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ISOZYME VARIATION IN THE MOSS *MEESIA TRIQUETRA* (MEESIACEAE)

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ABSTRACT. Isozyme variation in eight enzyme systems in plants from 15 fens from three regions (boreal, subarctic, and high arctic) indicate that the gene diversity of *Meesia triquetra*, at 0.151, and genetic identity values (0.80–1.00) between populations of *M. triquetra* are comparable to those reported for many tracheophyte plant species. Gene diversity decreases significantly with increasing latitude, however patterns of gene diversity of the site level were more complex and suggest a highly dynamic species. In particular, subarctic sites have high between site gene diversity, while boreal sites have high within site gene diversity and high arctic sites are consistently low. Genetic identities are highest among the high arctic sites and lowest among the subarctic sites. The data suggest that the present-day regional gene diversity has evolved differently in each region.

INTRODUCTION

Throughout the last decade bryologists have debated rates of evolution in mosses and hepatics. Traditional views regard bryophytes as evolutionarily unspecialized in comparison to tracheophytes, because they are phylogenetically older than phanerogams, but are far less differentiated (Crum 1972; Szweykowski 1984). In fact, Crum (1966) has gone so far as to say that evolution at the specific level appears to be at a standstill.

Five lines of evidence have been used to support the view that bryophytes evolve slowly. Firstly, some taxonomic groups are morphologically uniform, with very few narrowly endemic taxa and a relatively small number of species per genus. Also, the fossil record indicates that bryophytes had diversified into the major taxonomic ranks of mosses, hepatics, and hornworts by the Permian and that few major morphological changes have occurred since (Anderson 1963; Crum 1972; Krzakowa and Szweykowski 1979; Cummins and Wyatt 1981; Dewey 1989; Wyatt et al. 1989a). At least some modern moss genera were present by the early Cenozoic (Vitt 1984). However, several bryologists have suggested that the fossil record is far too scant to be used as conclusive evidence on the rate of evolution in bryophytes (Khanna 1964; Krassilov and Schuster 1984; Miller 1984). Finally, hepatics have a much earlier fossil record than mosses and hornworts, and it is unjustified to consider these three bryophyte groups to be of similar age; there is no evidence that mosses are as old as hepatics.

Secondly, some bryophyte species occur as disjunct populations as far apart as the two polar regions. Tracheophytes, with similar distributions, have disjunct populations related to each other at the generic or familial rank, whereas disjunct populations of bryophytes are often of the same species (Anderson 1963; Crum 1966; Krzakowa and

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Szweykowski 1979; Cummins and Wyatt 1981; Szweykowski 1984; Dewey 1989). Disjunct populations of bryophytes may have become established relatively recently through long-range dispersal; however, many species distributions reflect tectonic events just as disjunct populations of vascular plants. Moreover, current understanding of bryophyte distributions indicates that long-range dispersal may be less important than slow step-by-step dispersal across wide areas (van Zanten and Pocs 1981; Wyatt et al. 1989a).

Thirdly, many bryologists believe that the slow rate of evolution in mosses and liverworts is chiefly due to the dominamt haplophase in the bryophyte life cycle, in which all alleles are expressed. Haploid organisms are believed to have low genetic diversity because a slightly deleterious mutation will be strongly selected against in the gametophyte stage, and since mutations that are deleterious in one environment may be advantageous in another, the chances of adapting to new environments through mutation alone are reduced (Crum 1972; Longton 1976; Krzakowa and Szweykowski 1979; Cummins and Wyatt 1981; Yamazaki 1981; Daniels 1982; Szweykowski 1984; Innes 1990).

Fourthly, because of their small stature and seemingly restricted range of niches, bryophyte species are thought to be subjected to very few new selective pressures (Crum 1966; Longton 1976; Cummins and Wyatt 1981; Dewey 1989). Mosses are thought to avoid macroenvironmental change because they are well suited to specific micro-environments, thus they avoid the pressures that are exerted on larger plants through geologic time (Anderson 1963; Crum 1972) or presumably over large environmental gradients such as changes in latitude.

Lastly, bryophytes have particularly short gene flow distances that are thought to increase inbreeding, reduce genetic recombination, and reduce the rate of evolution (Anderson 1980; Cummins and Wyatt 1981; Wyatt et al. 1989b). Since sexual reproduction is restricted by short gene flow distances, fragmentation of vegetative portions of moss plants can become an important mode of reproduction and gene dispersal because almost every part of the moss plant, except the antheridia, can regenerate (Anderson 1980). Fragmentation and vegetative reproduction are particularly important in polar regions where sporophyte production is much lower than in temperate or tropical regions (Holmen 1960, Crum 1972; Longton 1976; Schofield 1985; Smith 1987). Inbreeding and vegetative reproduction can lead to reduced gene diversity which in turn reduces the evolutionary flexibility of a species; prior gene diversity is required before temporal, spatial, or ecological isolating mechanisms can affect rates of speciation (Farris 1988; Macnair 1989; Ennos 1990). Therefore, it can be expected that gene diversity might be lower in polar mosses relative to mosses of lower latitudes, and possibly that populations of mosses in the north will have lower genetic diversities relative to their conspecifics in the south.

These five lines of evidence have led some bryologists to believe that evolution is slow in bryophytes. However, all of the above hypotheses are based on inference and rarely on empirical data. Evolution is based, for the most part, on changes in gene frequencies, and so it is to gene frequencies that we should look for information on the

rate of evolution in bryophytes (Krzakowa and Szweykowski 1979; Wyatt 1982). Several electrophoretic studies indicate that the level of gene diversity in bryophytes is much higher than expected and in some species is comparable to gene diversity in angiosperms (Krzakowa and Szweykowski 1979; Cummins and Wyatt 1981; Yamazaki 1981; Daniels 1982; Szweykowski 1982, 1984; de Vries et al. 1983, 1989; Wyatt et al. 1987, 1989a; Innes 1990; Meagher and Shaw 1990). Apparently, bryophytes are not as genetically depauperate as would be expected, given the above lines of evidence.

Levels of diversity at isozyme loci may not reflect levels of genetic diversity for ecologically important characters, but if the electrophoretically detectable genetic variation is high and the variation in ecologically important characters is low, it may be suggested that natural selection has acted to stabilize the ecologically important characters. Thus, genetic diversity in selectively neutral traits can indicate the potential of a species to evolve.

Most investigators have found that genetic distances between populations do not relate in any way to spatial distances or to differences in ecology between populations (de Vries et al. 1989; Dewey 1989; Innes 1990). Such patterns can provide information on the evolutionary history of a species (Crouau-Roy 1989a). Spieth (1975), however, found similarities between patterns of genetic distance and patterns of spatial distance only when he expanded the geographical range of his studies. He concluded that in a small area, the microhabitats in which *Neurospora intermedia* (a haploid fungus) occurs are more ecologically similar than different in comparison to microhabitats across a wide geographical area. Differing selective pressures may be evident only over wide geographical ranges. Also Wyatt et al. (1989a) found that there was more gene diversity in mosses from old growth forests than in secondary growth forests, possibly indicating that a genetic bottleneck had taken place in the not too distant past.

Morphological variation over geographical gradients in bryophytes has not been studied extensively. However, the few studies available suggest that bryophytes do exhibit morphological variation and that it is often related to broad-scale geographic patterns. Vitt (1980) showed that geographically separated populations of the widespread moss *Macrocoma tenue* are morphologically different. *Schlotheimia* species occurring in New Zealand exhibit some morphological characters that vary with latitude (Vitt 1989), and morphological features of *Meesia triquetra* not only vary relative to latitude, but are more variable in the southern [boreal] part of the species' North American range than in the northern part [arctic] (Montagnes and Vitt 1991).

In this study we examine genetic variation in *Meesia triquetra* (Richt.) Aongstr., a rare, rich fen indicator species of high fidelity (Slack et al. 1980). The gametophytes of *M. triquetra* are unisexual. It is a circumboreal moss that occurs in North America from northernmost Ellesmere Island and Alaska, south to Montana and California, and east to Wisconsin, Pennsylvania, and Newfoundland (Montagnes, 1990a). There are three objectives to this study: 1) to quantify levels of gene variation in *M. triquetra* and to relate the degree of variability to gene diversity records in other mosses and organisms, 2) to determine how genetic variation in *M. triquetra* is patterned between sites from southern, mid, and northern parts of the species geographic range, and 3) to

suggest a biogeographic hypothesis that accounts for the modern distribution and gene diversity patterns found.

Materials and Methods

Study Regions

Plants of *Meesia triquetra* were collected from three regions (boreal, subarctic, and high arctic) along a 3000 km arctic-boreal gradient in northern and western Canada. Within each region, five fens (sites) were selected; the boreal sites are located between Edson and Nordegg, Alberta (between 55°35′N, 116°26′W and 52°50′N, 116°05′W). The subarctic sites are located along the Dempster Highway, Yukon Territory, between km 96 and 190 (between 64°30′ and 65°30′N at approximately 138°50′W). The high arctic sites are located at Princess Marie Bay on Ellesmere Island, N.W.T. (79°29′N, 75°47′W). The subarctic site is approximately half the distance between the boreal and high arctic site.

Exact locations for all fifteen sites and details of the geology, vegetation, and climate of each are outlined by Montagnes (1990b), and voucher specimens of *M. triquetra* are located at ALTA.

Collection and Electrophoresis

Fifty collections of live moss (approximately 24 cm^2, 7 cm deep), hereafter referred to as "demes", each containing at least ten *M. triquetra* stems, were collected from each of the 15 sites. Thus, collections were made in a nested fashion, with ten stems within each of 50 demes from each of five sites from each of three regions. Deme collections were made no less than 1 m apart. The demes were placed in plastic bags and kept cool for three months when they were placed in plastic greenhouse cell trays and left to grow in a growth chamber. The trays were set in a 4-cm deep water bath to ameliorate temperature differences due to lighting on the growth bench. Tbe lighting was held constant with 16 daily hrs of light at an intensity of 300 $\mu mol\, s^{-1}\, m^{-2}$. The water bath had daily maximum temperatures of 18°C and daily minimum temperatures of 10°C. Relative humidity was maintained at 65%. Every day the trays were watered with distilled, deionized water.

One stem from each of 30 randomly chosen demes per site (450 in total) was assayed for enzyme phenotype using horizontal starch-gel electrophoresis following the methods of Bayer (1988). Stems were ground with mortar and pestle on ice in two drops of an ice-cold extraction buffer: 1 M Tris-HCl, pH 7.5, 4.0 mM 2-mercaptoethanol, 1.0 mM EDTA (disodium salt), 0.2 M sucrose, 0.6% polyvinyl-polypyrrolidone (5 : 1 ratio of 40 K : 360 K m.w.), 2.0% PEG (8 K m.w.), 0.1% BSA, and 0.002 M ascorbic acid. The extract was absorbed on two filter paper wicks, which were frozen at −20°C for 24 hrs and then loaded into 12.5% starch gels. Malate dehydrogenase (MDH), phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), and aldolase (ALDO) were resolved on a system consisting of a gel buffer of 0.016 M L-histidine (free base) and 0.002 M citric acid-H_20 (pH 6.5) and an electrode buffer of 0.065 M L-histidine (free base) 0.007 M citric acid H_20 (pH 6.5). Glucose-3-phosphate dehy-

drogenase (G3PDH), glutamate oxaloacetate transaminase (GOT), alcohol dehydrogenase (ADH), and triosephosphate isomerase (TPI) were resolved on a system composed of a gel buffer consisting of one part 0.038 M lithium hydroxide-H_20-0.188 M boric acid (pH 8.3), and 9 parts 0.045 M Tris-0.007 M citric acid (pH 8.4), with the electrode buffer consisting only of the lithium borate constituent.

Isozyme variation was used to determine total gene diversity (H, Nei 1973) as follows: total gene diversity [H_t]; gene diversity within sites (between demes) [H_s]; gene diversity between sites [D_{st}]; and the relative amount of between site diversity to total diversity [G_{st}] using the GENESTAT program (Whitkus 1985). Also the mean gene diversity of each site was calculated as $(\sum H_{ik})/n$; where H_{ik} is the gene diversity of the i^{th} site at the k^{th} locus and n is the total number of loci, and regressed against latitude. Principal components analysis (PCA) was used to determine how each site related to isozyme variation using NTSYS-pc (Rohlf 1987). Allele frequencies were used to determine genetic distances (D) and identities (I) (Nei 1972) between regions and between sites. A phenogram was constructed based on genetic identities using NTSYS-pc.

RESULTS

Enzyme band interpretation is facilitated because only one allele can be carried at each locus due to the haploid condition of *M. triquetra* gametophytes. The chromosome number of *M. triquetra* is $n=10$ (Steere 1954a, 1954b; and Inoue 1979). The 18 putative isozymes (and their allozymes) detected are: MDH-1 (A and B), MDH-2 (A to C), MDH-3 (A to C), PGI-1 (A), PGI-2 (A and B), PGI-3 (A to C), PGM-1 (A), PGM-2 (A), PGM-3 (A to C), TPI-l (A and B), TPI-2 (A and B), GOT-1 (A), G3 PDH-1 (A), G3PDH-2 (A and B), ALDO-1 (A and B), ALDO 2 (A to C), ADH-1 (A and B), and ADH-2 (A and B). ADH-1 and G3PDH-1 were often not expressed, in which case they were not considered in the analysis.

Total gene diversity (H_t) of the regions and within site gene diversity (H_s) within regions show a decreasing trend with increasing latitude; however, between site gene diversity is highest in the subarctic region and lowest in the high arctic (Table 1, Fig. 1). Between site diversity accounts for 49% of the total diversity in the subarctic region, but only 27–28% in the high arctic and boreal regions (Table 1, Fig. 1). Five of 18 loci were polymorphic in the high arctic sites, nine loci showed variation in the subarctic sites, and 11 loci showed variation in the boreal sites. Most of the loci that were variable in the north were also variable in the south; exceptions are *Adh-1*, which varied in the high arctic and boreal sites, but not in the subarctic sites, and *Pgi-2* and *Tpi-2* which varied in the subarctic sites, but not in the boreal sites. Mean gene diversities of boreal sites are highest, while those of high arctic sites are lowest, with mean gene diversity decreasing with increasing latitude (Fig. 2). Seventy percent of the variation in mean gene diversity data is accounted for by the latitudinal gradient ($p \leq 0.005$).

The high arctic sites are positioned in the PCA in a relatively small area, with a high positive principal component (PC) 1 and high negative PC2 and PC3 loadings,

Table 1. Total gene diversity (H_t), within site gene diversity (H_s), between site gene diversity (D_{st}), and coefficient of gene differentiation (G_{st}) for *Meesia triquetra* at all sites and within each of the three regions.

	H_t	H_s	D_{st}	G_{st}
All sites	0.151	0.082	0.069	0.454
High Arctic	0.080	0.057	0.023	0.286
Subarctic	0.145	0.074	0.070	0.485
Boreal	0.181	0.131	0.050	0.274

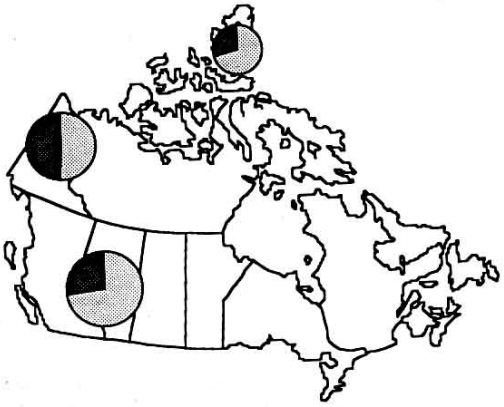

Fig. 1. Map of Canada with relative total gene diversity (H_t) shown by size of circle; between site gene diversity (D_{st}) represented by dark shading and within site gene diversity (H_s) by light shading.

indicating a strong influence from the alleles *Tpi-1*^{a}, *Tpi-1*^{b}, and *Adh-1*^{b}. Conversely, the boreal sites are scattered across PC1, but have high PC2 and PC3 loadings, indicating strong influence from *Mdh-1*^{a}, *Mdh-1*^{b}, *Pgm-3*^{a}, *Pgm-3*^{b}, *Aldo-1*^{a}, and *Aldo-1*^{b}, and moderate influence from *Mdh-2*^{c}, *Pgi-2*^{a}, *Pgi-2*^{b}, and *G3pdh-2*^{a}. Finally, the subarctic sites are located high on the PC1 axis, but throughout the PC2 and PC3 axes. The subarctic and high arctic sites overlap considerably, and are both well separated from the boreal sites. Between site variation is greatest for the subarctic sites and least for high arctic and boreal sites (Fig. 3).

Genetic identities (I) between pairs of sites range from 0.8010–0.9997 (Table 2). Genetic identities between high arctic sites range between 0.933 and 0.999 with a mean of 0.964; those of subarctic sites range between 0.801 and 0.999 with a mean of 0.903, and those of the boreal sites range between 0.842 and 0.970 with a mean of 0.923. Thus high arctic sites have most similarity to one another, while subarctic sites have least similarity among sites. A UPGMA phenogram of the mean genetic identity by region shows that the subarctic and high arctic regions are much more similar to each other

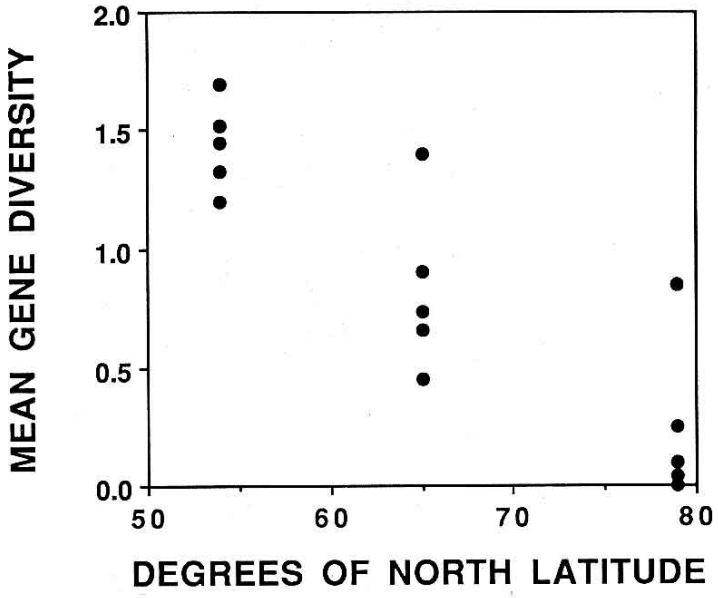

Fig. 2. Relationship of mean gene diversity (H_t) of *Meesia triquetra* from 15 sites (fens) to latitude.

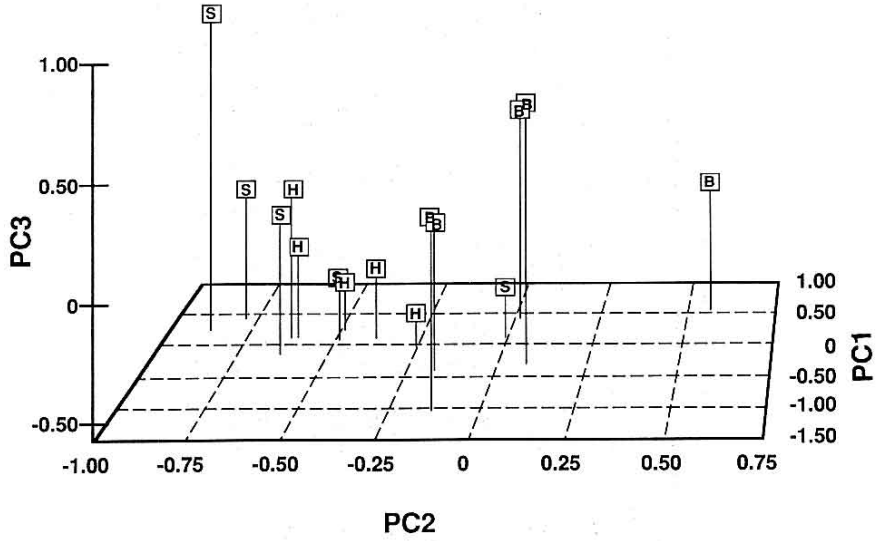

Fig. 3. Principal components analysis of allele frequency variation from 15 sites (fens) in *Meesia triquetra*. (B=boreal; S=subarctic; H=high arctic).

Table 2. Genetic identities (*I*) (above) and distances (*D*) (below) of *Meesia triquetra* from between sites from the high arctic region (H), subarctic region (S), and boreal region (B).

Population	H1	H2	H3	H4	H5	S1	S2	S3	S4	S5	B1	B2	B3	B4	B5
H1	-.---	0.999	0.953	0.967	0.933	0.892	0.903	0.929	0.916	0.997	0.939	0.954	0.976	0.9655	0.950
H2	0.000	-.---	0.948	0.961	0.928	0.931	0.887	0.917	0.904	0.997	0.930	0.950	0.973	0.961	0.943
H3	0.048	0.053	-.---	0.979	0.997	0.875	0.987	0.992	0.925	0.917	0.991	0.983	0.958	0.908	0.899
H4	0.033	0.040	0.021	-.---	0.973	0.848	0.947	0.978	0.925	0.956	0.924	0.963	0.929	0.952	0.913
H5	0.069	0.075	0.003	0.027	-.---	0.864	0.929	0.992	0.928	0.894	0.962	0.975	0.929	0.889	0.823
S1	0.114	0.072	0.134	0.164	0.147	-.---	0.801	0.816	0.918	0.999	0.831	0.871	0.860	0.848	0.872
S2	0.102	0.120	0.013	0.055	0.074	0.221	-.---	0.957	0.873	0.879	0.945	0.909	0.919	0.891	0.865
S3	0.074	0.087	0.008	0.022	0.008	0.203	0.044	-.---	0.919	0.913	0.903	0.970	0.875	0.916	0.852
S4	0.088	0.101	0.078	0.078	0.075	0.086	0.136	0.085	-.---	0.951	0.906	0.906	0.907	0.868	0.895
S5	0.003	0.003	0.086	0.045	0.112	0.001	0.130	0.091	0.050	-.---	0.812	0.941	0.885	0.973	0.943
B1	0.063	0.073	0.009	0.080	0.038	0.185	0.057	0.102	0.099	0.208	-.---	0.962	0.970	0.857	0.842
B2	0.048	0.051	0.018	0.037	0.025	0.138	0.095	0.030	0.099	0.061	0.039	-.---	0.947	0.948	0.925
B3	0.025	0.028	0.043	0.074	0.074	0.151	0.085	0.134	0.098	0.123	0.030	0.054	-.---	0.898	0.916
B4	0.035	0.040	0.096	0.049	0.118	0.165	0.116	0.088	0.141	0.027	0.154	0.060	0.108	-.---	0.964
B5	0.051	0.059	0.107	0.091	0.195	0.137	0.145	0.160	0.112	0.059	0.172	0.078	0.088	0.036	-.---

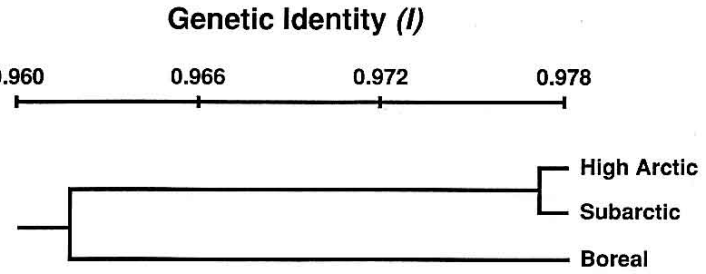

Fig. 4. UPGMA Phenogram based on Nei's genetic identity (I) for populations of *Meesia triquetra*.

than they are to the boreal region (Fig. 4).

DISCUSSION

Genetic Diversity

The overall value for gene diversity (H_t) of *M. triquetra* is near those reported for several species of bryophytes, including some species of *Racopilum*, *Plagiomnium ciliare*, and *Conocephalum conicum* (Table 3). The two *Pellia* species reported by Zielinski (1987) and other gene diversity records for hepatics cited by Wyatt et al. (1989b) indicate that overall, hepatics may have lower gene diversities than mosses. Khanna (1964) argued that since hepatics, compared to mosses, have a smaller number of species, less variation in chromosome number, less effective spore dispersal mechanisms, and are less ecologically successful, hepatics have a slower rate of evolution than mosses. Lower genetic diversities in hepatics would support Khanna's views, but as of yet the evidence is scant.

Meesia triquetra has H_t values much higher than those of selfing vascular plants such as *Hordeum spontaneum* or *Phlox cuspidata* and even higher H_t values than the outcrossing *Gaura longiflora*, although *M. triquetra* has a much lower H_t value than does *Picea abies*. In terms of mean genetic heterogeneity, mosses appear to be slightly more genetically homogeneous than tracheophytes (Loveless and Hamrick 1984). Although gene diversity in the dioicous *M. triquetra* is close to that of apomictic vascular plants (Table 3), it also has H_t values close to those reported for dioecious tracheophytes. Only *Racopilum spectabile* and *R. cuspidigerum* have H_t values near the averages reported for outcrossing and all sexual plants in general, and none of the mosses reported has diversities as high as those reported for autogamous, hermaphroditic, or facultatively apomictic tracheophytes (Loveless and Hamrick 1984).

The range of genetic identities between sites of *M. triquetra* are similar to those reported for populations of other moss species. Some mosses have wide ranges of I between populations. For instance, values for genetic identity between *Racopilum capense* populations range from 0.520 to 0.990 in identity (de Vries et al. 1989) and those of *Sphagnum recurvum* var. *mucronatum* range from 0.430 to 0.864 (Daniels

Table 3. Total gene diversity (H_t) within species of bryophytes and tracheophytes.

	Species	H_t	Authority
Mosses	*Meesia triquetra*	0.151	this paper
	Racopilum strumiferum	0.180	de Vries et al. 1989
	Racopilum tomentosum	0.170	de Vries et al. 1989
	Racopilum intermedium	0.080	de Vries et al. 1989
	Racopilum capense	0.080	de Vries et al. 1989
	Racopilum spectabile	0.260	de Vries et al. 1983
	Racopilum cuspidigerum	0.260	de Vries et al. 1983
	Plagiomnium ciliare	0.177	Wyatt et al. 1989a
Hepatics	*Conocephalum conicum*	0.167	Yamazaki 1981
	Pellia neesiana	0.025	Zielinski 1987
	Pellia borealis	0.045	Zielinski 1987
Tracheophytes	*Antennaria rosea*	0.183	Bayer 1989
	Hordeum spontaneum	0.003	Nevo et al. 1979
	Phlox cuspidiata	0.008	Levin 1978
	Gaura longiflora	0.074	Gottlieb and Pilz 1976
	Picea abies	0.370	Lundkvist 1979
	Calamagrostis canadensis	0.183	MacDonald and Lieffers (unpubl.)
General-Tracheophytes:	Autogamous	0.291	Loveless and Hamrick 1984
	Mixed mating	0.242	Loveless and Hamrick 1984
	Predominantly outcrossing	0.251	Loveless and Hamrick 1984
	Hermaphroditic	0.284	Loveless and Hamrick 1984
	Monoecious	0.224	Loveless and Hamrick 1984
	Dioecious	0.155	Loveless and Hamrick 1984
	Obligately apomictic	0.172	Loveless and Hamrick 1984
	Facultatively apomictic	0.356	Loveless and Hamrick 1984
	Sexual	0.261	Loveless and Hamrick 1984

1985). Within many tracheophyte populations, I values between conspecific populations are rarely lower than 0.700, and animals such as the cave dwelling beetle, *Speonomus zophosinus* (Crouau-Roy 1989b), and the Opossum, *Didelphis virginianum* (Kovacic and Guttman 1979), do not have values of I between populations below 0.900. Genetic identities between populations within some bryophyte species are as low as values of I between most tracheophyte species (Table 4).

Gene diversity and genetic identities in *M. triquetra* are comparable to that of many tracheophyte and animal species. Evidently, if *M. triquetra* (and other mosses) are evolving slowly compared to other organisms, it is not because they are genetically depauperate.

Genetic Variation With Latitude

Overall gene diversity in *M. triquetra* declines with increasing latitude, with high arctic gene diversity only 44% of boreal and 55% of subarctic diversity. Subarctic gene

Table 4. Genetic identities (I) among populations from mosses, tracheophytes, and animals.

Species	Identity	Authority
Mosses		
Meesia triquetra	0.801–0.9997	this paper
Plagiomnium ciliare	0.813–0.998	Wyatt et al. 1989a
Racopilum spectabile	0.853–0.899	de Vries et al. 1983
Racopilum strumiferum	0.880–0.960	de Vries et al. 1983
Racopilum tomentosum	0.960–0.990	de Vries et al. 1983
Racopilum capense	0.520–0.990	de Vries et al. 1983
Sphagnum pulchrum	0.657–0.967	Daniels 1982
Sphagnum recurvum var. *mucronatum*	0.430–0.864	Daniels 1985
Tracheophytes		
Dedeckera eurekensis	0.855–0.974	Nickrent and Wiens 1989
Senecio flavus	0.857–0.984	Liston et al. 1989
Antennaria rosea	0.718–0.990	Bayer 1989
Coreopsis nuecensis	0.900–0.990	Crawford and Smith 1982
Elymus canadensis	0.960	Sanders et al. 1979
Pseudotsuga menziesii	0.990	Yeh and O'Malley 1980
Picea abies	0.980	Lundkvist 1979
Sullivantia hapemanii	0.900–1.000	Soltis 1981
Hordeum spontaneum	0.890	Nevo et al. 1979
Gaura longiflora	0.990	Gottlieb and Pilz 1976
Calamagrostis canadensis	0.986–0.997	MacDonald and Lieffers (unpub.)
Animals		
Speonomus hydrophilus	0.952–0.981	Crouau-Roy 1989a
Speonomus zophosinus	0.960–1.000	Crouan-Roy 1989b
Didelphis virginiana	0.904–0.955	Kovacic and Guttman 1979

diversity is 80% of boreal diversity. However, perhaps more significant are the patterns at the site and deme levels. Within site diversity (deme diversity) in the high arctic is only 44% of the within site boreal diversity, while subarctic within site diversity is 56% of the boreal diversity. Thus individual sites (fens) in the subarctic and especially in tbe arctic are genetically more uniform than individual fens in the boreal region.

Gene diversity between sites reveals a completely different pattern. Highest between site gene diversity, lowest mean genetic identity, and greatest range of individual genetic identities is in the subarctic. The boreal region between site gene diversity is 71% that of the subarctic, while high arctic between site gene diversity is 33% of the subarctic. Identities show similar patterns, and it is clear that subarctic sites have greater differences between themselves than do either high arctic and boreal sites. Finally, identities and the PCA analysis clearly show that the high arctic populations are more closely allied to the subarctic ones than to the boreal ones.

We suggest three possible reasons for these patterns of gene diversity in *Meesia triquetra*. Firstly, low genetic diversity may be due to founder effect. Northern

populations of *M. triquetra* may be the result of a relatively small number of propagules immigrating north from southern populations relatively recently. Such a founder effect would be amplified by the haploid, unisexual condition and reduced sexual reproduction in the high arctic. Variation in the number of sporophytes produced by *M. triquetra* over the three regions was not investigated quantitatively, but far fewer sporophytes were observed in high arctic sites than in subarctic and boreal sites, both in the growth chamber during the culturing period and in the field. Founder effects could explain the relatively low genetic diversity in northern populations of *M. triquetra* if the northern populations are younger than the southern populations.

Secondly, relatively low genetic diversity in northern populations of *M. triquetra* could be the result of genetic drift. This is particularly likely if the Ellesmere populations are indeed comparatively older than the boreal, or even the subarctic populations. According to England and Bradley (1978), Ellesmere Island was not completely glaciated during the Wisconsinan Glaciation because of the aridity of the climate. This implies that the high arctic popnlations could be older or as old as the boreal populations. Thus, low genetic diversity in high arctic populations of *M. triquetra* may result from loss of variability in isolated, relatively old, relict populations.

Thirdly, the relatively low genetic diversity in the northern populations of *M. triquetra* could be the result of strong selective forces acting in the harsh arctic environment. If, in fact, there is less sexual reproduction in *M. triquetra* in northern populations, it is likely that the electrophoretically detectable loci have undergone fixation with selectively advantageous genetic backgrounds.

Biogeographic Corollaries

Differences in patterns of gene diversity are clearly evident for populations from boreal, subarctic, and high arctic regions of North America. Historically, the boreal sites were glaciated several times in the Pleistocene, and became ice free about 10,000 years ago, however the sites are near to the western Canadian Ice Free Corridor (Prest 1984) and also relatively close to the southern extent of Wisconsinan Glaciation. The subarctic sites, in present-day eastern Beringia, were never glaciated, while the high arctic sites may or may not have been glaciated (Prest 1984), but it is doubtful that the severe Pleistocene climate of the area would have allowed the presence of permanent rich fens as they occur today.

Based on our data, we suggest the following geographic history for *Meesia triquetra* in northwestern North America.

1. The boreal populations are descendants from relatively old, extensive, interbreeding populations that survived glacial advances in relatively large populations, either south of the maximum extent of glaciation or in the Ice Free Corridor, migrating relatively short distances to their present day sites. These populations were never genetically impoverished and they have been little affected by founder effects, genetic drift, nor strong selective forces as evidenced by the large total gene diversity, large within site gene diversity, and rather low between site gene diversity. They did not contribute significantly to founding northern populations of this species.

2. The subarctic populations are relatively old; they survived glaciation in relatively small populations under strong selective pressures. Inter-site breeding was restricted due to isolation of sites. Thus they exist today with moderate amounts of total gene diversity, little gene diversity within sites, and large gene diversity between sites. They served as ancestral populations for those farther north.

3. The high arctic populations are recent, immigrants originating from subarctic populations. The lack of diversity can be attributed to founder effects, with strong selection having previously acted on ancestral populations in the subarctic. The small amounts of both within and between site diversity suggest recent introduction with relatively large amounts of asexual reproduction. The strong genetic identities with subarctic populations (and lack of with boreal ones) indicate that the high arctic populations are derived from subarctic ones. As indicated by the low between site gene diversity, it is unlikely that the high arctic populations are survivors of glacial periods, as the subarctic ones appear to be.

CONCLUSIONS

Meesia triquetra is one of several bryophytes with genetic diversities comparable to those of vascular plants and some animals. The existence of these genetically diverse species of mosses and hepatics contradicts the view that bryophytes have low genetic diversity because of their dominant haploid state, short gene flow distances, and low incidence of sexual reproduction. The amount of genetic variation in bryophytes is certainly as high as in many tracheophyte species, which indicates that bryophytes may have the potential to evolve as vascular plants. Indeed, it may be that bryophytes have not evolved simply because selective pressures are acting to stabilize their characters rather than to modify them. When genetic diversities are considered, it appears that populations of *Meesia triquetra* from boreal, subarctic, and high arctic regions of North America have different genetic compositions that reflect the complex histories of populations from the three regions. Indeed, the patterns in genetic diversity of *Meesia triquetra* suggest a highly dynamic, regionally differentiated species.

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