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Variation in the structure of *Matteuccia struthiopteris* populations in Lithuania

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Demographic data and associated phytosociological and environmental variables were sampled from 25 populations dominated by the fern *M. struthiopteris* studied in different parts of Lithuania. The main aim was to study the variation in demographic variables such as rootstock thickness, trophophyll size, plant density and sporophyll production within the populations and to analyse this variation in relation to environmental variables and floristic composition. The fern is relatively rare in Lithuania, and the populations were, with few exceptions, small. In total, 71 different vascular plant species were associated with the fern, but the average number of vascular plants was only 4.7 per m^{-2}. The variation in species composition was significantly correlated with the distance from the coast ($p = 0.001$) and a growth site on river-banks or not ($p = 0.001$). Compared to studies in other countries, the rootstocks and fronds were generally big, and the rootstock density was very low. All rootstocks were connected to a parental plant, indicating that they were all results of vegetative reproduction. The sporophyll production was highly variable, and it decreased strongly with increasing canopy cover ($p = 0.001$). Based on the rootstock sizes, all the populations studied were considered to be old. Most of the populations appeared to be in healthy condition, but some suffered from dry soil and a dense canopy cover.

Key words: ramets, trophophyll, sporophyll, fern, density, ordination

INTRODUCTION

Ecological studies of individual species have as a primary objective analysis of species adaptation to their environments, and in such studies data on population structure may provide important information whether the actual specimens are growing in a favourable site. Especially important may be comparisons of how the plants allocate resources to reproduction under different environmental conditions. In many plant species, recruitment through the production of vegetative offshots (clonal growth) is an important method of establishment and spread. Clonal ramets, like individual plants (genets), have individual demographic profiles. But ramets differ in that they often remain attached to one another (via rhizomes) and may therefore remain physiologically interconnected. Clonal growth may result in the development of large, dense stands consisting of a single genotype. Analysis of how plants allocate resources to sexual (spores or seeds) and asexual structures (new ramets) in the field is essential for the understanding of the relationship between growth and reproduction as well as the constraints imposed upon reproduction under different environments. All plants exhibit a certain range of morphological variation, and this applies to all plant organs both above and below ground. In ecological studies, plants are frequently used as environmental indicators, and then it may be useful to know the morphological characteristics of an "average plant" and the extent of their variation.

The ostrich fern, *Matteuccia struthiopteris* (L.) Todaro, is widely distributed in Cold Temperate and Boreal North America and Eurasia. It is confined to areas with rich and moist soils, often on fluvial deposits. Here the fern may produce large homogeneous stands, with or without a tree canopy [1, 2]. In Europe it is scattered or missing in the northernmost, southernmost, and westernmost parts. *M. struthiopteris* is widely used as an ornamental plant, and in parts of the world it has also a long history as an edible plant [3, 4]. Recently there has been interest in both management of wild fern populations and field cultivation [1]. Harvesting the ostrich fern as a green vegetable involves the removal of the fronds (fiddleheads) as they emerge in the spring, prior to any degree of uncoiling. Studies have been carried out in order to document effects of crozier removal on growth and long-term viability of the plants [5].

Studies of plant populations in different geographic areas, which involve sampling of both floristic, demographic, and environmental data, may give valuable information about the ecological demands of the actual species, its responses to different environmental conditions, and give a basis for the evaluation of its future survival and possible needs for remedial management actions. This paper describes the relationships among demographic, environmental and floristic data on *Matteuccia* populations in different parts of Lithuania, with emphasis on the relative variation in allocation of resources to sexual (sporophyll production) and asexual reproduction (production of new small ramets). The results of this investigation will be followed by a study of the variation in fern population genetics in Lithuania [10].

MATERIALS AND METHODS

The sampling of field data was carried out in July during 2003–2005. In total, 25 populations were investigated in different parts of Lithuania, most of them situated within regional or national Parks. A stratified random sampling method was applied: only the populations where *M. struthiopteris* was dominant (more than 75% of the cover) were selected, and the populations had also to be mature, i.e. that some of the rootstocks had to be thicker than 50 mm. Then the effects of population dynamics and succession should be strongly reduced. Within each population, a representative 2 × 2 m sample plot was randomly selected for collection of floristic data, morphological measurements, demographic data and environmental variables.

The abundances of all species in the studied quadrats were subjectively estimated according to the following cover scale: 1: 1%, 2: 2–5%, 3: 6–10%, 4: 11–25%, 5: 26–50%, 6: 51–75%, 7: >75% of the cover. The total cover of the canopy layers was estimated in percentage. Slope was estimated in degrees. The distance of the populations from the coast (Klaipëda) was measured in km. Growth site in a river bank subjected to sedimentation or not and growth site influenced by fallen logs (from storm) were given on a nominal scale. DCA axes of 1–4 sample scores were included as floristic explanatory variables.

M. struthiopteris is a clonal plant, and consequently all rootstocks within a population may genetically represent the same genome. This study was based on the morphology and demography of the different upright rootstocks within the samples. The fern produces both fertile (sporophyll) and sterile (trophophyll) fronds, both in variable numbers and sizes. The following morphological data were sampled for each rootstock: number of trophophylls (nT), number of sporophylls (nS), sporophyll height (hS), trophophyll height (hT), and rootstock diameter (dR).

Based on the sampled morphological data, the following demographic variables were calculated for each quadrat: number of rootstocks (nR), height of the tallest frond on the actual rootstock (hTmax), total number of fertile rootstock within the quadrat (nF), mean trophophyll height for the quadrat (mTh), mean number of trophophylls within the quadrat (mnT), mean rootstock diameter for the quadrat (mdR), maximum rootstock thickness in the quadrat (maxR), number of rootstocks with trophophyll smaller than 6 dm (n6), number of rootstocks with trophophyll taller than 12 dm (n12), number of rootstocks with a diameter smaller than 2 cm (d2), number of rootstocks with a diameter larger than 10 cm (d10), and percentage of rootstocks producing sporophylls (F%).

Statistical analyses were performed on different data-matrices: (1) morphological variation, (2) variation of species composition, (3) relationships between floristic composition and environmental variables, and (4) relationships between floristic composition and demographic variables. These data-sets were analysed by different numerical methods: Principal Components Analysis (PCA), Detrended Correspondence Analysis (DCA), Canonical Correspondence Analysis (CCA), and Redundancy Analysis (RDA) were run on the CANOCO 4.5 program package [11]. *M. struthiopteris* was introduced as a supplementary species in the DCA and CCA analysis. In PCA, "Center by species" was selected, and in RDA, "Center and Standardize" was selected. Otherwise default settings were selected (no down weighting of rare species).

Monte Carlo permutation tests (available in CCA and RDA) were run to test the significances of the different variables. Both forward and manual selection of the variables were tested. Marginal effects (λ_M) give the variance they explain singly, i.e. when that particular variable is used as the only explanatory factor. Conditional effects (λ_C) give the variance they explain in the order of their inclusion in the model together with the additional variance each variable explains at the time it was included. In Monte Carlo tests, the significance (p value) of the variable at that time together with its test statistics (F value) is given based on 1000 permutations. Prior to the statistical analyses, all variables were square-root transformed ($\sqrt{x+1}$) in order to try to normalize the data and to remove the dependency of the variance upon the mean.

RESULTS

1. Morphological variation

In total, 506 rootstocks were measured, and these had in total developed 3552 trophophylls and 227 sporophylls. The morphology of *M. struthiopteris* in

Table. Geographic location of study populations and demographic data on sampled quadrats (Q). lb = lake bank, rb = river bank, rt = river terrace, rv = river valley, f = forest. Areas: 1–3 Aukštaitija NP, 4–6 Dzūkija NP, 7–9 Krekenava RP, 10–12 Anykščiai RP, 13–16 Utena district, 17–19 Rambynas RP, 20–22 Žemaitija NP, 23–24 Venta RP, 25 Kaišiadorys district. NP = national park, RP = regional park. Size = Approximate population size in m^2. For explanation of demographic abbreviations see Methods

Q	Site	Size	nR	mTh	mnT	mhS	mdR	maxR	n6	n12	nS	nF	d2	d10	F%
1	Linkmenas lb	48	41	113.8	7.9	51.9	64.0	100	3	21	18	7	3	7	17.1
2	Linkmenas lb	60	28	106.6	10.0	42.4	73.2	122	3	7	14	6	1	9	21.4
3	Buka rb	200	16	142.6	7.4	46.0	97.2	120	0	15	1	1	0	10	6.3
4	Merkys rt	63	19	110.7	6.5		71.1	110	1	7	0	0	1	5	0.0
5	Merkys rt	300	21	107.4	7.1	35.5	68.8	120	1	6	3	2	1	4	9.5
6	Merkys rt	135	23	91.0	5.9	39.5	61.7	121	3	4	6	2	3	3	8.7
7	Liaudė rv	1800	21	134.6	6.7	75.0	64.1	102	0	16	4	1	0	4	4.8
8	Liaudė rv	600	15	155.4	9.0	52.0	87.3	127	0	14	4	2	0	4	13.3
9	Liaudė rv	50	15	140.8	8.9	73.2	73.0	124	1	12	21	5	0	2	33.3
10	Variaus rv	700	25	66.9	5.3	40.0	41.3	120	9	0	7	2	3	1	8.0
11	Variaus rv	150	19	98.3	5.0		57.2	96	2	0	0	0	1	0	0.0
12	Variaus rv	400	11	115.1	6.4	39.3	88.4	114	0	6	10	6	0	1	54.5
13	Laukonis rv	1200	16	118.0	7.4	51.0	90.8	123	2	9	2	1	1	3	6.3
14	Laukonis rv	700	21	94.1	6.3		60.5	100	1	1	0	0	1	0	0.0
15	Laukonis rv	28000	12	126.6	7.8	49.7	99.7	125	1	8	10	3	0	2	25.0
16	Laukonis rv	28000	11	118.3	6.5		79.5	124	1	8	0	0	1	3	0.0
17	Šereitlaukis f	5000	33	118.7	5.3	42.0	50.5	108	0	21	1	1	0	2	3.0
18	Šereitlaukis f	5000	15	163.9	6.9	57.5	80.7	124	0	15	7	2	0	4	13.3
19	Šereitlaukis f	5000	15	95.5	5.0		43.3	80	0	2	0	0	0	0	0.0
20	Pilis isle f	6000	18	135.2	9.9	42.0	76.3	127	1	12	14	6	1	6	33.3
21	Pilis isle f	6000	18	133.2	9.2	47.7	88.4	130	2	13	24	7	2	9	38.9
22	Plokštinė f	30	15	98.1	4.7	45.0	60.7	110	3	4	5	2	3	2	13.3
23	Uogis rv	150	19	97.1	8.1	43.5	47.9	80	0	0	16	4	0	0	21.1
24	Uogis rv	80	42	104.1	6.8	48.4	47.4	130	3	11	28	7	5	4	16.7
25	Lomena rv	100	40	114.0	6.5	43.2	43.7	105	2	20	32	9	2	1	22.5
	Mean		21.2	116.0	7.1	48.2	68.7		1.6	9.3	9.1	3.0	1.2	3.4	14.8
	SD		9.0	22.0	1.5	10.3	17.5		1.9	6.5	9.4	2.8	1.3	2.9	14.0

Lithuania exhibits a certain range of variation, and there were several significant relationships among the different fern organs: trophophyll height varied between 15 and 185 cm, and the number of trophophylls per plant varied from 1 to 17. There was a general increase in trophophyll height with increasing the number of trophophylls per plant, but when the number of trophophylls exceeded eleven there was no general increase in frond height (Fig. 1, Table).

Rootstock diameter varied from 1 to 130 mm (mean, 68.7 mm), and there was a general linear increase in the number of trophophylls with increasing the rootstock thickness (r^2 = 59.1, p = 0.000) (Fig. 2). There was also a linear increase in trophophyll height with increasing the rootstock thickness (r^2 = 52.7, p = 0.000). The number of sporophylls per plant varied from 1 to 9, with a majority between 1 and 4. No plant with trophophylls smaller than 100 cm and a rootstock thickness smaller than 55 mm produced sporophylls, but above these thresholds there was a general increase in the number of trophophylls per plant (Figs. 3 and 4).

Sporophyll height varied between 28 and 80 cm, but the majority were between 40 and 50 cm (Fig. 5). There was a significant linear increase in sporophyll height with increasing the number of trophop-

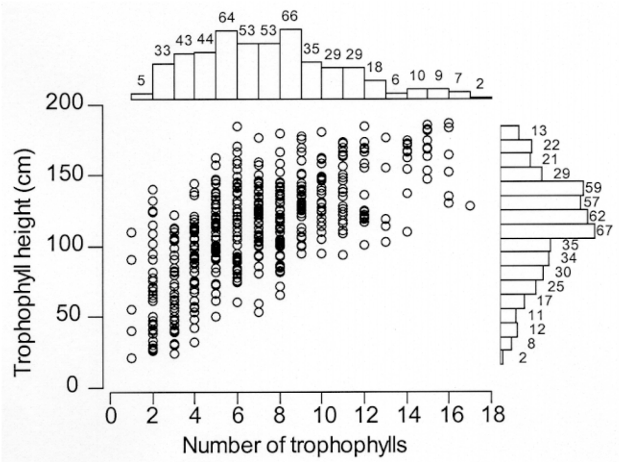

Fig. 1. Relationship between number of trophophylls and trophophyll height for the 506 studied rootstocks. The figure also shows histograms of the size distributions

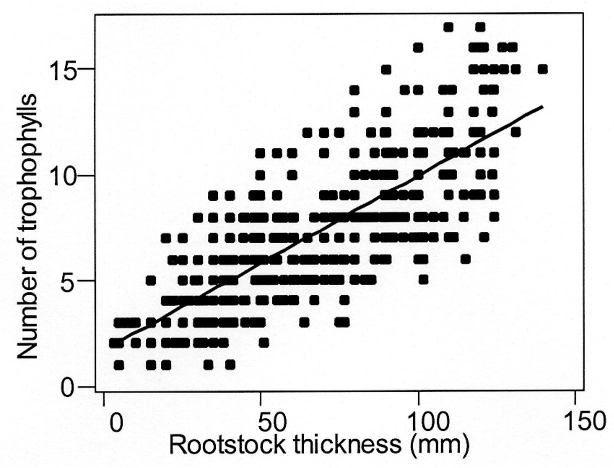

Fig. 2. Relationship between rootstock diameter and number of trophophylls. The fitted linear regression line is drawn

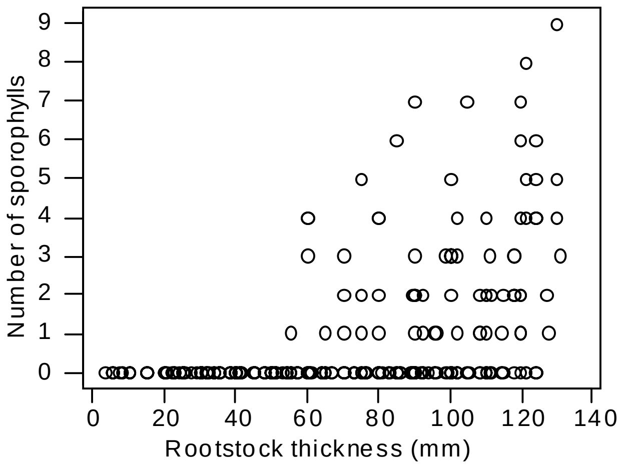

Fig. 3. Relationship between rootstock diameter and the number of sporophylls developed

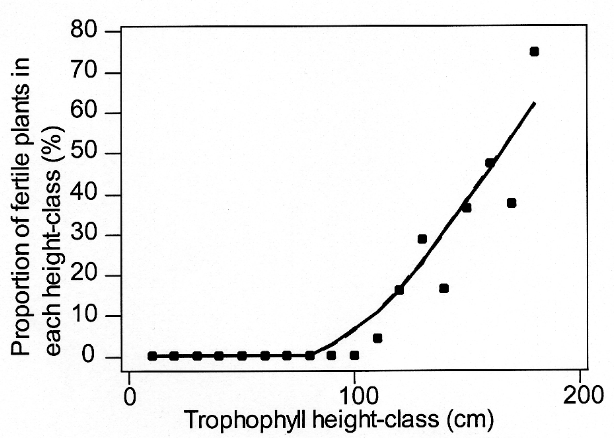

Fig. 4. Proportion of rootstocks producing sporophylls in different trophophyll size classes. A locally weighted scatter plot line (LOWESS) is drawn

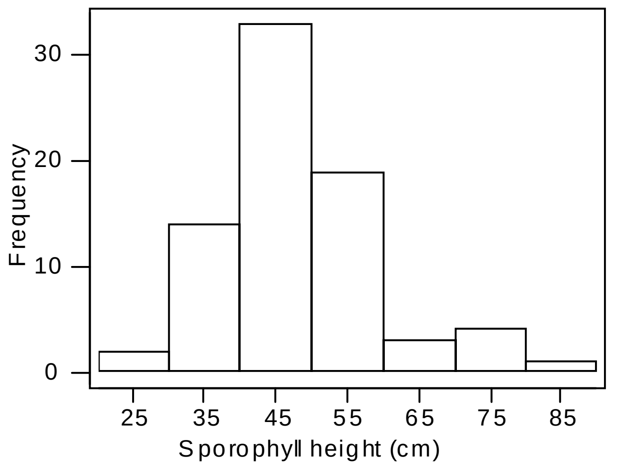

Fig. 5. Histogram of the sporophyll size distribution

hyll (r^2 = 19.7, p = 0.000) and with increasing the trophophyll height (r^2 = 16.7, p = 0.000), though the highest sporophylls were found on trophophylls with heights between 150 and 170 cm. In general, it appeared that *M. struthiopteris* started to produce sporophylls when the number of trophophylls exceeded 7, trophophyll size exceeded 110 cm, and rhizome thickness exceeded 60 mm.

2. Variation in floristic composition

The DCA ordination showed that the lengths of the three main DCA axes were 2.75, 2.59, and 2.42 SD units, and the eigenvalues were 0.433, 0.315, and 0.190 respectively. When the environmental variables were included, the sum of all canonical variables explained 57.1% of the total inertia. DCA axis 1 was most correlated with slope (r = – 0.41, p < 0.001), the second was most correlated with the distance from the coast (r = – 0.65, p < 0.001) and R-bank (r = – 0.65, p < 0.001), and the third was most correlated with slope (r = – 0.42, p < 0.001).

DCA analysis with the demographic data introduced as supplementary variables is shown in Fig. 6. The sum of all canonical variables explained 50.7% of the total inertia. DCA axis 1 is most correlated with the number of rootstocks larger than 10 cm (r = –0.55), the number of fertile rootstocks (r = –0.35), mean trophophyll height (r = –0.31) and the mean number of trophophylls (r = –0.31). DCA axis 2 is most correlated with the number of rootstocks larger than 10 cm (r = 0.23), the number trophophylls smaller than 60 (r = –0.22). DCA axis 3 is most correlated with the number of rootstocks smaller than 2 cm (r = –0.43), the number of fertile rootstocks (r = –0.35), mean trophophyll height (r = 0.54) the mean number of trophophylls (r = 0.43) and number of trophophylls taller than 120 cm (r = 0.49).

All the populations studied had a tree canopy cover or they were growing within canopy gaps. The most frequent plants associated with *M. struthiopteris* in the 25 studied stands were *Aegopodium podagraria* L. (100%), *Urtica dioica* L. (96%), *Myosoton aqu-*

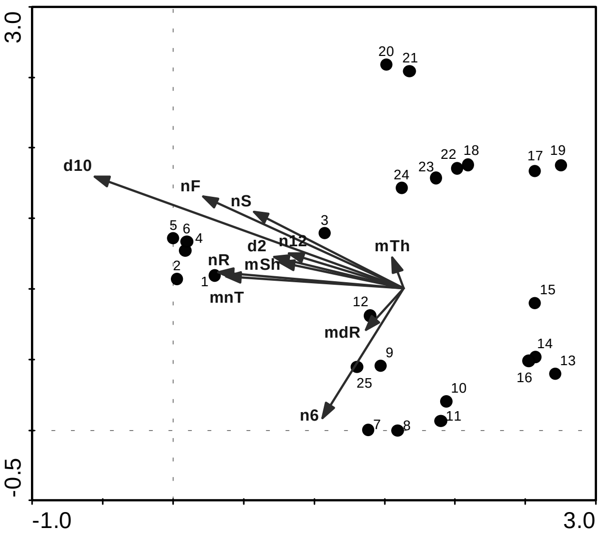

Fig. 6. Scatter plot showing the relative position of the 25 samples in relation to DCA axis 1 and 2. The demographic variables are plotted as supplementary vectors. Abbreviations are explained in Materials and Methods

aticum (L.) Moench (56%), *Equisetum pratense* Ehrh. (48%), *Padus avium* Mill. (48%), *Oxalis acetosella* L. (48%), and *Alnus incana* (L.) Moench (48 %), *Alnus glutinosa* (L.) Gaertn. (44%), *Rubus idaeus* L. (44%), and *Chaerophyllum aromaticum* L. (44%). There were geographical and/or environmental differences in the species composition. In the western parts, species such as *Salix fragilis* L., *Alnus incana* (L.) Moench, *Padus avium* Mill., *Corylus avellana* L., *Mercurialis perennis* L., *Fraxinus excelsior* L., *Anemone ranunculoides* L., *Circaea lutetiana* L., *Allium ursinum* L., *Brachypodium sylvaticum* (Huds.) P. Beauv., *Cirsium oleraceum* (L.) Scop., and *Chaerophyllum aromaticum* L. occurred. *Alnus glutinosa* (L.) Gaertn., *Padus avium* Mill., *Asarum europaeum* L., *Chelidonium majus* L., *Impatiens parviflora* DC, and *Rhamnus catharctica* L. were most frequent in the eastern parts. Also some rare or red-listed species (*Allium ursinum* L., *Circaea lutetiana* L., and *Lunaria rediviva* L.) were recorded within the stands.

3. Variation in population structure

The mean percentage of rootstocks producing sporophylls in 25 quadrats was 14.8, ranging between 0 and 54.5%, the average number of sporophylls was 2.3, and the number of fertile plants was 0.75 m^{-2}. Mean rootstock density was 5.3 m^{-2}, with a variation from 10.3 to 2.7 m^{-2}. Except for quadrat 10 (Table), all quadrats had a very low number (less than 1 per m^2) of small (young) plants (frond height less than 60 cm and a rootstock diameter less than 2 cm) (Table). All the rootstocks studied were connected to a parental plant which indicated that they were all ramets.

Most of the populations were situated within 1–5 metres from rivers or lakes. Plants on fluvial plains were heavily influenced by sedimentation, and often the whole rootstock was covered by sand. In other areas more than 10 cm of the rootstocks were growing up above the ground. The density of the canopy was poorly correlated with the main floristic differences among the stands. CCA analysis with automatic selection of environmental variables showed that the distance from the coast and growth-site in a riverbank or not were significantly ($p = 0.001$) correlated with the floristic differences among the populations. In manual selection, also slope degree was significant ($p = 0.006$).

CCA analysis with automatic selection of demographic variables showed that the number of large rootstocks (d10, $p = 0.003$) and large trophophylls (n12, $p = 0.004$) were significantly correlated with the floristic differences among the populations. In manual selection, also mean trophophyll height ($p = 0.044$) was significant. There was a quadratic relationship between the number of sporophylls per quadrat and quadrat DCA axis 1 sample score (r^2 =

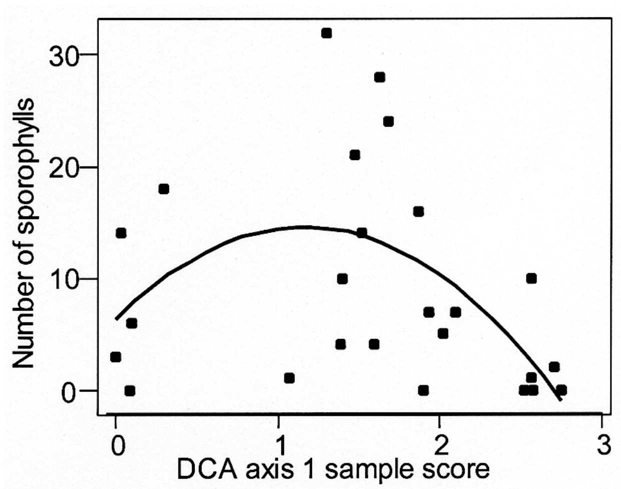

Fig. 7. Relationship between DCA axis 1 sample score and the number of sporophylls in the samples. The fitted quadratic regression line is drawn

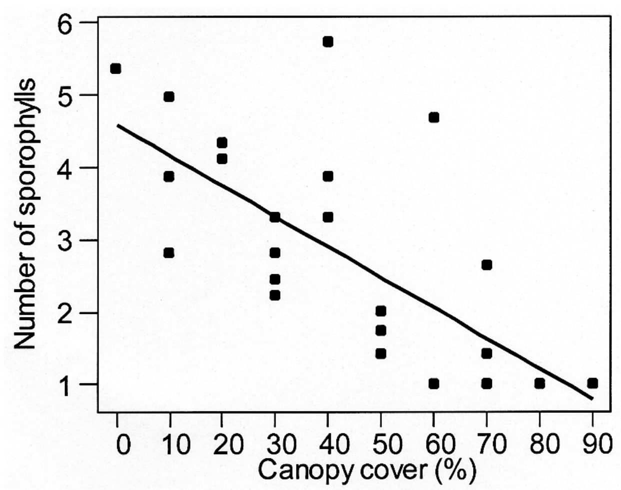

Fig. 8. Relationship between canopy cover and number of sporophylls in the samples. The fitted linear regression line is drawn

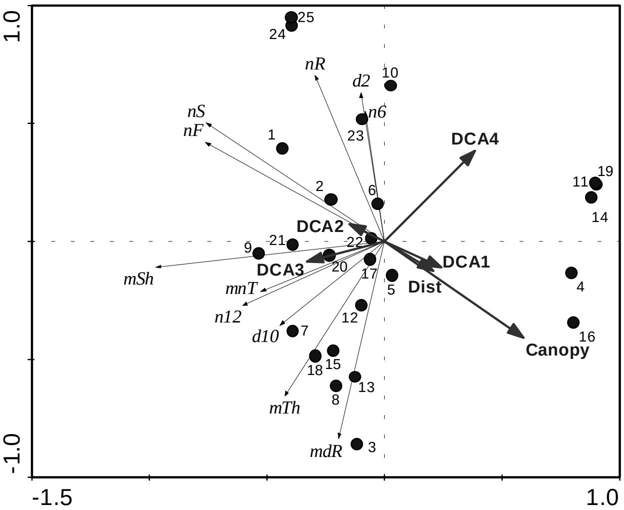

Fig. 9. PCA axes 1 and 2 triplot showing relative positions of the samples (1–25, Table) based on the demographic variables and associated environmental and explanatory variables plotted as supplementary variables. Abbreviations are explained in Materials and Methods. The positions "River bank", "Logs" and "Slope" are not shown, because they lie close to the origo

30.8, p = 0.018) (Fig. 7), and there was a general decrease in the number of sporophylls with increasing canopy cover, but the highest numbers of sporophylls were found in a plot with a 40% cover (Fig. 8).

PCA analysis showed that the main variation in population structure separated populations with large rootstocks and high sporophyll production from smaller plants with few sporophylls, while the second gradient separated samples with a high plant density and relatively small plants from populations with bigger plants and a low density. Figure 9 is a PCA triplot where the samples were plotted according to the demographic variables, and the environmental variables and floristic gradients were superimposed as supplementary vectors. RDA analysis of the demographic data with a subsequent automatic selection of environmental data and Monte Carlo permutation tests showed that canopy cover (p = 0.001), DCA axis 3 sample scores (p = 0.011), occurrence of fallen logs (p = 0.025), DCA axis 1 sample scores (p = 0.028) and DCA axis 4 sample scores (p = 0.041) were statistically significant.

DISCUSSION

A total of 71 different vascular plant species were recorded from the 25 plots analysed. The number of vascular plants per plot varied between 7 and 32, with a mean of 18.8 m^{-2}, which is quite similar to figures reported from W Norway [2]. Phytosociologically, the populations may be referred to the *Alnion incanae* alliance (also named *Alno-Ulmion* or *Alno-Padion* Knapp 1942 em. Medw.-Korn. ap. Mat. et Bor. 1957) [12, 13] due to the occurrence of species such as *Alnus incana* (L.) Moench, *Ulmus glabra* Huds., *Stellaria nemorum* L., *Filipendula ulmaria* (L.) Maxim, in addition to *Matteuccia* itself. A characteristic feature was also the space moss cover, only *Plagiomnium undulatum* (Hedw.) T. J. Kop. being found in some of the populations.

Matteuccia has been characterised as a shade-adapted plant with an Ellenberg light factor of 5 [14]. Both too much and too low light may therefore cause a problem for an optimal development. The tree canopy cover varied between 10 and 90%. In some cases the canopy cover of trees and shrubs was obviously too dense to be favourable for the fern, and therefore the tropophylls were small and sporophyll production low (e.g., quadrats in the lower right part of Fig. 9). In Canada, Prange & von Aderkas [1] found that only 1% of the plants produced sporophylls in shaded sites. Obviously, the dense tree canopy along the river-banks in Lithuania represents a serious problem for the persists and development of *M. struthiopteris* populations. It seems to benefit from tree fall, probably both because of more available light and nutrient supply through wood decay. No populations were found close to the Baltic Sea, which may indicate that a coastal climate, directly or indirectly, may be unfavourable for the fern. A similar pattern was also found in W Norway [2].

According to Prange & vonAderkas, von Aderkas & Green and Jonsell [1, 6, 7], *M. struthiopteris* is a clonal fern with fronds ascending from an erect rootstock that may be up to 10 cm in diameter. It is a fern with dimorphic fronds, and during the spring it produces 1–16 trophophylls (sterile fronds) and 0–8 fertile fronds (sporophylls) which normally are 30–60 cm tall. Prange & von Aderkas and von Aderkas & Green [1, 6] maintain that fern rootstocks must reach a certain age or stage in their development before a sporophyll can be developed, and that the rootstocks do not start to produce sporophylls until the third year, and then only irregularly. In natural populations sporophyll occur mainly on the largest plants (average rootstock width 58 mm). It has also been reported that there may be annual variation in morphological and demographic variables within a population [8, 9].

Hendrych [15] considered the populations in the Czech Republic, and probably in other parts of Central Europe, to have originated from cultivations in gardens and parks. This conclusion was based on the localities in the vicinity of parks and castles, settlements and water-mills, as well on the fact that these plants did not produce sporophylls. Alegro et al. [13], on the other hand, maintained that the populations in Croatia were vigorously developed with both sterile and fertile fronds, and they were assumed to be indigenous. One of the studied populations (quadrat 3) had developed from garden plants, but the others were all considered to be indigenous. Strongly clonal fern populations are considered to be long-lived, and they are in theory immortal [1]. The genomes within the different populations may therefore be the same as those established some time after the glaciers had retreated after the last ice-age.

The demographic data show that there are major differences among the populations as to the density of rootstocks (on average 5.3 rootstocks per m^2) and throphophyll height (mean, 116.0 cm). Trophophyll height can be used as an indication of plant age, both for angiosperms and pteridophytes [16]. The trophophyll size in Lithuania lied within the size ranges found in Norway, but on average they were higher than plants reported from Canada and Norway [6, 16]. A characteristic feature of the Lithuanian populations was that the plants were generally big, plant density was small, and few new ramets were present. In Canada, mean densities between 8 and 10 were reported by Kenkel [9], and a mean trophophyll height of 90 cm was found by von Aderkas & Green [6].

Matteuccia has the ability to produce offspring both sexually and asexually, and therefore there may be a trade-off between these two modes of reproduction. Investment in sexual reproduction can be quantified by sporophyll production, and the investment in vegetative reproduction may be quantified by the number of small newly developed rootstocks. New plants developed from gametophytes have not been recorded in this study, which is in accordance with studies from other areas [17]. According to Prange & von Aderkas and von Aderkas & Green [1, 6], new plants were only produced by stolon development within dense *M. struthiopteris* populations probably due to allelopatic effects. The relative number of small plants can therefore be used as a measure of recent clonal growth within the population [18].

The Lithuanian populations had generally a very low number of small, new rootstocks, while the proportion of rootstocks producing sporophylls could be high (54.5%), with a mean fertility percentage of 14.8%. In Canada, von Aderkas & Green [6] found that 17% of the plants produced sporophylls, and Kenkel [9] reported a variation between 0.45 and 4.45%. Annual production of new ramets was found to vary between 5 and 20 for a 25 m^2 quadrat during a five-year period [9]. The mean rootstock diameter was 68.7 mm in Lithuania, while in Canada it was 43 mm for fertile plants and 43 cm for sterile plants [6].

The generally large plants and their low production of small new ramets indicate that the Lithuanian plants have a relatively low annual investment in vegetative reproduction. This fits with general patterns of plant behaviour along temperature gradients; in warm areas plants with sexual reproduction are more frequent than in cold areas, and plants that can reproduce in both modes generally invest more in asexual reproduction in cold environments [19]. This has earlier been shown also for *Matteuccia* [20].

CONCLUSIONS

1. *M. struthiopteris* is a relatively rare plant species in Lithuania, the populations are with few exceptions small (<6000 m^2), and they were absent in the westernmost coastal areas.

2. In total, 25 populations were studied and 506 rootstocks measured. Maximum value was 185 cm for trophophyll height, 80 cm for sporophyll height, and 130 mm for rhizome thickness, and most of the populations were characterised by a high number of large plants and few small plants.

3. The populations were mainly found close to rivers or lakes, probably where the ground watertable is high, and where there was a gape in the dense tree canopy. The most frequent plants associated with *M. struthiopteris* was *Urtica dioica* L., *Aegopodium podagraria* L., *Equisetum pratense* Ehrh., *Rubus idaeus* L., *Padus avium* Mill., *Glechoma hederacea* L., *Oxalis acetosella* L., and *Humulus lupulus* L. Bryophytes and lichens were very rare.

4. The variation in the floristic composition among the populations was relatively small (DCA axes 1 and 2 are both less than 2.7 SD units), and this variation was significantly correlated with the distance from the coast ($p = 0.001$) and a river-bank growth site ($p = 0.007$).

5. The density of plants varied from 11 to 42 plants per 4 m^2, with a very low frequency of small, young plants (< 6 dm tall). This indicates that there was a very low production of new ramets within the populations. The number of sporophylls varied from 0 to 32 per 4 m^2, and the proportion of rootstocks with sporophylls varied from 0 to 54.5% (on average 14.8%). The variation in fertility was highly negatively correlated with the canopy cover ($p = 0.000$).

6. Before the Lithuanian plants start to produce sporophylls, the rootstock diameter has to reach a threshold of 60 mm, trophophyll height should exceed 110 cm, and the rootstock has to produce more than 7 trophophylls.

7. All plants found within the populations were connected to a parental plant, showing that no plant had originated from sexual reproduction.

8. Most of the populations appeared to be in a healthy condition, but a few (mainly those with no sporophyll production) suffered from a very dense tree canopy. These may go extinct without remedial actions.

9. The variation in morphology was quite similar to that reported from Norway. However, no intermediate fronds were found in Lithuania.

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MATTEUCCIA STRUTHIOPTERIS POPULIACIJŲ STRUKTŪROS POKYČIAI LIETUVOJE

Santrauka

Paupinis jonpapartis (*Matteuccia struthiopteris* (L.) Tod.) – gana retas Lietuvoje saugotinas blužniapapartinių (*Athyriaceae*) šeimos augalas. Nuo 2003 iki 2005 metų įvairiose Lietuvos vietose, daugiausia regioninių ir nacionalinių parkų teritorijose, ištirtos 25 šio augalo populiacijos. Absoliuti dauguma populiacijų yra upių arba ežerų pakrantėse. Pagrindinis tyrimo tikslas buvo nustatyti paupinio jonpaparčio populiacijų demografinius parametrus ir jų kintamumą Lietuvoje. Svarbiausi apibūdinantys rodikliai buvo individų skaičius ploto vienete, šakniastiebių dydis, trofofilų skaičius ir ilgis, sporofilų skaičius ir ilgis. Demografiniai tyrimai atlikti 4 m^2 dydžio laukeliuose, iš viso ištirti 506 paupinio jonpaparčio individai. Nustatyta, kad 4 m^2 dydžio tiriamuosiuose laukeliuose auga nuo 11 iki 42 paupinio jonpaparčio augalų. Jaunų vegetatyvinės kilmės augalų populiacijose yra labai mažai. Sprendžiant iš vyraujančių augalų šakniastiebių diametrų, visos tirtos paupinio jonpaparčio populiacijos yra ganėtinai senos, prieš daugelį metų susidariusios atitinkamose augavietėse. Vidutiniškai 14,8% paupinio jonpaparčio augalų yra su sporofilais. Nustatyti sporofilų susidarymo ekologiniai ir demografiniai parametrai. Generatyvinės kilmės augalų paupinio jonpaparčio populiacijose nerasta. Visos tirtos paupinio jonpaparčio populiacijos apskritai yra geros būklės, menkesnio gyvybingumo augalų padaugėja tankėjant medžių lajoms bei žemėjant gruntinio vandens lygiui. Atlikta palyginamoji paupinio jonpaparčio populiacijų struktūros Lietuvoje, Kanadoje ir Norvegijoje analizė.