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REVIEW ARTICLE

THE REVIEW OF WHEAT, ITS CONTROVERSIES AND THE ETHIOPIAN CONTEXT

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ABSTRACT

As a cereal wheat is also believed to originate from Fertile Crescent. On the other hand Ethiopia is a center of great diversity particularly for the tetraploid wheat. Genomic and taxonomic controversies are of the major points of debate among scientists working on the crop. Since wheat is known to compose A,B and D genomes the controversies stems from the fact that different findings suggested different results with regards to the progenitor specie of these genomes. Compared with B and A genomes the D genome, progenitor is found to be less arguable that it is widely accepted to be Aegilops tauschii. On the contrary the B genome donor has been a point of immense studies but remained controversial. This is attributed to the fact that B genome is relatively diverged from its putative diploid progenitors. Though the progenitors of the A genome are less debatable than the B genome three species were suggested as a probable progenitors of the A genome. These were T. monococcum, T.uratu and T.boeoticum. Taxonomically, different researchers follow either of the two different approaches, the traditional and genetic approaches naming, which are characterized by binomial and trinomial naming respectively. The traditional naming gives more emphasis to the separate habitats of the traditional species. On the other hand in the genetic classification approach the cultivated forms with the same ploidy level were considered as the same species. Despite this controversy it is most recommended to follow either of the naming in a given scientific writing. The emmer wheat found in Ethiopia given different names: T.dicoccum and T.dicoccun appeared to be the other point of debate as far as wheat nomenclature is concerned.

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INTRODUCTION

Wheat (*Triticum L.*) is an annual plant that belongs to the grass family Poaceae, tribe Triticeae and sub tribe Triticineae. The crop is thought to have originated on the Eurasian continent, a starting point from which man spread it throughout the world (Haider, 2010). The Fertile Crescent considered as the birth place of cultivated wheat about 8000 to 10000 years ago. Hence it is one of the earliest domesticated crop plants (Lev-Yadun *et al*., 2000). It is the world's most widely cultivated food crop followed by rice and maize (Gulbitti-onarici *et al*., 2009). In earlier times Ethiopia was considered to be the center of origin for cultivated tetraploid wheat (Vavilov, 1951). But it was agreed later on that Ethiopia is a center of diversity not origin as there are no wild relatives and ancestral forms of the crop. About seven species has been reported to be cultivated in Ethiopia but with significant in difference the area coverage. Emmer wheat, *Triticum dicocum* was the first to arrive (Feldman, 1976). Ethiopia is one of the few countries where *T. dicoccum* is still under production.

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But it is not clear however, whether the free threshing types replaced emmer after direct introduction or they evolved from emmer through mutations followed by selections (Tesfaye and Getachew, 1991). Despite the immense studies carried on the crop throughout the world there are still controversies. These controversies arose mainly from the origin of the genomes and the nomenclature of the crop. Hence the objective of this article is to review the controversies over the A and B genome donor and nomenclature of wheat.

Controversies on the genome donors of wheat

Wheat is a polyploid cereal consisting of different pliody levels, diploid (einkorn) 2n=2x=14 AA, tetraploid (emmer, durum, rivet, polish and Persian; 2n=4x=28, BBAA or GGAA) and hexaploid (spelt, bread, club, and Indian shot; 2n=6x=42, BBAADD or GGAADD) species (Feldman, 2001; Provan *et al*, 2004). It is derived from 3 homologous genomes, A, B and D (G instead of B in timopheevi group) each of which contributes 7 pairs of chromosomes to the wheat's total genome. The chromosomes (1 through 7) in various diploid genomes (B, A, and D) are considered to be evolutionarily related, that is, homoeologous in nature. When combined in the same nucleus, homoeologues can be induced to pair with each other (Gale and Devos, 1998). The D genome progenitor of hexaploid wheat is generally accepted to be *Aegilops TauschiiCoss*. (syn. *Aegilops. squarrosa*auct. non L.), since the chromosomes of *T.tauschii* show complete pairing with the D genome chromosomes of the *T. aestivum (Zhang et al, 2008)*. Besides the D genome is expected to show less variation than the other genomes (B and A). Hence there is no as such an ambiguity in the D genome donor of polyploidy wheat. This genome has contributed significantly to the wheat flour properties that make *T.aestivum* so valuable in bread making (Peterson *et al*., 2006); (Morris and Sears, 1967). Early Cytogenetic studies led to the conclusion that the A genome of the tetraploid species, *T. timpheevi* and *T. turgidum* was contributed by *T. monococum* (Sax 1922). Chapman *et al*, (1976) determined that the A genome originated from *T. uratu*. Konarev *et al* (1979) concluded from studies of the immunological properties of seed-storage proteins, that the A genome in *T. turgidum* was contributed by *T. uratu* and A genome of T. *timopheevi* was contributed by *T. monococum*. However, Nishikawa *et al*. (1994) suggested that the A genomes in both diploid species were contributed by *T. uratu.* Recently 3 species were suggested as the A genome donor to polyploidy wheat: *T. monococum* (Sourdille *et al*., 2001), *T. uratu* (Gulbiti-Onarici *et al*., 2007), and *T. boeoticum* (*T. monococum* var *boeoticum*) (Gulbiti-Onarici *et al*., 2009). The non brittleness and nakedness which is controlled by wheat domestication gene Q locus, located on chromosome 5 of genome A (Luo *et al*., 2000). This gene is considered to be the major wheat domestication gene since it governs the free-threshing character and square spike phenotype (Kristin *et al*., 2005).

the polypliod wheat (Peteresen *et al*., 2006), the incomplete chromosome pairing between B genome chromosomes and any diploid species and the fact that the B genome is relatively diverged from its putative diploid progenitors (Talbert *et al*., 1995). Morphological, geographical and cytogenetic evidence suggests that *Ae. Speltoides* is the donor of the B genome. However, chromosome banding, *in situ* hybridization and isozyme studies have indicated that the genome of *Ae. Speltoides* is not identical to that of the B genome common to *T. aestivum* and *T. turgidum* (Waines and Barnahart, 1992). Zhang *et al*. (2008) pointed out that the B genome donor is believed to be extinct, heavily modified, or not yet discovered, but agreed that it was probably an ancestor of *Ae. speltoides*. Talbert *et al*. (1991), suggested *Ae. speltoides* as the closest living species to the extant species. An alternative explanation to the donor of the B genome is its being polyphyletic in origin, that it is a recombined genome derived from 2 or more diploid *Aegilops* species (Liu *et al*., 2003).

Such a polyphyletic origin would result in a high level of differentiation in the B genome (Harlan, 1992). A polyphyletic origin of the B genome was also suggested based on enzyme analysis (Nishikawa *et al*., 1992) and a low copy non coding chromosome-specific DNA sequence (Liu *et al*., 2003). Blake *et al* (1999), however, supported the monophyly of the B genome of wheat. Several studies have shown that the B genome in *T. turgidum* and *T. aestivum* is closely similar to the S genome in section Sitopsis. Therefore, one or more of the sitopsis species were frequently proposed as B genome donor to polyploid wheat, including *Ae. bicornis, Ae. longissima, Ae. searsii, Ae. sharonensis and Ae. Speltoides,* for which the most positive evidence has been accumulated (Salina *et al*., 2006).

Table 1. The nomenclature of wheat based on both traditional and genetic approach

Common name	Genome(s)	Genetic approach	Traditional approach
Diploid (2x)			
Wild einkorn	A^m	*Triticum monococcum*L. subsp. *aegilopoides* Thell.	*Triticum boeoticum*Boiss.
	A^U	*Triticum uratu*Tumanian ex Gandilyan	*Triticum uratu*Tumanian ex Gandilyan
Einkorn	A^m	*Triticum monococcum*L. subsp. *Monococcum*	*Triticum monococcum*L.
Tetraploid (4x)			
Wild emmer	BA^u	*Triticum turgidum*L. subsp. *dicoccoides*(Korn. ex Asch. &Graebn.) Thell.	*Triticum dicoccoides*(Körn. ex Asch. & Graebner) Schweinf.
Emmer	BA^u	*Triticum turgidum*L subsp. d*icoccum* (Schrank ex Schübl.) Thell.	*Triticum dicoccum*Schrank ex Schübler
	BA^u	*Triticum ispahanicum*Heslot	*Triticum ispahanicum*Heslot
	BA^u	*Triticum turgidum*L. subsp. *paleocolchicum*Á.&D. Löve	*Triticum karamyschevii*Nevski
Durum or macaroni wheat	BA^u	*Triticum turgidum*L. subsp. *durum*(Desf.) Husn.	*Triticum durum*Desf.
Rivet or cone wheat	BA^u	*Triticum turgidum*L. subsp. *turgidum*	*Triticum turgidum*L.
Polish wheat	BA^u	*Triticum turgidum*L. subsp. *polonicum*(L.) Thell.	*Triticum polonicum*L.
Khorasan wheat	BA^u	*Triticum turgidum*L. subsp. *turanicum*(Jakubz.) Á.&D. Löve	*Triticum turanicum*Jakubz.
Persian wheat	BA^u	*Triticum turgidum*L. subsp. *carthlicum*(Nevski) Á.&D. Löve	*Triticum carthlicum*Nevski in Kom.
Tetraploid (4x) - *timopheevi* group			
	GA^u	*Triticum timopheevii* (Zhuk.) Zhuk.subsp. *armeniacum*(Jakubz .) Slageren	*Triticum araraticum*Jakubz.
	GA^u	*Triticum timopheevii* (Zhuk.) Zhuk. subsp. *Timopheevii*	*Triticum timopheevii* (Zhuk.) Zhuk.
Hexaploid (6x)			
Spelt wheat	BA^uD	*Triticumaestivum*L. subsp. *spelta*(L.) Thell.	*Triticum spelta*L.
	BA^uD	*Triticum aestivum*L. subsp. *macha*(Dekapr. & A. M. Menabde) Mackey	*Triticum macha*Dekapr. &Menabde
Common or bread wheat	BA^uD	*Triticum aestivum*L. subsp. *aestivum*	*Triticum aestivum*L.
Club wheat	BA^uD	*Triticum aestivum*L. subsp. *Compactum* (Host) Mackey	*Triticum compactum*Host
Indian dwarf or shot wheat	BA^uD	*Triticum aestivum*L. subsp. *sphaerococcum*(Percival) Mackey	*Triticum sphaerococcum*Percival

(Source: GRIN Taxonomy for Plants).

In polyploid wheat, the donor of the B genome has been the most controversial and is still relatively unknown, in spite of a large number of attempts to identify the parental species (Huang *et al*, 2002). This may be associated with the higher diversification rate of the B genome compared to A genome in

Ae.speltoides was even proposed as the mitochondrial genome donor of polyploid wheat (Wang *et al*., 2000). Provan *et al* (2004) suggested cytoplasm of *T. aestivum* is similar to the cytoplasm of the S-type of the 5 Sitopsis species of *Aegilops*. Uncertainty remains, however, regarding whether *Ae.*

speltoides is the sole source of the B genome or whether this genome resulted from an introgression of several parental species (Blake *et al*., 1999). Regardless, since the cytoplasm donor is the female in the original cross creating the polyploid it is always listed first in any pedigree. The tetraploid genome designations should technically be BBAA or GGAA instead of AABB or AAGG.

Taxonomic controversies

Although gene pool classification based on ease of crossability, fertility of hybrids, chromosome paring and ease of gene transfer has been rocomended, classification of *Triticum* with clear cut discontinuity at species level has been very difficult. Hence the classification of wheat has been the subject of much debate for over a century, and there is still no consensus of opinion as to the best system of nomenclature (Philips, 1995). Some authors follow the traditional classification approach where more weight is given to the separate habitats of the traditional species. In this system of classification, the reasonably stable and recognized types of wheat are given the taxonomic rank of species. Besides in such an approach there are pragmatic arguments that most species can be described in Latin binomials (Table 1). Hence emmer and durum wheat for instance are treated as a different species. The other approach that is still being followed by other authors mostly geneticists is the genetic classification approach. The proponents of this approach take the view that cultivated forms with in the same genome should be regarded as single species, hence each ploidy level is represented by only one species as follows: *T. monococum* (diploid); *T.turgidum* (tetraploid); *T. aestivum* (hexaploid). The different types of wheat are then relegated to subspecific rank or treated as cultivars (Mac Key, 1966). Similarly, Bowden (1959) argued that forms that are interfertile should be treated as one species. There is no crossing barrier for instance amongst the members of the BBAA teraploid groups together with the heterogeneous environment, this has resulted in continuous variation. Consequently, traditional morphological schemes of classification have been rather difficult to adopt. Thus emmer and durum wheat should both be treated as sub species of a single teraploid species defined by the genome BA^u. Latin trinomials are used to describe each species (Table 1). The other controversy related to the nomenclature of wheat is, the emmer wheat specie found in Ethiopia. Tesfaye and Getachew (1991) reported the presence of emmer wheat, (*T. dicocum)* in Ethiopia. It is assumed to be introduced to Ethiopia by the Hamites 5000 years ago (Feldman 1976 in Tesfaye and Getachew 1991). On the other hand Philips (1995) reported the emmer wheat found in Ethiopia is *T. dicoccon* whereas *T. dicocum* is different specie not found in Ethiopia. Kihara (1944) reported *T.dicoccon to be the wild emmer not the cultivated as a tetraploid parent.* Hence the argument here is since there is no wild emmer in Ethiopia how could the emmer wheat found in Ethiopia be dicoccon?

Conclusion

With the progress in scientific research particularly in phylogenetic studies the prevailing controversies won't continue as they are now. Genomic progenitors of the B and A genome will be verified following the continued immense studies on the matter. With regards to the naming of the crop the controversy remains but the most critical point is that different taxonomic schemes should not be mixed. In a given article or book only one of the schemes should be used at a time, otherwise, it will be unclear how the botanical names are being used.

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