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Phytogeographical and community similarities of alpine tundras of Changbaishan Summit, China, and Indian Peaks, USA

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Abstract. We compared the diversity, phytogeography, and plant communities in two mid-latitude alpine tundras with comparable aerial and elevational extents: Changbaishan Summit in eastern Asia and Indian Peaks in western North America. Despite wide separation, the two areas shared 72 species. In all, 43 % of the species on Changbaishan Summit are also distributed in the alpine zones of western North America, while 22 % of the species on Indian Peaks are also distributed in the alpine zones of eastern Asia. Almost all the shared species also occur in the Beringian region. Phytogeographical profiles of species and genera showed that 69 % of species and over 90 % of genera in both alpine tundras belong to the three phytogeographical categories: cosmopolitan, circumpolar, and Asian-North American. We attributed the current floristic relationship between these widely separated areas to the periodic past land connection between the two continents during the Tertiary and Pleistocene. Indian Peaks has a closer floristic relationship with the Arctic tundra than does Changbaishan Summit. Indian Peaks also has 45 % higher species richness and lower vegetation cover than Changbaishan Summit.

Plant communities from the two areas were completely separated in the two-way indicator species analysis and non-metric multidimensional scaling on floristic data at both species and generic levels, whereas ordination of communities by soil data produced a greater overlap. The plant communities on Changbaishan Summit in general have lower alpha diversity, higher beta diversity (lower between-community floristic similarity), and more rare species than does Indian Peaks. Mosaic diversity does not differ in the two alpine tundras, although the analysis suggests that Changbaishan Summit communities are more widely spaced on gradients than the Indian Peaks communities.

Keywords: Alpine vegetation; Asian-North American comparisons; Bering land bridge; Phytogeography.

Nomenclature: North American taxa: Kartesz (1994) for vascular plants, Anderson (1990) and Anderson et al. (1990) for mosses, Stotler & Crandall-Stotler (1977) for liverworts and hornworts, and Esslinger & Egan (1995) for lichens; taxa distributed outside North America: Qian (1989a).

Introduction

The alpine floras of temperate eastern Asia and temperate western North America are currently separated by 8000-10 000 km. During the colder climates and lower sea levels of the past, however, the Bering land bridge provided a corridor for plant migration between the two continents (Tiffney 1985). Literature reports, as well as our own field work (Qian 1989a, 1993; Qian & Gao 1990) suggest strong floristic relationships. Our objective in this paper was to compare the floristics, plant communities, and soil gradients of these now isolated alpine areas.

Studies of the relationships between the eastern Asian and western North American alpine tundras have been general (e.g. Zhu & Rowe 1987; Qian 1989a, 1993; Qian & Gao 1990) and no attempt has been made to compare plant communities of the two continents. Since most of the alpine tundras on either side of the Pacific Ocean have not been surveyed, a complete comparison is impossible. Here, we focus on two well-studied alpine tundra areas: Changbaishan Summit, China, and Indian Peaks, USA. We selected these areas for four reasons. First, the areas are located at comparable latitudes and have similar aerial and elevational extents (Table 1). Second, the two areas are similar in the major environmental factors such as annual mean temperature (Table 1). Third, the two areas have typical alpine vegetation and environments for the geographical regions in which they are situated, and are relatively undisturbed by humans. Finally, the floristics and vegetation of the two areas have been intensively surveyed.

We addressed two sets of questions. At the floristic level, we addressed: How comparable are the two areas in richness of vascular plants, bryophytes, and lichens? How do the two areas compare in the phytogeography of their species and genera? How much floristic overlap is there between the two alpine floras and between these areas and the Arctic tundra? At the community level, we addressed: How similar are the communities in composition, structure, soil properties, and vegetation-environment relations? How similar are the ecological diversities of the two areas?

Materials and Methods

Study areas

Changbaishan Summit (also called Changbai Mountain in China; and Baektu Mountain, Paektushan, or Mount Paektu in North Korea), is situated on the international border between China and North Korea. The highest summit of Changbaishan is 2749 m a.s.l. (at 42°00' N and 128°10' E), which is below the modern climatic snow line. The alpine tundra zone ranges from 1950 (at the treeline) to 2749 m a.s.l. (Table 1).

Changbaishan is of volcanic origin (Zhao 1987). The last volcanic eruption to cause severe devastation of the vegetation was in 404 (± 177 yr) A.D. (Qian 1989a). Since the pumice-ash layer was found mainly on the east, southeast, and south slopes, it is believed that the vegetation on the rest of Changbaishan, approximately 2/3 of the summit, was not destroyed by that eruption. Since the 15th century, Changbaishan volcano has erupted four times (1413, 1597, 1668, and 1702 A.D.) (Zhao 1987; Qian 1989a), however, none of these volcanic eruptions caused severe devastation to the vegetation not even around the caldera.

In the areas not destroyed by the eruption (404 A.D.), two alpine subzones are distinguished: low-alpine and high-alpine. Dwarf woody plant communities dominate the low-alpine subzone. Ericaceous plants such as *Vaccinium uliginosum*, *V. vitis-idaea*, *Rhododendron confertissimum*, *Rh. chrysathum*, *Therorhodion redowskianum*, *Arctostaphylos ruber* and *Phyllodoce caerulea* are common dominants, while the plant communities of *Empetrum nigrum* (var. *japonicum*), *Dryas octopetala* (var. *asiatica*), and *Juniperus communis* (var. *montana* = *J. sibirica*) are sporadic. In the high-alpine subzone vascular plants and bryophytes co-dominate.

Indian Peaks is in the Colorado Front Range of the southern Rocky Mountain province (Komárková 1979). The highest summit of Indian Peaks is 4115 m a.s.l. (North Arapaho), which is also below the modern climatic snow line. The alpine tundra zone roughly ranges from 3400 to 4115 m a.s.l., and has several small glaciers (Komárková 1979). Indian Peaks underwent two major ice advances during the Wisconsin stage of the Pleistocene glaciation (Komárková 1979), but some areas (e.g. Niwot Ridge) may not have been glaciated during Wisconsin time (Komárková & Webber 1978). Pleistocene and Holocene deposits cover considerable areas in the alpine zone (Benedict 1968).

Within the alpine zone of Indian Peaks two subzones have been distinguished. The mean elevation for the line of closed vegetation cover is 3553 m (Komárková 1979). Most of the area below that line is covered by alpine meadows dominated by *Kobresia* spp. and *Carex* spp., while in the area above that line, in the subnival belt, rock crevice vegetation dominates. Dwarf shrubs and ericaceous plants are rare in the Indian Peaks area (Komárková 1979).

Table 1. Geographical and meteorological data of Changbaishan Summit and Indian Peaks. Meteorological data for Changbaishan Summit (Qian 1989a) are from Tianchi station (2623 m a.s.l., 42°01' N and 128°05' E; data recorded from 1959 - 1980) and data for Indian Peaks (Komárková 1979; Greenland 1989) are from Niwot Ridge (D1) station (3749 m a.s.l., 40°03' N and 105°37' W; data recorded from 1952 - 1987). Note that the two climate stations differ in their placement. The station for Changbaishan Summit is at a higher position within the alpine zone than that for Indian Peaks.

	Changbaishan Summit	Indian Peaks
Geography		
Latitude	41°53'-42°04' N	40°00'-40°10' N
Longitude	127°57'-128°11' E	105°32'-105°44' W
Area (km^2)	160	164
Rel. height of alpine zone (m)	ca. 800	ca. 715
Climate		
Annual mean temperature (°C)	–7.3	–3.7
Mean temp. in warmest month (°C)	8.6	8.2
Mean temp. in coldest month (°C)	–23.2	–13.2
Annual precipitation (mm)	1332	1050
June–September precipitation (mm)	993	221

Data source

This study is based on two series of investigations: Qian (1989a, b, 1990a, b, c, d, 1992, 1993) and Qian & Gao (1990) on Changbaishan Summit and Komárková (1976, 1979, 1981, 1993) on Indian Peaks.

Floristics

Three major autotrophic groups (i.e. vascular plants, bryophytes, and lichens) were included. Nomenclature in the two original data sets was standardized and updated. Floristic data for Indian Peaks was updated with the addition of a few bryophyte and lichen species according to Flock (1978). Subspecific taxa were combined to the specific rank in this study.

Vegetation

A total of 1179 vegetation plots sampled using Braun-Blanquet methods were used in our analysis: 729 plots on Changbaishan Summit (Qian 1989a, 1992), and 450 plots on Indian Peaks (Komárková 1979, 1993). Vegetation was analysed at the association level (Mueller-Dombois & Ellenberg 1974). In the original data sets, 59 associations were recognized on Changbaishan Summit (Qian 1989a, 1992) and 63 on Indian Peaks (Komárková 1979, 1993). However, two associations from Changbaishan Summit were excluded from this study as they were vegetation types in human-disturbed areas. Thus, a total of 120 associations were used in this study. Methods for sampling vegetation in the field and the criteria of grouping vegetation plots into associations can be found in Qian (1989a) and Komárková (1979).

Importance values for species and genera were calculated separately using:

$$IV_{ijk} = \frac{O_{ijk} \cdot L_{jk}}{\sum_{i=1}^{n} O_{ijk}} \quad (1)$$

where IV_{ijk} is the importance value of species *i*, O_{ijk} is percent cover of species *i* in layer *k* (*k* = 1 for woody/herbaceous layer or 2 for bryophyte/lichen layer) of association *j* with a total of *n* species, and L_{jk} is the projected cover (in percent) of layer *k* of association *j*.

Although many soil physical and chemical properties were reported in the original data sources, only the soil variables measured following the same techniques in the two areas were considered here. Soil data are restricted to the top 30 cm. Further details on soil sampling and analysis can be found in Qian (1989a) and Komárková (1976, 1979).

Data analysis

Phytogeography

We assigned taxa to one of seven phytogeographical categories: (1) cosmopolitan taxa with worldwide or nearly worldwide distribution; (2) circumpolar taxa widespread in the Holarctic; (3) Asian-North American taxa occurring in eastern Asia and North America, but not in Europe; (4) Eurasian taxa present in Europe and Asia, but not in North America; (5) Euramerican taxa distributed in Europe and North America, but not in Asia; (6) Asian taxa restricted to Asia; and (7) North American taxa restricted to North America. Phytogeographical profiles (i.e. the distribution of taxa across the seven categories) were compared between the two study areas.

Classification and ordination of associations

To examine the relationships among the 120 associations within and between the study areas, two-way indicator species analysis (TWINSPAN; Hill 1979) and non-metric multidimensional scaling (NMDS; Minchin 1987) were used. TWINSPAN was used (1) to classify the 120 associations into association groups, and (2) to detect the degree to which the associations from different study areas are mixed in association groups. TWINSPAN was run on importance values using default options, except for pseudospecies (*sensu* Hill 1979) cut levels, which were set to 0, 25, 50 and 75.

The association groups derived from TWINSPAN (hereafter referred to as TWINSPAN groups) were tabulated into a diagnostic table using the concept of differential and dominant-differential species (e.g. Klinka et al. 1996), defined as: (1) differential species are those species that may be associated with more than one vegetation unit in a hierarchy, species presence class ≥ III and at least two species presence classes greater than in other units of the same category and circumscription, and (2) dominant-differential species are those species that may be associated with more than one vegetation unit in a hierarchy, species presence class ≥ III, mean species importance value class ≥ 5 and two or more species importance value classes greater than in other units of the same category and circumscription.

NMDS was used to ordinate associations based on floristic (presence/absence) data or soil data. On the floristic data, NMDS was performed for the species and generic ranks separately. We used the Jaccard coefficient as a measure of dissimilarity. On the soil data (nine selected soil variables), % clay, redundant by default (i.e. % clay = 100 - % sand - % silt), was excluded. To minimize the effect of using different measurement units for different soil variables, all soil variables were standardized using:

$$S_{ij} = \frac{O_{ij}}{\sum_{j=1}^{n} O_{ij}} \times 100 \quad (2)$$

where S_{ij} is the standardized value of soil variable *i*, O_{ij} with the original value in association *j*, and *n* is 120 - the total number of associations of Changbaishan Summit and Indian Peaks.

The results from TWINSPAN and NMDS using floristic data showed that there was no overlap of associations between Changbaishan Summit and Indian Peaks, whereas NMDS run on soil data showed a large overlap between the two areas; therefore, the relationships among the TWINSPAN groups were examined separately for the two study areas, using NMDS run on soil data and floristic data (importance values) separately.

Vegetation-environment relationships were examined using canonical correspondence analysis (CCA; ter Braak 1987). Environmental variables used in CCA were three community structure variables (total vegetation cover, woody/herbaceous layer cover, and bryophyte/lichen layer cover) and the eight soil variables (in original measuring units). CCA was performed separately on importance values and soil data for each study area.

Compositional ratio of major taxonomic groups

Triangular ordination, with each of the three taxonomic groups (vascular plants, bryophytes, and lichens) being one of the three axes, was used to examine patterns in vegetation structure at the TWINSPAN group level. Two triangular ordinations were constructed: one using species floristic (presence/absence) data, and the other using species importance values.

Ecological diversity

Alpha diversity of each association was measured as Shannon-Wiener's index (H'; Shannon & Weaver 1949):

$$H' = -\sum p_i \ln p_i \tag{3}$$

where p_i is the proportion of importance value contributed by species i (i = 1, 2, 3,…, S), and S is the total number of species in an association. Beta diversity between each pair of associations within and between the study areas was measured with Jaccard coefficient (SI_{ij}), calculated as (Mueller-Dombois & Ellenberg 1974):

$$SI_{ij} = \frac{c_{ij}}{a_i + b_j - c_{ij}} \tag{4}$$

where a_i and b_j are the numbers of species in the associations i and j, respectively; and c_{ij} is the number of species common to both associations i and j. To compare compositional similarities of associations within and between the TWINSPAN groups, a mean coefficient between associations within a TWINSPAN group (for within-group comparison) and a mean coefficient of associations between TWINSPAN groups (for between-group comparison) were calculated using the following formulas:

$$SI_{\mathrm{Mean}} = \begin{cases} \dfrac{2}{n(n-1)} \displaystyle\sum_{i<j}^{n(n-1)/2} SI_{ij} & \text{(for within-group comparison)} \\ \dfrac{1}{n \cdot l} \displaystyle\sum_{j=1}^{n}\sum_{i=1}^{l} SI_{ij} & \text{(for between-group comparison)} \end{cases} \tag{5}$$

where SI_{Mean} is the mean of SI_{ij} which is defined in Eq. (4); n is the number of associations in a group (for within-group comparison), or the number of associations in the first group of a pair under comparison (for between-group comparison); and l is the number of associations in the second group (for between-group comparison).

Mosaic diversity (m; *sensu* Istock & Scheiner 1987) was used to compare diversity patterns at the landscape (regional) level. Mosaic diversity is a function of the mean similarity among sites (i.e. associations in this study) measured using Jaccard coefficient, and the affinity among sites, calculated from their differences in similarity with all other sites. Mosaic diversity is measured as the slope of the line (standardized against the random expectation) of mean affinities plotted against mean similarities for sites in an area (Scheiner 1992):

$$m = r\frac{S_{\overline{AI}}}{S_{\overline{SI}}} \tag{6}$$

where r is the correlation coefficient of mean affinity indices ($\overline{AI}$) and mean similarity indices ($\overline{SI}$), and $S_{\overline{AI}}$ and $S_{\overline{SI}}$ are the standard deviations of mean affinity indices and mean similarity indices, respectively. Scheiner (1992) suggests that "values of $m < 1$ indicate disconnected landscape consisting of groups of sites that are similar within groups but with very little species sharing among groups. Values of m in the range of 1-3 indicate a simple landscape dominated by one or a few gradients. Values of $m > 3$ indicate a complex landscape with either many ecological gradients or no particularly strong gradients."

Species occurrence distribution

Species occurrence frequency distributions were analyzed with a two-way frequency tabulation method (i.e. species occurrence frequency vs. association frequency). Species occurrence frequency in associations was calculated for each species by dividing the number of associations in which a given species was present by the total number of associations in a study area (i.e. divided by 57 for Changbaishan Summit or 63 for Indian Peaks) and then multiplying by 100. Association frequency was calculated by dividing i by n (where i = 1, 2, 3,…, n, and n is the number of associations in a study area), and then multiplying by 100. The association frequencies were grouped into 10 classes (from I - X), each with 10 % in range (e.g. I = 0 - 10 %, II = 11 - 20 %,…, X = 91 - 100 %).

General statistics and computer software

Statistical tests were used to determine the significance of differences in comparisons (*t*-test for pairwise comparison and linear regression coefficient comparison, and the one-way analysis of variance (ANOVA) and Tukey's test for multiple comparison; Zar 1984). The Kolmogorov-Smirnov two-sample test was used to test the significance of the differences between the two study areas in phytogeographical category profiles and species occurrence frequency distribution (Sokal & Rohlf 1981). SYSTAT (Wilkinson et al. 1992) was used for all correlation analyses, statistical tests, and regression analyses. PC-ORD (version 3.0; McCune & Mefford 1997) was used for TWINSPAN classification, and NMDS and CCA ordinations. VTAB (Emanuel 1989) was used for generating a diagnostic species table for the association groups. AA program (Affinity Analysis; Scheiner 1992) was used to determine mosaic diversity for the two study areas. Jaccard coefficients were jackknifed to meet independence of data before statistical tests were conducted (Scheiner 1992).

Results

Comparison of the two alpine tundras at the floristic level

The flora of Indian Peaks is richer than that of Changbaishan Summit in all categories except for bryophyte families and species. Comparisons of the taxonomic richness of Changbaishan Summit vs. Indian Peaks are: 32 vs. 43 families, 87 vs. 122 genera, and 129 vs. 244 species for vascular plants; 37 vs. 35 families, 67 vs. 74 genera, and 128 vs. 118 species for bryophytes; 9 vs. 25 families, 21 vs. 50 genera, and 67 vs. 109 species for lichens.

The phytogeographical profiles of Changbaishan Summit and Indian Peaks do not differ at either the species rank ($D_{max} = 0.06 < D_{.01} = 0.11$) or the generic rank ($D_{max} = 0.05 < D_{.01} = 0.16$). The relative frequency of species found in the three shared phytogeographical categories are virtually identical for the two study areas (69 %; Table 2). The relative rank of these categories in the two areas are also the same, with the circumpolar category containing 48-52 % of the species, followed by the Asian/North American category containing 27-29 %, and then the cosmopolitan category containing 11-17 % (Table 2). At the generic rank, cosmopolitan and circumpolar categories combined contain most of the flora (>90 %) and again, the relative frequencies of genera across the categories are similar in the two areas (Table 2).

Vascular plant species had narrower geographical ranges than bryophyte and lichen species (Table 2). Most of the bryophytes (89-96 %) and lichens (79-93 %) were in the cosmopolitan, circumpolar, and joint (Asian-American) categories. When examined at the generic rank, all of the three taxonomic groups were distributed primarily in the cosmopolitan and circumpolar categories, with circumpolar being more important for vascular plants and cosmopolitan for bryophytes and lichens.

The two study areas had 72 species in common (i.e. 22, 38 and 12 species for vascular plants, bryophytes and lichens, respectively). Changbaishan Summit, with a lower richness (324 species), shared 22 % of its flora with Indian Peaks, which, with a higher richness (471 species), shared 15 % of its flora with Changbaishan Summit. The species overlap between the two study areas was greatest for bryophytes (Fig. 1). Expanding the geographical area of comparison generally resulted in an increase in the number of shared species, with bryophytes exhibiting the greatest amount of overlap (Fig. 1). For Changbaishan Summit, 43 % (139 species) of its flora also occurred in the alpine tundras of western North America, and for Indian Peaks, 22 % (104 species) of its flora in alpine tundras of eastern Asia. Among the total of 723 species found on either Indian Peaks or Changbaishan Summit, 171 species (23 %) were distributed in the alpine areas of both temperate eastern Asia and temperate western North America. Of the 171 species, 94 % also occurred in Beringia - the area of Chukotka (northeasternmost Asia) and Alaska (northwesternmost North America). However, the flora of Indian Peaks was more closely related to the flora of the Arctic than that of Changbaishan Summit, with 66 % of the vascular plants (vs. 49 %), 97 % of the bryophytes (vs. 77 %), and 93 % of the lichens (vs. 64 %) also found in the Arctic (Fig. 1).

Comparison of the two alpine tundras at the community level

The TWINSPAN classified the 120 associations into seven groups at the third division level (Fig. 2). The 57 associations on Changbaishan Summit were completely

Table 2. Relative frequency (%), according to phytogeographical categories (PGC), of the alpine tundra species or genera of Changbaishan Summit (CB) and Indian Peaks (IP). Species numbers of vascular plants (VASC), bryophytes (BRYO) and lichens (LICH) are respectively 129, 128 and 67 in Changbaishan Summit; and are respectively 244, 118 and 109 in Indian Peaks. Genus numbers of vascular plants, bryophytes and lichens are respectively 87, 67 and 21 in Changbaishan Summit, and are respectively 122, 74 and 50 in Indian Peaks. ALL = all plants.

Phytogeographical category (PGC symbol)	Mountain range	PGC symbol	Species VASC	Species BRYO	Species LICH	Species ALL	Genus VASC	Genus BRYO	Genus LICH	Genus ALL
Cosmopolitan (COSM)	CB	COSM	0.0	23.4	37.3	17.0	24.1	73.1	95.2	51.4
	IP	COSM	0.0	18.6	27.5	11.0	23.8	75.7	76.0	50.0
Circumpolar (CIRC)	CB	CIRC	40.3	63.3	31.3	47.5	65.5	22.4	4.8	41.7
	IP	CIRC	34.0	76.3	63.3	51.4	63.1	23.0	24.0	43.1
Asian-North American (ASNA)	CB	ASNA	4.7	2.3	10.5	4.9	3.5	1.5	0.0	2.3
	IP	ASNA	11.1	0.9	1.8	6.4	2.5	0.0	0.0	1.2
Eurasian (EUAS)/Euramerican (EUNA)	CB	EUAS	7.8	0.8	3.0	4.0	5.8	1.5	0.0	3.4
	IP	EUNA	3.3	1.7	2.8	2.8	0.0	0.0	0.0	0.0
Asian (AS)/North American (NA)	CB	AS	47.3	10.2	17.9	26.5	1.2	1.5	0.0	1.1
	IP	NA	51.6	2.5	4.6	28.5	10.7	1.4	0.0	5.7

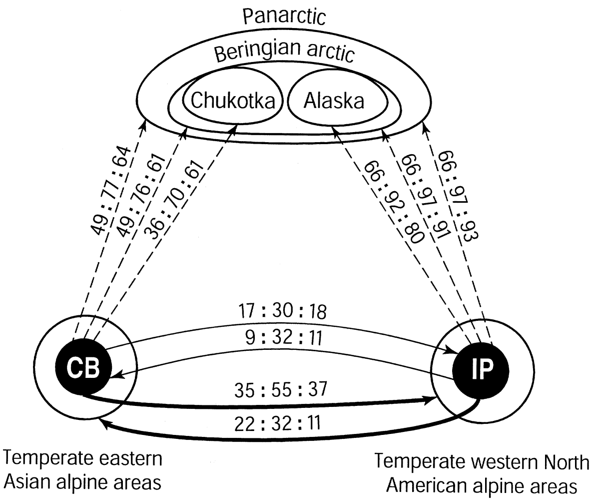

Fig. 1. Comparisons of floristic overlap between (1) the alpine tundras of the two study areas: Changbaishan Summit (CB) and Indian Peaks (IP) (fine line); (2) the alpine tundra of each study area and the alpine tundra areas on the opposite continent (heavy line); and (3) the alpine tundra of each study area and arctic tundras (dashed line). The Beringian arctic, a part of the Panarctic (the entire arctic region of Eurasia and North America) is divided into the Chukotka arctic (northeasternmost Russia) and the Alaskan arctic (Alaska and Yukon in northwesternmost USA and Canada). Values close to a line represent the percentage of shared species out of the total for each study area according to major taxonomic groups of plants (vascular plant : bryophyte : lichen).

separated from the 63 associations on Indian Peaks at the first division (eigenvalue = 0.826). Examination of the diagnostic table (Table 3) suggests that: (1) Indian Peaks had more diagnostic (differential and dominant-differential) species than Changbaishan Summit, and (2) there were very few diagnostic species which could completely separate TWINSPAN groups within each study area.

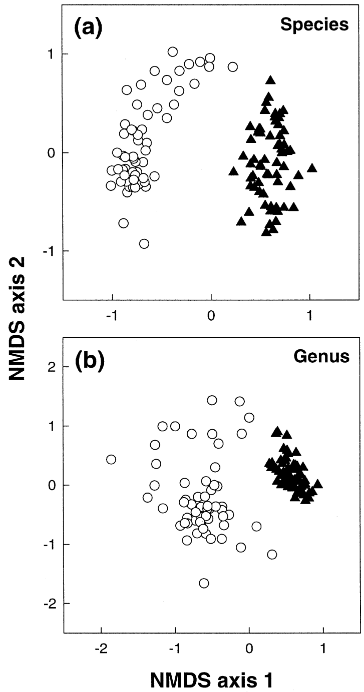

Fig. 3. Non-metric multidimensional scaling (NMDS) ordinations of the 120 associations of Changbaishan Summit (open circles) and Indian Peaks (solid triangles) using presence/absence data of (a) species and (b) genera.

Community structure and soil properties were not, in most cases, statistically different among the TWINSPAN groups within each study area, but were more likely to be significantly different ($P < 0.05$) between the two study areas (Table 4). Total vegetation cover was higher, woody/herbaceous cover and bryophyte/lichen cover tended to be higher, and bryophyte frequency tended to be lower for the TWINSPAN groups of Changbaishan Summit. In general, the TWINSPAN groups of Changbaishan Summit had a soil with higher silt, lower clay,

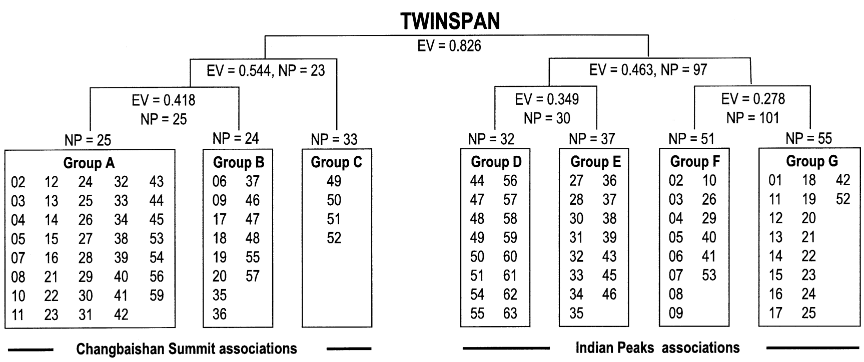

Fig. 2. Seven association groups (A through G) derived by TWINSPAN using the 120 associations in the alpine tundras of Changbaishan Summit and Indian Peaks. Association codes (numbers in boxes) are the same as in the original data sources (Qian 1993 and Komárková 1979). EV = eigenvalue; NP = the number of preferential species.

Table 3. Diagnostic combinations of differential and dominant-differential species for the seven TWINSPAN groups of the associations on Changbaishan Summit (groups A through C) and Indian Peaks (groups D through G). Abbreviations for plant groups are: V = vascular plant, B = bryophyte, and L = lichen. Species presence classes (as percent of frequency) are: I = 1 - 20 %, II = 21 - 40 %, III = 41 - 60 %, IV = 61 - 80 %, and V = 81 - 100 %. Species mean importance value classes are: + = 0.1 - 0.3, 1 = 0.4 - 1.0, 2 = 1.1 - 2.1, 3 = 2.2 - 5.0, 4 = 5.1 - 10.0, 5 = 10.1 - 20.0, 6 = 20.1 - 33.0, 7 = 33.1 - 50.0, 8 = 50.1 - 70.0, and 9 = 70.1 - 100.

Study area and species	Plant group	**Species presence and mean importance value classes by TWINSPAN group**													
		A		B		C		D		E		F		G	
Changbaishan Summit															
Rhodiola sachalinensis	V	**I**	**+**	**III**	**1**	**V**	**3**								
Calamagrostis angustifolia	V	**I**	**+**	**I**	**3**	**III**	**4**								
Carex eleusinoides	V	**I**	**+**	**I**	**4**	**IV**	**+**								
Oxytropis anertii	V	**IV**	**1**	I	+										
Saussurea alpicola	V	**IV**	**2**	I	+										
Vaccinium uliginosum	V	**III**	**4**	I	+										
Lloydia serotina	V	**III**	**+**	I	+	I	+					III	+	IV	1
Tofieldia coccinea	V	**III**	**+**												
Dryas octopetala	V	**IV**	**5**											I	2
Rhytidium rugosum	B	**III**	**5**							I	+				
Cetraria laevigata	L	**IV**	**3**	I	+										
Sanionia uncinata	B	I	3	**IV**	**6**					I	+	I	+	I	+
Fragaria orientalis	V			I	+	**III**	**+**								
Angelica saxatile	V	I	+			**III**	**+**								
Saussurea alpina	V	I	+			**III**	**4**								
Veratrum album	V					**IV**	**3**								
Sanguisorba canadensis	V			II	1	**V**	**7**								
Brachythecium kuroishicum	B					**III**	**1**								
Indian Peaks															
Carex scopulorum	V							**V**	**4**	**IV**	**1**	**II**	**1**	**II**	**+**
Luzula congesta	V							**I**	**+**	**II**	**1**	**V**	**+**	**IV**	**1**
Deschampsia cespitosa	V	I	+	I	+			**III**	**1**	**IV**	**1**	**III**	**+**	**II**	**3**
Festuca brachyphylla	V							**I**	**+**	**II**	**+**	**V**	**1**	**V**	**1**
Poa arctica	V	I	+	II	+			**III**	**+**	**IV**	**3**	**II**	**+**	**I**	**+**
Trisetum spicatum	V	I	+					**I**	**+**	**II**	**+**	**V**	**1**	**IV**	**1**
Polygonum bistortoides	V							**III**	**1**	**III**	**+**	**II**	**1**	**V**	**2**
Geum rossii	V							**II**	**1**	**II**	**+**	**IV**	**1**	**V**	**3**
Artemisia scopulorum	V							**I**	**+**	**II**	**+**	**II**	**1**	**IV**	**2**
Cerastium arvense	V							**I**	**+**	**I**	**+**	**I**	**+**	**III**	**1**
Trifolium parryi	V							**I**	**+**	**I**	**+**	**II**	**1**	**IV**	**3**
Potentilla diversifolia	V							**II**	**+**	**II**	**+**	**I**	**1**	**IV**	**1**
Bryum turbinatum	B							**III**	**1**	**IV**	**1**	**III**	**+**	**I**	**+**
Hypnum revolutum	B							**III**	**+**	**I**	**+**	**V**	**3**	**IV**	**1**
Polytrichum piliferum	B	I	+					**I**	**+**	**III**	**3**	**V**	**3**	**IV**	**1**
Cladonia pyxidata	L							**II**	**+**	**III**	**1**	**V**	**1**	**V**	**1**
Ligusticum tenuifolium	V							**III**	**2**	I	+	I	+	I	+
Sedum rhodanthum	V							**III**	**1**	I	1	I	+	I	+
Caltha leptosepala	V							**IV**	**4**	II	+	I	1	I	+
Warnstorfia exannulata	B							**IV**	**3**	II	3				
Philonotis fontana	B							**IV**	**4**	II	3	II	2		
Brachythecium nelsonii	B							**III**	**2**	I	+	I	+	I	+
Brachythecium turgidum	B							**III**	**+**	I	+	I	+		
Antennaria alpina	V									**III**	**3**	I	+	I	+
Erigeron melanocephalus	V									**IV**	**1**	I	+	I	+
Rorippa alpina	V									**III**	**2**				
Carex pyrenaica	V									**III**	**3**	I	+	I	+
Distichium capillaceum	B											**III**	**+**		
Selaginella densa	V									I	+	I	+	**V**	**1**
Oreoxis alpina	V							I	+			II	+	**IV**	**1**
Achillea millefolium	V							I	+			I	+	**III**	**1**
Antennaria umbrinella	V									I	+	I	+	**IV**	**+**
Erigeron pinnatisectus	V											I	+	**III**	**+**
Solidago simplex	V									I	+	I	+	**III**	**+**
Campanula rotundifolia	V							I	+					**IV**	**+**
Arenaria fendleri	V											I	+	**IV**	**1**
Minuartia obtusiloba	V							II	+			II	1	**V**	**2**
Sedum lanceolatum	V											I	+	**V**	**1**
Carex rupestris	V											II	+	**V**	**3**
Trifolium dasyphyllum	V											I	+	**IV**	**2**
Poa fendleriana	V							I	+					**III**	**+**
Poa glauca	V							I	+			II	+	**IV**	**1**
Phlox pulvinata	V													**III**	**1**
Saxifraga rhomboidea	V							I	+			I	+	**IV**	**+**
Castilleja occidentalis	V											II	+	**IV**	**+**
Encalypta vulgaris	B							I	+			I	+	**III**	**+**
Cetraria aculeata	L							I	+			I	+	**III**	**+**
Peltigera rufescens	L							I	+			II	+	**IV**	**+**
Physconia muscigena	L											II	+	**IV**	**+**
Xanthoparmelia coloradoensis	L	I	+									II	+	**IV**	**+**

Table 4. Means of the selected community structure and soil variables for each of the seven TWINSPAN groups of the associations from Changbaishan Summit and Indian Peaks. A number in parentheses under a TWINSPAN group code indicates the number of associations in that TWINSPAN group. Different superscript letters on the same row within the same study area indicate significant differences between the TWINSPAN groups of that area (Tukey multiple comparison tests; $P < 0.05$). *P*-values in the last column are the probabilities from *t*-test for the significance of differences in each pair of two means between Changbaishan Summit and Indian Peaks regardless of the TWINSPAN groups.

Community structure and soil variable	Variable code	Changbaishan Summit A (39)	B (14)	C (4)	Indian Peaks D (16)	E (15)	F (14)	G (18)	*P*-value
Community structure									
Total vegetation cover (%)	COVTOT	91.10^{a}	90.57^{a}	92.00^{a}	89.44^{a}	67.53^{b}	55.71^{b}	72.89^{ab}	< 0.001
Woody/herbaceous cover (%)	COVWH	61.82^{a}	69.96^{a}	87.50^{a}	71.94^{a}	39.47^{b}	40.07^{b}	67.28^{a}	0.080
Bryophyte/lichen cover (%)	COVBL	70.55^{a}	46.36^{a}	32.88^{a}	19.13^{a}	29.60^{a}	16.29^{a}	5.61^{b}	< 0.001
Vascular plant frequency (%)	FREQV	67.40^{a}	67.39^{a}	76.33^{a}	63.63^{a}	62.28^{a}	58.89^{a}	68.75^{a}	0.078
Bryophyte frequency (%)	FREQB	19.12^{a}	25.15^{a}	23.67^{a}	34.91^{a}	31.47^{a}	27.81^{a}	14.90^{b}	0.008
Lichen frequency (%)	FREQL	13.48^{a}	7.46^{ab}	0.00^{b}	1.46^{a}	6.25^{a}	13.30^{b}	16.35^{b}	0.370
Soil variables									
Sand (%)	SAND	62.62^{a}	57.22^{a}	48.18^{a}	38.35^{a}	68.71^{b}	67.52^{b}	64.40^{b}	0.834
Silt (%)	SILT	30.15^{a}	34.46^{a}	41.26^{a}	38.61^{a}	20.78^{b}	23.25^{b}	23.34^{b}	0.044
Clay (%)	CLAY	7.31^{a}	8.37^{a}	10.57^{a}	23.04^{a}	10.51^{b}	9.23^{b}	12.26^{b}	< 0.001
pH	pH	5.68^{a}	5.66^{a}	5.30^{a}	5.24^{a}	5.37^{a}	5.46^{a}	5.43^{a}	0.003
Organic matter content (%)	ORGMAT	8.28^{a}	7.32^{a}	5.44^{a}	20.84^{a}	6.27^{b}	8.01^{b}	11.29^{ab}	0.032
Exchangeable Ca (meq/100g)	Ca	4.30^{a}	3.71^{a}	4.50^{a}	5.51^{a}	1.96^{a}	2.14^{a}	4.47^{a}	0.395
Exchangeable Mg (meq/100g)	Mg	0.97^{a}	1.96^{b}	1.36^{ab}	0.49^{a}	0.17^{a}	0.30^{a}	0.59^{a}	< 0.001
Cation exchange capacity (meq/100g)	CEC	14.00^{a}	17.87^{a}	15.15^{a}	9.01^{a}	4.18^{b}	4.61^{b}	7.77^{ab}	< 0.001
Base saturation (%)	BASESAT	49.09^{a}	51.25^{a}	47.27^{a}	65.38^{a}	48.03^{a}	58.12^{a}	55.72^{a}	0.092

and higher cation exchange capacity, and tended to be lower in organic matter content and higher in exchangeable Mg.

NMDS ordinations of the 120 associations completely separated the associations of Changbaishan Summit from those of Indian Peaks on the first NMDS axis at both species and generic ranks (Fig. 3). When NMDS was run on soil data, the associations of the two areas were interspersed, though with some tendency to segregate (ordination not shown). About 63 % and 80 % of the lengths of the first and second NMDS axes, respectively, were occupied by associations from both study areas.

Three-dimensional ordination diagrams generated from NMDS for each study area (based on species importance values) showed that the TWINSPAN groups within each study area were relatively well differentiated (Fig. 4a, b). For the associations of Changbaishan Summit, for example, the group C was completely separated from groups A and B, which were in turn largely separated from each other, on the ordination facet of axes 1 vs. 3 (Fig. 4a). Similarly, the associations of different TWINSPAN groups of Indian Peaks were also mostly separated with one another. For instance, the groups D, E and G were almost completely separated from one another on the ordination facet of axes 2 vs. 3 (Fig. 4b), and most of the associations in group F were separated from the associations of the other three groups on the ordination facets of axes 1 vs. 3 and of axes 2 vs. 3 (Fig. 4b). However, with soil data being used in the NMDS ordination, the TWINSPAN groups were mixed with one another for both study areas (Fig. 4c, d).

In the CCA ordination with Changbaishan Summit data, the total inertia (sum of all eigenvalues) was 23.8. The fraction of variance explained was 14.4 % for the first axis and 12.9 % for the second axis. In the CCA ordination with Indian Peaks data, the total inertia was 33.8. The fraction of variance explained was 12.2 % for the first axis and 11 % for the second axis. For both areas, pH and Ca were the variables with the two strongest correlations with the first CCA axis; for both areas, silt and sand were the two variables with the strongest correlation with the second CCA axis (Table 5; Fig. 5).

Compositional ratio of major taxonomic groups

The pattern in compositional ratio of the three major taxonomic groups was shown in triangular ordination diagrams (Fig. 6). When the species presence/absence data were used, all of the 120 associations clustered in a triangular space with more than 20 % of vascular plants, less than 60 % of bryophytes, and less than 40 % of lichens (Fig. 6a), with no substantial difference between Changbaishan Summit and Indian Peaks in the proportional contributions of the three groups. All the associations of group C and most associations of group D had a lichen proportion of 0 %, while group G tended to occupy a space with lower proportion of bryophytes (Fig. 6a;

Table 5. Canonical coefficient and inter-set correlation of environmental variables (plant community structure and soil properties) for the first two (species) axes of CCA for Changbaishan Summit (CB) and Indian Peaks (IP). Full names for the environmental variables are given in Table 4.

Environmental variables	Canonical coefficient				Inter-set correlation			
	CB		IP		CB		IP	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
COVTOT	– 0.137	– 0.018	– 0.826	– 0.552	0.068	– 0.174	0.202	0.220
COVWH	0.127	– 0.529	0.999	0.893	– 0.129	– 0.700	– 0.079	0.527
COVBL	0.362	0.014	1.083	0.243	0.225	0.184	0.341	– 0.500
Sand	0.886	1.375	0.454	– 1.077	– 0.152	– 0.338	– 0.272	– 0.681
Silt	1.104	1.661	0.290	– 0.287	0.193	0.433	0.246	0.617
pH	1.471	– 0.302	1.352	– 0.343	0.549	– 0.142	0.725	0.416
ORGMAT	0.135	0.247	0.149	– 0.314	– 0.214	0.285	0.018	– 0.046
Ca	– 0.392	0.294	0.526	– 0.807	– 0.268	– 0.091	0.288	0.462
Mg	– 0.024	0.697	0.081	0.160	– 0.031	0.060	0.159	0.272
CEC	– 0.689	– 0.603	– 1.018	0.388	– 0.008	– 0.024	0.186	0.472
BASESAT	0.271	– 0.731	– 0.149	1.016	– 0.181	– 0.227	0.261	0.448

Table 4). When the species importance values were used, 94 % of the associations were located in a zone with lichens less than 20 % and bryophytes and vascular plants ranging from 0 to 100 % (Fig. 6b). The associations of Changbaishan Summit tended to have a higher percentage of bryophytes than those of Indian Peaks.

Ecological diversity

Diversity (Shannon-Wiener's index; *H*') was, on average, significantly lower ($P < 0.001$) for the associations of Changbaishan Summit (1.24 ± 0.08 SE) than for those of Indian Peaks (1.87 ± 0.09 SE).

Comparisons of the TWINSPAN groups in beta diversity (Jaccard coefficient) revealed several patterns (Table 6). For example, mean Jaccard coefficients between associations within each TWINSPAN group were lower for the groups of Changbaishan Summit than for the groups of Indian Peaks. This indicates that the beta diversity of the TWINSPAN groups was higher for Changbaishan Summit than for Indian Peaks.

Mosaic diversity in the plant communities of Changbaishan Summit and Indian Peaks was 3.85 and 4.02 (slopes of lines in Fig. 7), respectively. After being jackknifed, mosaic diversity (± 1 s.d.) was 3.85 ± 0.04 and 4.03 ± 0.03, respectively, for Changbaishan

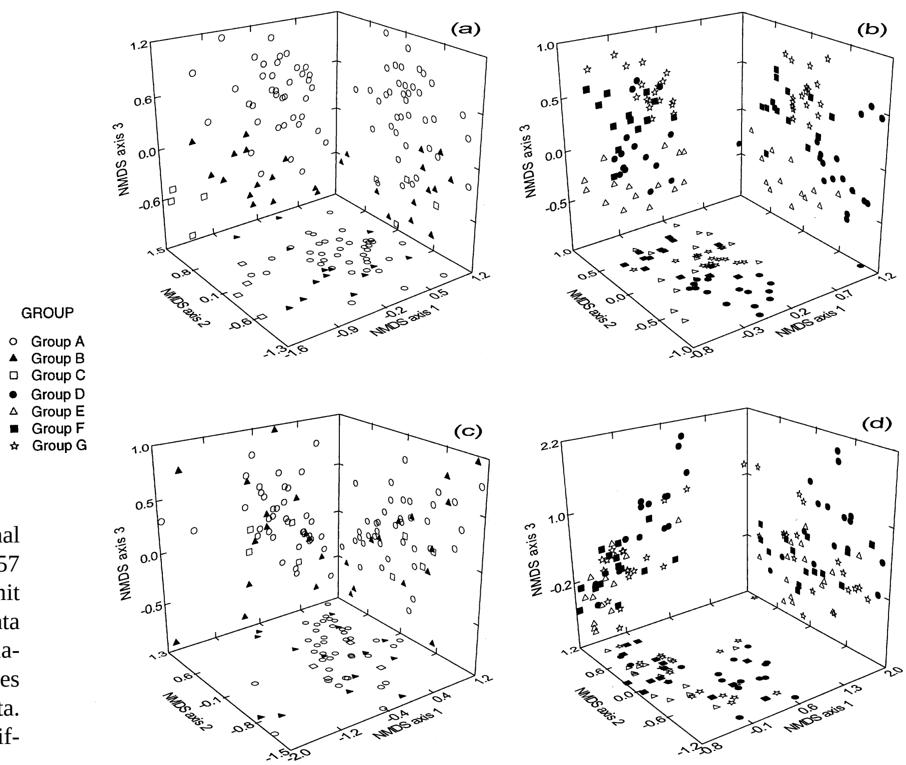

Fig. 4. Non-metric multidimensional scaling (NMDS) ordinations of the 57 associations of Changbaishan Summit using (a) species importance value data and (c) soil data; and of the 63 associations of Indian Peaks using (b) species importance value data and (d) soil data. The seven TWINSPAN groups are differentiated by symbols.

Table 6. Means of Jaccard (similarity) coefficients for the within and between TWINSPAN group comparisons using the 120 associations from Changbaishan Summit and Indian Peaks. The total number of pairwise comparisons between associations is 7140. Numbers in boldface are the largest means in each row and/or each column.

Group A	**0.181**						
Group B	0.071	**0.100**					
Group C	0.020	0.053	**0.112**				
Group D	0.009	0.012	0.005	**0.193**			
Group E	0.013	0.023	0.007	0.164	**0.291**		
Group F	0.015	0.015	0.004	0.102	0.180	**0.242**	
Group G	0.014	0.009	0.001	0.081	0.131	0.214	**0.321**
	A	B	C	D	E	F	G
	Changbaishan Summit			Indian Peaks			

Summit and Indian Peaks. The fact that the two lines in Fig. 7 tended to be parallel suggests that the mosaic diversities of the two study areas did not differ (t = 1.937, $t_{0.05(2),116}$ = 1.981, P > 0.05). However, for a given mean affinity value, Indian Peaks had a higher mean similarity than Changbaishan Summit (Fig. 7). The identical mosaic diversities of Changbaishan Summit and Indian Peaks suggests that the two study areas have the same number of underlying gradients, but the Changbaishan Summit communities, with lower mean similarity, lie further apart on the gradients (S. M. Scheiner pers. comm.).

Ecological amplitude

Species occurrence frequencies (%) across the 10 association frequency classes (ordered from I - X) were 67.8, 16.9, 9.0, 2.8, 1.7, 1.1, 0.6, 0.0, 0.0 and 0.0 for Changbaishan Summit, and are 50.6, 21.8, 10.5, 8.8, 3.9, 2.1, 1.8, 0.5, 0.0 and 0.0 for Indian Peaks. Comparisons of Changbaishan Summit and Indian Peaks showed that their species occurrence frequency distributions were in two significantly different profiles (P < 0.01; Kolmogorov-Smirnov test). The frequency profile for Changbaishan Summit had a greater proportion of species with narrow ecological amplitude (i.e. occurring in a small number of associations) than with wide ecological amplitude (i.e. widespread or common in a large number of associations). Forty-three percent of the Changbaishan Summit species in class I occur in one association, while, in contrast, only 26 % of the Indian Peaks species in the same class occur in one association.

Discussion

Despite generally similar environments and strong floristic relationships, Changbaishan Summit and Indian Peaks differed in significant ways in plant diversity and their floristic relationships with the Arctic flora. With the overall floras of the two areas being compared, Indian Peaks had 1.5 and 1.4 times as many species and genera,

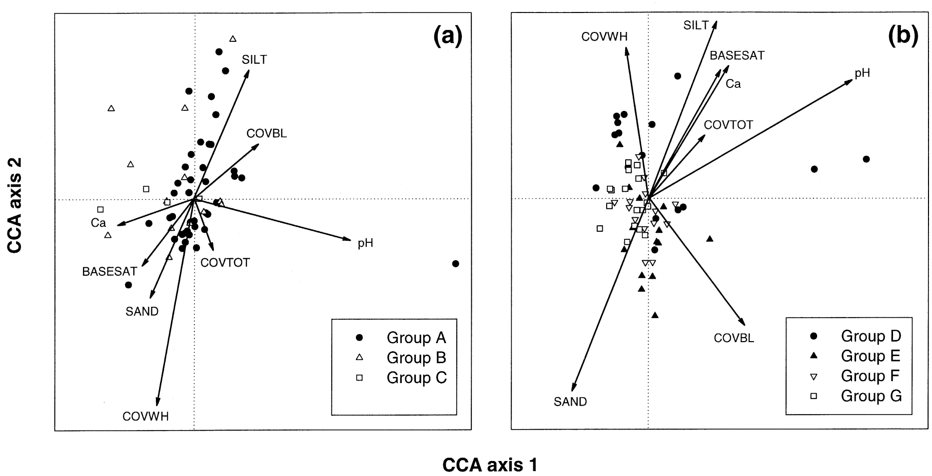

Fig. 5. Biplots of canonical correspondence analysis (CCA) ordinations of (a) the 57 associations from Changbaishan Summit, and (b) the 63 associations from Indian Peaks, using important value data in relation to three community structure and eight soil variables (abbreviations as in Table 4). Community structure and soil variables are plotted at a scale factor of 6. The seven TWINSPAN groups are differentiated by symbols.

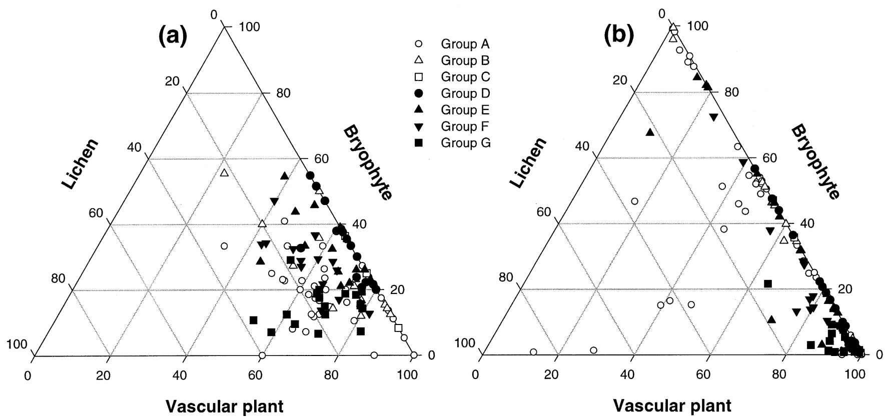

Fig. 6. Triangular ordination of the 120 associations from Changbaishan Summit and Indian Peaks according to the relative frequency (%) of the three major taxonomic groups (vascular plants, bryophytes, and lichens) using (a) species floristic (presence/absence) composition data and (b) species importance value data. The seven TWINSPAN groups are differentiated by symbols.

respectively, as Changbaishan Summit. At the community level, Indian Peaks had a higher Shanon-Wiener index than Changbaishan Summit. Furthermore, the results of similarity analysis, NMDS ordinations, affinity analysis, mosaic diversity, and species occurrence frequency analysis all showed higher similarity in species composition among plant communities on Indian Peaks than on Changbaishan Summit. The mosaic diversity analysis also showed that Changbaishan communities were more widely spaced on gradients and frequency analysis showed that Changbaishan species had lower ecological amplitudes, compared to Indian Peaks. These results suggest higher beta diversity on Changbaishan Summit than on Indian Peaks. With respect to the floristic relationship with the Arctic flora, Indian Peaks had a stronger relationship than did Changbaishan Summit. The causes of the differences include environmental differences, volcanic eruption, and glacial history.

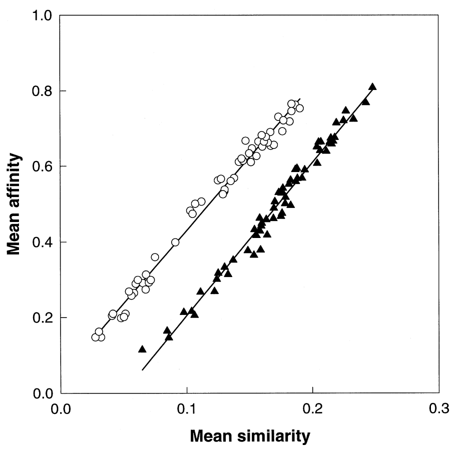

Fig. 7. Affinity analysis graph showing mosaic diversities (m, the slope of fitted line) of Changbaishan Summit (open circles, $m = 3.85$) and Indian Peaks (solid triangles, $m = 4.02$).

Although the two areas are comparable in terms of total area, the areas that can support plant growth and community establishment are not. One third of Changbaishan Summit is surfaced with a volcanic pumice-ash layer, where the vegetation cover usually is less than 0.5%. While it has been 1592 ± 177 yr since the last devastating eruption, we believe a greater time span is required for flora and plant community recovery, because of the environmental severity (strong winds and periglacial processes), slow growth rate of alpine plant species (annual ring width being 0.07 ± 0.02 mm for *Dryas octopetala* var. *asiatica*; Qian 1989a), and slow colonization rate due to isolation (see below).

Results from this study and others (e.g. Zhu & Rowe 1987; Qian 1989a, 1990a, 1992, 1993; Qian & Gao 1990) have shown that the alpine tundra floras and ecosystems in mid-latitude eastern Asia and western North America are related, and have high affinities to the Arctic tundra. Of the two study areas, Indian Peaks showed a greater floristic relationship with the Arctic. In terms of distance, Indian Peaks is actually further away from the arctic region than Changbaishan Summit. However, in terms of topographic barriers, Indian Peaks has a mountain range configuration that has probably been far more conducive to the north-south migration of plants. In eastern Asia, most of the mid-latitude mountain ranges generally run in an east-west orientation. For example, the mountain ranges in Northeast China (including Changbaishan Mountain Range) are separated from the mountain ranges farther north by the Manchurian Plain and the Amur River valley (Zhu & Rowe 1987). Under this configuration, the warmer climates of the valley bottoms serve as a barrier to the migration of plants between alpine areas. In contrast, the mountain ranges of western North America generally run in a north-south orientation, making plant migration along the north-south axis possible during much of glacial and post-glacial time.

In addition, the two areas have different histories of glacial development. During the last glacial maximum (18 000 yr ago), the Cordilleran ice sheet extended from Alaska through British Columbia to its southernmost margin in northern Washington, Idaho and Montana (about 45 - 46° N latitude; Ritchie 1987). As the glacial margin moved southward, tundra vegetation moved southward as well. At the same time, alpine tundra moved to lower elevations and the two floras came to occupy the same areas (Delcourt & Delcourt 1993). In contrast, there was no glaciation in eastern Asia except for a few isolated glacial areas in Siberia north of 60 °N. Because of the lack of glacial advance and retreat in much of eastern Asia, the interchanging of floristic components between alpine tundras and the Arctic tundra would presumably be much lower in eastern Asia than in western North America. Our data support this conclusion.

94 percent of the vascular plants, bryophytes, and lichens which are common to the eastern Asian and western North American alpine floras and are present on Changbaishan Summit and/or Indian Peaks, also occur in Beringia. Several of these species, such as *Salix rotundifolia* and one vascular plant genus, i.e. *Therorhodion*, are restricted to Beringia and the alpine areas close to the coast of the North Pacific Ocean. They are primarily amphi-Beringian floristic elements.

27 percent of vascular plants and 8.3 % of bryophytes common to Changbaishan Summit and Beringia are absent from the Asian side of Beringia; and 5.3 % of bryophytes and 12.1 % of lichens common to Indian Peaks and Beringia occur only on the Asian side of Beringia. These species may have been distributed on both sides of Beringia but have since become extinct from one of the two Beringian sides. It is also possible that some of these species migrated from Asia to North America, or vice versa, using only the southernmost portion of the Bering land bridge (Yurtsev 1974) or the Commander-Aleutian chain (Yurtsev 1984), which linked southern Kamtchatka and southern Alaska. These species might have never had direct connections to the Arctic regions, but have had access to alpine areas of opposite continents.

Both Changbaishan Summit and Indian Peaks have much lower relative frequencies (< 4 %) in the Eurasian and Euramerican phytogeographical categories than in cosmopolitan, circumpolar, and Asian-North American categories (69 %). A similar pattern has also been found in the Beringian arctic. For example, Komárková (1993) reported that 45 % of vascular plant taxa at Atkasook (170 km^2, on the north slope of the Brooks Range of Alaska) are circumpolar, 42 % are Asian-North American, 12 % are North American, and only 0.4 % are Euramerican. This pattern suggests that the floristic exchange between the alpine floras of eastern Asia and Europe, or between western North America and Europe, seldom occurred unless complete circumpolar exchange was also possible.

While we have argued that the alpine tundra floras of eastern Asia and western North America reflect past connections, the floras have also developed during periods of isolation. This is particularly true for vascular plants. Roughly half of vascular plants on Changbaishan Summit (47 %) and Indian Peaks (52 %) are limited to their respective continents, and many of them are eastern Asian or western North American alpine endemics. For example, *Aconitum monanthum*, *Cerastium baischanense*, *Salix polyadenia*, *Cardamine baishanensis*, *Geranium paishanense*, *Coelopleurum nakaianum*, *C. saxatile*, and *Gymnomitrion uncrenulatum* are the eastern Asian alpine endemics almost entirely restricted to the alpine areas of the Changbaishan Mountain Range, while *Angelica grayi*, *Arenaria fendleri*, *Besseya alpina*, *Carex perglobosa*, *Chionophila jamesii*, *Gentianopsis barbellata*, *Oreoxis alpina*, and *Primula angustifolia* are western North American alpine endemics restricted to the southern Rocky Mountains. The evidences of the independent development of the eastern Asian and western North American floras have been also shown in forests, especially the treeline forests adjacent to alpine or arctic tundra zones. There are no coniferous tree species shared by the two continents (Lausi & Nimis 1985) and the treeline species on either side of the North Pacific Ocean are different. The arctic-boreal treeline forests of eastern Asia and western North America probably did not form a continuous belt during the Pleistocene (Lausi & Nimis 1985; Qian 1993), although the Bering land bridge was more than 1000 km wide at that time (Yurtsev 1974).

In contrast, the arctic floras of northeasternmost Asia and northwesternmost North America are very similar. About 83 % of Chukotkan vascular plant species have been found in Alaska and about 72 % of Alaskan vascular plant species have also been found in Chukotka (Qian 1993). At a smaller geographical scale, the percentage of the shared species can be higher. For example, 78 % of vascular plant taxa in Arrigetch Peaks (200 km^2, in central Brooks Range of Alaska; Cooper 1989) and 88 % of vascular plant species in Atkasook (Komárková 1993) in the arctic region of northwestern North America are also present in the arctic region of northeastern Asia. The similarities in vegetation and floras of Chukotka and Alaska are so high that phytogeographers (e.g. Meusel et al. 1965; Hultén 1973; Aleksandrova 1980; but see Yurtsev 1994) recognize Chukotka and Alaska as a single amphi-Beringian province. The current discontinuity of the floristic province has lasted since the Bering land bridge was broken up about 10 000 yr ago (Hultén 1968).

In general, Changbaishan Summit has more woody plants and a higher vegetation cover (on areas which have not been severely damaged by volcanic eruptions) than Indian Peaks. The lower vegetation cover in the plant communities of Indian Peaks is partly due to the scattering of vegetation amongst boulders – a considerable portion of Indian Peaks is covered by Pleistocene and Holocene deposits (Komárková 1979). With respect to vegetation composition, it is believed that regional climate plays a major role in determining whether woody or herbaceous plants dominate. The stable vegetation on Changbaishan Summit is dominated by dwarf woody species especially ericaceous plants in the low-alpine subzone, and codominated by dwarf woody plants, herbaceous plants, and bryophytes in the high-alpine subzone. On Indian Peaks, the dominant vegetation is alpine meadows/grasslands dominated by *Kobresia* spp., *Carex* spp., or other herbaceous species (Komárková 1981). The fact that the plant communities dominated by dwarf woody plants such as ericaceous species are also present in alpine zones of coastal mountains in western North America (such as coastal British Columbia; Archer 1963) as well as some mountain ranges in Europe (Dahl 1956), and that the plant communities dominated by *Kobresia* are also present in Altai Mountains (Kuminova 1960) as well as many mountains in Siberia (see Kuvaev 1960; Malyshev 1965, 1976; Krasnoborov 1976), suggests that the major differences in vegetation features between Changbaishan Summit and Indian Peaks are a result of regional climate, rather than of a separation of continents.

Although both Changbaishan Summit and Indian Peaks have relatively high annual precipitation, the growing season precipitation (June to September) is much higher on Changbaishan Summit than on Indian Peaks (72 % vs. 24 % of annual precipitation). In general, higher precipitation in the growing season favors the development of alpine vegetation dominated by woody plants.

The two areas overlap more in soil properties than in floristic compositions of vegetation. Further, the same soil variables emerge in both areas as strongly correlated with ordination results: pH, Ca, and soil texture. The differences in soil properties between the two areas are presumably the result of differences in soil development and parent material. The soils on Changbaishan Summit have developed from volcanic materials deposited mainly during Tertiary and Quaternary times in a climate with wetter summers (Qian 1989a), while the soils on Indian Peaks have developed from postglacial deposits in a climate with drier summers. The differences in soil properties between Changbaishan Summit and Indian Peaks were at least in part responsible for the differences in plant diversity between the two areas.

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