



Chloroplast phylogeny and phylogeography of *Stellera chamaejasme* on the Qinghai-Tibet Plateau and in adjacent regions

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ABSTRACT

Historic events such as the uplift of Qinghai-Tibet Plateau (Q-T Plateau) and climatic oscillations in the Quaternary period greatly affected the evolution and modern distribution of Sino-Tibetan flora. *Stellera chamaejasme*, a perennial herb with flower color polymorphism that is distributed from the mountainous southeastern Q-T Plateau (Hengduan Mountains, H-D Mountains) to the vast platform of the Q-T Plateau and the adjacent plain of northern China, provides an excellent model to explore the effects of historic events on the origination and variation of species. In this study, we conducted a phylogenetic and phylogeographical study using three chloroplast sequences (*trnT-L*, *trnL-F* and *rpl16*) in 26 populations of *S. chamaejasme* and 12 outgroups from the Thymeleaceae. Phylogenetic analysis and molecular clock estimation revealed that the monophyletic origin of *S. chamaejasme* occurred ca. 6.5892 Ma, which is consistent with the radical environment changes caused by the rapid uplift of the Q-T Plateau ca. 7 Ma. Intra-specific differentiation of *S. chamaejasme* is estimated to have occurred after ca. 2.1 Ma. Twelve haplotypes were revealed from combined *trnL-F* and *rpl16* sequences. High genetic diversity ($h_T = 0.834$) and population differentiation ($N_{ST} = 0.997$ and $G_{ST} = 0.982$) imply restricted gene flow among populations and significant geographical or environmental isolation. All populations from the vast plain of northern China were dominated by one haplotype (H1), and the same haplotype was fixed in most populations from the high elevation platform of the western and northern Q-T Plateau. In contrast, the majority of the haplotypes were found in the relatively narrow area of the H-D Mountains, in the southeastern distribution of *S. chamaejasme*. The contrasting haplotype distribution patterns suggested that the H-D Mountains were either a refugium for *S. chamaejasme* during the Quaternary climatic oscillations or a diversification center of this species. The present wide distribution of this species on the Q-T Plateau platform and in northern China is likely to have resulted from a rapid post-glacial population expansion from the southeastern refugium involving founder effects, facilitated by the adjacent geographic range with a similar grassland habitat.

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1. Introduction

The Qinghai-Tibet Plateau (Q-T Plateau) is the highest and largest plateau in the world, with a mean elevation of 4500 m and an area of 2.5×10^6 km² (Zheng, 1996). More than 12,000 species from 1500 genera are found in this region, of which more than 20% are endemic (Wang, 1993, 1994; Wu, 1987; Wu and Wu, 1996). The uplift of the Q-T Plateau, which was followed by the formation of high mountains and deep valleys within the plateau (Li et al., 1995), was one of the most important geological events to have occurred since the Cenozoic, and this event modified the global climate and influenced monsoon intensity (An et al., 2001; Raymo and Ruddiman, 1992; Spicer et al., 2003). The Hengduan Mountains (H-D Mountains) are located at the southeastern edge of the Q-T Plateau (Li, 1987, 1989; Wu,

1988), and this area is referred to as the core area of the Himalayan hotspot, one of the world's biodiversity hotspots, due to its high level of species and generic richness (Boufford and Dijk, 2000; Boufford et al., 2004; Myers et al., 2000; Raven and Axelrod, 1978; Wilson, 1992; Ying et al., 1993). The high species richness in the H-D Mountains (ca. 8000 angiosperm species) has led to the hypothesis that this region is a distribution and diversity center for many alpine genera, for example *Gentiana*, *Androsace*, *Pedicularis*, *Primula*, *Rhododendron* and *Saussurea* (Sun, 2002; Sun and Li, 2003; Wu, 1988). Many taxa (genera or species) are thought to have originated recently in this region as a result of the severe alteration of topography and climate since the uplift of the Q-T Plateau between the Miocene and the Quaternary (Chen et al., 2005; Liu et al., 2006; Wang et al., 2005, 2007). Furthermore, the H-D Mountains have been hypothesized to have been a refugium for plants on the Q-T Plateau platform and in the north temperate zone of eastern Asia during the Quaternary Ice Age (Wu, 1987).

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The dominant vegetation types of the Q-T Plateau platform are alpine meadow and desert-steppe, with scattered and disjunct forests (Wu, 1980). It was suggested that the present vegetation in the region developed during the late Pliocene with the major uplift of the plateau (Axelrod et al., 1996; Shi et al., 1998; Wu, 1980), which was followed by large-scale climatic changes (Ni, 2000; Shi et al., 1998; Thompson et al., 2000; Zhang et al., 1996). During the Quaternary, climatic oscillations caused repeated retreats and advances of many species' ranges, resulting in shifts in the dominant vegetation during glacial and interglacial cycles (Hewitt, 1996, 1999; Tang and Shen, 1996). The distribution of many Q-T Plateau plant species is characterized by colonization due to a rapid expansion from the refugia located on the eastern edge area, especially the H-D Mountains (Chen et al., 2008; Meng et al., 2007; Yang et al., 2008), although some species are suspected to have survived in ice-free areas on the plateau platform during the glaciations (Shi et al., 1998; Wang et al., 2009).

The natural vegetation of northern China is dominated by steppes with a relatively homogeneous environment (Wu, 1980, 1995). Numerous plant species have extended their distribution from Q-T Plateau to northern China (e.g., *Stellera chamaejasme*, *Incarvillea sinensis*, *Ranunculus tanguticus*, *Hyecoum leptocarpum*), and some of these species could have originated and expanded northeastwardly from the H-D Mountains (Wang, 1992a, 1992b). Reduction of genetic diversity is expected under a scenario of rapid post-glacial expansion into homogeneous grassland, as has been found in northern Europe and America (Hewitt, 1996). Because northern China is believed not to have been glaciated during the Quaternary (Hewitt, 2000; Liu, 1988; Zhao and Li, 1990), it is an open question whether species with the range from southwestern China (Q-T Plateau) to northern China experienced past northern expansion and southern retreat during the Quaternary climatic oscillations. Northward expansion from southern refugia was demonstrated for *Picea crassifolia* and *Pinus tabulaeformis*, which are tree species of the fragmented forest (Chen et al., 2008; Meng

et al., 2007). However, no similar phylogeographical study had ever been conducted on herbaceous plants.

The availability of new phylogenetic and phylogeographical molecular tools, such as non-recombining and uniparentally inherited chloroplast DNA markers (cpDNA) (Dumolin et al., 1995; Rajora and Dancik, 1992), has resulted in intensive investigation of vegetation of the Q-T Plateau and the adjacent eastern mountain area (Chen et al., 2005; Liu et al., 2006; Meng et al., 2007; Wang et al., 2009; Yang et al., 2008; Zhang et al., 2005). However, these studies did not consider the relationship of the studied vegetation with the vast adjacent northeastern plain in northern China, which is dominated by homogeneous grassland, despite the fact that many plant species are common to these two regions. In addition, most of the species studied have been trees (Meng et al., 2007; Zhang et al., 2005), while herbaceous vegetation has received much less attention (Chen et al., 2008; Yang et al., 2008). Therefore, it would be of great interest to study the phylogeography of an herbaceous species with a distribution that covers both desert steppe and grassland to understand the evolution and modern distribution of the vegetation of the Q-T Plateau and adjacent regions.

We conducted a phylogenetic and phylogeographic study on a perennial herbaceous plant, *S. chamaejasme* L. This species has a wide geographic range from the northwestern Yungui Plateau through the H-D Mountains northwestward to the Q-T Plateau platform and northeastward to the plain of northern China (Grey-Wilson, 1995; Wang and Gilbert, 2007; Zhang, 1999). This plant exhibits flower color polymorphism (Fig. 1), which served in the past as the basis for the delimitation of two separate species, *S. chamaejasme* L. and *S. bodinieri* H. Léveillé (Léveillé, 1912; Linnaeus, 1753), or two forms of this species (Diels, 1912; Huang, 1985). The white-red flower type (hereafter referred to as TypeWR), *S. chamaejasme* f. *chamaejasme*, with a red calyx tube and white tube lobe flowers (Fig. 1A), has a vast distribution from the Q-T Plateau to northern China (Fig. 2). The pure-yellow flower type (hereafter referred to as TypeY), *S. chamaejasme* f. *angustifolia*



Fig. 1. Different flower color populations of *S. chamaejasme*. A. white-red flower morphological type (TypeWR). B. pure-yellow flower morphological type (TypeY). C. white-yellow flower morphological type (TypeWY). D. pure-red flower morphological type (TypeR).

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