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Geographic variation and dispersal history in Fennoscandian populations of two forest herbs

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Abstract. *Carex digitata* and *Melica nutans* are forest understorey herbs with wide European distributions and their northern range margins in Fennoscandia. The species have closely similar habitat requirements, occur in small populations in old forest stands on base-rich to neutral soils and have restricted dispersal abilities at the present day. This study investigates the structure of allozyme variation (12 and 8 loci, respectively) in material of both species (38 and 37 populations, respectively) from throughout southern Sweden and southern Finland. Both species show a relatively low overall genetic diversity (H_T excluding monomorphic loci = 0.17 and 0.18, respectively). The hierarchic structuring of allelic diversity in the species is similar, with a relatively high between-population component of diversity ($G_{ST} = 0.36$ and 0.37, respectively). Neither of the species shows a clear intraspecific pattern of geographic differentiation. The lack of large-scale patterns of geographic differentiation is not consistent with a simple scenario of discrete and independent waves of immigration into Fennoscandia. However, particularly in *M. nutans*, a group of populations from a lowland belt across southwestern Finland and southern central Sweden is somewhat differentiated from populations to the north and south. A number of rare alleles in both species are widely, but patchily distributed in low frequencies. Hybridization may account for the scattered occurence of some of the rare alleles in *Carex digitata*, but cannot explain the distribution of rare alleles in *Melica nutans*.

Key words: *Carex digitata*, *Melica nutans*, allozymes, genetic diversity, geographic differentiation

The Fennoscandian and northern European ranges of many nemoral and boreal forest species lie within areas that were ice-covered or contained tundra-like habitats during the Weichselian glacial maximum at 20 000 BP. European tree species are known to have overwintered the last glaciation in refugia in southern Europe, the Caucasian region or in the southern Ural mountains (Bennett et al. 1991, Taberlet et al. 1998, Tarasov et al. 2000) and it is reasonable to believe that the majority of forest understorey forest herbs overwintered in the same areas. Range expansion, over distances of up to 3000 km, to include the present-day distributional limits in Fennoscandia would imply an average rate of migration of at least 150 m/year. However, at present, the yearly rate of spread for understorey herbs migrating into secondary forests has been estimated to be between 0.2 and 15 m per year (Matlack 1994, Brunet and von Oheimb 1998). Diffusion models, parametrized with data on population growth and mean distances of diaspore dispersal, have not been able to explain how forest understorey herbs could have migrated more than 100 km over the last 16 000 years (Cain et al. 1998). It has been

concluded that, in general, the colonization of previously glaciated areas must have depended on rare long-distance dispersal events resulting, for example, from meteorological accidents or transport by migrating vertebrates or birds (Wilkinson 1997, Cain et al. 1998). Several studies dealing with the postglacial migration of North American trees have reached similar conclusions (Webb 1986, Johnson and Webb 1989, Green and Johnson 1989).

The primary source of information on large-scale postglacial plant migrations is the pollen record (cf. Huntley and Birks 1983). The Weichselian ice sheet began its retreat from northern Europe around 18 000 BP, and time-series of pollen maps show a rapid postglacial expansion of the ranges of many tree species into northwestern Europe (Huntley and Birks 1983). Isopoll maps also reveal that several tree species, such as spruce (*Picea abies*), colonized Europe from more than one geographic source (Huntley and Birks 1983). However, while extensive palynological data are available for many wind-pollinated tree taxa, most herbaceous forest species are sparsely represented in the pollen record.

Historical migration patterns and changes in species distributions have played an important role in determining the present-day geographic structure of intraspecific genetic variation (Hewitt 1996). Genetic patterns formed by historical processes may persist for thousands of generations (cf. Nichols and Hewitt 1994) and recent studies of intraspecific geographic differentiation have shown that directions of postglacial migration and spread may be inferred from the present-day distributions of genetic characters or molecular markers (Avise 1986, Taberlet et al. 1998).

Phylogeographic studies have revealed that the postglacial colonization of Fennoscandia by a range of animal species involved immigrants from more than one direction and more than one population pool (e.g. Fredga 1973, Tegelström 1987, Jaarola and Tegelström 1992, Taberlet et al. 1995, Jaarola et al. 1999). Some forest trees also show patterns of genetic differentiation that suggest that Fennoscandia was colonized by populations that had different geographic origins (e.g. Ferris et al. 1998, King and Ferris 1998).

Because non-woody plants are rarely represented in the pollen and macrofossil records, genetic data may provide the only means of inferring directions of postglacial migration for many herbaceous plant species. It has also been suggested that genetic methods may provide a means of assessing the importance of long-distance dispersal events in forest understorey herbs (Cain et al. 2000). However, there have been few studies of genetic differentiation in widespread herbs in Fennoscandia, and even fewer studies of forest understorey herbs. So far, most investigations of genetic variation in Fennoscandian plants have focussed on species that depend on open habitats and that have disjunct distributions (e.g. Prentice 1992, Jonsell et al. 1995, Rosquist and Prentice 2000). Only one study of a widespread northwest European forest understorey herb includes material from Fennoscandia (Schiemann et al. 2000).

As well as reflecting directions of postglacial migration, the present-day structure of genetic variation within species may also provide information on population processes that took place during range expansion. It has been suggested that the rapid postglacial range expansion in many species is likely to have involved long-distance dispersants that were able to establish colonies in advance of the main distributional front. These advance colonies, in their turn, may have expanded rapidly and acted as sources for further long-distance dispersal events (e.g. Hewitt 1996, 1999). This model of range expansion is consistent with the fact that long-distance seed dispersal events need to be invoked if we are to explain the postglacial spread of forest understorey herbs (cf. Cain et al. 1998). With this mode of range expansion, genetic bottlenecks associated with repeated founder effects are expected to have led to the loss of much of the original allelic variation that was present in the refugial populations (cf. Nei et al. 1975).

Within-population levels of genetic diversity are, thus, expected to decrease with increasing distance from the source populations in the glacial refugia. Hewitt (1996, 1999) further suggested that the effects of density and of logistic population growth might prevent later immigrants from contributing significantly to the genetic diversity of established populations within colonized areas. However, if range expansion proceeds through the gradual spread of large and continuous populations, then most or all of the genetic variation in the source of refugial populations may be retained throughout the expanding range of the species.

Many recent studies of the distribution of within-species genetic variation in various organisms support the prediction that populations from recently deglaciated areas will be less genetically variable than populations from unglaciated areas (e.g. Mercure et al. 1993, Demesure et al. 1996, Mahy et al. 1997, Broyles 1998, Cronberg 2000), but there are also several studies that do not reveal a relationship between proximity to glacial refugia and levels of genetic variation (e.g. Tigerstedt 1973, Levin 1977, Yeh and O'Malley 1980, Betancourt et al. 1991, Ford et al. 1997, Jaarola et al. 1999, Schiemann et al. 2000).

In the present study, we investigate whether patterns of genetic variation or the structure of genetic diversity in a pair of ecogeographically similar species can provide evidence on the immigration of forest understorey herbs into Fennoscandia or clues about the population history of this group of plants. Present-day plant communities do not represent historically stable species-associations (Huntley 1991). It is also clear that differences in the directions, modes and rates of spread as well as competitive interactions with other species may lead to idiosyncratic phylogeographic patterns (Comes and Kadereit 1998). Nevertheless, comparative investigations of species with currently similar habitats and distributions may provide insights into the population history of groups of species with broadly similar niches. A study of an array of North American plants showed that species with similar geographic distributions often had similar patterns of genetic variation, suggesting that they have had comparable biogeographic histories (Soltis et al. 1997).

We investigate and compare the geographic structure of allozyme variation in two Fennoscandian understorey forest herbs that have closely similar distributions and habitat preferences. The species, *Carex digitata* and *Melica nutans*, both show an inability to colonize new localities in the modern landscape (cf. Tyler and Olsson 1997). Both species are mainly restricted to relatively undisturbed forest habitats with long historical continuity and both show short dispersal-distances at the present-day (Brunet and von Oheimb 1998). This combination of ecological characteristics suggests that the spread of the two species is unlikely to have been strongly influenced by humans and that patterns of genetic differentiation may still retain a historical structure.

Materials and methods

The species. *Carex digitata* L. (Cyperaceae) is a c. 25 cm high, paroecious (i.e. with separate male and female inflorescences on the same individual) long-lived perennial sedge that forms dense tussocks 5–20 cm in diameter. Swedish material of *C. digitata* has the chromosome number $2n = 52$, but aneuploids with $2n = 48$–52 have been reported from other parts of the species' distribution (Davies 1956). In Fennoscandia the species flowers in April, and the tussocks produce multiple culms, each with 1–5 unisexual spikes. The flowers are wind-pollinated. When cultivated in a private garden, a single plant produced large amounts of viable seeds indicating self-compatibility (H.C. Prentice, pers. obs.). *Carex digitata* is known to hybridize with *C. ornithopoda* Willd.. Hybrids were considered to be relatively common by Hylander (1966) but there are few confirmed records of hybrids within the area of the present study. The utricles are c. 3 mm long and show no apparent adaptation for any kind of specialized dispersal.

Melica nutans L. (Poaceae) is a diploid ($2n = 18$) (Sorsa 1962), c. 35 cm high, synoecious (i.e. with all flowers bisexual), shortly-rhizomatous perennial grass. It forms loose tussocks or patches of up to 1 m in diameter. Gradual vegetative

expansion by rhizomes can take place over distances of a few meters over many years (T. Tyler, pers. obs.). Flowering occurs in June in Fennoscandia. *Melica nutans* is wind-pollinated and is not known to hybridize with any other species in Fennoscandia. The achenes are ca. 3 mm long and show no adaptation for specialized dispersal but, because the seeds and their enclosing glumes are relatively light (c. 4 mg), they may be transported by wind over shorter distances.

Both species grow in open to semi-closed forests, usually on well-drained neutral or slightly acidic, sandy or gravelly soils (Oberdorfer 1962). In southern Fennoscandia, the species typically co-occur in forests on steep slopes with shallow, circumneutral and unstable soil overlying calcareous or ultrabasic bedrock or boulders. Both species are rare in areas with exclusively acidic bedrock or moraine and, in such areas, they are confined to steep ridges or to unstable soil at the base of cliffs. *Carex digitata* is rarely found on level ground with deep soil. Most of Fennoscandia is covered by acidic bedrock and outcrops of base-rich bedrock are spatially restricted. Populations of *M. nutans* and *C. digitata* typically consist of relatively few (tens to hundreds) individuals within a restricted area. Both species are common throughout southern and central Fennoscandia but become somewhat more scattered in the extreme south of Sweden. The distribution of *C. digitata* extends northwards to the arctic circle and *M. nutans* occurs in scattered localities even further north.

Outside Fennoscandia, both species have a subcontinental distribution in Eurasia (Hultén and Fries 1986). They are absent from the most oceanic parts of western Europe but are continuously distributed from central France to the Ural mountains. They extend southwards into the northern part of the Mediterranean region in Italy and the Balkan peninsula.

Sampling methods. Thirty seven populations of *C. digitata* (22 Swedish, 14 Finnish and 1 Estonian) and 38 populations of *M. nutans* (24 Swedish and 14 Finnish) were sampled in 1997 and 1998. Whenever possible, both species were sampled from the same localities, or at least from adjacent sites. The geographic positions of all the sampling sites are given in Fig. 1 and Appendix 1. The most closely adjacent populations were c. 3 km apart and the longest distance between sampled populations was c. 1200 km. We aimed to sample 20–25

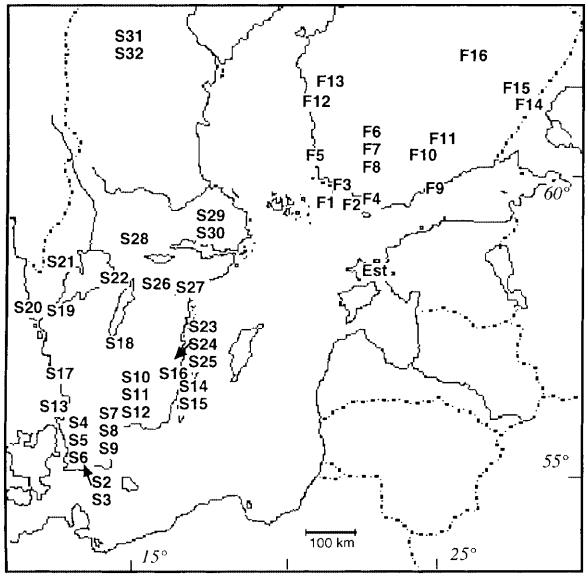

Fig. 1. Map of southern Fennoscandia indicating the geographic positions of the sampling sites. Further site details are given in Appendix 1

ramets ('individuals') from each population and the ramets were collected from the whole area occupied by the population (usually 0.1–3 ha). To avoid over-representation of closely related ramets, or ramets belonging to the same clone, only individuals separated by at least 3 m were sampled. All collected material was transported to Lund, planted in pots in standard soil and grown in cold frames prior to analysis.

Enzyme electrophoresis. Basal tissue from young leaves was ground, together with washed sand, in 80 ml chilled extraction buffer consisting of 2.42 g Tris, 1 g Na-bisulfate, 0.1 g EDTA, 0.2 g $MgCl_2$, 200 ml di-Mercaptoethanol and 2 g PVP, in 100 ml buffer. The extracts were absorbed onto wicks of Whatman 3 MM chromatography paper and stored at −80 °C until used. Electrophoresis was carried out in horizontal gels prepared from 10–12% hydrolyzed potato starch (Reppin PSG 1000). Two buffer systems were used. The enzyme systems aspartate aminotransferase (AAT: E.C.2.6.1.1), diaphorase (DIA: E.C.1.6.99), phosphoglucose isomerase (PGI: E.C.5.3.1.9) and triosephosphate isomerase (TPI: E.C.5.3.1.1) were resolved using a lithium-borate/tris-citrate buffer system at pH 8.4/8.1 (Ashton and Braden 1964 with slight modification). Aconitase (ACO: E.C.4.2.1.3), isocitrate dehydrogenase (IDH: E.C.1.1.1.42), malic enzyme

(ME: E.C.1.1.1.40), 6-phosphogluconate dehydrogenase (6PGD: E.C.1.1.1.44), phosphoglucomutase (PGM: E.C.5.4.2.2.), shikimate dehydrogenase (SKD: E.C.1.1.1.25) and uridine 5′ diphosphoglucose pyrophosporylase (UGPP: E.C.2.7.7.9) were run in a morpholine-citrate buffer system at pH 6.1 (system 2 in Wendel and Weeden 1989). After a prerun of 20 min at 20 mA, electrophoresis was run at a constant current of 40 mA (c. 5.5 h for the morpholine-citrate buffer system, and c. 4.5 h for the lithium-borate system). Staining protocols for ACO, IDH, 6PGD, SKD and TPI followed Wendel and Weeden (1989), and UGPP followed Manchenko (1994), with some alterations of substrate concentrations. PGI was stained in a 0.2 M pH 8.0 Tris buffer containing 30 mg fructose-6-phosphate, 40 U glucose-6-phosphate dehydrogenase, 0.1 g $MgCl_2$, 10 mg NADP, 4 mg PMS and 20 mg MTT per 100 ml buffer. ME was stained in a 0.2 M pH 8.5 Tris buffer containing 10 ml 2 M malic acid, 20 mg NADP, 0.2 g $MgCl_2$, 4 mg PMS and 20 mg MTT per 100 ml buffer. DIA was stained in a 0.2 M pH 8.0 Tris buffer containing 20 mg 2,5-indole phosphate, 80 mg NADH and 80 mg MTT per 100 ml buffer. Two staining protocols were used for AAT. For *C. digitata* the gels were stained in a 0.2 M Tris buffer containing 0.5 g L-aspartic acid, 70 mg α-ketoglutaric acid, 50 mg pyridoxal-5-phosphate and 200 mg Fast Blue BB-salt per 100 ml buffer. For *M. nutans* the gels were stained according to Wendel and Weeden (1989).

Preliminary screening and gel interpretation. Preliminary screening, to identify variable and consistently interpretable loci, was carried out on a subset of c. 200 Swedish and 50 Finnish individuals (representing all the sampled populations) of each species. Only enzyme systems that included consistently interpretable polymorphic (with more than one allele) loci were analyzed in the full samples of 720 individuals of *C. digitata* and c. 700 individuals of *M. nutans*.

Putative loci and alleles were numbered in order of descending anodal mobility. In *C. digitata*, the preliminary screening revealed 12 consistently interpretable loci. Seven of these (*Aat-2*, *Dia-2*, *Dia-3*, *6Pgd-1*, *6Pgd-2* and *Skd*) were monomorphic. The enzyme systems ACO and UGPP showed no activity in this species and, although PGM and ME were variable, these two systems could not be interpreted in terms of loci and alleles. The five polymorphic loci that were included in the analyses of the full set of *C. digitata* individuals were *Aat-1*, *Dia-1* and *Pgi* (with 3 alleles each) and *Tpi-1* and *Tpi-2* (2 alleles each).

In *M. nutans*, the preliminary screening revealed 8 consistently interpretable loci. Three of these loci (*Aat-1*, *Aco-2* and *Aco-3*) were monomorphic. The enzyme systems DIA and TPI showed weak and unreliable activity; ME, 6PGD, PGI and UGPP were variable, but could not be consistently interpreted in terms of loci and alleles. The five polymorphic loci that were included in the final analyses of *M. nutans* were *Skd* (4 alleles) and *Aat-2*, *Aco-1*, *Idh*, and *Pgm* (each with two alleles).

Statistical analyses. The statistical calculations were based on the five polymorphic loci in each species. The mean (over loci) total genetic diversity (Nei 1973) is given by H_T, the mean (over loci) within-population diversity by H_{pop} and the mean (over loci and populations) within-population genetic diversity by H_S. The between-population component of the total genetic diversity is given by G_{ST} ($G_{ST} = (H_T - H_S)/ H_T$). For each species, H_T, H_S and G_{ST} values were calculated for the total material and separately for the Swedish and Finnish material.

The observed number of heterozygotes (H_{obs}) and the number of heterozygotes expected under Hardy-Weinberg equilibrium (H_{exp}) were calculated for each locus and population. The less common alleles, at loci with more than two alleles, were pooled in the calculations of heterozygosity. The numbers of comparisons showing positive or negative deviations from random mating (null hypothesis: $H_{obs} = H_{exp}$) were compared with a one-tailed sign test (Sokal and Rohlf 1995).

Rogers' genetic distance (Rogers 1972) based on within-population allele frequencies for the five loci for each species was calculated for each pair of populations. UPGMA cluster analysis and nonmetric multidimensional scaling (MDS, Kruskal 1964a, b) were used to analyse patterns of between-population differentiation within each species. The cluster analyses and MDS analyses were carried out with NTSYS-pc (Rohlf 1994) using the procedure 'SAHN' and 'MDSCALE', respectively. The MDS calculations were repeated ten times and the solution with the lowest stress value (differences between the ranking order of the original distances and the order of distances in the resulting MDS solution, Kruskal 1964a) was chosen.

Table 1. Summary of (mean over polymorphic loci) population genetic statistics for *Carex digitata* and *Melica nutans*. H_T is the total within-species genetic diversity. H_S is the mean (over populations) within-population genetic diversity and G_{ST} is the between-population component of the total diversity. For each of the species, analyses were carried out on the total material and separately on the material from Sweden and Finland

	Carex digitata			*Melica nutans*		
	Total	Finland	Sweden	Total	Finland	Sweden
H_T	0.169	0.231	0.128	0.180	0.208	0.151
H_S	0.112	0.139	0.093	0.118	0.120	0.115
G_{ST}	0.355	0.367	0.303	0.367	0.428	0.272

Results

Carex digitata. The within-population genetic diversity (H_{pop}) ranged from 0.000 to 0.300 and the mean (over population) within-population genetic diversity (H_S) was 0.112 for the five polymorphic loci that were analysed for the full set of *C. digitata* individuals (Table 1). The total (mean over loci and populations) genetic diversity (H_T) for the species, in the whole of the investigated area, was 0.169. Thirty six percent of the total diversity was explained by the between-population component of diversity (G_{ST}). In the separate analyses for the Swedish and Finnish material, both H_T and G_{ST} were higher in Finland than in Sweden (0.231; 37% and 0.128; 30%, respectively, Table 1). The numbers of alleles per population for the five polymorphic loci ranged from 5 to 10 (mean for Sweden = 7.1, mean for Finland = 7.4). The number of alleles per locus (including monomorphic loci) was 1.67 when all loci and populations were considered.

Cluster analysis (Fig. 2) and MDS (Fig. 3) did not group populations according to their geographic origin in any consistent way. Finnish and Swedish, and northern and southern populations were intermixed in the cluster diagram (Fig. 2). In many cases, geographically adjacent populations were placed in different subclusters (cf. Fig. 1). However, there is a tight group of (mainly) Swedish populations in the centre of the MDS plot (Fig. 3) and this group contains the majority of the populations that were fixed at all five loci or showed low allelic richness. Most of these populations are from southernmost

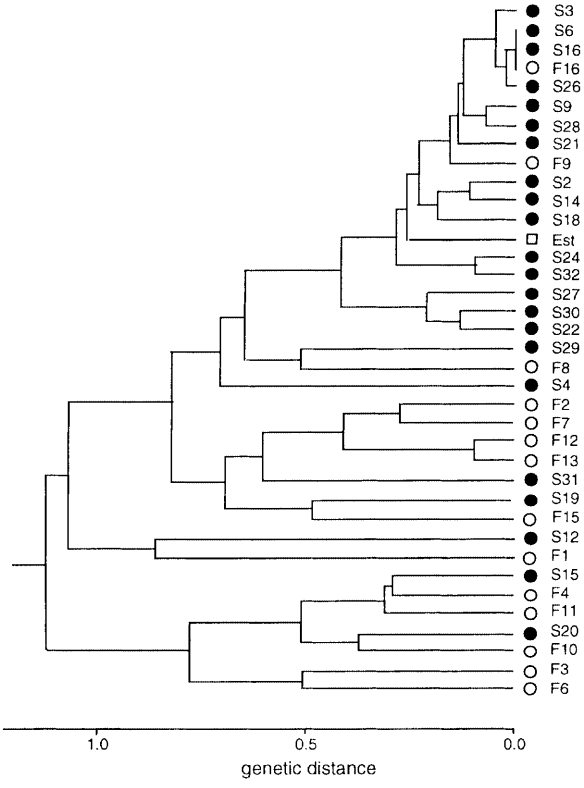

Fig. 2. UPGMA dendrogram based on Rogers' genetic distances between populations of *Carex digitata*. Populations from Finland are represented by open circles, populations from Sweden by filled circles and the Estonian population by an open square. Population numbers refer to Fig. 1 and Appendix 1

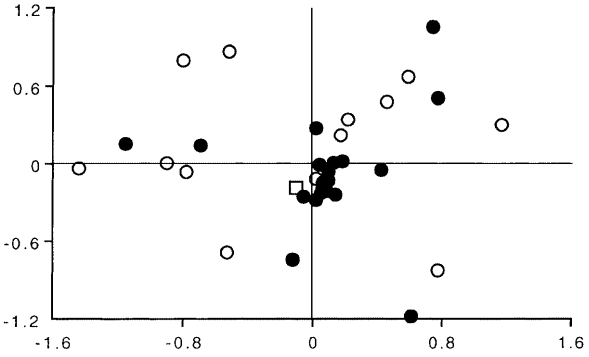

Fig. 3. MDS plot based on Rogers' genetic distance between populations of *Carex digitata* (stress = 0.237). Populations from Finland are represented by open circles, populations from Sweden by filled circles and the Estonian population by an open square

Sweden. The Finnish populations tend to be more separated from each other than the Swedish populations. The geographic distributions of some of the less common alleles are illustrated in Fig. 4. The alleles *Pgi* (c) and *Dia* (a) were only found, at low frequencies, in populations S4 & S29 and S18 & F1, respectively, and are not illustrated. Within-population allele frequencies at the five polymorphic loci are given in Appendix 2.

The number of heterozygotes was lower than would be expected at Hardy-Weinberg equilibrium for a significant majority of all the locus-population combinations that did not show fixation (one-tailed sign-test, $P < 0.001$).

Melica nutans. The within population genetic diversity (H_{pop}) ranged from 0.004 to 0.223 and the mean within-population genetic diversity (H_S) was 0.118 (Table 1). The total (mean over loci and populations) genetic diversity (H_T) for the species in the whole of the investigated area was 0.180. Thirty seven percent of this diversity was due to the between-population component of diversity (G_{ST}). As in *C. digitata*, the total genetic diversity was higher in Finland than in Sweden (0.208 compared to 0.151) and the between-population component of diversity (G_{ST}) was substantially higher in Finland than in Sweden (43% compared to 27%, Table 1). The numbers of alleles per population for the five polymorphic loci ranged from 6 to 9. The mean number of alleles per population was somewhat higher in Finland than in Sweden (7.1 and 6.8, respectively). The number of alleles per locus was 1.88 (including monomorphic loci) when all loci and populations were considered.

None of the major clusters in Fig. 5 contains solely Swedish of Finnish populations. However, there is some geographic differentiation into Swedish and Finnish groups of populations in the MDS plot (Fig. 6). In addition, all the populations that have negative scores on the first MDS axis are either from coastal localities in Finland or from a distinct belt across Sweden (Fig. 7). The relatively tight group of populations (with high scores on axis 1 and intermediate scores on axis 2) in the MDS plot (Fig. 6) contains the majority of the populations that had the lowest total numbers of alleles. These populations are mainly from the southernmost part of Sweden. The distributions of some of the less common alleles are illustrated in Fig. 8. The alleles *Idh* (b) (only found at medium frequency in population S9), *Pgm* (a) and *Skd* (a) (only found at low frequencies in population S7 and S23 & S25, respectively), and *Aat* (b) (only found at medium frequency in population F14) are not illustrated. Within-population allele frequencies at the five polymorphic loci are given in Appendix 3.

The number of heterozygotes were lower than would be expected at Hardy-Weinberg equilibrium for a significant majority of all the locus-population combinations that did not show fixation (one-tailed sign-test, $P < 0.001$).

Discussion

Levels of variation and the hierarchic structuring of genetic diversity. It is predicted that the postglacial range expansion of plant and animal species will often have involved phases of rapid migration, during which genetic variation was successively reduced by a combination of long-distance dispersal, repeated founder

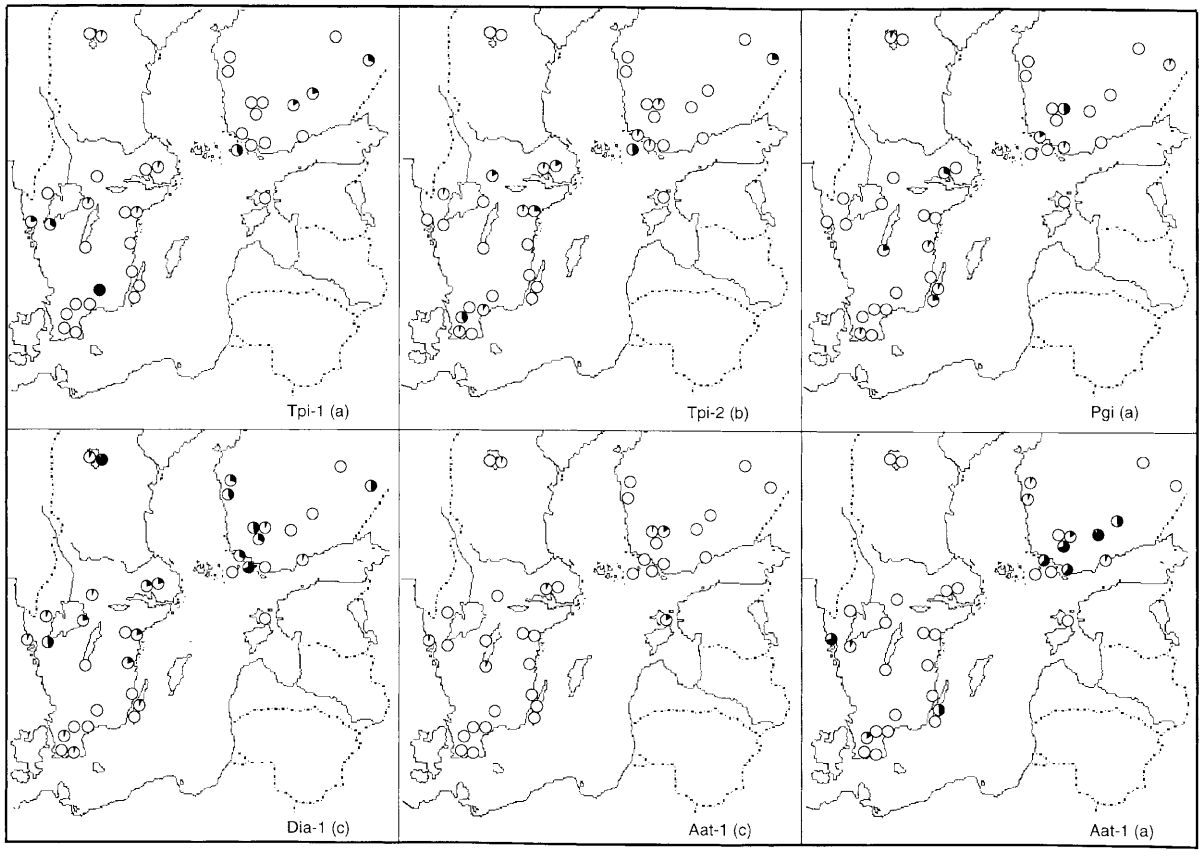

Fig. 4. Within-population relative frequencies of the less common alleles (represented by black sectors) at five polymorphic loci in *Carex digitata*

effects and episodes of small population size (e.g. Comes and Kadereit 1998; Hewitt 1996, 1999). Studies of several European and North American plant species reveal, as predicted, lower levels of genetic variation in populations within areas that were ice-covered during the last glacial period, and higher levels of variation in populations that are near to the species' presumed refugial sites (eg. Broyles 1998, Cronberg 2000). Scandinavian populations of another sedge species, *C. arenaria*, show substantially lower levels of allozyme diversity than populations from the Iberian Peninsula, and the SW to NE decline in diversity is interpreted in terms of postglacial spread, northwards, along the coasts of Europe (Jonsson and Prentice 2000). The present study shows that Fennoscandian *C. digitata* and *M. nutans* both have a smaller proportion of polymorphic loci and a lower level of overall genetic diversity (H_T; Table 1) than is typical of widespread perennial herbs (Hamrick and Godt 1989). It is plausible that the low levels of allozyme variation in Fennoscandian populations have resulted from the loss of alleles during immigration to the region. However, studies of populations from throughout the range of the species, including unglaciated regions, are needed to support or reject this scenario.

Both species also showed a relatively high between-population component of allozyme diversity (G_{ST}). Populations of *C. digitata* and *M. nutans* are generally small and are restricted to sites with relatively uncommon geomorphological conditions. High G_{ST} values may thus be a consequence of genetic drift and the random loss of alleles from fragmented, small

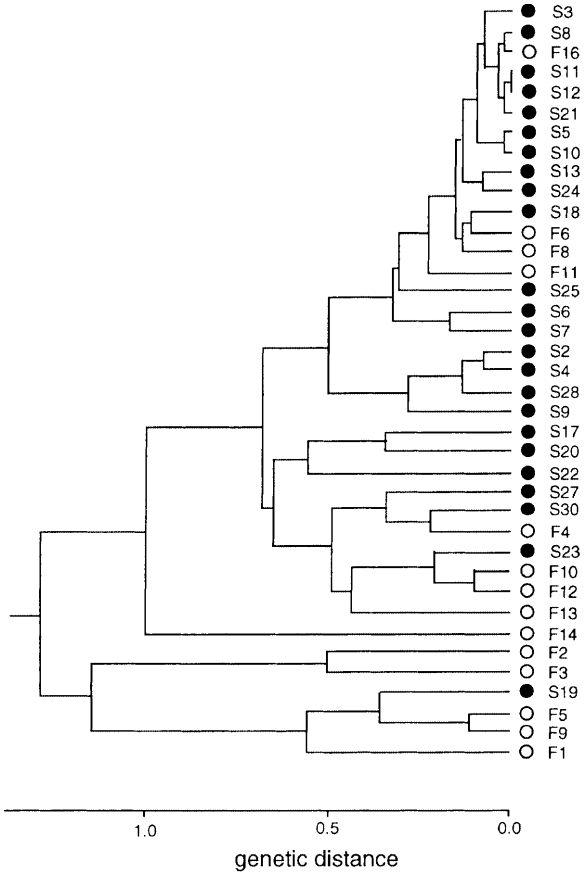

Fig. 5. UPGMA dendrogram based on Rogers' genetic distances between populations of *Melica nutans*. Populations from Finland are represented by open circles, populations from Sweden by filled circles. Population numbers refer to Fig. 1 and Appendix 1

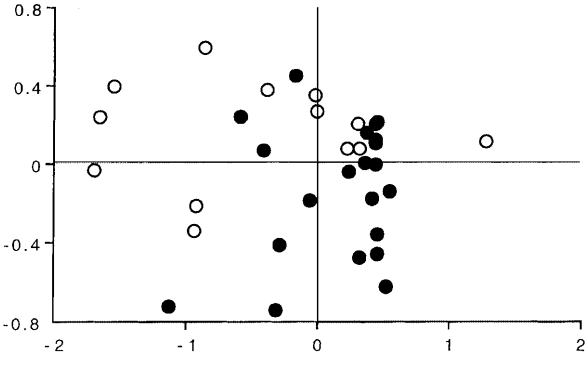

Fig. 6. MDS plot based on Rogers' genetic distances between populations of *Melica nutans* (stress = 0.184). Populations from Finland are represented by open circles, populations from Sweden by filled circles

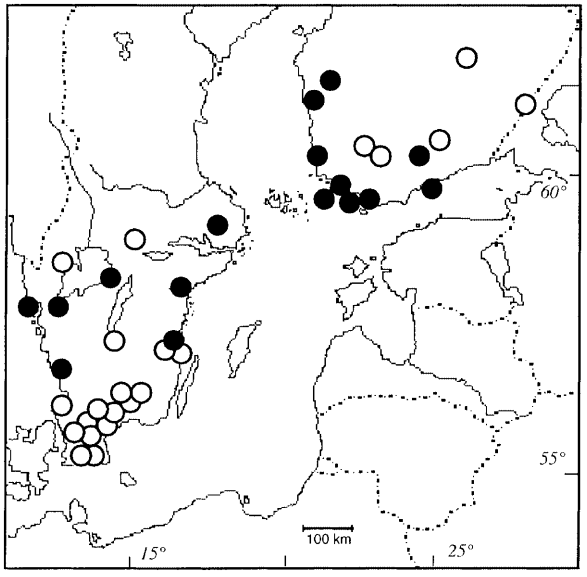

Fig. 7. Geographic distribution of the populations of *Melica nutans* that show negative (filled circles), and positive (open circles) scores on the first MDS axis in Fig. 6

and isolated populations (Barrett and Kohn 1991, van Treuren et al. 1991, Dolan 1994, Rosquist and Prentice 2000). Relatively high G_{ST} values are also typical in predominantly selfing species. Breeding system is one of the most important determinants of genetic structure in plants and reviews of allozyme studies show that selfing species are generally less variable than outcrossers and have a higher between-population component of diversity (e.g. Hamrick and Godt 1989). Sedges and grasses are usually wind-pollinated (Oberdorfer 1962). This mode of pollination allows long-distance gene dispersal and is characteristically associated with relatively low values of G_{ST} (Hamrick and Godt 1989). However, in the case of *C. digitata* and *M. nutans*, the observed within-population deviations from Hardy-Weinberg expectations suggest relatively high levels of selfing and inbreeding, given that neither species shows extensive clonal spread.

The proximity of inflorescences within tussocks may be expected to promote selfing in caespitose or shortly-rhizomatous grasses and sedges, despite the fact that the taxa are

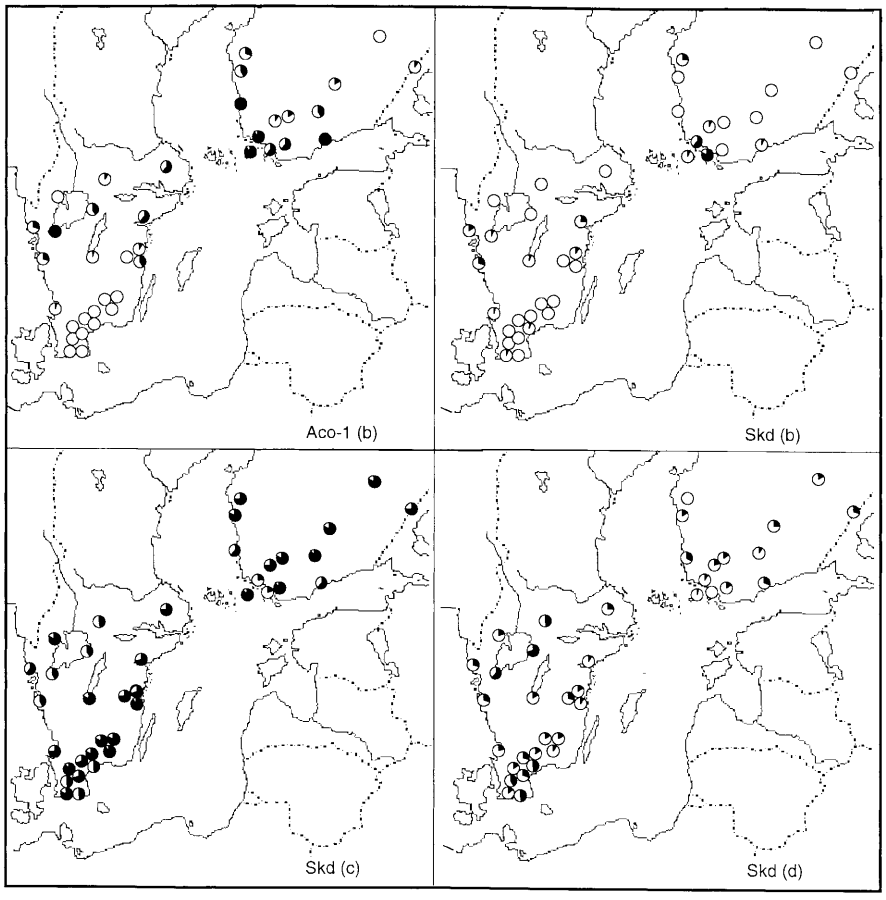

Fig. 8. Within-population relative frequencies of the less common alleles (represented by black sectors) at two polymorphic loci in *Melica nutans*

wind-pollinated. Within *Carex*, it has been shown that caespitose species have higher fixation indices than extensively-spreading rhizomatous species (B.O. Jonsson, M. Hedrén, A. Nilsson and P. Stenroth, unpublished manuscript). Both *C. digitata* and *M. nutans* are patchily distributed within sites, and their sheltered, forest-floor habitat is also likely to reduce pollen dispersal distances and to further promote inbreeding.

Patterns of geographic differentiation. Neither *C. digitata* nor *M. nutans* shows pronounced, large-scale patterns of geographic differentiation in allele frequencies within Fennoscandia. In both species, there is a somewhat patchy pattern of geographic variation in allele frequencies (Figs. 4, 8) and adjacent populations are often more similar to populations from other regions than to their geographic neighbours (cf. Figs. 2, 3, 5 and 6). Rare alleles in both species (not illustrated) are often present in several, geographically distant, populations.

More-or-less pronounced contact zones between, genetically-distinct, southern/western and northern/eastern groups of Fennoscandian populations are found in many mammals (e.g. Fredga 1973, Tegelström 1987, Jaarola and Tegelström 1992, Taberlet et al. 1995, Jaarola et al. 1999). These clear, large-scale, patterns of geographic differentiation provide strong support for independent colonization of Fennoscandia by genetically-differentiated populations from different geographic sources. There is also genetic evidence that indicates that several Fennoscandian plant taxa have

colonized the region from different geographic directions (e.g. Lönn et al. 1995, Ferris et al. 1998, Nordal and Jonsell 1998).

The lack of large-scale, strong patterns of geographic differentiation in *Carex* and *Melica* is not consistent with a simple scenario of discrete and independent waves of immigration into Fennoscandia from different geographic sources. However, populations of *M. nutans* from SW Finland and from a belt across the lowland area around the large lakes in southern central Sweden are somewhat differentiated from the rest of the Swedish and Finnish populations (Figs. 6, 7). These populations are characterized by, for example, a higher frequency of allele b at the locus *Aco-1* (Fig. 8). This group of populations is found within the area that was mostly deglaciated by 10 000 to 9900 BP but which was not above water until the Ancylus Lake Stage, around 9000 to 8900 BP (Björck 1995). These areas will have become available for colonization later than the southernmost part of Sweden and it seems plausible that the genetic differentiation of this group of populations has a historical explanation. There is also a weak aggregation of some *C. digitata* alleles in the same region (cf. Fig. 4). One of the genetic races within the triploid form of the weevil *Otiorhynchus salicis* shows a somewhat similar distribution across the southern boreal region in southern Finland and southern central Sweden (Soumalainen, Saura and Lokki, cited in Lönn et al. 1998) and there is a concentration of tetraploid populations of *Parnassia palustris* that follows a similar belt across southern central Sweden (Hultgård 1987). Other plant taxa show patterns of allozyme differentiation between populations in southern Sweden that are more easily interpreted in terms of the Holocene palaeogeography of the region (Hedrén and Prentice 1996, Runyeon and Prentice 1997).

Both species show both a higher between-population component of diversity (G_{ST}), and higher total genetic diversity (H_T) in Finland than in Sweden (Table 1). Southern Finland has a more continuous forest cover than southern Sweden and the populations of *Carex digitata* and *Melica nutans* are often found on long and inter-connecting systems of moraine ridges. The more pronounced between-population structure in Finland is unlikely, therefore, to be a consequence of greater disjunction and isolation of suitable habitats. However, Finland has a continuous mainland connection with the rest of Eurasia whereas the postglacial immigration to Sweden must have taken place across water, between islands or over narrow historic land-bridges. Thus the colonization of Finland may have involved larger numbers of migrants and a more diverse gene-pool than the immigration of Sweden.

The dispersal biology of Holarctic forest floor herbs presents a paradox – "Reid's paradox" (Cain et al. 1998). Long-distance dispersal and migration must necessarily have taken place during the recolonization of glaciated regions. Yet the majority of woodland herbs lack obvious mechanisms for long-distance seed dispersal. Many forest floor species currently reproduce mainly by clonal spread and show a limited ability to disperse by seed and colonize new sites (Cain et al. 1998).

Recent ecological studies of secondary forest successions have provided estimates of levels of short-distance spread and establishment for a range of woodland herbs. In a study by Brunet and Oheimb (1998) in southern Sweden, both *C. digitata* and *M. nutans* showed particularly poor dispersal abilities with estimated migration speeds of 0.0 and 0.42 m per year, respectively. A study of the overall dynamics of populations of a range of S Swedish species also showed that both *C. digitata* and *M. nutans* rarely colonize new sites and that they are almost totally restricted to localities where they have been known for more than 40 years (Tyler and Olsson 1997).

However, despite observational and experimental evidence for restricted dispersal in many plant species, it is becoming increasingly clear that rare events of long-distance seed dispersal play an important role in both metapopulation dynamics and in the process of large scale migration (Le Corre et al. 1997,

Cain et al. 2000). Similarly, it is also clear that gene dispersal by pollen may be considerably more extensive than was earlier assumed on the basis of leptokurtic pollen dispersal curves (Ellstrand 1992).

Carex digitata and *M. nutans* have closely similar present-day habitat preferences. Populations of the two species often occur in the same sites and the similarity of the geographic structure of genetic variation in the two species is consistent with their also having had similar types of immigration history. The spread of both species into Fennoscandia must have involved seed dispersal events over greater distances than are observed in present day populations and forest habitats in southern Sweden. It is possible that the large-scale patchiness of the variation in the frequencies of the commoner alleles in both species is a reflection of multiple colonization events.

The scattered distribution of rare alleles among geographically separated populations in both species is more difficult to explain. The presence of the same, rare, alleles in widely-separated populations might also be a reflection of occasional long-distance dispersal by pollen, seeds or vegetative propagules, but this pattern is unlikely to result from random changes in allele frequencies in small populations. Populations of *Carex arenaria* in the Baltic region show a similar, disjunct distribution of rare alleles at several loci (Jonsson and Prentice 2000). In *C. arenaria*, the distribution of the rare alleles can be explained by introgression from the closely-related *C. ligerica* in areas where the two species are sympatric at the present day (Jonsson and Prentice 2000). In *M. nutans*, recent introgression is unlikely because the species is not known to hybridize with any related Fennoscandian species. In contrast, interspecific hybridization is common within the genus *Carex*, although most reported hybrids show high levels of sterility (Chater 1980). *Carex ornithopoda* Willd. and *C. pallens* (Frist.) Harmja are the closest relatives of *C. digitata* in Fennoscandia. A pilot study of allozyme variation in these two species showed that they share the same alleles as *C. digitata* at most loci (T. Tyler, unpubl. data). Further studies of related species will be needed to confirm or exclude the suggestion that the rare alleles in *C. digitata* may have been derived from introgression.

We would like to thank Ursula Malm for help with fieldwork, Mikael Hedrén and Mikael Lönn for distributional discussions, and Torbjörn Säll for statistical advise. The study was funded by grants from the Swedish Natural Sciences Research Council (NFR) to HCP and the Swedish Council for Forestry and Agricultural Research (SJFR) to BW.

Appendix 1. List of sampling sites for *Carex digitata* and *Melica nutans*. Population codes are followed by the province, parish, sampling locality and habitat details. Numbers of analysed ramets of *Melica nutans* (M) and *Carex digitata* (C) are given in parentheses

Sweden:

S2. Skåne, Öved, Charlottenlund. Old *Fagus* forest on stabilized sand dune. (M = 9, C = 17–20)
S3. Skåne, Öved, Frualid. Mixed deciduous forest on ultrabasic cliff. (M = 18–20, C = 17–20)
S4. Skåne, Höör, Bjäret. *Fagus* forest on ultrabasic basalt bedrock. (M = 16–19, C = 20–25)
S5. Skåne, Matteröd, Tommaholma. *Carpinus* forest with ultrabasic boulders. (M = 15–20)
S6. Skåne, N. Mellby, Stångeryd. *Carpinus* forest on calcareous moraine ridge. (M = 20, C = 14–15)
S7. Skåne, Österslöv, Gårrö. Herb-rich forest margin. (M = 18–20)
S8. Skåne, Oppmanna, N of Arkelstorp. Herb-rich *Quercus* forest on moraine ridge. (M = 14–15)
S9. Skåne, Österslöv, Bokenäset. Old, herb-rich *Fagus* forest. (M = 17–20, C = 11–19)
S10. Småland, Urshult, 2 km S of lake Mien. Boulder-strewn, mixed forest. (M = 14–18)
S11. Småland, Urshult, Midingstorp. Open cattle-grazed *Quercus* forest. (M = 15–19)
S12. Småland, Urshult, Kurrebo. Herb-rich, broad leaved deciduous forest. (M = 13–17, C = 19–20)
S13 Skåne, V. Karup, WSW of church. Grazed, deciduous forest with gneiss cliffs. (M = 19)

Appendix 1 (continued)

S14. Öland, Torslunda, Tveta. Deciduous forest on calcareous soil. (C = 20)
S15. Öland, Räpplinge, NW of crossroad Lindby-Hageby. *Quercus* forest on calcareous soil. (C = 20–21)
S16. Småland, Ryssby, Skäggenäset peninsula, Rosendal. *Picea* forest on deep moraine. (C = 16–19)
S17. Bohuslän, Billdal-Askim, N-NE of Årekärr. *Quercus* forest on dioritic bedrock. (M = 21–23)
S18. Småland, Rogberga, Högagärde. Steeply-sloping, mixed forest with dioritic cliffs. (M = 20, C = 25)
S19. Västergötland, V. Tunhem, western slope of Mt. Hunneberg. Mixed deciduous forest on ultrabasic basalt cliffs and shale. (M = 21, C = 19–20)
S20. Bohuslän, Skredsvik, Dalen, Mixed forest on steep coastal amphibolite cliffs. (M = 17, C = 25)
S21. Dalsland, Edelskog, Skackerud. *Picea* forest on calcareous spilite bedrock. (M = 17, C = 27)
S22. Västergötland, Amnehärad, by lake Skagern N of Delebäck. Deciduous forest. (M = 7, C = 21)
S23. Småland, Tuna, Karlsberg. Mixed *Quercus-Corylus* forest. (M = 20)
S24. Småland, Tuna, Vånghult. *Corylus* stand. (M = 20, C = 19–20)
S25. Småland, Hallingeberg, between lakes Lingsjön and Långsjön. Ravine in *Quercus-Corylus* forest. (M = 20)
S26. Östergötland, Kvillinge, Torshag. Mixed forest at the foot of a porphyritic cliff. (C = 16–20)
S27. Östergötland, Krokek, Marmorbruket. Deciduous shrub on marble rocks. (M = 18–19, C = 19–20)
S28. Västmanland, Grythyttan, NW of the southern point of lake Torrvarpen. Mixed deciduous forest on marble bedrock. (M = 17, C = 23)
S29. Uppland, Sunnersta, between Sunnersta, Gottsunda and Bäcklösa. Steep mixed deciduous forest. (C = 17–22)
S30. Uppland, Uppsala, Lunsen. Mixed conifer forest on silicious moraine. (M = 13–19, C = 16–20)
S31. Jämtland, Frösö, E of Frösö camping site. (C = 19–21)
S32. Jämtland, Odensala, W of lake Lillsjön. Forest-margin. (C = 15)

Finland
F1. Regio Aboensis, Korpoo. Mixed conifer forest on granitic bedrock. (M = 16, C = 23)
F2. Regio Aboensis, Parainen, Solliden camping site. Open *Pinus* forest on granitic bedrock with intermixed marble. (M = 19–20, C = 20–21)
F3. Regio Aboensis, Åbo, Ruissalo peninsula. Coastal *Pinus-Betula* forest on moraine. (M = 21, C = 22)
F4. Regio Aboensis, Kisko, Härkähaka. Outcrop of ultrabasic hyperite bedrock in mixed *Pinus-Populus* forest. (M = 16–17, C = 15–16)
F5. Satakunta, Rauma, on the peninsula Petäjäs. *Pinus* forest on silicious bedrock. (M = 16)
F6. Tavastia australis, Kalvola, Mt. Oikalanvuori. Rocky *Pinus* forest on copper-ore bedrock. (M = 13, C = 15)
F7. Tavastia australis, Valkeakoski, E of lake Vallonjärvi. Herb-rich *Picea*-forest with large boulders. (C = 20)
F8. Tavastia australis, Sääksmäki. Mixed conifer forest on steep moraine ridge. (M = 17, C = 17–20)
F9. Nylandia, Helsinki, N of Bastöviken. Sloping herb-rich *Picea* forest. (M = 19–21, C = 22)
F10. Tavastia australis, Lammi, Mt. Reväsvuori. Herb-rich mixed forest on steep ultrabasic cliff. (M = 18–21, C = 20)
F11. Tavastia australis, 2 km N of Hartola. *Pinus* forest on slightly calcareous moraine ridge. (M = 17–19, C = 13–16)
F12. Ostrobotnia australis, Metsäle. Herb-rich *Pinus-Corylus* forest on former hay-meadow. (M = 11–12, C = 19–20)
F13. Ostrobotnia australis, WSW of Karijokki, Kruvunahole. Herb-rich *Pinus-Populus* forest. (M = 14–15, C = 15–17)
F14. Karelia ladogensis, 10 km NE of Parikkala, Rasvaniemi. Grazed deciduous forest on moraine ridge. (M = 17)

Appendix 1 (continued)

F15. Savonia australis, 15 km SW of Punkaharju, Mt. Petramonvuori. *Populus* forest on silicious rocks. (C = 17–19)

F16. Savonia australis, NW of Kangasniemi. Deciduous forest between a lake and an abandoned garden. (M = 3, C = 10)

Estonia

Est. Hiiuma (Dagö), S of Heltermaa. (C = 17).

Appendix 2. Allele frequencies at the five polymorphic loci that were included in the statistical analyses of genetic variation in the 38 investigated populations of *Carex digitata*. Population numbers refer to Fig. 1 and to Appendix 1

Locus	*Aat-1*			*Pgi*			*Dia-1*			*Tpi-1*		*Tpi-2*	
Allele	(a)	(b)	(c)	(a)	(b)	(c)	(a)	(b)	(c)	(a)	(b)	(a)	(b)
Population													
EST	0	0.85	0.15	0	1	0	0	1	0	0	1	1	0
F1	0	1	0	0	1	0	0.04	0.96	0	0.46	0.54	0.52	0.48
F2	0	1	0	0	1	0	0	0.33	0.67	0	1	0.95	0.05
F3	0.59	0.39	0	0.16	0.84	0	0	0.66	0.34	0	1	0.93	0.07
F4	0.60	0.40	0	0.03	0.97	0	0	1	0	0	1	1	0
F6	0.73	0.27	0	0	1	0	0	0.63	0.37	0	1	1	0
F7	0	0.95	0.05	0	1	0	0	0.47	0.53	0	1	1	0
F8	0.13	0.74	0.13	0.50	0.50	0	0	0.91	0.09	0	1	0.92	0.08
F9	0.05	0.95	0	0	1	0	0	0.95	0.05	0	1	1	0
F10	0.90	0.10	0	0	1	0	0	1	0	0.13	0.87	1	0
F11	0.47	0.53	0	0	1	0	0	1	0	0.16	0.84	1	0
F12	0.08	0.92	0	0	1	0	0	0.63	0.37	0	1	1	0
F13	0.07	0.93	0	0	1	0	0	0.70	0.30	0	1	1	0
F15	0	1	0	0.11	0.89	0	0	0.47	0.53	0.32	0.68	0.74	0.26
F16	0	1	0	0	1	0	0	1	0	0	1	1	0
S2	0	1	0	0.10	0.90	0	0	1	0	0	1	0.97	0.03
S3	0	1	0	0	1	0	0	0.97	0.03	0	1	1	0
S4	0.17	0.83	0	0	0.90	0.10	0	0.95	0.05	0	1	0.60	0.40
S6	0	1	0	0	1	0	0	1	0	0	1	1	0
S9	0	1	0	0	1	0	0	1	0	0	1	0.91	0.09
S12	0	1	0	0	1	0	0	1	0	1	0	1	0
S14	0	1	0	0.20	0.80	0	0	1	0	0	1	1	0
S15	0.48	0.52	0	0.07	0.93	0	0	0.90	0.10	0	1	1	0
S16	0	1	0	0	1	0	0	1	0	0	1	1	0
S18	0	0.92	0.08	0.18	0.82	0	0.04	0.96	0	0	1	1	0
S19	0.08	0.92	0	0	1	0	0	0.52	0.48	0.35	0.65	1	0
S20	0.70	0.26	0.04	0	1	0	0	0.90	0.10	0.16	0.84	1	0
S21	0	1	0	0	1	0	0	0.93	0.07	0	1	0.94	0.06
S22	0	1	0	0	1	0	0	0.81	0.19	0.07	0.93	1	0
S24	0	1	0	0.10	0.90	0	0	0.82	0.18	0	1	1	0
S26	0	1	0	0	1	0	0	1	0	0	1	0.97	0.03
S27	0	1	0	0	1	0	0	0.79	0.21	0.05	0.95	0.74	0.26

Appendix 2 (continued)

Locus / Allele	*Aat-1*			*Pgi*			*Dia-1*			*Tpi-1*		*Tpi-2*	
	(a)	(b)	(c)	(a)	(b)	(c)	(a)	(b)	(c)	(a)	(b)	(a)	(b)
S28	0	1	0	0	1	0	0	0.98	0.02	0	1	0.85	0.15
S29	0	0.93	0.07	0.28	0.67	0.05	0	0.79	0.21	0	1	0.97	0.03
S30	0	1	0	0	1	0	0	0.80	0.20	0.08	0.92	0.87	0.13
S31	0	0.95	0.05	0	1	0	0	0.11	0.89	0.05	0.95	1	0
S32	0	1	0	0.07	0.93	0	0	0.87	0.13	0	1	1	0

Appendix 3. Allele frequencies at the five polymorphic loci that were included in the statistical analyses of genetic variation in the 37 investigated populations of *Melica nutans*. Population numbers refer to Fig. 1 and to Appendix 1

Locus / Allele	*Skd*				*Idh*		*Aco-1*		*Pgm*		*Aat-2*	
	(a)	(b)	(c)	(d)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)
Population												
F1	0	0.07	0.90	0.03	1	0	0.03	0.97	0	1	0	1
F2	0	0.82	0.18	0	1	0	0.40	0.60	0	1	0	1
F3	0	0.67	0.26	0.07	1	0	0.10	0.90	0	1	0	1
F4	0	0	0.87	0.13	1	0	0.36	0.64	0	1	0	1
F5	0	0	0.63	0.37	1	0	0	1	0	1	0	1
F6	0	0.05	0.77	0.18	1	0	0.91	0.09	0	1	0	1
F8	0	0	0.85	0.15	1	0	0.88	0.12	0	1	0	1
F9	0	0.05	0.65	0.30	1	0	0	1	0	1	0	1
F10	0	0	0.90	0.10	1	0	0.65	0.35	0	1	0	1
F11	0	0	0.78	0.22	1	0	0.83	0.16	0	1	0	1
F12	0	0	0.85	0.15	1	0	0.65	0.35	0	1	0	1
F13	0	0.27	0.73	0	1	0	0.71	0.29	0	1	0	1
F14	0	0	0.72	0.28	1	0	0.94	0.06	0	1	0.64	0.36
F16	0	0	0.84	0.16	1	0	1	0	0	1	0	1
S2	0	0	0.50	0.50	1	0	1	0	0	1	0	1
S3	0	0.05	0.80	0.15	1	0	1	0	0	1	0	1
S4	0	0	0.55	0.45	1	0	1	0	0	1	0	1
S5	0	0	0.88	0.12	1	0	1	0	0	1	0	1
S6	0	0	0.65	0.35	1	0	1	0	0	1	0	1
S7	0	0	0.69	0.31	1	0	1	0	0.10	0.90	0	1
S8	0	0	0.83	0.17	1	0	1	0	0	1	0	1
S9	0	0.06	0.47	0.47	0.85	0.15	1	0	0	1	0	1
S10	0	0	0.89	0.11	1	0	1	0	0	1	0	1
S11	0	0	0.82	0.18	1	0	1	0	0	1	0	1
S12	0	0	0.82	0.18	1	0	1	0	0	1	0	1
S13	0	0.03	0.74	0.23	1	0	0.95	0.05	0	1	0	1
S17	0	0.31	0.40	0.29	1	0	0.65	0.35	0	1	0	1
S18	0	0.05	0.82	0.13	1	0	0.95	0.05	0	1	0	1
S19	0	0.05	0.38	0.57	1	0	0	1	0	1	0	1
S20	0	0.12	0.59	0.29	1	0	0.71	0.29	0	1	0	1

Appendix 3 (continued)

Locus	*Skd*				*Idh*		*Aco-1*		*Pgm*		*Aat-2*	
Allele	(a)	(b)	(c)	(d)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)
S21	0	0	0.81	0.19	1	0	1	0	0	1	0	1
S22	0	0	0.36	0.64	1	0	0.57	0.43	0	1	0	1
S23	0.05	0	0.90	0.05	1	0	0.55	0.45	0	1	0	1
S24	0	0	0.75	0.25	1	0	1	0	0	1	0	1
S25	0.10	0.10	0.66	0.14	1	0	0.90	0.10	0	1	0	1
S27	0	0.25	0.69	0.06	1	0	0.37	0.63	0	1	0	1
S28	0	0	0.50	0.50	1	0	0.91	0.09	0	1	0	1
S30	0	0	0.74	0.26	1	0	0.38	0.62	0	1	0	1

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