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Genetic Structure of *Galitzkya macrocarpa* and *G. potaninii*, Two Closely Related Endemics of Central Asian Mountain Ranges

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• *Background and Aims* Habitats in mountains are often isolated. Plants growing in these sites face severe dispersal limitations, but also difficulties for recruitment. The focus was laid on the magnitude of genetic differences among populations but also on the size of potentially occurring clones.
• *Methods* RAPD fingerprints were obtained from 23 populations in southern Mongolia. Sampling covered the entire distribution range of *Galitzkya macrocarpa*; samples of *G. potaninii* represented only the Mongolian part of its mainly northern Chinese range.
• *Key Results* The Mongolian endemic *G. macrocarpa* showed moderately strong population differentiation ($\Phi_{ST} = 0{\cdot}251$), and limited evidence for isolation by distance. Local genetic diversity was not positively correlated to habitat size, and not reduced in peripheral populations. Clonal growth is possible, but most plants originate from sexual reproduction. In contrast, populations of *G. potaninii* were highly differentiated ($\Phi_{ST} = 0{\cdot}550$); and the most remote outposts had reduced genetic diversity. In these areas, isolation is expected to date back to glacial times.
• *Conclusions* Effects of natural fragmentation differ among species. Both are rare, but *G. macrocarpa* appears to be able to maintain genetic diversity over its range. Clonal growth is an option in its mixed reproduction strategy and allows survival under harsh conditions. In contrast, genetic structure in *G. potaninii* gives reason for concern, and further studies on population dynamics are needed.

Key words: Conservation, *Galitzkya macrocarpa*, *Galitzkya potaninii*, clonal growth, fragmentation, endemics, genetic diversity, isolation, Mongolia, mountains.

INTRODUCTION

Mountain habitats experience special climatic conditions that often differ tremendously from the surrounding lowlands and valleys. Steep topographic and therefore climatic gradients lead to heavily fragmented habitats characterized by barriers to migration and genetic exchange. Levels of natural fragmentation are thus generally high and several studies have demonstrated strong genetic effects and isolation by distance (Bauert *et al.*, 1998; Schönswetter *et al.*, 2002, 2004). Effects of habitat isolation should be especially pronounced where mountains rise from dry lowlands like the Central Asian Gobi. Several montane species of the Altay and Tien Shan mountains have relatively high moisture requirements and populations are widely isolated (Jäger, 2005). This renders genetic exchange — at least under current climatic conditions — difficult. So far only a few Central Asian mountain taxa have been studied in terms of genetic structure (Chen *et al.*, 2005; Wesche *et al.*, 2005*c*; Xia *et al.*, 2005; Zhang *et al.*, 2005). Thus, it is largely unknown whether natural fragmentation has strongly affected genetic exchange among populations, which would raise a need for subsequent studies on possible consequences for fitness parameters (Reed and Frankham, 2003; Frankham, 2005).

Genetic exchange relies on movement of pollen or seeds. However, climatic conditions in Central Asia are generally harsh and seedling establishment is exceedingly difficult (Lavrenko and Karamysheva, 1993; Gunin *et al.*, 2003). Most dominant plant species are therefore perennial, and clonality is widespread (Li and Ge, 2001; Song *et al.*, 2002; Setsuko *et al.*, 2004). Patterns are similar in mountain areas where several species are known to survive unfavourable conditions by extended clonal growth over dozens or hundreds of years (Steinger *et al.*, 1996; Escaravage *et al.*, 1998; Keeler *et al.*, 2002; Young *et al.*, 2002; Yu *et al.*, 2004; Wesche *et al.*, 2005*c*). However, despite the fact that genetic diversity is expected to decrease with clonal growth being the dominant reproduction type (Honnay *et al.*, 2006), recent studies on alpine plants found relatively high levels of clonal diversity (Li and Ge, 2001; Pluess and Stöcklin, 2004).

Here, is presented a study on the genetic structure of two closely related, long-lived Central Asian rock endemics: *Galitzkya macrocarpa* and *G. potaninii* (Brassicaceae). Both species are capable of clonal growth and occur in comparable habitats in south-western Mongolia and north-western China (Gubanov, 1996; Grubov, 2001). They have distinct distribution ranges with the range of *G. macrocarpa* being exclusively restricted to Mongolia. Populations are rare and known from few scattered locations in southern Mongolia (Gubanov, 1996; Grubov, 2001), where they are restricted to widely isolated mountain habitats (Wesche *et al.*, 2005*a*). Whether isolation has caused genetic differentiation among populations was unknown. In the same region, an earlier study confirmed an almost complete reproductive collapse in stands of the clonal *Juniperus sabina* (Wesche *et al.*,

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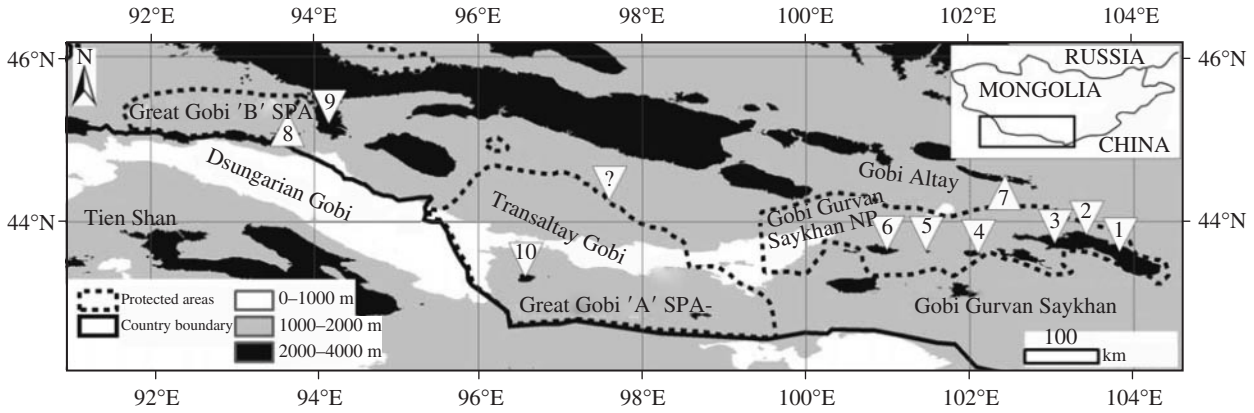

FIG. 1. Position of sampling localities in southern Mongolia. Numbers of ranges refer to Table 1; the question mark indicates the site Edrengiyn Nuruu, where both species had previously been recorded (Grubov, 2001) but were not found in this study. Dotted lines demarcate the nature reserves (Great Gobi 'A' and 'B' Special Protected Areas, Gobi Gurvan Saykhan National Park) in the region.

2005*c*), so similar problems were expected for the species in the present study.

Patterns of random amplified DNA (RAPD) variation were examined for 23 Mongolian *Galitzkya* populations in order to answer the following questions: (*a*) How is genetic variation distributed among and within populations of *G. macrocarpa* and *G. potaninii*? Is there any evidence for restricted gene flow among populations; and is genetic similarity correlated with spatial distance? (*b*) How large is the genetic diversity of populations, and is there any correlation to habitat size of *G. macrocarpa*? (*c*) Is there evidence for extensive clonal growth in the fine-scale genetic structure of *G. macrocarpa* populations? (*d*) What are the implications for conservation of the Mongolian populations?

MATERIALS AND METHODS

Study species and study region

The genus *Galitzkya* (Brassicaceae) is restricted to Central and Middle Asia and comprises three species: *Galitzkya spathulata* (Steph. ex Willd.) V. Boczantzeva occurs from northern China to western Kazakhstan (Pavlov, 1961; Zhou *et al.*, 2001) and is not included here for logistical reasons. *Galitzkya macrocarpa* (Iconn.-Galitz.) V. Boczantzeva is a true endemic of mountain ranges in southern Mongolia (Boczantzeva, 1979; Gubanov, 1996), while *G. potaninii* (Maxim.) V. Boczantzeva grows in mountains of south-west Mongolia, and in the Tien Shan and Quilian Shan in north-western China. So far neither species has been studied in terms of genetic structure, nor is there any information on ploidy levels.

Galitzkya macrocarpa and *G. potaninii* are suffruticose plants characterized by broad rosulate leaves. Individuals develop one main caudex which can form several branches (three to five) with increasing age. Plants are often successively buried in moving scree, resulting in the development of subterranean shoots. The number of laterally developed inflorescences ranges between 0 and 27 (mean of 5; R. Undrakh, unpbl. res.); these bear on average three to five silicles, each of which contains four to eight seeds. Both species have light seeds (mean weight: *G. macrocarpa*, 1·72 mg; *G. potaninii*, 1·05 mg) which are flat (mean surface area: *G. macrocarpa*, 5·69 mm^2; *G. potaninii*, 5·19 mm^2) with broad wings (mean width: *G. macrocarpa*, 1·66 mm; *G. potaninii*, 1·43 mm). Seeds are thus capable of dispersal by wind, but no detailed data are available. Plants are self-compatible, insect-pollinated (R. Undrakh, unpbl. res.), and seeds germinate readily without any apparent sign of dormancy.

The study area comprises three protected areas in south-western Mongolia and covers some 80 000 km^2 (Fig. 1). Here, *G. potaninii* occurs in the Dsungarian Gobi and Transaltay Gobi, while *G. macrocarpa* is restricted to the Gobi Altay region and the Transaltay Gobi where it was previously described from a single mountain range only (Edrengiyn Nuruu; Grubov, 2001). However, it was not possible to relocate that population, nor was it possible to find any of the two species in that mountain range. Both species avoid the relatively flat piedmont regions, which reach higher altitudes in central southern Mongolia; instead species prefer rock fissures or boulder areas. *Galitzkya macrocarpa* occurs between 1800 and 2600 m a.s.l., while *G. potaninii* covers the altitudinal range of 1500–2100 m a.s.l. in south-western Mongolia (Table 1). Both species grow on barely accessible rocks and boulders and are virtually unaffected by nomadic land use. Thus, the current levels of isolation and population fragmentation are not determined by human impact but by natural causes.

There are hardly any climate stations in the mountains but short-term measurements are available for the Dund Saykhan (east Gobi Gurvan Saykhan National Park; Fig. 1) and are expected to be fairly typical for the region. These suggest that mountains above 2300 m a.s.l. receive a total annual precipitation of 160–200 mm (Retzer, 2004). This renders them dry but nonetheless moister than the surrounding lowlands (mean annual precipitation <130 mm).

Data collection

Sample sizes differ among species because more populations of *Galitzkya macrocarpa* than of *G. potaninii*

TABLE 1. *List of sampled mountain ranges, populations, spatial extent of suitable moist mountain steppes, and number of specimens sampled (sample size is higher in population 1 due to the analysis of small-scale genetic structure)*

Range no.		Latitude/longitude (decimal degrees)	Elevation (m a.s.l.)	Habitat (km^2)	Population no.	Sample size	No. used for population level analysis
Galitzkya macrocarpa							
1	Dund Saykhan	43·620/103·820	2480	67·7	1	30 (+31)	10
	Dund Saykhan	43·630/103·810	2520		2	6	6
	Dund Saykhan	43·630/103·777	2750		3	5	5
2	Gegetiyn Am	43·830/103·330	2070	60·5	4	10	10
	Gegetiyn Am	43·800/103·190	2050		5	9	9
	Bayan Bor Nuruu	43·792/103·134	2150	16·1	6	3	
3	Bayan Tsagaan	43·794/102·515	2040	23·8	7	9	9
	Bayan Tsagaan	43·717/103·101	2330		8	9	9
	Khavtsgaitiyn Am	43·690/102·970	1950		9	1	
4	Sevrey Uul	43·647/102·045	2080	7·2	10	10	10
	Sevrey Uul	43·601/101·978	2300		11	6	6
5	Gilbent Uul	43·636/101·500	2050	2·7	12	5	5
6	Nemegt Uul	43·666/100·900	2600	28·3	13	2	
	Nemegt Uul	43·700/100·910	2400		14	10	10
	Nemegt Uul	43·622/100·434	2300		15	10	10
7	Arts Bogd	44·730/102·200	1800	78·6	16	3	
	Arts Bogd	44·418/102·211	1830		17	9	9
	Arts Bogd	44·483/102·561	2160		18	1	
Galitzkya potaninii							
8	Gun Tamgijn Us	45·250/93·667	1700	No data	19	10	10
	Takhin Tal	45·561/93·613	1800		20	10	10
9	Mongolian Altay	46·423/94·221	2010		21	10	10
10	Atas Bogd	43·321/96·645	2300		22	16	10
	Atas Bogd	43·390/96·411	1700		23	4	

were found. Whereas the 18 populations of *G. macrocarpa* cover its entire distributional range, those of *G. potaninii* (five populations) represent only the northern part of that species' range (Fig. 1). DNA samples are kept at our institute Halle; voucher specimens were deposited at the herbarium at the Martin-Luther-University Halle-Wittenberg (HAL). A population was defined as a group of plants separated from their closest conspecific by at least 1 km. The minimum and maximum distances between two populations were 1 and 275 km, respectively, for *G. macrocarpa* and 20 and 367 km, respectively, for *G. potaninii*.

The mountain steppes colonized by *G. macrocarpa* in the Gobi Gurvan Saykhan region have a mean inclination of 20° (Wesche *et al.*, 2005*b*); suitable microhabitats are usually even steeper and several populations grew on vertical cliffs. Access is exceedingly difficult due to the heavily weathered rock. Whenever possible, at least nine plants per population (>1 m apart), which were always taken within a radius of 10 m, were sampled. In some cases, the terrain rendered sampling of nine plants impossible (Table 1). For the same reason, it was impossible to estimate population numbers. However, as *G. macrocarpa* is restricted to relatively moist mountain steppes (Gubanov, 1996), a vegetation map (von Wehrden *et al.*, 2006) was used to estimate the extent of this habitat type in a given mountain range as a proxy for the potential population size (Table 1).

To assess the small-scale genetic structure of *G. macrocarpa*, all 67 shoots on a reasonably accessible site in the Dund Saykhan were mapped and sampled for genetic fingerprinting (range 1, population 1, Table 1; plot size 7 × 14 m, mean density 0·68 shoots m^{-2}).

RAPD-PCR

Anonymous RAPD-, AFLP- and ISSR-markers are widely used in population genetics. All share the problem of dominance, and have been demonstrated to yield mostly similar results (Nybom and Bartish, 2000; Nybom, 2004). RAPDs were chosen as these have been employed previously for identifying clones in small-scale spatial studies (e.g. Steinger *et al.*, 1996; Wesche *et al.*, 2005*c*). As RAPDs formerly have been criticized in terms of reproducibility (Bachmann, 1994), reliability of data was ensured by repeating PCRs.

Tissues were stored in silica-gel directly after sampling. Genomic DNA was extracted from 25 mg of dried leaves with a standard kit (QIAGEN 2000; DNeasy Plant Mini Kit). Sixty primers were screened for readability and reproducibility (Random Primer Kits, Roth). This resulted in the selection of nine primers (D02, GGACCCAACC; D05, TGAGCGGACA; D07, TTGGCACGGG; D12, CACCGTATCC; D20, ACCCGGTCAC; N05, ACTGAACGCC; N09, TGCCGGCTTG; N12, CACAGACACC; N20, GGTGCTCCGT). DNA was amplified in 10-µL reaction volumes containing 8 ng DNA, 0·6 µmol L^{-1} primer (Roth), 0·2 mmol L^{-1} of each dNTP (Peqlab), 0·5 units Taq polymerase (Qbiogene), 1 µL buffer ×10 (Qbiogene) and 6·5 µL H_2O. PCR was carried out in a thermocycler (Flexigene 384, Techne) that allowed for the simultaneous processing of all samples. The thermocycler

TABLE 2. *Summary of genetic information available for analysis*

	G. macrocarpa	*G. potaninii*	Both species
No. of samples	138 (+31)	50	188
No. of polymorphic bands	126	68	150
No. of monomorphic bands	9	14	
No. of missing bands	15	68	
No. of shared bands			67
No. of private bands	68	15	
of these polymorphic	68	11	
of these monomorphic	0	4	
Bands with frequency <5%			
of these private	16	0	
of these shared	12	10	

was programmed for one cycle of 2 min at 94 °C followed by 36 cycles of 12 s at 94 °C, 45 s at 36 °C and 120 s at 72 °C with a final cycle of 7 min at 72 °C.

DNA fragments were separated by electrophoresis in 2% agarose gels with a TAE (Tris-acetate-EDTA) buffer system at 150 V for 150 min (equalling 10 cm distance) and stained with ethidium bromide. DNA bands were then visualized by UV light and documented using a video camera. Each sample was run in at least two independent RAPD-PCR amplification reactions. Gel pictures were analysed visually and digitalized with the help of the software RFLPSCAN PLUS Version 3.0 (Scanalytics); only bands in the range between 240 and 1500 bp were scored.

Data analysis

The nine primers used in the PCR yielded 150 polymorphic bands. RAPD data were coded into a simple matrix with '0' for absent and '1' for present bands. Only polymorphic bands were used as recommended by Nybom and Bartish (2000); these totalled 126 in *G. macrocarpa* and 68 in *G. potaninii*; 67 bands were shared among species (Table 2). It was possible to amplify DNA for 61 of the 67 mapped shoots of *G. macrocarpa* within population 1. The matrix for analysis of possible clonal structures contained 73 bands, of which 51 were polymorphic.

In dominant markers, application of standard measures of genetic diversity relies on several assumptions including presence of a Hardy–Weinberg equilibrium. For that reason, several approaches are usually combined to analyse dominant markers (e.g. Schönswetter *et al.*, 2005). Sörensen similarity was chosen as an asymmetrical index that places strong weight on bands shared among individuals. Values were transformed to a distance measure by subtracting them from 1 (Legendre and Legendre, 1998). The distance matrix was used to calculate mean distance among individuals, as well as within and among populations. Sörensen distance was also used in ordination; principal co-ordinate analysis was performed on all samples on square-root transformed distances as these have metric properties (Legendre and Legendre, 1998). As ordinations confirmed clear differences among species, further analyses were performed separately for *G. macrocarpa* and *G. potaninii*.

A second approach was based on symmetric measures of genetic diversity. Data of all populations with a sample size $\geqslant 5$ (13 of *G. macrocarpa*, four of *G. potaninii*) were subjected to a hierarchical analysis of molecular variance (AMOVA) (Excoffier *et al.*, 1992) with three levels for variance partitioning: among mountain regions, among populations within mountain regions, and within populations (Table 1). In parallel to *F*-statistics, Φ-statistics were calculated to assess the genetic differentiation among populations. Significances were tested by a permutation procedure with 9999 runs. Measures for intra-population diversity used in this study include the percentage of polymorphic loci, the percentage of polymorphic bands among those present in a given population, the number of private bands (those restricted to the given population or mountain range, respectively), mean Sörensen distance among plants in a population, and average gene diversity over all loci (Schneider *et al.*, 2000).

In populations 1 and 22 more than ten specimens were sampled, so statistics were compared on the population level for populations with subsample size $n \geqslant 5$ with those with $n \geqslant 9$, and again for those with $n \geqslant 9$, but with a maximum of ten specimens included. Except for the number of polymorphic sites, no statistic was affected by changing sample size, confirming that RAPD-based assessments are relatively insensitive to sampling intensity (Nybom and Bartish, 2000). Thus, figures based on those 13 populations with at least five samples available are reported (Table 1). In populations 1 and 22, ten samples were randomly chosen from the larger data set for analysis at the population level.

For *G. macrocarpa*, isolation by distance was tested with Mantel tests. Pairwise Φ_{ST}-values were used as symmetrical measures of genetic distances, which were tested against a matrix of spatial distances in kilometres. Mean Sörensen distances among populations were also tested against the same geographic distances. In all Mantel tests, significances were tested with 9999 permutations.

Asymmetric analyses were performed with PC-ORD 4·32 (McCune and Mefford, 1999) and CANOCO 4.5 (ter Braak and Smilauer, 2002); genetic analysis was done with Arlequin ver. 2.000 (Schneider *et al.*, 2000). Simple bivariate correlations were calculated with SPSS 12.0 (SPSS, 2003).

RESULTS

Differences between *Galitzkya macrocarpa* and *G. potaninii*

Among the 188 bands obtained, 68 were only found in *G. macrocarpa*, while G. *potaninii* had 15 private bands (Table 2). No single band was sufficient to characterize samples of *G. macrocarpa* as all 68 private bands were polymorphic. Of the 15 private bands of *G. potaninii*, four were monomorphic and characterized that species. Principal co-ordinate analysis of all 23 populations sampled showed that species were clearly and unequivocally differentiated along ordination axis 1 (Fig. 2), which

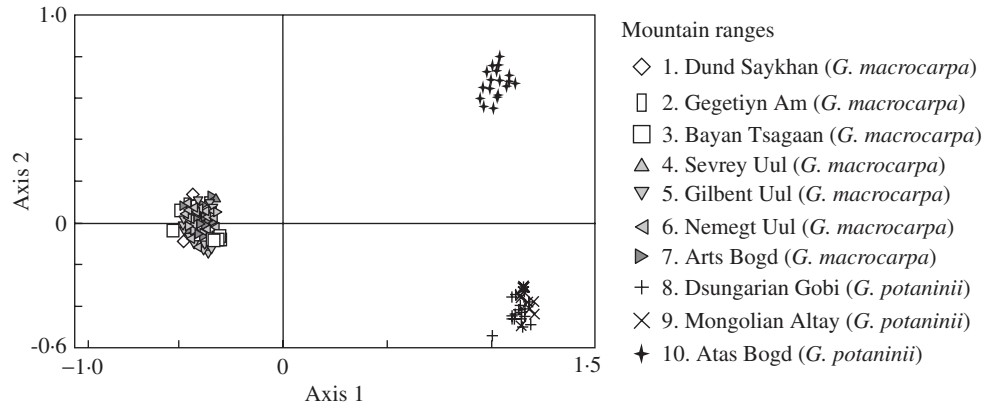

FIG. 2. Principal co-ordinate analysis of RAPD data for *G. macrocarpa* and *G. potaninii* (based on square-root transformed Sörensen similarity; explained variance axis 1 = 43·7 %; axis 2 = 7·9 %; axis 3 = 3·4 %).

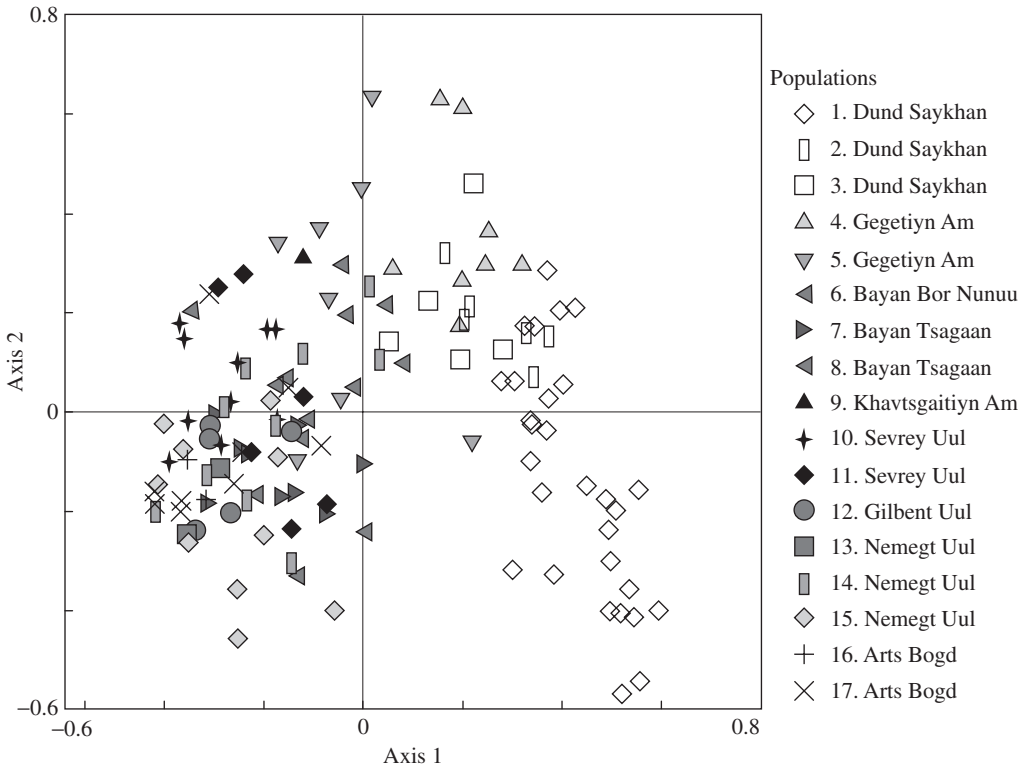

FIG. 3. Principal co-ordinate analysis of RAPD data for *G. macrocarpa* (all 138 available samples; PCA based on square-root transformed Sörensen Similarity; explained variance axis 1 = 8·6 %; axis 2 = 6·1 %; axis 3 = 5·2 %).

captured 43·7 % of the total variance. The much less important axis 2 (7·9 % explained variance) differentiated populations of *G. potaninii* of the Dsungarian Gobi (lower right corner) from those in the Transaltay Gobi. In comparison, samples of *G. macrocarpa* formed a closed group in the left-hand part of the ordination diagram.

Inter-population structure

Except for one sample (in population 4), all others in this data set, and in that for *G. potaninii*, had distinct phenotypes, and specimens were thus considered genetic individuals. The ordination revealed relatively weak genetic differentiation between *G. macrocarpa* populations and mountain ranges (Fig. 3). The first three axes together explained only 14·7 % of the variance, indicating the absence of any simple genetic structure. Although samples within populations generally clustered together, populations — and even different mountain ranges — showed clear overlaps in the ordination diagram. This pattern was supported by the AMOVA (Table 3A) that found 74·9 % of the total genetic variation within populations, and 16·2 % among populations. This left 8·9 % for differences between mountain ranges.

Differences among groups and among ranges, as well as values for Φ-statistics, were highly significant. The overall Φ_{ST}-value of 0·251 gives evidence for spatial isolation.

TABLE 3. *AMOVA table for (A) populations of* Galitzkya macrocarpa *in the South Gobi, which were nested within the main mountain ranges (13 populations,* n ⩾ *5 and* ⩽ *10):* $\Phi_{SC} = 0{\cdot}178$; $\Phi_{ST} = 0{\cdot}251$; $\Phi_{CT} = 0{\cdot}088$; *and (B)* G. potaninii *populations, which were nested within the regions Dsungarian Gobi and Transaltay Gobi (only those four populations with* n = *10):* $\Phi_{SC} = 0{\cdot}181$; $\Phi_{ST} = 0{\cdot}550$; $\Phi_{CT} = 0{\cdot}451$

Source of variation	d.f.	Sum of squares	Variance components	% variation
(A) *G. macrocarpa*				
Among regions	6	257·700	1·106***	8·9
Among populations within regions	6	156·272	2·029***	16·2
Within populations	95	889·944	9·368***	74·9
Total		1303·917	12·504	
(B) *G. potaninii*				
Among regions	2	159·175	5·067	45·1
Among populations within regions	1	16·250	1·120***	10·0
Within populations	36	181·900	5·053***	44·9
Total	39	357·325	11·240	

***$P < 0{\cdot}001$.

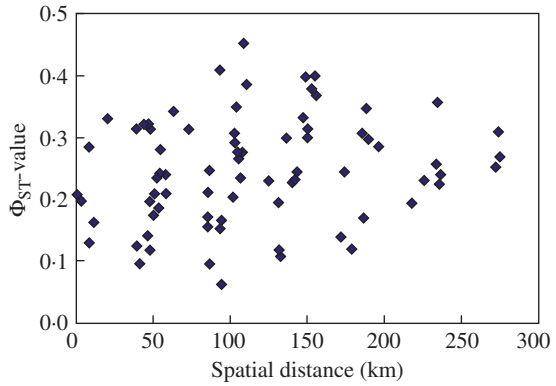

FIG. 4. Scatterplot indicating the relationship between geographic and genetic distance among populations.

This is confirmed by pair-wise Φ_{ST}-values, which tended to be lower within mountain ranges than among them (Fig. 4). The results of the Mantel tests indicated limited isolation by distance, as the pair-wise Φ_{ST}-values among populations and their geographical distances showed a weak and not significant correlation (standardized Mantel statistic $R_M = 0{\cdot}213$, $P = 0{\cdot}100$; 9999 permutations). The respective correlation for mean Sörensen distance between populations was higher than that for the Φ_{ST}-values and significant (standardized Mantel statistic $R_M = 0{\cdot}345$, $P = 0{\cdot}008$, 9999 runs).

A separate PCoA for *G. potaninii* yielded a similar picture as the general ordination (Fig. 2), so the data are not shown. The AMOVA also indicated strong differentiation in *G. potaninii*, and suggested a moderate degree of variability within the populations (44·9 %, Table 3B), while 45·1 % of the variation was accounted for by the different regions. The Φ_{ST}-value of 0·550 indicates strong genetic differentiation among populations. This differentiation was highly significant, as were differences among regions.

Intra-population diversity

Values for average gene diversity were <0·18 and those of mean Sörensen distance within populations were <0·22 for the 13 populations of *G. macrocarpa* (Table 4). Values within the more extensively sampled population 1 were similar, when several subsets were compared. The number of private alleles was low for most populations. However, when data were pooled on the level of mountain ranges, five out of seven mountain ranges were characterized as having exclusive alleles: Dund Saykhan (five), Gegetiyn Am/Bayan Bor Nuruu (two), Bayaan Tsagaan (three), Gilbent Uul (one) and Nemegt Uul (two). Genetic diversity within populations was not correlated with the size of the suitable habitat (for average gene diversity, Pearson's $r = -0{\cdot}01$, n.s.; for mean Sörensen distance within populations, $r = 0{\cdot}03$, n.s.).

Genetic diversity within populations of *G. potaninii* was lower in the Dsungarian Gobi than in the Transaltay Gobi (Table 4). Strong isolation among regions colonized by *G. potaninii* was also indicated by the higher numbers of private bands at the population level (Table 4). Moreover, 20 bands were restricted to populations found in the Dsungarian Gobi and 14 were restricted to samples from the Transaltay Gobi.

Spatial extent of clones in G. macrocarpa

Non-sexual regeneration occurs in *G. macrocarpa* (Fig. 5). Shoots tended to grow together and there was evidence of clumping. The 51 polymorphic bands constituted 52 different phenotypes, five of which occurred twice, and two, three times. Thus, most shoots originated from sexual reproduction. Shoots with identical phenotypes — though rare overall — always grew next to each other. The maximum distance covered by one clone was 2 m. The importance of sexual reproduction was also suggested by the intense flowering of the species, and also ramets within clones were usually flowering (Fig. 5).

DISCUSSION

Genetic structure

Our analyses of genetic structure revealed clear differentiation among populations, but levels differed tremendously among the two *Galitzkya* species. The Φ_{ST}-value of 0·251 for *G. macrocarpa* is not unexpectedly high. Meta-analysis of RAPD-based estimates of F_{ST}/Φ_{ST}-values (Nybom and Bartish, 2000; Nybom, 2004) demonstrated that Φ_{ST}-values are significantly related to live-form, with long-lived perennials showing the lowest figures (mean 0·25), and species with a mixed-breeding system being characterized by intermediate levels (means 0·25–0·4; Nybom and Bartish, 2000; Nybom, 2004). Endemics do not differ from more widespread species in this respect. Compared with other alpine perennials, pairwise Φ_{ST}-values among *G. macrocarpa* populations are also intermediate (Fig. 4),

TABLE 4. *Genetic diversity within populations of* G. macrocarpa *and* G. potaninii

Population no.	Range no.	*n*	No. of bands present	No. of bands polymorphic	% polymorphic	Private bands	Gene diversity	Sörensen distance
Galitzkya macrocarpa								
1	1	10	76	42	55	1	0·134	0·163
2	1	6	71	37	52	0	0·146	0·184
3	1	5	71	33	46	1	0·141	0·170
4	2	10	73	40	55	0	0·116	0·143
5	2	9	79	57	72	1	0·172	0·222
7	3	9	75	49	65	1	0·153	0·191
8	3	9	86	57	66	1	0·165	0·205
10	4	10	84	62	74	1	0·170	0·215
11	4	6	64	36	56	0	0·129	0·182
12	5	5	78	44	56	1	0·165	0·190
14	6	10	82	57	70	1	0·158	0·203
15	6	10	76	53	70	0	0·155	0·199
17	7	9	84	45	54	0	0·127	0·142
r			0·374	0·541	0·491	0·022	0·017	0·164
Galitzkya potaninii								
19	8	10	41	21	51	3	0·111	0·124
20	10	10	43	23	53	3	0·138	0·152
21	9	10	41	20	49	2	0·106	0·117
22	10	10	47	42	89	14	0·240	0·336

Figures refer to symmetrical measures of molecular diversity (average gene diversity over all loci, see Schneider *et al.*, 2000), and the mean of the asymmetrical Sörensen distance among samples of a given population (only those with $n \geqslant 5$).

Percentages of polymorphic bands were calculated with respect to the number of bands present in a given population.

For *G. macrocarpa*, Pearson correlations of diversity measures and specimen number are given.

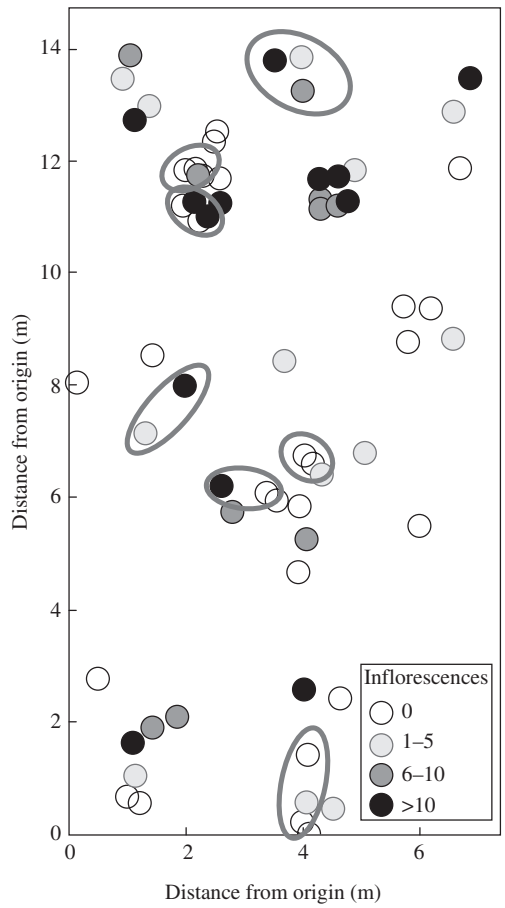

FIG. 5. Small-scale distribution of shoots of *G. macrocarpa*. Dots indicate individual shoots, shading corresponds to its number of inflorescences. Outlined areas include shoots with an identical marker phenotype.

as values between 0·1 and 0·5 are widely reported (e.g. Gugerli *et al.*, 1999; Stehlik *et al.*, 2001; Schönswetter *et al.*, 2002, 2004; Young *et al.*, 2002). In comparison, the overall Φ_{ST}-value of 0·550 for *G. potaninii* appears relatively high. In alpine plants, similarly high Φ_{ST}-values were usually interpreted as evidence of prolonged isolation, assumed to date back to the last glacial period (Schönswetter *et al.*, 2002, 2004; Reisch *et al.*, 2003). Pronounced differentiation in Dsungarian populations of *G. potaninii* may also be related to founder effects, and subsequent severe isolation. Another option is that populations in the Dsungarian Gobi and in the Transaltay Gobi originated from different refugia, which can not be assessed without data from the Chinese part of the range, but seems less likely with respect to the regional topography. Thus, there are good reasons to suspect that *G. potaninii* populations in the Dsungarian Gobi have been isolated for extended periods of time.

Comparatively low levels of population differentiation imply that in *G. macrocarpa*, isolation may be less severe or has occurred much more recently (Max *et al.*, 1999). This is indicated by the overlap of populations in the PCoA (Fig. 3) and by the results of the AMOVA analysis (Table 3). Most of the genetic variance is kept within populations (>70 %), a pattern often described for mountain plants (Gugerli *et al.*, 1999; Cotrim *et al.*, 2003; Pluess and Stöcklin, 2004), for endemic plants from Tibet (Chen *et al.*, 2005) and from Central Asian deserts (Li and Ge, 2001; Ge *et al.*, 2003; Sheng *et al.*, 2005). However, available data does not allow a generalization of such a pattern, as higher levels of population differentiation have also been reported, both from Tibet (Chen *et al.*, 2005; Xia *et al.*, 2005) and from Central Asia (Ge *et al.*, 2003, 2005).

Variation among populations and regions was nonetheless significant in *G. macrocarpa*, so there clearly is an impact of spatial isolation, albeit less severe than that documented for *G. potaninii*. Correspondingly, only part of the Mantel tests of spatial and genetic differences gave significant values for the standardized Mantel statistic, suggesting that much of the variation among populations of *G. macrocarpa* is not related to spatial distance. Because *Galitzkya* species are insect-pollinated, long-distance seed dispersal, rather than pollen flow, is likely to be responsible for gene flow among mountain ranges (Pluess and Stöcklin, 2004). Available data for the similarly sized Brassicaceae *Biscutella laevigata*, which also has winged seeds and grows on exposed rocks in Europe, suggests a limited dispersal capacity with <1·5 % of the seeds flying >100 m (Tackenberg, 2001; Tackenberg *et al.*, 2003). However, as micro-scale wind patterns are of outmost importance for seed uplift, and weather observations suggest that upgoing winds can be very strong in the region studied (>8 on the Beaufort scale), there is at least a potential for effective uplift of seeds and, consequently, occasional long-distance dispersal.

Within population diversity

RAPDs are dominant markers and estimates of genetic diversity are relatively crude. However, values of average gene diversity obtained for the study species were closely related to those calculated based on simple multivariate similarity (Sörensen distance *vs*. average gene diversity, $r = 0{\cdot}921$). This supports the notion that relative comparisons within datasets should be possible (Nybom and Bartish, 2000; Nybom, 2004). In *G. macrocarpa*, genetic diversity of populations was not positively correlated to habitat size, and figures did not differ much between mountains. In all mountain ranges, the potential habitat size was above 7 km^2, which provides ample space for a relatively small plant like this, but results of the AMOVA indicate that there is significant genetic variation among populations within a given mountain range, so habitats are probably not continuously colonized. Thus, the real populations of *G. macrocarpa* may be much smaller than that suggested by the estimates derived from the vegetation map (scale 1 : 250 000; von Wehrden *et al.*, 2006).

Figures for intra-population genetic diversity are nonetheless relatively low when compared with studies on other fragmented plant species performed by the present working group with the same methodology (Dittbrenner *et al.*, 2005; Hensen and Oberprieler, 2005; Hensen *et al.*, 2005) and, also, though this has to be treated with caution because of differing marker systems, compared with other alpine plants (Schönswetter *et al.*, 2002, 2004; Cotrim *et al.*, 2003). It cannot be ruled out that the low genetic diversity is related to random losses of alleles in small populations. However, genetic variability was not further reduced in peripheral populations, and there was only limited evidence for isolation by distance. Thus, it is suspected that current patterns are more easily explained by effects on the entire species. Pronounced range contractions and possible bottlenecks are plausible with respect to the strong climatic changes that these dry mountain ranges experienced in the Quaternary (Gunin *et al.*, 1999).

Galitzkya potaninii differs also in this respect. Low levels of genetic diversity were found in the Dsungarian Gobi, where habitats are relatively small and populations are widely isolated from the main range in the northwestern Chinese uplands (Fig. 1). However, levels were higher in the population from the Atas Bogd, which is geographically less isolated from the remainder of its range. Thus, in the peripheral populations in the Dsungarian Gobi, isolation has apparently prevented genetic exchange resulting in overall lower levels of genetic diversity than in the less isolated populations. Similar results have been obtained for montane plants in North America (Godt *et al.*, 1996).

Clonal growth in G. macrocarpa

Identical specimens were hardly found in the overall sample of 13 *G. macrocarpa* populations, and the small-scale mapping revealed that 61 ramets on 98 m^2 represent 52 genets (Fig. 5). The few clones reached a maximum extension of up to 2 m, which should translate to an age of several decades, or even centuries. However, sexual reproduction is clearly the more important mode of recruitment in the life cycle of *G. macrocarpa* and suggests that establishment of sexual propagules, and thus also gene flow, is possible. Studies on genetic structure have demonstrated higher importance of clonal growth in a number of Central Asian desert species (Li and Ge, 2001; Su *et al.*, 2003; Xu *et al.*, 2003), and the number of clonal plants is thought to increase with increasing aridity of the sites (Song *et al.*, 2002). Clonal growth in alpine plants has been described for several growth forms including perennial grasses (Steinger *et al.*, 1996; Linhart and Gehring, 2003), perennial herbs (Diggle *et al.*, 1998; Jones and Gliddon, 1999), and shrubby species (Escaravage *et al.*, 1998; Young *et al.*, 2002). In some alpine plants such as *Saxifraga cernua* (Bauert *et al.*, 1998) extensive clonal growth correlates with reduced genetic diversity. In the region studied, the prostrate *Juniperus sabina* forms clones totalled up to 100 m in diameter while sexual reproduction had practically ceased (Wesche *et al.*, 2005*c*).

It is concluded that sexual reproduction is apparently effective in *G. macrocarpa*, gene flow seems to be present and there is no direct evidence for loss of genetic diversity due to clonal growth. In these respects, *G. macrocarpa* compares well with the clonal alpine species *Geum reptans* that maintains local clonal and genetic diversity, and shows only moderated isolation by distance among populations (Pluess and Stöcklin, 2004). A similarly mixed strategy of sexual and asexual reproduction was found in *Lloydia serotina* (Jones and Gliddon, 1999), *Carex scopulorum* (Linhart and Gehring, 2003) and *Rutidosis leiolepis* (Young *et al.*, 2002). If site conditions become unfavourable for seed production or seedling establishment, extended periods of time can be survived by vegetative growth while at the same time guarding against potential risks associated with exclusively clonal growth (Honnay and Bossyut,

2005). Thus, *G. macrocarpa* appears to be well adapted to an essentially harsh environment where pronounced intra-annual variability renders opportunities for sexual regeneration rare events.

Recommendations for species' conservation

Galitzkya macrocarpa is completely restricted to Mongolia. Its overall distribution range is approx. 30 000–40 000 km^2, though the actual potential habitats cover well below 1000 km^2 (Table 1). It clearly is a rare species, but no evidence of shrinking populations was found (Wesche *et al.*, 2005*a*). Thus, at present the species cannot be regarded as vulnerable according to standard criteria (IUCN, 2001).

Current levels of fragmentation could still threaten long-term survival. Estimates of gene flow based on Φ_{ST}-values (Wright, 1931) are crude but still widely used (Wang, 2004). In the case of *G. macrocarpa*, gene flow is estimated at 0·75 exchanged individuals per generation (Φ_{ST} = 0·251). This is less than the minimum of one migrant per generation — a rule-of-thumb value that is thought to be sufficient to maintain genetic exchange. On the other hand, a Φ_{ST} value of 0·251 is not an unusual figure compared with other species of perennial herbs, and similar levels of population differentiation have also been described for naturally fragmented montane species (Pluess and Stöcklin, 2004; Chen *et al.*, 2005). In the present case, fragmentation is largely controlled by the current levels of aridity. Less drought-tolerant vegetation types were more widespread in the southern Mongolian mountains some 4000–2000 years BP (Gunin *et al.*, 1999; Jäger, 2005), and current levels of fragmentation in *G. macrocarpa* should have been reached later than that.

With respect to its overall limited distribution, Mongolian populations of *G. potaninii* certainly have importance for conservation of that species. The present estimate for the Φ_{ST}-value of 0·550 corresponds to only 0·20 exchanged individuals per population, a very low figure that indicates 'severe fragmentation' (IUCN, 2001). Further data on distribution and population structure, especially in the Chinese part of its range, are thus urgently needed to assess if the species has not already become endangered.

At present, there is no immediate need for conservation action in *G. macrocarpa*, but levels of fragmentation and genetic diversity imply that some monitoring is also required. As possible threats may be related to climate change, rather than land use, they may be beyond conservation action *in situ*. Because the greater part of genetic variability is captured within populations, sampling for conservation *ex situ* should concentrate on representing a high number of individuals rather than representing all populations; a strategy which has already been proposed for other Central Asian endemics (Young *et al.*, 2002; Ge *et al.*, 2003).

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