DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
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COMPARATIVE ECOLOGY OF THREE FERN SPECIES: *DRYOPTERIS CARTHUSIANA* (VILL.) H.P. FUCHS, *D. EXPANSA* (C. PRESL) FRASER-JENKINS & JERMY AND *D. DILATATA* (HOFFM.) A. GRAY (DRYOPTERIDACEAE)

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following articles, which are referred to in the text by their Roman numerals.

I Rünk, K., Moora, M. & Zobel , M. 2006. Population stage structure of three congeneric *Dryopteris* species in Estonia. Proceedings of the Estonian Academy of Sciences. Biology. Ecology 55: 15–30.

II Rünk, K. & Zobel, K. 2007. Phenotypic plasticity and biomass allocation pattern in three *Dryopteris* (Dryopteridaceae) species on an experimental light-availability gradient. Plant Ecology (in press; http://springerlink.metapress.com/content/681jp73486607010/?p=4ba137a33e614e99b57e5788a72bef5b&pi=1).

III Rünk, K., Moora, M. & Zobel, M. 2004. Do different competitive abilities of three fern species explain their different regional abundances? Journal of Vegetation Science 15: 351–356.

IV Rünk, K. & Zobel, M. The different reproductive capacity of three fern species could help explain their varying regional abundances. Manuscript.

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1. INTRODUCTION

1.1. General introduction

The central goal of ecology is to detect which factors and mechanisms control the abundance and distribution of species (Krebs, 1994; Crawley, 1997; Kunin & Gaston, 1997; Grime, 2001). The understanding of why some species are common whereas others are rare provides us with essential information about the dynamics of those species in space and time. This information helps to explain not only the present patterns of the distribution and abundance of species, but also to predict their possible changes in future, hence also having an essential practical implication for the conservation management of rare species. A species may be rare for various different reasons. The species' biology, ecological requirements and biotic interactions are the main reasons that may determine the species' abundance and geographic distribution, i.e. the degree of species rarity (Fiedler & Ahouse, 1992; Kunin & Gaston, 1997).

In order to classify, compare and evaluate the level of species rarity, several classification schemes based on different parameters have been elaborated (e.g. Harper, 1981; Rabinowitz, 1981; Fiedler & Ahouse, 1992; Gaston, 1994a; Kean & Barlow, 2004). At least one of following parameters: breadth of geographic range, size of local population/local abundance, degree of habitat specificity and taxon age is present in all schemes. A rare species is considered to be a species with at least one of the following attributes: small geographic range, small local population size/low local abundance, narrow habitat specificity or young taxon.

The rarity of species can be assessed/compared at different spatial scales e.g. local (smaller area within a country), regional (specific region e.g. one country or group of countries) or higher (continental or global) scales.

The simplest way to measure species rarity is to quantify species distribution (its geographic range). IUCN (Hilton-Taylor, 2000) suggested two measures for this purpose: the extent of occurrence (EOO; the area of the minimum convex polygon containing all sites of the present occurrence of a species) and the area of occupancy (AOO; sum of occupied grid cells). The sum of occupied grid cells (distribution frequency of a species) or the percentage of the occupied grid cells of the sum of all grid cells of the area (relative distribution frequency of a species) can be used for the definition of rarity/rare species with different criteria on different spatial scales (Broennimann *et al*., 2005; Pärtel *et al*., 2005; Pocock *et al*., 2006). These parameters can also be used for the direct comparison of the geographic distribution area of different species and the estimation of the relative rarity of the species.

The local abundance of a species (the total number of individuals of a species in an area or population) can be assessed by using the local density of a species (the number of individuals within a given area).

In the present study, a rare species was defined as a species with the lowest relative distribution frequency among three species compared in regional scale in Estonia.

One possible approach for the investigation of the causes of rarity is the comparison of taxa with contrastingly different levels of rarity (rare and common; reviewed in Bevill & Louda, 1999; e.g. Baskauf & Eickmeier, 1994; Sultan, 2001; Simon & Hay, 2003; Pohlman *et al*., 2005) in order to detect the differences in key traits between species. The studied pairs or the larger number of evolutionarily closely related taxa with different distribution and/or abundance help to minimize the confounding of phylogenetic differences existing between species (Silvertown & Dodd, 1996), and may more distinctly reveal factors or processes limiting the abundance and distribution of rare species.

In order to explain the general pattern that closely related and widely distributed species are locally abundant, and narrowly distributed ones are rare (Brown, 1984; Gaston, 1994b; Gaston, 1996; Gaston *et al*., 2000), the 'the resource breadth hypothesis' (Brown, 1984) and 'the resource availability hypothesis' (Gaston *et al*., 1997) have been elaborated. According to the first hypothesis, the abundance and distribution reflect the species' ability to use resources, i.e. species with wide niche breadth are expected to be more abundant and more widespread than species with narrow niches (Thompson *et al*., 1998; Kolb & Diekmann, 2005).

The expected positive correlation between niche breadth and geographical distribution offers us the possibility to study the plausible factors that might cause species rarity, and has been tested in numerous studies in which the morphological and physiological responses of related species with different ecological breadth (e.g. Bell & Sultan, 1999; Valladares *et al*., 2000; Sultan, 2001) or geographical range (Pohlman *et al*., 2005) have been compared to different levels of different environmental factors. Certain differences between the responses of studied species and thus some supportive evidence for the positive relationship between environmental tolerance and geographical distribution have been found.

Phenotypic plasticity may enable plants to grow and reproduce in spatially or temporally heterogeneous environments (Bradshaw, 1965) and therefore might help explain differences in the ecological and geographical distribution of closely related rare and common taxa (Petit *et al*., 1996). Although high plasticity in a phenotypic trait does not necessarily indicate adaptation (Weiner, 1988), several empirical studies of presumably adaptive phenotypic plasticity rely heavily on the assumption that plastic response is adaptive (see e.g. Bonser & Aarssen, 1994; Winn, 1996). Given that being plastic can be a wasteful maladaptive strategy in certain situations (Pigliucci, 2001), the nature of the relationship between the degree of plasticity in certain traits and local or large-scale ecological success remains largely unclear.

Competition is often claimed to be the most significant biotic interaction in plants, and different competitive abilities of rare and common species have been declared to be important causes of plant rarity (Kunin & Gaston, 1997; Lloyd *et al*., 2002). Experimental studies of competitive abilities have, however, often yielded contrasting results. In some cases, a common species was a superior competitor (Walck *et al*., 1999; Binney & Bradfield, 2000; Moora & Jõgar, 2006), while Rabinowitz *et al*. (1984) found the opposite. In an experiment by Snyder *et al*. (1994), the competitive ability of a rare congener was lower than the competitive ability of one common congener and higher than that of another. Lloyd *et al*. (2002) experimentally investigated the largest set of species so far, and obtained mixed results. They concluded that although rare species may in some cases have low competitive ability, this is not the necessary cause of rarity. Bush and Van Auken (2004) found some evidence that the competitive ability of rare species could be conditional and depend on environmental factors (e.g. soil salinity).

The contrasting results of different competition studies may partly be due to different experimental designs – the use of replacement series, additive series and combined series, as well as the use of both artificial potting substrates and natural soil mixtures with intact microbial communities in the experiments. On the other hand, however, the results of the above-mentioned studies indicate that the interrelations between competitive ability and rarity are conditional and depend on the biology of the particular species and on the local environmental conditions.

Starting from a plant propagule stage, biotic interactions may compress the fundamental niche of a species and determine its realized niche – the range of environments where it actually grows (Hutchinson, 1957) – hence determining the level of rarity of a species. Only by studying both the fundamental environmental requirements and biotic interactions of species can one determine the forces that shape different abundance and distribution patterns and elucidate the relative role of biotic interactions in the formation of a synecological niche.

The investigation of different ecological factors and mechanisms behind rarity may be addressed via both observational and experimental studies. Observational studies include the description of fern species and populations along environmental gradients or in conditions of different human impact. Here the description of population life stage structure may be a vital approach for obtaining necessary information about the mechanisms behind the different local abundance of species. In particular, the observation of the status and changes in plant population structure may exhibit significant information (Aguraiuja *et al*., 2004). In general, the status of plant populations may be studied on four levels: population distribution, the quantitative monitoring of population size/condition, the monitoring of population structure, and the demographic investigation of the population (Hutchings, 1991; Menges & Gordon, 1996). Demographic studies provide valuable information about the

condition of populations. They are, however, laborious, and take years to complete, which prevents their wide use, both in population studies and 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 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 the populations of such species in a single census is by determining the relative abundance (proportions of individuals) of the different stages in 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).

1.2. The biology and ecology of ferns

This thesis focuses on the comparative ecology and causes of distribution of three fern species. The causal relationships between ecological factors and the rarity of fern species have seldom been addressed (Suzuki *et al*., 2005; Wild & Gagnon, 2005). Several features of pteridophyte biology compared to angiosperms is an essential matter to consider in describing and explaining the distribution and abundance of pteridophyte taxa. In particular, ferns are distinguished by two independent alternating generations – by a small ephemedral non-vascular gametophyte developing from the spore and spore-bearing diploid vascular sporophyte that finalizes the life cycle.

The generative propagules of homosporous ferns are small lightweight haploid spores (30–100 μm) (Tryon & Lugardon, 1990). One plant may produce an enormous number of spores (from 75,000 to 750,000,000 per fertile frond; Page, 1979). Nevertheless, even if airborne spores may in very favourable circumstances be dispersed over very long distances (Tryon, 1970; Smith, 1972; Tryon, 1985), the highest abundance of fern spores has been found within a relatively short distance – 2 to 10 m – from the source (Peck *et al*., 1990; Penrod & McCormick, 1996). In natural conditions, for example, 90% of the spores of *Dryopteris dilatata* are deposited within 3 m of sporophytes (Glaves, 1991).

Ferns' mating systems include outcrossing, intragametophytic and intergametophytic selfing (Klekowski, 1979). Haploid gametophytes develop the reproductive structures and may become unisexual (male or female) or hermaphroditic. In many species, a pheromone antheridiogen that stimulates spore

germination and induces maleness in neighbouring gametophytes determines their mating system (Näf, 1979). Fern sperm need external water in order to move to an egg cell for fertilization.

Fern spores have been found to disperse widely, and gametophytes temporarily grow in a greater area than that in which sporophytes are recorded (Page, 1979). Although comparative studies of the different life phases of fern ecology (spores, gametophytes and sporophytes) have shown the different amplitude of the abiotic factors under study, usually broader in the case of spores (comparing spores and gametophytes; Hill, 1971; Prada *et al*., 1995) and gametophytes (comparing gametophytes and sporophytes; Sato & Sakai, 1981), the persistence of species in a habitat is possible only if the realized niches of spores, gametophytes and sporophytes match. However, the importance of gametophyte stage in the life history of ferns as big as of sporophyte stage, their small size and the absence or lack of knowledge of morphological differences complicate their investigation, especially in field conditions. Nevertheless, even if the geographical distribution of a fern taxon in reality shows the distribution of its sporophytes, it also provides some information about the spores' and gametophytes' ecology.

The distribution and level of abundance of a given plant species at a particular site is primarily dependent on the availability of diaspores and on the correspondence between plant traits and local ecological conditions, i.e. the abiotic environment and biotic interactions. As fern species are independent from pollen and seed, there are also no records about zoochory, and only a few co-evolved fern herbivores (Page, 1979) are known, it has been suggested that the distribution of ferns is mostly determined by abiotic factors of the environment – climatic or edaphic (e.g. Petersen, 1985; Odland *et al*., 1990; Marquez *et al*., 1997). On the other hand, the high number of spores and their capability for long-distance dispersal, e.g. to reach remote oceanic islands (Tryon, 1970), suggests that ferns are not dispersal-limited (Tryon, 1970; 1986) or are less than angiosperms. Several recent studies have focused on the relative importance of the dispersal and environmental determinants of fern distribution. On both a local scale (Richard *et al*., 2000; Wild & Gagnon, 2005) and a regional scale (Guo *et al*., 2003), the evidence indicates that habitat availability and not dispersal capability is responsible for fern distribution. A study on two contrasting local spatial scales (local fine and local mesoscale) showed similar results (Karst *et al*., 2005) – the abiotic environment was the main determinator of fern species distribution. Fern distribution on a local mesoscale (135–3515 m) was linked to water regime and on a local fine scale (4–134 m), both dispersal and the abiotic environment were jointly responsible for fern distribution.

Although there are several studies concerning the responses of related seed plant species with narrow and broad ecological/geographical distribution to different light conditions (Walters & Field, 1987; Baskauf & Eickmeier, 1994;

Gonzáles & Gianoli, 2004), pteridophyte species growing in different light conditions have been compared in only a few studies (Nasrulhaq-Boyce & Haji Mohamed, 1987; Brach *et al*., 1993; Saldaña *et al*., 2005).

In the case of ferns, the availability of photosynthetically active radiation (PAR) is, alongside water availability, undoubtedly the key resource to explain their distribution patterns. Modern ferns have been claimed to be evolutionarily relatively young species that have probably adapted to exploit shady habitats (Schneider *et al*., 2004) predominated by more competitive higher seed plants (Kawai *et al*., 2003). Although ferns also inhabit open habitats such as rocks, heathlands, etc., the diversity of ferns is highest in shaded forests (Tryon, 1964; Page, 1979; Grime, 1985) where the probability of gametophyte and sporophyte survival is greatest. The study of autecological reaction norms to light in different ferns would enable us to test whether ferns are truly restrictively adapted to the deep shade they are usually found in, or whether the real autecological optimum lie in a more illuminated part of the PAR gradient.

Although the potential role of both interspecific and intraspecific competition in determining species distribution and abundance has repeatedly been mentioned in a number of studies on fern ecology (Page, 1979; 1997; Willmot, 1985; Grime *et al*., 1988; Bartsch & Lawrence, 1997; Mütter *et. al*., 1998), there are only a handful of experimental studies on this topic (den Dubbelden & Knops, 1993; Russell *et al*., 1998; Bell *et al*., 2000). In natural communities, the abundance of pteridophytes may be restricted by the susceptibility of gametophytes and young sporophytes to competition from herbaceous angiosperms (Grime, 1985; Grime *et al*., 1988) and bryophytes (Gilbert, 1970; Cousens *et al.*, 1985). Consequently, the ability of a young sporophyte to tolerate competitive pressure from the surrounding vegetation would be extremely important for the fate of a particular fern individual, as well as for the abundance and distribution of that particular fern species.

Evidence shows that rare flowering plant species exhibit lower fitness than common species, e.g. reduced amounts of viable pollen (Burne *et al*., 2003) and lower pollen viability (Banks, 1980), smaller seeds (Münzbergová, 2005), lower seed production per plant individual (Peat & Fitter, 1994; Eriksson & Jakobsson, 1998) or lower pollinator effectiveness (Rymer *et al*., 2005).

Analogous studies about spore plants, including ferns, are extremely scarce, but the results coincide with those of seed plants – rare mosses produce fewer spores than common ones (Hedderson, 1992). Accordingly, one may presume that the trait connected with reproduction may be crucial in controlling the relative abundance and distribution of species.

In order to estimate the spore production of fern species, two different methods have been used: (i) the direct counting of sporangia and the calculation of the number of spores (Farrar, 1976; Peck *et al.,* 1990) and (ii) the indirect estimation of spores on the basis of the volume of spores collected from fern individuals (Cousens, 1981), by counting the number of fertile leaves (Conway,

1957; Bremer, 1995) or by calculating the area covered by spores (Greer & McCarthy, 2000).

1.3. Aims of the thesis

The main objective of this study was to test the relative role of different abiotic and biotic factors in determining the different relative distribution and abundance of three fern species in Estonia – the common *Dryopteris carthusiana*, the scarce *D. expansa,* and the rare *D. dilatata*.

First, we aimed to investigate whether the population structure of the three fern species fluctuates differently in different sites and different years. In particular, we hypothesized that the population structure of the rare *D. dilatata* is the most dynamic and may be characterized either by a greater proportion of premature individuals, due to edaphic factors, the 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.

Second, we studied the responses of *D. carthusiana*, *D. expansa* and *D. dilatata* to different levels of light availability (PAR), with the aim of testing whether the degree of response to PAR is related to the different distribution patterns of the three species. We hypothesized that three fern species with different regional frequency possess different biomass allocation strategies in response to different levels of PAR – the species with the greatest ability to shift allocation patterns in response to changes in PAR availability is the most competitive and hence the most frequent.

Third, we tested the hypothesis that the competitive response of three fern species in a young sporophyte stage is related to their regional distribution frequency. We expected that the more frequent species would show the smallest response to competition, and *vice versa***.**

Finally, we were interested in the capacity of generative reproduction (the quantity of spore production) of all three fern species, and tested the hypothesis that the regionally rare species *D. dilatata* has a lower fitness in terms of spore production than the more common *D. expansa* and *D. carthusiana*.

2. MATERIAL AND METHODS

2.1. Study species

All three plant 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, occurring in Europe, Northern America and Asia. Tetraploid (2n=164) *D. dilatata* (Hoffm.) A. Gray is a European endemic distributed mostly in Western and Central Europe. Diploid (2n=82) *D. expansa* (C. Presl) Fraser-Jenkins & Jermy occurs in Northern America and Asia. In Europe *D. expansa* is restricted to mountainous areas, with a more north-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* (Fig. 1) is recorded (at least once since 1970) in 441, *D. expansa* (Fig. 2) in 145 and *D. dilatata* (Fig. 3) in 20 of the 513 6 x 10 minute grid squares covering Estonia.

All three species are rhizomatous small to large-sized arbuscular mycorrhizal (AM) (Berch & Kendrick, 1982; Harley & Harley 1987) perennials with 3-pinnate fronds and orbicular sori covered with a reniform indusium (Fraser-Jenkins, 1993). There is no registered data about antheridiogen system in the case of all three species. In Estonia, all three species grow mainly in mesic woodlands. In particular, they occur (and frequently co-occur) in moderately moist mesotrophic *Picea abies* and *Pinus sylvestris* boreal forests. *D. carthusiana* also grows in forests on peaty soils and *D. dilatata* in oligo-mesotrophic boreal forests. *D. expansa* and *D. carthusiana* also grow together in eutrophic boreo-nemoral forest (Rünk, 2002). According to Raunkiaer's (1934) life form classification, all three species are hemicryptophytes. According to the Ellenberg ecological indicator values for light, characterising the synecological optima of species along the illumination gradient (using ordinal scores ranging from 1 to 9; Ellenberg et al., 1991), *D. carthusiana* is characterised as a semi-shade-tolerant species (Ellenberg's score = 5), and *D. expansa* and *D. dilatata* as being between shade and semi-shade-tolerant species (Ellenberg's score = 4).

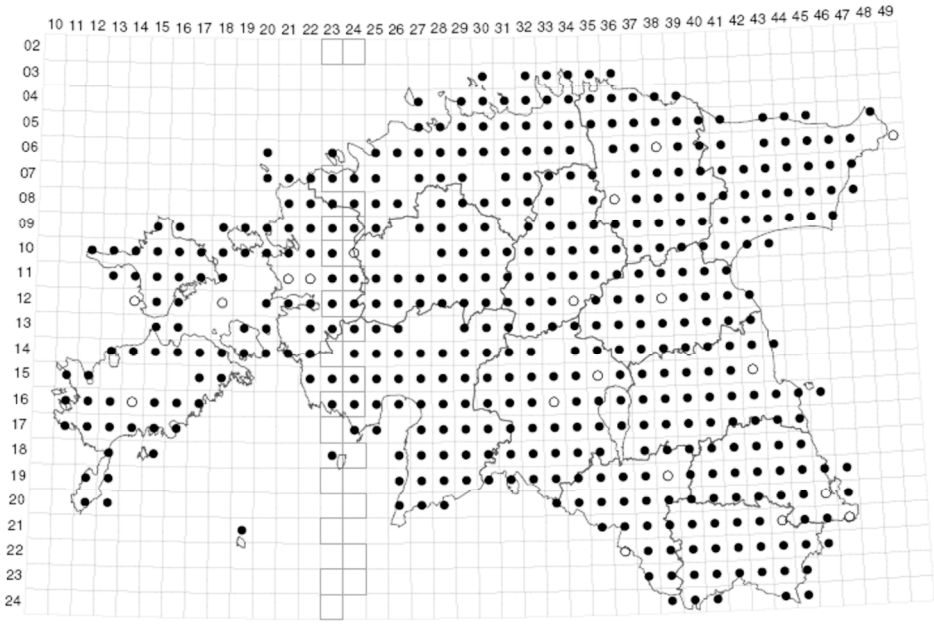

Figure 1. Distribution of *Dryopteris carthusiana* in Estonia. Filled circles – recordings after 1970; open circles – 1921–1970 (Kukk & Kull, 2005).

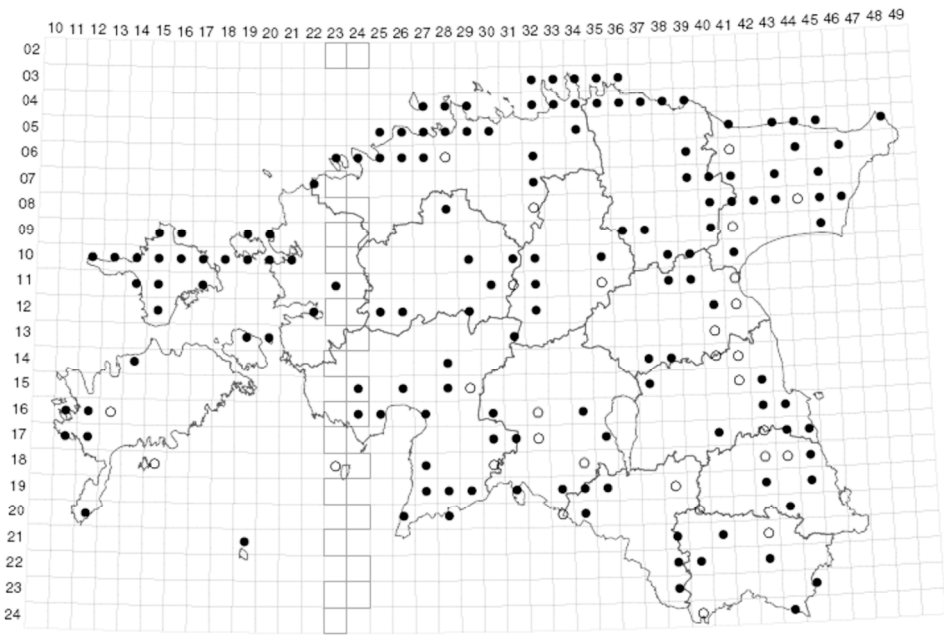

Figure 2. Distribution of *Dryopteris expansa* in Estonia. Filled circles – recordings after 1970; open circles – 1921–1970 (Kukk & Kull, 2005).

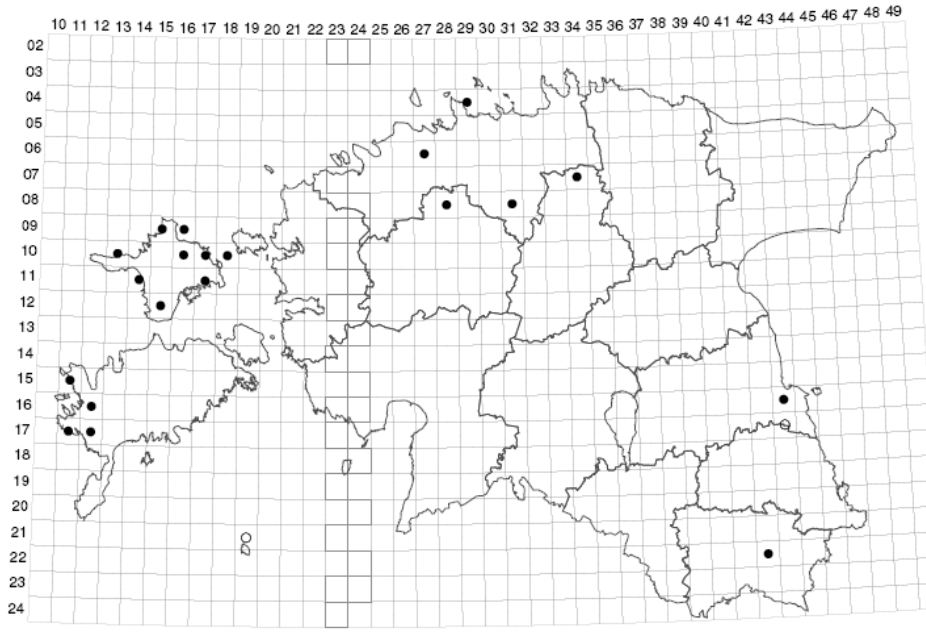

Figure 3. Distribution of *Dryopteris dilatata* in Estonia. Filled circles – recordings after 1970 (Kukk & Kull, 2005).

In Estonia *D. expansa* overwinters as a leafless rhizome, and fronds of *D. carthusiana* and *D. dilatata* sometimes remain green until the following spring (K. 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* and *D. dilatata* on natural substrates showed a maximum of 79% and 35% of intragametophytic self-fertilisation respectively (Seifert, 1992).

In competition experiments, we used as a neighbour species *Deschampsia flexuosa* (L.) Trin. (Poacea), which is a common perennial grass species in Estonia, coexisting in dry and mesic coniferous forests with all three of the above-mentioned fern species.

Species nomenclature follows Fraser-Jenkins 1993.

2.2. Study sites

The population stage structure and dynamics of three coinciding local sporophyte populations of *D. carthusiana*, *D. dilatata*, and *D. expansa* in Estonia were studied at Õngu and Sääre, both on the Baltic island of Hiiumaa, and in Jäneda, central North Estonia (Fig. 1/I). The locations were situated in different parts of Estonia, the pairwise distances between the locations being 40 km, 205 km and 243 km. Fern spores for all experiments were collected from the same three sites. At each location, spores from five plants of each species were collected. *Deschampsia flexuosa* seeds for the competition experiment were collected from Sääre (Fig. 1/I). In fact, in 2000, at the beginning of the study, those three study sites were the only localities known and practically suitable for research in Estonia and where all three species coexisted; this made it possible to compare their population structure in similar abiotic conditions.

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 impact is relatively low at all three sites. The 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 and a lower annual mean are observed (Table 2/I). The mean annual precipitation at 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) there was less precipitation at all three sites in 2002 than in 2001 and also than in 2000 (Table 2/I).

The experimental garden in which all of the experiments were conducted was located in Tartu (Fig. 1/I) (58°21´25´´N, 26°42´5´´E, 68 m a.s.l.), in south-eastern Estonia, where the average annual temperature is 5.0°C and the average amount of annual precipitation is 550 mm (Jaagus, 1999).

All shade treatment was provided using tents made of aluminium-coated shade cloths (spectrum neutral; Ludvig Svensson, Kinna, Sweden).

2.3. Population life stage structure and dynamics (I)

Within each of the three study sites (Jäneda, Sääre and Õngu), which had areas of 2000–3000 m², five permanent plots of 4 x 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 2/I). Individuals of the three fern species were monitored in detail. The field surveys were conducted during the same phenological stage of the fern individuals, either during the end of July or the beginning of August in 2001, 2002 and 2003. In 2001 all sporophytes in plots and in 2002 and 2003 also all newly recruited sporophytes were labelled and mapped in order to locate and identify each individual. As there was no possibility to understand whether an individual rhizome apex with fronds had arisen due to vegetative or generative reproduction, all fern individuals were treated as genets.

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 the individuals, the individual sporophytes of *D. carthusiana*, *D. dilatata*, and *D. expansa* were classified into three different life stages: premature individuals (sporulation was not recorded in census years), vegetative adults (without fertile fronds in the 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 only used in 2002 and 2003.

2.4. Experiment with different levels of light availability (II)

Plasticity in relation to light availability was assessed in a garden experiment in 2004. The spores of all fern species were collected in the wild in July 2003. The substrate used for spore germination was sterilised and consisted of 3 parts horticultural peat and 1 part fine-grade sand. Spores were sown on 20 October, 2003.

Even-aged young fern sporophytes were planted in plastic pots on 23 June, 2004. The soil mixture consisted of 3 parts horticultural peat and 1 part fine-grade sand. The pots were placed in a greenhouse and watered as required to keep the soil moist. After 15 days the pots were relocated to the experimental garden and distributed randomly among four neutral (no change in the quality of the active radiation) shading treatments: 100, 50, 25 and 10% of full daylight, with ten replicate plants in each, and were grown there for another 85 days. We believe that in a comparative study the use of neutral shade does not provide a bias in estimating the responses of closely related species to light availability. Though the effect of neutral and “green” canopy shade on plant growth is different in several aspects, the only really consistent difference between the neutral and green shade is that the effect of the latter is stronger (except on biomass; Stuefer & Huber, 1998; Dorn *et al*., 2000; Weinig, 2000). Therefore,

the use of neutral shade instead of "green" shade probably causes systematically lower plasticity to light availability, and consequently increases the probability of Type II error in statistical analyses, but can hardly cause artifacts and biased statistical inferences.

Initially all treatments were represented by 10 replicates but, due to the mortality of plants in the full light treatment and due to plants that were excluded from the analysis because of herbivoral or mechanical damage, the final number of replicates was lower in some treatment variants (the lowest being seven).

The numbers of fronds were counted once, immediately before harvesting. After harvesting, plants were separated into fronds (the leaf of a fern), rhizomes and roots (below-round organs), and dried at 75ºC for 48 h. All biomass fractions were weighed separately. The length of the stipe (the stalk of the frond) was obtained by subtracting blade length from frond length.

Blade area was measured using a scanner (ScanJet5p), DeskScan II 2.9, and Pindala 1.0 software. Specific blade area (specific leaf area, SLA) was calculated as blade area (cm^2) per unit of blade dry mass (g).

2.5. Competition experiment (III)

The spores of all fern species and seeds of *Deschampsia flexuosa* for the competition experiment were collected in the wild in August 2001. The spores were sown on 8 November 2001 and the seeds on 17 January 2002. The substrate used for spore and seed germination was sterilised and consisted of one part horticultural peat, one part leaf mould and one half part fine sand. Individuals of even-aged young fern sporophytes and individuals of *Deschampsia flexuosa* were planted in plastic pots on 17 April 2002, both as single controls and as two-species mixtures – single fern individuals together with 2, 4 and 8 individuals of *Deschampsia flexuosa* (referred to as 2n, 4n and 8n respectively). Since we were interested in the performance of fern species under different competitive effects, ferns were considered to be target species and *Deschampsia flexuosa* to be neighbour species. Initially, all treatment combinations (altogether 12) were represented by 15 replicates but, due to the misidentification of some young sporophytes, the final number of replicates was lower. The substrate used for the competition experiment consisted of four parts forest soil and one part medium-grade sand. The soil originated from the same sites (1:1 mixture of Õngu and Sääre soils) from which the spores and seeds of the experimental plants were collected. The pots were placed in a greenhouse and watered as required to keep the soil moist. After 65 days the pots were relocated to the experimental garden and grown in shaded light (a tent with a shade value of 65%) for another 82 days.

The length of the fronds and frond blades (leafy part of the frond) of every fern individual were measured, and the numbers of the fronds of all plants were counted once, before the harvest. The length of the stipe (the stalk of the frond) was obtained by subtracting blade length from frond length. The above-ground parts (blade and stipe) and below-ground parts (rhizome and roots) of all plants were harvested, dried at 85°C for 24 hrs, and weighed. These parameters allowed us to calculate total biomass and the ratios between different biomass fractions.

2.6. Comparison of reproductive capacity and vegetative growth (IV)

Species' traits with regards to vegetative growth, reproduction, morphology and biomass were assessed in a garden experiment conducted in 2004 and 2005. The spores of all fern species were collected in the wild in July 2003. The substrate used for spore germination was sterilised, and consisted of 3 parts horticultural peat and 1 part fine-grade sand. Spores were sown on 20 October 2003. Young fern sporophytes were first planted 9 individuals per box on 16 May 2004. The specimens were replanted individually in plastic pots on August 2. All three species were initially represented by 60 replicates, but for the final harvest and analysis, 15 individual plant specimens per species were randomly selected.

The soil mixture consisted of 4 parts horticultural peat and 1 part fine-grain sand. The boxes were placed in a greenhouse at 22 ±2°C with a photoperiod of 12:12 h (fluorescent light: daylight tubes, photon flux density 40 μmol $s^{-1}m^{-2}$) and watered as required to keep the soil moist. On August 10 the pots were relocated to the experimental garden and grown in shaded light (a tent with a shade value of 65%) for another 14 months.

During winter 2004/2005, plants were covered with horticultural peat, imitating fallen leaves and their decay.

During both vegetation periods, a total of 9 measurements – 5 (nos. 1–5) in 2004 and 4 (nos. 6–9) in 2005, were performed every 28–34 days starting from 9 June 2004 – in the case of each fern individual, the number of fronds was counted and the length of the longest frond was measured. In generative individuals, the number of fertile (spore-bearing) fronds was also counted.

Leaf elongation rate (LER, mm/day) was recorded on the longest frond of each fern individual by subtracting the result of the previous (e.g. first) measurement from the following (e.g. second) one and dividing the difference by the time period (number of days) between the measurements. Measurements were calculated separately for 2004 and 2005. LER was recorded for all 7 periods between the measurements – 4 (nos. 1–4) for 2004 and 3 (nos. 5–7) for 2005.

After the final harvest in October 2005, three biomass fractions – fronds (fern leaves), rhizomes and roots – were separated, dried at 75ºC for 48 h and weighed. The length of all fronds and frond blades were measured to the nearest millimetre just before the final harvest. The length of the stipe was obtained by subtracting blade length from frond length.

Blade area and blade area (pinnae) covered with sori was measured using a scanner (ScanJet5p), DeskScan II 2.9, and Pindala 1.0 software.

Specific blade area (specific leaf area, SLA) was calculated as blade area (cm^2) per unit of blade dry mass (g).

2.7. Data analysis

2.7.1. Population life stage structure and dynamics (I)

Differences in the overall population densities of *D. carthusiana*, *D. dilatata* and *D. expansa* in three study sites in the years 2001–2003 were tested using repeated measures ANOVA (using the Statistica software version 6.0; StatSoft Inc., 1998). Species (three levels) and study site (three levels) were included in the model as fixed factors and census year (three levels: 2001, 2002 and 2003) as a repeated measure factor. Data on plant densities in permanent plots were square root transformed to meet the assumptions of ANOVA (Zar, 1999).

Differences in the population densities of the three different life stages of *D. carthusiana*, *D. dilatata*, and *D. expansa* in three study sites in the years 2002–2003 were tested using repeated measures ANOVA. Species (three levels), life stage (three levels), and study site (three levels) were included in the model as fixed factors and census year (two levels: 2002 and 2003) as a repeated measure factor. As it was impossible to distinguish between premature individuals and vegetative adults (sporulated in the previous year, but without sori in the census year), in the first census year the three-stage classification was used only for 2002 and 2003. Relative plant densities on plots (the proportions of individuals representing certain life stages) were arcsine square root transformed to meet the assumptions of ANOVA (Zar, 1999).

The differences in the mean number of leaves per individual and in the mean length of leaves per individual (data from 2002–2003) where analysed in a model including 'year', with two levels as the repeated measure factor (2002 and 2003) and 'life stage' (three levels) as the fixed categorical factor. In the case of the mean number of fertile leaves per generative adult (only one life stage under observation), data from all the three observation years (2001–2003) were used. Differences between the coverage of vegetation layers (tree, herb and bryophytes layer; Table 2/I) in the three study sites were tested using 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 the percentage cover of vegetation layers (bryophyte and herb layer) in the study sites were analyzed using Spearman rank correlation.

2.7.2. Experiment with different levels of light availability (II)

In order to analyse the effects of species and light availability on biomass fractions and ratios and the morphological traits of ferns, two-way ANOVA (using the Statistica software version 6.0; StatSoft Inc., 1998) was conducted, with percent of light availability (three levels) and species (three levels) as fixed factors. All variables were log transformed. To test the differences between the three light availability levels and three species levels, the Tukey HSD multiple-comparison test with 0.05 significance level was used (Sokal & Rohlf, 1995).

The plasticity of a plant morphological trait (Π) in response to light availability was defined as the absolute value of the slope of the reaction norm between trait and illumination (Gavrilets & Scheiner, 1993; Scheiner, 1993; McLellan *et al*., 1997; Schlichting & Pigliucci, 1998; Stratton, 1998; Pigliucci & Schmitt, 1999; Lepik *et al*., 2005). Such a plasticity estimate is comparable across different traits and species, provided that the trait value is log-transformed and the allometric effect of biomass (passive or inevitable plasticity) is considered and removed in order to reveal true plasticity (ontogenetic or active plasticity), which is frequently shaded by a strong allometric effect of plant size (Coleman & McConnaughay, 1995; McLellan *et al*., 1997; Casper *et al*., 1998; García-Berthou, 2001; Cheplick, 2003; Gehring, 2003; Lepik *et al*., 2005; Semchenko & Zobel, 2005). The plasticity estimation procedure started with a testing for an allometric relationship between plant total biomass and trait value separately for each species. Regressions of the log-trait value on total biomass were performed to fit the allometric relationship. There was no need to fit more complex allometric curves, since the log-trait *vs* log-biomass regression was clearly significant and linear in all cases where an allometric relationship was detectable. Residual trait values (after fitting the allometric curve) were used for the estimation of the slope of the reaction norm in a regression analysis of residuals versus percent light availability. If there was no significant effect of total biomass on a morphological trait, the original log-transformed trait values were used for determining the slope of the reaction norm (plasticity).

We performed pairwise comparisons of the plasticity of 11 traits in the three species (a total of 33 comparisons). For one comparison, a general linear model was fitted with a residual log-trait (in cases where there was a significant allometric relationship between trait and total biomass) or log-trait (in cases where there was no significant allometrical relationship), serving as a dependent variable. Percent illumination was included as a continuous independent

variable, and species as a categorical independent variable with two levels. The significance of the variable 'species', after correcting for multiple tests using the Bonferroni criterion ($p<0.0015$) (Sokal & Rohlf, 1995), was considered to be an indication of the different plasticity of the trait between the two species.

2.7.3. Competition experiment (III)

For statistical analysis, two-way ANOVA (using the Statistica software version 6.0; StatSoft Inc., 1998) was conducted, with neighbour density (four levels) and species (three levels) as fixed factors. All variables were log transformed. The summary total biomass of *D. flexuosa* individuals was significantly different between all neighbour density treatments (one-way ANOVA; $F = 24.523$; $p < 0.001$). In order to estimate the differences between the four neighbour density treatments and three species treatments, the Tukey HSD multiple-comparison test with 0.05 significance level was used (Sokal & Rohlf, 1995).

2.7.4. Comparison of reproductive capacity and vegetative growth (IV)

Differences in vegetative growth (the length of the longest frond and the number of fronds) in the years 2004 and 2005 were tested separately for each year with repeated measures of ANOVA (using the Statistica software version 6.0; StatSoft Inc., 1998), with species (three levels) as fixed factors, and measurement time (five levels in 2004 and four levels in 2005) as a repeated factor.

Differences in LER (leaf elongation rate) between *D. carthusiana*, *D. dilatata* and *D. expansa* in the years 2004 and 2005 were tested separately for each year, with repeated measures of ANOVA with species (three levels) as fixed factors and period of time between measurements (four levels in 2004 and three levels in 2005) as a repeated measures factor.

Differences in morphological, biomass and reproductive parameters between *D. carthusiana*, *D. dilatata* and *D. expansa* in the experiment were tested using one-way ANOVA with species (three levels) as fixed factors.

All variables were log transformed, except in the case of relative biomass allocation, when data (proportions) were arcsine square root transformed.

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).

3. RESULTS

3.1. Population life stage structure and dynamics (I)

3.1.1. Population density

The overall fern population densities differed significantly between species and between Jäneda, Sääre and Õngu study sites over the three census years (2001–2003) (Table 2/II). 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 density of the overall fern population was higher than at the other two sites, and lower in 2001 than it was in 2002 or in 2003.

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

3.1.2. Population life stage structure

The life stages were represented differently across all studied fern populations in 2002–2003 – the relative 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. In general, over two years, all three species had similar population stage structures, in that premature individuals and generative adults had a significantly higher share in local populations than vegetative adults.

The local populations of *D. carthusiana* and *D. expansa*, however, had a nonsignificantly higher relative density of generative adults than premature individuals, while in the case of *D. dilatata* the proportion of prematures was nonsignificantly higher than the proportion of generative individuals.

A significant three-way interaction between species, life stage, and study site became evident. 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 – this difference was significant compared to vegetative adults, 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 to the Jäneda population 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. In the Õngu population, premature and generative stages were significantly more numerously represented than the vegetative adult stage.

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 altogether absent. 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 were a significantly higher proportion of generative adults than of vegetative adults.

The significant three-way interaction between year, species, and life stage indicates the species-specific annual differences in the 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 numerously represented than vegetative adults in the case of both fern species. In the case of *D. expansa*, the population stage structure was only similar to the other two *Dryopteris* spp. in 2002. This pattern changed in 2003 – the proportion of vegetative adults was not different 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 (Fig. 2/I). In 2002, the relative densities of premature individuals of *D. dilatata* and *D. expansa* at Jäneda were higher than the densities of vegetative adults. At Sääre in 2002, the relative densities of generative adults of *D. carthusiana* and *D. dilatata* were higher than those of vegetative adults. At Õngu the relative density of premature individuals of *D. dilatata* was higher than that of vegetative adults in both years.

3.1.3. Morphological parameters

3.1.3.1. 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 longest at Õngu and 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*.

3.1.3.2. 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.

3.1.3.3. Mean number of fertile fronds per generative adult

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

3.1.4. Relationships between layers of vegetation in study sites

There were no differences between the percentage of tree layer cover (Table 2/I) in different study sites. The percentage of herb layer cover at Sääre was significantly lower than at Jäneda or Õngu ($F = 25.130$, $p < 0.001$). The bryophyte cover was highest at Sääre, intermediate at Jäneda, and lowest at Õngu ($F = 61.667$, $p < 0.001$). The bryophyte cover was negatively correlated with the herbaceous plant cover ($r = –0.71$, $n = 15$, $p < 0.05$).

3.2. Experiment with different levels of light availability (II)

3.2.1. Plant survival

In full sunlight the mortality of young sporophytes of all three fern species was considerable – it was highest (90%) in *D. carthusiana,* lower in *D. dilatata* (60%) and lowest in *D. expansa* (20%). Hence data from the full-light treatment will not be used in the analysis.

3.2.2. Plant total biomass

There were distinct differences in total plant size at harvest (*D. carthusiana* > *D. expansa* > *D. dilatata* (Table 1/II; Fig. 1/II). There was also an obvious divergence in how biomass changed along the light gradient in different species. In the two more common species there was a steep but non-linear increase in biomass with increasing light, with *D. carthusiana* already showing near-maximum growth at 25% of full light, and *D. expansa* only responding strongly at 50% of full light (Fig. 1 a, c/II). In *D. dilatata* there were hardly any differences in total biomass at different light conditions (Fig. 1 e/II).

3.2.3. General biomass allocation pattern

All of the measured biomass characteristics responded significantly to the light treatment and, with one exception (root:frond mass ratio), did so in a different fashion in different species. Interestingly, the single common feature of the three species in the biomass allocation pattern was a gradual decrease in relative allocation to roots with increasing light (Fig. 1 b, d, f/II), a response that is opposite to that usually observed in plants. The general response pattern of biomass partitioning on the light gradient allowed us to distinguish between two distinct strategies of biomass allocation, shown by the common species *D. carthusiana* and the rare species *D. dilatata* (with *D. expansa* demonstrating intermediate behaviour). The contrasting strategies were mostly revealed in how resources were partitioned between fronds and rhizomes (or fronds and below-ground organs) in *D. carthusiana* and *D. dilatata*. *D. carthusiana* allocated a nearly constant share of resources to its rhizome, and thus relative frond biomass increased steadily (on account of the decreasing share of root and below-ground organs) with increasing light (Fig 1 b/II). *D. dilatata*, on the contrary, showed a plastic switch towards increased resource storage in its rhizome (and below-ground biomass) and a simultaneous decrease in relative

frond biomass in benign conditions (Fig. 1 f/II). In *D. expansa,* a more or less constant proportion of biomass was allocated to fronds and below-ground organs. Here the decrease in relative root mass with increased light was compensated by a slight increase in relative stipe and rhizome mass.

3.2.4. Morphological traits

All of the measured morphological characteristics responded to the light treatment, with the exception of blade length (in blade area, the effect of light is also only marginally significant). In all cases there were significant morphological differences among species and, with the exception of the blade:stipe length ratio, the response patterns of species to light treatment were different (Table 1/II). Out of the six considered morphological traits, four were significantly allometrically related to plant biomass in all species (the number of fronds, blade area, blade length, blade:stipe length ratio). In these traits, residuals from the model that gave the best fit for the trait *vs* biomass relationship were observed parallel to absolute trait values, in order to differentiate between ontogenetic plastic responses (ontogenetic change in plant trait) and passive (those explainable through total plant size) plastic responses. In all cases the best fit was provided by a linear relationship between log-trait and log-biomass.

Specific leaf (blade) area (SLA), as well as blade area, showed the expected plastic responses to light in all species – blades grew thicker and had a relatively smaller area in increased light supply (Fig. 2/II, 3/II). In *D. carthusiana* and *D. dilatata,* an abrupt decrease of SLA already occurred in 25% light, while *D. expansa* responded more gradually. The absolute decrease in mean blade area with increasing light could only be seen in *D. dilatata* (Fig. 3 a/II); in *D. carthusiana* and *D. expansa* there was no clear response. Fig 3 b/II reveals that when the allometric effect of plant biomass had been removed, a steady plastic response was present in all species, with *D. dilatata* showing the steepest reaction norm.

The number of fronds per plant was a trait regarding which only *D. carthusiana* showed a clear response, and even there, most of the observed response was due to passive (inevitable) plasticity – when the effect of biomass had been removed, there remained no evidence of the slope of the reaction norm being different from zero because of a great deal of unexplained variation (Fig. 4 a, b/II). The relative importance of blade as a vertical spacer increased in all species with improved illumination, with *D. dilatata* showing the strongest response (Fig. 5/II). When stipe length and blade length were observed separately, it became clear that the response pattern was actually quite complicated (Fig. 6/II, 7/II). Stipe length shortened with increased illumination, steeply in *D. dilatata*, slowly but steadily in *D. carthusiana*, and showed no clear response

in *D. expansa* (Fig. 6/II). Blade length showed passive plastic responses, as well as clear ontogenetic plasticity to light (Fig. 7 a/II and 7 b/II comparatively).

3.2.5. Morphological plasticity

In five traits – rhizome mass, below-ground:frond ratio, blade area, specific leaf area (SLA) and stipe length – there were significant interspecific differences in the degree of ontogenetic plasticity to light. In all five cases *D. dilatata* was significantly more plastic than *D. expansa,* and in four cases more plastic than *D. carthusiana*. Plasticity of blade area was not significantly different in *D. dilatata* and *D. carthusiana.* It is clear that *D. dilatata* is by far the most morphologically plastic species of the three.

3.3. Competition experiment (III)

3.3.1. Biomass

The general responses of all biomass fractions (total, fronds [leaf of the fern], rhizome and root biomass) to competition treatment were similar, but all biomass fractions differed among fern species. *D. expansa* had the lowest biomass (total and all fractions), while the biomasses of *D. carthusiana* and *D. dilatata* did not differ significantly (Fig. 1 a/III). Biomass was inversely related to neighbour density. A significant interaction was found between species and neighbour density. *D. carthusiana* and *D. dilatata* were less vulnerable to increasing neighbour density – a significant decrease in the biomass of target plants was observed from the 4n treatment upwards. *D. expansa* responded more strongly to increasing neighbour density. A significant decrease in biomass compared to the control was observed from the 2n treatment upwards.

3.3.2. Biomass ratios

D. carthusiana had a significantly higher root:frond ratio than *D. dilatata.* Increasing neighbour density increased the root:frond ratio and total below-ground:frond ratio, and there were also significant interactions between species and neighbour density. In the case of *D. carthusiana*, both the root:frond and total below-ground:frond ratio increased with increasing neighbour density up to the 4n treatment and then stabilized (Fig. 1 b/III). In the case of *D. expansa* and *D. dilatata*, both ratios increased up to the 4n treatment and then dropped strongly from 4n to 8n. As concerns the rhizome:frond ratio, *D. carthusiana* had

a significantly higher ratio than *D. expansa* or *D. dilatata*. The ratio did not change with neighbour density. The root:rhizome ratio was dependent only on neighbour density; it was significantly higher in the 4n treatment than in the control.

3.3.3. Morphological variables

D. expansa had shorter fronds and blades than *D. carthusiana* and *D. dilatata*. Increasing neighbour density significantly reduced frond and blade lengths; there was also a significant interaction between species and neighbour density. The frond and blade length of *D. carthusiana* and *D. dilatata* were reduced from the 4n treatment upwards, those of *D. expansa* from the 2n treatment.

The ratio between blade length and stipe length decreased significantly with increasing neighbour density. There were no significant differences between species, though a higher ratio of *D. dilatata* at the 8n treatment neighbour density became evident (Fig. 1 c/III).

There was a significant difference in the number of fronds among species. *D. expansa* had fewer fronds than *D. carthusiana* and *D. dilatata*. Increasing neighbour density reduced the number of fronds quite smoothly (Fig. 1 d/III). There was also a significant interaction between species and neighbour density. In the case of *D. expansa* and *D. carthusiana*, the neighbour effect became evident in the 4n treatment as a reduction in the number of fronds compared to the control. In the case of *D. dilatata*, no effect of neighbours was observed.

3.4. Comparison of reproductive capacity and vegetative growth (IV)

3.4.1. Vegetative growth and LER (leaf elongation rate)

In both 2004 and 2005, *D. carthusiana* and *D. dilatata* were characterised by longer fronds and by a higher number of fronds than *D. expansa* – all differences were significant except in the case of the length of fronds between *D. dilatata* and *D. expansa* in 2004. There were also differences in the timing of vegetative growth between species in 2004 – *D. carthusiana* had the longest period of intensive growth – the production of new fronds and the growth of the longest frond continued until September. *D. expansa* had the shortest period of intensive growth of the three species – the number of leaves only increased until July, and the length of the longest frond until August. Similar to *Dryopteris carthusiana*, *D. dilatata* produced new fronds until September; nevertheless, the growth period of the longest frond matched that of *D. expansa*, continuing until August.

Differences in LER were more distinct – significantly, *D. carthusiana* had the highest LER in 2004 (Fig. 1 a/IV) and *D. dilatata* in 2005 (Fig. 1 b/IV). Although the differences between the other two species were nonsignificant in both years, *D. carthusiana* had the lowest LER in 2005. *D. carthusiana* also had a significantly higher LER in August 2004, than the two other species. There were also differences in LER between 2004 and 2005. At the beginning of the experiment in 2004, LER dropped during July and rose to its peak in August, and dropped again at the end of the vegetation period. In 2005, LER was highest at the beginning of the vegetation period and fell gradually until the end of the period.

3.4.2. Morphological traits and biomass allocation

D. carthusiana had longer fronds (Fig. 2/IV) and stipes than the other two species, and longer blades at the end of the experiment (*at the final harvest*) than *D. expansa*. *D. carthusiana* and *D. dilatata* both had significantly higher biomass in regard to all fractions studied (total, frond [leaf of a fern], rhizome and root) and also larger blade area compared to *D. expansa*. There were no differences in SLA between species. The relative biomass allocation pattern was different between species – *D. expansa* allocated significantly more biomass to the rhizome and less to the blades than *D. dilatata* and *D. carthusiana* (Fig. 3/IV).

3.4.3. Reproductive traits

D. dilatata had the lowest proportion of generative individuals in the final harvest – 80.0%, whereas *D. expansa* and *D. carthusiana* had more – 93.3% and 86.7% respectively. *D. dilatata* had significantly less fertile fronds per generative individual than *D. carthusiana* by the end of the experiment, in October 2005 (Fig 4/IV). *D. dilatata* also had a smaller pinnae area covered with sori per generative individual at the final harvest compared to *D. carthusiana* and *D. expansa* (Fig. 5/IV). In the case of *D. carthusiana* and *D. dilatata*, vegetative reproduction was also observed – *D. carthusiana* had on average 1.07 and *D. dilatata* 0.07 vegetative offspring per plant individual. There was no difference among the species at the time the first fertile frond appeared – in the case of all three species, this event was registered in August 2005.

4. DISCUSSION

4.1. Population life stage structure and dynamics (I)

The population life stage structure and dynamics of three coinciding local sporophyte populations of *D. carthusiana*, *D. dilatata*, and *D. expansa* were studied in Estonia, at Õngu and Sääre, both on the Baltic island of Hiiumaa, and at Jäneda in north-central Estonia.

The density of ferns in the study sites was smallest in 2001, and increased significantly in 2002. In 2001 the precipitation recorded in the Hiiumaa study sites – the total annual precipitation (Table 2/I), 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 combined, data not shown) in the period when the ferns' spores ripen and germinate in Estonia (July-September) created particularly favourable moisture conditions for 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 relatively similar population stage structures – premature individuals and generative adults had quite similar proportions in populations, exceeding that of vegetative adults.

The density of vegetative adults in 2003 was significantly higher than in 2002. One explanation for this 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* (K.Rünk, personal observations). The very dry vegetation period in 2002 and the possible water deficiency in the period of the fronds' pre-formation may have inhibited the formation of sporangia in the next year's fronds. Also, as has been discovered in the case of *Asplenium scolopendrium*, fertile individuals may become sterile after a severe winter (Bremer, 1995), and the winter of 2002/2003 was the coldest since 1999 (data not shown).

The population stage structures of *D. expansa* at Jäneda and Õngu were quite similar, and corresponded to the general stage structure pattern described above, indicating the 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 in population stage structure 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 at 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 at this site, and the transition of some individuals between life stages had a very great impact on the whole life stage structure.

Even though the results show that the most widespread species in the region – *D. carthusiana* – was also locally the most abundant over the three study areas, its population stage structure was quite inconsistent between the sites. Although the density of *D. carthusiana* was lower at Sääre than at Jäneda, this species with a weak competitive response tolerates the pressure of bryophytes and could hold a stable population structure. The domination of the generative plants of *D. carthusiana* in local populations at Õngu and Sääre in 2002 could be explained by their rapid maturation. Fast-growing *D. carthusiana* plants frequently mature during their first year of life (K. 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. A similar population structure of *D. dilatata* – an excess of sterile plants over fertile ones – was observed in England (Willmot, 1985). The 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 area of distribution. Although the density of *D. dilatata* at Jäneda was the lowest compared with the other two species, the premature stage was well represented at the Jäneda site. Also, *D. dilatata* had a higher number of fertile fronds than *D. carthusiana*, the longest fronds among the three species studied over all sites, and its young sporophytes performed relatively well in a competition experiment (III).

The habitat that meets the requirements of the gametophytes or young sporophytes may be less suitable or not at all suitable for sporophytes. The simplest reason why the density of generative individuals may be lower than that of premature ones could be the unsuitable microhabitat in which sporophyte' rooting is impeded. The different life stages of pteridophytes could have also different freezing tolerance, as shown by a study of 14 cool temperate fern

species (Sato & Sakai, 1981). The younger stages – gametophytes of all species – were more cold tolerant than the older ones – sporophytes. One may hypothesize that the bottleneck in the expansion of local populations is not the younger, premature stage, but the generative one, which suffers due to edaphic or climatic factors.

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 at 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; Grime, 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 could be referred to as senile (Oostermeijer *et al*., 1992). Possible reasons for this may be unfavourable light and moisture conditions and the 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.

4.2. Biomass allocation pattern and phenotypic plasticity at different levels of light availability (II)

The poor survival and low vitality of the studied fern species in the full daylight treatment was not surprising. It has been shown that most modern ferns have actually diversified as understory species in the shadow of angiosperms and are thus true shade species (Schneider *et al*., 2004). In shade-tolerant species, reduced performance, decreased biomass and leaf damage is frequently observed when plants experience radiation stress due to an excess of photosynthetically active radiation and increased absorption of UV radiation (Demmig-Adams & Adams, 1992; Davidson *et al*., 1998, 2002; Olsen *et al*., 2002; Larcher, 2003). Given that *D. carthusiana* has been found to be more sensitive to water stress (Page, 1997) than the other two species, its higher mortality could be explained by the combined effect of both intense light and increased evapotranspiration. It should be noted here that, in this experiment, illumination should be treated as a complex factor, as it actually is in natural ecosystems, which is closely correlated with evaporation and transpiration intensities, the impact of wind, etc.

The comparison of total plant biomasses in different light treatments reveals a possible cause for the rarity of *D. dilatata* in the given climate – in more or less benign conditions (50% of full daylight) after one growing season, its total

biomass is nearly two times smaller than that of *D. expansa* and more than two times smaller than that of *D. carthusiana*. This evidently makes *D. dilatata* an inferior competitor in the young sporophyte stage in productive habitats with intense competition for light.

Graphs a, c and e in Fig. 1 (II) provide certain information about the possible optima for light availability in the three species. *D. expansa* appears to be the least shade tolerant, since its biomass in 25% illumination is only half of that in 50% illumination. The biomasses of the remaining two species do not differ much between 25% and 50% treatments. The comparison of *D. carthusiana* and *D. dilatata* shows that *D. dilatata* could be considered the more shade tolerant of the two, since it could produce nearly as much biomass in deep shade as in half daylight.

Surprisingly, all species demonstrated a steady decrease in the relative allocation to roots with improving illumination. This contradicts the usual response pattern in plants, where increased root growth is mostly induced by increased light. This trend most likely does not actually show a truly inverse plastic response to light, but simply indicates that in deep shade plants develop more slowly and are therefore ontogenetically younger (i.e. have relatively more roots) at harvesting than those in more illuminated conditions. Ontogenetic shifts towards lesser root growth have been observed in several species (Ledig *et al*., 1970; Hawthorn & Cavers, 1982; McConnaughay & Coleman, 1999). Also, in the competitive study (III), allocation to below-ground parts decreased with increasing neighbour density in both *D. expansa* and *D. dilatata*, in conditions where no extreme shade was imposed as a treatment. This shows that the usual plastic response to shading – decreased relative allocation to roots – is nevertheless present in the three fern species under observation.

In the relative plant biomass allocation pattern, the most notable difference among species was the relative share of biomass stored in belowground organs – specifically in rhizomes. In the two more common species this share was nearly constant and independent of the illumination conditions (ca 26% of total biomass). *D. dilatata*, in contrast, allocated very little biomass to its rhizome in deep shade but was able to increase this share more than twofold in 50% light. Such plasticity in allocation could be beneficial in competitive situations where an abrupt change of allocation strategy is clearly a property that can give a certain advantage in the struggle for mutual overtopping. Apparently *D. dilatata* has certain competitive disadvantages (poor initial growth in half-shade) as well as advantages (plastic allocation pattern), making the success of the species vulnerably dependent on the particular environmental situation.

The directions of autecological responses to the illumination treatment presented are conventional – in better light, plants had a greater number of thicker and relatively smaller fronds. At the same time, the specific leaf area (SLA) was a trait that varied independently of plant total biomass, showing that the effect of plant size on SLA was negligible, and the observed changes were

mostly true plastic responses. In mean blade area, passive plasticity to some extent overshadowed the true plasticity, and the even decrease in relative blade size with increasing illumination could be seen in all species only when the allometric effect of biomass was removed. The change in the number of fronds, in contrast, was mainly explainable through passive plasticity – after the effect of plant biomass was removed, there remained a great deal of unexplained variation and no clear response patterns. It is clear that the number of fronds was not a truly plastic trait in any of the species.

The change in the relative importance of blade as a vertical spacer (blade:stipe length ratio) along the illumination gradient was most pronounced in *D. dilatata* – this ratio increased steadily with increased illumination. In the remaining two species there was no difference between 10% and 50% light treatments. Figures 6 (II) and 7 (II) reveal the cause of the change in blade:stipe length ratio. Stipe length appeared to be largely independent of illumination in *D. carthusiana* and *D. expansa*, and shortened steeply with increased light in *D. dilatata*. At the same time, the blades of *D. carthusiana* and *D. expansa* slightly elongated with increasing light, while *D. dilatata* showed the opposite response – blades were clearly shorter in better light. Thus, in *D. carthusiana* and *D. expansa*, the observed increase in the blade:stipe length ratio was due to a slight increase in blade length with a simultaneous slight decrease in stipe length. In *D. dilatata,* both blade and stipe shortened with increasing light, and the intense response in the ratio of blade:stipe length was due to a considerably steeper decrease in blade length than in stipe length. Figure 7 b (II) shows that the ontogenetic part of the total plastic response was unidirectional (and matches the expectation from the earlier experience) in all three species – in better light there is less blade length per biomass unit in all species. Again, *D. dilatata* demonstrates the steepest reaction norm.

The results clearly show that the rare *D. dilatata* is by far the most morphologically plastic species of the three (Table 2/II). In terms of rhizome mass, below-ground:frond mass ratio, stipe length, as well as SLA, its plasticity (the slope of the reaction norm of the trait) is significantly higher than that of *D. carthusiana* or *D. expansa*. Additionally, the plasticity of *D. dilatata* (and *D. carthusiana*, although nonsignificantly) exceeds that of *D. expansa*, making the latter the least plastic species of the three. Again, *D. dilatata* demonstrates the active foraging strategy already observed in the previous competition experiment (III). The more plastic biomass allocation strategy of *D. dilatata*, when compared to the other two species, would possibly enable it to exploit a wider range of light environments, as well as different substrate and humidity conditions (Page, 1997).

4.3. Competitive ability (III)

In natural populations, fertile *D. carthusiana* individuals are significantly smaller than those of *D. dilatata*, but not those of *D. expansa*. In the competition experiment, young sporophytes of *D. expansa* had the smallest biomass parameters and frond number and length compared to *D. carthusiana* and *D. dilatata*. During the experimental period, *D. carthusiana* sporophytes on average reached 25% of their final natural frond length, while *D. expansa* reached 23% and *D. dilatata* only reached 20%.

The response to competition from neighbouring *Deschampsia flexuosa* individuals differs among the fern species. In the case of all biomass fractions (frond, rhizome, root, and total biomass) and length parameters (frond length, blade length), the species-specific responses to competition were similar. In the case of *D. expansa*, a decrease in biomass or length was already observed in the 2n (2 neighbouring plants) treatment, where the competitive effect was assumed to be relatively weak. In the case of *D. carthusiana* and *D. dilatata*, a negative response to neighbour density was only observed in the 4n (4 neighbouring plants) and 8n (8 neighbouring plants) treatment. Our results show that *D. expansa* is relatively more vulnerable to competition than *D. carthusiana* and *D. dilatata.*

As to biomass allocation pattern, *D. carthusiana* had larger relative allocation to the rhizome than the other two species, and a larger allocation to roots than *D. dilatata.* The rhizome:frond biomass ratio did not change under different neighbour density, so the response of the belowground:above-ground ratio to competition was due to changes in root biomass. In the case of *D. carthusiana*, root:frond ratio and total below-ground:frond ratio increase along the neighbour density gradient, while in *D. expansa* and *D. dilatata,* the ratios decreased from treatment 4n to 8n.

Plants respond to low nutrient availability by shifting the allocation of carbohydrates to below-ground organs, and to low light availability by allocating more biomass above-ground (Grace, 1997). Since resource availability is associated with ambient competitive pressure, release from competition may result in the re-arrangement of the allocation pattern (Lewis & Tanner, 2000). There is, however, little and mixed evidence on the influence of competition on allocation to above-ground tissues and below-ground organs (Nötzold *et al*., 1998; Cheplick & Chui, 2001; Cheplick & Gutierrez, 2000).

The increase in the root:frond ratio of all three fern species along the gradient of neighbour density indicated an increase in nutrient competition. The rapid decrease in the root:frond ratio of *D. expansa* and *D. dilatata* in the 8n treatment may be connected with the relative increase in the significance of light competition under high plant density. *D. carthusiana* lacked such a response, perhaps because of its light competition tolerance. The decrease in the blade length:stipe length ratio with increasing intensity of competition indicated

that within fronds, allocation is directed at a decrease in blade length rather than stipe length. The number of fronds per fern individual decreases only slightly when competition increases, suggesting that module size is more plastic than module number. One explanation may be the so-called organ preformation (Geber *et al*., 1997), which is common in many gymnosperm and angiosperm species, also including fronds of *D. carthusiana*, *D. dilatata* (Seifert, 1992), and *D. expansa* (K. Rünk, personal observations). In general, *D. dilatata* seems to represent the 'foraging type' of competitive response (Keddy *et al*., 1998) due to the increase of stipe length in the most crowded and shaded conditions. *D. carthusiana* evidently represents the transition between the 'foraging type' (increased allocation to roots in crowded conditions) and the 'persistence type' (high allocation to the rhizome in all neighbour densities).

The competitive responses of *D. carthusiana* and *D. expansa* were clearly different, and the more vulnerable species (*D. expansa*) was also less abundant than competition-tolerant *D. carthusiana*. The biomass of *D. carthusiana* was higher, and hence the competitive ability might also be higher than that of *D. expansa* all over the experimental light availability gradient (II). Neither of those two species is at their northern distribution limit in Estonia. Thus the scattered distribution and relatively low local and regional abundance of *D. expansa* may well be one of the consequences of the weak competitive ability of this species. *D. dilatata*, the rarest species in Estonia but the most common among the studied species in Central Europe, was as tolerant to competition in conditions of 35% light availability, probably near its light availability optimum, as the most frequent species in Estonia, *D. carthusiana*. Nevertheless, it is plausible that as *D. dilatata* had lower biomass than *D. carthusiana* in differently illuminated conditions (25% and 50% full daylight), the competitive ability of *D. dilatata* might also be lower. Consequently, the vulnerability of a species to competition may limit its regional distribution and local abundance, but the relationship between competitive ability and species abundance may also be conditional, depending on the particular species and on the local environmental conditions.

4.4. Vegetative growth and reproductive capacity (IV)

D. carthusiana showed stronger initial growth for a longer period of time than the other two species – the differences between the lengths of the longest frond were significant for almost the whole first vegetative period, until August 2004. The more vital growth of *D. carthusiana* in terms of the number of fronds and in the length of the longest frond at the beginning of the experiment resulted in the highest number of the longest fronds by the final harvest.

The high LER of young *D. carthusiana* individuals during the first vegetation period and particularly in August, after replantation, is probably one of

the crucial preconditions for its high abundance in natural ecosystems. Achieving higher fertility or utilizing more resources for reproduction could support why there was a reduced LER of *D. carthusiana* in 2005. The lower LER of all three species in July 2004, before replanting, is probably the result of competition between plants growing together in relatively small boxes. All morphological and biomass parameters registered at the end of the experiment showed the more vital growth of *D. carthusiana* than of *D. expansa* and *D. dilatata*. The individuals of *D. carthusiana* were significantly larger than that of *D. expansa*, though the differences with *D. dilatata* were in most cases nonsignificant.

According to the results of the experiment on light availability gradient (II), the total biomass of *D. dilatata* does not depend significantly on light conditions, and could only be as high as that of *D. carthusiana* in less illuminated conditions (10% of total daylight), when the biomass of the latter species is significantly decreased compared to the better illuminated conditions. As the biomass of *D. dilatata* does not change due to light conditions, the relative success of *D. dilatata* may depend mostly on the biomasses of neighbouring species. The lower total biomass of *D. dilatata* compared to *D. expansa* (and *D. carthusiana*), in more illuminated conditions (50%) could be connected with the different ploidy level and habitat requirements differentiation of *D. dilatata* and *D. expansa*. Diploid *D. expansa* is one of the parental species of allotetraploid *D. dilatata*. Moore (1977) has shown that hybrids are frequently less fit than their parents in parental habitats, but more fit than either parent in other habitats.

There was a significant difference between *D. expansa* and the other two species in relative biomass allocation, since *D. expansa* invested more biomass in its storage organ, the rhizome, and less in the blades. This fact may be connected with the habitat preferences of this species – better tolerance to severe climatic factors in the mountains or in extreme northern regions of Europe. In Scandinavia, the distribution limit of *D. expansa* is the northernmost of the three species (Jonsell, 2000). Above the timberline in the Polish Tatras, it reaches 2098 m a.s.l. (Piękoś-Mirkova, 1991).

Propagule availability may be an important factor determining the presence of a plant species in a particular site. The difference between numbers of propagules could explain the different distribution and abundance of species.

All of the registered generative reproduction parameters of *D. dilatata* were lower than those of the other two species or lower than that of *D. carthusiana* – *D. dilatata* had the lowest number of fertile (spore producing) individuals, less fertile fronds than *D. carthusiana*, and the lowest number of spores (the smallest area of pinnae covered with sori) at the end of the experiment. Such low fertility (reduction of fertility or even sterility toward their distribution limit) in some fern species has been registered near their distribution limit in Norway (Odland, 1998). At the same time, the illumination conditions of the

present experiment (35% of full daylight) were close to the probable autecological optima of *D. dilatata*, and its total biomass is as high as that of *D. carthusiana*. The lower fitness – generative reproduction capacity – resulting from the lower number of spores produced by *D. dilatata*, could be the main reason why the vegetatively vigorous species *D. dilatata* has the lowest regional abundance in Estonia, near its northerly distribution limit.

4.5. *Dryopteris carthusiana*

D. carthusiana is the most widespread of the three species on the global and European as well as on the regional scale, and is evenly distributed in Estonia (Kukk & Kull, 2005). The results of a three-year study of natural conditions on permanent plots also showed the highest overall local density of this species. In all experiments, *D. carthusiana* performed better than *D. expansa* or better than two other species in many respects. *D. carthusiana* had the highest total biomass in more illuminated conditions – in 25% and in 50% of full daylight and higher biomass and weaker competitive response than *D. expansa* in conditions of 35% illumination. In the first vegetation period in 2004 *D. carthusiana* had the highest LER and relatively longer-lasting and stronger growth than the other two species. By the end of the second vegetative period *D. carthusiana* had the higher number of longer fronds and higher total biomass than *D. expansa*, despite its slow LER in the second year.

D. carthusiana also matured first – spore-bearing fronds appeared at the end of the first vegetative period (competitive experiment [III], control treatment; data not shown) and had more vegetative offspring than *D. dilatata* by the end of second vegetative period. Other traits of reproductive capacity – the number of fertile fronds and the number of spores per generatative individual – were also highest among the three species, but the difference with *D. expansa* was nonsignificant.

In near-natural conditions – in interactions with *Deschampsia flexuosa*, *D. carthusiana* was able to stand against the competitive pressure of the graminoid species better than *D. expansa* (III). Although in permanent plots the length of the longest frond and the number of fertile fronds were not highest, *D. carthusiana* maintained its dominance over both other fern species in terms of number of fronds (I) in natural conditions and interactions with other species.

The high ability of *D. carthusiana* to self-fertilize (in experimental conditions 55% of gametophytes grown on soil and even 79% on decomposed wood formed sporophytes [Seifert, 1992]), and the consequently high potential for colonization (Flinn, 2006) may be the most important factor behind its broad distribution.

The vigorous initial growth in the first vegetative period, the larger biomass and therefore better competitive ability than *D. expansa* and *D. dilatata* in more

illuminated productive habitats, and also its high colonisation ability, are probably the other factors behind the highest local abundance and regional frequency of *D. carthusiana* among the three species in Estonia.

4.6. *Dryopteris expansa*

In Europe *D. expansa* is restricted to mountainous areas and distributed more north-easterly than *D. dilatata* and more northerly than *D. carthusiana*. In Europe, *D. expansa* is a less frequent species than *D. carthusiana*, and its area of distribution is smaller. In Estonia *D. expansa* is distributed in scattered localities throughout the country.

The local population density of *D. expansa* is lower than that of *D. carthusiana*. Although in nature individuals of *D. expansa* are the smallest of the three species, with the lowest number of fronds – the stable population structure (with similar proportions of premature individuals and generative adults exceeding that of vegetative adults) may be an indicator that suitable habitats for this species are present in the region.

D. expansa appears to be the least shade-tolerant of the three fern species – its total biomass in 10% and 25% illumination is only about half of that in 50% illumination. In better illuminated conditions, *D. expansa* had smaller total biomass than *D. carthusiana*, and thus possibly a stronger competitive response. In particular light conditions (35% of full light – probably near the light availability optima for *D. dilatata*) and in competition with neighbouring plants, *D. expansa* had the strongest competitive response and also smaller biomass than *D. dilatata*. Weaker competitive ability (possibly in combination with unfavourable light and moisture conditions), slower LER and shorter growth time in the first vegetation period of *D. expansa* than *D. carthusiana* may be not only the reason for interrupted regeneration in habitats with dense bryophyte cover and thus the overall low population density of *D. expansa* (e.g. in Sääre on the island of Hiiumaa) but also the lower population density of *D. expansa* than that of *D. carthusiana* throughout the region.

The higher light conditions optima than that of the other two fern species and the lowest mortality in full light conditions, changed and different relative biomass allocation (relatively more biomass was allocated into the rhizome than into the blades) by the end of the second vegetation period and the relatively short period of intense growth in the first vegetative period of *D. expansa* may also be connected with the habitat preferences of this species on a larger scale – better tolerance to severe climatic factors in the mountains or in the extreme northern regions of Europe.

Although the reproductive success of *D. expansa* in terms of fertile fronds, both in natural (data from permanent plots; I) and experimental conditions (IV), as well as the number of spores, were not lower than that of *D. carthusiana*, the

low mean intragametophytic selfing rate of 0.34 (Soltis & Soltis, 1987) and thus low colonization ability may have had an effect on the distribution frequency of the species.

Diploid *D. expansa* is probably the most ancient species, one of the ancestors of the allotetraploid *D. dilatata*, while the other ancestor is *D. intermedia*. The allotetraploid *D. carthusiana* originates from *D. intermedia* and *D. semicristata* (Gibby & Walker, 1977; Stein *et al*., 2002). Tetraploid fern species are generally larger (Page, 2002) and, due to heterosis, have higher rates of spore germination and faster growth rates (Kott & Peterson, 1974). Tetraploids usually have higher selfing rates and hence better colonizing ability (Seifert, 1992; Schneller & Holderegger, 1996; Soltis & Soltis, 2000; Trewick *et al*., 2002; Flinn, 2006).

The lower regional frequency and lower local density of diploid *D. expansa* in Estonia compared to tetraploid *D. carthusiana* could first of all be connected with their lower growth rate, low biomass and hence weak competitive ability during the young sporophyte stage, and may be caused by the diploid origin and mating system (comparatively low intragametophytic selfing rate) of the species, that may be related to the fact that diploid fern species can exhibit a higher level of inbreeding depression than their polyploid relatives (Masuyama & Watano, 1990).

4.7. *Dryopteris dilatata*

D. dilatata has the lowest regional frequency in Estonia. In contrast to *D. carthusiana* and *D. expansa*, the distribution limit of this species lies in Estonia or in the close proximity to Estonia, in the north-west (Hultén & Fries, 1986). Consequently, we may assume that factors and processes that limit the regional frequency of *D. dilatata* also determine its distribution limit. Considering the different aspects of the determination of the species border, three primary groups of circumstances should be taken into account – niches, spatial variation in environments, and dispersal (Brown & Lomolino, 1998). The exact position of the range boundary is determined by the interaction of the population processes of birth, death, and dispersal with the spatial and temporal variation in the environment (Brown *et al*., 1996). The local population density of *D. dilatata* was lower than that of the most common species *D. carthusiana* throughout the study area, but not lower than that of *D. expansa*. At two sites (Õngu, Jäneda), the population structure of *D. dilatata* was dominated by premature stages, indicating the dynamic status of these populations (I). In the case of ferns, the realized niches of two life stages should not absolutely overlap, therefore we hypothesized that the bottleneck in the expansion of local populations is not the younger, premature stage, but the generative one, which suffers due to edaphic or climatic factors.

The comparison of total biomasses in different light treatments revealed one more possible cause for the rarity of *D. dilatata* in the given climate – in more or less benign conditions (50% of full daylight) and after one growing season, its total biomass was nearly two times lower than that of *D. expansa* and more than two times lower than that of *D. carthusiana* (II). On the other hand, *D. dilatata* was the most shade-tolerant of the three species – it could produce nearly as much biomass in deep shade as in half daylight, and as much as the other two species. Also in shade of 65%, probably near its light optima, *D. dilatata* had an equally high biomass and hence should at that level of light conditions have had as high a competitive ability as *D. carthusiana* (III). Furthermore, relative irradiance reaching plants under the forests of the temperate zone is on average 3–10% (Larcher, 2003), i.e. the light conditions in which *D. dilatata* may be as vigorous in terms of biomass as the other two species. Indeed, the local densities of *D. dilatata* in all three research areas are lower than the density of *D. carthusiana* at the Jäneda site (I) alone. In addition, the more plastic biomass allocation strategy of *D. dilatata* compared to the other two species would possibly enable it to exploit a wider range of light environments, as well as different substrate and humidity conditions (Page, 1997).

D. dilatata individuals studied in natural populations were taller than individuals of the two other species, had more leaves than *D. expansa* and had more fertile leaves than *D. carthusiana*. Also, vigorous vegetative growth – the higher number of leaves and the higher total biomass of *D. dilatata* compared to *D. expansa*, although not different from *D. carthusiana* at the end of the comparative vegetative growth experiment, supports the assumption that under appropriate environmental conditions, *D. dilatata* would be as successful in Estonia in term of local abundance as *D. carthusiana* and *D. expansa*. The present study of the population and vegetative traits of three fern species could not find many reasons for the lower local abundance of *D. dilatata* than *D. carthusiana*: firstly the factor (probably edaphic or climatic) that limits the number of generative individuals in populations and comparatively low biomass traits (and hence low competitive ability) in light conditions of 25% and 50% of full daylight.

According to the metapopulation theory, a species occupies discrete suitable patches within a matrix of otherwise unsuitable habitats (Hanski, 1999). The distribution of a species may therefore be limited by the lesser number of suitable patches or by patches with lower quality at the periphery. In the case of the more or less stable distribution border of *D. dilatata*, the lack of suitable habitats may be the one reason why the regional frequency of the species is low. The lower production of dispersal propagules by occupied patches is another factor that may limit species distribution (Holt *et al*., 2005). Low fertility (the reduction of fertility or even sterility) toward their distribution limit in some fern species has been registered in Norway (Odland, 1998). Our experimental

results (IV) showed a similar pattern – all of the registered generative reproduction parameters of *D. dilatata* were lower than those of both other species – *D. dilatata* had the lowest number of fertile (spore producing) individuals and the lowest number of spores (the smallest area of pinnae covered with sori) by the end of the experiment. The number of fertile fronds per fertile individual of *D. dilatata* was also the lowest among three species, although the difference with *D. expansa* was not significant. The shorter intensive leaf growing period in the case of *D. dilatata* in the first vegetative period may indicate that the growth and development of spores could be interrupted by some climatic factor, despite the simultaneous appropriate conditions for the vital vegetative growth of *D. dilatata*.

Not only habitat quality and the low number of spores may limit the distribution of *D. dilatata*, but also the comparatively low self-fertilization rate (only 19.2% gametophytes on soil and 35.2% on decomposed wood produced sporophytes; Seifert, 1992) and therefore low colonization potential. The fact that even though the long-distance dispersal of fern spores is possible, over 90% of spores of *D. dilatata* in natural conditions were deposited within 3 m of sporophytes (Glaves, 1991), and this may explain the low frequency of this species in Estonia.

Although the brief duration and the methods of the present study do not make it possible to assess the dynamics of the distribution of *D. dilatata* in the region, the dynamic population structure and high plasticity of the species are good preconditions for the expansion of distribution. The data from 2003 (Blamey *et al*.) has already shown the expansion of the distribution of *D. dilatata* in Great Britain and Ireland during the last forty years. One reason behind the expansion of its distribution may be the relatively young age of *D. dilatata* (allotetraploid, originated from *D. expansa* and *D. intermedia*), and another explanation could be the expansion of this species due to climate warming, as already predicted by Bakkenes *et al*. (2002).

4.8. Suggestions for conservation

Only one of the three studied fern species – the relatively rare *D. dilatata* with its small and patchy populations – is included in the Red Data Book of Estonia (Lilleleht, 1998). None of the three species is protected by law in Estonia. By the time of the compiling of the last, third Estonian Red Data Book (1998), there was insufficient data to specify the exact degree of endangerment, and *D. dilatata* was specified as an ‘indeterminate species’. According to this study, the main threat to *D. dilatata* may be the strong change in light conditions in the habitats of this species. The experiment in light availability gradient (II) revealed a relative disadvantage of *D. dilatata* – its lower total biomass and hence lower competitive ability compared to other species in better-illuminated

conditions. Accordingly, the decline in the quality of habitats – the disappearance of canopy shade as a result of forestry activities e.g. after clear cutting, may be a serious threat to existing individuals and populations of *D. dilatata*. The reduction of suitable habitats for *D. dilatata* in the region as a result of the decrease in forest area by the intensive forestry in Estonia may endanger the existence of the species.

In summary, the present status (e.g. land ownership in localities, the possibility of human threats, population size, habitat conditions) of most of the populations of *D. dilatata* and hence the whole species in Estonia is still unclear. There is also no information about the long-term dynamics of the populations and population dynamics after the changes in environmental conditions. In order to assess the status of rare *D. dilatata* in Estonia and specify the exact Red List category, the necessity and level of legal protection, the corresponding analysis (the long-term population monitoring and inventory of the habitats) is required.

CONCLUSIONS

1. According to the present study, the local abundance of the most frequent species, *D. carthusiana*, was higher than the abundances of the regionally rare *D. dilatata* and the sparse *D. expansa*. In general, all fern species showed relatively similar population stage structures – premature individuals and generative adults had rather similar proportions in populations, exceeding that of vegetative adults. In the case of *D. expansa,* the population structure remained almost the same in sites and between years, and may thus serve as a template of the stable stage structure of a successfully performing fern species. In only one site, in Sääre on the island of Hiiumaa, where all three species more or less tolerated the competitive pressure of bryophytes, the premature stage was almost absent in this local population in the case of only one species – *D. expansa*. 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. 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.
2. Radiation stress in full daylight in experimental conditions caused poor survival and low vitality in all three species, although the effect varied between species and was strongest in the case of *D. carthusiana*. In different light conditions all three species performed differently – *D. expansa* was the least shade tolerant, since its biomass in 25% illumination is only half of that in 50% illumination, and *D. dilatata* was the most shade tolerant of the three – it could produce nearly as much biomass in 90% of shade as in half daylight. *D. carthusiana* performed better than the other two species in more illuminated conditions – in 25% and 50% of full daylight (its total biomass was the highest in both treatments) than in shade of 90%. In the relative plant biomass allocation pattern, the most notable difference among the species was the relative share of biomass stored in belowground organs – specifically in rhizomes. In the two more common species this share was nearly constant and independent of the illumination conditions (ca 26% of total biomass). *D. dilatata*, in contrast, allocated very little biomass to its rhizome in deep shade, but was able to increase this share more than twofold in 50% light. Such plasticity in allocation could be beneficial in competitive situations, where an abrupt change in allocation strategy is clearly a property that can provide a certain advantage in the struggle for mutual overtopping. The results clearly show that the rare *D. dilatata* is by far the most morphologically plastic species of the three. In terms of rhizome mass, below-

ground:frond mass ratio, stipe length, as well as SLA, its plasticity (the slope of the reaction norm of the trait) is significantly higher than that of *D. carthusiana* or *D. expansa*. The more plastic biomass allocation strategy of *D. dilatata* than the other two species would possibly enable it to exploit a wider range of light environments, as well as different substrate and humidity conditions.

3. The response to competition from neighbouring *Deschampsia flexuosa* individuals also differs between fern species. This experiment was performed in the fixed light conditions of 65% of shade. In the case of all biomass fractions (frond, rhizome, root, and total biomass) and length parameters (frond length, blade length), the species-specific responses to competition are similar. In the case of *D. expansa*, a decrease in biomass or length is already observed in the 2n treatment (2 neighbouring individuals), where the competitive effect is assumed to be relatively weak. In the case of *D. carthusiana* and *D. dilatata*, a negative response to neighbour density is only observed from the 4n treatment (4 neighbouring individuals) upwards. Our results show that in light conditions of 35% full daylight, *D. expansa* is relatively more vulnerable to competition than *D. carthusiana* and *D. dilatata.* In general, *D. dilatata* seems to represent the 'foraging type' of competitive response due to the increase in stipe length in the most crowded and shaded conditions. *D. carthusiana* evidently represents the transition between the 'foraging type' (increased allocation to roots in crowded conditions) and 'persistence type' (high allocation to the rhizome in all neighbour densities). It may concluded that in many cases the vulnerability of a species to competition may limit its regional frequency and local abundance, but the relationship between competitive ability and species abundance may also be conditional, depending on the particular species and on local environmental conditions.
4. The results of comparative vegetative growth showed the stronger initial growth of *D. carthusiana* for a longer period of time than the other two species – differences between the lengths of the longest frond were significant for almost the entire first vegetative period. The more vital growth of *D. carthusiana* than that of *D. expansa* in terms of the number of fronds and the length of the longest frond at the beginning of the experiment resulted in the higher number of the longer fronds by the final harvest. The high LER (leaf elongation rate) of young *D. carthusiana* individuals during the first vegetation period is probably one of the crucial preconditions for its high abundance in natural ecosystems. All morphological and biomass parameters registered at the end of the experiment showed the superiority of *D. carthusiana* over *D. expansa* and also *D. dilatata*. The individuals of *D. carthusiana* were significantly larger than of *D. expansa*, though the differences with *D. dilatata* were in most cases nonsignificant.

5. The differences between the experimental reproductive capacity of the three species were significant – almost all of the registered generative reproduction parameters of *D. dilatata* were lower than those of the two other species – *D. dilatata* had the lowest number of fertile (spore producing) individuals and the lowest number of spores (the smallest area of pinnae covered with sori) at the end of the experiment. *D. dilatata* also had less fertile fronds then *D. carthusiana*. Insufficient production of spores for the colonisation of new habitats may be the limiting factor for the distribution of the species.
6. *D. carthusiana*, the most frequent and locally abundant of the three *Dryopteris* species in Estonia, performed better than the two other species or better than *D. expansa* in all of our experiments in many respects. The vigorous initial growth in the first vegetative period on the one hand, the overall greater biomass and therefore better competitive ability than *D. expansa* and *D. dilatata*, but significantly in more illuminated productive habitats, as well the high generative and vegetative reproductive capacity, are probably the other factors behind the highest local abundance and regional frequency of *D. carthusiana* among the three species in Estonia.
7. *D. expansa* is distributed in Estonia in scattered localities throughout the country, and its local abundance is lower than that of *D. carthusiana*. The stable population structure (similar proportions of premature individuals and generative adults exceeding that of vegetative adults) may be an indicator of the existence of suitable habitats for this species in the region. The slower LER and shorter growth time in the first vegetation period, lower biomass and hence stronger competitive response than that of *D. carthusiana* may not be the only reason for the interrupted regeneration in habitats with dense bryophyte cover and thus overall low population density of *D. expansa*, but also the lower population density of *D. expansa* than *D. carthusiana* throughout the region. The higher light conditions optima than that of the other two fern species, different relative biomass allocation (relatively more biomass was allocated to the rhizome than to the blades) by the end of the second vegetation period and the relatively short period of intense growth in the first vegetative period of *D. expansa* may also be connected with the habitat preferences of this species – greater tolerance to severe climatic factors in mountains or in extreme northern regions of Europe.
8. *D. dilatata* has the lowest regional frequency in Estonia. In contrast to *D. carthusiana* and *D. expansa*, the distribution limit of this species lies in Estonia or in close proximity to Estonia. The local population density of *D. dilatata* was lower than that of the most common species *D. carthusiana* all over the study area, but not lower than that of *D. expansa*. Also, in experimental and natural conditions *D. dilatata* performed as well as *D. carthusiana* or at least as well as *D. expansa* in terms of biomass and morphological traits. In addition, *D. dilatata* was the most shade tolerant and

plastic species compared to the other two species. Nevertheless, the local abundance of *D. dilatata* may be limited by its comparatively low biomass and hence low competitive ability in conditions of 25% and 50%, as well by its generative population stage, which may suffer due to edaphic or climatic factors. Consequently, in the case of the more or less stable distribution border of *D. dilatata*, the lack of suitable habitats may be the one reason why the species' regional frequency is low. Despite its vigorous vegetative growth, *D. dilatata* showed a comparatively lower reproduction capacity in registered generative reproduction parameters than both of the other two species – *D. dilatata* had the lowest number of fertile (spore producing) individuals, the lowest number of spores (the smallest area of pinnae covered with sori), and a lower number of fertile fronds than *D. expansa* at the end of the experiment. The short intensive leaf growing period of *D. dilatata* in the first vegetative period may indicate that the growth and development of spores could be interrupted by some climatic factor, despite the simultaneous appropriate conditions for the vital vegetative growth of *D. dilatata*.

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SUMMARY IN ESTONIAN

KOLME SÕNAJALALIIGI: OHTESE SÕNAJALA *DRYOPTERIS CARTHUSIANA* (VILL.) H.P. FUCHS, LAIUVA SÕNAJALA *D. EXPANSA* (C. PRESL) FRASER-JENKINS & JERMY JA AUSTRIA SÕNAJALA *D. DILATATA* (HOFFM.) A. GRAY (DRYOPTERIDACEAE) VÕRDLEV ÖKOLOOGIA

Taimeökoloogia üheks põhieesmärgiks on uurida faktoreid ja protsesse ning leida seaduspärasusi, mis põhjustavad liikide erinevat levikut ning arvukust ruumis ja ajas. Erineva ruumilise skaala tasemega haruldaste, kas siis väikese levilaga ja/või vähese arvukusega liikide harulduse põhjuste väljaselgitamine on oluline ka nende praktilise, sageli just regionaalse (riigisisese) kaitse korraldamiseks. Üheks harulduse põhjuste uurimise meetodiks on erineva leviku ja/või arvukusega lähedaste liikide võrdlemine.

Kolm lähedase morfoloogia, päritolu ja ökoloogiaga sõnajalaliiki esinevad Eestis erineva sagedusega: tetraploidne ohtene sõnajalg *Dryopteris carthusiana* on tavaline liik, diploidset laiuvat sõnajalga *D. expansa* võib leida paiguti ja tetraploidne austria sõnajalg *D. dilatata* on haruldane. Ohtest sõnajalga on registreeritud (vähemalt üks kord alates 1970 aastast) 441 (86%) Eesti floora atlase 513 6 x 10' ruudus, laiuvat sõnajalga vastavalt 145 (27%) ja Austria sõnajalga 20 (4%) ruudus.

Käesoleva töö eesmärgiks oli uurida erinevate abiootiliste ning biootiliste tegurite mõju kolmele sõnajalaliigile ning hinnata nende tegurite mõju osatähtsust nende liikide erinevale esinemissagedusele. Aastatel 2001–2003 uuriti kolmel uurimisalal Eestis nimetatud liikide segapopulatsioonidesse rajatud prooviruutudel liikide populatsioone võrdlemaks populatsioonide arenguastmete struktuuri ja populatsioonistruktuuride fluktueerumist. Tulemused näitasid, et regionaalselt kõige sagedasem ohtene sõnajalg oli ka lokaalselt kõige arvukam, haruldast austria ja kohati kasvavat laiuvat sõnejalga oli vähem, kuid nende arvukus omavahel oluliselt ei erinenud. Üldiselt oli kõigil liikidel sarnane populatsioonistruktuur – juveniilseid ja generatiivseid isendeid oli võrdselt ning vegetatiivseid isendeid neist mõlemast vähem. Laiuva sõnajala selline populatsioonistruktuur jäi suhteliselt muutumatuks läbi aastate ja üle kohtade ning võib seega nendes tingimustes olla stabiilse populatsioonistruktuuri mudeliks. Vaid ühel uurimisalal, Säärel Hiiumaal, kus kõik kolm liiki kannatasid tõenäoliselt sammaltaimede tugeva konkurentse mõju tõttu, puudusid juveniilsed isendid laiuva sõnajala populatsioonist peaaegu täielikult. Austria sõnajala populatsioonistruktuur oli kõige dünaamilsem ja varieerus kohtade vahel. Õngul Hiiumaal, aga ka Jänedal Järvamaal domineerisid populatsioonis juveniilid, Säärel aga generatiivsed isendid. Võib oletada, et austria sõnajala arvukuse lokaalset suurenemist ei piira mitte juveniilne, vaid generatiivne arengustaadium, millele kasvukoht ei sobi – kas mõjub negatiivselt kohalik

mikrokliima või on edaafilised tingimused ebasobivad. Kuna sõnajalgade puhul võivad erineda kahe arengustaadiumi, eellehtede ja sporofüütide kasvukohanõudlusd, siis põhjuseks, miks sporofüüt ei saa kasvada seal, kus kasvas eelleht, võib lihtsalt olla juurdumisvõimaluse puudumine sporofüüdil kohas, kus kasvas eelleht.

Kolme liigi biomassi allokatsiooni ja morfoloogilist plastilisust valgusgradiendil uuriti potikatses, mis viidi läbi kolmes erineva varjutugevusega telgis (50%, 25% ja 10% valgust) ja täisvalguses. Täisvalgus mõjus kõikide liikide kasvule ja arengule negatiivselt, kuid kõige tugevamini ohtesele sõnajalale – selle liigi isenditest hukkus 90%. Erinevad valgustingimused mõjusid liikide biomassile ja morfoloogilistele tunnustele erinevalt. Biomassi suuruse järgi otsustades oli laiuv sõnajalg vähem varjutaluv ja austria sõnajalg kõige varjutaluvam kolmest liigist. Ohtene sõnajalg aga oli mõlemast liigist suurema kogubiomassiga valgemates tingimustes. Liikide biomassi allokatsioon maa-alustesse organitesse, eriti risoomi oli erinev – kui ohtene ja laiuv sõnajalg paigutasid risoomi püsivalt enam-vähem ühepalju biomassi (26% kogubiomassist), seda valgustingimustest sõltumata, siis austria sõnajalg paigutas vähema valguse tingimustes risoomi suhteliselt vähe biomassi, kuid oli võimeline paremates valgustingimustes (50% täisvalgusest) suurendama risoomi paigutatava biomassi ostähtsust rohkem kui kaks korda. Eksperimendi tulemused näitasid, et austria sõnajalg on plastilisem kui kaks teist liiki. Austria sõnajala risoomi massi, maa-aluse massi:lehemassi suhte, leherootsu pikkuse ja lehe eripinna plastilisus on oluliselt suurem kui ohtesel ja laiuval sõnajalal ning lehelaba pindala plastilisem kui laiuval sõnajalal. Selline plastiline biomassi allokatsioonistrateegia – võime valgustingimuste muutumisel kiiresti muuta suhtelist biomassi allokatsiooni võib osutuda liigile kasulikuks konkurentsitingimustes ning võimaldama austria sõnajalal kasvada erinevamate valgustingimustega, aga ka mulla ning niiskustingimustega kasvukohtades kui ohtesel ja laiuval sõnajalal.

Liikide konkurentsvõimet võrreldi potikatses, kus iga sõnajalaliigi üks noor isend kasvas potis kas üksinda, koos kahe, nelja või kaheksa võnk-kastevarre *Deschampsia flexuosa* isendiga. Katse viidi läbi eksperimentaalaias 65% varjuga telgis. Tulemused näitasid, et erinevate osabiomasside (lehe, leherootsu, risoomi) ja kogubiomassi ning morfoloogiliste parameetrite (lehe- ning lehelaba pikkuse) vastusmuster konkurentsi kasvule oli liigiti sarnane. Laiuv sõnajalg oli kõige tundlikum konkurentsi suhtes, biomassi ning pikkusparameetrite oluline vähenemine algas juba kahe naabertaimega konkureerides. Ohtene ja austria sõnajalg olid konkurentsile rohkem vastupidavamad, biomassi ja pikkusparameetrite vähenemine algas alles konkurentsis nelja naabertaimega. Seega võib laiuv sõnajalg keskmistes valgustingimustes (35% täisvalgust) olla konkurentsiõrnem kui tetraploidsed ohtene ja austria sõnajalg. Ohtese ja laiuva sõnajala erineva konkurentse vastusega võib seletada, miks on ohtese sõnajala regionaalne esinemissagedus suurem kui laiuval sõnajalal, kuna ohtese sõnajala bio-

mass ja seega tõenäoliselt ka konkurentsivõime olid laiuva sõnajala omadest suuremad ka kogu eksperimentaalsel valgusgradiendil. Austria sõnajalg, kes 35% valgustingimustes oli tõenäoliselt oma valgusoptimumi lähedal ja näitas ohtese sõnajalaga võrdselt tugevat konkurentsivõimet, mida ta aga ei pimedamates (25%) ega valgemates (50%) tingimustes tõenäoliselt oma väiksema biomassi tõttu ei suudaks. Seega võib katsetulemustest järeldada, et nõrk konkurentsivõime võib piirata liigi levikut, kuid seos konkurentsivõime ja liigi harulduse vahel võib olla ka tingimuslik, sõltudes konkreetsest liigist ja keskkonnatingimustest.

Kolme liigi vegetatiivse kasvu ja generatiivse paljunemisega seotud parameetreid võrreldi kaks vegetatsiooniperioodi kestnud potikatses aastatel 2004 ja 2005. Kõigi kolme liigi isendeid kasvatati katse algul laboris ning hiljem eksperimentaalaias 65% varjuga telgis. Tulemused näitasid, et ohtese sõnajala kasv katse algul jõulisem ja ajaliselt pikem kui laiuval ja austria sõnajalal – erinevused pikema lehe pikkuses olid olulised peaaegu kogu esimese vegetatsiooniperioodi jooksul. Katse lõpuks oli ohtesel sõnajalal suurem arv pikemaid lehti kui laiuval sõnajalal. Ohtese sõnajala suurim (kõige pikema) lehe kasvukiirus esimesel kasvuperioodil on tõenäoliselt üheks selle liigi kõrge arvukuse eelduseks looduslikes ökosüsteemides. Kõik morfoloogilisete ja biomassi tunnuste väärtused oli ohtesel sõnajalal samuti oluliselt kõrgemad kui laiuval sõnajalal ja enamus mitteoluliselt kõrgemad kui austria sõnajalal. Katse tulemuste järgi erinesid kolm liiki oluliselt oma generatiivselt paljunemisvõimelt. Peaaegu kõik tunnuste väärtused oli austria sõnajalal madalamad kui kahel teisel liigil. Katse lõpus oli austria sõnajalal kõige vähem fertiilseid (eoseid kandvaid) isendeid ja vähem eoseid (soorustega kaetud lehepind oli väiksem) fertiilse taime kohta. Ka oli austria sõnajalal vähem fertiilseid lehti isendi kohta kui ohtesel sõnajalal. Generatiivsete leviste, sõnajalgade puhul eoste vähene toodang võib olla oluliseks uute kasvukohtade kolonisatsiooni piiravaks teguriks.

Ohtene sõnajalg, kolmest liigist Eestis kõige sagedasem ja arvukam liik oli mõlemast teisest liigist või vähemalt laiuvast sõnajalast käesoleva töö tulemuste järgi mitme tunnuse järgi edukam. Ohtesel sõnajalal oli kõige jõulisem kasv esimesel kasvuaastal ning suurim kogubiomass kogu eksperimentaalsel valgusgradiendil, oluliselt laiuvast ja austria sõnajalast suurem just valgemates tingimustes. Ohtesel sõnajalal oli ekperimentaaltingimustes ka kõrge vegetatiivse ja hea generatiivse paljunemise võime – suurim tütartaimede arv ning austria sõnajalast rohkem eostega lehti ning eoseid. Kõik need omadused, aga tõenäoliselt ka suhteliselt parem kolonisatsioonivõime on tõenäoliselt selle liigi laiuvast sõnajalast laiema regionaalse leviku ja suurema lokaalse arvukuse taga.

Laiuv sõnajalg on Eestis väiksema levikusagedusega kui ohtene sõnajalg, samuti on väiksem liigi lokaalne arvukus. Laiuva sõnajala stabiilne populatsioonistruktuur, kus võrdse osatähtsusega juveniilseid ja generatiivseid isendeid on rohkem kui vegetatiivseid isendeid, võib viidata liigile sobivate kasvu-

kohtade olemasolule regioonis. Aeglasem lehe kasvukiirus ning lühem kasvuperiood esimesel aastal, väiksem biomass ja seega tõenäoliselt väiksem konkurentsivõime kui ohtesel sõnajalal võivad olla mitte ainult pidurdunud regeneratsioonivõime ja madalama arvukuse põhjusteks tiheda samblakattega kasvukohtades, vaid ka ohtesest sõnajalast madalama arvukuse põhjusteks üle kogu regiooni. Laiuva sõnajala kõrgem valgustingimuste optimum kui kahel teisel liigil, erinev biomassi allokatsioonistrateegia (biomassi paigutus enam risoomi kui lehelabadesse) teise kasvuaasta lõpuks ning suhteliselt lühike intensiivse kasvu periood esimesel aastal võivad olla seotud selle liigi kasvukohtadega mägedes, külmemates kliimatingimustes ja Euroopa äärmistes põhjapiirkondades.

Austria sõnajala regionaalne levikusagedus on madalaim kolme liigi hulgas. Erinevalt ohtesest ja laiuvast sõnajalast on austria sõnajalg Eestis oma levikupiiril või selle lähedal. Austria sõnajala üldine lokaalne arvukus oli madalam kui ohtesel sõnajalal, kuid mitte madalam laiuva sõnajala omast. Samuti olid austria sõnajala biomassi ning morfoloogiliste tunnuste väärtused nii eksperimentaal- kui ka looduslikes tingimustes sama kõrged kui ohtesel sõnajalal või vähemalt sama kõrged kui laiuval sõnajalal. Austria sõnajalg oli kolme liigi hulgas kõige varjutaluvam ja kõige plastilisem. Siiski, käesoleva töö tulemused näitavad, et austria sõnajala lokaalset arvukust võib piirata austria sõnajala ohtesest sõnajalast oluliselt väiksem biomassi ja seega tõenäoliselt ka väiksem konkurentsivõime valgemates tingimustes (25% ja 50% täisvalgust). Samuti võib austria sõnajala populatsioonistruktuur, kus kahel uurimisalal domineerisid juveniilsed isendid, viidata sellele, et liigi lokaalset arvukust ja levimist võib limiteerida generatiivne arengustaadium, mida piiravad mikroklimaatilised või edaafilised tegurid. Seega, juhul kui austria sõnajala areaalipiir on stabiilne võib liigi madala esinemissageduse üheks põhjuseks olla sobivate kasvukohtade puudus. Teiseks põhjuseks võib olla leviste puudus – vaatamata oma jõulisele vegetatiivsele kasvule oli austria sõnajala suhteline paljunemisvõime kõigi generatiivse paljunemise tunnuste järgi madalam kui kahel teisel liigil – tal oli madalaim fertiilsete isendite arv, väikseim eoste arv (eoslatega kaetud lehelaba pidala oli väikseim) ja väiksem fertiilsete lehtede arv kui laiuval sõnajalal eksperimendi lõpus. Austria sõnajala intensiivse kasvu periood oli esimesel kasvuaastal lühem ja võis katkeda mingi kliimafaktori mõju tõttu. Seega võib oletada, et kliimafaktor võib katkestada ka eoste normaalse arengu, isegi kui tingimused vegetatiivseks kasvuks on samal ajal veel sobivad.

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PUBLICATIONS

THE DIFFERENT REPRODUCTIVE CAPACITY OF THREE FERN SPECIES COULD HELP EXPLAIN THEIR VARYING REGIONAL ABUNDANCES

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ABSTRACT

Despite the large number of comparative studies on species with differing distribution and abundance, no clear general pattern of attributes explaining the species' rarity has yet been found. Although studies of regenerative traits of spore plants are extremely scarce, there is some evidence that rare spore plant species have lower fitness than common species. We were interested in whether the contrasting regional distribution patterns of three congeneric fern species – common *Dryopteris carthusiana,* scattered *D. expansa* and rare *D. dilatata* – could be explained by their different reproductive capacity. We grew the species in a garden experiment for two vegetation periods, until the first sporulation. *D. carthusiana* had larger biomass and longer dimensions than *D. expansa*. The highest LER and longest initial growth in the first vegetation period is probably one of the crucial preconditions for the high abundance of *D. carthusiana* in the natural ecosystems of Estonia. The different biomass allocation strategy of *D. expansa* – more biomass was invested into storage organ, rhizome, and less into blades – may be connected with the habitat preferences of this species and its better tolerance to a cold seasonal climate. *D. dilatata* did not differ from two other species, or even showed several higher values of vegetative growth and biomass parameters than *D. expansa*. Results differed in regard to reproductive parameters. The lower proportion of generative individuals, as well as the number of fertile fronds and spores among the three species could be reasons for the lowest regional abundance of *D. dilatata* in Estonia.

Keywords: *Dryopteris*, Rarity, Pteridophyte, Reproduction, Spore production

INTRODUCTION

The central goal of ecology is to detect which factors and mechanisms control the relative abundance and distribution of species (Kunin and Gaston, 1997; Crawley, 1997). Understanding why some species are more common than others provides us with basic information about the distribution and regional dynamics of different species and is, essential for the practical conservation management of rare species (species with a low relative abundance/ distribution).

One possible approach for investigating the mechanisms behind rarity is through the comparison of taxa with contrastingly different distribution and abundance patterns (e.g. Baskauf and Eicmeier, 1994; Sultan, 2001; Simon and Hay, 2003; Pohlman et al., 2005). The study of pairs or even larger numbers of closely related taxa helps to minimize the confounding effect of phylogenetic differences between species (Silvertown and Dodd, 1996; Gitzendanner and Soltis, 2000) and may reveal factors limiting rare species (Baskin and Baskin, 1986). Despite a large number of comparative studies on the subject (e.g. reviewed in Bevill and Louda, 1999; Binney and Bradfield, 2000; Brown et al., 2003; Rymer et al., 2005), no clear pattern of general attributes explaining species' rarity has yet been found. Nevertheless, evidence shows that rare flowering plant species exhibit lower fitness than common species, e.g. reduced amounts of viable pollen (Burne et al., 2003) and lower pollen viability (Banks, 1980), smaller seeds (Münzbergová, 2005), lower seed production per plant individual (Peat and Fitter, 1994; Eriksson and Jakobsson, 1998) or lower pollinator effectiveness (Rymer et al., 2005).

Analogous studies about spore plants, including ferns, are extremely scarce, but the results coincide with those of seed plants – rare mosses produce fewer spores than common ones (Hedderson, 1992). Accordingly, one may presume that the trait connected with reproduction may be crucial in controlling the relative abundance and distribution of species.

In order to estimate the spore production of fern species, two different methods have been used: (I) the direct counting of sporangia and the calculation of the number of spores (Farrar, 1976; Peck et al., 1990) and (II) the indirect estimation of spores on the basis of the volume of spores collected from fern individuals (Cousens, 1981), by counting the number of fertile leaves (Conway, 1957; Bremer, 1995) or by calculating the area covered by spores (Greer and McCarthy, 2000).

The current study is part of a larger project investigating three closely related co-occurring fern species – *Dryopteris carthusiana*, *D. expansa*, *D. dilatata* (Rünk, 2002; Rünk et al., 2004; Rünk et al., 2006; Rünk and Zobel, in press). The aim of the project is to specify what causes differences in the local and regional abundances of the three species. In this paper, we aim to test the hypothesis that the regionally rare species *D. dilatata* has a lower fitness than

the more common *D. expansa* and *D. carthusiana*. First of all, we were interested in the capacity of generative reproduction (quantity of spore production) of all three fern species. Secondly, we compared the time of the first maturation (emerging of sporangia) and production of vegetative offspring between *D. dilatata* and the other two species. Finally, we took measurements of individual fern specimens during the two-year experiment and at the time of the final harvest, which also allowed us to compare the vegetative growth, leaf elongation rate, biomass and morphological parameters of the three species.

MATERIAL AND METHODS

Study species

The three species studied are closely related from an evolutionary point of view (Gibby and Walker, 1977). They are also morphologically similar pteridophytes (Fraser-Jenkins and Reichstein, 1984; Page, 1997). Tetraploid (2n=164) *D. carthusiana* (Vill.) H.P. Fuchs is the most common of the three species, and it can be found throughout Europe, North America and Asia. 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 restricted to mountainous regions of Europe, and has a more northerly and easterly distribution than *Dyopteris dilatata*. *Dyopteris expansa* can also be found in North America and Asia. In Western and Central Europe, *D. dilatata* is a more common species than *D. expansa* (Fraser-Jenkins and Reichstein, 1984; Hultén and Fries, 1986; Fraser-Jenkins, 1993; Page, 1997). In Estonia the opposite 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. The regional abundance of *D. carthusiana* is the highest of the three species, and this species is evenly distributed across the country. According to the Atlas of the Estonian Flora (Kukk and Kull, 2005), *D. carthusiana* was recorded in 441, *D. expansa* in 145 and *D. dilatata* in 20 of the total of 513 unit (6 x 10 minute grid) squares covering Estonia. Similarly to its regional abundance, the local abundance (population density) of *D. carthusiana* is the highest among the three species as well (Rünk et al., 2006).

All three species are rhizomatous, medium-sized, herbaceous plants with 3-pinnate fronds and orbicular sori covered with a reniform indusium (Fraser-Jenkins, 1993). In Estonia all the species can be found growing in mesic woodlands (Rünk, 2002), frequently in mixed populations.

Species nomenclature follows Fraser-Jenkins 1993.

Experimental design

Species' traits with regards to vegetative growth, reproduction, morphology and biomass were assessed in a garden experiment conducted in 2004 and 2005. Spores of all fern species were collected in the wild in July 2003 and stored in a refrigerator (at 2±1ºC) until the beginning of the experiment. The substrate used for spore germination was sterilised and consisted of 3 parts horticultural peat and 1 part fine-grade sand. Spores were sown on October 20, 2003. Young fern sporophytes were first planted 9 individuals per box. They were spaced together evenly in plastic boxes (12x8x8 cm), on May 16, 2004. The specimens were replanted individually in plastic pots (10 cm diameter, 8 cm deep) on August 2. Initially all three species were represented by 60 replicates, but for the final harvest and analysis, 15 individual plant specimens per species were randomly selected.

The soil mixture consisted of 4 parts horticultural peat and 1 part fine-grade sand. The boxes were placed in a greenhouse at 22 ±2°C with a photoperiod of 12:12 h (fluorescent light: daylight tubes, photon flux density 40 μmol $s^{-1}m^{-2}$ and watered as required to keep the soil moist. On August 10 the pots were relocated to the experimental garden and grown in shaded light (screen with shade value 65%) another 14 months. As in Estonia, all three species can be found growing mainly in mesic woodlands, frequently in mixed populations, and a screen with shade value 65% was used for shading. Shade treatment was provided using a tent made of aluminium-coated shade cloth (spectrum neutral; Ludvig Svensson, Kinna, Sweden).

During winter 04/05, plants were covered with horticultural peat imitating fallen leaves and their decay.

The experimental garden was located in Tartu (58°21´25´´N, 26°42´5´´E, 68 m a.s.l.), in south-eastern Estonia, where the average annual temperature is 5.0°C and the average amount of annual precipitation is 550 mm (Jaagus, 1999).

Data collection

During both vegetation periods, a total of 9 measurements – 5 (1–5) in 2004 and 4 (6–9) in 2005, were performed every 28–34 days starting from June 9 2004 – in the case of each fern individual, the number of fronds was counted and the length of the longest frond was measured. In this case, the longest frond length was measured to the nearest millimetre. In generative individuals, the number of fertile (spore-bearing) fronds was also counted.

Leaf elongation rate (LER, mm/day) was recorded on each individual fern between the base of the stipe (stalk of the frond) and the tip of the longest frond by subtracting the result of the previous (e.g. first) measurement from the following (e.g. second) one and dividing the difference by the time period

(number of days) between the measurements. Measurements were calculated separately for 2004 and 2005. LER was recorded for all 7 periods between the measurements – 4 (1–4) for 2004 and 3 (5–7) for 2005.

After the final harvest in October 2005, three biomass fractions – fronds (fern leaves), rhizomes and roots – were separated and dried at 75ºC for 48 h. All biomass fractions were weighed separately. The length of all fronds and frond blades (the leafy part of the frond) were measured to the nearest millimetre just before the final harvest. The length of the stipe was obtained by subtracting blade length from frond length.

All three fern species: *D. carthusiana*, *D. dilatata* and *D. expansa* are sexually reproducing species (Manton, 1950) with sporangia that contain 64 spores (Schneller, 1975; Fraser-Jenkins and Reichstein, 1984) per sporangium. Consequently, the equal number of spores per sporangium enables us to compare the production of spores using the comparison of fertile areas (pinnae covered with sporangia), without counting the number of spores.

Blade area and blade area (pinnae) covered with sori was measured using a scanner (ScanJet5p), DeskScan II 2.9, and Pindala 1.0 software.

Specific blade area (specific leaf area, SLA) was calculated as blade area (cm^2) per unit of blade dry mass (g).

Statistical analysis

Differences in vegetative growth (the length of the longest frond and the number of fronds) in the years 2004 and 2005 were tested separately for each year with repeated measures of ANOVA (using the Statistica software version 6.0; StatSoft Inc., 1998) with species (three levels) as fixed factors and measurement time (five levels in 2004 and four levels in 2005) as a repeated factor.

Differences in LER (leaf elongation rate) between *D. carthusiana*, *D. dilatata* and *D. expansa* in the years 2004 and 2005 were tested separately for each year with repeated measures of ANOVA with species (three levels) as fixed factors and period of time between measurements (four levels in 2004 and three levels in 2005) as a repeated measurement factor.

Differences in morphological, biomass and reproductive parameters between *D. carthusiana*, *D. dilatata* and *D. expansa* in experimental garden experiment were tested by one-way ANOVA with species (three levels) as fixed factors.

All variables were log transformed, except in the case of relative biomass allocation, when the data (as proportions) was arcsine square root transformed.

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 and Rohlf, 1995).

RESULTS

Vegetative growth and LER (leaf elongation rate)

In both years 2004 and 2005, *D. carthusiana* and *D. dilatata* were characterised by longer fronds and by the higher number of fronds (Table I) than *D. expansa* – all differences were significant except in the case of the length of fronds between *D. dilatata* and *D. expansa* in 2004. There were also differences in the timing of vegetative growth between species in 2004 – *D. carthusiana* had the longest period of intensive growth. The production of new fronds and the growth of the longest frond continued until September. *D. expansa* had the shortest period of intensive growth of the three species – the number of leaves increased only until July and the length of the longest frond until August. Similar to *Dryopteris carthusiana*, *D. dilatata* produced new fronds up until September; however the growth period of the longest frond matched that of *D. expansa*, continuing until August.

Differences in LER (Table II) were more distinct – *D. carthusiana* had significantly the highest LER in 2004 (Fig. 1a) and *D. dilatata* in 2005 (Fig. 1b). Although the differences between the other two species were nonsignificant in both years, *D. carthusiana* had the lowest LER in 2005. *D. carthusiana* also had a significantly higher LER in August 2004, compared to the two other species. There were also differences in LER between 2004 and 2005. In the beginning of the experiment in 2004, LER dropped during July and rose to its peak in August and dropped again at the end of the vegetation period. In 2005, LER was the highest at the beginning of the vegetation period and fell gradually until the end of the period.

Table I. Results of repeated measures ANOVA: effects of species, measurement time and their interaction on the length of the longest frond and on the number of fronds of *Dryopteris carthusiana*, *D. expansa* and *D. dilatata* in 2004 and in 2005.

Source of variation	Species			Time			Species*time		
	Df	F	P	Df	F-ratio	P	Df	F	P
Length of the longest frond in 2004	2	4.47	0.019	4	291.56	<0.000	8	9.16	<0.000
Length of the longest frond in 2005	2	9.50	<0.000	3	528.74	<0.000	6	5.69	<0.000
Number of fronds in 2004	2	14.71	0.009	4	298.53	<0.000	8	3.50	0.001
Number of fronds in 2005	2	12.20	<0.000	3	238.25	<0.000	6	1.609	0.150

Table II. Results of repeated measures ANOVA: effects of species, period of time between measurements and their interaction on the LER of *Dryopteris carthusiana*, *D. expansa* and *D. dilatata* in 2004 and 2005.

Source of variation	Species			Time period			Species*time period		
	Df	F	P	Df	F	P	Df	F	P
LER 2004	2	8.717	<0.000	3	332.93	<0.000	6	3.216	0.006
LER 2005	2	12.17	0.000	2	76.8	<0.000	4	1.137	0.345

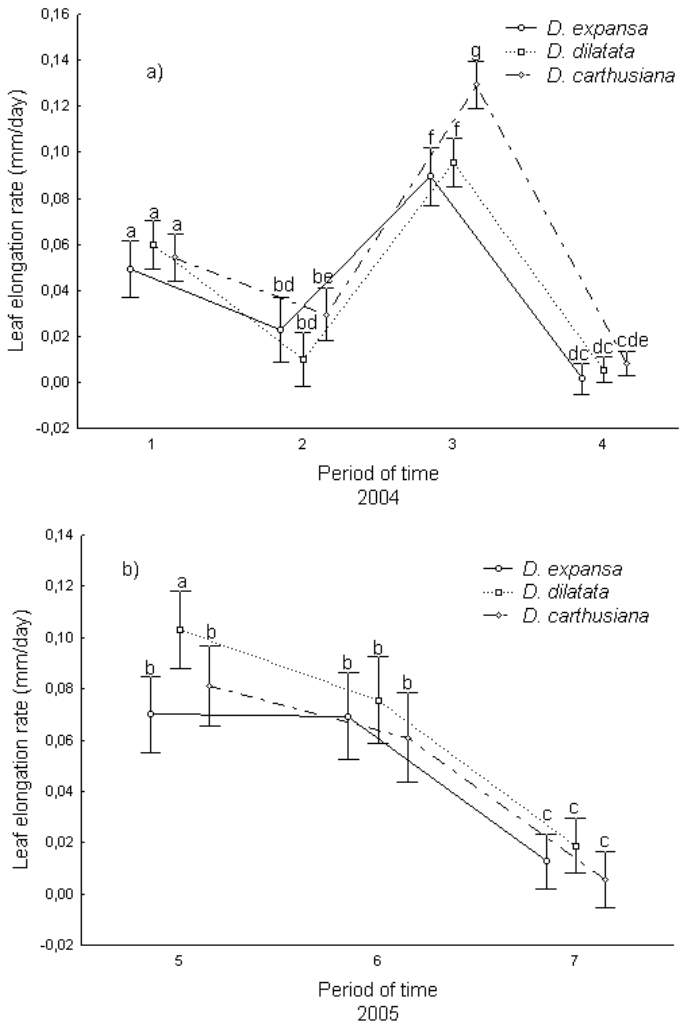

Figure 1. Mean ± SE of the LER (mm/day) of *Dryopteris expansa*, *D. dilatata* and *D. carthusiana* in time period 1 (9/6–9/7), 2 (9/7–9/8), 3 (9/9–10/9), 4 (10/9–8/10) in 2004 (a) and in time period 5 (22/6–27/7), 6 (27/7–25/8), 7 (25/8–30/9) in 2005 (b). Whiskers with the same letter are not significantly different ($p<0.05$, Tukey test).

Morphological traits and biomass allocation

The effects of species on the morphological traits and biomass allocation of *D. carthusiana*, *D. expansa* and *D. dilatata* are summarized in table III. *D. carthusiana* had longer fronds (Fig. 2) and stipes than the other two species, and longer blades at the end of the experiment (*at the final harvest*) than *Dryopteris expansa*. *Dryopteris carthusiana* and *D. dilatata* both had significantly higher biomass in regard to all fractions studied (total, frond, rhizome and root) and also larger blade area compared to *D. expansa*. There were no differences in SLA between species. The relative biomass allocation pattern was different between species – *D. expansa* allocated significantly more biomass into the rhizome and less into the blades than *D. dilatata* and *D. carthusiana* (Fig. 3).

Table III. Results of one-way ANOVA: effects of species on the morphological, biomass and reproductive traits of *Dryopteris carthusiana*, *D. expansa* and *D. dilatata*.

Source of variation	Species (Df=2)	
	F	P
Frond length	6.65	0.003
Blade length	4.51	0.017
Stipe length	23.93	<0.000
No of fertile fronds	3.754	0.033
Total mass	13.85	<0.000
Rhizome mass	5.968	0.005
Root mass	13.35	<0.000
Frond mass	17.67	<0.000
Relative biomass allocation to blade	14.20	<0.000
Relative biomass allocation to rhizome	13.97	<0.000
Blade area	22.91	<0.000
SLA	3.41	0.042
Pinnae area covered with sori	5.472	0.009

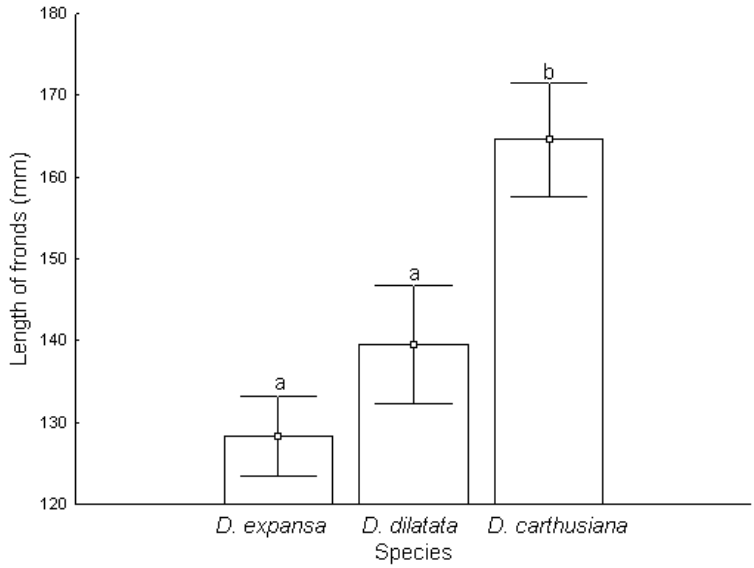

Figure 2. Mean ± SE of the mean length of the fronds per fern individual (mm) of *Dryopteris expansa*, *D. dilatata* and *D. carthusiana* at the final harvest. Bars with the same letter are not significantly different ($p<0.05$, Tukey test).

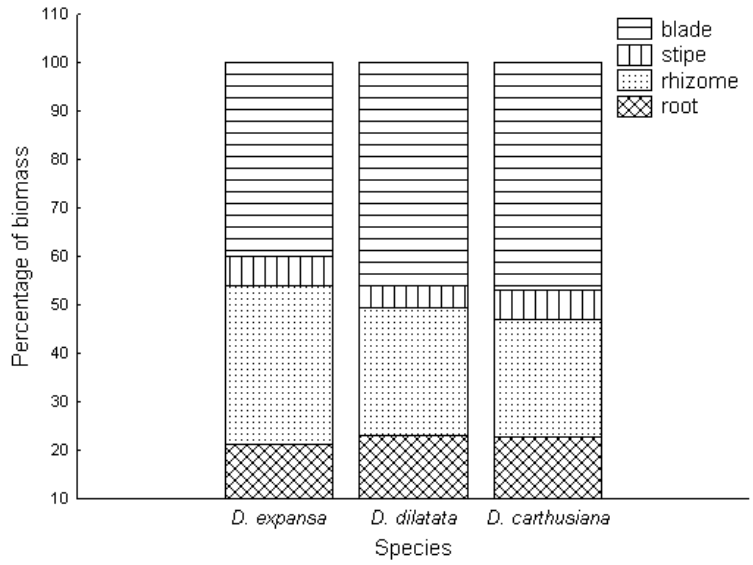

Figure 3. Absolute (a) and relative (b) mean biomass allocation pattern in *Dryopteris carthusiana*, *D. expansa* and *D. dilatata*.

Reproductive traits

D. dilatata had the lowest proportion of generative individuals in the final harvest – 80.0%, whereas *D. expansa* and *D. carthusiana* had more – 93.3 % and 86.7% respectively. *D. dilatata* had significantly less fertile fronds (Table III) per generative individual than *D. carthusiana* in October 2005, by the end of the experiment (Fig. 4). *D. dilatata* also had a smaller pinnae area covered with sori per generative individual (Table III) at the final harvest compared to *D. carthusiana* and *D. expansa* (Fig. 5). In the case of *D. carthusiana* and *D. dilatata*, vegetative reproduction was also observed – *D. carthusiana* had in average 1.07 and *D. dilatata* 0.07 vegetative offspring per plant individual. There was no difference among the species at the time when the first fertile frond appeared – in the case of all three species, it was registered in August 2005.

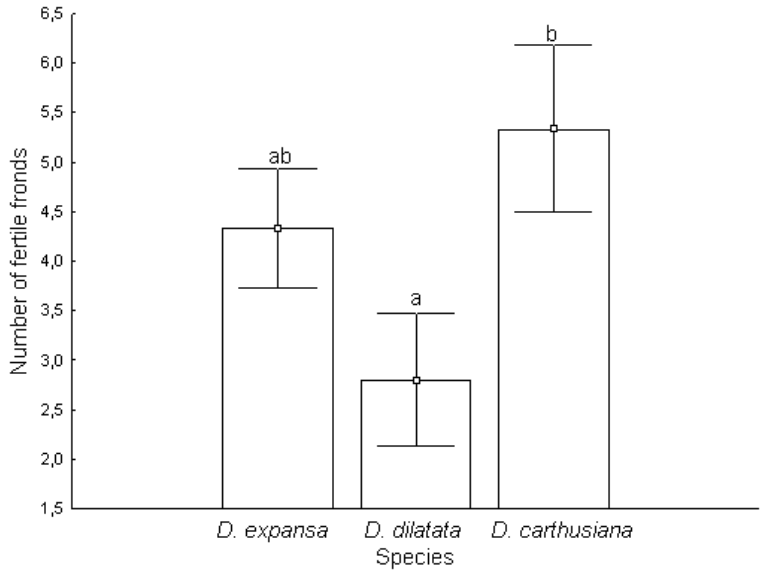

Figure 4. Mean ± SE of the number of fertile fronds per generative individual of *Dryopteris expansa*, *D. dilatata* and *D. carthusiana* at the final harvest. Bars with the same letter are not significantly different ($p<0.05$, Tukey test).

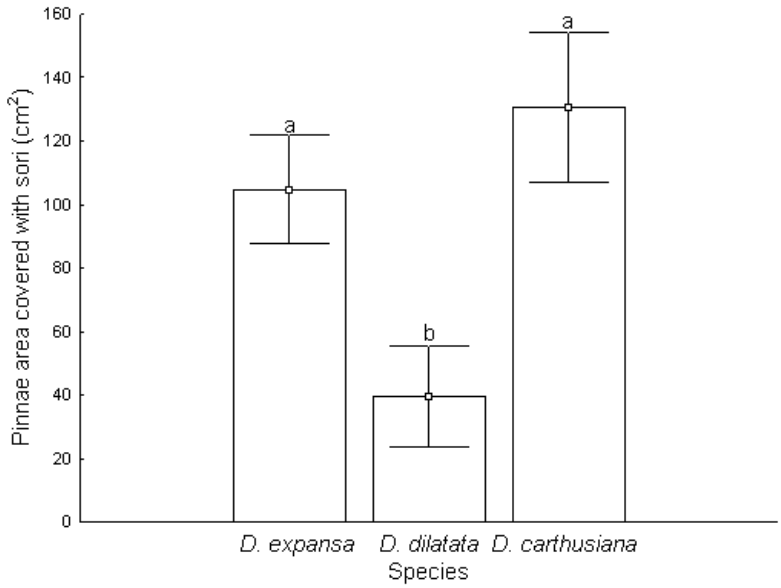

Figure 5. Mean ± SE of pinnae area covered with sori (cm²) per generative individual of *Dryopteris expansa*, *D. dilatata* and *D. carthusiana* at the final harvest. Bars with the same letter are not significantly different ($p<0.05$, Tukey test).

DISCUSSION

D. carthusiana showed stronger initial growth for a longer period of time than the other two species – the differences between the lengths of the longest frond were significant for almost the whole of the first vegetative period, until August 2004. The more vital growth of *D. carthusiana* in terms of the number of fronds and in the length of the longest frond at the beginning of the experiment resulted in the highest number of the longest fronds by the final harvest.

The high LER of young *D. carthusiana* individuals during the first vegetation period and particularly in August, after replanting, is probably one of the crucial preconditions for its high abundance in natural ecosystems. Achieving higher fertility or using more resources for reproduction could support why there was a reduced LER of *D. carthusiana* in 2005. The lower LER of all three species in July 2004, before replanting, is probably the result of competition between plants growing together in relatively small boxes. All morphological and biomass parameters, registered at the end of the experiment, showed the more vital growth of *D. carthusiana* than *D. expansa* and *D. dilatata* as well. The individuals of *D. carthusiana* were significantly larger than those of *D. expansa*, though the difference with *D. dilatata* was in some cases nonsignificant.

In all of our earlier experiments, *D. carthusiana* – the most abundant of the three species described by us on both a local (Rünk et al., 2006) and regional (Kukk and Kull, 2005) scale – was a superior species in many respects. *D. carthusiana* had a higher competitive ability (Rünk et al., 2004) and larger biomass in conditions of 25% and in 50%of full daylight (Rünk and Zobel, in press) than *D. expansa*.

Although none of the reproductive traits of *D. carthusiana* were significantly higher than that of *D. expansa* in this experiment, the high ability of *D. carthusiana* to self-fertilize (in experimental conditions 55% of gametophytes grown on soil and even 79% on decomposed wood formed sporophytes [Seifert, 1992]), and consequently high potential for colonization (Flinn, 2006) may be the key factor behind its broad distribution.

The relatively high leaf elongation rate in the first vegetation period, the high values of the vegetative parameters in different light conditions and hence high competitive ability on the one hand, and the high potential for colonisation on the other, are probably the main factors behind the highest local and regional frequency of *D. carthusiana* of the three species.

The results of the present experiment showed the lower values of the vegetative growth of *D. expansa* in both years of the experiment compared to the other two species, and the smallest biomass parameters at the end of the experiment.

D. expansa appears to be the least shade tolerant of the three fern species – its total biomass in 10 % and 25 % illumination is only about half of that in 50% illumination (Rünk and Zobel, in press). *D. expansa* had lower total biomass than that of *D. carthusiana* in all experimental light conditions, but significantly lower in better illuminated conditions, and thus possibly a stronger competitive response. In particular light conditions (35 % of full light – probably near the light availability optima for *D. dilatata*) as in present experiment and in competition with neighbouring plants (Rünk et al., 2004), *D. expansa* had the strongest competitive response and also lower biomass than *D. dilatata*.

There was a significant difference between *D. expansa* and the other two species in terms of relative biomass allocation, since *D. expansa* invested more biomass in its storage organ, the rhizome, and less in the blades. This fact may be connected with the habitat preferences of this species – better tolerance to severe climatic factors in mountains or in extreme northern regions of Europe. In Scandinavia, the distribution limit of *D. expansa* is the northernmost of the three species (Jonsell, 2000). Above the timberline in the Polish Tatras, it reaches 2098 m a.s.l. (Piękoś-Mirkova, 1991).

Although the reproductive success of *D. expansa* in terms of fertile fronds, both in natural (data from permanent plots; Rünk et al., 2006) and experimental conditions, as well as in the number of spores, were not lower than that of *D. carthusiana*, the low mean intragametophytic selfing rate of 0.34 (Soltis and

Soltis, 1987) and thus low colonization ability may have had an effect on the distribution frequency of the species.

The lower regional frequency and lower local density (Rünk et al., 2006) of diploid *D. expansa* in Estonia compared to tetraploid *D. carthusiana* could first of all be connected with the lower growth rate, low biomass and hence weak competitive ability during the young sporophyte stage, and may be caused by the diploid origin and mating system (comparatively low intragametophytic selfing rate) of the species, which may be related to the fact that diploid fern species can exhibit a higher level of inbreeding depression than their polyploid relatives (Masuyama and Watano, 1990).

In contrast to *D. carthusiana* and *D. expansa*, the distribution limit of rare species *D. dilatata* lies in Estonia or in the close proximity to Estonia, in the north-west (Hultén and Fries, 1986). Consequently, we may assume that the factors and processes that limit the regional frequency of *D. dilatata* determine its limit of distribution too. Considering the different aspects of the determination of the species border, three main groups of circumstances should be taken into account – niches, spatial variation in environments, and dispersal (Brown and Lomolino, 1998).

The results of this experiment showed that the vegetative growth of rare *D. dilatata* did not significantly differ from the growth of *D. carthusiana*. In addition, *D. dilatata* also had more and longer fronds than *D. expansa* in the second year of the experiment. Even if the LER of *D. dilatata* was lower than that of *D. carthusiana* in the first year of the experiment, in the second year the LER of *D. dilatata* was the highest of the three. Both *D. dilatata* and *D. carthusiana* exceeded *D. expansa* in terms of all observed biomass parameters in the present experiment with fixed (35% of full daylight) light conditions. The comparison of total biomasses in different light treatments (Rünk and Zobel, in press) revealed one more possible cause for the rarity of *D. dilatata* in the given climate – in more or less benign conditions (50% of full daylight) and after one growing season, its total biomass was nearly two times lower than that of *D. expansa* and more than two times lower than that of *D. carthusiana.* In reality the relative irradiance that reaches plants under the forests of the temperate zone is on average 3–10% (Larcher, 2003) – the light conditions in which *D. dilatata* may be as vigorous in terms of biomass as other two species. Indeed, our three-year study (Rünk et al., 2006) on permanent plots of mixed populations of three species showed that the local abundance of *D. dilatata* did not differ from *D. expansa*, although it was lower than *D. carthusiana*. Also, vigorous vegetative growth – the higher number of leaves and the higher total biomass of *D. dilatata* compared to *D. expansa*, although not different from *D. carthusiana* at the end of the present experiment, supports the assumption that under appropriate environmental conditions, *D. dilatata* would be as successful in Estonia as *D. carthusiana* and *D. expansa*.

According to metapopulation theory, a species occupies discrete suitable patches within a matrix of otherwise unsuitable habitats (Hanski, 1999). The distribution of a species may therefore be limited by the lesser number of suitable patches or by patches with lower quality at the periphery. In the case of the more or less stable distribution border of *D. dilatata*, the lack of suitable habitats may be the one reason why the regional frequency of the species is low. The lower production of dispersal propagules by occupied patches is another factor that may limit species distribution (Holt et al., 2005).

Low fertility (reduction of fertility or even sterility) toward their distribution limit in some fern species has been registered in Norway (Odland, 1998). Our experimental results showed a similar pattern – all of the registered generative reproduction parameters of *D. dilatata* were lower than those of both other species – *D. dilatata* had the lowest number of fertile (spore producing) individuals and the lowest number of spores (the smallest area of pinnae covered with sori) at the end of the experiment. The number of fertile fronds per fertile individual of *D. dilatata* was also the lowest of the three species, although the difference with *D. expansa* was not significant. The shorter intensive leaf growing period in the case of *D. dilatata* in the first vegetative period may indicate that the growth and development of spores could be interrupted by some climatic factor, despite the simultaneous appropriate conditions for the vital vegetative growth of *D. dilatata*.

Not only the habitat quality and low number of spores may limit the distribution of *D. dilatata*, but also its comparatively low self-fertilization rate (only 19.2 % gametophytes on soil and 35.2 % on decomposed wood produced sporophytes; Seifert, 1992) and therefore low colonization potential. The fact that even though long-distance dispersal of fern spores is possible, over 90% of spores of *D. dilatata* in natural conditions were deposited within 3 m of sporophytes (Glaves, 1991) may also have an effect on the frequency of this species in Estonia.

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