2007), many *Triticeae* gene loci have been sequenced and characterized. Some of these are responsible for spike morphology or grain characteristics, *Q* of *T. aestivum* (Faris *et al.* 2003), *Ha* (*Hardness*) of *Triticum* and *Aegilops* (Chantret *et al.* 2005), *Vrs1* of *H. vulgare* L. (Komatsuda *et al.* 2007), and *Nud* of *H. vulgare* (Taketa *et al.* 2008). *Q* is thought to be a major regulatory gene for floral development (Muramatsu 1986), and Chantret *et al.* (2005) proposed an *APETALA2* (*AP2*)-like gene as a candidate for *Q* gene because *AP2* is known to play a major role in controlling floral homeotic gene expression. This was also confirmed by Simons *et al.* (2006). A wide array of molecular techniques has allowed us to understand the genetic basis of other important traits. We can also hope that such progress will enable us to understand why differences in genomes result in different morphologies.

When using the tribe *Triticeae* as a gene pool for breeding of indispensable cereals, we must view the tribe from biodiversity and conservation angles as well (e.g. Holubec 2005, Knüpffer 2009). Species identification is an urgent problem, not only for the practical utilization of genetic resources but also in understanding the whole evolutionary history of this tribe. In identifying species, we still need to develop a species-level treatment of the tribe. Barkworth and von Bothmer (2005) proposed an approach to develop illustrated, multi-entry keys using programs such as DELTA (Dallwitz 1980, Dallwitz *et al.* 1993, 1995, 2000) or Lucid ID (Centre for Bioinformation Technology 2004). Adopting such an approach would undoubtedly facilitate the identification of species of the tribe *Triticeae*.

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