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Circumpolar phylogeography of *Juncus biglumis* (Juncaceae) inferred from AFLP fingerprints, cpDNA sequences, nuclear DNA content and chromosome numbers

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Abstract

We explored the circumpolar phylogeographic history of the arctic-alpine *Juncus biglumis* using amplified fragment length polymorphisms (AFLPs), sequences of cpDNA, relative nuclear DNA content and chromosome numbers. The analyses of the AFLP and cpDNA data gave congruent results and revealed three distinct clades. One of them, represented by a single population from the Taymyr peninsula in northern Siberia, had approximately fourfold larger genome size than the other samples and produced an AFLP pattern that was too aberrant to be analysed together with the rest of the data set. The two other clades represented different ploidy levels ($2n=60$ and 120) as judged from chromosome counts of selected populations but differed only in c. 6% relative DNA content. Based on the AFLP and partly also on the cpDNA data, each of the two main clades was further subdivided into two well-supported subgroups. Three of the subgroups were widespread and exhibited largely overlapping distribution patterns. The fourth subgroup seems to be absent from the North Atlantic region and from western Siberia. We suggest that the four subgroups diverged during isolation in different glacial refugia during the Quaternary. Interestingly, individuals of both main clades were encountered in geographically close populations in eastern Greenland and even within a single population from Svalbard, indicating that both areas were colonised at least twice. The different genome sizes and ploidy levels strongly suggest that the three main clades represent distinct gene pools and act as cryptic species.

Keywords: AFLP; Arctic-alpine; cpDNA; Flow cytometry; Immigration; *Juncus*; Ploidy levels

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1. Introduction

In contrast to the growing body of literature exploring circumpolar phylogeographic patterns in arctic animals (reviewed in Hewitt, 2004), few studies have searched for such patterns in arctic plant species. Five years have passed since it was stated that further range-wide phylogeographic studies on circumpolar plants "should lead to a more complete understanding of arctic plant evolution since the late Tertiary and make clear whether isolation in glacial refugia was as important in shaping patterns of biodiversity within arctic plants as in temperate species" (Abbott et al., 2000). So far, only two such studies have been published in full, namely a pioneering study on the purple saxifrage, *Saxifraga oppositifolia* (Abbott et al., 2000) and a recent study on the bog bilberry, *Vaccinium uliginosum* (Alsos et al., 2005). Whereas phylogeographic breaks in arctic animals exhibit some well-founded congruencies across the investigated species (Hewitt, 2004), the low number of relevant

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studies has impeded a comparative phylogeographic approach towards understanding the driving forces that shaped the distribution patterns of arctic plants.

In the arctic-alpine *S. oppositifolia*, there are two main clades of cpDNA haplotypes with mainly Eurasian and North American distributions, respectively, overlapping on the Taymyr Peninsula in northern Central Siberia and in northern Greenland (Abbott et al., 2000; Abbott and Brochmann, 2003; Abbott and Comes, 2004). One clade is distributed from eastern North America over Greenland and Europe to Taymyr, and the other ranges from Taymyr over North America to Greenland. The authors suggest that *S. oppositifolia* first occurred in the Arctic in the Taymyr area, from where it migrated east- and westwards to achieve a circumpolar distribution (Abbott et al., 2000; Abbott and Brochmann, 2003). Late-Tertiary fossils from Greenland suggest that, that area had already been colonised before the Pleistocene. The populations in the southern European mountain ranges (Alps, Pyrenees) have widespread Eurasian haplotypes. In the more boreal-montane *V. uliginosum* sensu lato three cpDNA clades were identified, one amphi-Atlantic, one Beringian and one "arctic-alpine" lineage (Alsos et al., 2005). The latter has a circumpolar distribution and also includes one fully circumpolar haplotype. The divergence among the three clades was estimated to have taken place before the onset of the major Quaternary glaciations >700,000 years ago.

Our study taxon, *Juncus biglumis* L., belongs to a group of closely related species with its centre of diversity in the Himalayas (Kirschner, 2002). It is one of the most characteristic vascular plants of the Arctic (Polunin, 1940) and has a continuous circumpolar distribution reaching well over 80° north on Greenland and Ellesmere Island (Canada; Hultén and Fries, 1986). The species also grows in more southern mountain ranges such as the Rocky Mountains of North America, the Central Asian mountain ranges from the Altai north-eastwards, and— isolated from the arctic populations—in the European Alps (Fig. 1). In the North Atlantic region, it is found on several islands and archipelagos, e.g., in the British Isles (Scotland), Iceland, Greenland and Svalbard. Two ploidy levels ($2n = 60$, 120) have been documented in *J. biglumis* so far, both of them in Scandinavia (Knaben and Engelskjøn, 1967; Engelskjøn and Knaben, 1971). Chromosome counts from other areas have only revealed the higher ploidy level ($2n = >100$, Johnson and Packer, 1968; $2n = 130 \pm 10$, Mosquin and Hayley, 1966), but are less exact.

The aim of the present study is to unravel the phylogeographic history of *J. biglumis* mainly focussing on western Eurasia and Greenland using amplified fragment length polymorphisms (AFLPs), sequences of chloroplast DNA (cpDNA), flow cytometry data and chromosome numbers. In particular, we ask (1) whether the Alpine populations are most closely related to the Scandinavian populations as hypothesised in the classical biogeographic literature (Vierhapper, 1918; Noack, 1922); and (2) what are the source areas for the colonisation of Greenland and Svalbard.

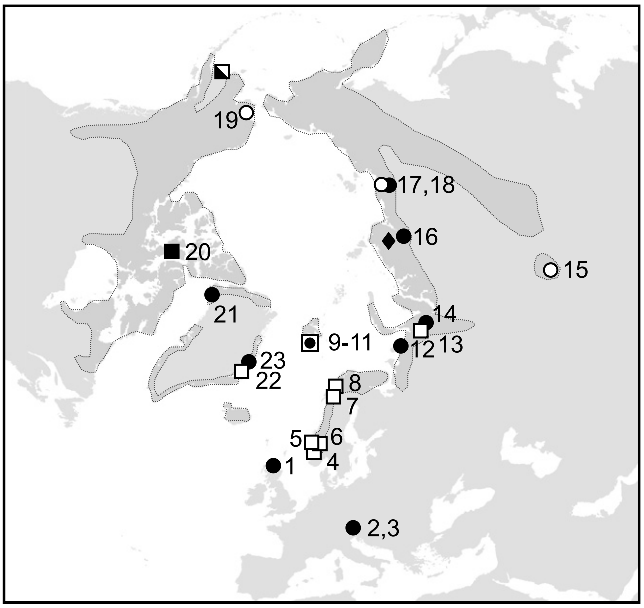

Fig. 1. Total distribution (broken line) and sampled populations of *Juncus biglumis*. Symbols indicate different nuclear DNA content and phylogeographical groups: filled circles, *Alps-group*, open circles, *W. Canada-group*, open squares, *Scandinavia-group*, and filled square, *E. Canada-group* (see the text for more details). A diamond symbolises the putatively highly polyploid Ary–Mas population with approximately fourfold nuclear DNA content. The sample from Cape Espenberg, Alaska (semi-filled square, not numbered) was not included in the AFLP study; its affiliation to the group with lower relative DNA content was determined with flow cytometry. Note that on Svalbard (populations 9–11), both the *Alps*- and the *Scandinavia-groups* occur. See Table 1 for details of the sampled populations.

2. Materials and methods

2.1. The study species

Juncus biglumis L. is a low-growing (2–30 cm) perennial rush forming small dense tufts. It grows in a wide range of rather wet habitats in different successional stages (Aiken et al., 1999). The species is wind-pollinated, but apparently nothing is known about its breeding system. Seed dispersal may be partly anemochorous since the seeds are small and light. Hydrochory may also be important, as it has been shown that seeds can float for about a year (Goodson et al., 2001).

2.2. Sampling

Twenty-five populations of *J. biglumis* were sampled in 2003 and 2004, covering the entire range of the species but focusing on the North Atlantic region (Table 1). Typically, leaf material of 10 plants was collected per population. Voucher specimens are deposited at the Faculty Centre Botany, University of Vienna (WU), or in the Botanical Museum, University of Oslo (O). Living plants from populations 2 and 6 were collected in 2005 and cultivated in the Botanical Garden of the University of Vienna (HBV), to confirm flow cytometry results conducted with silica