BIODIVERSITY OF THE ALPINE VASCULAR FLORA OF THE N.W. NORTH AMERICAN CORDILLERA: THE EVIDENCE FROM PHYTO-GEOGRAPHY

With 9 figures, 3 tables and 1 appendix

STUART A. HARRIS

Zusammenfassung: Biodiversität der alpinen Gefäßpflanzenflora der nordwestlichen nordamerikanischen Kordillere: Belege einer vegetationsgeographischen Betrachtung

Am Ende der Late Wisconsin-Vereisung stand der alpinen Gefäßpflanzenflora lediglich ein Zeitraum von ca. 3.500 Jahren zur Verfügung, um das sich ca. 1.600 km erstreckende, ehemals vergletscherte Gebiet im westlichen Kanada wieder zu besiedeln, bevor die Temperaturen zu einer Isolierung in einzelnen Gebirgsregionen führten. In diesem Artikel werden die Ursprungsgebiete (Refugien) beschrieben und es erfolgt eine Abschätzung der Effizienz der Migration aus den einzelnen Ursprungsgebieten.

Datengrundlage bildet die aktuelle Vegetation von 29 alpinen Standorten zwischen der Nordküste Alaskas und Colorado. Über 70% der alpinen Arten der kanadischen Kordillere sind in ihrer Verbreitung auf diesen Kontinent beschränkt. Die Verbreitung einzelner Arten ist sporadisch; wahrscheinlich eine Folge der nur kurzen Zeit, die für die Wiederbesiedlung zur Verfügung stand.

Während der letzten Vereisung haben Mutationen zu standörtlichen Anpassungen und zu spezifischen Artenveränderung in den Refugien geführt. Anhand der neuen Arten lässt sich die Flora der einzelnen Refugien identifizieren. Die ca. 629 vorkommenden Arten wurden auf der Grundlage ihrer aktuellen Verbreitung in neun Gruppen unterteilt. Anhand von Karten, welche die prozentuale Artenzusammensetzung darstellen, ist ersichtlich, dass Arten aus den Refugien der mittleren Kordillere, aus der Umgebung des Plateau Mountain und von den Königin-Charlotte-Inseln hauptsächlich nördlich und südlich entlang der angrenzenden Gebirgsketten wanderten. Aufgrund feuchterer und kühlerer Bedingungen in den ehemals vergletscherten Gebieten wanderten nur wenige Arten aus dem Bereich der südlichen Kordillere ein. Der Erfolg neuer Bering-Arten war unterschiedlich, während Arten der nördlichen Kordillere sowie die der nordamerikanischen und Kordilleren-Florengruppe den gesamten Gebirgsraum in der zur Verfügung stehenden Zeit wieder besiedelten. Lediglich wenige Arten aus den angrenzenden Präriegebieten wanderten ein.

Die Ergebnisse legen den Schluss nahe, dass während wiederholter Kaltphasen alpine Arten ihren Lebensraum ausdehnen können und sich mit der Kordilleren-Flora vermischen. Besonders anpassungsfähige Arten mit effizienten Verbreitungsmechanismen können sich weit verbreiten und gehen in die nordamerikanische Flora ein. Besteht eine Landverbindung zwischen Asien und Amerika, können diese Arten nach Eurasien wandern und Teil der zirkum-subarktischen Flora werden. Die Anzahl der diesen Wanderungsprozess durchlaufenden Arten ist jedoch gering, aufgrund der dazu notwendigen Zeit, ineffizienter Verbreitungsmechanismen, der Bewältigung von Wanderungshindernissen und der Verfügbarkeit einer für ausreichende Zeit bestehenden Landverbindung.

Summary: At the end of the Late Wisconsin glaciation, the alpine vascular flora had only about 3.5 ka in which to colonize the 1,600 km north-south extent of the formerly glaciated terrain in western Canada as soon as the ice melted, before the temperatures caused them to become isolated on individual mountains. This paper describes the source areas/refugia, and estimates the efficacy of the migration from each source.

Basic data consists of details of the present-day vegetation from 29 alpine sites between the north coast of Alaska and Colorado. Over 70% of the alpine species in the Canadian Cordillera are only found on this continent. Distribution of individual species is sporadic, probably due to the short time available for colonization. Considerable speciation had occurred in each refugium during the glaciation, probably due to the greater success of mutations that could survive better than their parents in the new conditions. These new species allow the flora of each refugium to be identified.

The ca. 629 species present were categorized into nine groups based on existing distributions. Plots of the percentages of species in each category produced maps showing that the species present in the Middle Cordilleran refugium in the vicinity of Plateau Mountain and on the Queen Charlotte Islands mainly migrated north and south along the adjacent mountain ranges. There was limited recruitment from the Southern Cordilleran species due to the wetter and colder conditions in the formerly glaciated terrain. New Beringian species showed mixed success, whereas the North Cordilleran, North American and Cordilleran species colonized the whole Cordillera in the available time. There was limited invasion of a few species from the adjacent Prairies.

The results suggest that during repeated cold events, the alpine species can extend their ranges, becoming mixed to form the Cordilleran flora. The more plastic species with efficient dispersal mechanisms can spread and become part of the North American group. When the Bering Land Bridge is open, these species can then move to Eurasia, and have the potential to become part of the Circum-Subarctic group. However the number of species completing this process is small due to the time requirement, the inefficiency of dispersal, the overcoming of filters, and the availability of an open Bering Strait at a suitable time.

1 Introduction

The early collections by HOOKER and GRAY (1880) provided evidence of arctic species having migrated southwards along the Cordilleran mountain ranges as far south as the mountains of Colorado. Looking at these results, DARWIN (1883) proposed that the species moved south during prior glaciations when the climate was colder and tundra conditions were therefore widespread. Subsequently, evidence accumulated to indicate that there had been migrations of species across the Bering Strait in both directions (HULTÉN 1928). This prompted TOLMACHEV (1959) and HULTÉN (1962, 1971) to conclude that the vascular flora had undergone a more complex evolution than previously recognised.

HULTÉN (1962) quantified the migration of the flora across the Bering Strait but could not make further progress. The main problems stopping him were:

1. The flora contains many species that were unique to North America (ca. 70% HARRIS 2002). This is the result of the isolation of this continent from Eurasia during the Tertiary period resulting in the development of a largely endemic flora, although closely related to that of Eurasia.

2. The vast areas with different climates and topography.

3. Lack of data on the distributions of the vascular plant species on the North American continent.

4. Uncertainties concerning the synonymy between the Eurasian and North American species.

5. Lack of information on actual numbers and ages of the glaciations.

6. Lack of information on the timing and frequency of the opening and closing of the Bering Land Bridge.

Over the last 40 years, these problems have largely been solved, so it is now possible to obtain a reasonable idea of the overall picture. While a recent summary of the biodiversity of the alpine vegetation of the mountains south of the former Late Wisconsin ice front has been published (BOWMAN a. DAMM 2002), there has been no similar examination of the results of revegetation of the alpine areas in the areas vacated by the former ice sheets. Since the post-glacial period is short

(10–13.5 ka), the vascular plants have had limited time to move through the 1,600 km (N–S) void left after the Late Wisconsin glaciers melted (PREST et al. 1968; HARRIS 1985). This problem was especially acute for the alpine species that had less than 3,500 years for migration into the newly deglaciated areas before warmer temperatures caused them to become isolated on the upper mountain slopes. By 8,000 years BP, grasslands had moved north of Calgary and Drumheller, and the boreal forest was limited to the Foothills near Calgary and to the Foothills area 100 km west of Edmonton, i.e., the vegetation zonation was similar to today. This was followed by the Hypsithermal warm period which reached a climax about 6 ka BP in this area. Evidence from Plateau Mountain in SW Alberta indicates that mean annual air temperatures reached 2 °C warmer than at present on the tops of the mountains, so the vegetation zones had to migrate upwards, resulting in some species "walking the plank" off the top of the upper parts of the mountains (HARRIS 2002). Thereafter, the climate cooled resulting in two or three Neoglacial events starting about 4 ka, the last one producing the most extensive ice advances, thus wiping out much of the evidence of the earlier Neoglacial events (LUCKMAN a. OSBORN 1979). In between these cold events, the climate warmed, the last warm period from ca. 1200 to 1400 AD being slightly warmer than that today.

We now know that there were four main source areas or refugia from which alpine plant could emigrate into the formerly glaciated areas. These were the eastern part of Beringia in western Yukon Territory and Alaska (HARRIS 2004), the Queen Charlotte Islands (CALDER a. TAYLOR 1968), the nunataks around Plateau Mountain in southwestern Alberta (HARRIS 1991; HARRIS a. PRICK 1997), and the vast unglaciated areas in the northern Cordillera of the United States. BOWMAN and DAMM (2002) have discussed the available evidence for vascular plant diversity of the alpine plants in the area south of the main Wisconsin ice sheet. In the case of the montane boreal forest, revegetation of the formerly glaciated zone in western Canada was most effectively accomplished by the species from the Beringian refugium, since the vegetation was moving south into warmer areas which generally had enough precipita-

Table 1: Ages of the major cold events, marine transgressions and the Bering Land Bridge connections in the last 4 Ma (after HARRIS 2005)

Die Hauptkaltzeiten, marine Transgressionen und die Bering-Landverbindungen in den letzten 4 Mio. Jahren (nach HARRIS 2005)

Period	Cold event	Age (Ma)	Marine Transgression	Bering Land Bridge
Quaternary	Late Wisconsinan	0.011–0.025		
	Middle Wisconsinan	0.03–0.04		
	Early Wisconsinan	0.055–0.07		X
			Simpsonian	
	Middle Sangamon	0.088–0.1		
			Pelukian	
	Illinoian	0.125–0.22		
	Middle Yarmouthian	0.266–0.4		
			Anvillian	
	Kansan	0.5–0.6		X
	Aftonian	0.63–0.68		
	Nebraskan	0.7–1.0		
	Columbian	1.1–1.3		X
	Yukonian	1.35–1.6		
Pliocene	Montanan	1.9		X
	Wyoming	2.2		
			Fishcreekian	
	Alaskan	2.58		X
			Bigbendian	
	Californian	3.0		
			Colvillian	
	Patagonian	3.5–3.6		X

tion to support the species. The migration north from the southern refugia were limited by the differences in climate, both temperature and precipitation regimes (HARRIS in press).

This paper examines the effectiveness of the migration of alpine vascular plant species from these four refugia and the source areas involved. It also demonstrates that while the migrations across the Bering Strait were important in mixing North American and Eurasian floras as discussed by the earlier workers, they play a negligible role in explaining the present-day distribution of vegetation that recolonized the alpine areas of the Cordillera in Canada that were recently covered by the Late Wisconsin ice sheet. In the areas of the Cordillera south of the former main Wisconsin ice sheet, there is no significant relationship between numbers of species in the alpine zone and latitude (BOWMAN a. DAMM 2002). It will be shown that there are significant differences in numbers north of the former ice front, and the probable causes of these will be examined.

2 Glacial history

There were 14 cold events commencing 3.6 Ma ago (see Tab. 1, modified from HARRIS 2005, 219). A glaciation took place where sufficient precipitation occurred. Elsewhere, the colder climates resulted in the development of permafrost accompanied by expansion of the alpine tundra, thus allowing the alpine plant species to migrate into large areas at lower elevations. Many glacial events involved limited areas covered by ice sheets, so that spreading of the distributions of arctic and alpine species was facilitated. However, the glaciations became more extensive and frequent with time (BARENDREGT a. IRVING 1998), culminating in the Late Wisconsin glaciation which covered most of Canada (Fig. 1). It wiped out the pre-existing vegetation cover from a 1,600 km north-south section of the Cordillera including the mountain tops. Many arctic and alpine species survived on the tundra-covered mountains south of the ice sheets (WEBER 1965) which therefore served as a refugium.

3 Bering Land Bridge events

A small lowering in present-day sea levels would expose a wide corridor joining Asia and North America. This was realized by botanists early on, and HULTÉN (1928) described some of the North American species then recognized in the flora of Eastern Siberia. It was thought that each glaciation was accompanied by the opening of the land bridge, and its importance was discussed in HOPKINS (1967). However, studies of the timing of introduction of new microtine rodents into Alaska by REPENNING (1973) show that there were only eight exchanges of biota in the last 5.8 Ma. These migrations can be divided into four groups:

Group 1: Migration of subtropical species at 5.3 Ma and 4.8 Ma. These species currently have disjunct distributions in Colorado and Kirghizstan (WEBER 1965).

Group 2: Migration of warm temperate species during the first limited glaciation at 3.5 Ma. These species currently have northern limits to their distributions well south of the Bering Strait, e.g., *Heracleum lanatum* Michx.

Group 3: Exchange of biota at 2.5 Ma, 1.8 Ma, 1.2 Ma, and 0.45 Ma. These would have consisted of arctic species, and the earlier they entered the new continent, the greater the number of subsequent glaciations during which they could migrate across the continent and south along the Cordillera.

Group 4: The Late Wisconsin (^{16}O isotope stage 6) migration between 25 ka and 12 ka. These arctic species could only move south along the mountains from unglaciated Beringia during the short, late-glacial climate prior to 10.2 ka, and then only after the ice had retreated.

summer dry season and warmer weather than in the other centres.

Each refugium has some characteristic species that appear to have evolved during the last glaciation (Fig. 2). At times of extreme changes in climate, the biota is put under extreme stress and any mutants that have special advantages which help deal with the new environment will tend to out-compete the parent stock. In the case of the North Cordilleran refugium, about 60 new species were evolved in 15 ka, representing about 39% of the present-day alpine flora. The more southerly refugia showed a lower percentage of new species, e.g., 8% at Plateau Mountain, probably due to less extreme climatic changes. This is in contrast to the mountain ranges south of the former ice sheet, where BOWMAN and DAMM (2002, 38) conclude that only 2–7% of the species existing today are endemics, and these have been evolved over a much longer time span which included interglacials. There is a clear trend to increasing speciation with a more northerly latitude in a given time in the Cordillera which indicates that the more severe climatic conditions at higher latitudes favours natural selection at times of changing climates, as would be expected following the theory of natural selection of DARWIN (1883).

A similar pattern is seen in the Alps in Europe (FAVARGER 1972), where maximum endemism is seen in the Swiss and Austrian Alps (18%) where the last glaciation was most extensive. In the French Alps, the endemics make up only 13% of the alpine flora, while in the Carpathians, they represent 12%.
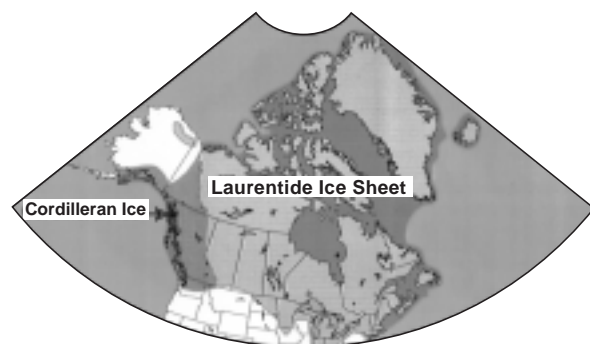
4 Refugia: source areas for post-glacial migration

Four principal areas acted as refugia for the vascular plant species displaced from the Cordillera during the Late Wisconsin event. In the north, the unglaciated east Beringia of Alaska and the Yukon Territory provided a source for the northern parts of the Cordillera (HARRIS 2004). On the west coast, the Queen Charlotte Islands provided a refugium for species that thrive under wet, maritime conditions (CALDER a. TAYLOR 1968; MATHEWES 1989). The third centre occurs in Southwest Alberta, on part of the front ranges of the eastern Cordillera centred on Plateau Mountain on limestone (HARRIS 1991; HARRIS a. PRICK 1997). South of the ice sheet, the ranges of the Cordillera in the northern United States provided a haven characterized by a

Fig. 1: The areas of North America that were glaciated during the Late Wisconsin event

Die vergletscherten Gebiete Nordamerikas während der Late Wisconsin-Vereisung

5 Sources of information

There are at least 29 sites (Fig. 3) along the north and central parts of the North American Cordillera (40–7°N) where there are sufficiently detailed studies of the alpine flora to provide reasonably reliable quantitative data on the species present (Appendix A). This table is based on published literature, coupled with field work by the writer to confirm and/or add information where possible. The collections of plants by the author were identified with the help of Bonnie Smith (University of Calgary), William J. Cody (Research branch, Department of Agriculture, Ottawa), Peter W. Ball (Erindale College, University of Toronto) and George W. Argus (Museum of Nature, Ottawa). The specimens are in the personal collection of the author (ca. 13,400 sheets). The names of the plants were standardised using KARTESZ and KARTESZ (1980), while plant distributions were checked using CHARKEVICZ (1985–1996), CODY (2002), CRONQUIST et al. (1972–1997), DORN (1992), GREAT PLAINS FLORA ASSOCIATION (1986),
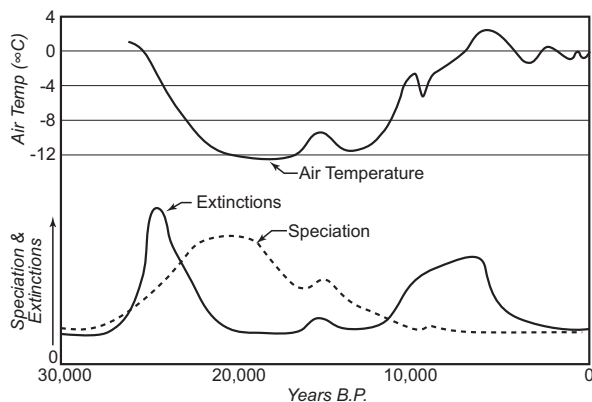

Fig. 2: Diagram showing the apparent timing of the phases of extirpation of species and the evolution of new taxa (speciation) in the alpine areas around the Late Wisconsin ice sheets during the last 30 ka. It is based on the fact that the more extreme the climatic condition during the last major cold event, the more abundant are the new species that evolve at a given site (see the text for the details)

Offenbarer Verlauf von Phasen des Artenaussterbens und der Entwicklung neuer Taxa (Speziation) in den alpinen Gebieten im Umfeld des Eisschilds der Wisconsin-Vereisung in den letzten 30.000 Jahren. Das Diagramm basiert auf der Tatsache, dass je extremer die klimatischen Bedingungen während der letzten großen Kaltzeit waren, desto ausgeprägter sich die Abundanz neu entwickelter Arten an einem Standort darstellt (für Details, siehe Text)

HADLEY (1987), HITCHCOCK et al. (1955–1969), HULTÉN (1958, 1962, 1968), PORSILD and CODY (1980), and WELSH et al. (1993).

In the case of the stations in Alaska, published sources of information included EDWARDS and ARMBRUSTER (1989), MURRAY (1992), NOBLE (1978), NOBLE and SANDGREN (1976), SHELTON (1962) and SANDGREN and NOBLE (1978). This was augmented by field work by the author and by colleagues including Bonnie Smith. The data for the Yukon and Northwest Territories were collected during annual visits from 1980 to the present, but includes the results of the biologists from the University of British Columbia collected from the Kluane Lake area (see HARRIS 2004), as well as the collections of other botanists whose collections are deposited in the herbarium in the Biology Department of the University of Calgary (UAC). A considerable amount of data is also available in CODY (1996), COOK and ROLAND (2002), PORSILD (1951), and PORSILD and CODY (1980).

LORD and LUCKHURST (1974) and PRATT (1991) have data on the Summit Lake area, northern British Columbia, but this has been augmented by more detailed field collecting. The data for Pink Mountain, south to Plateau Mountain, Alberta is based primarily on field work, augmented by data from collections deposited in the UAC herbarium and by published data by BAPTIE (1968), BEDER (1967), BROAD (1973), CRACK (1977), HARRIS (1991), HARRIS and PRICK (1997), KNAPIK (1973), KNAPIK et al. (1973) and KUCHAR (1975).

There is a considerable body of literature on the Waterton Lakes-Glacier National Peace Park (see CHOATE a. HARBECK 1967; KUIJT 1982; LESICA 2002, and the references contained therein). BAMBERG and MAJOR (1968) and DORN (1992) provide data on the Flint Creek region of Montana while JOHNSON and BILLINGS (1962) described the alpine flora of the Beartooth Mountains. To the south, the classic study by KOMÁRKOVÁ (1979) provides data on the Indian Peaks area of the Colorado Front Range.

Westwards, ELLISON (1954) and WELSH et al. (1993) have worked on the alpine flora of the Wasatch Plateau in Utah, while the flora of the Beaverhead National Forest, Montana, has been studied by COOPER et al. (1997). The Mount Hood area in Oregon has been discussed in HALL (1967) and more recently by TITUS and TSUYUZAKI (1999), and the alpine flora of the Olympic Peninsula, Washington State, was studied by DOUGLAS (1971, 1972).

Finally in Canada, ACHUFF et al. (1984) described the flora of the Mount Revelstoke region, and the author has subsequently made additional studies. The

Table 2: The nine categories of geographical distribution represented amongst the alpine species used in Appendix A. This grouping follows the concepts of HULTÉN (1962) and BOWMAN and DAMM (2002) in distinguishing between taxa with markedly different distributions closely related to geography, climate and the history of the species, but the categories have been modified where necessary to cope with the study area.

Die neun Kategorien der geographischen Verbreitung zur Untergliederung der alpinen Arten in Appendix A. Diese Gruppierung folgt den Konzepten von HULTÉN (1962) und BOWMAN and DAMM (2002) dahingehend, dass zwischen Taxa mit deutlich unterschiedlicher Verbreitung (eng verknüpft mit Geographie, Klima und Artgeschichte) differenziert wird. Wo notwendig wurden jedoch die Kategorien modifiziert und an den Untersuchungsraum angepasst.

Geographical Distribution	Characteristics
Circum-Subarctic	Found throughout the Northern hemisphere south of the Arctic coast.
Cordilleran	Distributed from Alaska and Yukon south to the unglaciated portions of Washington, Montana and Idaho, or even further south.
Beringian	Species found on both sides of the Bering Strait.
South Cordilleran	Taxa mainly distributed south of the area glaciated during the Late Wisconsin event.
Middle Cordilleran	Species limited in distribution to the region around the unglaciated portions of the west coast (mainly the Queen Charlotte Islands) or the Front ranges of the Rocky Mountains around Plateau Mountain, west of Claresholme.
North Cordilleran	Taxa with their distribution centred on the unglaciated area of east Beringia in Alaska and the western Yukon Territory.
Amphi-Atlantic	Species mainly occurring around both sides of the Atlantic Ocean.
North American	Taxa found across the width of North America.
Prairie-Cordilleran	Found in the drier regions of both the mountains and the plains.

classic work of CALDER and TAYLOR (1968) deals with the flora of the Queen Charlotte Islands in extensio.

The species present at each site were divided into nine categories by distribution in North America and elsewhere (Tab. 2), and these were used to produce maps showing the post-glacial migration or lack of it for each category. The numbers were also recalculated as percentages of the total flora found at that site. The categories were selected along the lines of the traditional Holarctic ones used by HULTÉN (1962) and by BOWMAN and DAMM (2002), modified to deal with the distinct distributions of vascular plants found in the Cordillera of Canada.

Most categories are obvious, but the Amphi-Atlantic category, first invoked by HULTÉN (1958), and has resulted in considerable debate. ABBOTT and BROCHMANN (2003) re-examined the evidence for it and concluded that it was a valid category. The *"in situ glacial survival"* (the nunatak hypothesis, first suggested by BLYTT 1876, 1882) was widely accepted until the 1960s. Since then evidence has accumulated to indicate presumed postglacial migration of at least 77 north boreal, alpine and arctic taxa across the Atlantic Ocean (BROCHMANN et al. 2003). Additional species can be identified in the North American literature, but the exact method of immigration has yet to be determined.
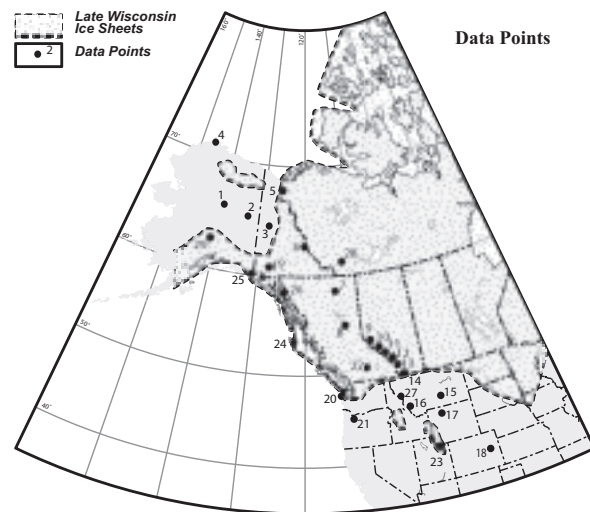

Fig. 3: Locations of the 29 alpine sites used in this study together with the maximum extent of the Late Wisconsin ice sheet

Lage der in dieser Studie verwendeten 29 alpinen Standorte und maximale Ausdehnung des Eisschildes während der Late Wisconsin-Vereisung

Whether the migrations were entirely post-Wisconsinan may also bear further study since some Amphi-Atlantic species also occur as far west in North America as the eastern slopes of the Rocky Mountains, e.g., *Pedicularis flammea* L., *Armeria maritima* (Mill.) Willd. ssp. *labradorica* (Walln.) Hultén, *Typha angustifolia* L., and *Saxifraga aizoides* L. (Fig. 4). They would have had to migrate thousands of kilometers immediately after deglaciation to produce this distribution during the early Holocene. The palaeogeography during the Wisconsin deglaciation argues against this being possible. On the other hand, if species of organisms could cross the Atlantic Ocean during the Holocene period, why could they not have done so during previous postglacial climatic events? Regardless of these problems, the evidence currently available argues for the inclusion of the Amphi-Atlantic as a valid category in the present study.

6 Results

Although there were at least 629 species found at the 29 sites (see Appendix A), the largest number of species reported from a given site was only 281. Most northern sites had 50 to 90 species present, and the numbers generally increased southwards. One obvious conclusion from examining the data in Appendix A is that the actual numbers of species present on the alpine slopes of the mountains in the formerly glaciated montane areas are noticeably lower than the numbers from the areas on the nunataks, e.g., Plateau Mountain (192), as well as those for the areas to the south of the former ice front, e.g., the Beaverhead National Forest, Montana (281), and the Indian Peaks area of the Colorado Front Range (245). The higher number found at Sunshine Ski Area (144) is probably due to the much higher precipitation that falls in that area. The higher numbers at Slims River, Kluane Lake (163), are from mountains on the margin of the unglaciated area of eastern Beringia.

BOWMAN and DAMM (2002, Fig. 3.3) found only a minor increase in number of species in the alpine zone with decreasing latitude in the area south of the former Late Wisconsin ice sheets. The increase was not statistically significant, but statistics of the kind are questionable since the mountain ranges have varying ranges of altitudes above tree line. Accordingly they inevitably have varying amounts of land and micro-environments suitable for colonisation by vascular plants. Furthermore, the alpine plants occupy specific zones on mountains that are high enough to have a wide range of available elevation. In any case, snow cover (OGILVIE 1969), moisture availability (OBERBAUER a. BILLINGS 1981), drainage (CHABOT a. BILLINGS 1972), nutrient availability (BOWMAN a. DAMM 2002), slopes, substrates and their stability (OGILVIE 1969) vary from mountain
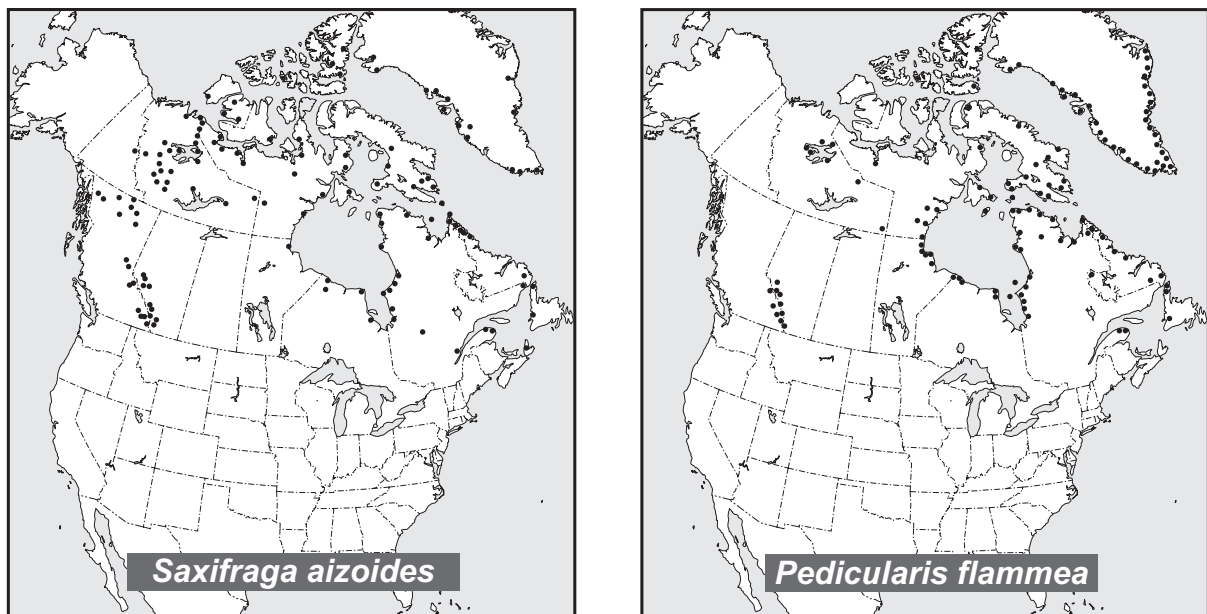

Fig. 4: Distribution of *Saxifraga aizoides* Michx. and *Pedicularis flammea* L. in North America

Verbreitung von *Saxifraga aizoides* Michx. und *Pedicularis flammea* L. in Nordamerika

to mountain, and a given alpine species may not find a suitable habitat in which they can live. Thus the use of alpine vegetation to demonstrate the expected increase in numbers of species with decreasing latitude is not valid. For this reason, no comparisons of numbers of species with individual environmental factors such as climate can be employed using the data in Appendix A.

Distributions of individual species are sporadic and scattered (HARRIS 2002), reflecting the difficulties in colonizing the vast deglaciated region in such a short time. This is also indicated by the fact that in both Alberta and British Columbia, approximately 30% of the flora is regarded as rare (KERSHAW et al. 2001; DOUGLAS et al. 2002).

The actual and relative abundances of the 629 arctic/alpine species in the nine geographical distributions are shown in table 3. It will be seen that the South Cordilleran and Circum-Subarctic groups are by far the most abundant, but they show markedly different efficiency in dispersal. The Circum-Subarctic species are spread fairly evenly along the formerly glaciated area, whereas the South Cordilleran species disappear a short distance northwards of the former ice margin (Fig. 5), as previously noted by OGILVIE (1962). This is probably due to the South Cordilleran species being adapted to a marked dry summer season and warmer growing temperatures in contrast to the colder and continuously wet weather characteristic of the alpine zone in the deglaciated areas. The Circum-Subarctic species are plastic species capable of coping with a much wider range of environmental conditions.

Table 3: Relative abundances of the 629 arctic/alpine taxa in Appendix A, arranged by categories of geographical distribution (see Tab. 2)

Relative Abundanz von den 629 arktisch-alpinen Taxa in Appendix A, gegliedert nach Kategorien der geographischen Verbreitung (siehe Tab. 2)

Category	Number of taxa
South Cordilleran	200
Circum-Subarctic	122
Beringian	74
Cordilleran	62
North American	55
North Cordilleran	45
Middle Cordilleran	33
Prairie-Cordilleran	32
Amphi-Atlantic	6
Total	629

The Middle Cordilleran species characteristic of the Queen Charlotte Islands refugium spread north and south along the wet coastal ranges but generally did not enter the drier interior of the Cordillera (Fig. 6). The species from the Plateau Mountain refugium were calciphiles, so were limited to the areas of limestone bedrock east of Revelstoke. They, too, spread north to about 58° latitude along the eastern ranges of the Rocky Mountains (Fig. 6). The North Cordilleran species had the advantage of being adapted to cold
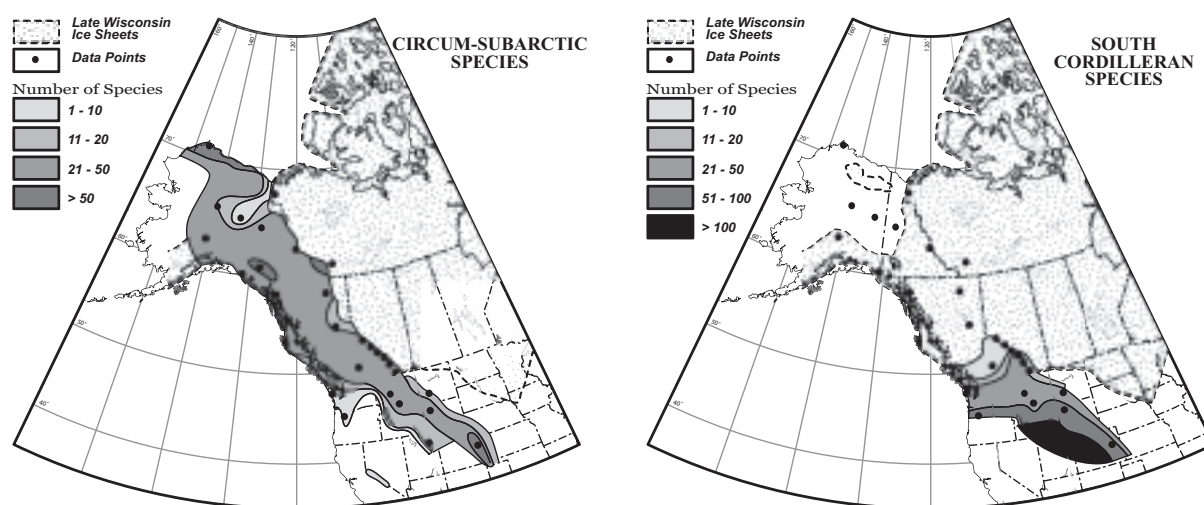

Fig. 5: Present-day distribution of Circum-Subarctic and South Cordilleran alpine species along the Cordillera

Aktuelle Verbreitung von zirkum-subarktischen und alpinen Arten der südlichen Kordillere entlang der Gebirgskette

conditions and about 10 of them had no difficulty spreading their range southwards (Fig. 7). Longer growing seasons, more sunlight and warmer summer temperatures in the areas to the south obviously aided the migration.

Cordilleran and North American species moved throughout the deglaciated zone, but were noticeably more successful along the western ranges (Fig. 8), some even reaching the unglaciated area south of the front

of the former ice sheets in Montana. The Beringian species moved reasonably efficiently southwards, but note the peak numbers in Colorado. These are presumably due to their arrival there as a result of migrations following earlier glaciations. A few species spread into the dry Front Ranges of the Rocky Mountains from the Prairies adjacent to southern Alberta (Fig. 9), while a few Amphi-Atlantic species also reached the Front Ranges of the Rocky Mountains of the Eastern
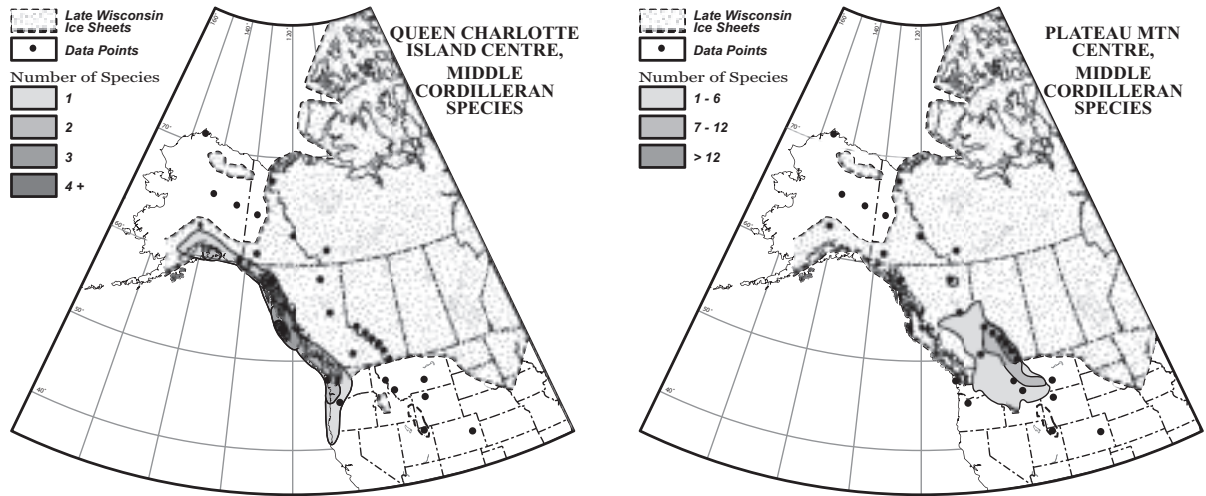
Fig. 6: Present-day distribution of the Middle Cordilleran alpine species of the Queen Charlotte and Plateau Mountain refugia along the Cordillera

Aktuelle Verbreitung alpiner Arten der mittleren Kordillere aus den Queen Charlotte- und Plateau Mountain-Refugien entlang der Gebirgskette
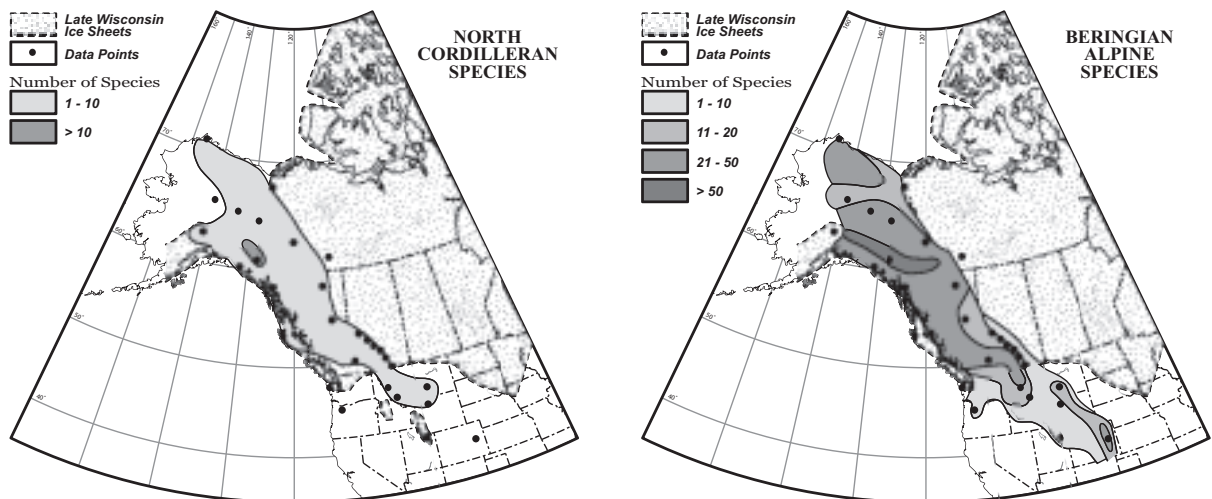
Fig. 7: Present-day distribution of the North Cordilleran and Beringian alpine species along the Cordillera

Aktuelle Verbreitung alpiner Arten der nördlichen Kordillere und Bering-Kategorie entlang der Gebirgskette

Cordillera. As noted above, it seems more probable that they migrated west prior to the last major glaciation and survived the latter in one of the refugia.

7 Origin of the Circum-Subarctic flora

One of the questions that still needs to be resolved is the origin of the Circum-Subarctic flora. The evolution of new species in specific regions is relatively easy to explain, but to get a given new species spread across the mountains throughout the Northern Hemisphere while others remain in limited areas is more difficult. HULTÉN (1971) was able to explain how lowland species might evolve in Eastern Asia and the more plastic species could then spread across to Europe, but explaining the origin of the Circum-Subarctic alpine flora is more difficult. The flora is currently found on isolated mountain ranges and peaks at the middle and lower latitudes,
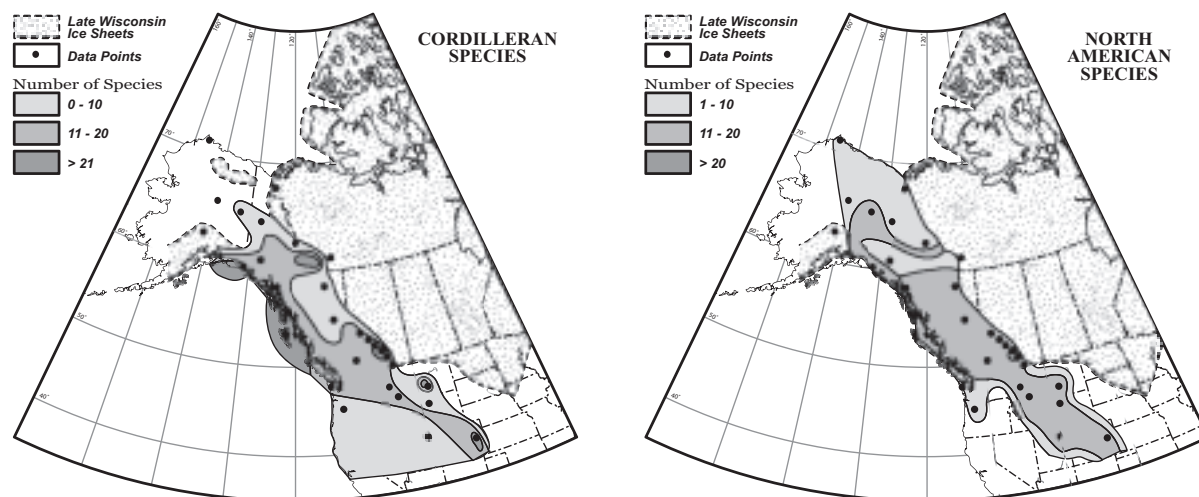
Fig: 8: Present-day distribution of the Cordilleran and North American alpine species along the Cordillera

Aktuelle Verbreitung alpiner Arten der Kordilleren-Gruppe und nordamerikanischen Gruppe entlang der Gebirgskette
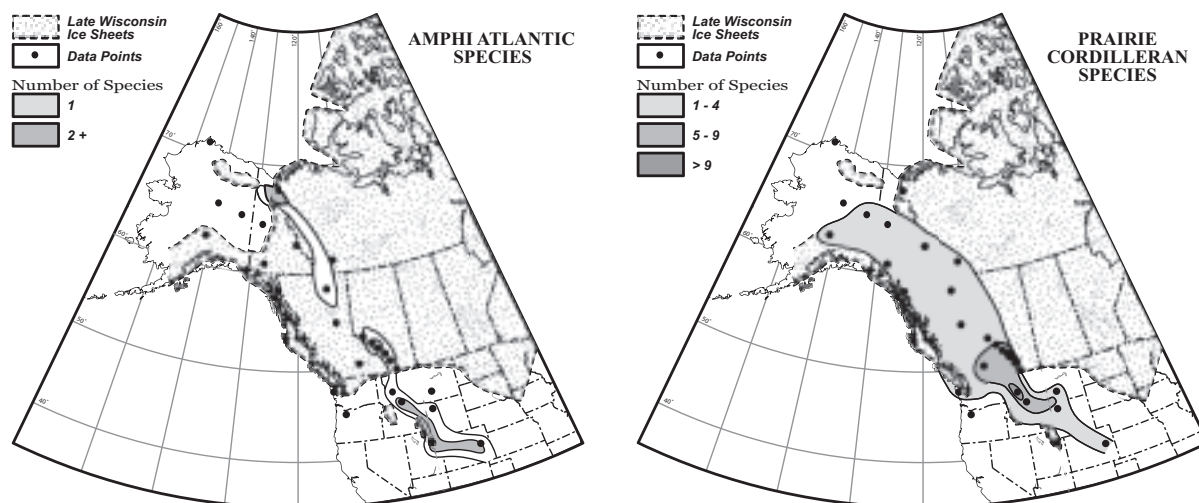
Fig. 9: Present-day distribution of the Amphi-Atlantic and Prairie-Cordilleran alpine species along the Cordillera

Aktuelle Verbreitung alpiner Arten der Amphi-Atlantischen Gruppe und der Prärie-Kordilleren-Gruppe entlang der Gebirgskette

and it is very difficult for the species to cross an intervening inhospitable area to move to another location. At higher latitudes in North America, the widespread glaciation of the environment would have interrupted any mingling of the arctic species and resulted in the destruction of the pre-existing vegetation in vast areas. This would also be true in parts of Northern Europe.

The results of the present study suggest a mechanism for producing the Circum-Subarctic flora by a process of gradual expansion of the ranges of individual species at the beginning and end of cold events. It starts with the evolution of mutations that enable the mutant species to out-compete the parent species under the stress of changing environmental conditions. Maximum speciation occurs in the colder northern environments, resulting in new taxa more capable of handling the harsh new environment. On deglaciation, many of these species (46 out of about 60 in the case of the North Cordilleran alpine flora) readily move south in the limited time available before the climate becomes too warm for further migration. Given multiple glaciations, these species would have a number of opportunities to expand their distribution and become part of the Cordilleran and North American species in a relatively short time. New species that evolved in more southern refugia are generally less well adapted to rapid migration into the deglaciated areas due to the colder and wetter climate there. In any case, they will also be able to spread across the region of arctic Canada, north of the tree line, so mingling with the other species and producing a North American distribution.

Once the species are established throughout the Cordillera, they are in a position to move across the Bering Strait, if and when a land bridge develops. Thereafter, they can spread across northern Eurasia unless constrained by filters, and will eventually become part of the Circum-Subarctic flora. If this is correct, then the Circum-Subarctic flora is a conglomeration of the most plastic species that mainly evolved under harsh environmental conditions during times of climatic change, usually at high latitudes, and then spread rapidly across all the areas of the world using cold climatic events and land bridges when the opportunity rose.

8 Conclusions

When a glaciation occurs, the alpine species become restricted to harsh conditions in refugia around the ice sheet, but can spread out, colonising lower lying areas that develop a suitable climate but lack glaciers. Both during the beginning and the end of the glaciation, any

mutations which help the species survive the climatic changes that are occurring will tend to cause speciation. This speciation is roughly proportional to the degree of stress that the species are encountering.

In the case of the Late Wisconsin glaciation, four key refugia were sources for colonization of the deglaciated alpine areas in the short time available. The South Cordilleran area was home to the largest number of species, but proved an ineffective source due to the drier and warmer conditions with more insolation at lower latitudes. The Queen Charlotte Island and Plateau Mountain refugia of the Middle Cordillera were more effective, but the new species from these centres were adapted to specific environmental conditions not found throughout the Cordillera. Although the North Cordilleran area had fewer total species, it had a higher proportion of new, mutant species, and most of these were able to migrate south to less harsh alpine conditions in a very short period of time. Repetition of this process with each cold event can result in the new species developing first a Cordilleran distribution and also a North American distribution.

Actual distributions of individual species remain very patchy, indicating that the time available for establishment throughout the formerly glaciated area was too short before the warming of the climate curtailed further colonization. Undoubtedly another cold event without actual glaciation of the Cordillera would permit completion of the migration process.

The Cordilleran and North American species can migrate into new deglaciated environments very rapidly and appear to be derived primarily from the incorporation of such new species into the more widespread flora of the Cordillera and arctic tundra across northern Canada during successive cold events. These species could also take advantage of any opening of the Bering Land Bridge and so have the potential of becoming part of the Circum-Subarctic flora.

References

ABBOTT, R. J. a. BROCHMANN, C. (2003): History and evolution of the arctic flora: in the footsteps of Eric Hultén. In: Molecular Biology 12, 299–313.

ACHUFF, P. L.; HOLLAND, W. D.; COEN, G. M. a. VAN TIGHEM, K. (eds.) (1984): Appendix A. Plants of Mount Revelstoke and Glacier National Parks, British Columbia. In: ACHUFF, P. L.; HOLLAND, W. D.; COEN, G. M. a. VAN TIGHEM, K. (eds.): Integrated Resource Description 1. Publication, Alberta Institute of Pedology M-84-11. Edmonton, 191–212.

BAMBERG, S. A. a. MAJOR, J. (1968): Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. In: Ecological Monographs 38, 127–168.

BAPTIE, B. (1968): Ecology of the alpine soils of Snow Creek valley, Banff National Park, Alberta. Unpubl. M.Sc. thesis. Calgary.

BARENDREGT, R. W. a. IRVING, E. (1998): Changes in the extent of the North American ice sheets during the Late Cenozoic. In: Canadian Journal of Earth Sciences 35, 505–509.

BEDER, K. (1967): Ecology of the alpine vegetation of Snow Creek valley, Banff National Park. Unpubl. M.Sc. thesis. Calgary.

BLYTT, A. (1876): Essay on the immigration of the Norwegian flora during alternating rainy and dry periods. Christiania.

– (1882): Die Theorie der wechselnden kontinentalen und insularen Klimate. In: Botansk Jahrbuch 2, 1–50.

BOWMAN, W. D. a. DAMM, M. (2002): Causes and consequences of Alpine vascular plant diversity in the Rocky Mountains. In: KÖRNER, C. a. SPEHN, E. M. (eds.): Mountain biodiversity: a global assessment. Boca Raton, 35–47.

BROAD, J. (1973): Ecology of alpine vegetation at Bow Summit, Banff National Park. Unpubl. M.Sc. thesis. Calgary.

BROCHMANN, C.; GABRIELSEN, T. M.; NORDAL, I.; LANDVIK, J. Y. a. ELVEN, R. (2003): Glacial survival or *tabula rasa*? The history of the North Atlantic biota revisited. In: Taxon 52 (3), 417–450.

CALDER, J. A. a. TAYLOR, R. L. (1968): Systematics of the vascular plants. Flora of the Queen Charlotte Islands 1. Monograph, Research Branch Agriculture Canada 4. Ottawa.

CHABOT, B. F. a. BILLINGS, W. D. (1972): Origins and ecology of the Sierra alpine flora and vegetation. In: Ecological monographs 42, 163–199.

CHARKEVICZ, S. S. (1985–1996): Vascular plants of the Soviet Far East. Leningrad. (in Russian)

CHOATE, C. M. a. HARBECK, J. R. (1967): Alpine plant communities at Logan Pass, Glacier National Park. In: Proceedings of the Montana Academy of Sciences 27, 36–54.

CODY, W. J. (1996): Flora of the Yukon Territory. Ottawa.

COOK, M. B. a. ROLAND, C. A. (2002): Notable vascular plants from Alaska in Wrangell-St. Elias National Park and Preserve with comments on the floristics. In: Canadian Field-Naturalist 116 (2), 192–304.

COOPER, S. V.; LESICA, P. a. PAGE-DUMROESE, D. (1997): Plant Community classification for alpine vegetation on the Beaverhead National Forest, Montana. General Technical Report 362. Ogden, UT.

CRACK, S. N. (1977): Flora of Wilcox Pass, Jasper National Park, Alberta. Unpubl. M.Sc. thesis. Calgary.

CRONQUIST, A.; HOLMGREN, A. H.; HOLMGREN, N. H.; REVEAL, J. L. a. HOLMGREN, P. K. (1972–1997): Intermountain Flora: vascular plants of the Intermountain West, USA 1–6. Bronx, NY.

DARWIN, C. (1883): Origin of the species. London.

DORN, R. D. (1992): Vascular plants of Montana. Cheyenne.

DOUGLAS, G. W. (1971): The alpine-subalpine flora of the North Cascade Range, Washington. In: Wasmann Journal of Biology 29, 129–168.

– (1972): Subalpine plant communities of the western North Cascades, Washington. In: Arctic and Alpine Research 4, 147–160.

DOUGLAS, G. W.; MEIDINGER, D. a. PENNY, J. T. (2002[2]): Rare native vascular plants of British Columbia. Victoria.

EDWARDS, M. E. a. ARMBRUSTER, W. S. (1989): A tundra-steppe transition on Kathul Mountain, Alaska, USA. In: Arctic and Alpine Research 21, 296–304.

ELLISON, L. (1954): Subalpine vegetation of the Wasatch Plateau, Utah. In: Ecological Monographs 24, 89–184.

FAVARGER, C. (1972): Endemism in the montane floras of Europe. In: VALENTINE, D. H. (ed.): Taxonomy, phytogeography and evolution. London, 191–204.

GREAT PLAINS FLORA ASSOCIATION (1986): Flora of the Great Plains. Lawrence.

HADLEY, K. S. (1987): Vascular plant distributions within the central and southern Rocky Mountains, USA. In: Arctic and Alpine Research 19, 242–251.

HALL, L. (1967): A survey of vascular plants above timberline on Mount Hood, Oregon. In: Madroño 19, 130–137.

HARRIS, S. A. (1985): Evidence for the nature of the early Holocene climate and palaeogeography, High Plains, Alberta Canada. In: Arctic and Alpine Research 17, 49–67.

– (1991): Vascular plant checklist – Plateau Mountain area. In: Pica 11 (3), 14–22.

– (2002): Biodiversity of the vascular timberline flora in the Rocky Mountains of Alberta. In: KÖRNER, C. a. SPEHN, E. M. (eds.): Mountain biodiversity: a global assessment. Boca Raton, 49–57.

– (2004): Source areas of North Cordilleran endemic flora: evidence from Sheep and Outpost Mountains, Kluane National Park, Yukon Territory. In: Erdkunde 58, 62–81.

– (2005): Thermal history of the Arctic Ocean environs adjacent to North America during the last 3.5 Ma and a possible mechanism for the cause of the cold events (major glaciations and permafrost events). In: Progress in Physical Geography 29 (2), 1–19.

– (in press): Diversity of vascular plant species in the Montane Boreal Forest of western North America. In: Erdkunde 62 (1).

HARRIS, S. A. a. PRICK, A. (1997): The periglacial environment of Plateau Mountain: an overview of current periglacial research. In: Polar Geography 27, 113–136.

HITCHCOCK, C. L.; CRONQUIST, A.; OWNBEY, M. a. THOMPSON, J. W. (1955–1969): Vascular plants of the Pacific Northwest 1–5. Seattle.

HOOKER, J. D. a. GRAY, A. (1880): The vegetation of the Rocky Mountain region and a comparison with that of other parts of the world. In: U.S. Geol. and Geog. Surv. Bull. 6, 1–62.

HOPKINS, D. M. (ed.) (1967): The Bering Land Bridge. Stanford, CA.

HULTÉN, E. (1928): On the American component of the flora of eastern Siberia. In: Svensk Botanisk Tidskrift 22, 220–229.

– (1958): The amphi-Atlantic plants and their phytogeographical connections. Kungliga Svenska Vetenskapsakademiens Handlingar, series 1, 8. Stockholm.

– (1962): Vascular cryptograms, conifers, monocotyledons. The circumpolar plants 1. Kungliga Svenska Vetenskapsakedemiens Handlingar, series 4, 8. Stockholm.

– (1968): Flora of Alaska and neighboring territories. Stanford, CA.

– (1971): Dicotyledons. The cicumpolar plants 2. Kungliga Svenska Vetenskapsakedemiens Handlingar, series 4, 13. Stockholm.

JOHNSON, P. L. a. BILLINGS, W. D. (1962): The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. In: Ecological Monographs 32, 105–135.

KARTESZ, J. T. a. KARTESZ, R. (1980): A synonymized checklist of the Vascular Flora of the United States, Canada, and Greenland. Chapel Hill.

KERSHAW, L.; GOULD, J.; JOHNSON, D. a. LANCASTER, J. (2001): Rare vascular plants of Alberta. Edmonton.

KNAPIK, L. J. (1973): Alpine soils of the Sunshine area, Canadian Rocky Mountains. Unpubl. M.Sc. thesis. Edmonton.

KNAPIK, L. J.; SCOTTER, L. W. a. PETTAPIECE, W. W. (1973): Alpine soils and plant communities of the Sunshine Area of Banff National Park. In: Arctic and Alpine Research, 5, A161–A170.

KOMÁRKOVÁ, V. (1979): Alpine vegetation of the Indian Peaks area, Front Range, Colorado Rocky Mountains. Flora et vegetatio mundi 7. Vaduz.

KUCHAR, P. (1975): Alpine tundra communities and *Dryas octapetala* ssp. *hookeriana* in the Bald Hills, Jasper National Park. Unpubl. Ph.D. thesis. Edmonton.

KUIJT, J. (1982): A flora of Waterton Lakes National Park. Edmonton.

LESICA, P. (2002): A flora of Glacier National Park, Montana. Corvallis.

LORD, T. M. a. LUCKHURST, A. J. (1974): Alpine soils and plant communities of a Stone sheep habitat in northeast British Columbia. In: Northwest Science 48, 38–51.

LUCKMAN, B. H. a. OSBORN, G. (1979): Holocene glacier fluctuations in the middle Canadian Rocky Mountains. In: Quaternary Research 11, 52–77.

MATHEWES, R. W. (1989): The Queen Charlotte Islands refugium: a paleoecological perspective. In: FULTON, R. J. (ed.): Quaternary Geology of Canada and Greenland. Ottawa, 486–491.

MOSS, E. H. (1983²): Flora of Alberta. Toronto.

MURRAY, D. F. (1992): Vascular plant diversity in Alaskan arctic tundra. In: Northwest Environment Journal 8, 29–52.

NOBLE, M. G. (1978): Sherman Glacier vegetation. In: Northwest Science 52, 351–357.

NOBLE, M. G. a. SANDGREN, C. D. (1976): A floristic survey of the Muir Point, Glacier Bay National Monument, Alaska. In: Bulletin of the Torrey Botanical Club 103, 132–136.

OBERBAUER, S. a. BILLINGS, W. D. (1981): Drought tolerance and water use by plants along an alpine topographic gradient. In: Oecologia 50, 325–331.

OGILVIE, R. T. (1962): Notes on plant distribution in the Rocky Mountains of Alberta. In: Canadian Journal of Botany 40, 1091–1094.

– (1969): The mountain forest and alpine zones of Alberta. In: NELSON, J. G. a. CHAMBERS, M. J. (eds.): Vegetation, soils and wildlife. Toronto, 26–44.

PORSILD, A. E. (1951): Botany of southeastern Yukon adjacent to the Canol Road. National Museums of Canada Bulletin 121, Biolog. Ser. 41. Ottawa.

PORSILD, A. E. a. CODY, W. J. (1980): Vascular plants of continental Northwest Territories, Canada. Ottawa.

PRATT, V. E. (1991): Wildflowers along the Alaska Highway. Anchorage.

PREST, V. K.; GRANT, D. R. a. RAMPTON, V. N. (1968): Glacial Map of Canada. Geological Survey of Canada, Map 1253A.

REPENNING, C. A. (1973): Faunal exchanges between Siberia and North America. In: Canadian Journal of Anthropology 1, 37–44.

SANDGREN, C. D. a. NOBLE, M. G. (1978): A floristic survey of a subalpine meadow on Mt. Wright, Glacier Bay National Park. In: Northwest Science 52 (4), 329–336.

SHELTON, N. (1962): A study of vegetational zonation in Mount McKinley National Park, Alaska. Unpubl. M.Sc. thesis. Durham, NC.

TITUS, J. H. a. TSUYUZAKI, S. (1999): Ski slope vegetation of Mount Hood, Oregon, USA. In: Arctic and Alpine Research 31, 283–292.

TOLMACHEV, A. (1959): Sur l'origine de la flore arctique: quant ou, et comment surgit la flore arctique? In: Proceedings of the IX International Botanical Congress, August 19–29, 1959, Montreal, Canada 2: Abstracts. Toronto, 399.

WEBER, W. A. (1965): Plant geography of the southern Rocky Mountains. In: WRIGHT, H. E. Jr. a. FREY, D. G. (eds.): The Quaternary of the United States. Princeton, 433–468.

WELSH, S. L.; ATWOOD, N. D.; GOODRICH, S. a. HIGGINS, L.C. (eds.) (1993): A Utah flora. Provo, UT.

Appendix A: Alpine taxa present at the 29 sites along the North American Cordillera shown in figure 3

Appendix A: An den 29 Standorten entlang der nordamerikanischen Kordillere (siehe Abb. 3) vorkommende alpine Taxa

Location	Latitude	Longitude	Circum-Subarctic	Beringian	N. Cordilleran	M. Cordilleran	S. Cordilleran	Cordilleran	Cordilleran-Prairie	N. American	Amphi-Atlantic	Introduced	Total Species
1. Fairbanks, Alaska.	64 59' N	147 40' W	47.6% (20)	28.6% (12)					2.4% (1)	21.4% (9)			40
2. Eagle, Alaska.	65 21' N	142 16' W	14.0% (7)	38.0% (19)	14.0% (7)			2.0% (1)	4.0% (2)	28.0% (14)			40
3. North Fork Pass, Y.T.	64 32' N	138 13' W	38.9% (28)	43.1% (31)	5.5% (4)			2.8% (2)		9.7% (7)			72
4. Barrow, Alaska.	71 19' N	156 40' W	61.4% (54)	31.8% (28)	2.3% (2)					2.3% (2)		2.3% (2)	88
5. Rat Pass, Y.T./N.W.T.	68 00' N	133 00' W	30.8% (12)	41.0% (16)	2.6% (1)				2.6% (1)	17.9% (7)	5.1% (2)		39
6. MacMillan Pass, Y.T.	63 30' N	130 00' W	44.3% (31)	30.0% (21)	1.4% (1)			10.0% (7)	2.9% (2)	11.4% (8)			70
28. Nahanni Park, N.W.T.	61 50' N	128 10' W	38.8% (64)	24.8% (41)	4.2% (7)			15.2% (25)	1.8% (3)	13.9% (23)	0.6% (1)	0.6% (1)	165
7. Summit Lake, B.C.	57 45' N	124 30' W	32.5% (27)	41.0% (34)	3.6% (3)			4.8% (4)	1.2% (1)	15.7% (13)	1.2% (1)		83
8. Pink Mountain, B.C.	57 04' N	122 52' W	25.0% (11)	34.1% (15)	2.3% (1)			2.3% (1)	2.3% (1)	34.1% (15)			44
9. Jasper, Alberta.	52 47' N	118 07' W	40.2% (37)	13.0% (12)	5.4% (5)		6.5% (6)	20.7% (19)	1.1% (1)	13.0% (12)			92
10. Parker Ridge, Alberta.	52 11' N	117 07' W	23.1% (15)	9.2% (6)	6.2% (4)	3.1% (2)	12.3% (8)	26.2% (17)		18.5% (12)	1.5% (1)		65
11. Bow Summit, Alberta.	51 40' N	116 30' W	30.0% (23)	9.1% (4)	6.1% (4)	3.0% (2)	7.6% (5)	27.3% (18)	1.5% (1)	22.7% (15)	1.5% (1)	1.5% (1)	74
12. Sunshine, Alberta.	51 04' N	115 45' W	24.3% (35)	11.1% (16)	6.9% (10)	3.4% (5)	11.1% (16)	23.6% (34)	4.2% (6)	12.5% (18)	2.1% (3)	0.7% (1)	144
13. Plateau Mountain, Alberta.	50 13' N	114 31' W	21.9% (42)	8.9% (17)	3.6% (7)	6.3% (12)	15.6% (30)	16.7% (32)	7.8% (15)	17.7% (34)	1.0% (2)	0.5% (1)	192
14. Waterton-Glacier Parks, Alta-Ma.	49 00' N	113 40' W	22.7% (27)	12.6% (15)	1.7% (2)	5.9% (7)	24.4% (39)	15.1% (18)	5.0% (6)	10.9% (13)	0.8% (1)	0.8% (1)	129
15. Flint Creek, Montana.	46 10' N	113 10' W	14.3% (16)	13.4% (15)	0.9% (1)	3.6% (4)	26.8% (30)	19.6% (22)	3.6% (4)	17.0% (19)			111
16. Beartooth Mountains, Montana.	45 00' N	109 30' W	26.0% (44)	13.6% (23)	0.6% (1)	0.6% (1)	40.8% (69)	4.1% (7)	3.0% (5)	10.7% (18)	0.6% (1)		169
17. Big Snowy Mountains, Montana.	46 50' N	109 20' W	30.0% (27)	7.7% (7)	2.2% (2)	3.3% (3)	26.8% (30)	13.2% (12)	6.6% (6)	15.6% (14)			101
18. Indian Peaks, Colorado.	40 03' N	105 36' W	32.2% (79)	12.2% (30)			38.8% (95)	8.2% (20)	1.2% (3)	6.5% (16)	0.8% (2)		245
29. Mount McKinley, Alaska. #	64 00' N	151 00' W	50.0% (25)	32.0% (16)	4.0% (2)			2.0% (1)	4.0% (2)	8.0% (4)			50
19. Slims River, Kluane, Y.T.	61 02' N	138 27' W	23.3% (51)	36.8% (56)	9.8% (15)	0.7% (1)	0.7% (1)	7.8% (12)	0.7% (1)	15.7% (24)	0.7% (1)	0.7% (1)	163
22. Mount Revelstoke, B.C.	51 40' N	118 30' W	13.6% (6)	9.0% (4)		4.5% (2)	20.0% (9)	34.1% (15)		18.2% (8)			44
27. Beaverhead National Forest, Ma.	45 00' N	113 40' W	13.5% (38)	9.3% (26)		0.7% (2)	51.2% (144)	12.5% (35)	3.9% (11)	7.5% (21)	1.1% (3)	0.3% (1)	281
23. Wasatch Plateau, Utah.	39 30' N	111 20' W	8.4% (14)	1.2% (2)			74.6% (123)	2.4% (4)	0.6% (1)	9.8% (16)		3.0% (5)	165
25. Glacier Bay, Alaska.	58 38' N	136 10' W	31.9% (36)	33.3% (38)	5.3% (6)	0.9% (1)		19.5% (22)		8.8% (8)			111
26. Juneau Icefields, Alaska.	58 30' N	145 00' W	40.6% (37)	30.8% (28)	5.5% (5)			15.4% (14)	1.1% (1)	6.6% (6)			91
24. Queen Charlotte Islands, B.C.	53 30' N	132 30' W	20.3% (25)	28.5% (35)	3.3% (4)	2.4% (3)		30.9% (38)		8.1% (10)			115
20. Olympic Peninsula, Washington.	47 40' N	123 30' W	11.1% (8)	2.8% (2)		1.4% (1)	52.8% (38)	16.7% (12)	5.6% (4)	9.7% (7)			72
21. Mount Hood, Oregon.	45 30' N	121 40' W	7.1% (6)	4.8% (4)	1.2% (1)		71.4% (60)	9.5% (8)		4.8% (4)			83

No grasses, sedges or rushes included.