Complete chloroplast genomes of Aegilops tauschii Coss. and Ae. cylindrica Host sheds light on plasmon D evolution

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ORIGINAL ARTICLE

Complete chloroplast genomes of *Aegilops tauschii* Coss. and *Ae. cylindrica* Host sheds light on plasmon D evolution

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Abstract Hexaploid wheat (*Triticum aestivum* L., genomes AABBDD) originated in South Caucasus by allopolyploidization of the cultivated Emmer wheat *T. dicoccum* (genomes AABB) with the Caucasian *Ae. tauschii* ssp *strangulata* (genomes DD). Genetic variation of *Ae. tauschii* is an important natural resource, that is why it is of particular importance to investigate how this variation was formed during *Ae. tauschii* evolutionary history and how it is presented through the species area. The D genome is also found in tetraploid *Ae. cylindrica* Host ($2n = 28$, CCDD). The plasmon diversity that exists in *Triticum* and *Aegilops* species is of great significance for understanding the evolution of these genera. In the present investigation the complete nucleotide sequence of plasmon D (chloroplast DNA) of nine accessions of *Ae. tauschii* and two accessions of *Ae. cylindrica* are presented. Twenty-eight SNPs are characteristic for both TauL1 and TauL2 accessions of *Ae. tauschii* using TauL3 as a reference. Four SNPs are additionally observed for TauL2 lineage. The longest (27 bp) indel is located in the intergenic spacer *Rps15-ndhF* of SSC. This indel can be used for simple determination of TauL3 lineage among *Ae. tauschii* accessions. In the case of *Ae. cylindrica* additionally 7 SNPs were observed. The phylogeny tree shows that chloroplast DNA of TauL1 and TauL2 diverged from the TauL3 lineage. TauL1 lineage is relatively older then TauL2. The position of *Ae. cylindrica* accessions on *Ae. tauschii* phylogeny tree constructed on chloroplast DNA variation data is intermediate between TauL1 and TauL2. The complete nucleotide sequence of chloroplast DNA of *Ae. tauschii* and *Ae. cylindrica* allows to refine the origin and evolution of D plasmon of genus *Aegilops*.

Keywords Chloroplast DNA · Illumina · Indels · Sequencing · SNP · *Aegilops*

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Introduction

Hexaploid wheat (*Triticum aestivum* L., genomes AABBDD) originated in South Caucasus by allopolyploidization of the cultivated Emmer wheat *T. dicoccum* Schrank (genomes AABB) with the Caucasian *Ae. tauschii* ssp *strangulata* (Eig) Tzvelev (genomes DD) (Kihara 1944; McFadden and Sears 1946, cited according Wang et al. 2013; Dvorak et al. 1998; Dubcovsky and Dvorak 2007). *Ae. tauschii* Coss. (syn. *Ae. squarrosa* auct non L.) is a diploid ($2n = 14$, genome DD) goat-grass species which donated its genome D to common wheat, *T. aestivum* L. It is considered as the most important donor of agriculturally important genes for improvement of common wheat (Kimber and Feldman 1987). Genetic variation of *Ae. tauschii* is an important natural resource, that is why it is of particular importance to investigate how this variation was formed during *Ae. tauschii* evolutionary history and how it is presented through the species area. The D genome is also found in

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tetraploid *Ae. cylindrica* Host ($2n = 28$, CCDD). The parents of *Ae. cylindrica* are *Ae. caudata* L. ($2n = 14$, CC) and *Ae. tauschii*. *Ae. caudata* and *Ae. tauschii* overlap the area of *Ae. cylindrica*, but have no area in common (Nakai 1981). The term Plasmon is used for cytoplasmic (organellar) genomes—chloroplast and mitochondria (Tsunewaki et al. 2002; Gill and Friebe 2002). The plasmons of *Ae. tauschii* Coss.and *Ae. cylindrica* Host both belong to the D type. According to Tsunewaki et al. the plasmon diversity that exists in *Triticum* and *Aegilops* species is of great significance for understanding the evolution of these genera.

Ae. tauschii is presented by two subspecies, *Ae. tauschii* Coss. ssp *tauschii* and *Ae. tauschii* Coss. ssp *strangulata* (Eig) Tzvelev with cylindrical and moniliform types of spike, respectively (Eig 1929). In ssp *strangulata* a relict lineage "t-9^{1}s" was found which considerably differ genetically from other accessions of this subspecies (Dudnikov 1998, 2012; Pestsova et al. 2000). The three markedly different gene-pools of *Ae. tauschii*, i.e. those of ssp *tauschii*, "usual" ssp *strangulata*, and relict lineage "t-9^{1}s" of ssp *strangulata*, were designated by Matsuoka et al. (2013, 2015) as TauL1, TauL2 and TauL3, respectively. These designations were finally used after several investigations (Matsuoka et al. 2007, 2008, 2009, 2013, 2015; Mizuno et al. 2010). Chloroplast DNA variation in *Ae. tauschii* was studied by Matsuoka et al. (2007, 2008, 2009) and four major haplogroups, HG7, HG9, HG16 and HG17 were identified. From those, HG16, HG9 and HG17 belonged to ssp *tauschii*, ssp *strangulata* and relict lineage "t-9^{1}s", respectively; while haplogroup HG7 contained *Ae. tauschii* accessions from both ssp *tauschii* and ssp *strangulata* (Matsuoka et al. 2007, 2008, 2009). Analysis of AFLP polymorphism revealed two major gene-pools in *Ae. tauschii*: those of ssp *tauschii* and ssp *strangulata*, designated as L1 and L2 respectively; and *Ae. tauschii* accessions belonging to HG17 cpDNA (Chloroplast DNA) haplogroup had an intermediate position between L1 and L2 (Mizuno et al. 2010). Later on, the same three gene-pools, L1, L2 and HG17 were identified using DArT analysis (Matsuoka et al. 2015); they were renamed as TauL1, TauL2 and TauL3, respectively; and it was outlined that TauL3 is related to TauL2 (Matsuoka et al. 2013).

Ae. tauschii occupies the vast range, from Turkey to Kirgizia. The Georgian part of the area is of particular interest. Despite it is relatively very small, an essential part of *Ae. tauschii* genetic variation was pointed out here (Dudnikov 2000, 2012; Pestsova et al. 2000). Therefore Georgia is the only country where relict gene-pool TauL3 is rather common. Besides Georgia, it was pointed out only once, as a local population t-9^{1}s in Dagestan (Dudnikov 1998, 2012).

Traditionally, extranuclear DNA, such as cpDNA is considered as an effective tool of genealogic studies (Yamane and Kawahara 2005; Matsuoka et al. 2005; Tabidze et al. 2014; George et al. 2015; Kong and Yang 2015; Vieira et al. 2015; Oldenburg and Bendich 2015). Next-generation sequencing technologies, which have been developed in recent years, enable the determination of the complete nucleotide sequence of both, chloroplast and mitochondrial DNAs of many higher plants, including wheat and its relatives. Recently this technology was used in our lab to sequence cpDNA of three species of Zanduri wheat (*T. timopheevii*, *T. zhukovskyi*, *T. monococcum* var. *hornemannii*) as well as wild species *T. araraticum* (Gogniashvili et al. 2015). The new methodology of cpDNA sequencing was developed (see Tabidze et al. 2014; Gogniashvili et al. 2015). A study, in which complete cpDNA would be sequenced in a set of *Ae. tauschii* accessions originated from Georgia—the part of the area which is of particular importance for understanding the species evolution, seems to be of particular interest. Intraspecies divergency of *Ae. tauschii* was previously studied by Dudnikov (2012)—four regions of non-coding cpDNA, about 3000 bp in total, were sequenced in 112 accessions of *Ae. tauschii*. But the genealogy patterns obtained were complicated and rather contradictory. The root of phylogenetic tree was located between relict lineage t-9^{1}s of ssp. *strangulata* and the lineage "AE-725" of ssp *tauschii*. The latter was the ancestor for all the other lineages of both ssp *tauschii* and *stangulata* (Dudnikov 2012).

To date complete sequence of cpDNA of two ssp *strangulata* accessions and one accession of *Ae. cylindrica* is known (Middleton et al. 2014; Gornicki et al. 2014). In the present investigation we sequenced total cpDNA in nine *Ae. tauschii* and two *Ae.cylindica* accessions of Georgian origin. So, the data on eleven *Ae. tauschii* accessions was used for the analysis of its intraspecies phylogeny, and the data on tree accessions of *Ae. cylindrica* was used for investigation of peculiarities of plasmon origin of this spesies.

Materials and methods

Plant material

The seeds of *Ae. tauschii* Coss. and *Ae. cylindrica* Host were collected in East Georgia in 2010 (Jinjikhadze et al. 2010). In *Ae. tauschii*, the ssp determination was done according to Dudnikov (2000) on the basis of ssp index "SI", which is a ratio between spikelet glume width and rachis segment