Pan-Arctic variation in *Juniperus communis*: historical biogeography based on DNA fingerprinting

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Abstract

Twelve populations of *Juniperus communis* L. were sampled from throughout the arctic, world-wide and DNA fingerprinting (RAPDs, Random Amplified Polymorphic DNAs) was performed. Based on 152 RAPD bands, all of the populations (*J. communis* var. *depressa* Pursh and *J. communis* var. *megistocarpa* Fern. and St. John) from the western hemisphere formed one group and all of the populations of the eastern hemisphere (including Greenland and Iceland), formed another group that included *J. communis* var. *communis* and *J. communis* var. *saxatilis* Pall., except for the Kamchatka population that was quite dissimilar to any population examined. Most likely, the current sites of all of the populations were covered with ice or otherwise inhospitable, up to or during the late Pleistocene (ca. 12,000 BP). Therefore, these populations are recent in origin. The path of re-colonization appears to have been northward in North America. Greenland appears to have been colonized from Iceland plants, which in turn came from northern Europe. The Kamchatka population seems likely to have come from Japan.
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1. Introduction

The genus *Juniperus* consists of approximately 68 species and 36 varieties (using the more widely accepted variety category instead of the subspecies category) (Adams, 1999, 2000a,b,c,d, 2001; Adams et al., 2002 a,b). All the taxa grow on the Laurasian land mass, except *J. procera* Hochst. ex. Endl. which grows along the rift mountains in east Africa, thence into the southern hemisphere (Adams et al., 1993) and some of the Mediterranean *Juniperus* species such as *J. oxycedrus* L., *J. phoenicea* L., and *J. thurifera* L. that grow in the mountains of the northernmost part of Africa (Morocco, Algeria).

Juniperus communis is the only *Juniperus* species that occurs in both hemispheres (Fig. 1). Farjon (1998) recognized var. *communis* L. (n. Europe), var. *depressa* Pursh (North America), var. *megistocarpa* (e. Canada), and var. *saxatilis* Pall. (Europe, Siberia, central Asia, far east, Greenland, Iceland, and far western North America). Farjon did not recognize var. *hemispherica* (J. and C. Presl.) Nyman (Sicily, Mediterranean) nor var. *oblonga* (M.-Bieb.) Parl. (Caucasus Mountains). In addition, Adams et al. (2002 a) have recently reported that in Japan, var. *saxatilis* and var. *nipponica* (Maxim.) E.H. Wilson are quite distinct from var. *saxatilis* from Europe.

Most of the northern portion of *J. communis*' range was glaciated during the Pleistocene (Flint, 1971; Graham, 1999). Comparing the distribution of *J. communis* (Fig. 1) versus the ice cover (Fig. 2), only the Alaska and Kamchatka populations might have been ice-free. However, whether *J. communis* survived in either location is uncertain. Vast areas of the northern hemispheres that now have populations of *J. communis* have been colonized since the last glacial maximum (12,000–18,000 BP; Flint, 1971). During the maximum of the Wisconsin glaciation, which occurred ca. 18,000 BP, the ice covered nearly all of Canada, except a large part of the Yukon, and the Arctic Archipelago, reaching the Columbia Plateau in the west and the Ohio–Mississippi basin and New England in the east (Fig. 2). In Alaska, ice cover was restricted to southern Alaska and the Aleutians. Greenland was completely covered by ice. In North America, two large and confluent ice masses constituted the ice cover: the Cordilleran Ice Sheet, which occupied the Canadian Cordillera and the Laurentian Ice Sheet which covered the regions east of the Rocky Mountains. Smaller ice sheets occupied the High Arctic and Newfoundland. Mountain glaciers were also present in the western USA. Sea levels lowered by as much as 200 m and large expanses of the continental shelf were colonized by vegetation. Between 14,000 and 9,000 BP, in response to the warming of the climate, the ice receded and ice sheets separated and broke into several domes. The Cordilleran sheet thinned and fractionated into ice caps and then into families of valley glaciers. By the end of this period, much of the Arctic and coastal areas of Greenland were ice-free. The retreat of the Laurentide ice mass, north of the St Lawrence Valley allowed marine transgression. Large post-glacial lakes, such as Agassiz and McConnnell, existed along the western margins. Recession of the ice further accelerated and by 8400 years BP, ice remained in the Canadian Cordillera and Arctic only in areas where glaciers persist today. The Laurentide sheet receded rapidly following the marine invasion of the Hudson's Bay
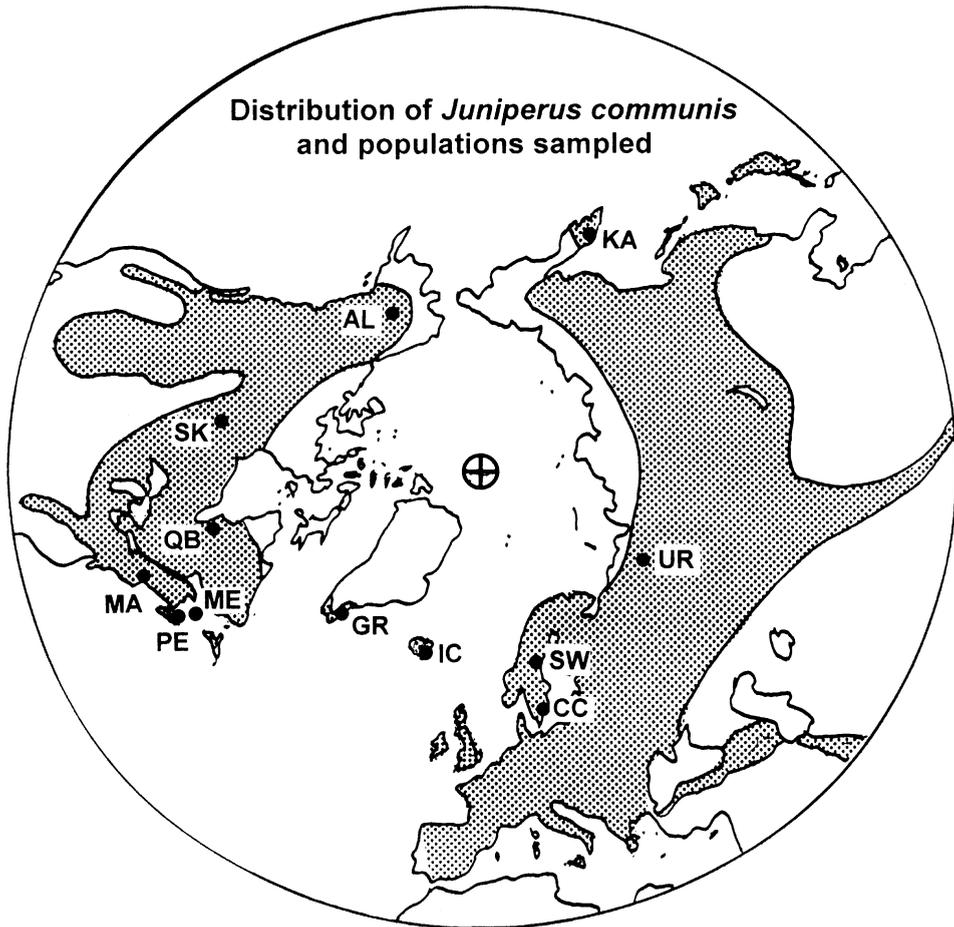
Fig. 1.   Distribution of *J. communis* and populations sampled. AL, Alaska; SK, Saskatchewan; QB, Quebec; ME, *J. commuis* var. *megistocarpa*, Magadalene Island, Quebec; PE, Prince Edward Island; MA, Massachusetts; GR, Greenland; IC, Iceland; SW, Sweden (*J. communis* var. *saxatilis*); CC, *J. communis* var. *communis*, Sweden; UR, Ural Mountains, Russia; KA, Kamchatka Peninsula.

region, separating into Labrador and Keewatin domes. By 8000 years BP, the Tyrrel sea was transgressing the Hudson's Bay Lowlands and the Champlain sea had almost retreated from the St Lawrence Valley. Ice gradually disappeared from Keewatin, New Quebec, and Labrador. In Greenland, the ice sheet reached a minimum about 5000 BP, followed by a readvancement to it present limits (Flint, 1971; Clague, 1989; Dyke et al., 1989; Occhietti, 1989).

J. communis appeared as soon after or at the end of the last glacial period in northern Britain (Bennett et al., 1992), in North America (Yu, 1997) and in Siberia (Pisaric et al., 2001). Whether *J. communis* existed in the Kamchatka peninsula during the last ice age is unknown to the present authors. It is now generally thought

Fig. 2.   Pleistocene ice cover with populations of *J. communis* sampled indicated by solid circles. Map based on Flint (1971).

that the Kamchatka peninsula probably lacked ice sheets and only local alpine glaciers occurred during the peak of the last glacial period (Savoskul, 1999). But severe conditions in western Beringia up to 12,800 BP (Lozhkin et al., 1993) probably made the area inhospitable for *J. communis*.

Of particular biogeographical interest is the colonization of Iceland and Greenland, and the question of the migration of *Juniperus* across the Bering land bridge between Siberia and Alaska. The purpose of this study was to sample populations in northern latitudes (Fig. 1) and examine their historical biogeography.

2. Materials and methods

Specimens used (plus acronyms used, and see Fig. 1) in this study: *J. communis* var. *communis*: Adams 7846, 7848, Stockholm, Sweden (CC); *J .communis* var. *saxatilis*: Adams 9211–13 (ex. K. Hoegh) 60°43′ N, 46°22′ W, Qaqortoq, Greenland (GR); Adams 9207–9 (ex. T. Thorfinnsson) Egilsstadir, Iceland (IC); Adams 9213–15 (ex. G. Samuelson) Umea, Sweden (SW); Adams 9178–80 (ex. J.W. Leverenz), 25 km NW of Labytnangi, near the Ural Mountains, Russia (UR); Adams 9181–83 (ex. J.W. Leverenz), Esso, Kamchatka Peninsula, Russia (KA); *J. communis* var. *depressa*: Adams 7582–84, Denali National Park, Alaska, USA (AL); Adams 7094–96, Neimembian Lake, Saskatchewan, Canada (SK); Adams 8572–75, Boxbourough, Massachusetts, USA (MA); Adams 9394 (ex. M. Blondeau TQ 92293, 58°42″ N, 69° 56′ W, Quebec, Canada), Adams 9395 (ex. N. Dignard 3773, 52°31′07″ N, 79°09′33″ W, Quebec, Canada) (QB); Adams 8578, Greenwich, Prince Edward Island, Canada (PE); *J. communis* var. *megistocarpa*, Adams 8575–77, Magdalen Islands, Quebec, Canada (ME). Voucher specimens are deposited at SRCG herbarium.

One gram (fresh weight) of the foliage was placed in 20 g of activated silica gel and transported to the lab, thence stored at−20 °C until the DNA was extracted. DNA was extracted from the leaves by use of the Qiagen Dneasy Plant Mini Kit. The Random Amplified Polymorphic DNA (RAPD) analyses follow that of Adams and Demeke (1993). Ten-mer primers were purchased from the University of British Colombia (5′–3′): 116:TAC GAT GAC G; 134: AAC ACA CGA G; 153: GAG TCA CGA G; 204: TTC GGG CCG T; 212: GCT GCG TGA C; 218: CTC AGC CCA G; 239: CTG AAG CGG A; 249: GCA TCT ACC G; 250: CGA CAG TCC C; 265: CAG CTG TTC A; 327: ATA CGG CGT C; 338: CTG TGG CGG T; 346: TAG GCG AAC G; 347: TTG CTT GGC G; 375: CCG GAC ACG A; 391: GCG AAC CTC G; 413: GAG GCG GCG A; 431: CTG CGG GTC A.

PCR was performed in a volume of 15 μl containing 50 mM Tris–HCl (pH 9), 2.0 mM MgCl$_2$, 0.01% gelatin and 0.1% Triton X-100, 0.2 mM of each dNTPs, 0.36 μM primers, 0.3 ng genomic DNA, 15 ng BSA and 0.6 unit of Taq DNA polymerase (Promega). A control PCR tube containing all components, but no genomic DNA, was run with each primer to check for contamination. DNA amplification was performed in an MJ Programmable Thermal Cycler (MJ Research, Inc.). The thermal cycle was: 94 °C (1.5 min) for initial strand separation, then 40 cycles of 38 °C (2 min), 72 °C (2 min), 91 °C (1 min). Two additional steps were used: 38 °C (2 min) and 72 °C (5 min) for final extension.

Bands that occurred once or did not show fidelity within the two replicated samples of each taxon were eliminated. It should be noted that these bands contain very useful information for the study of genetic variance and individual variation, but are merely 'noise' in the present taxonomic study. Bands were scored in four classes: very bright (=6); medium bright (=5), faint (=4) and absent (=0). See Adams and Demeke (1993) for details on electrophoresis and RAPD band scoring.

Similarity measures were computed using absolute character state differences (Manhattan metric), divided by the maximum observed value for that character over

all taxa (=Gower metric, Gower, 1971; Adams, 1975). Principal coordinate analysis (PCO) of the similarity matrix follows Gower (1966).

3. Results and discussion

One hundred and fifty-two RAPD bands were found to vary among the populations and these were used to construct a minimum spanning network (Fig. 3). This revealed
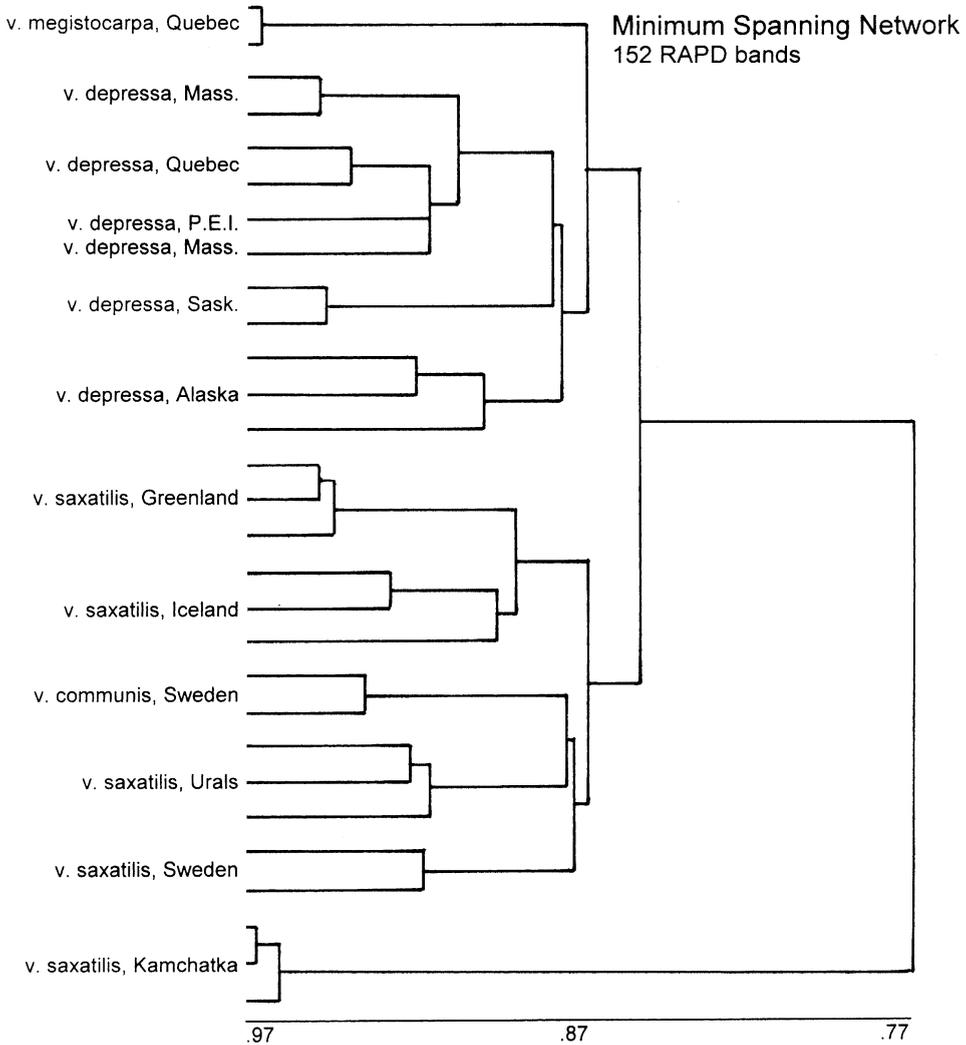

Fig. 3.   Minimum Spanning Network based on 152 RAPD bands. Note the divergence of the Kamchatka population and the clustering of populations by hemisphere.

several interesting facets: the Kamchatka population is the most distinct of any sampled; *J. communis* clusters by hemisphere not necessarily by traditional variety; variation among individuals, even after cleaning the data by removing single events (i.e. a single band not found in other individual) was often as large as between populations. Notice that the plants from Iceland and Alaska populations were linked at lower levels of similarity than many of the populations' links. One of the most uniform populations was the var. *megistocarpa* population from Magdalen Islands, where these endemic plants have very large fruits (9–13 mm). Magdalen Islands archipelago extends only approximately 70 km long and from less than a kilometer to 10 km wide. The plants are found on the fore dunes in limited locations on the islands. Inbreeding and the Founder's effect are very likely responsible for the small amount of variation found.

The other very uniform population is in the Kamchatka peninsula (Fig. 3). There was almost no variation among these individuals. This population is also very isolated from other populations.

Several of the varieties of *J. communis* were included in this study. All the plants in this study were small shrubs or prostrate plants except the small trees (2–3 m tall) of *J. communis* var. *communis* from Sweden. These var. *communis* plants (CC) link with var. *saxatilis* plants (UR) from the eastern hemisphere (Fig. 3). There appears to be no large distinction in the RAPDs of var. *communis* and var. *saxatilis* from Europe. Additional studies are being made involving all *J. communis* varieties to better address this question.

Factoring the similarity matrix by use of PCO enables one to isolate trends in the matrix. The major trend (coordinate 1, Fig. 4 and 26%), is the separation of the populations from the eastern and western hemispheres and, of course, the very distinct nature of the Kamchatka population. PCO 2 (16%) principally separates the Kamchatka population and PCO 3 (8%) separates the Greenland and Iceland populations from the European populations (Fig. 4). Notice that var. *communis* and var. *megistocarpa* (closed stars and open stars,respectively in Fig. 4) are not very separated from var. *saxatilis* (the rest of the individuals in Fig. 4).

To better visualize the geography of these similarities, the minimum spanning network was plotted onto the distribution map of *J. communis* (Fig. 5). Several important trends are now evident. The eastern North America plants are very similar (0.920, 0.921). The linkage of MA to PE and to QB is suggestive of a colonization pathway. The colonization pathway to Iceland (IC) and Greenland (GR) appears to be from Europe (Sweden, SW) and not from North America (however the second largest link from Greenland is to Saskatchewan (SK), but at a much lower level of similarity). Several bird species stop in Iceland en route between Europe and Greenland: geese (*Anser brachyrhyncus* Baillon; *Branta leucopsis* Bechstein; *Anser albifrontus* Scop. and *Branta bernicla* L.); waders (sandpiper, *Calidris canutus* L.; sanderling, *Calidris alba* Pallas; turnstone, *Arenaria interpres* L.) and passerines (the Lapland bunting, *Calcarius lapponicus* L.). Several bird species common in Greenland also occur in Iceland, such as the ptarmigan (*Lagopus mutus* Montin), snow bunting (*Plectrophenax nivalis* L.) and the Arctic redpoll (*Carduelis hornemanni* Holboll) that is closely related to the redpoll. As these species occur in both countries,
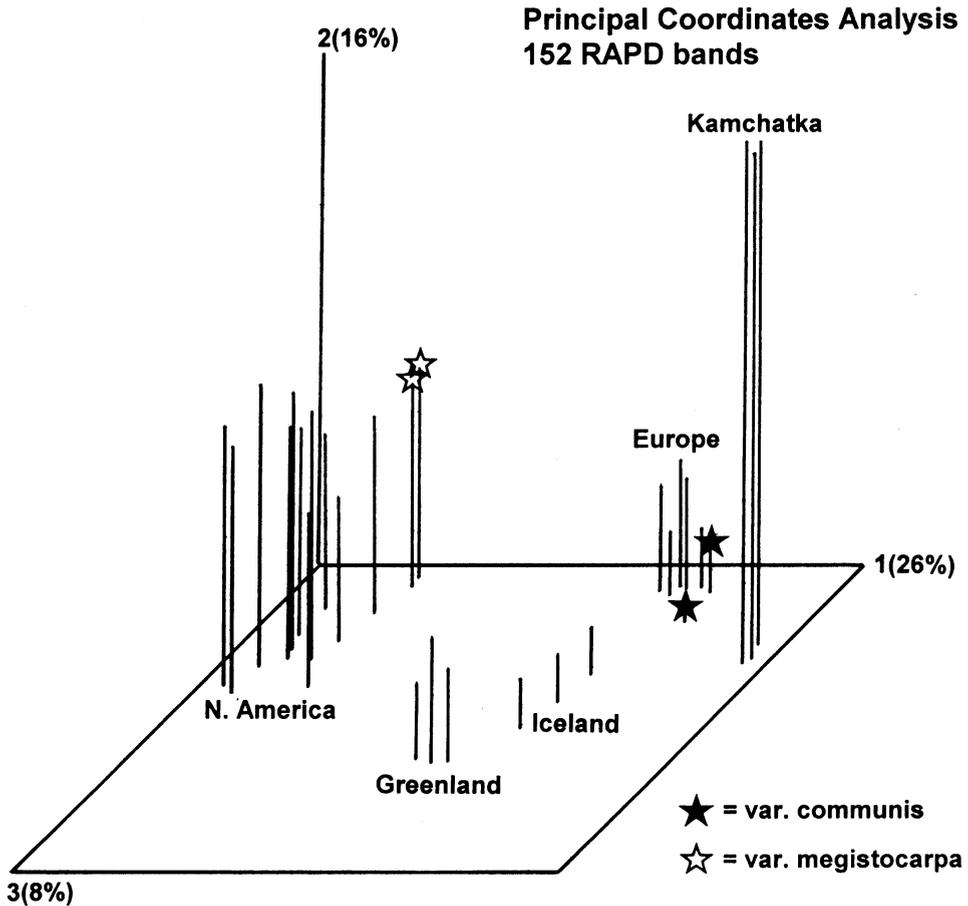
Fig. 4.   PCO of the similarity matrix based on 152 RAPD bands. Note the progression from Europe to Iceland to Greenland.

it is very likely that they migrate between Iceland and Greenland, and indeed snow buntings tagged in Iceland have been found in Greenland. The Greenland gerfalcon (*Falco rusticolus* Linnaeus) is known to visit Iceland (where there is an indigenous population). It is possible that they eat birds that feed on juniper berries. Falcons often gulp the crop whole and its remains have been found in their vomit.

There is no evidence that the Alaska population (AL) came from across the Bering Strait, but rather from inland in North America. Of course, it did not come from Saskatchewan (SK), because SK was glaciated. All of the northern populations likely were colonized by spring bird migrations from more southerly regions. In North America, the dispersion of juniper seeds by birds has long been documented (Holthuijzen and Sharik, 1985; McAtee, 1947; Phillips, 1910).

Again we see the divergence of the Kamchatka (KA) population by its lower similarity to the Ural Mountains (UR) population. On the Kamchatka peninsula, *J.*
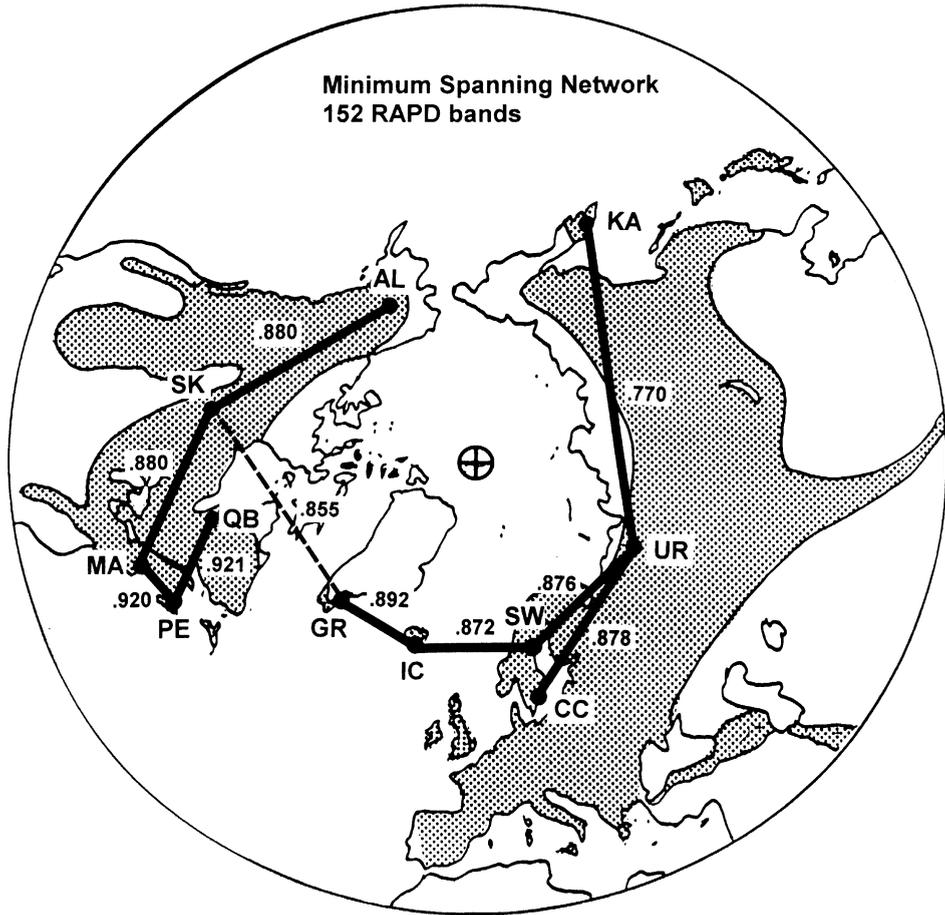
Fig. 5. Minimum spanning network linking populations. Notice the linkage of Greenland (GR) to Iceland (IC) to Sweden (SW). The dotted line is the second most similar link to GR (from SK).

communis is apparently restricted to the areas below about 56° N (Florin, 1963). Our collection site near Esso (55°58′ N, 158°38′ E) on the Kamchatka peninsula, thus, appears to be close to its northern limit on the peninsula. Hansson (1995) described *J. communis* as being locally abundant on the peninsula, and that was true at our collection site. No *J. communis* was found on a neighboring, colder slope which was dominated by *Pinus pumila*. The locally abundant distribution and restriction to the southern part of the peninsula may reflect the requirement of soil disturbance and places for birds to perch (Vedel, 1961), as well as competition from *P. pumila*. This may also reflect the retreat of the northern forest limits over the past 4000 years (except for the last 100 years, when the tree line again seems to be advancing (Kremenetski et al., 1998; MacDonald et al., 1998). These vegetational observations suggest that *J. communis* (and trees in general) did not likely grow at

our collection site during the last glaciation. It might be noted that *J. communis* is also reported to occur on the Commander Islands off the east coast of the Kamchatka peninsula, as well as on the Sakhalin Islands to the south (Florin, 1963). Thus, oceanic climates do not seem to restrict its distribution as much as some of the other conifers on the Kamchatka peninsula. The gap in the distribution of *J. communis*, which occurs in Beringia, is associated with a slower recovery from tundra conditions in that area in comparison with both eastern and western Beringia (Lozhkin et al., 1993).

The introduction (or re-introduction) of *J. communis* to Kamchatka since the last glacial maximum is certainly possible by migrating birds. A good candidate is the Naumann's Thrush (*Turdus naumanni* Temm.) that migrates to the Kamchatka peninsula from overwintering sites on the main island of Japan and China. It is reported to feed on berries during its migration during the winter months (Dement'ev and Gladkov, 1968, vol. 6, pp. 512–514). Northern bluetail (*Tarsiger cyanurus* Pallas) is also reported to feed on berries during migration from similar areas (Dement'ev and Gladkov, 1968, vol. 6, pp. 625–628). Locally, birds such as the Kamchatka Capercaillie (*Tetrao urogalloides kamtschaticus* Kittlitz) could be responsible for distributing the berries (Dement'ev and Gladkov, 1968, vol. 4, pp. 112–115).

It seems likely that *J. communis* was not present on the Kamchatka peninsula during the last glacial maximum, but was (re-) introduced by migrating birds. Considerable variation has been reported in *J. communis* from Japan (Adams, 2001). The Kamchatka *J. communis* may have come from Japan. Additional studies of all the *J. communis* varieties will be needed to address this question.

In summary, this study revealed that all of the populations (*J. communis* var. *depressa* and *J. communis* var. *megistocarpa*) from North America formed one group and all of the populations of the eastern hemisphere (including Greenland and Iceland), formed another group that included *J. communis* var. *communis* and *J. communis* var. *saxatilis*, except for the Kamchatka population that was quite dissimilar to any population examined. Most likely, the sites of all of the populations were covered with ice or uninhabitable to *J. communis* during the late Pleistocene (ca. 12,000 BP). Therefore, these populations are recent in origin. The path of re-colonization appears to have been northward in North America. Greenland appears to have been colonized from Iceland plants, which in turn came from northern Europe. The Kamchatka population seems likely to have come from Japan.

4. Acknowledgments

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