Horizontal Gene Transfer by the Parasitic Plant *Striga hermonthica*

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Horizontal gene transfer (HGT) plays an important role in genome evolution (1). In plants, the majority of reported cases of HGT have been limited to exchanges between plants and microbes, mitochondrial transfer, or the translocation of mobile elements among related species (1). Parasitic plants are known to be vectors of mitochondrial HGT, but it has been unclear whether they also mediate nuclear HGT (1, 2).

*Striga hermonthica* (Del.) Benth. is a devastating parasitic plant that infests members of the grass family (Poaceae), including major crops such as sorghum (*Sorghum bicolor*) and rice (*Oryza sativa*). *S. hermonthica* belongs to the eudicot Orobanchaceae family of the order Lamiales (fig. S1) (3) and only infects monocot plants. Thus, we reasoned that we may be able to detect nuclear HGT, if it occurs, by identifying monocot-specific genes in the *S. hermonthica* genome. From a large-scale expressed sequence tag analysis of *S. hermonthica* (4), we found one gene, designated *ShContig9483*, which shows high similarity to genes in sorghum and rice but has no homologs in eudicots (fig. S2A and table S1) (5). Southern blot analysis revealed *ShContig9483* cross-hybridization signals from sorghum, and rice to a lesser extent, reflecting its lower similarity, whereas no signals were detected from other closely related plants in Orobanchaceae nor from any nonparasitic eudicots (fig. S2B). This indicates that *ShContig9483* most likely originated in the monocots before its transfer to *S. hermonthica*.

*ShContig9483* encodes a 448-amino acid protein with unknown function. Phylogenetic analysis of *ShContig9483* and related protein-coding sequences clusters *S. hermonthica* with sorghum (Fig. 1A). This tree conflicts with the phylogenetic position of *Striga* (3), suggesting that *S. hermonthica* acquired *ShContig9483* from sorghum or a related grass species. The *S. hermonthica* genomic region containing *ShContig9483* resides near a nuclear gene encoding a putative cis-prenyltransferase (fig. S3A). In contrast to *ShContig9483*, this putative cis-prenyltransferase gene from *S. hermonthica* clusters with genes from other eudicot species (fig. S3B).

The genomic sequences of the sorghum homologs show similarities to the *ShContig9483* locus from about 150 base pairs (bp) up- and 800 bp downstream of the putative open reading frame (ORF), except for several insertions and deletions (Fig. 1B and fig. S4). The similarity to homologs from *Brachypodium* and rice covers a shorter region with lower identities (Fig. 1B). The high conservation of sequence between *S. hermonthica* and sorghum outside the ORF suggest that transfer was a relatively recent event. Indeed, a sequence highly similar to *ShContig9483* was found in *S. gesnerioides* but not in *Orobanche minor*, which is from a closely related genus (figs. S2B and S5). These data suggest that incorporation of the *ShContig9483* fragment occurred before speciation of *S. hermonthica* and *S. gesnerioides* but after differentiation of the genera *Striga* and *Orobanche*. Parasitic plants form an invasive organ called a haustorium, which interconnects their vasculature with that of their hosts to allow transfer of nutrients, water, and even mRNAs (2). Thus, one possibility is that *ShContig9483* was originally captured by *S. hermonthica* as mRNA or cDNA. Interestingly, we found 13 consecutive adenine (A) nucleotides at the 3' end of the *ShContig9483* genomic region (fig. S4). This sequence may be indicative of a poly-A tail added to a transcriptional unit of the originally transferred gene. In any case, our comparative genomics analysis of a eudicot parasite and its monocot hosts presents a clear case for nuclear HGT. Because the method used in this study is limited to the detection of nuclear HGT of genes that are unusual among eudicots, we suspect that more nuclear HGT will be found if other genes are investigated in detail.

Fig. 1. *ShContig9483* represents natural HGT in *S. hermonthica*. (A) Phylogenetic tree of *ShContig9483* homologs. Maximum likelihood bootstrap values (ML, top) and Bayesian inference posterior probability values (BI, bottom) are indicated at the nodes of a maximum likelihood tree. Bold lines indicate BI = 100 and ML > 95. (B) Comparison of genomic sequences of *ShContig9483* and its homologs from *S. bicolor* (Shb01 g013250 and Shb01s004030), *Brachypodium distachyon* (Bradi1g00410), and *O. sativa* (LOC_Os01g56900). Sequences with and without similarity to *ShContig9483* are indicated in green (with identities) and yellow, respectively, and similar regions between adjacent homologs are indicated by light blue.

Supporting Online Material

www.sciencemag.org/cgi/content/full/328/5982/1128/DC1

Materials and Methods

Figs. S1 to S5
Table S1

References

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