

Reticulate evolution in *Thuja* inferred from multiple gene sequences: Implications for the study of biogeographical disjunction between eastern Asia and North America

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Abstract

The eastern Asia–North America disjunction is one of the most interesting biogeographical patterns, but its formation is still in much debate. Here nucleotide sequences of five cpDNA regions, nrDNA ITS and two low-copy nuclear genes (*LEAFY*, *4CL*) were employed to reconstruct the phylogeny and to explore the historical biogeography of *Thuja*, a typical eastern Asia–North America disjunct genus. High topological discordance was observed between chloroplast and nuclear gene trees, even between different nuclear gene trees, suggesting that *Thuja* could have a reticulate evolutionary history due to multiple interspecific hybridization events. The eastern Asian species *Thuja koraiensis* might have obtained its chloroplast genome from the eastern North American species *T. occidentalis* by chloroplast capture, while the western North American species *T. plicata* is very likely to have inherited a recombinant cpDNA. Based on the phylogenetic analysis of multiple genes, DIVA-reconstruction of the distribution history, molecular clock estimation and fossil data, we inferred that *Thuja* could have originated from the high-latitude areas of North America in the Paleocene or earlier with subsequent expansion into eastern Asia through the Bering Land Bridge. The two eastern Asia species *T. standishii* and *T. sutchuenensis* have a sister relationship, and their split could have occurred in the Oligocene or early Miocene. In the present study, the selection of molecular markers in biogeographic studies was also discussed. Since most previous studies on the eastern Asia and North America disjunction are based on uniparentally inherited cpDNA and (or) directly sequenced nrDNA ITS data, the historical reticulate evolution in the studied groups might have been underestimated. Therefore, we suggest that multiple genes from different genomes, especially low-copy nuclear genes, be used in this research area in the future.

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1. Introduction

The geological changes and climatic cooling in the Cenozoic, especially in the late Tertiary and Quaternary, interrupted the continuity of the boreotropical flora or mixed mesophytic forests in the Northern Hemisphere and brought about the plant biogeographic patterns of intercontinental disjunction. The disjunction between east-

ern Asia and eastern North America (EA–ENA) is the most attractive one and has magnetized several generations of botanists in the past nearly 150 years (Gray, 1859; Boufford and Spongberg, 1983; Wen, 1999; Manos and Donoghue, 2001). Both eastern Asia and eastern North America sheltered their residents with complex geographical topologies when congeneric species became extinct in Europe and other areas (Tiffney, 1985a,b; Wen, 1999; Tiffney and Manchester, 2001). Tiffney (1985a,b) attributed the EA–ENA disjunct distribution to a layering of many events rather than a single historical event. The two landmark papers

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also emphasized the important roles of the Bering Land Bridge and the North Atlantic Land Bridge, two main land bridges connecting Asia, North America and Europe in the Tertiary, in shaping modern phytogeographic patterns of the Northern Hemisphere, especially the EA–ENA disjunction.

With the help of more and more molecular markers, newly developed analysis methods (e.g., DIVA, Multidivtime, r8s) and fossil records, the evolution of some plant groups with an EA–ENA disjunct distribution has been investigated in much more detail, including interspecific relationships, divergence times of different lineages, and biogeographical histories (e.g., Cunningham and Collins, 1994; Qiu et al., 1995; Wen and Zimmer, 1996; Gould and Donoghue, 1998; Wen, 1999; Xiang et al., 1998, 2000; Wen and Shi, 1999; Xiang and Soltis, 2001; Wang et al., 2003; Nie et al., 2006). However, most of the studies were based on uniparentally inherited chloroplast markers and (or) directly sequenced PCR products of nuclear ribosomal DNA internal transcribed spacers (ITS), which have limitations in discovering reticulate evolution events such as hybridization and introgression. As one mode of speciation in plant, hybrid speciation has occurred much more frequently in nature than previously envisioned. For example, several compelling ancient hybridization events and cryptic hybrid species have been revealed recently with both plastid and nuclear gene markers (e.g., Cronn et al., 2003; Oh and Potter, 2005; Fehrer et al., 2007). A robust phylogeny reconstructed with multiple gene markers from different genomes is very necessary to the historical biogeographical study that infers the development of distribution pattern of a group based on the gene tree topology. On the other hand, previous studies show that the EA–ENA disjunction could have originated at different times and by different pathways (Wen, 1999). In particular, a closer biogeographic relationship between eastern North America and western North America than between eastern Asia and eastern North America was reported from some groups, such as *Aralia* (Wen et al., 1998) and *Cornus* (Xiang et al., 1998). Therefore, more attention should be paid to the western North American species for the study of EA–ENA disjunction.

Thuja L., a small genus of Cupressaceae comprising five extant species, exhibits a disjunct distribution in eastern Asia, eastern and western North America (Farjon, 2005). The three eastern Asian species of the genus have quite restricted distributions, including *Thuja sutchuenensis* in Chengkou, Chongqing, China, *T. koraiensis* in the Changbai Mountain of northeastern China and the Korean Peninsula, and *T. standishii* native to Japan. *T. sutchuenensis* was once listed as a species extinct in the wild by IUCN-SSC and rediscovered in 1999 (Farjon and Page, 1999; Xiang et al., 2002). The two North American species of *Thuja* have much wider distributions. *T. occidentalis* occurs in eastern North America, occupying a geographical range between the subarctic taiga–tundra interface in the north and the belt of deciduous angiosperm forests in the south.

T. plicata is disjunctly distributed in the Pacific Coastal Mountains and the Rocky Mountains of western North America.

Based on fossil evidence, present distribution and morphological characters, especially seed cone structure, McIver and Basinger (1989) proposed a phylogeny of *Thuja* comprising both extant and fossil species. They inferred that *Thuja* had occupied much of the Northern Hemisphere in the early Tertiary and the subsequent dramatic climatic and geographic changes were responsible for the current disjunction of the genus. This phylogeny is topologically quite different from the molecular phylogeny of *Thuja* reconstructed with the directly sequenced nrDNA ITS region by Li and Xiang (2005), in which an eastern Asia origin and two dispersals to North America were suggested for the genus. The conflict between previous studies could be attributed to the slight morphological differences among species, the discontinuity and incompleteness of the fossil record, and the use of a single molecular marker. In addition, it is better to clone the PCR products when nrDNA ITS is used in the molecular systematic study of gymnosperms, in consideration that this DNA region might have marked intragenomic length and sequence variations due to the incomplete concerted evolution as reported from Pinaceae (Liston et al., 1996; Maggini et al., 1998; Germandt et al., 2001; Wei et al., 2003; Wei and Wang, 2004a; Campbell et al., 2005; Kan et al., 2007). It is obviously that more DNA markers, including both cytoplasmic and nuclear genes, should be used to reconstruct a robust phylogeny of *Thuja* and then to explore the historical biogeography of the genus.

Recently, several dozens of chloroplast DNA markers suitable for the study of interspecific relationships of plants have been screened out (Shaw et al., 2005, 2007). Meanwhile, the low-copy nuclear gene has the advantages of biparental inheritance and rapid evolutionary rates, and thus is increasingly used in systematic and biogeographic studies (Sang, 2002; Small et al., 2004; Whittall et al., 2006). For example, the *LEAFY* gene involved in the formation of the flower meristem (Frohlich and Parker, 2000) has been used as a single copy gene in the phylogenetic reconstruction of some seed plants (e.g., Grob et al., 2004; Oh and Potter, 2005; Won and Renner, 2005). Also, the *4CL* gene, encoding 4-coumarate: coenzyme A ligase in the general phenylpropanoid metabolism essential to plant development and environmental interactions (Cukovic et al., 2001; Hamberger and Hahlbrock, 2004), has been successfully used in molecular phylogenetic studies of conifers (Wang et al., 2000; Wei and Wang, 2004b; Syring et al., 2005). In the present study, we employed nucleotide sequences of five chloroplast non-coding regions (*rpl16*, *AtpI-rpoC1*, *trnS-trnfM*, *trnS-trnG*, and *trnT-trnF*) and two low-copy nuclear genes (*LEAFY* and *4CL*), together with the cloned nrDNA ITS sequences, to reconstruct the phylogeny and to investigate the historical biogeography of *Thuja*. Based on the results, we also discussed the utilities of multiple genes from different genomes

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