

Population stage structure of three congeneric *Dryopteris* species in Estonia

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Received 29 November 2004, in revised form 8 February 2005

Abstract. There are three congeneric fern species in Estonia that show similar morphology and ecology, but whose regional distribution is different – *Dryopteris carthusiana* is common, *D. expansa* is distributed in scattered localities, and *D. dilatata* is rare. We studied *D. carthusiana*, *D. dilatata*, and *D. expansa* in localities where all three fern species co-occur in Estonia. Our aim was to compare the population stage structure of the three species and to observe whether their population structure fluctuates differently in different sites in different years. We observed an unfavourable condition of *D. expansa* in one site (Sääre), which we interpreted as a possible result of competitive pressure from bryophytes. Also, we observed a predomination of premature stages of *D. dilatata* in two sites (Jäneda, Öngu), indicating the dynamic status of these populations. Because of a more westerly distribution of this species in Estonia compared to the other two, one may hypothesize that *D. dilatata* is able to expand its range due to climate warming.

Key words: *Dryopteris*, population dynamics, population stage structure, rarity.

INTRODUCTION

There are three congeneric fern species in Estonia that show similar morphology and ecology, but whose distribution pattern is quite different – *Dryopteris carthusiana* is common, *D. expansa* is distributed in scattered localities, and *D. dilatata* is rare. We were interested in the mechanisms behind the different distribution frequency and local abundance of these three species. In natural communities, the contribution of pteridophytes may be restricted by the suscepti-

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bility of gametophytes and young sporophytes to competition from herbaceous angiosperms (Grime, 1985; Grime et al., 1988) and bryophytes (Gilbert, 1970; Cousens et al., 1985). Thus, the ability of a young sporophyte to tolerate competitive pressure from the surrounding vegetation would be extremely important for the distribution frequency and abundance of that particular fern species. We found that scarce *D. expansa* was distinguished from the other two species by its weaker ability to resist interspecific competition (Rünk et al., 2004). Thus, scattered distribution of diploid *D. expansa*, compared to tetraploid *D. carthusiana*, may be explained by its weaker competitive ability. Tetraploid fern species have also been found to be generally larger (Page, 2002), with higher rates of spore germination, and faster growth rates (Kott & Peterson, 1974; Seifert, 1992). Since *D. dilatata* showed good competitive ability, other mechanisms should be behind its distribution frequency.

According to Page (1997), in Northern and Eastern Europe the border-line of the *D. dilatata* distribution area follows quite well the isothermal line along which the coldest month is between -5 and -8°C (Boucher, 1987). We hypothesized that in Estonia its distribution and growth may be climatically restricted.

One possibility for getting more information about the different behaviour of the three fern species in different years is to observe the dynamics of local populations. Regional dynamics of plant populations can be estimated on the basis of the condition of local populations (Agurauja et al., 2004). In general, the status of plant populations may be studied on four levels: population distribution, quantitative monitoring of population size/condition, monitoring of population structure, and demographic study of the population (Hutchings, 1991; Menges & Gordon, 1996). Demographic studies give valuable information about the condition of populations. They are, however, laborious, and take several years to complete, which prevents their wide use both in population studies and in conservation biology (Harvey, 1985; Oostermeijer et al., 1994; Eckstein et al., 2004). Another, less time-consuming way to relate the demographic performance of populations of perennial plants to overall vegetation change is to analyse their structure in different plant communities. The structure of a population may be described by classifying the individual plants either by age, size, or their life stage (Gatsuk et al., 1980; Rabotnov, 1985). Since it is often impossible to establish the age of perennial herbaceous plant individuals, and both size and reproductive capacity are poorly correlated with age (Harper, 1977), the best way of describing populations of such species in a single census is by determining the relative proportions of individuals in the different stages of their life cycle. This method has proved to be successful in a number of studies of perennial plant species, including rare and endangered species (Rabotnov, 1985; Oostermeijer et al., 1994; Bühler & Schmid, 2001; Hegland et al., 2001; Brys et al., 2003; Eckstein et al., 2004).

We studied *D. carthusiana*, *D. dilatata*, and *D. expansa* in the only three localities in Estonia where all the three fern species occur together. Our aim was

to compare the population stage structure of the three species and to observe whether their population structures fluctuate differently in different sites in different years. In particular, we hypothesized that the population structure of rare *D. dilatata* is the most dynamic and may be characterized either by a greater proportion of premature individuals, due to lesser freezing resistance of adults than of younger life stages, or by a greater proportion of vegetative adults, due to climatically unfavourable years. Also, we hypothesized that *D. expansa* is distinguished by a relatively lower proportion of more juvenile life stages in sites where the vegetation canopy is more developed and the competitive pressure is assumed to be higher.

MATERIALS AND METHODS

Study species

All three species studied are evolutionarily closely related (Gibby & Walker, 1977) and morphologically similar pteridophytes (Fraser-Jenkins & Reichstein, 1984; Page, 1997). Tetraploid ($2n = 164$) *D. carthusiana* (Vill.) H. P. Fuchs is the most widespread of the three species in the whole of Europe. Tetraploid ($2n = 164$) *D. dilatata* (Hoffm.) A. Gray is distributed mostly in Western and Central Europe. Diploid ($2n = 82$) *D. expansa* (C. Presl) Fraser-Jenkins & Jermy is mainly a mountain species in most of Europe, and has a more northerly and easterly distribution than *D. dilatata*. In Western and Central Europe, *D. dilatata* is a more frequent and common species than *D. expansa* (Fraser-Jenkins & Reichstein, 1984; Hultén & Fries, 1986; Fraser-Jenkins, 1993; Page, 1997).

In Estonia the converse is true: *D. expansa* is distributed in scattered localities throughout Estonia, while *D. dilatata* is rare and comes close to its north-eastern distribution limit. *D. carthusiana* is the most widespread of the three species and is evenly distributed in Estonia. According to the Atlas of the Estonian Flora (Kukk & Kull, 2005), *D. carthusiana* is recorded (at least once since 1971) in 441, *D. expansa* in 145, and *D. dilatata* in 20 of the 920, 6×10 minute grid squares covering Estonia.

All three species are rhizomatous small to large-sized, in Estonia mainly terrestrial woodland ferns (Rünk, 2002) with 3-pinnate fronds and orbicular sori covered with a reniform indusium (Fraser-Jenkins, 1993). According to Raunkiaer's (1934) life form classification, all three species are hemicryptophytes. In Estonia *D. expansa* overwinters as a leafless rhizome, fronds of *D. carthusiana* and *D. dilatata* sometimes remain green until next spring (Rünk, personal observations).

According to Soltis & Soltis (1987), diploid *D. expansa* possesses a mixed mating system (mean intragametophytic selfing rate of 0.34). Gametophyte cultures of *D. carthusiana* showed a maximum of 79% intragametophytic self-fertilization, those of *D. dilatata* a maximum of 35% (Seifert, 1992).

Study sites

Three coinciding local sporophyte populations of *D. carthusiana*, *D. dilatata*, and *D. expansa* were studied in Estonia (Fig. 1). In fact, those three study sites were the only localities in Estonia where all three species coexist; this makes it possible to compare their population structure in identical abiotic conditions.

The study sites were located at Õngu and Sääre, both on the Baltic island of Hiiumaa, and at Jäneda, central North Estonia (Fig. 1). The soil was a weakly developed podzol at Õngu and Sääre and a peaty forest soil at Jäneda. In all sites, the plant community is a natural mesophyte boreal coniferous forest, with predominating *Picea abies* at Õngu and Jäneda, and *Pinus sylvestris* at Sääre. The degree of human activity is low in all three sites. Sites on Hiiumaa Island are characterized by milder climate, with a higher mean temperature in January and a higher annual mean, while at Jäneda, a colder January, as well as a lower annual mean are observed (Table 1). The mean annual precipitation in the study sites was 621 mm at Õngu, 632 mm at Sääre, and 685 mm at Jäneda (Jaagus, 1999).

According to data from the three nearest meteorological stations – Vanaküla (Jäneda), Ristna (Õngu), and Heltermaa (Sääre) – in 2002 there was less precipitation in all three sites than in 2001 and also than in 2000 (Table 1).



Fig. 1. Location of the study sites.

Table 1. Environmental characteristics of the study sites

| Characteristic | Jäneda | Sääre | Õngu |
|--|----------|----------|----------|
| Latitude | 59°14' N | 58°58' N | 58°51' N |
| Longitude | 25°41' E | 22°56' E | 22°27' E |
| Mean annual temperature, °C ^a | 4.3 | 5.8 | 6.0 |
| Mean temperature in January, °C ^a | -6.1 | -3.4 | -2.6 |
| Mean annual precipitation, mm ^a | 685 | 632 | 621 |
| Precipitation in 2001, mm/year ^b | 796 | 824 | 750 |
| Precipitation in 2002, mm/year ^b | 540 | 493 | 477 |
| Precipitation in 2003, mm/year ^b | 792 | 479 | 485 |
| Mean percentage of tree layer ($n = 5$) ^c in plots | 68.0 | 60.0 | 66.0 |
| Mean percentage of herb layer ($n = 5$) ^c in plots | 66.0 | 32.0 | 66.0 |
| Mean percentage of bryophyte layer ($n = 5$) ^c in plots | 60.0 | 90.0 | 20.0 |

^a Jaagus, 1999.

^b Jaagus, 2004, personal communication.

^c The cover of vegetation layers was determined visually as a percentage cover (with an accuracy of 10%) of each layer in each plot.

Field methods

Within each of the three study sites with areas of 2000–3000 m², five permanent plots of 4 × 4 m were established in order to represent the sporophyte individuals of all three (or at least two) species in each plot.

In these plots, plant community composition was described in August 2001 by estimating the cover of all vegetation layers and the cover of all herbaceous plant species. The cover of vegetation layers was determined visually as a percentage cover (with an accuracy of 10%) of each layer in each plot (Table 1).

Individuals of the three fern species were monitored in detail. The field surveys were conducted during the same phenological stage of fern individuals, either during July or August, in 2001, 2002, and 2003. In 2001 all sporophytes in plots and in 2002 and 2003 newly recruited sporophytes were labelled and mapped in order to locate and identify each individual. As there was no possibility of determining the origin of existing individuals, every crown (rhizome apex with fronds) was treated as an individual (genet). In the case of each fern individual, the number of fronds was counted and the length of the longest frond was measured in 2001, 2002, and 2003. In generative individuals, the number of fertile (spore-bearing) fronds was also counted.

Based on the reproductive status of individuals, the individual sporophytes of *D. carthusiana*, *D. dilatata*, and *D. expansa* were classified into three different life history stages: premature individuals (sporulation has not been recorded in census years), vegetative adults (without fertile fronds in census year, but

with sporulation recorded in one of the previous years), and generative adults (with fertile fronds). As it was impossible to distinguish between premature individuals and vegetative adults in the first census year, the three-stage classification was used only in 2002 and 2003.

Statistical analyses

Differences in population densities and morphological parameters of the three different life stages of *D. carthusiana*, *D. dilatata*, and *D. expansa* in three study sites in the years 2001–2003 were tested with repeated measures of ANOVA (using the Statistica software version 6.0; Anonymus, 2003) with species (three levels), life stage (three levels), and study site (three levels) as fixed factors and census year (two levels – 2002 and 2003) as a repeated measure factor. In the case of analysis of population density in 2001–2003, the factor ‘life stage’ was not used, and, in the case of the factor ‘census year’, all three levels (2001–2003) were used. Before the analysis, data on plant individual densities on plots (as proportions) were arcsine square root transformed to meet the assumptions of ANOVA (Zar, 1999). In order to analyse the differences in the mean number of leaves per individual and in the mean length of leaves per individual, the data of population densities for 2002–2003 and the factor ‘year’ with two levels (2002 and 2003) were used, while in the case of mean number of fertile leaves per generative adult, the data from 2001–2003 and the factor ‘year’ with three levels (2001, 2002, and 2003) were used. Differences between the coverage of vegetation layers in the three study sites were tested by one-way ANOVA.

The significance of the differences among means was estimated with the help of the Tukey HSD multiple-comparison test with a 0.05 significance level (Sokal & Rohlf, 1995). The relationships between vegetation layers in the study sites were analysed using Spearman correlation analysis.

RESULTS

Population density

The overall fern population densities differed significantly among species and study sites over the three census years (2001–2003) (Table 2). The population density of *D. carthusiana* was significantly higher than the densities of *D. dilatata* and *D. expansa*. The population densities differed between study sites – at Jäneda the fern population density was higher than in the other two sites. The overall density of fern populations was lower in 2001 than it was in 2002 or in 2003.

There was a significant interaction between species and study site. Population densities of *D. carthusiana* and *D. expansa* were higher at Jäneda than in the other two sites. At Jäneda the population density of *D. carthusiana* was significantly

Table 2. Results of repeated measures ANOVA: effects of species, study site (site), life stage (stage), census year (year) and their interaction on the population densities of *D. carthusiana*, *D. dilatata*, and *D. expansa*

| Source of variation | Population density 2001–2003 | | | Population density 2002–2003 | | |
|--------------------------|---------------------------------|-----------------|----------|---------------------------------|-----------------|----------|
| | df | <i>F</i> -ratio | <i>P</i> | df | <i>F</i> -ratio | <i>P</i> |
| Species | 2 | 14.079 | 0.001 | 2 | 0.192 | 0.826 |
| Site | 2 | 19.834 | <0.000 | 2 | 0.206 | 0.814 |
| Stage | | | | 2 | 66.664 | <0.000 |
| Species* site | 4 | 7.591 | 0.001 | 4 | 0.060 | 0.993 |
| Species* stage | | | | 4 | 4.733 | 0.002 |
| Stage* site | | | | 4 | 11.21 | <0.000 |
| Species* stage* site | | | | 8 | 2.765 | 0.009 |
| Year | 2 | 37.179 | <0.000 | 1 | 0.284 | 0.596 |
| Year* species | 4 | 0.932 | 0.446 | 2 | 0.167 | 0.846 |
| Year* site | 4 | 0.874 | 0.479 | 2 | 0.384 | 0.682 |
| Year* stage | | | | 2 | 29.620 | <0.000 |
| Year* species* site | 8 | 1.366 | 0.210 | 4 | 0.156 | 0.960 |
| Year* species* stage | | | | 4 | 7.532 | 0.001 |
| Year* stage* site | | | | 4 | 20.781 | <0.000 |
| Year* species* age* site | | | | 8 | 7.049 | <0.000 |

higher than that of *D. dilatata* but did not differ significantly from the population density of *D. expansa*. Also, there were no differences between the densities of *D. dilatata* and *D. expansa*. At Sääre *D. carthusiana* and *D. dilatata* also had significantly higher population densities than *D. expansa*. There were no differences between fern population densities at Öngu.

Population stage structure

The life stages were represented differently in overall fern populations in 2002–2003 (Table 2) – the densities of premature individuals and generative adults were higher than the density of vegetative adults. There was no significant difference between premature individuals and generative adults.

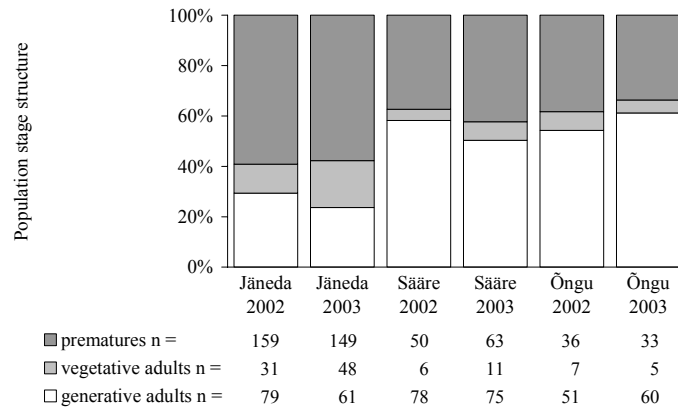
The interaction between species and life stage was also significant (Table 2). In general, all the three species had similar population stage structures in that premature individuals and generative adults had a significantly higher share in local populations compared to vegetative adults. The local populations of *D. carthusiana* and *D. expansa*, however, had an insignificantly greater density of generative adults than premature individuals, while in the case of *D. dilatata* the proportion of prematures was insignificantly greater than the proportion of generative individuals.

A significant three-way interaction between species, life stage, and study site was detected (Table 2). There were different population stage structure patterns in different sites in the case of all three species. In the case of *D. carthusiana*, no statistical differences between stage proportions were observed at Jäneda. At Sääre premature and generative individuals were represented in significantly higher proportions than vegetative adults. At Õngu the proportion of premature individuals did not differ from that of vegetative and generative adults, but there was a significantly higher proportion of generative than vegetative adults. The population of *D. dilatata* at Jäneda was predominated by premature individuals – the difference compared to vegetative adults was significant, and marginally nonsignificant compared to generative adults. The proportions of the two adult stages did not differ from each other. In the Sääre population, the reverse pattern compared with Jäneda was detected – the proportion of generative individuals was significantly higher than that of vegetative ones, and nonsignificantly higher than that of premature individuals. The proportions of premature and vegetative individuals did not differ. Premature and generative stages were significantly more numerous represented than the vegetative adult stage in the Õngu population. In the *D. expansa* population at Jäneda, proportions of premature and generative individuals were both higher than the proportion of vegetative adults. The population at Sääre had a different stage structure, since it was dominated by generative individuals, while prematures were absent all together. The population stage structure of *D. expansa* at Õngu was similar to *D. carthusiana* at the same site – the proportion of premature individuals did not differ from that of vegetative and generative adults, but there was a significantly higher proportion of generative adults than vegetative adults.

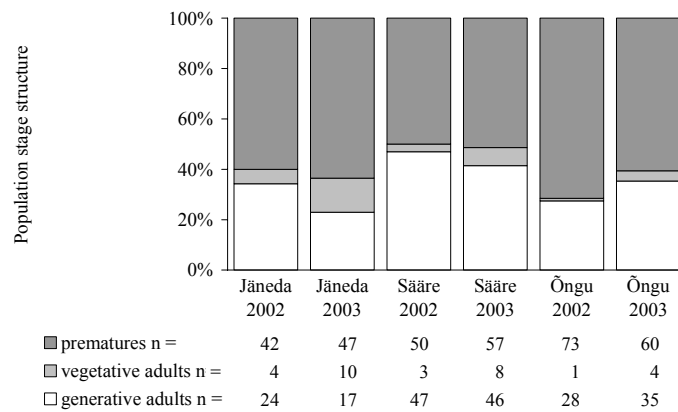
The significant three-way interaction term between year, species, and life stage (Table 2) indicates the species-specific annual differences in population life stage structures of *Dryopteris* species. *Dryopteris carthusiana* and *D. dilatata* shared a similar population stage structure in both census years – premature individuals and generative adults were significantly more numerous represented than vegetative adults in the case of both fern species. In the case of *D. expansa*, the population stage structure was similar to the other two *Dryopteris* spp. only in 2002. This pattern changed in 2003 – the proportion of vegetative adults still did not differ from that of prematures, but was significantly lower than that of generative adults. The proportions of premature and generative individuals did not differ from each other.

There was a significant four-way interaction between study site, life stage, species, and year (Table 2). In 2002, the densities of premature individuals of *D. dilatata* and *D. expansa* at Jäneda were higher than the densities of vegetative adults (Fig. 2). At Sääre in 2002, the densities of generative adults of *D. carthusiana* and *D. dilatata* were higher than that of vegetative adults. At Õngu the density of vegetative individuals of *D. dilatata* was higher than that of vegetative adults in both years.

Dryopteris carthusiana



Dryopteris dilatata



Dryopteris expansa

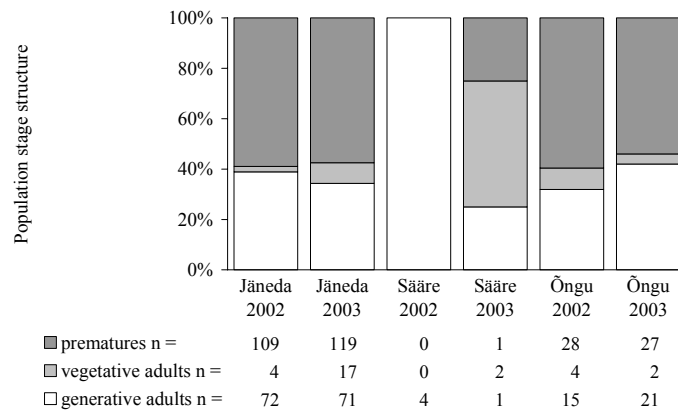


Fig. 2. The local population stage structure of *Dryopteris* ssp. at Jäneda, Sääre, and Õngu in 2002 and 2003.

Morphological parameters

The effects of species, study site, life stages, and census year on different morphological parameters (mean length of fronds, mean number of fronds per individual, and mean number of fertile fronds per generative adult) of *Dryopteris carthusiana*, *D. dilatata*, and *D. expansa* are summarized in Table 3.

Mean length of fronds

D. dilatata had the longest, *D. carthusiana* intermediate, and *D. expansa* the shortest fronds. The fronds of the three species were the longest at Õngu and the shortest at Sääre. Generative adults had the longest, vegetative adults intermediate, and premature individuals the shortest fronds.

All three species had the same patterns of frond lengths in different life stages in both census years – generative adults had the longest fronds, while the difference between premature individuals and vegetative adults was nonsignificant.

In 2002 the vegetative adults of *D. expansa* had shorter fronds than *D. carthusiana* and the generative adults of *D. dilatata* had longer fronds than *D. carthusiana*.

Table 3. Results of repeated measures ANOVA: effects of species, study site (site), life stage (stage), census year (year), and their interaction on the morphological parameters of *D. carthusiana*, *D. dilatata*, and *D. expansa*.

Abbreviations: Number of fronds = mean number of fronds per individual, Length of fronds = mean length of fronds per individual, Number of fertile fronds = mean number of fertile fronds per generative adult

| Source of variation | df | Number of fronds in 2002–2003 | | Length of fronds in 2002–2003 | | Number of fertile fronds in 2001–2003 | | |
|----------------------|----|----------------------------------|----------|----------------------------------|----------|--|-----------------|----------|
| | | <i>F</i> -ratio | <i>P</i> | <i>F</i> -ratio | <i>P</i> | df | <i>F</i> -ratio | <i>P</i> |
| Species | 2 | 12.54 | <0.001 | 9.566 | <0.001 | 2 | 5.723 | 0.007 |
| Site | 2 | 0.309 | 0.735 | 5.190 | 0.008 | 2 | 7.905 | 0.002 |
| Stage | 2 | 104.91 | <0.000 | 311.38 | <0.000 | | | |
| Species* site | 4 | 2.091 | 0.090 | 1.680 | 0.163 | 4 | 1.216 | 0.323 |
| Site* stage | 4 | 3.872 | 0.006 | 4.877 | 0.001 | | | |
| Species* stage | 4 | 0.729 | 0.575 | 5.539 | <0.001 | | | |
| Species* site* stage | 8 | 1.506 | 0.169 | 1.619 | 0.133 | | | |
| Year | 1 | 0.304 | 0.583 | 0.322 | 0.572 | 2 | 1.920 | 0.154 |
| Year* species | 2 | 1.275 | 0.285 | 0.319 | 0.727 | 4 | 3.559 | 0.011 |
| Year* site | 2 | 15.154 | <0.001 | 2.245 | 0.113 | 4 | 6.196 | <0.001 |
| Year* stage | 2 | 0.994 | 0.375 | 0.766 | 0.468 | | | |
| Year* species* site | 4 | 2.204 | 0.076 | 0.525 | 0.717 | 8 | 0.362 | 0.937 |
| Year* site* stage | 4 | 3.949 | 0.006 | 2.410 | 0.056 | | | |
| Year* species* stage | 4 | 3.315 | 0.015 | 5.364 | 0.001 | | | |

Mean number of fronds per individual

D. carthusiana had the highest, *D. dilatata* intermediate, and *D. expansa* the lowest number of fronds per individual. The generative adults had a higher number of fronds than the other two life stages.

The mean number of fertile fronds per generative adult

A higher number of fertile fronds over the three census years was observed in *D. dilatata* and *D. expansa*, while *D. carthusiana* had significantly fewer fertile fronds compared to *D. dilatata*.

Relationships between layers of vegetation in study sites

There were no differences between the percentage cover of the tree layer (Table 1) in different study sites. The percentage cover of the herb layer at Sääre was significantly lower than at Jäneda or Öngu ($F = 25.130$, $P < 0.001$). The cover of bryophytes was the highest at Sääre, intermediate at Jäneda, and the lowest at Öngu ($F = 61.667$, $P < 0.001$). The cover of bryophytes was negatively correlated with the cover of vascular plants ($r = -0.71$, $n = 15$, $P < 0.05$).

DISCUSSION

The density of ferns in the study sites was the smallest in 2001, and increased significantly in 2002. In 2001 the precipitation recorded in Hiiumaa study sites – the total annual precipitation (Table 1), as well as the rainfall in summer and early autumn (July–September, data not shown) – was the highest compared to the other years in the three-year observation period. The high rainfall in 2001 (almost twice as high as in 1999–2000 together, data not shown) in the period when the ferns' spores ripen and germinate in Estonia (July–September) created particularly favourable moisture conditions for the spore germination in this year and could be the main cause of the overall population density change in 2002.

In general, all fern species showed rather similar population stage structures – premature individuals and generative adults had rather similar proportions in populations, exceeding that of vegetative adults.

The density of vegetative adults in 2003 was significantly higher compared to 2002. One explanation here may be the so-called organ pre-formation (Geber et al., 1997), which is common in many gymnosperm and angiosperm species, especially in seasonally cold environments (Bliss, 1971; Yoshie & Yoshida, 1989). Such a process is characteristic also of *D. carthusiana*, *D. dilatata* (Seifert, 1992), and *D. expansa* (Rünk, personal observations). The very dry vegetation period in 2002 and the possible water deficiency in the period of fronds' pre-formation could have inhibited the formation of sporangia in the next-year fronds. Also, as

it has been found in the case of *Asplenium scolopendrium* the fertile individuals may become sterile after a severe winter (Bremer, 1995) and the winter 2002/2003 was the coldest since 1999 (data not shown).

The population stage structures of *D. expansa* at Jäneda and Õngu were rather similar and corresponded to the general stage structure pattern described above, indicating a stable condition of the populations. Since the population stage structure of *D. expansa* at Õngu and Jäneda remained almost the same in the sites and between years, it may serve as a stable stage structure model of a successfully performing fern species. Local populations of this species were characterized by approximately equal frequencies of premature individuals and generative adults, while the proportion of vegetative adults was considerably smaller.

In the case of *D. expansa*, only a slight fluctuation was detected among sites and between years. The domination of the juveniles of *D. expansa* at Jäneda in 2002 could be explained by the recruitment of young sporophytes following the very successful germination and fertilization event in 2001.

In contrast, the population stage structure of *D. expansa* was different in the Sääre site, since the premature stage was almost absent in this local population. The between-years differences of the Sääre population indicated its peculiar structure, as the abundance of *D. expansa* was extremely low in this site and the transition of some individuals between life stages had a very large impact on the whole life stage structure.

Even though the results show that regionally the most frequent species – *D. carthusiana* – was also locally the most abundant over the three study areas, its population stage structure was rather inconsistent between the sites. Although at Sääre the density of *D. carthusiana* was lower than at Jäneda, this species with a weak competitive response (Rünk et al., 2004) tolerates the pressure of bryophytes and could hold a stable population structure. The domination of the generative plants of *D. carthusiana* at Õngu and Sääre in 2002 could be explained by features of its possible ruderal strategy *in sensu* Grime (2001). Fast-growing *D. carthusiana* plants could mature also rapidly – in their first year of life (Rünk, personal observations); so the sporophytes derived from spores germinated in the favourable year of 2001 could be generative plants in 2002.

The population stage structure of the rarest species – *D. dilatata* – varied between the sites and was more dynamic. Particularly at Õngu, but also at Jäneda, the population of *D. dilatata* was dominated by premature individuals, but at Sääre generative adults predominated. The similar population structure of *D. dilatata* – an excess of sterile plants over fertile ones – was also observed in England (Willmot, 1985). A high proportion of premature individuals of *D. dilatata* in the Õngu population may indicate that under favourable conditions the rare *Dryopteris* may demonstrate a dynamic population stage structure (Oostermeijer et al., 1992), which may indicate that this species could enlarge its distribution. Although the density of *D. dilatata* at Jäneda was the lowest compared with other two species the premature stages were well represented in the Jäneda site. Also, *D. dilatata* had a higher number of fertile fronds than *D. carthusiana*, the longest fronds

among the three species studied, and its young sporophytes performed relatively well in a competition experiment (Rünk et al., 2004). At the same time, one has to keep in mind that rare *D. dilatata* is less abundant than *D. carthusiana* all over the study area.

Different life stages of pteridophytes could have different freezing tolerance as a study of 14 cool temperate fern species showed. The younger stages – gametophytes of all species were more cold tolerant than the older ones – sporophytes (Sato & Sakai, 1981).

One may hypothesize that the bottleneck in the performance of local populations is not the younger, premature stage, but the generative one, which suffers due to climatic factors. However, the particular mechanism behind climatic restrictions still remains open to debate.

Among the three study sites, Sääre was the most unfavourable for the *Dryopteris* species, especially for *D. expansa*, but also for *D. dilatata* and *D. carthusiana*. The low density at Sääre may partly be explained by the fact that the mean cover of bryophytes in plots was significantly higher than in the other sites. At the same time, competition with bryophytes may be a critical factor for the survival of gametophytes (Gilbert, 1970; Cousens et al., 1985).

The completely different stage structure of *D. expansa* at Sääre could be an indication of unsuccessful performance at this site. Although generative individuals of *D. expansa* persist in low numbers at Sääre, the regeneration of the population has almost stopped and this population might be called senile (Oostermeijer et al., 1992). Possible reasons for this may be unfavourable light and moisture conditions and inability to establish due to the dense moss cover, in combination with the poor competitive ability of the fern species itself, especially at the early establishment stage (Rünk et al., 2004).

It has been suggested that the status of plant populations may be studied by monitoring population stage structure (Hutchings, 1991; Menges & Gordon, 1996). This approach may reveal, for instance, the response of populations to local management conditions (Oostermeijer et al., 1994; Bühler & Schmid, 2001; Hegland et al., 2001).

Brys et al. (2003) reported a relationship between population size and stage structure. In the case of three *Dryopteris* species in Estonia, the population stage structure revealed some differences in population conditions. These differences agreed with our expectations. We observed the most unfavourable condition of *D. expansa* in one site (Sääre), which we interpreted to be the result of competitive pressure from bryophytes. The differences in the population structure of *D. carthusiana* could be explained by its possible faster growth rate, earlier maturation, and weaker competitive response. Also, we observed predomination of premature stages of *D. dilatata* in two sites (Õngu, Jänedä), indicating the dynamic status of these populations. Because of the more westerly distribution of this species in Estonia compared to the other two species, it may be hypothesized that *D. dilatata* could enlarge its range due to climate warming as it was already shown by Bakkenes et al. (2002). It may be concluded that the population stage structure can reveal useful information about the condition of local populations,

though a demographic approach that estimates the probability of transitions between life stages would be required for a better understanding of the mechanisms behind population dynamics.

ACKNOWLEDGEMENTS

We are grateful to Elgi Brand from Öngu for her help and support. This study was financed by the Estonian Science Foundation (grants 5809 and 5535) and the University of Tartu (grants DBGBO1896 and TBGBO 2540).

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Kolme sõnajala *Dryopteris* liigi populatsioonide arenguastmete struktuurist Eestis

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Kolm sarnase ökoloogia ja morfoloogiaga sõnajalaliiki esinevad Eestis erineva sagedusega: ohtene sõnajalg *Dryopteris carthusiana* on tavaline liik, laiuvat sõnajalga *D. expansa* võib leida paiguti ja austria sõnajalga *D. dilatata* harva. Aastatel 2001–2003 uuriti kolmel uurimisalal Eestis nimetatud liikide segapopulatsioonidesse rajatud prooviruutudel nende liikide populatsioonide struktuuri. Töö eesmärgiks oli võrrelda nimetatud aastatel liikide arenguastmete struktuuri ja populatsioonistruktuuride fluktueerumist uurimisaladel. Sääre uurimisalal (Hiiumaal) leiti laiuva sõnajala populatsioon ebasoodsates tingimustes, mis võivad olla tekkinud sammaltaimede konkurentse mõju tulemusel. Kahel uurimisalal, Jänedal (Järvemaal) ja Õngul (Hiiumaal), domineerisid austria sõnajala populatsioonides varasemad arengujärgud, millest võib järeldada nende populatsioonide dünaamilisemat iseloomu. Kuna austria sõnajala levila on Eestis oma kirdepiiril ja kahe teise uurimisaluse liigi levilaga võrreldes läänepoolsem, on võimalik austria sõnajala levila laienemine ida suunas tänu kliima üldisele soojenemisele.