

## Letters

Multiple rounds of ancient and recent hybridizations have occurred within the *Aegilops*–*Triticum* complex

In response to the Letter by Sandve *et al.* (2015) in *New Phytologist* (this issue, pp. 9–10), we reiterate our earlier conclusion that multiple rounds of both ancient and recent hybridizations have likely occurred within the *Aegilops*–*Triticum* complex.

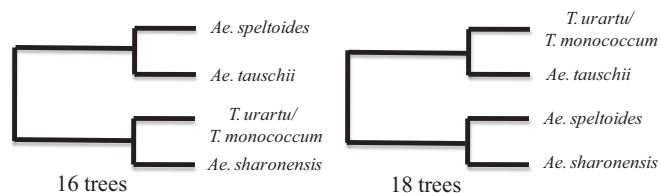
The nomenclature of *Aegilops*–*Triticum* complex

We agree with Sandve *et al.* (2015) that the nomenclature of *Aegilops*/*Triticum* lineages is complex. Indeed, there is a contradiction in how they themselves have defined ‘the D genome lineage’ in their Letter (Sandve *et al.*, 2015), compared to their earlier paper (Marcussen *et al.*, 2014). Fig. 1 of Sandve *et al.* (2015) defines it as a clade comprising D + S\* + M genome species; this definition is consistent with the clade we identified in our cpDNA phylogeny (Fig. 1 of Li *et al.*, 2015). By contrast, the nuclear gene phylogeny of Marcussen *et al.* (2014) places M-genome species (e.g. *Ae. comosa*) within the B-genome lineage, not the D-genome lineage (see Fig. S6 of Marcussen *et al.*, 2014). This contradiction between the chloroplast and nuclear phylogenies is consistent with our previous inference of a complex hybridization history for the D-genome lineage. It is not consistent with a single homoploid hybrid origin of the D + S\* + M clade, as inferred by Sandve *et al.* (2015).

Moreover, contrary to the assertion by Sandve *et al.* (2015) that we confounded the modern D genome and the D-genome lineage (as defined in Fig. 1 of Sandve *et al.*, 2015), we explicitly drew this distinction in our analyses (e.g. Table 2 of Li *et al.*, 2015; showing results both for extant D-genome species and for ‘the ancient D-genome lineage’). We also explicitly considered the single homoploid hybrid origin model favored by Sandve *et al.* (2015) for the D-genome lineage (see Fig. 2a of Li *et al.*, 2015); however, the conflicting chloroplast and nuclear phylogenies described earlier led to our inference of a more complex hybridization history.

Ancient and recent hybridizations within the *Aegilops*–*Triticum* complex

Regarding the timescale of the hybridization event(s), we agree with Sandve *et al.* (2015) that ancient homoploid hybridization between ancestral genomes of A- and B-genome lineages likely played a role



**Fig. 1** Topologies of 34 nuclear genes used in Marcussen *et al.* (2014), outgroup rooted (outgroups not shown). *Ae.*, *Aegilops*; *T.*, *Triticum*.

in the formation of the ancestor of the D-genome lineage. However, we reassert that the inference of a single, ancient homoploid hybrid origin specific to the D-genome lineage (D + S\* + M species) – is not conclusively supported by the nuclear gene trees of Marcussen *et al.* (2014). Under their hypothesis, *Aegilops tauschii* and *Ae. sharonensis* should share the same pre-speciation ancestry because they are included in the (D,(S\*,M)) clade. As such, the two species should be phylogenetically sister, relative to species in the lineages of the two putative ancestral genome donors, S and A. However, as we noted in our previous Letter, in 40% of the nuclear gene trees, one of these D-genome lineage species is grouped as sister to an S- or A-genome lineage species (Li *et al.*, 2015). Two of these topologies are shown in Fig. 1. These data imply a more complex evolutionary history than can be explained by any single hybridization event.

Finally, we agree with Sandve *et al.* (2015) that sequencing and analysis of additional diploid and polyploid *Aegilops*–*Triticum* species will likely provide new evidence for additional hybridization events.

## Acknowledgements

This study was supported by the National Natural Science Foundation of China (31290210, 31470010) and the Program for Introducing Talents to Universities (B07017).

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**Key words:** *Aegilops*, bread wheat, chloroplast phylogeny, homoploid hybridization, *Triticum*.



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