POLIBOTÁNICA
Núm. 24, pp. 25-51, ISSN 1405-2768; México, 2007

A COMPARATIVE STUDY OF THE FLORAS OF CHINA AND CANADA

Zhiyao Su
College of Forestry, South China Agricultural University, Guangzhou 510642 - P. R. China

J. Hugo Cota-Sánchez
Department of Biology, University of Saskatchewan, Saskatoon, SK S7N 5E2 - Canada
E-mail: hugo.cota@usask.ca

ABSTRACT

In this study, we investigated the floristic relationships between China and Canada based on comparative analysis of their spermatophyte floras. Floristic lists were compiled from standard floras and then subjected to cluster analysis using UPGMA and NMS ordination methods. Our data demonstrate that the Chinese spermatophyte flora is considerably more diverse than that of Canada and that the taxonomic richness of seed plants in the floras of China and Canada shows significant variation at the specific and generic levels. China contains 272 families, 3 318 genera, and 27 078 species (after taxonomic standardization), whereas the spermatophyte flora of Canada includes 145 families, 947 genera, and 4 616 species. The results indicate that out of 553 genera shared by the Chinese and Canadian floras, 60 of them have an eastern Asia-North American disjunct distributional pattern. These disjunct genera show a similar geographic distribution in both eastern and western Canada. There is a higher degree of similarity at higher taxonomic levels between the two intercontinental floras, which suggests ancient floristic relationships, but there are significant differences at the generic and specific levels that are correlated with more recent geological and climatic variations and ecoenvironment diversity, resulting in differences in floristic composition. Overall, western and eastern Canada have a similar number of shared genera, which suggests multiple migration events of floristic elements via the Atlantic and Pacific connections and corridors that existed in past geological times.

Keywords: China, Canada, floristic relationships, taxonomic richness, shared taxa, intercontinental disjunction.

RESUMEN

En este estudio se investigaron la relaciones florísticas entre Canadá y China basados en análisis comparativos de las floras de espermatofitas de ambos países. Los listados florísticos se compilaron de una extensa revisión de literatura con respecto a inventarios florísticos, floras y trabajos relacionados a la fitogeografía y vegetación de China y Canadá. Esto incluyó también varios sitios de Internet que contienen información referente a este tema. La riqueza florística en las diferentes regiones políticas de China y

Canadá se obtuvo a partir de una serie de hipótesis nulas usando *G*-test, con las cuales se evaluaron las diferencias taxonómicas a niveles ordinales, genéricos y específicos. Las listas florísticas se organizaron en taxa compartidos en las diferentes categorías taxonómicas entre ambos países y se tabularon en una matriz de datos binaria.

Posteriormente, después de estandarizar los aspectos nomenclaturales, los datos se sometieron a análisis de UPGMA (Unweighted Pair-Group Method with Arithmetic Mean) y NMS (non-metric multidimensional scaling) para estimar y comparar los índices de similitud florística entre estos países.

Nuestros resultados indican que la flora espermatofita de China es mucho más diversa que la flora canadiense. Además, la riqueza taxonómica de estas floras exhibe diferencias significativas a niveles específicos y genéricos. La flora de China es aproximadamente seis veces más rica que su contraparte canadiense. China incluye 272 familias, 3 318 géneros, y 27 078 especies, mientras que la flora de Canadá abarca 145 familias, 947 géneros y 4 616 especies. Estas estadísticas representan una contribución a nivel mundial estimada en 12% para China y 1.4-1.5% de Canadá. Asimismo, el número de géneros distribuidos en ambos países es de 533. Este número representa un valor estimado de 5.4 veces más elevado en la cantidad de especies en la flora de China (12 967) comparada con 2 384 en Canadá. En general, existen 123 taxa que exhiben distribución disjunta entre China y Canadá. Las provincias de la región este de Canadá comparten un número de especies más alta con China, y por lo tanto tienen mayor grado de afinidad florística, comparadas con las provincias del lado oeste del país. Consideramos que cuatro factores principales han contribuido a las diferencias florísticas entre China y Canadá. Éstos son: clima, migración de especies de regiones circunvecinas, stasis, y efectos de refugio.

A pesar de que la diferencia en extensión territorial entre China y Canadá no es extremadamente marcada, la diversidad en relieve topográfico y tipos climáticos de China han favorecido la existencia de una gran variedad de regiones ecogeográficas y ambientales en ese país. Estas variables han contribuido a la formación de patrones de vegetación geográficos de distribución y composición taxonómicas más complejas. En general, la diversidad taxonómica, composición florística y regiones fitogeográficas de Canadá son mucho más simples que aquellas existentes en ese país oriental. De hecho, China es el único país del mundo donde aún existe una conexión continua entre los bosques tropicales, subtropicales, templados y boreales. De la misma manera, las floras adyacentes del centro, norte y sur de Asia tienen gran influencia en la composición florística de China dado que eventos migratorios pasados y presentes han permitido el intercambio de elementos florísticos, divergencia de especies y casos de especiación. A su vez, stasis ha tenido un papel importante en los complejos procesos de especiación y diversidad de especies, es decir, que los niveles taxonómicos más altos representan los linajes filogenéticos más ancestrales. Finalmente, la noción de áreas de refugio también han contribuido en los niveles de diversidad y diferencias taxonómicas así como la existencia de especies actuales poco comunes pero con distribución disjunta. Esto a su vez sugiere que la ruta migratoria florística de elementos a través del Estrecho de Bering contribuyó significativamente a la distribución de especies en ambos países. En conclusión, nuestro

estudio confirma que un buen número de especies comunes entre China y Canadá tienen distribución vicariante o disjunta y comparten historia biogeográfica como resultado de eventos geológicos pasados, y que las floras de estos países han evolucionado independientemente a consecuencia de aislamiento geográfico y factores climáticos y geológicos, entre otros.

Palabras claves: China, Canadá, relaciones florísticas, riqueza taxonómica, taxa compartidos, disjunción intercontinental.

INTRODUCTION

The study of the floristic relationships between eastern Asia and North America is an example of long-standing research focusing on biogeograpical floristic affinities and intercontinental disjunctions. According to Wood (1972), the eastern Asia North American floristic relationships were first mentioned by Linnaeus in 1750 and later in a series of publications between 1840 and 1878 by Asa Gray, who brought this topic to the attention of other American and European scientists. More recently, a number of sources (Li, 1952; Boufford and Spongberg, 1983; White, 1983; Wu, 1983; Tiffney, 1985; Guo *et al.*, 1998; Xiang *et al.*, 1998; Qian, 1999, 2001) have provided evidence that the two floras have similarities in taxonomic diversity and geographic distribution patterns.

The occurrence of intercontinental disjunction in plants stands as one of the most intriguing circumstances regarding the floristic relationships between eastern Asia and North America. In fact, the distributional pattern and affinities of the North American and eastern Asia floristic elements has been explained from biogeographical (Raven, 1972; Wood, 1972), ecological (Ricklefs and Latham, 1992;), geological (Wu, 1983), and phylogenetic (Wen and Stuessy, 1993; Xiang *et al.*, 1998) perspectives. The temperate floristic elements exhibiting intercontinental disjunct distribution are considered Tertiary relicts that were once widely distributed across Laurasia (Li, 1952; Wolfe and Leopold, 1967; Xiang *et al.*, 1998). Other references (Kruckeberg, 1983; Wu, 1983, 1991; Ricklefs and Latham, 1992; Wen, 1999) have focused on compiling taxonomic lists of species with disjunct distribution in eastern Asia and North America, particularly China and the United States.

In order to address the floristic relationship of eastern Asia and North America, previous studies (Cheng, 1983; Hou, 1983; Hsu, 1983; Wu, 1983; Ying, 1983; Xiang *et al.*, 1998; Qian, 1999) have compared the flora of China with that of the United States as representative elements of eastern Asia and North America, respectively. The geographical and environmental similarities and the remarkable interest in plant disjunctions between China and the United States have justified such comparisons (Qian, 1999). In spite of the progress made in understanding the intercontinental disjunctions between eastern Asia and North America, additional floristic and monographic work is needed to complete a catalogue of species. The Flora of China project is an ongoing collaborative study with completion estimated in 2010 (reviewed in Heywood, 2001; see also Flora of China Website available at: http://flora. huh. harvard.edu/china/).

The flora of Canada, on the other hand, has received relatively little attention despite the historical floristic migrations and extant examples of disjunt species mediated by past hypothetical land bridges between northern North America and Eurasia across the Atlantic and the Pacific Oceans. In general, the Canadian flora is diverse due to topographic variation and a wide range of ecoregions with particular climatic and environmental conditions. Canada's plant biodiversity is primarily found in the wet west coast temperate forests, the warmer temperate broad-leaf forests in southern Ontario, the central deserts and grasslands, the tundra plains, and the northern arctic plains (Scoggan, 1978).

In order to investigate plant disjunct patterns, we have undertaken this study to address issues concerning the taxonomic richness, distribution, and floristic relationships between the extant spermatophyte floras of China and Canada. The objectives of this research include 1) to compare the floristic richness of the Chinese and Canadian floras and to determine the dominant plant groups or families in these areas, 2) to establish a correlation of the affinity of Canadian and Chinese plants distributed in similar phytogeographical areas, and 3) to provide a taxonomic list of elements shared between the two floras.

MATERIAL AND METHODS

Our study is primarily based on a compilation of published data. We conducted extensive literature research to compile information and provide data regarding species composition, taxonomic richness, distribution, and affinities between the Chinese and Canadian spermatophyte floras. Our searches included library and on-line references. The floristic data were tabulated in three Microsoft Access datasheets: 1) the China taxa datasheet, 2) the Canada taxa datasheet, and 3) the shared genera datasheet. In addition to data matrices produced from these datasheets, we used Microsoft Access utilities to generate a series of queries, such as sorting and filtering. Data sources for tabulation were mainly from published literature, including national and provincial floras, as well as floristic checklists and monographs. The main sources for the flora in China included the Institute of Botany of the Chinese Academy of Sciences (1987), the Flora of China (FOC) project (Wu and Raven, 1994) web site, Flora of Taiwan Editorial Board (1979), Hou (1986), and Wu (1991). Once the taxonomic tabulation was completed, the scientific name distribution of some dubious Chinese genera was verified using the FOC.

Checklists and web sites available at http://mobot.mobot.org/W3T/Search/FOC/projs-foc.html. The primary data sources for the Canadian flora included Scoggan (1957, 1978), Baldwin (1958), Erskine (1960), Roland and Smith (1969), Porsild and Cody (1980), Moss (1983), Looman and Best (1987), Douglas *et al.* (1989-1991), Cody (1996), and Hinds (1999).

For standardization purposes the taxonomy used in this study follows that of Mabberley (1998) at the generic level and Kubitzki's proposed modifications to Cronquist's 1981 system (listed in Mabberley 1998, pp. 771-781) for higher taxa. Other bibliographic sources, such as Hou (1986) and Kartesz (1994), were consulted to confirm questionable taxa. Our floristic databases also include the family names as proposed by the Angiosperm Phylogeny Group (APG, 1998; also see Judd, *et al.*, 2002), reflecting the most recent phylogenetic scheme.

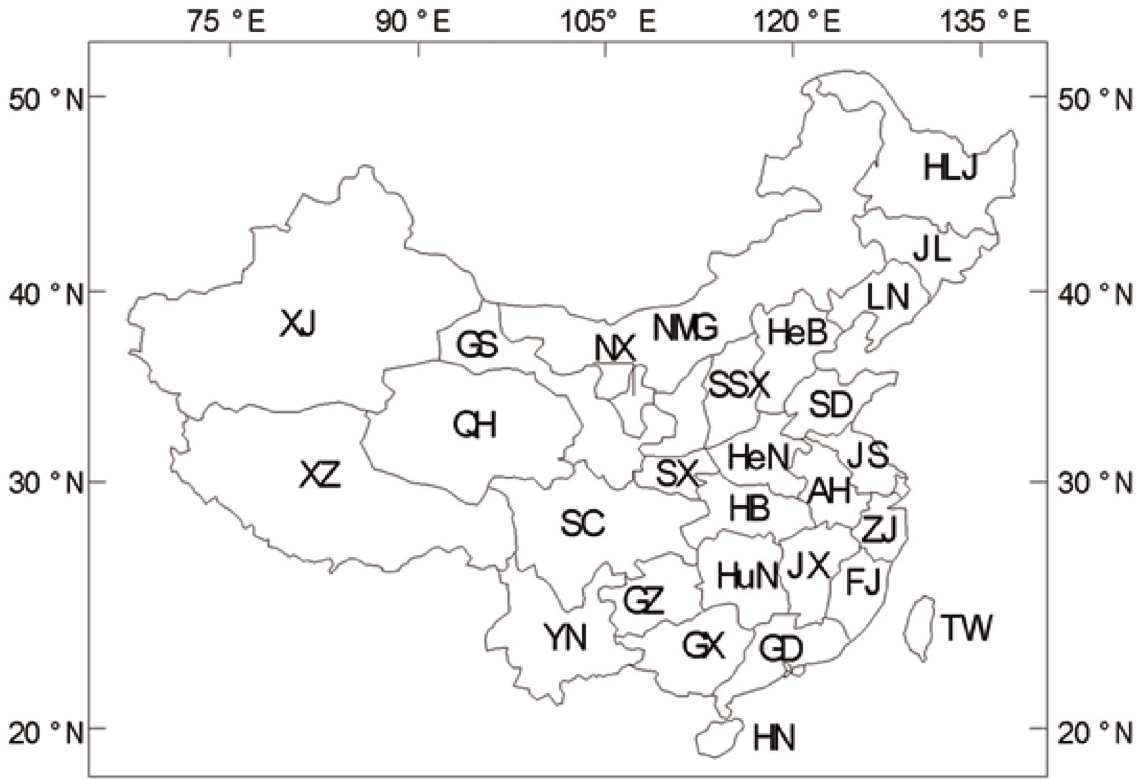
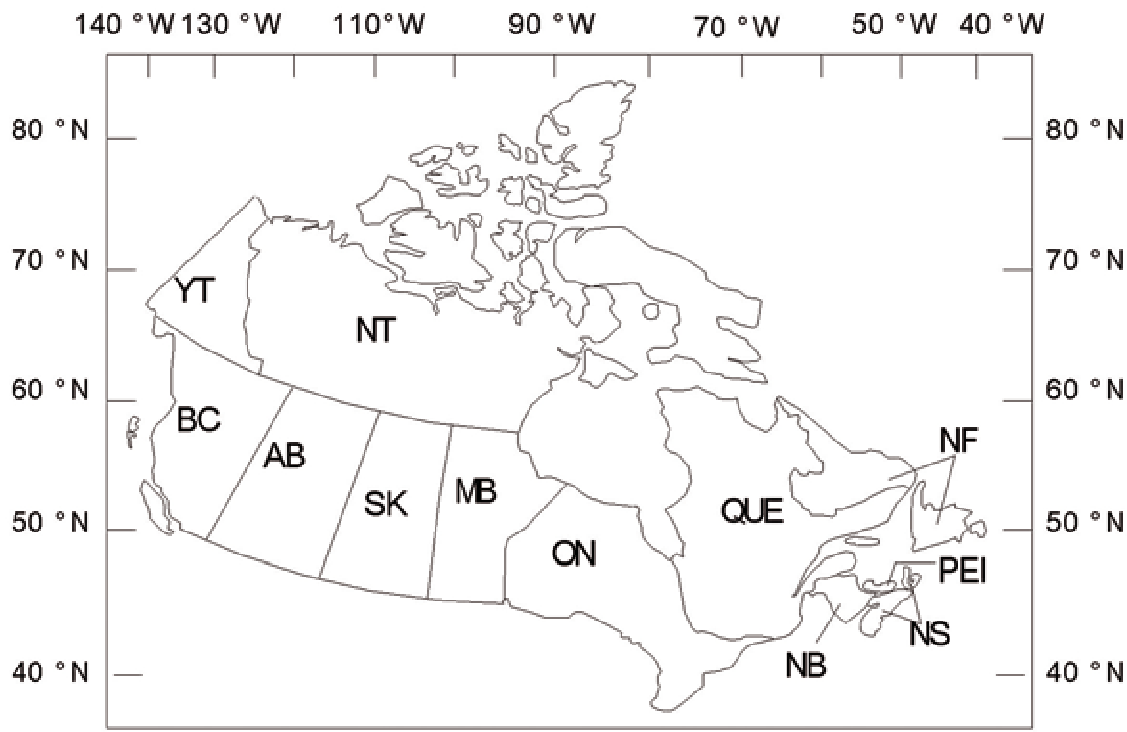


Fig. 1. China and Canada maps showing the political regions (mainly provinces) considered in this floristic analysis. Abbreviations are as follow: **China:** GD = Guangdong; GX = Guangxi; HN = Hainan; TW = Taiwan; FJ = Fujian; JS = Jiangsu + Shanghai; ZJ = Zhejiang; SD = Shandong; SC = Sichuan + Chongqing; HuB = Hubei; HuN = Hunan; HeB = Hebei + Beijing + Tianjin; HeN = Henan; SX = Shanxi; JX = Jiangxi; SSX = Shaanxi; AH = Anhui; LN = Liaoning; JL = Jilin; HLJ = Heilongjiang; NMG = Neimenggu; GZ = Guizhou; YN = Yunnan; XZ = Xizang; QH = Qinghai; NX = Ningxia; XJ = Xinjiang.



Continuación Fig. 1. Canada: BC = British Columbia; YT = Yukon Territory; NWT = Northwest Territories + Nunavut; AB = Alberta; SK = Saskatchewan; MB = Manitoba; ON = Ontario; QUE = Quebec; NB = New Brunswick; NS = Nova Scotia; NF = Newfoundland; PEI = Prince Edward Island.

However, the corresponding ordinal categories of the latter treatment were not used in our analysis because of the ambiguous and/or unassigned position of some species in different plant families, which would have made the overall floristic comparison more difficult.

The floristic richness and generic distribution in the political regions or provinces between China and Canada were generated based on the construction of a series of null hypotheses. Foremost, we used the *G*-test (Sokal & Rohlf, 1995) to evaluate the difference between the floras of China and Canada at different taxonomic levels (order, family, genus, and species) for both the Gymnospermae and the Angiospermae. We used the same approach to determine the general distribution patterns of cosmopolitan, tropical, temperate, and eastern Asia-North American disjunct species. Finally, we used *G*-statistics to test our null hypothesis: H_0 = the general distribution patterns of the shared genera between eastern and western Canada are similar.The shared genera between the floras of China and Canada were tabulated in the form of a binary data matrix based on their distribution in the political regions of both countries (Fig. 1).

This data matrix was then subjected to cluster analyses (Legendre and Legendre, 1998) using the Unweighted Pair-Group Method with Arithmetic Mean (UPGMA) algorithm based on the overall similarity among the political regions. In order to produce a second matrix, the genera shared between China and Canada underwent additional grouping into particular distribution patterns, specifically the areal types of seed plants proposed by Wu (1991). We used this second matrix to map the interrelationships in an ordination by non-metric multidi-mensional scaling (NMS) (Legendre and Legendre, 1998). As an ordination method, NMS provides superior results compared to analytical methods used in ecological and biogeographical studies (Rohlf, 1972; Clarke, 1993). Additionally, the Bray-Curtis distance measure (McCune and Mefford, 1999) was applied to both the cluster analysis and NMS, which were performed using the multivariate statistical package PC-ORD 4.20 (McCune and Mefford, 1999). The *G*-test analyses were conducted using PopTools (Hood, 2002). The remaining calculations were performed using the Statistica software (Statsoft, Inc., 1997) package.

Results

Taxonomic Richness: China's Flora versus Canada's Flora

The taxonomic richness of seed plants in the floras of China and Canada exhibits considerable variation at the generic and specific levels. According to Polhill (1990) and Heywood (2001), the Flora of China project, which includes an estimated 29 500 species, formally published 8 256 species from its beginning in the mid-1980s up to 2001 (less that 50% of its flora). Meanwhile, the Flora of China web site reports that China is home to approximately 31000 species representing about 12% of the world's flora. Of these, ca. 10 000 are endemic, at least 8 000 species are of economical and medicinal uses, and roughly 3 000 are in danger of extinction. Overall, the Flora of China is much larger than the 20 000 native species representing the combined flora of Canada and U.S.A.

There are discrepancies regarding the number of species in Canada. According to Heywood and Davis (1994), Canada's estimated number of vascular plant species

is 3 270, of which 147 (4.5%) are endemic. The Natural Heritage Information Centre (NHIC) lists 4 839 plant species (1 431 non-vascular and 3 408 vascular). Based on the most recent estimate of 320 000 plant species worldwide (Prance, 2001), Canada's flora makes up an estimated 1% of the world's plant species diversity and roughly 24% relative to the continental flora of the U.S.A., which is estimated to be 20 000 species (Heywood and Davis, 1994). From a taxonomic perspective, our bibliographic of research indicates that Canada's flora contributes about 1.4 to 1.5% to the world flora: 3 990 to 4 153 to 4 839 species in 154 to 179 families and 842 to 934 genera (Fig. 3).
There is a marked contrast in the total number of taxa (after taxonomic standardization) between the floras of China and Canada (Fig. 2). The species richness of seed plants in China is quite remarkable and is approximately six-fold higher (29 500 to 31 000) compared to that of Canada (ca. 4 000). The divergence is less significant at the generic level, with an estimated four-fold difference (ca. 1 100 genera in Canada and ca. 4 000 in China).

The taxonomic richness of the Chinese flora relative to the Canadian flora shows some similarities but also some important differences (Fig. 3) at different taxonomic ranks. The *G*-test values (Table 1) indicate that the taxonomic distribution in Gymnospermae

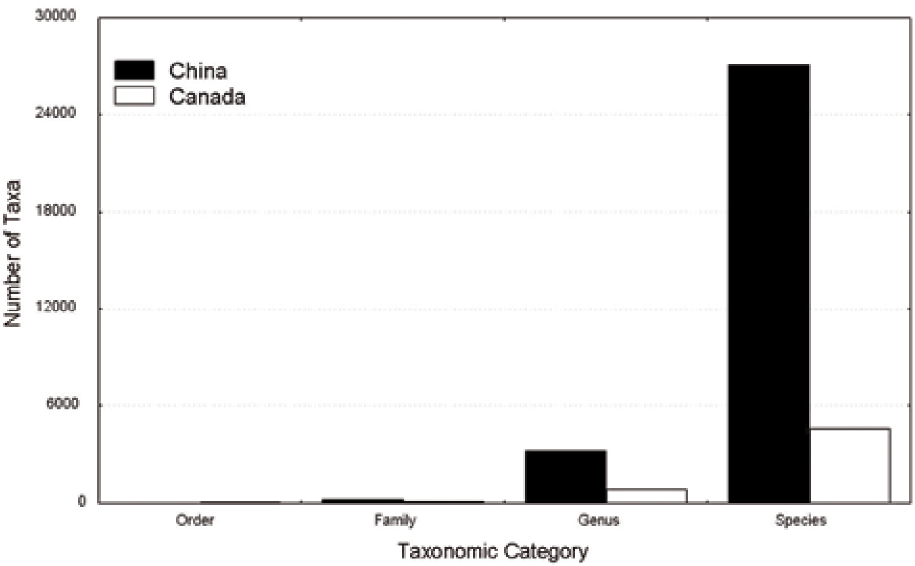


Fig. 2. Total number of taxa in the spermatophyte floras of China and Canada. Number of orders includes Angiospermae only.

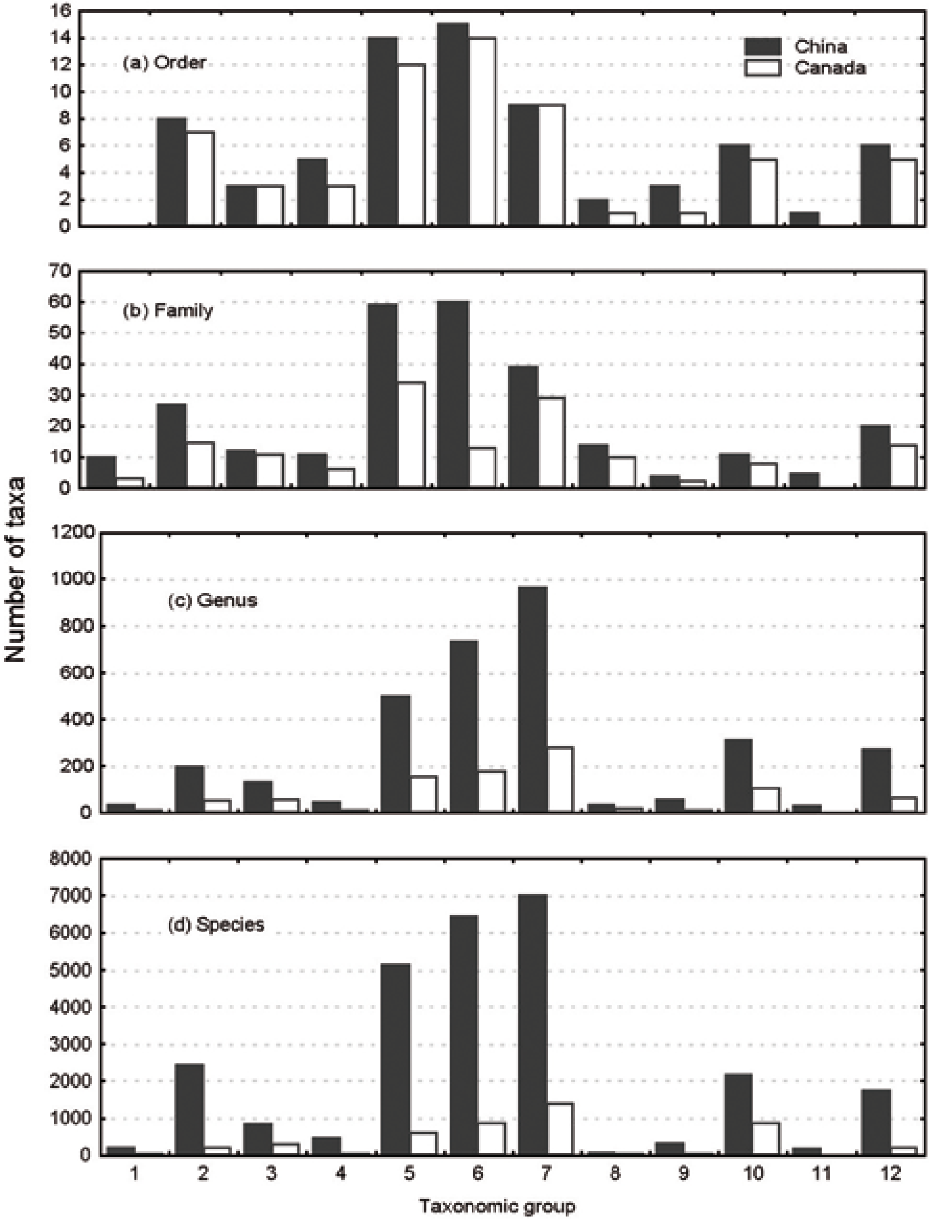


Fig. 3. Number of taxa at the ordinal, familial, generic, and specific levels in Gymnospermae and the subclasses of Angiospermae in the floras of China and Canada. Gymnospermae families are not grouped into orders.

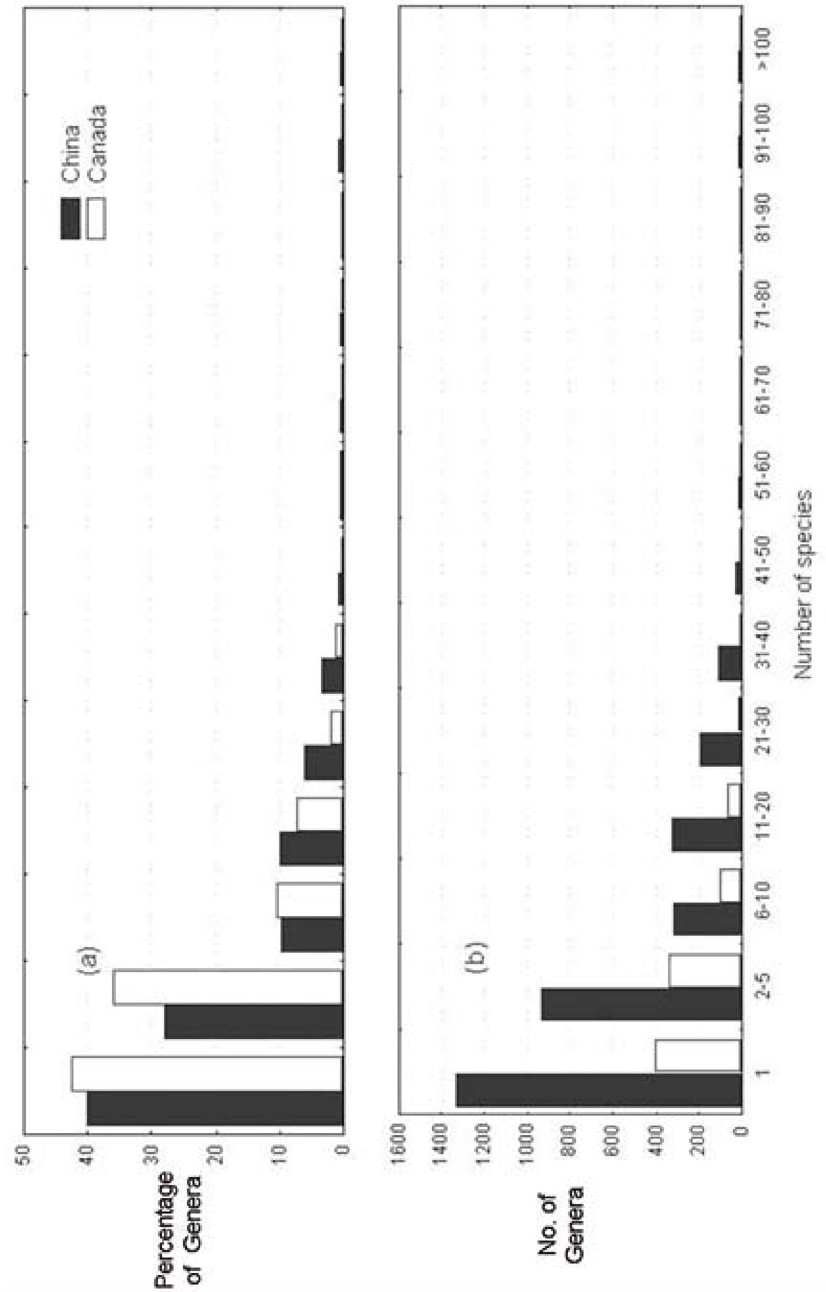


Fig. 4. Frequencies of major genera in the floras of China and Canada (a) comparison of frequency, and (b) comparison of relative frequency.

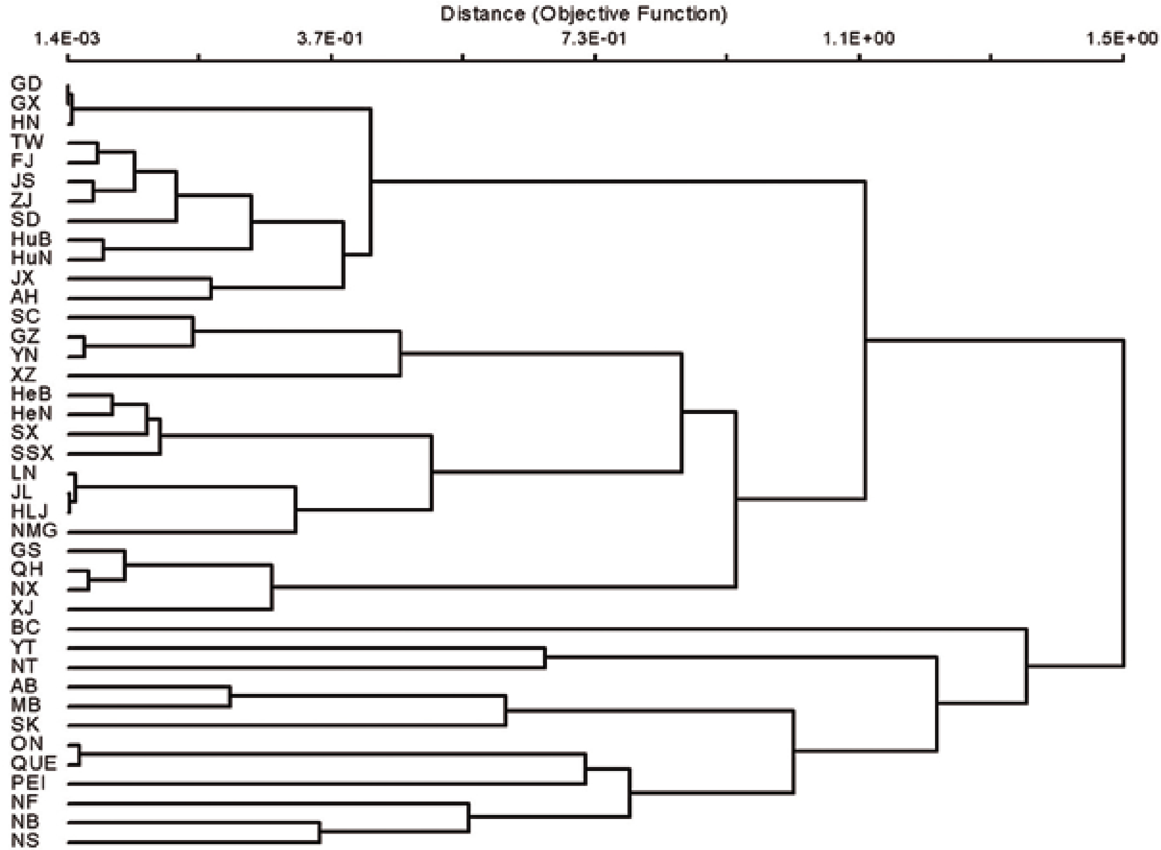


Fig. 5. Dendrogram showing degree of similarity among the political regions of China and Canada based on the presence/absence of shared genera. (See Fig. 1 for abbreviations and locations of political regions.)

and all the subclasses of Angiospermae in both floras is similar at the ordinal and familial levels, significant at the generic level (p = 0.00089), and very significant (p = 0) at the specific level (Table 1). The contrast in the total number of species between the two countries also reflects a major difference in number of genera (Fig. 4). The generic incidence in an artificially divided species class limit is significantly different between China and Canada (Gadj = 78.87, G-critical = 21.03, $p = 6.77\times10^{\text{ÿ}12}$) (Fig. 4a). However, the relative frequencies of genera of the two floras have similar distributions (G-adj = 4.17, G-critical = 21.03, p = 0.98), indicating that their distributions correlate in proportion to the number of species of the two floras (Fig. 4b).

Shared Genera and Geographic Patterns

We identified a total of 553 shared genera between the Chinese and Canadian floras. These 553 genera include an estimated number of species 5.4 times higher in China (12 967) relative to Canada (2 384). A dendogram indicating the floristic relationships between the political regions of China and Canada (Fig. 5) was generated from a matrix containing binary data (presence/absence) based on the distribution of all shared genera between the two countries. All shared genera were weighted equally in the cluster analysis. As expected, the floras of China and Canada form two large, distinct clusters (Fig. 5).

These two major groups reflect the difference in generic composition in the two floras. In the China cluster, seven groups of floristically similar regions can be identified, each with a different coefficient distance. Group 1 (GD, GX, and HN) represents the southern China provinces distinguished by numerous tropical floristic elements; Group 2 (TW, FJ, JS, ZJ, and SD) includes the eastern and southeastern coastal provinces characterized by humid subtropical forest environments; Group 3 (HuB, HuN, JX, and AH) corresponds to approximately the central to east China floristic region; Group 4 (SC, GZ, YN, and XZ) characterizes the flora in western and southwestern China; Group 5 (HeB, HeN, SX, and SSX) represents the provinces from central to north China dominated by deciduous broad-leaf forest; Group 6 (LN, JL, HLJ, and NMG) is the northern and northeastern floristic region of China characterized by the dominance of coniferous forests; Group 7 (GS, QH, NX, and XJ) includes the provinces in northwestern China, the floras of which consist of many arid, ephemeral elements. These groups are in agreement with the ecological regions (Wu, 1980) and floristic zonation of China (Wu and Wu, 1998). Although other subgroups can be distinguished in the dendrogram, they do not correspond to any of the recognized Chinese ecological regions

The large cluster representing the Canadian elements consists of three groups separated by similar distance coefficients, with the BC group being the most distant. Group 1 includes YT and NWT (including the semiautonomous territory of Nunavut), mainly characterized by arctic and subarctic elements; Group 2 represents the prairie and boreal forest elements and consists of the provinces of AB, MB, and SK; and Group 3 includes all the eastern Canadian provinces (ON, QUE, PEI, NF, NB, NS), which form the eastern Canadian floristic region. Further, the Canadian provinces of Ontario, New Brunswick, and Quebec have a high proportion of shared genera (Fig. 7).

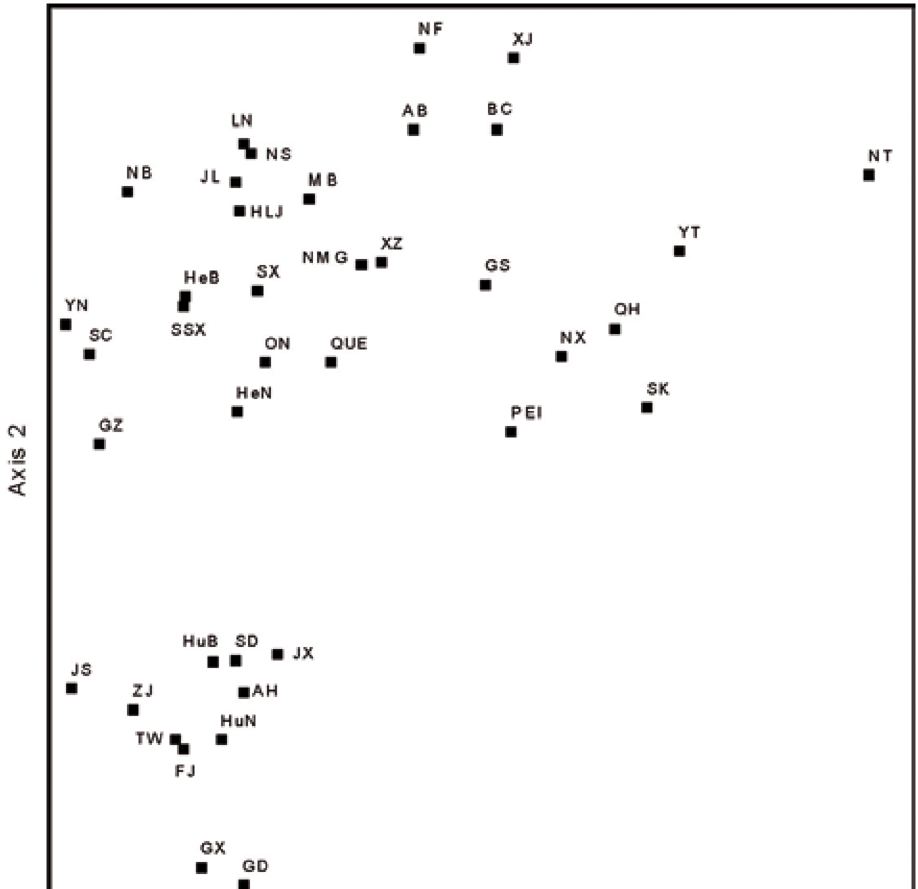


Fig. 6. Two-dimensional ordination plots from non-metric multidimensional scaling, showing relationships of the political regions between the floras of China and Canada as determined by the richness of shared genera grouped by areal-types.

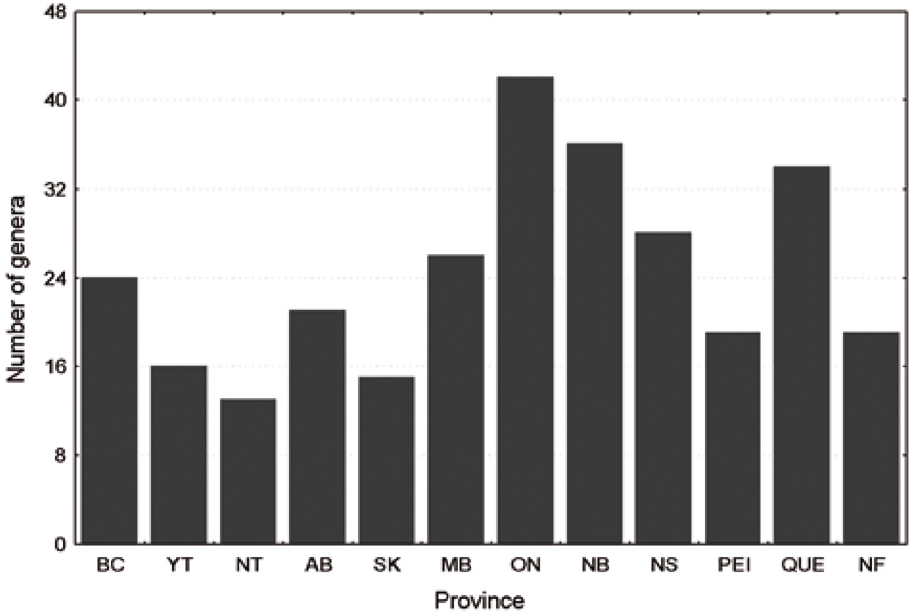


Fig. 7. Number of genera with an eastern Asia-North American disjunction pattern in provinces and territories of Canada.

Within Group 3, the ON-QUE subgroup is clearly distinguished as it represents part of the temperate broad-leaf forests.

Geographic Elements of Shared Genera

Our data were arranged in generic areal types, including number of species/genus based on the areal types concept (Table 2) of Wu (1991), who grouped the Chinese seed plant genera into 15 areal types and 35 subtypes. Our data indicate that the shared genera of seed plants between China and Canada can be grouped into 24 areal types and subtypes following Wu's (1991) concept. These areal types and subtypes can be subdivided into four general geographical elements, namely, cosmopolitan, tropical, temperate, and eastern Asia-North American disjunct. Further, we treated the eastern Asia-North American disjunct pattern as a separate geographical element in parallel with cosmopolitan, tropical, and temperate elements because of its relative importance in providing insight regarding the biogeographical link between the two floras.

Based on the areal types obtained from shared taxa, we generated a second matrix to map the generic interrelationships among the political regions in both floras using an ordination analysis employing NMS. In this analysis, each of the shared genera had different weights relative to the equal weight used in the areal types, which resulted in different groupings of the political regions in relation to their floristic components (Fig. 6) as compared with cluster analysis. All the regions of southern and southeastern China, which represent the tropical rain forest and subtropical evergreen broad-leaved forest zones, formed a cluster in the lower part of the box plot, whereas the northern, northeastern, and northwestern regions of China clustered with Canadian regions in the upper part of the plot as a result of temperate affinities (Fig. 6). These floristic similarities suggest that mainland China and southern Canada share comparable latitudinal ranges and climatic characteristics. These groups, directly related to variations in climate and vegetation types, may provide useful information to infer historical links between the two floras in forthcoming studies.

Shared Genera with an Eastern Asia-North American Disjunct Distribution

Overall, our data indicate that there are 123 spermatophyte genera with the China-North American disjunct distribution pattern. Sixty of these genera are represented in the flora of Canada (Table 3). A number of the genera extend their distribution beyond the area of study. For instance, *Castilleja* Mutis ex L. extends to Europe and Central America, and *Tsuga* (Antoine) Carrière ranges to southern Vietnam. Although most of the 60 disjunct genera occur in the eastern provinces of Canada, a number of them are also found in the western provinces.

The eastern Canadian provinces share a relatively higher number of genera with China than the western provinces (Fig. 7; Tables 4 and 5). However, there is little difference in the generic distribution by geographical elements between three western and three eastern Canadian provinces (Table 5). Furthermore, some of the genera shared with China are confined to the western part of Canada, e.g., *Achlys* D.C. and *Glehnia* F. Schmidt ex Miq. occur only in BC; *Oplopanax* (Torrey & A. Gray) Miq. occurs only in BC, YT, and AB; *Boschniakia* C. Meyer ex Bong. is only found in BC, YT, AB, and NWT. These four genera have an eastern Asia-western or northwestern American disjunct distribution pattern (Table 3), which can be explained from a historical floristic point of view. Graphical representation of NMS ordination (Fig. 6) also shows the close floristic relationship between western Canada and China.

Discussion

Although Canada is slightly larger than China, China's topographic relief and more diverse climate favour a greater diversity of eco-environments/regions, resulting in complex patterns of vegetation with much greater taxonomic richness at the generic and specific level of seed plants. There are four major factors that may account for the significant differences at the generic and specific categories in seed plants between China and Canada. First, climate and the resulting eco-environment may play a major role modelling distribution and different types of vegetation, while similar latitude and climatic zones determine floristic affinities. In general, the taxonomic complexity, floristic composition, and phytogeographic regions of the vegetation of Canada are much simple compared with those of China. In fact, China is the only place on Earth where there is an unbroken connection between tropical, subtropical, temperate, and boreal forests. This vegetational continuum has resulted in associations of plants that are rarely seen in other parts of the world, many of which are relicts of a once widespread flora. In China, tropical rain forests, subtropical evergreen broad-leaf forests, temperate deciduous broad-leaf forests, and boreal forest, harbour the country's mega-diversity of species from south to north. Further, from east (at about 30°N) to west and northwest, vegetation types change from broad-leaf forests, grassland, and steppe to desert. Conversely, the vegetation of Canada is characterized by high arctic tundra and polar desert, low arctic tundra, boreal forest or taiga from coast to coast, pacific coast conifer forest, and western mountain conifer forest (Barbour and Christensen, 1993).

Second, the adjacent floras of central, northern, and southern Asia largely influence the Chinese flora. In all likelihood past and current plant migration events have allowed the interchange of floristic elements and promoted species divergence and speciation. We believe that the different migration rates and dispersal capacity of species have a landscape effect and reflect variation in taxonomic patterns and colonization rates in different geographic areas of China and Canada.

Statis, the third factor, may also play a role in complex patterns of diversity and speciation. Ricklefs and Latham (1992) suggested that time is stasis in ecological traits of relict genera of temperate perennial herbs. In our view, taxonomic levels represent the phylogeny of seed plants, i.e., higher levels represent older phylogenetic lineages. Accordingly, the similarity in higher-level taxa versus the great difference at the generic and specific levels suggests stasis in the seed plants of the Canadian flora. Nonetheless, the extreme divergences are consistent with morphological stasis at lower hierarchical ranks, i.e., the specific level.
Lastly, availability of refugia may also account for differences in species diversity. It has been reported that numerous taxa that occurred in both eastern Asia and North America in past geological times became extinct from the modern flora of North America due to Quaternary glacial events (Wolfe and Leopold, 1967; Xiang *et al.*, 1998). For example, fossil records of *Liquidambar* L. have been found in Canada (Scoggan, 1978). In contrast, during the Quaternarty China was relatively warm and served as refugia for numerous temperate species, as evidenced by the many taxa presumed extinct that were later found in China, notable examples being *Ginkgo* L. and *Metasequoia* Miki ex Hu & W. C. (Chinese redwood), two famous genera of "living fossils" found in the modern flora of China.

When it comes to the historical floristic links between eastern Asia and North America, our study shows that both western and eastern Canada is floristically closely related to China. This indicates that the migration route of floristic elements through the Bering Strait had a major influence in facilitating species distribution. In addition, there is well-supported evidence that floristic elements of eastern Asia migrated to North America through Europe in past geological times, resulting in eastern North America being more similar to eastern Asia in geographical elements (Raven, 1972; Tiffney, 1985; Wen, 1999). On the other hand, the migration route through the Bering Strait has been a matter of discussion because the history of Beringia needs further consideration in light of plate tectonics (see Raven, 1972). However, other studies have suggested the existence of the Bering Land Bridge (e.g., Cox, 1974; Kruckeberg, 1983; McKenna, 1983; Lindstrom, 2001), thus supporting paleodistribution patterns of plants and animals.

In view of the close similarity between western Canada and China, it is unlikely that the western floristic elements originated from Europe via the Atlantic connections but rather from Beringia. In fact, it has been proposed that the floristic disjunction involving eastern Asia and eastern and western North America probably arose at different geological times in different genera (Li, 1952), an idea supported by Xiang *et al.* (1998), who proposed that some of the most remarkable examples of intercontinental disjunction are those between eastern Asia and eastern and western North America.

In summary, this study confirms that while a number of shared taxa exhibiting intercontinental disjuntion share biogeographic history, the floras of China and North America have evolved independently due in part to geographical isolation and climatic patterns, among other factors. Similarly, Xiang *et al.* (1998) propose that intercontinental disjunct taxa share historical biogeographic patterns and their current vicariant distribution represents a fragmentation of a past more continuous mixed mesophytic forest. Overall, the general information on the taxonomy and distribution of plants in China and Canada provided here along with palaeobotanical and geological data can assist in the understanding of migratory routes and in estimating times of disjunction between eastern Asian and North America and taxonomic diversification in regards with geological events.

ACKNOWLEDGEMENTS

The authors thank Theodore Cochrane for reviewing this manuscript and providing valuable comments. The China Scholarship Council provided a fellowship to Z. Su to conduct floristic research at the University of Saskatchewan, which in turn funded fieldwork of JHCS in China. The assistance of the staff of the Herbarium of the University of Saskatchewan (SASK) is also greatly appreciated.

LITERATURE CITED

APG (Angiosperm Phylogeny Group), 1998. "An ordinal classification for the families of flowering plants". *Annals of the Missouri Botanical Garden*, **85**: 531-553.

Baldwin, W. K. W., 1958. *Plants of the Clay Belt of Northern Ontario and Quebec*. Ottawa: National Museum of Canada.

Barbour, M. G., and N. L. Christensen, 1993. "Vegetation". *In:* Flora of North America Editorial Committee, Eds. *Flora of North America*, **1**: 97-131. New York: Oxford Univ. Press.

Boufford, D. E. and S. A. Spongberg, 1983. "Eastern Asian-eastern North American phylogeographical relationships: A history from the time of Linnaeus to the twentieth century". *Annals of the Missouri Botanical Garden*, **70**: 423-439.

Cheng, Z., 1983. "A comparative study of the vegetation in Hubei Province, China, and in the Carolinas of the

United States". *Annals of the Missouri Botanical Garden* **70**: 571-575.

Clarke, K. R., 1993. "Non-parametric multivariate analysis of changes in community structure". *Australian Journal of Ecology* **18**: 117-143.

Cody, W. J., 1996. *Flora of the Yukon Territory*. Ottawa: NRC Research Press.

Cox, C. B., 1974. "Vertebrate paleo-distributional patterns and continental drift". *Journal of Biogeography*, **1**: 75-94.

Douglas, G. W., G. B. Straley, and D. Meidinger, 1989-1991. *The Vascular Plants of British Columbia.* Part 1-Part 3. Ministry of Forests, Province of British Columbia.

Erskine, D. S., 1960. *The Plants of Prince Edward Island*. Ottawa: Plant Research Institute Research Branch, Canada Department of Agriculture.

Flora of Taiwan Editorial Board, 1979. *Flora of Taiwan*. vol. 6. Taipei: Epoch Pub. Co., Ltd.

Guo, Q., R. E. Ricklefs, and M. L. Cody, 1998. "Vascular plant diversity in eastern Asia and North America: Historical and ecological explanations". *Botanical Journal of the Linnaean Society*, **128**: 123-136.

Heywood, V. H., 2001. "Floristics and monography – an uncertain future?" *Taxon*, **50**: 361-380.

Heywood, V. H. and S. D. Davis, 1994. *Centres of Plant Diversity: A guide and strategy for their conservation in Europe, Africa, South West Asia and the Middle East*, Vol. I. S. D. Davis, V. H. Heywood, and A. C. Hamilton, eds. Cambridge, U.K.: The WWF and IUCN.

Hinds, H. R., 1999. *Flora of New Brunswick.* 2nd ed. Fredericton: Department of Biology, University of New Brunswick.

Hood, G., 2002. *PopTools*. CSIRO, Canberra, Australia.

Hou, F. C. (Revised by Wu, D. L.), 1986. *A Dictionary of the Families and Genera of Chinese Seed Plants*. 2nd ed. Beijing: Science Press.

Hou, H. Y., 1983. "Vegetation of China with reference to its geographical distribution". *Annals of the Missouri Botanical Garden*, **70**: 509-549.

Hsu, J., 1983. "Late Cretaceous and Cenozoic vegetation in China, emphasizing their connection with North America". *Annals of the Missouri Botanical Garden*, **70**: 490-508.

Institute of Botany, Chinese Academy of Sciences, 1987. *Claves familiarum generumque cormphytorum Sinicum*. Beijing: Science Press.

Judd, W. S., C. S. Campbell, E. A. Kellogg, P.F. Stevens, and M. J. Donohue, 2002. *Plant Systematics: A phylogenetic approach*. 2nd ed. Sunderland, MA: Sinauer Assoc. Inc.

Kartesz, J. T., 1994. *A Synonymized Checklist of the Vascular Flora of the United*

States, Canada and Greenland. 2nd ed. Portland, OR: Timber Press.

Kruckeberg, A. R., 1983. "Temperate floras: The North Pacific connection". *Annuals of the Missouri Botanical Garden*, **70**: 591-596.

Legendre, P., and L. Legendre, 1998. *Numerical Ecology*. 2nd ed. New York: Elsevier.

Li, H. L., 1952. "Floristic relationships between eastern Asia and eastern North America". *Transactions of the American Philosophical Society* N.S., **42**: 371-429.

Lindstrom, S. C., 2001. "The Bering Strait connection: Dispersal and speciation in boreal macroalgae". *Journal of Biogeography*, **28**: 243-251.

Looman, J. and K. F. Best, 1987. *Budd's Flora of the Canadian Prairie Provinces.* Ottawa: Research Branch, Agriculture Canada, Publication 1662.

Mabberley, D. J., 1998. *The Plant-Book: A portable dictionary of the vascular plants.* 2nd ed. Cambridge: Cambridge University Press.

McCune, B. and M. J. Mefford., 1999. *PC-ORD. Multivariate analysis of ecological data,* Version 4.20. Gleneden Beach, OR: MjM Software Design.

McKenna, M. C., 1983. "Holarctic landmass rearrangements, cosmic events, and Cenozoic terrestrial organisms". *Annals of the Missouri Botanical Garden*, **70**: 459-489.

Moss, E. H., 1983. *Flora of Alberta.* 2nd ed. (Revised by J. G. Packer). Toronto, ON: University of Toronto Press.

Natural Heritage Information Centre. Species List of Vascular Plants. Ministry of Natural Resources. Ontario.

Polhill, R. M., 1990. "Production rates of major floras". *Fl. Males. Bull.* Special Vol. **1**: 11-20.

Porsild, A. E. and W. J. Cody, 1980. *Vascular Plants of Continental Northwest Territories, Canada.* Ottawa: National Museums of Canada.

Prance, G. T., 2001. "Discovering the plant world". *Taxon*, **50**: 345-359.

Qian, H., 1999. "A comparison of the taxonomic richness of vascular plants in China and United States". *American Naturalist*, **154**: 160-181.

———, 2001. "A comparison of generic endemism of vascular plants between East Asia and North America". *International Journal of Plant Science*, **162**: 191-199.

Raven, P. H., 1972. "Plant species disjunctions: A summary". *Annals of the Missouri Botanical Garden*, **59**: 234-246.

Ricklefs, R. E. and R. E. Latham, 1992. "Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs". *American Naturalist*, **139**: 1305-1321.

Rohlf, F. J., 1972. "An empirical comparison of three ordination techniques in numerical taxonomy". *Systematic Zoology*, **21**: 271-280.

Roland, A. E. and E. C. Smith, 1969. *The Flora of Nova Scotia.* Halifax: The Nova Scotia Museum.

Scoggan, H. J., 1957. *Flora of Manitoba.* Ottawa: National Museum of Canada Bulletin No.140.

________, 1978. *The Flora of Canada*, Part 1-Part 4. Ottawa: National Museums of Canada.

Sokal, R. R. and F. J. Rohlf, 1995. *Biometry: The principles and practice of statistics in biological research.* 3rd ed. San Francisco: W. H. Freeman and Co.

Statsoft, Inc., 1997. *STATISTICA for Windows* (Computer program manual). Tulsa: Statsoft, Inc.

Tiffney, B. H., 1985. "Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America". *Journal of the Arnold Arboretum*, **66**: 73-94.

Wen, J., 1999. "Evolution of eastern Asian and eastern North American disjunct distributions in flowering plants". *Annual Review of Ecology and Systematics*, **30**: 421-455.

Wen, J. and T. F. Stuessy, 1993. "The phylogeny and biogeography of *Nyssa* (Cornaceae)". *Systematic Botany*, **18**: 68-79.

White, P. S., 1983. "Eastern Asian-eastern North American floristic relations: The plant community level". *Annals of the Missouri Botanical Garden*, **70**: 734-747.

Wolfe, J. A. and E. B. Leopold, 1967. "Neogene and Early Quaternary vegetation of northwestern North America and northeastern Asia". *In: The Bearing Land Bridge,* D. M. Hopkins, ed. Pp. 193-206. Stanford, CA: Stanford University Press.

Wood, C. E., 1972. "Morphology and phytogeography: The classical approach to the study of disjunctions". *Annals of the Missouri Botanical Garden*, **59**: 107-124.

Wu, C. Y., 1980. *The Vegetation of China.* Beijing: Science Press.

________, 1983. "On the significance of pacific intercontinental discontinuity". *Annuals of the Missouri Botanical Garden*, **70**: 577-590.

________, 1991. "The areal types of Chinese genera of seed plants". *Acta Botanica Yunnanica* (suppl.) **4**: 1-139.

Wu, C. Y. and P. H. Raven, 1994. *Flora of China*. [Published volumes available at: Brach, A. R. (ed.). 1996. *Flora of China.*

Wu, C. Y. and S. G. Wu, 1998. "A proposal for a new floristic kingdom (realm)". *In: Floristic characteristics and diversity of East Asian plants.* A. Zhang and S. Wu, eds. Pp. 3-42. New York: Springer.

Xiang, Q. Y., D. E. Soltis, and P. S. Soltis, 1998. "The eastern Asia and eastern and western North American floristic disjunction: Cogenetic patterns in seven diverse genera". *Molecular Phylogenetics and Evolution*, **10**: 178-190.

Ying, T. S., 1983. "The floristic relationships of the temperate regions of China and the United States". *Annals of the Missouri Botanical Garden*, **70**: 597-604.

Recibido: 20 septiembre 2006. Aceptado: 21 junio 2007.

Table 1. Results of the *G*-tests conducted to examine the difference between the floras of China and Canada at the ordinal, familiar, generic, and specific levels of the Gymnospermae and Angiospermae.

Taxonomic level	df value	*G*-adj value	*G*-critical	*P* value
Order	10	1.30337	18.30703	0.99943
Family	11	16.69475	19.67515	0.11723
Genus	11	31.56298	19.67515	0.00089
Species	11	931.02550	19.67515	0

Table 2. List of the generic areal types and number of species of shared genera between China and Canada.

Areal type (according to Wu, 1991)	Code (Wu, 1991)	Number of genera	Number of species China	Number of species Canada
Cosmopolitan	1	88	3 288	88
Pantropic	2	59	1 315	154
Tropical Asia and tropical America disjunction	3	3	28	9
Old World tropics	4	1	24	1
Tropical Asia to tropical Africa	6	3	36	3
Tropical Asia	7	4	82	16
Tropical subtotal (2 to 7)		70	1 485	183
North temperate	8	164	6 101	1 294
Circumpolar	1-8	7	8	10
Arctic-alpine	2-8	9	62	20
Arctic to Altai and N. America disjunction	3-8	1	1	11
N. temperate and S. temperate disjunction	4-8	46	869	318
Eurasia and S. temperate and South America disjunction	5-8	1	6	8
Old World temperate	10	48	420	128
Mediterranean, W. and E. Asia disjunction	1-10	8	66	14
Mediterranean and Himalaya disjunction	2-10	1	3	1
Eurasia and temperate S. America disjunction	3-10	7	72	33
Temperate Asia	11	8	126	13
Mediterranean, W. to C. Asia	12	28	77	54
Mediterranean to C. Asia and Mexico to USA	2-12	1	8	6
Mediterranean to temperate-tropical Asia, Australasia and S. America disjunction	3-12	2	9	3
Pan-Mediterranean	5-12	2	3	3
W. Asia to W. Himalaya and Tibet	3-13	1	4	1
C. Asia to Himalaya-Altai and Pacific N. America disjunction	4-13	1	3	4
Temperate subtotal (8 - 13-4)		335	7 838	1 921
E. Asia and N. America disjunction	9	60	356	192
Total		**553**	**12 967**	**2 384**

Table 3. Generic list of seed plants with an eastern Asia-North American disjunction pattern recorded in the floras of China and Canada. Abbreviations for distributions are: E As = eastern Asia, NE As = northeastern Asia, N Am = North America, E N Am = eastern North America, W N Am = western North America, NE N Am = northeastern North America, NW N Am = northwestern North America.

Taxonomic Group	Family	Genus	Number of species			Distribution
			China	Canada	World	
Gymnospermae	Cupressaceae	*Chamaecyparis*	2	1	8	E As-N Am
	Cupressaceae	*Thuja*	2	2	5	E As-N Am
	Pinaceae	*Pseudotsuga*	5	1	6	E As-W N Am
	Pinaceae	*Tsuga*	5±	3	14±	E As-N Am
Angiospermae						
Monocotyledons						
Alismatidae	Zosteraceae	*Phyllospadix*	1	2	5	E As-W N Am
Arecidae	Aracaeae	*Acorus*	1	1	2	E As-N Am
Arecidae	Araceae	*Symplocarpus*	1	1	1	NE As-NE N Am
Commelinidae	Gramineae	*Brachyelytrum*	1	1	3	E As-N Am
Commelinidae	Gramineae	*Zizania*	1	1	3	E As-N Am
Liliidae	Liliaceae	*Aletris*	13	1	15	E As-N Am
Liliidae	Liliaceae	*Zigadenus*	1	4	15	E As-N Am
Liliidae	Liliaceae	*Clintonia*	1	2	6	E As-N Am
Liliidae	Liliaceae	*Disporum*	10	4	20	E As-W N Am
Liliidae	Orchidaceae	*Pogonia*	3	1	7	E As-N Am
Liliidae	Trilliaceae	*Trillium*	3	8	30-45	E As-N Am
Dicotyledons						
Asteridae	Apocynaceae	*Apocynum*	1-2	3	12	E As-N Am
Asteridae	Bignoniaceae	*Campsis*	1	1	2	E As-E N Am
Asteridae	Bignoniaceae	*Catalpa*	7	3	11	E As-N Am
Asteridae	Caprifoliaceae	*Symphoricarpos*	1	4	18	E As-N Am

Table 3. Continuación.

Taxonomic Group	Family	Genus	Number of species			Distribution
			China	Canada	World	
Asteridae	Caprifoliaceae	*Triosteum*	3	2	10	E As-N Am
Asteridae	Labiatae	*Agastache*	1	4	9	E As-N Am
Asteridae	Orobanchaceae	*Boschniakia*	2	2	3	E As-NW N Am
Asteridae	Phrymaceae	*Phryma*	1	1	1-2	E As-E N Am
Asteridae	Rubiaceae (Naucleaceae)	*Cephalanthus*	1	1	17	E As-N Am to tropical Am
Asteridae	Rubiaceae	*Mitchella*	1-2	1	2	NE As-E N Am
Asteridae	Scrophulariaceae	*Castilleja*	1	33	90	E As-N Am to Europe and C Am
Asteridae	Scrophulariaceae	*Orthocarpus*	1	10	25	E As-W N Am
Asteridae	Scrophulariaceae	*Veronicastrum*	15	1	20	NE As-NE Am
Dilleniidae	Ericaceae	*Hypopitys*	1	1	1	E As-N Am
Hamamelidae	Hamamelidaceae	*Hamamelis*	2	1	6	E As-E N Am
Hamamelidae	Juglandaceae	*Carya*	4	7	15±	E As-E N Am
Magnoliidae	Lauraceae	*Sassafras*	2	1	3	E As-E N Am
Magnoliidae	Berberidaceae (Podophyllaceae)	*Achlys*	1	1	3	E As-W N Am
Magnoliidae	Berberidaceae (Podophyllaceae)	*Jeffersonia*	1	1	2	NE As-E N Am
Magnoliidae	Fumariaceae	*Adlumia*	1	1	2	NE As-NE N Am
Magnoliidae	Fumariaceae	*Dicentra*	2	4	20	E As-N Am
Magnoliidae	Magnoliaceae	*Liriodendron*	1	1	2	E As-E N Am
Magnoliidae	Magnoliaceae	*Magnolia*	30±	1	90±	E As-E N Am
Magnoliidae	Menispermaceae	*Menispermum*	1	1	3	E As-E N Am

Table 3. Continuación.

Taxonomic Group	Family	Genus	Number of species			Distribution
			China	Canada	World	
Magnoliidae	Nelumbonaceae	*Nelumbo*	1	1	2	E As-E N Am
Magnoliidae	Papaveraceae	*Stylophorum*	2	1	3	E As-E N Am
Magnoliidae	Saururaceae	*Saururus*	1	1	2	E As-E N Am
Rosidae	Araliaceae	*Aralia*	30+	4	36+	E As-N Am
Rosidae	Araliaceae	*Oplopanax*	1	1	3	E As-NW N Am
Rosidae	Araliaceae	*Panax*	6	2	8	E As-N Am
Rosidae	Cornaceae	*Nyssa*	6	1	10	E As-N Am
Rosidae	Hydrangeaceae	*Hydrangea*	45	1	80±	E As-N Am
Rosidae	Leguminosae	*Gleditsia*	10	1	14	E As-E N Am
Rosidae	Leguminosae	*Desmodium*	5	13	450	E As-N Am
Rosidae	Leguminosae	*Lespedeza*	65	7	90	E As-N Am
Rosidae	Leguminosae	*Amphicarpa*	3	1	10-15	E As-N Am
Rosidae	Leguminosae	*Apios*	6	1	10	E As-N Am
Rosidae	Rosaceae	*Physocarpus*	1	2	10	NE As-N Am
Rosidae	Rosaceae	*Amelanchier*	2	15	25	E As-N Am
Rosidae	Saxifragaceae (Penthoraceae)	*Penthorum*	1	1	3	E As-E N Am
Rosidae	Saxifragaceae	*Boykinia*	1	1	9	E As-N Am
Rosidae	Saxifragaceae	*Tiarena*	1	2	5	E As-N Am
Rosidae	Umbelliferae	*Glehnia*	1-2	1	1-2	NE As-W N Am
Rosidae	Umbelliferae	*Osmorhiza*	1-3	5	15	E As-N Am to S Am
Rosidae	Vitaceae	*Parthenocissus*	9-10	2	15	E As-N Am

Table 4. Distribution of shared genera according to areal types in Canada.

Geographical elements	BC	YT	AB	SK	MB	NWT	ON	QUE	NF	NB	NS	PEI
Cosmopolitan	56	60	71	62	74	55	65	65	67	82	82	71
Tropical	21	17	25	25	31	8	39	30	17	42	31	26
Temperate	234	204	255	186	243	210	220	209	260	250	247	186
E Asia-N Am	24	16	21	15	26	13	42	34	19	36	28	19
Total	**335**	**297**	**372**	**288**	**374**	**286**	**366**	**338**	**363**	**410**	**388**	**302**

Table 5. A summary of *G*-tests conducted to examine the generic distribution according to geographical elements between three western (BC, YT, AB) and three eastern (ON, QUE, NF) Canadian provinces.

Geographical elements	df value	*G*-adj value	*G*-critical	*P* value
Cosmopolitan	2	0.72183	5.99148	0.69704
Tropical	2	6.99630	5.99148	0.03025
Temperate	2	0.52852	5.99148	0.76778
E Asia-N Am Disjunction	2	4.16983	5.99148	0.12432
Total	**2**	**2.21173**	**5.99148**	**0.33092**