Contents lists available at ScienceDirect

Biochemical Systematics and Ecology

journal homepage: www.elsevier.com/locate/biochemsyseco

# Molecular phylogeography and intraspecific divergence of *Spiraea alpina* (Rosaceae) distributed in the Qinghai-Tibetan Plateau and adjacent regions inferred from nrDNA

Gulzar Khan [a, d, 1], Faqi Zhang [a, b, 1], Qingbo Gao [a], Peng-cheng Fu [a], Rui Xing [a, d], Jiuli Wang [a, d], Hairui Liu [a, d], Shilong Chen [a, c, *]

[a] *Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810001, PR China*
[b] *Key Laboratory of Eco-environments of Three Gorges Reservoir Region, Ministry of Education, School of Life Sciences, Southwest University, Chongqing 400715, PR China*
[c] *Key Laboratory of Crop Molecular Breeding, Qinghai Province, Xining 810001, PR China*
[d] *University of Chinese Academy of Sciences, Beijing 100039, PR China*

## ARTICLE INFO

*Article history:*
Received 21 January 2014
Accepted 22 August 2014
Available online

*Keywords:*
Genetic diversity
Glacial refugia
Allopatric divergence
Phylogeography
Qinghai-Tibetan plateau
Speciation

## ABSTRACT

The Qinghai-Tibetan plateau (QTP) uplift had a decisive effect on climatic and eco-environmental evolution in East Asia during the Quaternary. In the current study phylogeographic structure and diversification history of *Spiraea alpina* across the QTP were investigated for the first time based on nuclear internal transcribed spacer. The nuclear internal transcribed spacers ($ITS_{1a}$–$ITS_4$) were generated for a total of 284 individuals distributed within 31 natural populations. A clear phylogeographic structure was found for *S. alpina*. The results showed that this species colonized in three different glacial refugia during the Quaternary extensive glaciation and expanded during the Interglacial period. Analysis of molecular variance (AMOVA) showed 74.13% genetic diversity among populations and 25.87% genetic variation within populations with distinct phylogeographic structure ($F_{ST} = 0.741^*$). The estimated divergence time revealed that the main lineages of *S. alpina* diversified during the Quaternary 1.2–0.6 million years ago. The study concluded that severe climatic oscillations during Quaternary and the uplift of QTP had a profound effect on intraspecific divergence of *S. alpina*.

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## 1. Introduction

The response of species towards eco-environmental changes has been considered a highly dynamic process consisting of repeated retreats into refugia during glacial periods and range expansions from the refugia during interglacial periods. The Qinghai-Tibetan Plateau (QTP) is considered as the most sensitive region for historical climatic changes. The Flora and fauna

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[*] Corresponding author. Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810001, PR China.

*E-mail addresses:* gulzar.palynology@gmail.com (G. Khan), fqzhang@nwipb.cas.cn (F. Zhang), qbgao@nwipb.cas.cn (Q. Gao), fupengc@sina.com (P.-c. Fu), xingruialex@gmail.com (R. Xing), wangjiuli12@mails.ucas.ac.cn (J. Wang), 1440331027@qq.com (H. Liu), slchen@nwipb.cas.cn (S. Chen).

[1] These authors contributed equally to this work.

http://dx.doi.org/10.1016/j.bse.2014.08.013
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found at QTP should have traced the climatic variations to shift their distributional ranges (Zheng and Rutter, 1998). These range shifts can be detected from the genetic structure of current populations, especially glacial retreats (into refugia) and postglacial re-colonization (Avise, 2000; Hewitt, 2004). Such types of retreat and re-colonization patterns have been identified in some alpine species distributed in the QTP (Meng et al., 2007; Chen et al., 2008). Different studies have suggested that the last glacial maximum (LGM) did not seriously affect species ranges shift and the species survived in multiple refugia, while the largest glaciation occurred at the QTP may have had a great impact on the distribution or evolution of species (Wang et al., 2009a; Opgenoorth et al., 2010). The cold age occurred between 1.2 MYA (million years ago) and 0.4 MYA when the largest glaciation developed at QTP, however this glaciation did not result in a massive ice sheet (Shi et al., 1998; Zhou et al., 2006). Some of the previous studies showed that plants species with different habitats and morphologies responded differently to Quaternary severe climatic episodes. The Qinghai-Tibetan Plateau has more than 1800 alpine species at high-altitude (Wu et al., 1995). However, the phylogeographic patterns of most species remain unknown. In the current study, the phylogeographic structure and intraspecific divergence of *Spiraea alpina* (Rosaceae) based on nuclear DNA is reported. This alpine shrub is endemic to the QTP, with wide distribution at high altitudes between 2000 and 4500 m; partly extended to adjacent regions (Lu et al., 2003). The nuclear ribosomal internal transcribed spacer (ITS) is a suitable nuclear marker to trace population range shifts of species, dispersed through seeds (Gao et al., 2012; Wang et al., 2009b). In this study the nuclear internal transcribed spacers ($ITS_{1a}$-$ITS_4$) were used to trace the range shifts of this alpine shrub in response to the past eco-environmental changes. The main objectives were (I) to investigate whether this species survived in multiple refugia during the LGM, as other alpine shrubs found on the QTP, or underwent through range expansion, (II) to find out the intraspecific diversification in *S. alpina* based on nrDNA, and (III) to compare genetic diversity of biparentally inherited nrDNA with that of maternally inherited plastid cpDNA in *S. alpina*.

## 2. Materials and methods

### 2.1. Sampling

A total of 284 individuals, distributed in 31 natural populations of *S. alpina* were collected from the QTP and adjacent regions (Table 1; Fig. 1). Three to nineteen individuals (spaced at least 100 m apart) were collected for each population. Voucher specimens were deposited in the herbarium of the Northwest Institute of Plateau Biology (HNWP) at the Chinese Academy of Sciences.

**Table 1**
Population codes, locations, geographical coordinates, No of individuals used for nrDNA (each population column shows the number of individuals sampled for that population, followed by the number of haplotypes in parentheses), estimates of gene diversity ($h$), nucleotide diversity ($\pi$), mean number of pairwise differences (P.D), and haplotype composition for 31 *Spiraea alpina* populations. YN = Yunnan, SC = Sichuan, QH = Qinghai, T = Tibet, GS = Gansu.

| POP | Locality | Latitude (N) | Longitude (E) | Altitude (m) | No. of individuals used for nr(DNA) | Nuclear DNA haplotypes(N) | Gene diversity($h$) | Nucleotide diversity ($\pi$) | P.D |
|---|---|---|---|---|---|---|---|---|---|
| P1 | Datong, QH | 36°59′ | 101°25′ | 3210 | 3(3) | A1,A2,A5 | 1.000 ± 0.272 | 0.002 ± 0.002 | 1.333 ± 1.098 |
| P2 | Shanglaxiu,QH | 32°46′ | 96°39′ | 4090 | 6(2) | A12,A21 | 0.333 ± 0.215 | 0.0006 ± 0.001 | 0.333 ± 0.380 |
| P3 | Xialaxiu, QH | 32°45′ | 96°34′ | 3900 | 4(1) | A13 | 0.000 ± 0.000 | 0.000 ± 0.000 | 0.000 ± 0.000 |
| P4 | Zaduo, QH | 32°52′ | 95°19′ | 4030 | 11(3) | A1,A11,A13 | 0.473 ± 0.161 | 0.009 ± 0.005 | 5.127 ± 2.691 |
| P5 | Yushu, QH | 32°52′ | 97°04′ | 3810 | 17(6) | A13,A21,A15,A17,A12,A9 | 0.654 ± 0.122 | 0.009 ± 0.005 | 5.103 ± 2.603 |
| P6 | Hongyuan, SC | 32°46′ | 102°21′ | 3654 | 7(3) | A2,A3,A5 | 0.523 ± 0.208 | 0.001 ± 0.001 | 0.762 ± 0.629 |
| P7 | Litang, SC | 29°38′ | 100°21′ | 3891 | 16(5) | A5,A8,A19,A15,A10 | 0.650 ± 0.108 | 0.004 ± 0.003 | 2.575 ± 1.456 |
| P8 | Yajiang, SC | 30°04′ | 101°20′ | 4280 | 7(4) | A4,A5,A8,A10 | 0.809 ± 0.129 | 0.002 ± 0.002 | 1.428 ± 0.984 |
| P9 | Luhuo, SC | 31°37′ | 100°43′ | 3460 | 11(4) | A2,A3,A5,A10 | 0.690 ± 0.127 | 0.002 ± 0.001 | 1.090 ± 0.773 |
| P10 | Rangtang, SC | 32°18′ | 101°03′ | 3820 | 10(4) | A2,A4,A5,A10 | 0.777 ± 0.090 | 0.002 ± 0.001 | 1.022 ± 0.744 |
| P11 | Dari, QH | 33°17′ | 100°23′ | 4370 | 19(5) | A2,A3,A4,A5,A18 | 0.690 ± 0.094 | 0.002 ± 0.001 | 1.169 ± 0.787 |
| P12 | Maqin, QH | 34°36′ | 100°34′ | 3380 | 9(4) | A2,A3,A4,A17 | 0.777 ± 0.110 | 0.004 ± 0.002 | 2.111 ± 1.295 |
| P13 | Angqian, QH | 31°58′ | 96°25′ | 4290 | 11(7) | A1,A2,A5,A12,A16,A19,A21 | 0.909 ± 0.065 | 0.003 ± 0.002 | 1.927 ± 1.183 |
| P14 | Leiwuqi, T | 31°32′ | 96°22′ | 4210 | 10(6) | A1,A5,A10,A16,A17,A21 | 0.889 ± 0.075 | 0.004 ± 0.003 | 2.444 ± 1.443 |
| P15 | Mozhugongka, T | 29°42′ | 92°04′ | 4150 | 9(1) | A14 | 0.000 ± 0.000 | 0.000 ± 0.000 | 0.000 ± 0.000 |
| P16 | Basu, T | 30°07′ | 97°17′ | 4320 | 7(2) | A13,A14 | 0.476 ± 0.171 | 0.002 ± 0.001 | 0.952 ± 0.733 |
| P17 | Changdu, T | 31°11′ | 97°02′ | 3380 | 8(1) | A13 | 0.000 ± 0.000 | 0.000 ± 0.000 | 0.000 ± 0.000 |
| P18 | Jiangda, T | 31°21′ | 97°42′ | 4490 | 9(5) | A1,A2,A12,A5,A22 | 0.805 ± 0.119 | 0.002 ± 0.001 | 1.333 ± 0.910 |
| P19 | Dege, T | 31°57′ | 98°54′ | 4410 | 15(5) | A2,A5,A9,A12,A21 | 0.733 ± 0.089 | 0.003 ± 0.002 | 1.714 ± 1.058 |
| P20 | Shiqu, SC | 32°30′ | 98°27′ | 4380 | 7(3) | A3,A11,A21 | 0.523 ± 0.208 | 0.002 ± 0.002 | 1.142 ± 0.835 |
| P21 | Songpan,SC | 32°35′ | 103°37′ | 2830 | 14(1) | A13 | 0.000 ± 0.000 | 0.000 ± 0.000 | 0.000 ± 0.000 |
| P22 | Qilian, QH | 38°14′ | 99°57′ | 2880 | 8(2) | A17,A19 | 0.250 ± 0.180 | 0.0004 ± 0.0006 | 0.250 ± 0.311 |
| P23 | Menyuan, QH | 37°24′ | 101°57′ | 3150 | 4(2) | A19,A20 | 0.500 ± 0.265 | 0.0009 ± 0.001 | 0.500 ± 0.519 |
| P24 | Huzhu,QH | 36°55′ | 102°22′ | 2690 | 15(2) | A19,A20 | 0.133 ± 0.112 | 0.0002 ± 0.0004 | 0.133 ± 0.209 |
| P25 | Pingan, QH | 36°17 ′ | 101°58′ | 3160 | 11(3) | A11,A16,A19 | 0.563 ± 0.134 | 0.002 ± 0.001 | 1.127 ± 0.791 |
| P26 | Lingxia, GS | 34°53 ′ | 102° 49′ | 3220 | 11(4) | A5,A11,A19,A20 | 0.709 ± 0.099 | 0.003 ± 0.0022 | 1.781 ± 1.113 |
| P27 | Xiahe, GS | 34°45′ | 102° 34′ | 3210 | 6(3) | A2,A3,A5 | 0.600 ± 0.215 | 0.0015 ± 0.001 | 0.866 ± 0.700 |
| P28 | Zoigê, SC | 34° 07′ | 102° 38′ | 3280 | 4(2) | A2,A5 | 0.500 ± 0.265 | 0.0008 ± 0.001 | 0.500 ± 0.519 |
| P29 | Shagong, SC | 29° 08′ | 100°02′ | 4610 | 4(1) | A7 | 0.000 ± 0.000 | 0.000 ± 0.000 | 0.000 ± 0.000 |
| P30 | Ganzi, SC | 31° 36′ | 100° 09′ | 3830 | 3(1) | A12 | 0.000 ± 0.000 | 0.000 ± 0.000 | 0.000 ± 0.000 |
| P31 | Lhasa, T | 31° 50′ | 102°41′ | 3370 | 3(1) | A6 | 0.000 ± 0.000 | 0.000 ± 0.000 | 0.000 ± 0.000 |

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