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Ecology and Syntaxonomy of *Gymnocarpium dryopteris* L. in the Netherlands

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ABSTRACT.—Ecology, syntaxonomy and population size of *Gymnocarpium dryopteris* have been studied, especially during the period 1979–1991 by collecting data on 419 colonies in the Kuinderbos (a planted woodland in the Noordoostpolder, a polder reclaimed from the former Zuiderzee in 1942) and 74 colonies elsewhere in the Netherlands. In this paper the Kuinderbos population is compared with other Dutch populations (pleistocene area) in order to provide more insights in the ecology of the species and circumstances facilitating high density. Populations in Germany were studied as reference. In the period 1979–1991 the species was recorded in the Netherlands with at least 670 colonies, of which 89% are in the Kuinderbos. *Gymnocarpium dryopteris* prefers shadowed ditches and drainage trenches, but can grow at various other habitats as well. Especially at the western and southern part of the Netherlands, the species grows on canal walls. Sites with *Gymnocarpium dryopteris* belong to different communities. In the Kuinderbos stands of *Picea sitchensis* are preferred, while elsewhere in the Netherlands the species prefers the *Quercion roboris-petrae* (*Fago-Quercetum*) or *Pseudotsuga mensiezii*-stands. *Gymnocarpium dryopteris* is accompanied by 14 fern species, at the Kuinderbos by 12 fern species, with *Athyrium filix-femina* as characteristic species, often indicating potential sites. Rhizomes are shallow creeping, at average 2.6 cm below the surface (0.5–8 cm). It grows in the ecto-organic layer or just below this layer. At trench sides it often grows in the mineral layer. Most colonies are within the influence of the watertable. The Dutch colonies are small and colonies with more than 1000 fronds are rare. This probably indicates that most colonies are less than 20 years old. Colonies with more than 100 fronds are often fertile, with less than 20% of the fronds bearing sori. At the wall habitat small-sized individuals may be fertile as well. The high density in the Kuinderbos can be attributed to an optimal water supply from a peat subsoil, the composition of the ecto-organic layer consisting of *Picea* needles and an optimal light climate. The high density in *Picea sitchensis* within the Kuinderbos is unprecedented in Europe and makes these stands resemble the natural habitat of *Picea sitchensis* at the west coast of N. America.

KEY WORDS.—*Gymnocarpium*, syntaxonomy, ecology

Though *Gymnocarpium dryopteris* L. is one of the rarest fern species in the Netherlands (Mennema *et al.*, 1985), it is not endangered (van der Meijden *et al.*, 2000). Since 1979, many new sites of this species have been discovered, the most important being in the Kuinderbos, one of the woodlands planted in the former Zuiderzee (Noordoostpolder). The large number of sites where the density of the species is locally high has provided an opportunity to describe the ecology of the species in this woodland (Bremer, 1980; Bremer, 2007). In the Kuinderbos, *G. dryopteris* is closely associated with *Picea sitchensis* (Bong.) Carrière, whereas elsewhere in the Netherlands the species has been recorded in woodlands, on stream banks and sometimes from unlikely habitats, such as canal walls (Weevers *et al.*, 1948; van Ooststroom, 1973).

This raised the question: what are the optimal ecological conditions for *G. dryopteris* in the Netherlands to develop and form large patches?

First, it was important to do a thorough ecological study of the large population in the Kuinderbos. Subsequently a more detailed study of colonies elsewhere in the Netherlands was initiated, to ascertain the conditions under which the species is able to establish but is seldom able to form a population of appreciable size, and also to look at the types of vegetation in which *G. dryopteris* occurs. It is the composition of the vegetation and the abundance of its constituent species that provide information about the abiotic conditions and management (e. g., Grootjans, 1985; Schaminée *et al.*, 1995), in so far that constraints to dispersion do not strongly influence the composition of the vegetation, and provided the communities are saturated (no impact of seed or spore limitation). When comparing populations, aspects of performance were also considered, measured from the size and fertility of the colonies. It is the small and young colonies that provide information about the potential for establishment: the microhabitat in which they have established is often still discernable in the field. The colonies that have been able to survive in certain places for a long time yield different information. The environment in which prothallia can establish successfully may differ greatly from the environment of the mature colonies, as is the case for *Pteridium aquilinum* (L.) Kuhn (Page, 1982).

MATERIAL AND METHODS

A questionnaire on the characteristics of the locality and site was compiled and sent out to botanists and vegetation scientists who had sent in observations to the National Herbarium (Leiden University). In total, 26 respondents completed the questionnaire or supplied other information. In addition, documentation at the National Herbarium was consulted – including the descriptions in the herbarium collection. I visited 60% of the sites in the Netherlands where the species has been found and described them. Most of the data on the Kuinderbos were collected in 1979 (Bremer, 1980). Data on the other sites elsewhere in the Netherlands were collected from 1979 to 1990.

In the field the composition of the tree layer was noted. The soil composition was determined by taking multiple samples of the top 30 cm with a soil auger and describing the soil composition (e.g., Wiggers *et al.*, 1962). The pH was determined at 28 locations from soil collected from the root zone (ecto-organic layer plus soil from the underlying 5 cm layer). This entailed collecting 15 g of soil and mixing it with 20 ml of distilled water (pH H₂O) in the laboratory. The next day the mixture was shaken and then analyzed. The pH-KCl was measured after adding 2.5 ml 1 N KCl. The thickness and composition of the ecto-organic layer were determined by carefully scraping off this layer several times in each colony (Klinka *et al.*, 1981). In the Kuinderbos, the water table was determined from the water levels in piezometers (filter at 80–100 cm). Elsewhere, the mean highest water table (MHWT) was estimated from the water table in nearby watercourses or using soil features (rust phenomena).

The associated fern species were those within a radius of 3 m from the edge of a patch. If there were microtopographic differences in the site (as was

particularly the case in drainage trenches) slope was measured with a clinometer. Aspect was determined from the topographical map. In all colonies the number of fronds colony⁻¹ and the number of fertile fronds were counted. The data supplied by respondents were not always complete. This accounts for the differences between the numbers of colonies for which data on the aforementioned parameters are available.

Vegetation relevés were made in the habitats the species had been found ($n = 37$ sites). In woodlands these relevés were 10×15 m in size, in other habitats smaller. Data were analysed with TWINSPAN (Hill, 1979). Twinspan analyzes sets of relevés by calculating the similarity between all possible combinations. Relevés with high level of similarity are grouped in the same cluster and later on syntaxonomically interpreted.

Data on vegetation and other aspects were also collected from colonies in four mountain areas in Germany (Harz, Weserbergland, Teutenergebirge, Allgäu). Chi-square tests were used to compare the actual distributions of *G. dryopteris* over various habitats versus those that would be predicted. The scientific names in this paper are based on van der Meijden (2005).

RESULTS

Ecology.—*Gymnocarpium dryopteris* can be found in a large number of different habitats in the Netherlands (Table 1). There are significant differences in the distribution of the sites over the various habitats in the Netherlands prior to and since 1979 ($\chi^2 = 52.8$, $p < 0.001$, d.f. = 5). Prior to 1979, the species was found in a larger number of different habitats. In the period since 1979, the habitat preference in the Kuinderbos has been very different to that elsewhere in the Netherlands ($\chi^2 = 305.0$, $p < 0.001$, d.f. = 8); it is strongly related to the great preference in the Kuinderbos for trenched coniferous woodland. *Gymnocarpium dryopteris* occurs mostly in locations with some differences in microtopographic position: this applies to 89% of the clones in the Kuinderbos and 75% of the clones elsewhere in the Netherlands. The differences in microtopographic position are often associated with sides of trenches, but this category also includes walls. In the past, the species has also been recorded on pollarded willows, in wells and on wooded banks, but there have been no recent sightings in these habitats. Only since 1984 have individual specimens been recorded growing between the basalt blocks on former sea dikes (Lauwersmeer and IJsselmeer dikes: van der Ploeg, 1984).

In the Netherlands, *G. dryopteris* occurs most in stands of *Pseudotsuga menziesii* (Mirb.) Franco and *Quercus robur* L. Eighty seven percent of sites in the west and south of the Netherlands have something to do with walls ($n = 15$). In the Kuinderbos, 79% of the clones were found under *Picea sitchensis* (Table 2). The distribution over Kuinderbos sites with different tree species is significantly different from that elsewhere in the Netherlands (period 1979–1981) ($\chi^2 = 289.1$, $p < 0.001$, d.f. = 5). For the entire country and the period 1979–1991, two clones (3.1%) occurred under *Fagus sylvatica* L. In the Kuinderbos there was also a different preference in relation to the distribution

TABLE 1. Habitat preference of *Gymnocarpium dryopteris* in the Netherlands. The table shows the number of colonies per habitat. A distinction is made between populations that disappeared prior to 1979 and have not been recorded since, populations present in the period 1979–1991 (Pleistocene area in particular) and populations in the Kuinderbos (benchmark population: the entire population in 1979) (Values ≤ 3 were clustered in the chi-square analysis in order to fulfil the requirements of this test).

	Pleistocene area				Kuinderbos	
	Number of colonies before 1979	%	Number of colonies 1979–1991	%	Number of colonies in 1979	%
Soil under conifer stands			6	9.2	57	13.6
Soil under broadleaved stands			9	13.8	1	0.2
Trench in coniferous woodland			9	13.8	347	82.8
Trench in deciduous woodland			1	1.5	14	3.3
Not shaded ditch/drainage trench			10	15.4	-	
<i>subtotal woodlands/trench</i>	24	35.8	35	53.7		
Stream	8	11.9	8	12.3	-	
Canal wall/quay wall	16	23.9	8	12.3	-	
Brick wall (dry)	8	11.9	2	3.1	-	
Basalt dike	-		9	13.8	-	
Roadside verge	-		3	4.6	-	
Wooded bank	3	4.5	-		-	
Drainage canal	2	3.0	-		-	
Pollarded willow	2	3.0	-		-	
Well	2	3.0	-		-	
Hollow way	1	1.5	-		-	
Edge of steep drop	1	1.5	-		-	
<i>Total</i>	67	100	65	100	419	100

of the top 10 cm of soil compared with the rest of the Netherlands ($\chi^2 = 105.2$, $p < 0.001$, d.f. = 9) (Table 3). In the Netherlands, *G. dryopteris* occurs most often on moderately fine, coarse and loamy sandy soils, whereas in the Kuinderbos the soil composition is humic to peaty fine sand. Outside the Kuinderbos the soil is lime-poor with a measured pH-KCl of $3.9 (\pm 1.0, n = 12)$. In the Kuinderbos the fine sand is always calcareous, whereas peat and clay are lime-poor. In 52 of the 141 sites studied where clones were found, limy material occurred in the top 10 cm (Bremer 1980) and the mean pH-KCl was $6.6 (\pm 0.9, n = 16)$.

The average maximum thickness of the ecto-organic layer within patches is 4.7 cm outside the Kuinderbos but 1.5 cm in the Kuinderbos (Table 4). The difference is not statistically significant ($\chi^2 = 9.2$, $p = 0.06$, d.f. = 4). The thin average ecto-organic layer in the Kuinderbos is associated with the marked preference for trench banks. On these banks the ecto-organic layer is either less developed or is absent due to land slip, while litter decomposition is faster because the pH is high. Here, the rhizomes are at a shallow depth in a basic soil, whereas at the top of the trench, fronds of the same clone are usually growing in the ecto-organic layer, where the pH is much lower (Table 5). Elsewhere in the Netherlands, the pH at the top of trenches and on the trench sides is low.

TABLE 2. Habitat preference in relation to dominant tree species in the tree layer. A distinction is made between populations that disappeared prior to 1979 and have not been recorded since, populations present in the period 1979–1991 (Pleistocene area in particular) and populations in the Kuinderbos (benchmark population: 1979). * indicates no information on tree species (Values ≤ 3 were clustered in the chi-square analysis in order to fulfil the requirements of this test).

	Pleistocene area				Kuinderbos	
	Number of colonies before 1979	%	Number of colonies in 1979–1991	%	Number of colonies	%
<i>Pseudotsuga menziesii</i>	2	3.0	16	25.1	-	
<i>Pinus spp.</i>	5	7.5	2	3.1	-	
<i>Picea abies</i>	1	1.5	2	3.1	5	1.2
<i>Quercus robur</i>	1	1.5	10	15.6	53	12.6
<i>Picea sitchensis</i>	-		2	3.1	325	77.5
<i>Fagus sylvatica</i>	-		2	3.1	5	1.2
<i>Larix sp.</i>	-		2	3.1	2	0.5
<i>Betula spp.</i>	-		5	7.8	-	
Other tree species	22*	32.8	5	7.8	29	6.9
Other habitats	36	53.7	18	28.2	-	
<i>Total</i>	<i>67</i>	<i>100</i>	<i>64</i>	<i>100</i>	<i>419</i>	<i>100</i>

Shallow rooting also occurs in places where clones are growing in roadside verges and where there is no accumulation of litter. Here, the rhizomes grow in the mineral soil. Where colonies are growing on level ground under *Picea spp.* or *Pseudotsuga mensiezii*, the rhizomes may be growing in the mineral layer or the fermentation layer (litter layer), depending on the thickness of both these layers. At one site clones are growing in a trench with 2–10 cm litter overlying a fermentation layer that is up to 8 cm thick. Here, the rhizomes are mostly growing in the litter layer. The rooting depth varied from 0.5 to 8 cm.

The mean rooting depth based on measurements in three areas in the Netherlands is 3.3 cm ($n = 82$, Table 5a–c), in the Kuinderbos 1.8 cm (four

TABLE 3. Composition of the top 10 cm of soil under clones of *Gymnocarpium dryopteris* in the Netherlands (particular Pleistocene area, period 1979–1991) and in the Kuinderbos (1979).

Soil composition	Pleistocene area		Kuinderbos	
	Number of colonies	%	Number of colonies	%
Humic, moderately fine sand	16	27.2	-	
Moderately coarse sand	14	23.7	16	11.3
Sand on loam or loamy sand	10	16.9	-	
Stony substrate	10	16.9	-	
Between basalt blocks	8	13.6	-	
Loam	1	1.7	-	
Humic, very fine sand	-		59	41.9
Peaty, very fine sand	-		27	19.1
Peat	-		30	21.3
Clay	-		9	6.4
<i>Total</i>	<i>59</i>	<i>100</i>	<i>141</i>	<i>100</i>

TABLE 4. Thickness of the ecto-organic layer in sites of *Gymnocarpium dryopteris* in the Netherlands (Pleistocene area in particular) and in the Kuinderbos. The highest value is given for each clone.

Thickness (cm)	Pleistocene area		Kuinderbos	
	Number of colonies	%	Number of colonies	%
0.0–2.0	6	31.6	67	68.0
2.1–4.0	3	15.8	18	18.0
4.1–6.0	4	21.0	11	11.0
6.1–8.0	1	5.3	3	3.0
8.1–10.0	5	26.3	0	0.0
<i>Total</i>	<i>19</i>	<i>100</i>	<i>99</i>	<i>100</i>
<i>mean</i>	<i>4.7</i>		<i>1.5</i>	

populations together, 2.6 cm). Rooting depth also varies greatly in natural sites outside the Netherlands (Table 5e–f). On walls, the rhizomes of *G. dryopteris* grow shallowly, between the bricks. In the Kuinderbos, most clones are growing within the influence of the groundwater. This is particularly true for the clones growing lowest down the sides of trenches. Sometimes these clones endure brief soaking or even submergence. Elsewhere in the Netherlands, clones (or their parts) also generally occur within the influence of groundwater, but they can live outside this influence too (Table 6; $\chi^2 = 23.3$, $p < 0.001$, d.f. = 4). Many clones (55.3% outside the Kuinderbos, 88.5% in the

TABLE 5. The depth of rhizomes at various sites in the Netherlands and elsewhere. The measurements are based on 1–4 different colonies per area. The depth for each clone has been determined for places where the stipes are attached to the rhizomes. n = number of observations. **a.** Delden, shady roadside drainage trench. **b.** Lonnekerberg, shady roadside drainage trench, **c.** 't Velde estate, shady trench, **d.** Kuinderbos, clones on forest soil and trench sides under *Picea sitchensis*, **e.** Harz, Bremketal, in *Luzulo-Fagetum*, on mountainside, 51°40'N 10°20'E, **f.** Allgäu (southern Germany), Wiederhofen, in *Abieti-Fagetum* on mountainside 47°26' N 10°25'E. Total = total number of determinations.

Depth (cm)	Netherlands											
	Pleistocene area						Kuinderbos		Germany			
	a		b		c		d		e		f	
n	%	n	%	n	%	n	%	n	%	n	%	
1	10	71.4	17	100	-	-	32	42.7	-	-	24	48.0
2	-	-	-	-	6	11.8	16	21.3	4	6.2	18	36.0
3	4	28.6	-	-	1	2.0	9	12.0	8	12.3	5	10.0
4	-	-	-	-	7	13.7	12	16.0	21	32.3	3	6.0
5	-	-	-	-	8	15.7	2	2.7	20	30.8	-	-
6	-	-	-	-	19	37.2	4	5.3	3	4.6	-	-
7	-	-	-	-	9	17.6	-	-	5	7.7	-	-
8	-	-	-	-	1	2.0	-	-	3	4.6	-	-
9	-	-	-	-	-	-	-	-	1	1.5	-	-
<i>Total</i>	<i>14</i>	<i>100</i>	<i>17</i>	<i>100</i>	<i>51</i>	<i>100</i>	<i>75</i>	<i>100</i>	<i>65</i>	<i>100</i>	<i>50</i>	<i>100</i>
<i>mean</i>	<i>1.3</i>		<i>0.5</i>		<i>4.8</i>		<i>1.8</i>		<i>4.3</i>		<i>1.5</i>	

TABLE 6. Mean highest water table (MHWT) in metres for clones of *Gymnocarpium dryopteris* in the Netherlands (in particular in Pleistocene area) and in the Kuinderbos.

MHWT	Pleistocene area		Kuinderbos	
	Number of colonies	%	Number of colonies	%
≤ 0.4	15	38.4	23	46.0
0.41–0.8	4	10.3	27	54.0
0.81–1.2	1	2.6	-	
> 1.2	9	23.1	-	
on walls	10	25.6	-	
<i>Total</i>	<i>39</i>	<i>100</i>	<i>50</i>	<i>100</i>

Kuinderbos, both for the period 1979–1991) grow on unstable, steep, trench sides. The large difference between the Kuinderbos and the rest of the Netherlands in the slope of the sites ($\chi^2 = 39.5$, $p < 0.001$, d.f. = 8) is because outside the Kuinderbos the sites include walls and quays (with a slope of 80°–90°), whereas in the Kuinderbos many clones are growing on the level woodland floor (Table 7). Within the Dutch population, the species is found significantly more often on northerly aspects than on southerly aspects ($\chi^2 = 8.2$, $p < 0.01$, d.f. = 1) (Table 8). Most of the trenches in the Kuinderbos run NW – SE, but there is no preference for either aspect ($\chi^2 = 0.8$, $p > 0.1$). Hence there is a difference between the distribution of the colonies in the Kuinderbos compared with elsewhere in the Netherlands ($\chi^2 = 99.1$, $p < 0.001$, d.f. = 3).

Composition of the vegetation.—*Gymnocarpium dryopteris* co-occurs with 97 higher plants and 38 mosses and liverworts ($n = 37$ relevés). Several clusters are discernable in the synoptic table (Table 9). In general, the clusters do not fit precisely into one community. Group I comprises wall vegetations. Among the species associated with *G. dryopteris* are *Dryopteris filix-mas* (L.) Schott and *Thelyperis palustris* Schott. The vegetation of group I are related to the *Asplenietum trichomano-ruta-murariae*. Group II comprises vegetation

TABLE 7. Inclination of colonies on walls and in trenches in the Netherlands (Pleistocene area in particular). Slope per colony is based on the highest value.

Slope	Pleistocene area		Kuinderbos	
	Number of colonies	%	Number of colonies	%
< 10°	2	4.6	17	25.5
11–20°	5	11.7	2	3.0
21–30°	5	11.7	1	1.4
31–40°	2	4.6	5	7.4
41–50°	13	30.2	12	17.9
51–60°	3	7.0	20	29.9
61–70°	1	2.3	6	8.9
71–80°	0	0.0	4	6.0
81–90°	12	27.9	0	0.0
<i>Total</i>	<i>43</i>	<i>100</i>	<i>67</i>	<i>100</i>

TABLE 8. Aspect of sites in the Netherlands (Pleistocene area in particular) with slope $> 10^\circ$ and in the Kuinderbos.

Aspect	Pleistocene area		Kuinderbos	
	Number of colonies	%	Number of colonies	%
NW-NE	26	42.6	172	41.0
E or W	12	19.7	0	0.0
SW-SE	9	14.7	190	45.4
none	14	23.0	57	13.6
<i>Total</i>	<i>61</i>	<i>100</i>	<i>419</i>	<i>100</i>

with relatively many acidophile species. Some of the relevés were in stands of exotics. The relevés display a clear relationship with the *Quercion roboris-petreae* (and within this, with the *Fago-Quercetum* and also the *Betulo-Quercetum*). The relevés made under *Picea sitchensis* (Kuinderbos) also fall into this group. Group III comprises relevés in which species such as *Sorbus aucuparia* L., *Fagus sylvatica* (seedling or juvenile) and *Lonicera periclymenum* L. are differentiating. These relevés are clearly assignable to the *Fago-Quercetum*, actually being a damp form of this association with *Athyrium filix-femina* (L.) Roth and *Lysimachia vulgaris* L. Group IV comprises a single relevé which includes, among others, *Geranium robertianum* L., *Aegopodium podagraria* L., *Oxalis europaea* L. and *Conocephalum conicum* (L.) Dumort, which are assignable to the *Pruno-Fraxinetum*. Group V comprises relevés with relatively many grasses. The characteristic species for this group include, among others, *Festuca rubra* L., *Holcus lanatus* L., *Cerastium fontanum* Baumg. and *Taraxacum officinale* F.H.Wigg. These sites are of *G. dryopteris* on basalt dikes and in roadside trenches; the relevés contain many species that occur in the adjacent roadside verges. The most reliable species associated with *G. dryopteris* are *Athyrium filix-femina*, *Dryopteris dilatata* (Hoffm.) A.Gray, *Rubus fruticosus* L., with *Athyrium filix-femina* in particular being an indicator of potential sites of *G. dryopteris*.

Accompanying fern species were recorded for 128 colonies in total. The most common within the Dutch population are *Athyrium filix-femina*, *Dryopteris filix-mas*, *D. dilatata* and *D. carthusiana* (Vill.) H.P.Fuchs. Outside the Kuinderbos there are 14 fern species that occur as associated species: on average, 2.2 species colony⁻¹. The various uncommon species recorded as associated fern species on canal walls include *Gymnocarpium robertianum*, *Polystichum aculeatum* (L.) Roth and *Asplenium trichomanes* L. In the Kuinderbos, *G. dryopteris* is associated with 12 fern species (Table 10). Four of the five patches of *Phegopteris connectilis* (Michaux) Watt in the Kuinderbos are associated with *G. dryopteris*. In some localities outside the Kuinderbos, both species occur directly next to each other or in the same area. The frequencies of *G. dryopteris* in the Kuinderbos and in the rest of the Netherlands being associated with other fern species are significantly different ($\chi^2 = 13.1$, $p < 0.001$, d.f. = 4); this is primarily because of the high frequency of *Dryopteris carthusiana* in the Kuinderbos.

TABLE 9. Synoptic table based on relevés with *Gymnocarpium dryopteris*. The data have been classified on the basis of a TWINSpan computation of 37 relevés, two of which were made in Germany (Teutoburgerwoud) and the rest in the Netherlands. The table does not show the mosses, liverworts and vascular plant species recorded only once. Tree and shrub layer were not included in computation. The table gives the number of relevés per relevé group in which the species in question was found. Exclusive characteristic species have been printed in grey. These are species that have only been recorded in a single species group, with a presence of 25% or more. I = wall vegetations, II = exotic stands, III = *Fago-Quercetum*, IV = *Pruno - Fraxinetum*, V = vegetation of dikes and ditch banks.

Relevé group	I	II	III	IV	V
Number of relevés	4	16	8	1	8
<i>Gymnocarpium dryopteris</i>	4	16	8	1	8
<i>Asplenium ruta-muraria</i>	2	-	-	-	-
<i>Asplenium trichomanes</i>	2	-	-	-	-
<i>Thelypteris palustris</i>	3	-	-	-	-
<i>Sagina procumbens</i>	2	-	-	-	-
<i>Capsella bursa-pastoris</i>	2	-	-	-	-
<i>Rubus idaeus</i>	-	7	-	-	-
<i>Betula pendula</i>	-	5	-	-	-
<i>Ceratocarpus claviculata</i>	-	5	-	-	-
<i>Quercus robur</i>	-	4	-	-	-
<i>Cardamine pratensis</i>	-	3	-	-	-
<i>Viola palustris</i>	-	2	-	-	-
<i>Festuca ovina</i>	-	2	-	-	-
<i>Humulus lupulus</i>	-	2	-	-	-
<i>Eupatorium cannabinum</i>	-	2	-	-	1
<i>Chamaenerion angustifolium</i>	-	6	-	-	1
<i>Oxalis europaea</i>	-	1	-	1	-
<i>Lonicera periclymeum</i>	-	-	6	-	-
<i>Equisetum arvense</i>	-	-	2	-	-
<i>Luzula multiflora</i>	-	-	2	-	-
<i>Oxalis stricta</i>	-	-	2	-	-
<i>Cerastium fontanum</i>	-	-	-	-	4
<i>Taraxacum vulgare</i>	-	-	-	-	6
<i>Tussilago farfare</i>	-	-	-	-	3
<i>Lolium perenne</i>	-	-	-	-	2
<i>Athyrium filix-femina</i>	2	7	8	1	1
<i>Dryopteris filix-mas</i>	4	4	3	1	2
<i>Dryopteris dilatata</i>	1	14	4	-	-
<i>Rubus sp.</i>	4	9	6	-	-
<i>Epilobium sp.</i>	1	1	-	-	1
<i>Stellaria media</i>	-	2	1	1	1
<i>Urtica dioica</i>	-	3	4	1	2
<i>Agrostis cappilaris</i>	-	3	6	-	1
<i>Galium aparine</i>	-	1	3	-	2
<i>Lysimachia vulgaris</i>	-	2	6	-	1
<i>Hieracium laevigatum</i>	-	2	2	-	1
<i>Juncus effusus</i>	-	4	1	-	1
<i>Poa trivialis</i>	-	2	1	-	2
<i>Dryopteris carthusiana</i>	-	2	2	-	1
<i>Polypodium vulgare</i>	1	1	-	-	-
<i>Senecio vulgaris</i>	1	-	-	-	1
<i>Holcus mollis</i>	-	5	3	-	-

TABLE 9. Continued.

Relevé group	I	II	III	IV	V
<i>Deschampsia flexuosa</i>	-	4	3	-	-
<i>Sorbus aucuparia</i>	-	1	6	-	-
<i>Fagus sylvatica (j)</i>	-	1	5	-	-
<i>Galium saxatile</i>	-	2	2	-	-
<i>Molina coerulea</i>	-	1	2	-	-
<i>Rumex obtusifolius</i>	-	1	1	-	-
<i>Ajuga reptans</i>	-	1	1	-	-
<i>Phegopteris connectilis</i>	-	1	-	-	1
<i>Galium palustre</i>	-	1	-	-	1
<i>Heracleum sphondylium</i>	-	1	-	-	1
<i>Calamagrostis epigejos</i>	-	2	-	-	2
<i>Phragmites australis</i>	-	3	-	-	2
<i>Holcus lanatus</i>	-	4	-	-	5
<i>Ranunculus repens</i>	-	-	2	1	-
<i>Geranium robertianum</i>	-	-	1	1	-
<i>Anthriscus sylvestris</i>	-	-	1	1	-
<i>Angelica sylvestris</i>	-	-	1	1	-
<i>Festuca rubra</i>	-	-	1	-	7
<i>Potentilla erecta</i>	-	-	1	-	1
<i>Prunella vulgaris</i>	-	-	2	-	1

Size of colonies.—Sixty nine percent of the colonies in the Netherlands have fewer than 100 fronds. Large specimens with over 1000 fronds are rare: in the period 1979–1981, this occurred in only a single patch (in the park of the Royal Het Loo palace). In this respect the distribution for the Kuinderbos (1990 situation) is very similar to that for the rest of the Netherlands (Table 11), though the Kuinderbos has relatively more colonies with more than 1000 fronds (maximum is 3000). Various populations in this woodland were monitored over 15 years (Bremer, 1994). In heavy shade, individuals may remain the same size for a long time. If the light increases suddenly (e.g., as a result of storm damage), the number of fronds may increase over a number of years, at a maximum rate of 400 fronds year⁻¹. Seventy five percent of the colonies in the Netherlands are smaller in extent than this annual increase. Young clones lack a clear shape. As they grow larger, patches become clearly discernable. They are often oval or round in shape. If the center dies, a fairy ring may arise. Along trenches or streams, the oval shape may become elongated. Old patches may break up, making it appear that several clones occur next to each other. This has seldom been recorded in the Netherlands, because the clones are relatively young and limited in extent.

In the Netherlands (outside the Kuinderbos), 74 clones were recorded in the research period (1979–1991). By 1992, seven (= 10%) had disappeared. Sites on walls are always small and vulnerable, but large patches, too, can decay in a couple of years. Eighty eight percent of the Dutch colonies whose age was known or could be estimated were no older than 20 years (n = 41). After long-

TABLE 10. Associated fern species (within a distance of approx. 3 m from the clone) in the Netherlands (Pleistocene area in particular) and in the Kuinderbos (n = number of clones) For chi-square analysis, species with a frequency < 5 were clustered in a single category in order to fulfil the requirements of this test.

Species	Pleistocene area (n = 63)		Kuinderbos (n = 65)	
	Number of colonies	%	Number of colonies	%
<i>Dryopteris dilatata</i>	40	63.5	50	76.9
<i>Athyrium filix-femina</i>	36	57.1	35	53.8
<i>Dryopteris filix-mas</i>	22	34.9	25	38.5
<i>Dryopteris carthusiana</i>	14	22.2	40	61.5
<i>Asplenium trichomanes</i>	4	6.3	1	1.5
<i>Phegopteris connectilis</i>	4	6.3	3	4.6
<i>Blechnum spicant</i>	4	6.3	-	
<i>Polypodium vulgare</i>	3	4.8	1	1.5
<i>Thelypteris palustris</i>	3	4.8	-	
<i>Pteridium aquilinum</i>	2	3.1	-	
<i>Asplenium ruta-muraria</i>	1	1.6	-	
<i>Polystichum aculeatum</i>	1	1.6	2	3.1
<i>Gymnocarpium robertianum</i>	1	1.6	1	1.5
<i>Asplenium scolopendrium</i>	1	1.6	4	6.1
<i>Polystichum setiferum</i>	-		2	3.1
<i>Dryopteris affinis</i>	-		1	1.5
Mean no. of species per clone	2.2		2.5	

term monitoring of four research plots in the Kuinderbos it was found that after 15 years, 43.7% of the population (n = 190) had disappeared (Bremer, 1994). The half-life varied from 3.5 to 4.6 years, with some colonies older than 30 years.

Fertile fronds generally occur in specimens with more than 50 fronds, except in the case of wall specimens, where, though fronds are few, they may be fertile. Usually, less than 20% of the fronds of large colonies are fertile. In some large colonies, more than 50% of the fronds were found to be fertile. In general, fertile fronds are longer than sterile fronds and extend beyond the other fronds.

FronD damage.—*Gymnocarpium dryopteris* is a deciduous species. Its fronds usually unfurl in early May, though they may appear at the end of April if the winter has been mild. The species is vulnerable to damage from late night frosts, as evidenced after the April frosts of 1991. Frost can also accelerate die-back in October, but even without frost, most fronds have died before November. Severe thunderstorms may also cause damage, as if bent, the fragile fronds will die. New fronds can be formed until September, though they are usually smaller. *G. dryopteris* rarely suffers pest damage. Sawfly caterpillars (*Symphya*, indet.) are regularly found on the fronds of specimens in the Kuinderbos, but rarely do they destroy entire fronds. Similar pest damage has been found on populations elsewhere in the Netherlands. Slug damage is rare. *Gymnocarpium dryopteris* growing on dikes in small crevices between basalt rocks may be damaged by browsing livestock.

TABLE 11. The size of colonies of *Gymnocarpium dryopteris*, based on the number of fronds colony⁻¹ n = number of colonies, % percentage of colonies. **a.** Dutch populations 1979–1991 (Pleistocene area in particular), **b.** population in Kuinderbos in 1979 52° 48'N, 5° 45'E, **c.** population in Kuinderbos in 1990, **d.** Harz, Bremketal (1989), in *Luzulo-Fagetum dryopteridetosum* 51°40'N 10°20'E, **e.** Weserbergland (1989), in Steinköpfe ancient woodland in *Fago – Quercetum*, 51° 28'N, 9° 20'E, **f.** Allgäu (1991) in *Abieti-Fagetum* 47°26' N 10°25'E.

Size	Netherlands																	
	Pleistocene area						Kuinderbos						Germany					
	a		b		c		d		e		f							
	n	%	n	%	n	%	n	%	n	%	n	%						
1–10	11	17.2	35	17.2	19	10.9	1	1.8	-	-	2	14.2						
11–100	29	45.3	124	60.8	75	43.1	13	24.1	5	12.8	6	42.9						
101–1000	23	35.9	45	22.0	72	41.4	18	33.3	18	46.2	6	42.9						
1001–10000	1	1.6	-	-	8	4.6	15	27.8	14	35.9	-	-						
10001–10 ⁵	-	-	-	-	-	-	4	7.4	2	5.1	-	-						
10 ⁵ –10 ⁶	-	-	-	-	-	-	3	5.6	-	-	-	-						
<i>Total</i>	<i>64</i>	<i>100</i>	<i>204</i>	<i>100</i>	<i>174</i>	<i>100</i>	<i>54</i>	<i>100</i>	<i>39</i>	<i>100</i>	<i>14</i>	<i>100</i>						

DISCUSSION

Gymnocarpium dryopteris is a very rare species in the Netherlands (van der Meijden, 2005). In the period 1979–1991, 670 clones were recorded. The only high density recorded was in the Kuinderbos. Here, the fern was closely associated with *Picea sitchensis* in 1979, whether the ecto-organic layer was overlying fine sand, peat or clay. The rhizome is frequently very shallow, and thus the species reacts strongly to the composition of the ecto-organic layer, which is determined by the dominant tree species. It is striking that all the sites have peat in the subsoil. This peat deposit supplies the uppermost deposits with water by capillary action, assuring a very stable moisture supply. In long droughts, like the one that occurred from May to August 1992, many specimens may display reduced vitality, but there is no massive die-back of fronds. The reason that rhizomes on trench banks are shallower than in the woodland may be that the moisture supply is better than in the adjacent woodland. Here, clones often occur almost as far as the bottom of the trench. In the Kuinderbos, most colonies are growing within the influence of the groundwater; elsewhere they also occur outside this sphere of influence. The species can thus be designated a local phreatophyte (Londo, 1988). Although it does not tolerate waterlogging in the root zone (Britten, undated), parts of clones will tolerate brief submergence. In the Netherlands the rooting depth varies from 0.5–8 cm, which is more than the 2–3 cm mentioned by Page (1982). The mean value does agree with Page (1982).

In the Netherlands (excluding Kuinderbos) *G. dryopteris* grows on acidic sites. Exceptions are the sites on canal walls, where the mortar has a high pH. In the Kuinderbos the pH is generally high, but this could be an artifact of the

soil sampling, as the ecto-organic layer is thin and when the root environment is being sampled, some of the underlying soil was also sampled. Clones growing on the transition from trench side to woodland floor may be growing in calcareous fine sand in the trench side, but in an acidic fermentation layer on the woodland floor. Hence within a single clone, the pH of the root zone may vary by several units. Page (1982) notes that in the United Kingdom, *G. dryopteris* can grow in various pH values. Dostál (1984) reported the species on limestone overlain by a layer of raw humus, on soils with a mull or a moder profile. In North America the species prefers weakly acid substrates (Lellinger, 1985). Ellenberg (1982) called the species a moder humus indicator, because it grows on litter under *Picea abies* (L.) H.Karst., for example.

Gymnocarpium dryopteris occurs in various woodland types, such as the *Fago-Quercetum* and *Pruno-Fraxinetum*, always in relatively damp places and often associated with *Athyrium filix-femina*. The data presented by Stortelder *et al.* (1999) are in agreement with this. Outside the Kuinderbos, stands of *Pseudotsuga mensiezii* are an important habitat. These have often been planted in places where the potential woodland type is the *Fago-Quercetum*. Sissingh (1970) goes so far as to call it a *Dryopterido-Pseudotsugetum* with, among others, acidophile mosses and various ferns, including *G. dryopteris* as characteristic species. *Gymnocarpium dryopteris* is found in natural Douglas fir forests in N. America (Snyder, 1993). The only localities in the Netherlands where the species has been observed in stands of *Picea sitchensis* are in East Flevoland and the Kuinderbos – especially the latter. On the west coast of the United States and Canada the species frequently occurs in the natural Sitka forests (Fonda 1974) and is common in the *Polystichum munitum* - *Picea sitchensis* association, which has been described as a closed coniferous forest thriving on the foggy and rainy coasts of British Columbia. It is also common in other associations of the montane and subalpine forests e.g. the *G. dryopteris* - *Abies amabilis* community (Barbour and Billings, 1988; Peinado *et al.*, 1997). The species has not been reported from the extensive plantations of *Picea sitchensis* in Scotland (Ford *et al.*, 1979; Peterken, 1985), or Wales (Hill and Jones, 1978), but can be expected in places where moisture is guaranteed.

After 1985 it was found that *G. dryopteris* could rapidly establish in many places in the Kuinderbos where very dense stands of *Picea abies* had been severely thinned. This suggests it is not strictly associated with *Picea sitchensis*. If the Kuinderbos had been planted with *Pseudotsuga mensiezii* rather than *Picea sitchensis*, similar densities could have been expected, given the similarities between both conifers in terms of the light climate and build-up of the ecto-organic layer. The colonization of thinned stands of *Picea abies* is in line with the behavior of the species in Central Europe. In southern Germany, *G. dryopteris* has been reported in 31 forest types (out of a total of 68); in eight forest types its frequency was more than 20%. The woodlands in question were in ravines (*Ulmo glabrae-Aceretum pseudoplatani*), or were beech (such as *Dentario-Fagetum* and *Aceri-Fagetum*) and *Picea abies* forests (such as *Asplenio-Piceetum*) (Oberdorfer, 1992). In the Harz mountains, it occurs in all types of beech forest, in subassociations in shady places with a

high relative humidity (Böttcher *et al.*, 1981). The center of the species' distribution in the United Kingdom is in the birch and oak woodlands in Scotland (Page, 1982), but it also occurs along brooks with woodland vegetation related to the *Pruno-Fraxinetum* (Tansley, 1965). Rodwell (1991) calls it from *Juniperus communis* - *Oxalis acetosella* woodland with *Betula* spp. in the tree layer. In Scandinavia, the species is common in spruce, pine and birch forests (Aune, 1982; Havas and Kubin, 1985), and also in *Carpinus betulus* forests (Mäkiriinta, 1982). In the farthest north it also occurs outside woodland, in grasslands (Westhoff and Schoof-van Pelt, 1982). Its occurrence in grazed vegetations on basalt dikes in the Netherlands is thus not unexpected, as this vegetation too is unshaded. In North America it is listed from 38 cover types, with a dominant role of types dominated by coniferous tree species (Snyder, 1993).

Gymnocarpium dryopteris is often associated with *Phegopteris connectilis* within its range. In the Netherlands *Phegopteris connectilis* co-occurs with *G. dryopteris* in seven places, and in the Kuinderbos, they often co-occur. It has been reported (Rasbach and Willmans, 1976) that in Central Europe *G. dryopteris* establishes on weathering chalk soils earlier than *Phegopteris connectilis* (Rasbach and Willmans, 1976) especially if an acid layer has formed on top of these soils. Page (1982) mentions that the ecological difference is that *Phegopteris connectilis* grows on slightly drier slopes. The ecological differences appear to be minor. It remains noteworthy that in the Netherlands and elsewhere, *Phegopteris connectilis* is much rarer than *G. dryopteris*. In the 1980s, the Dutch population of *G. dryopteris* was at least 670 clones, with approximately 80,000 fronds, compared with an estimated maximum of 50 clones of *Phegopteris connectilis*. In its favored sites (montane areas), more than 100,000 fronds may occur within 1 ha, as has been recorded in the Harz mountains (Germany). Colonies with more than 1000 fronds form 2% of the population in the Netherlands, 5% of the population in the Kuinderbos and 41% in the studied populations in the Harz mountains and Weserbergland. Although clones can increase their size rapidly if conditions are favorable, in the Netherlands they remain small.

Eighty eight percent of the Dutch colonies are less than 20 years old, which suggests many recent establishings, but also high mortality. Colonies tens of years old are rare. The species used to occur in Beekbergerwoud, before this last surviving ancient Dutch old growth was felled in 1871. The oldest existing sites are in the Royal park of Het Loo palace, where the species was first recorded in 1853. It is possible that the same clones are still present, which must therefore be at least 150 years old. In the Kuinderbos the mortality is related to the lack of light that causes clones to gradually diminish in size and to disappear after some years (Bremer, 1994). Elsewhere in the Netherlands, colonies have disappeared for reasons such as the destruction of biotopes, heavy trampling and structural depletion of groundwater. Colonies mostly remain discernable as clearly delimited patches. Oinonen (1971) established that in Finland, colonies were still discernable after 450 years. Only in ancient, undisturbed forests do such clones break up and become indistinguishable.

Peterken (1985) mentioned this phenomenon in rhizome geophytes in old deciduous woodland. In one of the most undisturbed ancient forests in Europe, the Bialowieza forest (Polen), *G. dryopteris* has been observed to have a very dispersed manner of growth that is interrupted only where the rootballs of windthrown trees have created a new habitat and there has been a concentration in the fronds per colony.

The final conclusion is that the population in the Kuiderbos differs from that of the rest of the Netherlands in many aspects. The high density of clones in this area makes it possible to identify which factors are important. These are: a good, constant supply of moisture from underground peat, the presence of an acid ecto-organic layer with both a litter layer and a fermentation layer, and a favourable light climate. These conditions can be met in moderately dense *Picea* stands. Although in the Kuinderbos the species is closely associated with Sitka spruce, *Picea sitchensis*, its occurrence elsewhere in the Netherlands under Douglas fir *Pseudotsuga menziesii* and the colonisation of *Picea abies* within the Kuinderbos indicate that moisture supply and the presence of the acid ecto-organic layer of Spruce needles are more important than the presence of *Picea sitchensis* in particular.

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