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***CREPIDOMANES LUNULATUM (HYMENOPHYLLACEAE:
PTERIDOPHYTA), A NEW FILMY FERN SPECIES FROM SOUTH
INDIA***

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Key words: *Crepidomanes lunulatum*, filmy fern, India.

ABSTRACT

Crepidomanes lunulatum, a new species (Hymenophyllaceae: Pteridophyta) is described from Kerala, South India. Presence of closely arranged, regularly pinnatifid, entire-margined fronds and lunulate sori with flared, involucral mouths are the discriminative features. Illustrations of the diagnostic characters of the taxon are provided.

INTRODUCTION

During the recent investigations on the filmy ferns of South India we collected a few new taxa from the dense evergreen forests of the Western Ghats (Madhusoodanan *et al.*, 1996; Madhusoodanan & Hameed, 1997; Hameed & Madhusoodanan, 1998). Another interesting species has been collected from Athirapally tropical evergreen forests (700 m alt., 3000 mm annual rainfall) near the Palghat gap in the Western Ghats. We found that this is a new species of *Crepidomanes* and it is described here as *Crepidomanes lunulatum* for the characteristic lunar-shaped sori.

Crepidomanes is a genus of about 20 species whose range extends from Africa to Japan and to New Zealand. *Crepidomanes* has four species in South India *i.e.* *C. intramarginale* (Hook. & Grev.) Copel., *C. kurzii* (Bedd.) Tagawa & K. Iwats., *C. bipunctatum* (Poir.) Copel. and *C. latealatum* (Bosch) Copel. (Beddome, 1883; Iwatsuki, 1985; Nair *et al.*, 1994). Recently *C. christii* (Copel.) Copel. has also been reported from here (Madhusoodanan & Hameed, 1997). Except for *C. latealatum* (Bosch) Copel. all the other four species have a continuous intramarginal false vein very close to, but distinct from, the margin throughout the frond. The new species resembles *C. kurzii* (Bedd.) Tagawa & K. Iwats., but differs in having a crescent-shaped sorus. *C. lunulatum* is so far only recorded from its type locality, Athirapally.

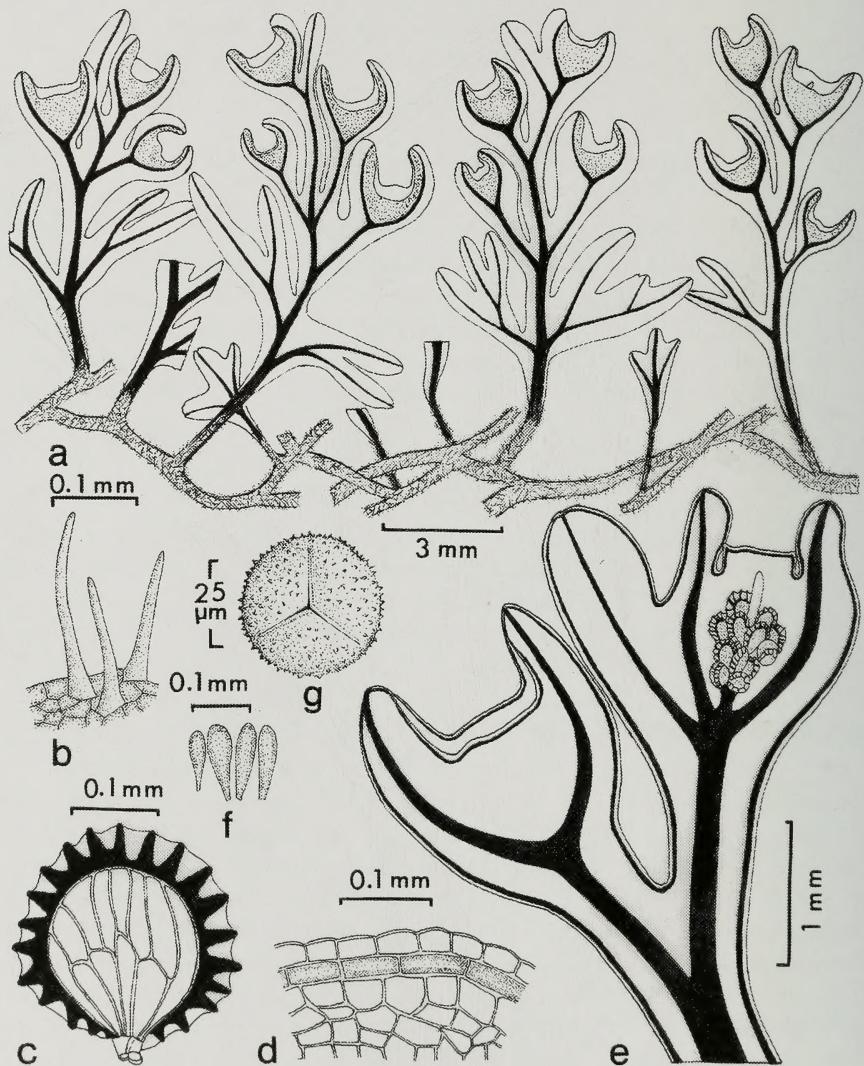


Figure 1: *Crepidomanes lunulatum* Madhus. & Hameed

a. Habit; b. Hairs on rhizome; c: Sporangium; d: Details of frond margin with submarginal false vein; e: Tip of fertile frond showing sori with sporangia; f: Club-like trichomes on veins; g : Spore.

***Crepidomanes lunulatum* Madhus. et Hameed sp. nov. (Fig. 1)**

Crepidomani kurzii similis, sed frondibus confertis atro-viridibus membranaceis profunde unipinnatis, segmentis primariis basalibus bi- vel trifidis differt. Sori 2-5 terminales anguste alati lunares (interdum urceolati) omnino immersi, cupula involucralis segmentis duobus longis superantibus costa furcata subtenta et sinu moderate profundiore et lato inter involucri segmenta.

Holotypus: C. Abdul Hameed CU34862, South India, Kerala, Athirapalli, Trichur Dt. (K).

A very small, lithophytic filmy fern growing in a thick mat, with a wide-creeping, slender, tomentose rhizome. Fronds very close, arranged at distance of 2-3 mm, dark green, membranous, pinnatifid, ovate or ovate-oblong (elliptic in some fertile fronds), 0.6-2 cm long and up to 1 cm broad; stipe terete, up to 5 mm long, covered by rudimentary, thin, dark brown, unicellular hairs; lowest pinnae bifid or trifid; segments thin, less than 1 mm broad, margin entire, apex obtuse to shallowly emarginate. Venation free, pinnate, distinct, with the costa slightly zig-zag and lateral veins ending at the apex of the segments; both sides of the veins bearing small clavate hairs. Fertile fronds more elongated than sterile ones, bearing a terminal lunular (sometimes urceolar) sorus produced in-between the forked upper pinnae. Sorus subtended by a costa dichotomising on either side of the receptacle, running into two long segments giving a characteristic appearance to the indusium; the lower swollen cupular portion of the involucre is completely embedded in the lamina and narrowly winged throughout; the involucral mouth is broad and flared with an included receptacle. Sporangia are simple, short-stalked and compressed having a spherical capsule with an oblique annulus of up to 22 cells without a definite stomium; the inner cells are thick-walled, elongated. Spores lacking a perine, globose, tetrahedral, up to 38 μm in diameter with an uniformly spinulose exine.

Type: C. Abdul Hameed CU34862, South India, Kerala, Athirapalli, Trichur Dt., 700 m alt. shady, moss-covered, wet rocks, 21 December 1997 (holotype: K; isotype: CALI, MH). Paratype: C. Abdul Hameed CU34873, South India, Kerala, Athirapalli, Trichur Dt., 800 m alt., 25 March 1998 (CALI).

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BOOK REVIEW

BIBLIOGRAPHÍA SOBRE GAMETOFITOS DE HELECHOS Y PLANTES AFINES
 (Bibliography for gametophytes of ferns and allied plants) B. Pérez-García & R. Riba. 1998. 98pp. Monographs in Systematic Botany, Vol.7, Missouri Botanical Garden Press. Price US\$20.00. ISBN 0-915279-61-4. ISSN 0161-1542. Paperback.

Environmental and laboratory studies of the haploid phase of pteridophytes are important for our understanding of their adaptations and role at the colonisation stage of the life cycle of these plants; also they have proved to be useful tools in our broader understanding of the alternation of generations life cycle and the genetic nature of pteridophytes and plants in general. This is a timely and extremely useful bibliography for anyone engaged in field or laboratory studies and teaching on any aspect of the biology of spores as the first cell of the haploid phase, or of gametophytes.

The short *Introduction* outlines the rise of spore and gametophyte research and its value to pteridologists in particular; the value of spores in facilitating the ease of management of laboratory studies is noted. Over 2000 references to such work, with full bibliographical details and published before 1996, are arranged in alphabetical order of author. Each entry is annotated with reference to all the categories to which it relates in a numbered list of thirty three research areas (termed *Claves de los Temas = Key to subjects*). The *Key* is in two parts: spore biology and gametophyte biology, and categories include culture methods, the various factors affecting germination, growth and development, aspects of cytology and histology, metabolism at different levels, aspects of the biology of sexual and vegetative reproduction and deviant forms of the life cycle, genetic studies, ecology, and morphological descriptions.

There are two useful indices, one thematic and sub-divided into the research areas listed in the *Key*, and the other taxonomic and sub-divided by families and genera in alphabetical order. (*Annual Review of Pteridological Research* please note!). Like the main list of references, the indices are cross-referenced, with papers relevant to more than one category being listed under all appropriate headings. Unfortunately, the listings of most of the sections in the *Thematic index* and a number in the *Taxonomic index* are very long and research workers will find it a daunting chore to seek out those papers relevant to their particular interest. But I suppose it only needs to be done once in a project! However, sub-divisions within such categories would have facilitated identification. What any user must **not** do is to ignore the *General* section, for therein lie a number of references which are not always found under other headings!

It is good to see references to fossil gametophytes included, but it is a pity that there is not a specific category for them. Though there are very few, to date, the only way of resourcing them in the Bibliography is through the name of a genus or family, as long as it is mentioned in a title, ...

YET ANOTHER FERN WITH STORAGE ROOTS - *CHEILANTHES BOLBORRHIZA* MICKEL & BEITEL (PTERIDACEAE: PTERIDOPHYTA) FROM MEXICO AND EL SALVADOR

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Key words: *Adiantum diaphanum*, *Afropteris*, anatomy, morphology, starch grains

ABSTRACT

Cheilanthes bolborrhiza has swollen root bases with enlarged pericycle cells, which contain starch grains. Storage roots are only known from two other fern genera, *Adiantum* and *Afropteris*. However, in the latter two taxa, the starch grains are deposited in the root cortex, while they are located in the pericycle cells in *Cheilanthes*. The root anatomy of these species and other cheilanthonid ferns is compared. Finally the biological importance of storage roots for xeric ferns is discussed.

INTRODUCTION

At present storage roots are known from only three fern species (Schneider, 1996). One of these is the epiphytic fern *Adiantum diaphanum* Blume with swollen lateral roots. The other two are members of the African genus *Afropteris* Alston; they are *A. barklyae* (Baker) Alston and *A. repens* (C.Chr.) Alston. Their short brown roots have a swollen base. In both, the storage cells are part of the root cortex. Deposition of starch grains is common in fern roots but in most cases this is not connected with a differentiation of the whole root or of parts of it. A few years ago Mickel and Beitel (1988) described a new species, *Cheilanthes bolborrhiza*, which occurs from Oaxaca (Mexico) to El Salvador. Its epithet reflects the swollen bases of the roots. The anatomy of roots with thickened parts has been compared to that of other species of the genus *Cheilanthes* with roots lacking modified parts. Here, an overview is given of the storage of starch in fern roots and the biological importance of such roots.

MATERIALS AND METHODS

Two vouchers were studied - Ruelas 16221, Mexico (UC) and Breedlove 64100, Mexico (UC). The roots were softened in 1.0 % Tinoventin solution for three days. They were then embedded in Kulzer Technovit 1700 following the method of Iggersheim and Cichocki (1996). Transverse sections of 5 µm thickness were produced with a Reichert-Jung Autocut 2040 microtome. Finally, sections were examined by optical microscopy using polarised light and various dyes, including KJJ, Ruthenium red, Sudan black, Sudan IV, and Toluidin blue.

RESULTS

1. Morphology of the roots

The base of the shoot-borne roots is swollen for a length of between 1-4 mm and a maximal thickness up to 2 mm. The shape of the swollen part is more or less ovate and broadest near the base. The remainder of the root is more than 5 cm long (not completely preserved in the herbarium specimens) and up to 0.4 mm thick. The body of this part of the root is more or less cylindrical and is densely covered with root hairs. Only a few root hairs are found on the swollen part. In both parts of the root the cells of the rhizodermis have an elongated-rectangular shape and are dark brown. Trichoblasts and atrichoblasts do not differ in cell shape and size.

2. Anatomy of the roots

- a. *Swollen root base* - The swollen root base is up to 1.2 mm thick in cross-section. The outer part is formed by a brown layer of 0.02 to 0.03 mm thickness. This layer consists of the one cell-layer thick rhizodermis and the root cortex of four to six cell-layers depth. The cells of the root cortex have slightly thickened, brown cell walls. However, these cells are mainly collapsed and form a compact layer around the central cylinder. The central cylinder and the single cell-layer of a secondary endodermis occupy the remaining part of the cross-section of the root. At the centre a small amount of vascular tissue consists of four metaxylem tracheids and two protoxylem poles, each with three tracheids. The main part of the root is formed by four to six cell layers of large pericycle cells which contain a lot of starch grains.
- b. *Root segment without swelling* - This part of the root is up to 0.4 mm thick. Both parts are nearly identical in the structure of the rhizodermis and root cortex, but in these younger parts of the root the cortex cells are not collapsed. Similar to the cells of the rhizodermis these cells become necrotic and collapse in older parts of the root. The pericycle consists of only one cell layer with remarkably smaller cells. Finally the central cylinder is only 0.03 mm thick. Its vascular tissue and endodermis are nearly identical to the swollen part. In conclusion, the only difference between both parts of the root is the structure of the pericycle.

DISCUSSION

1. Comparison with other storage roots in ferns (Table 1)

Whilst the storage organs of *Adiantum diaphanum* are lateral roots, the base of the shoot-borne root serves as storage organ in *Afropteris* and *Cheilanthes bolborrhiza*. Having ovate root bases, both taxa look very similar in their root morphology. However, in *Afropteris* and *Adiantum* the starch grains are stored in enlarged cells of the root cortex whereas they are stored in enlarged pericycle cells in *Cheilanthes bolborrhiza*. Based on the criteria of the anatomy and hierarchical structure of plant organs, the storage roots are formed in three different ways in the three genera and therefore they do not indicate relationships. Furthermore, all three genera grow in different habitats. Lastly, it is curious to note that storage roots have evolved independently three times in one fern family, the Pteridaceae (subfamilies Adiantoideae, Cheilanthoideae, Taenitidoideae), but not in any other family of ferns. *Afropteris* and *Cheilanthes bolborrhiza* share not only morphological

similarities in root and leaf morphology, but the species grow in similar habitats. However, they differ anatomically. Their distribution also indicates an independent evolution. *Adiantum diaphanum* differs from the other two especially in ecology and growth form.

Table 1: A comparison of ferns with storage roots

| | Modified part of the root | Tissue with starch grains | Ecology | Distribution |
|---|------------------------------|---------------------------|-------------|--------------------------------|
| <i>Adiantum diaphanum</i> | Lateral root | Cortex | Epiphyte | E. Asia to Australia |
| <i>Afropteris barklyae</i> and <i>A. repens</i> | Base of the shoot-borne root | Cortex | Terrestrial | Tropical Africa and Seychelles |
| <i>Cheilanthes bolborrhiza</i> | Base of the shoot-borne root | Pericycle | Terrestrial | Mexico (Oaxaca) and Salvador |

2. Comparison with roots of other Cheilanthoideae

Swollen root bases are not known from any other species of Cheilanthoideae. However, a root cortex structure as in *C. bolborrhiza* is common in this subfamily. As discussed earlier (Schneider, 1996) this structure of a root cortex, the so-called *Notholaena*-type, may be an adaptation to xeric environments and is found in Cheilanthoideae (Pteridaceae) and Anemoioideae (Schizaeaceae) only. Additionally, the pericycle consists of two layers of very large cells in cross-section and filled with starch grains in some species of *Cheilanthes* (*C. angustifolia* Humb., Bonpl. & Kunth, *C. aurea* Baker, *C. inaequalis* (Kunze) Mett.), *Chrysochosma* (*C. lemmmonii* (D.C.Eaton) Pic.-Serm.). There is not enough known about the correlation of ecology and starch grain deposition in the roots of cheilanthoid ferns.

3. Starch grains in fern roots

The deposition of starch grains is not uncommon in the roots of ferns. They are often found in cells of the cortex and pericycle. However, all these roots are unmodified at least in part. Only three taxa possess modified parts of the roots for the storage of starch grains. In all other cases the use of the roots as storage organ is more or less facultative and the amount correlates with growth conditions and seasons (Schneider, 1996). Starch grains are often found in roots of ferns growing in northern Europe and northern North America for instance in *Athyrium*, *Blechnum*, *Osmunda*, *Thelypteris*. Roots, collected at the end of summer show a high amount of starch grains but starch grains are absent in the root cortex in the late spring. Most fern genera store starch grains preferably in the root cortex while only a few species of cheilanthoid ferns possess starch grains in the root cortex. Most cheilanthoid ferns have starch grains in the pericycle cells, which are sometimes enlarged. The root cortex cells are often perishable and collapsed in the older parts of the roots. The dead cortex cells form a dense sheath around the central cylinder. This is composed of collapsed cells. In contrast the pericycle cells are living at least as long as the root meristem. This type of root cortex is called the *Notholaena*-type

(Schneider, 1996) and is found only in the Cheilanthoideae (Pteridaceae) and Anemoideae (Schizaeaceae). As shown, the occurrence of this root type correlates with the distribution of the taxon in xeric environments (Schneider, 1996). The roots are a part of a xeric fern syndrome which include various character complexes such as leaves, indumentum and roots. This correlation of morphological characters and ecology was first recognised by Hevely (1963) for cheilanthesoid ferns in Arizona.

The starch grains found in fern roots always have the structures described from Czaja (1978) for other parts of the plant. This type is called pteridophyte-starch grains. Such grains are found only in few seed plants (Czaja, 1978).

4. Biological importance of storage roots

The use of roots as storage organs may correlate with the need to survive a long period without a positive photosynthesis rate. Starch grains are deposited in the rhizome, roots and/or in the base of the petiole (trophopods) in many ferns growing in temperate regions. The starch is mobilised at the beginning of the growing season and stored from the middle to the end of this season. The roots may play an important role as storage organs if the shoot is small and the leaves wither completely in the winter and/or dry season. A similar cycle may exist in xeric ferns. However, it is known that the leaves of some cheilanthesoid ferns are poikilohydrous (Iljin, 1931) and recover after the dry period. This is especially the case in species with dense indument covering the leaves. In these species the reserves of assimilates are deposited in shoot, leaves and/or roots. In contrast the leaves of *C. bolborrhiza*, *Afropteris* and *Adiantum* lack a protecting indumentum. Additionally, they possess a creeping relatively thin rhizome. The leaves may be completely lost during the dry season and the relatively protected root can be an ideal storage organ. This may be especially the case in habitats with regular fires in the dry period. *C. bolborrhiza* and *Afropteris* are terrestrial ferns in forests with dry seasons and consequential regular fires. Both have also leaves of similar shape and size. In contrast, *Adiantum diaphanum* is an epiphyte in regions that have often also dry seasons and fires. Having storage roots can be one strategy where leaves are often lost in the dry, resting season. However, in most ferns the rhizome and petiole serve as storage organs. In evidence one may quote the cheilanthesoid from Zambia, growing in areas with frequent fires in the dry season: no storage roots are known from these ferns (Kornas, 1978a, b).

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BOOK REVIEWS

BIBLIOGRAPHÍA SOBRE GAMETOFITOS DE HELECHOS Y PLANTES

AFINES B. Pérez-García & R. Riba. Continued from p. 268

... or by looking at authors likely to have published on the subject. Any ignorance of either and articles on fossil gametophytes may well be missed - unless one is willing to search the full listing!!

Journals, symposia volumes and books have been searched for relevant literature, but it is unfortunate, I believe, that the actual resources examined have not been stated. Because of this, biologists, familiar with the journals and search resources pertinent to their area of interest, cannot easily identify those which have not been covered in the preparation of this volume. This could be significant to some researchers. For example, palaeobotanical journals do not appear to have been included despite the fact that some palaeo-articles which have occurred in non-palaeo-specific journals are given, and this should have suggested that the former were worth looking at. The result is the absence in the Bibliography of some pertinent references. There is also an absence of theses, suggesting that listings of theses, such as *Dissertation Abstracts* (Published by Ann Arbor University Microfilm International. Published in parts; part C is world-wide in its listings.) and *Index to Theses Accepted for Higher Degrees in Universities of Great Britain and Ireland* (Published by ASLIB [Association of Specialist Libraries and Information Services], London.) have not been explored. I know of one excellent thesis which should have been included and there must be others.

It is puzzling why a volume which is going to be an important reference source for workers world-wide for many years to come, is published in Spanish. I am not arrogant enough to think that all scientific publications should be in English but, because of its potential usefulness, one must query why it was not published in English or bilingual. The volume would be more accessible if it had been; the amount of text which needed to be translated is very small. Fortunately, for an English-speaking person at least, one can guess at the majority of the words of the sub-headings of the *Key* and *Thematic Index* and access to a Spanish scientific dictionary will resolve the rest. (It is not essential to be able to read the *Introduction* to use the Bibliography.)

A very small number of typographical errors have slipped through, e.g. *Pteridiums* in Bell (1960). Despite the deficiencies noted above, this is a valuable contribution to the study of the haploid phase of pteridophytes and the authors are to be congratulated on its compilation.

Jennifer M. Ide

FLORA DE MEXICO: Dryopteridaceae R. Riba & B. Pérez-García. 1999. 48 pp. Illus. Consejo Nacional de la Flora de México, Mexico, D.F. US\$23.00. ISBN 968-6144-18-8. Paperback.

FLORA DE MEXICO: Marsiliaceae R. Riba & B. Pérez-García. 1999. 17 pp. Illus. Consejo Nacional de la Flora de México, Mexico, D.F. US\$15.00. ISBN 968-6144-22-6. Paperback.

These books form parts 4 and 5 of the fern volume (Volume 6) of the *Flora de México*. The taxonomic information on Dryopteridaceae and Marsiliaceae is thorough, concise and clearly laid out in a way that appears user friendly and readily accessible even to non specialists. Line drawings are present for many species, they are beautifully produced and for those species illustrated, they are of great help in identification. It would have been beneficial to have provided small sketches to illustrate the main characters which differ between those species illustrated in full and other species in the same genus. Many specimens are cited and a distribution map is provided for every species. The treatments are well referenced, providing a guide to further literature at the end of each generic description and family treatment.

In the treatments of both Dryopteridaceae and Marsiliaceae the genera and species are arranged in alphabetical order which has the advantage that it is relatively easy to find a particular genus or species if you know the accepted name. Unfortunately if you have a name for a particular plant which is not the currently accepted name the Flora de México is harder to use as page numbering is not given in the index of scientific names. In small fascicles such as Dryopteridaceae and Marsiliaceae it is possible to search the work for synonymy however, for larger families finding a particular name could be frustrating. I would find the work more accessible if all the taxa were numbered and placed in phylogenetic order with all scientific names given page references in the index. A treatment based as far as possible on species relationships allows browsing through nearby species descriptions to compare characters and can be very helpful when unsure of an identification. For their size these treatments are rather expensive to buy if you are purchasing them outside Mexico, (working out at UK£14.30 and UK£9.30 respectively), however they form part of a very important work on one of the most biodiverse countries in the world. They will be of great use to botanists interested in Central American ferns and to non specialists working in land use and conservation projects in the region. Treatments of the Marattiaceae, Hymenophyllaceae and Dicksoniaceae are also available.

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HUMAN HEALTH RISKS FROM FERN SPORES? - A REVIEW

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INTRODUCTION

Ferns do not usually get bad publicity in relation to human health. The most famous exception to this rule is bracken (the genus *Pteridium*), which has been implicated as a health hazard in scientific literature, agricultural publications and British national newspapers (see Fig. 1 and Table 1)*. There are reports relating to adverse health effects of a few other species, but these largely concern livestock. Most cases relate to consumption of green leaves (fronds) or rhizomes, which is undoubtedly most unwise for bracken (see Table 1). Some reports, however, indicate that bracken spores may also pose a health risk (see Fig. 2). This has been recognised by the Forestry Commission, who issue their workers with face masks during the sporing season, and the Scout Association (pers. comm.) who discourage their members "from walking through bracken patches and from using bracken to construct backwoods shelters".

In assessing the risks posed by fern spores to human health there are two main aspects to consider. One is whether the spores of any fern species represent a health hazard. The other is to define the extent to which humans are exposed to fern spores, so as to assess the potential risk arising from this exposure. The aim of this review is to examine our current understanding of the potential health risks posed by bracken spores and to consider the extent to which spores of other fern species may present a human health hazard.

PTERIDOPHYTE SPORES AND ALLERGIC REACTIONS

Most reports of ill effects caused by fern spores relate to allergy-like symptoms. Devi *et al.* (1982, 1989) tested skin reactions to whole fern spores and sporangia in rats. All of eight fern species tested produced some kind of reaction. The ornamental species *Adiantum peruvianum*, *Anemia rotundifolia*, *Christella parasitica* and *Thelypteris augescens* induced histopathological changes

*In spite of this journal's requirement for plant (and animal) authorities, these have in some places been left out. The reason is that they were not presented in the original papers reviewed and we consider it scientifically indefensible to add them in the absence of assurances of taxonomic accuracy.



Figure 1. A range of newspapers and magazines have reported the adverse health effects caused by bracken.

Table 1. Fern species whose vegetative tissues (fronds and/or rhizomes) have been reported to induce adverse health effects in various animals.

| Species | Adverse health effects | Animals | Reference |
|-----------------------------|--|---------------------|---|
| <i>Cheilanthes sieberi</i> | acute toxic syndrome | cattle | Clark & Dimmock, 1971 |
| | bovine enzootic haematuria | cattle | Clark & Dimmock, 1971 |
| <i>Dryopteris filix-mas</i> | paralysis | tape-worm | Linnell, 1955 |
| | death | insects | Hartzell, 1947 |
| <i>Notholaena distans</i> | fits of trembling, fatal respiratory paralysis | cattle, goat, sheep | Radeleff, 1964 |
| | fits of trembling, fatal respiratory paralysis | cattle, goat, sheep | Radeleff, 1964 |
| <i>Pteridium aquilinum</i> | urinary bladder tumours, haematuria | guinea pig | Bringuier <i>et al.</i> , 1995 |
| | urinary bladder tumours, haematuria | llama | Peauroi <i>et al.</i> , 1995 |
| | thiamine deficiency | monogastric animals | Smith & Seawright, 1995 |
| | stomach cancer | human | Evans, 1976; Galpin <i>et al.</i> , 1990 |
| | apathy, death | pig | Evans <i>et al.</i> , 1972 |
| <i>P. sp.</i> | bright blindness | sheep | Barnett & Watson, 1970 |
| | bovine enzootic haematuria | cattle | Rosenberger & Heeschen, 1960 |
| | decrease in leukocytes and thrombocytes | cattle | Evans <i>et al.</i> , 1958 |
| <i>P. sp.</i> | oesophageal carcinoma | human | Kamon & Hirayama, 1975 |

(i.e. pathological changes detectable via microscopy). The changes started to subside when the exposure was interrupted. In rats exposed to spores of *Acrostichum aureum*, they observed sloughing of the stratum corneum and in those exposed to *Diplazium esculentum*, a slight skin oedema. Exposure to spores of *Abacopteris multilineata* and *Drynaria quercifolia* caused a slight slackening (laxity) of the skin.

Devi *et al.* (1979) used antigens prepared from spores of the ferns *Adiantum peruvianum* Kaulf., *Blechnum occidentale* L., *Cyclosorus parasiticus* (L.) Tardieu and *Microsorium punctatum* (L.) Copel. in clinical allergy tests on 136 patients of

Figure 2. Possible health effects suffered as a result of inhaling bracken spores have been highlighted in several papers and magazines. (Both of the illustrated reports herein depicted species other than bracken to illustrate the accounts!)

various ages and with different allergy backgrounds. A strong allergic reaction was induced by *A. peruvianum* and *M. punctatum* in 3-5% of the subjects.

Geller-Bernstein *et al.* (1987) reported positive skin test reactions to aqueous fern spore extracts in a group of patients suffering from hay-fever. Seven common household ferns were tested. *Dryopteris setigera* gave the strongest reaction. *Adiantum capillus-veneris*, *Cyrtomium falcatum* and *Pteris vittata* induced slightly milder reactions. *Nephrolepis exaltata*, *Platycerium bifurcatum* and *Polypodium glaucum* did not give any detectable reactions. Similar results were obtained by Bunnag *et al.* (1989) when spore extracts of *Achrostichum aureum* L. were used in skin tests and nasal provocation tests. The tests were carried out on patients

suffering allergic health problems and on non-allergic patients. Of the former group, 60-70% reacted to the fern spore extracts. Only 15-20% of the latter group did so.

In 1978, Hausen & Schulz reported contact dermatitis caused by *Arachniodes adiantiformis* (G.Forst.) Tindale in a florist. The dermatitis was traced to an allergen which was not specifically ascribed to the spores, but was found present in the plant only during the period of sporogenesis. At that time it was present in the fronds, sporangia and spores. Kobayashi (1980) reported a case of asthma in a dental technician caused by exposure to spores of *Lycopodium*.

In addition to the published literature we have been given anecdotal reports of adverse health effects of fern spores, such as skin rashes in horticulturists working with ferns in glasshouses (Hoshizaki, pers. comm.) and respiratory problems (e.g. constricted breathing and sneezing) and watering of the eyes in fern spore collectors and herbarium curators (Barrington, pers. comm.; Camus, pers. comm.).

DNA-DAMAGING POTENTIAL AND CARCINOGENICITY OF PTERIDOPHYTE SPORES

The DNA-damaging potential of *Pteridium* spores was reported by Povey *et al.* (1995, 1996). They showed that the DNA of mice fed spores or an aqueous extract of fronds from *Pteridium aquilinum* developed adducts, i.e. covalent modifications of the normal bases present in the DNA (O'Connor & Margison, 1990), in the gastrointestinal tract within 6-24 hours of the treatment. The adducts were detected by the ³²P-postlabeling assay (Gupta & Randerath, 1988). Preliminary studies of three other homosporous ferns, *Anemia phyllitidis* (L.) Sw., *Pteris vittata* L. and *Sadleria pallida* Hook. & Arn. indicate that their spores also induce DNA adducts when fed to mice (Winston, 1998). Research in our laboratory is currently extending these studies.

Evans (1984) showed that spores of *Pteridium aquilinum* caused leukaemia, gastric and mammary tumours in laboratory mice. Fifty mice were force-fed 0.2 g bracken spores on ten occasions and another 50 were used as controls. The animals in the control group were all alive after a year, whereas 39% of the animals fed bracken spores had developed tumours and died. Villalobos-Salazar (1995) reported lung and mammary tumours in mice caused by intake of *Pteridium aquilinum* spores. Sixty Swiss albino mice (30 of each gender) were fed a diet containing whole bracken spores for 48 weeks. Another 120 animals (60 of each gender) were used as controls and fed a basic grain diet. Mammary tumours developed in 26.6% of the female mice fed a bracken spore-containing diet, compared to 3% among the female controls, a difference that was statistically significant. Villalobos-Salazar (1995) also reported enlargement of the thymus, lower bodyweight and shorter life-span in the mice fed bracken spores compared with the controls. Spores of other ferns and pteridophytes have received less attention than those of bracken, but it is clear that *Lycopodium* spores can cause granuloma (e.g. Antopol, 1933; Erb, 1935).

THE CARCINOGENIC CONSTITUENT(S?) OF BRACKEN FERN

The convincing evidence that bracken spores are carcinogenic suggests that there is at least one carcinogenic compound present in the spores and it is possible that it would be the same compound as in the rest of the plant.

There has been some argument about which compound(s) in *Pteridium* tissues possess the DNA damaging and carcinogenic property. Evans & Osman (1974) suggested that the carcinogenesis was partly due to shikimic acid. This was based on a study in which 9 out of 14 mice treated with 1-100 mg shikimic acid developed cancerous or precancerous lesions within 70 weeks. However, Hirono *et al.* (1977) in a similar study, in which twelve rats (six of each gender) were fed a diet of 0.1% shikimic acid for 142 days, did not find any evidence to support the carcinogenic property of shikimic acid. The dose of shikimic acid per animal was more than twice that contained in an amount of bracken sufficient to induce tumours in 100% of animals in feeding experiments (Hirono *et al.*, 1977). El-Mofty *et al.* (1987) suggested that α -ecdysone was the carcinogenic compound of *Pteridium*. This compound is a natural constituent of *Pteridium aquilinum* (Kaplanis *et al.*, 1967) and has been reported to induce neoplastic lesions in the toad *Bufo regularis* (El-Mofty *et al.*, 1987). Quercetin and kaempferol have also been suggested to be the carcinogens of *Pteridium* (see Smith & Seawright, 1995). The carcinogenicity of quercetin has been investigated several times (see Ito, 1992) and though the results are somewhat controversial, they are mostly negative. Moreover, quercetin is a common compound in various fruits and vegetables and it has even been discussed as a possible anti-cancer drug (see Ito, 1992). Kaempferol is present in *Pteridium* and has been shown to be mutagenic, but there is doubt about its carcinogenic effects (see Smith & Seawright, 1995). Shikimic acid, quercetin and kaempferol have all been designated "unclassifiable as to carcinogenicity to humans" by the IARC (IARC, 1983; IARC, 1987). According to the IARC, there is limited evidence to suggest quercetin is carcinogenic to experimental animals, but inadequate evidence for shikimic acid and kaempferol.

In 1983, two research groups independently isolated and characterised a norsesterpene glucoside (van der Hoeven *et al.*, 1983; Niwa *et al.*, 1983) from *Pteridium aquilinum*. van der Hoeven *et al.* (1983) also confirmed the ability of this compound to cause mutations in *Salmonella* bacteria. The compound, named ptaquiloside, is unstable under both acid and alkaline conditions (Agnew & Lauren, 1991). In an alkaline environment it generates a dienone which can act as a very strong alkylating agent (Ojika *et al.*, 1987). This dienone, also known as activated ptaquiloside, has recently been reported to cause carcinomas in rats (Shahin *et al.*, 1998). Ptaquiloside has been reported to withstand boiling quite well (Hirono *et al.*, 1978), but this property is not generally accepted. According to Oelrichs *et al.* (1995) temperatures above 40 °C during isolation of ptaquiloside decrease the final yield of the compound. It has been shown that ptaquiloside treatment of thymocytes (cultured thymus cells) *in vitro* induces DNA adducts that are detectable by the ^{32}P -postlabeling assay (Smith & Seawright, 1995).

Ptaquiloside is ready soluble in water (Ojika *et al.*, 1987). This property lends support to the concerns about drinking water from sources close to *Pteridium*-infested areas (Wells & McNally, 1995) and milk from cows grazing in such areas (Alonso-Amelot *et al.*, 1996; Alonso-Amelot, 1997). So far ptaquiloside has only been found in one other fern species: *Cheilanthes sieberi* (Smith *et al.*, 1989), in which it was present in all tissues except the spores. We have not found any reports on attempts to extract and identify ptaquiloside from *Pteridium* spores.

HUMAN EXPOSURE TO FERN SPORES

Though measurements of human exposure to airborne biological particles are common (see e.g. Lacey & Dutkiewicz, 1994; Anon., 1996), data on fern spores are very scarce. Fern spores are usually either grouped with pollen or not measured. Extant data concerning fern spores are dominated by bracken studies conducted in out-door environments. Two types of methods have been used in these studies: personal and static air sampling. A few studies have been carried out by people using personal samplers. These instruments are designed to draw in air at a rate comparable to human breathing and to deposit any particulate material in the air on to a filter which can be examined under a microscope to determine the amount of the material potentially inhaled. Such studies suggest that a person walking through a stand of bracken which is sporing may inhale around 50,000 spores in 10 minutes (Smith, 1996). This corresponds to an air spore concentration of roughly 800 spores l^{-1} (calculated on a tidal volume of 0.5 l and a respiratory rate of 12 times min^{-1} (Guyton, 1987)).

Other studies have involved static air sampling in various locations. A short-term air sampler placed in a fertile bracken stand in Wales during the sporulation season recorded 800 spores l^{-1} air over some days (Povey *et al.*, 1995). A long-term air sampler placed 20 cm from a bracken stand throughout the sporulation season often recorded a daily mean of 750 spores m^{-3} air (equivalent to 0.75 spores l^{-1}). Most of the spores were caught in the morning and very few at night (Lacey & McCartney, 1994). In an on-going ten-year study a long-term volumetric spore trap has been placed on a roof-top 21 m above the ground in Edinburgh, UK. The air concentration of bracken spores has at no time exceeded 2 spores m^{-3} (equivalent to 0.002 spores l^{-1}). The closest sporing bracken stands are 1.6 and 5.5 km away (Caulton *et al.*, 1995; Caulton, pers. comm.). There are closer bracken stands, but they are infertile. Hence chronic exposure can occur in the U.K. in areas remote from bracken stands, but the very low dose suggests that this is unlikely to pose a human health risk. Elsewhere this may be different: e.g. in Bangkok, Bunnag *et al.* (1989) performed air sampling over a year with a Rotorod trap. The trap collects airborne particles on quickly rotating U-shaped arms coated with a sticky film. Fern spores were found to be the third most common airborne propagule in that area, occurring with a frequency of 17 %. Only pollen of sedges (23 %) and grasses (20 %) was more frequent.

It appears from the above mentioned studies that the collected spore load diminishes drastically with increasing distance from the spore source. This agrees with the results of studies designed to measure dispersal distance of fern spores. Nearly all (95%) trapped spores of an 8 m high tree fern were detected within 10 m of the plant (Conant, 1978) and 90% of trapped *Dryopteris dilatata* spores were deposited within 3 metres of the sporophyte in natural conditions (Glaves, 1991). From studies of spore dispersal patterns in *Osmunda* and *Dryopteris* Raynor *et al.* (1976) concluded that most spores settled within a short distance from the source and that only a few were carried further away. There are, however, reports of fern spores having travelled very long distances. Eight years after the formation of the volcanic island of Surtsey a *Cystopteris fragilis* plant was found growing in the bare

soil of the island (Fridriksson, 1975). This island is at least 20 km from the nearest possible source of spores. The Hawaiian islands are even further from possible sources and boast a rich and genetically diverse fern flora (e.g. Sheffield *et al.*, 1995). For more examples of long-distance spore dispersal in ferns, see Tryon (1986).

The problem, shared by all spore dispersal studies mentioned above, is that an unknown fraction of the total spore output is not trapped at all. Studies of moss spore dispersal distances (e.g. Stoneburger *et al.*, 1992) lend support to the contention of Conant (pers. comm.) that the trapped spores represent a very small proportion of the total. There have been too few studies on frond fertility or spore output to make generalisations about spore loads in air realistic.



Figure 3. The under-side of a sterile bracken frond shows no signs of sporangia along the pinnule edges. Inset shows indusial flap with no sporangia beneath.

It is important to note that while fertility is the rule for mature individuals of most ferns, infertility is frequent in bracken and, in most years and/or some locations, the majority of fronds are completely sterile (e.g. Conway, 1957; Dyer, 1989). Although a single fertile frond may indeed be capable of releasing up to 300,000,000 spores (Conway, 1952) and large stands may occasionally serve as a vast source of spores, the overwhelming majority of fronds and indeed stands of bracken studied in Scotland and the north of England during the autumn of 1998

were completely sterile (Wynn & Sheffield, pers. obs.). Infertility appears to be the most usual condition for these bracken stands, so it is little wonder that research has not revealed a link between acid soils and leukaemia clusters (Trotter, 1990). The study in question made the assumption that bracken could be mapped to acid soils and hypothesised that therefore the prevalence of leukaemia would be higher in those areas. There are no empirical data supporting the assumption that bracken has a preference for acid soils and the assumption that all bracken stands are a source of spores is untenable. It remains to be seen whether adverse health effects can be linked to proximity to **sporing** bracken stands.

Research is underway in our laboratory to attempt to determine the environmental and genetic factors that govern sporing behaviour of *Pteridium*. In the meantime we suggest that most of the media hype and public fear surrounding bracken stands is unwarranted. Simple inspection of the underside of fronds quickly distinguishes fertile from infertile material, as is shown in Figures 3 and 4, and where fronds are infertile, there is no cause for alarm or need for humans to take precautions against airborne contamination by this species.

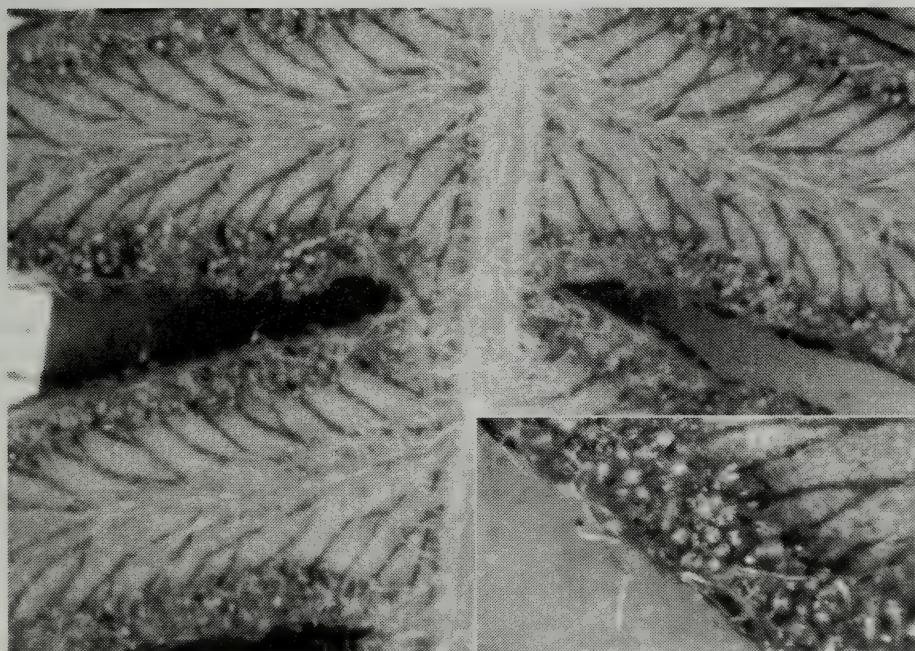


Figure 4. Dense clusters of sporangia line the edges of the under-side of a fertile bracken frond. Inset shows numerous sporangia, which would be visible to the naked eye. Individual spores would be revealed by a hand lens.

Only very limited pilot data are available for air concentrations and potential inhalation rates of fern spores in indoor environments, such as plant nurseries and conservatories (Winston, 1998). The steady increase in the popularity of ferns as ornamental plants (Gress, 1996) has prompted us to expand and extend these pilot

studies. Until such time as we are able to publish our findings we **would** advise caution when handling fertile fronds or fern spores. Potential risks from inhalation are easy to avoid by the simple, quick and cheap application of a face mask such as used by industrial workers to avoid inhaling particles (see Fig. 5).



Figure 5. It is advisable (and easy) to take some precautions when handling fertile fronds or fern spores. In the background, one of the many makes of face masks suitable for these cases.

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BOOK REVIEW

**FLORA MALESIANA SERIES II – FERNS AND FERN ALLIES. VOLUME 3
POLYPODIACEAE, DAVALLIACEAE, AZOLLACEAE, CHEIROPLEURIACEAE,
EQUISETACEAE, MATONIACEAE, PLAGIOGYRIACEAE.** Various authors. 1998.
iv + 334 pp. Illus. Foundation Flora Malesiana, Leiden. Price NLG100.00. ISBN 90-71236-
39-0. Paperback.

A long-awaited essential pteridophyte text has now been published! Volume 3 of Flora Malesiana Series II contains descriptions of 228 species in the following families: Polypodiaceae (183 species), Davalliaceae (31 species), Azollaceae (1 species), Cheiroleuriaceae (1 species), Equisetaceae (1 species), Matoniaceae (4 species) and Plagiogyriaceae (7 species). Descriptions and distributions are given for each family, genus and species, and keys are also provided for genera and species. Volume 3 differs from its two predecessors in being stand-alone and complete with its own index, thus avoiding the problems of some earlier user-unfriendly part numbers which had no individual index, but which were indexed in the final part of the volume. Another departure from the format of previous volumes is the very practical alphabetical arrangement of genera and species within families (except for the very small ones). Another welcome change is the inclusion of regional keys to species, in addition to the main key to species in Malesia, for the two largest genera *Microsorum* (31 species) and *Selliguea* (49 species). This innovation should be of great use to regional botanists who may have been intimidated in the past by the huge Malesia-wide keys to genera such as *Cyathea* (191 species) and *Sphaerostephanos* (152 species).

The accounts of Polypodiaceae and Davalliaceae are based on numerous previously published generic revisions. My main criticism of these revisions is that they seem to be almost overwhelmingly based on herbarium material and are backed up by apparently limited field knowledge of the taxa. In some genera, e. g. *Selliguea*, there is constructive discussion of morphological regional variation within some of the more widespread species which explains much of the synonymy. However as a field botanist with an in-depth knowledge of the pteridophyte flora of a few parts of Malesia, but less knowledge of the range of variation in the very widespread species, I thought some of the lumping rather extreme. Sure, identification is made easier if you have fewer taxa, but severe lumping is not conducive to keeping field botanists happy. *Davallia repens* has more than a page and a half of synonymy in this work, some of it no doubt richly merited, but in a small area of Borneo well-known to me four morphologically distinct taxa of this aggregate species are known and they are at least in part ecologically separated. '*Davallia vestita*' is an epiphyte at higher altitudes than the other three. '*Davallia pusilloides*' is a low altitude epiphyte and lithophyte restricted to limestone habitats. '*Davallia repens sensu stricto*' is also a low altitude epiphyte and lithophyte of limestone, but has not been found in the same areas as '*D. pusilloides*'; it also occurs on shale and sandstone substrates in lowland and montane forest. '*Davallia subvestita*' (the species combination has been made for *Humata* but is omitted here) is an epiphyte of montane forest on sandstone at an altitude intermediate between '*D. repens*' *sensu stricto* and '*D. vestita*'. It is disappointing to find no means of distinguishing these taxa in this volume.

Yes, this indispensable volume has flaws, but it is still required by all with an interest in the pteridophyte flora of Malesia and adjacent areas.

Lutetia Strange

COLONISATION OF POLDER WOODLAND PLANTATIONS WITH PARTICULAR REFERENCE TO THE FERNS

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Key words: clayey woods, colonisation, ferns, reclaimed polders, woodland species.

ABSTRACT

The plant species of 53 woods on clay soils in two reclaimed polders of the Zuiderzee, Netherlands: Noordoostpolder and O.-Flevoland, were surveyed. Total species number is correlated with woodland age and area, and distance to human habitation, whereas the number of purely woodland species is correlated with age and area. The number of fern species is correlated with woodland area. Monitoring demonstrated an effect of age as well. Colonisation by ferns is most rapid in coniferous plantations but deciduous woodland stands with *Fraxinus excelsior* support more species with time. The presence of trenches within woodlands promotes species diversity, with calcicole species particularly associated with them, but always present at low density. Observations as to the ecology, numbers and persistence of fern taxa occurring in the polder woodlands, but rare in the Netherlands, are presented.

INTRODUCTION

In 1932 the Zuiderzee was closed and subsequently four polders were reclaimed. This study is restricted to two of them: the Noordoostpolder (reclaimed in 1942) and O.-Flevoland (reclaimed in 1958) (Fig. 1). For over a millennium these polders were part of the sea floor covered by some 3-4 m of water; fresh-water at first, brackish to salty over the last centuries. After reclamation a natural vegetation arose (marshes, reedland, sometimes grasslands, e.g. Feekes & Bakker, 1954; Bakker, 1957; Jans & Drost, 1995), which was completely cultivated within 15 years. More than 12,000 ha of woods were planted on clayey soils after cultivation and drainage. At the beginning no woodland species were present so primary colonisation had to take place. The following questions were formulated:

- (1) what landscape ecological factors have an impact on the colonisation of woodland species with particular reference to the ferns ?
- (2) which habitats are preferred by ferns ?
- (3) how quickly do ferns colonise newly planted woods ?
- (4) for what ecological reasons is there a difference in composition in ferns when comparing woodlands in the polders with those on the mainland ?

Some authors have pointed out that woodlands which are isolated in an agricultural landscape are habitat islands. The number of species in such woodland islands depends on area, degree of isolation and time of isolation (e.g Scanlan, 1981; Peterken & Game, 1984; Grashof-Bokdam, 1997).

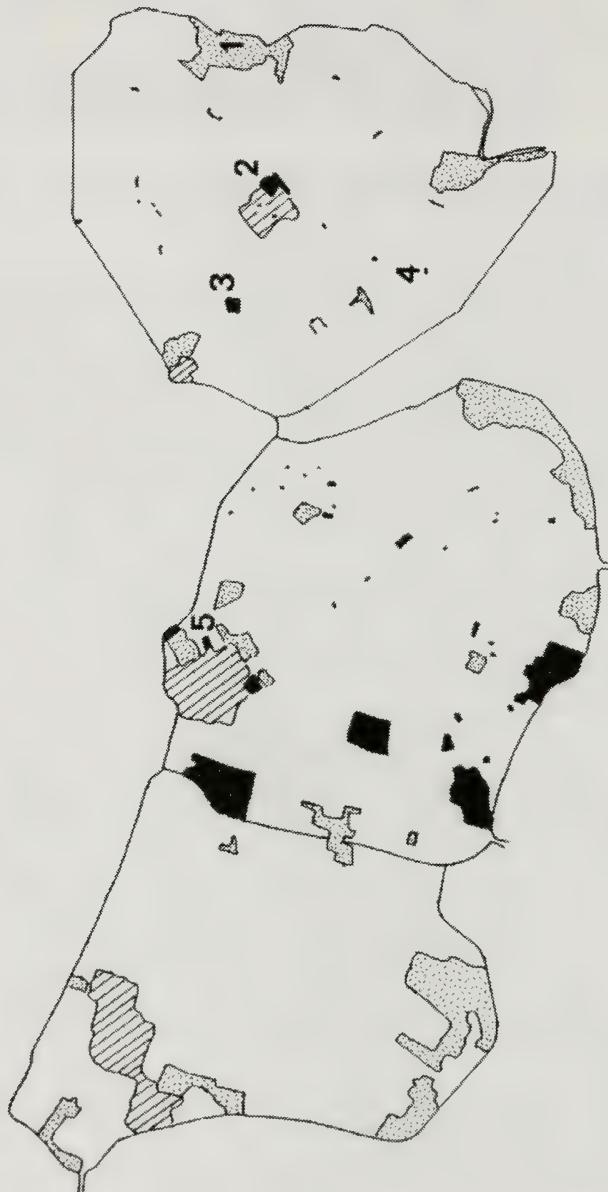


Figure 1. The woods examined in the province of Flevoland. Woods which were excluded (too young or not on clayey soil) are dotted. The following woods are mentioned in the text: 1 = Kuinderbos, 2 = Emmeloorderbos, 3 = Tollebeckerbos, 4 = Enserbos, 5 = Jagersveld.

Moreover the species richness of habitat islands may not always be explained in terms of the theory of island biogeography alone (McArthur & Wilson, 1967). The reason is that the number of species is not only a function of immigration and extinction rates, but also of habitat diversity, succession and the presence of a seedbank (Hermy, 1986). The studied woods are habitat islands surrounded by an intensively cultivated area. Isolation variables were selected in respect to the mainland and villages, due to the influence of man in other planted woods. Connectivity was not taken into account. Although 35 percent of the woods examined are linked with wooded banks these are rarely connected with other woods. Age, area and lutmum content (as habitat parameters) were taken into account.

Various trees and shrubs were planted, and we expected the most abundant colonisation of woodland species, including the ferns, in the more natural stands (*Fraxinus excelsior* L., *Salix alba* L.) corresponding with the *Fraxino-Ulmetum* (van der Werf 1991) in contrast to those of *Pinus* spp., *Acer pseudoplatanus* L. and *Fagus sylvatica* L. Since in the Kuinderbos the number of fern species was strongly correlated with trenches, we expected that woods drained by trenches would have more species than those without this habitat (Bremer 1980a, b). There was no reason to assume that other woodland species would prefer this habitat.

The *a priori* assumption was that anemochorous woodland species, especially ferns, would not to be influenced by isolation, as the species were presumed to be efficiently dispersed by wind. This had been demonstrated in the Kuinderbos, in the reclaimed Noordoostpolder, where 27 fern taxa were found, with first records in the Netherlands for various taxa. Here, most species were established after planting on calcareous sands deposited on peat (Bremer 1980a, b). For the other woodland species we expected that isolation would be important, especially in relation to the mainland as source of diaspores. For example, the colonisation of road verge plants started from the mainland and old roadsides were richer in species than young ones (Nip-van der Voort *et al.*, 1979).

We expected ferns to be the first species to colonise young woods and a saturation of the number of fern species with ageing. In the Kuinderbos the number of fern species was saturated within 30 years. We had no reason to assume that colonisation in the clayey woods would differ from those on other substrates.

In The Netherlands deciduous woods on drained, clayey soil resulted from afforestation. The best examples are those created at estates from the 17th century onwards (some 5,000 ha in The Netherlands, including undrained soils, Dirkse, 1993). The area of clayey woods prominently increased in the young polders, where more than 12,000 ha has been planted (Bremer, 1997). On the mainland no rare ferns, according to Dutch standards, were found and *Dryopteris filix-mas* (L.) Schott was most common. There was no reason to assume that in the polders the composition of the fern flora would be different.

THE STUDY AREA

In the polders over 8,300 ha of woods were laid out. In the Noordoostpolder 28% was afforested on clayey soils, in O.-Flevoland 73% of the woods were planted on these soils.

The composition of the clayey soils can differ from slightly clayey soils (5-12% lutum) to heavy clay (> 25% lutum), being always calcareous due to the high density of shells. Most woods are well drained, the phreatic level usually being more than one

meter under surface level in summer. Only a few of the examined woods are wet in winter or spring (average phreatic level < 0.5 m), due to seepage or water accumulation (slightly clayey soils). Here trenches were dug for drainage, with a density of up to 1.1 km per ha, and on average c. 0.5 m deep.

Various trees were planted, particularly *Populus × canadensis* Moench, *Quercus robur* L., *Fraxinus excelsior*, *Fagus sylvatica*, *Salix alba* and *Acer pseudoplatanus*. At some localities species such as *Pinus* spp., *Picea* spp. and other foreign tree species were planted. Each wood is divided into many woodland parcels separated from each other by ditches. Each parcel is bisected (lengthwise) by a parcel-path (rides). The parcels are drained by trenches running from the parcel-paths to the ditches.

METHODS

The area of investigation is situated in the province of Flevoland, The Netherlands. In the period 1990-1994 53 woods were surveyed and woodland species mapped in the Noordoostpolder and O.-Flevoland (Fig. 1). Various younger and older woods were visited on the mainland to act as a comparison with the woods on the former sea floor. Field work was carried out in spring when chances of finding all species are best. The species were designated by Tansley's code (Tansley, 1946). Small woods were visited once, sometimes twice, larger woods more frequently. For the respective species, including rare fern species, substrate and composition of the canopy were noted and the relationship to trenches. In order to compare the types of stands, the maximum number of wood inhabiting species per ha, per stand was surveyed for 14 woods.

Table 1. Dependent and independent variables used in the study on woods on clayey soils in Flevoland.

Independent variables

patch size

lnA = natural logarithm of area

habitat quality

kl = lutum content of the soil (upper dm)

isolation

d1 = distance to the mainland

d2 = distance to large wooded area on the mainland

ld3 = natural logarithm of distance to nearby wood, larger than 1 ha

ld4 = natural logarithm of distance to nearest village

other variables

l = age

Dependent variables

s1 = number of species per wood (shaded habitat)

s2 = number of wood inhabiting species (corrected for some sown species) per wood

s3 = number of fern species per wood

On the clayey soils a *Fraxino-Ulmetum* is evolving. Species correlated with this syntaxon were designated as woodland species (Westhoff & Den Held, 1969; van der Werf, 1991). Other species with an optimum in other types of wood and wood edges in the Netherlands were also taken into account.

Independent variables such as age and area were calculated using information gathered from plantation maps, isolation variables from topographic maps (at a scale of 1:25,000) and lutum from soil maps (with composition of the soil profile). The dependent variables were analysed by linear multiple regression. Independent variables (Table 1) were added by using stepwise forward selection (Norusis, 1986). Because frequency distributions of some of the independent variables were skew, they were transformed logarithmically. As level of significance $p=0.05$ was used. For some regressions the nominal Tansley code was transformed to an ordinal scale.

In the Jagersveld monitoring has been going on since 1979. During most years all rare ferns on trench banks were mapped, the number of fronds per specimen counted and the length of the longest fronds measured. When specimens were found for the first time their age was estimated by using demographic data from the Kuinderbos (*Asplenium scolopendrium* L., unpublished data; *Polystichum setiferum* (Forssk.) Woyn., Bremer, 1995).

At three medium-sized woods the colonisation was monitored since c. 1970. Estate woods on the mainland, planted in the 17th or 18th century, were used as reference. Near Zwolle (province of Overijssel) a recently planted wood was monitored during 15 years.

RESULTS

Species and habitat islands

In the 53 woods 135 plant species were detected; 42 designated as woodland species, including 12 fern species (Table 2). *Ribes rubrum* L. was the most frequent phanerogam (77% of the woods), *Dryopteris filix-mas* the most frequent fern (43% of the woods). *Galium aparine* L., *Poa trivialis* L., *Taraxacum* section *Vulgaria* and *Urtica dioica* L. are most common on the wood floor. All fern species known from other Dutch clayey woods were detected and 75% of the other woodland species, although many species only appeared at low density, indicating the beginning of colonisation. Various species of ancient woods, such as *Carex sylvatica* Huds. and *Ranunculus auricomus* L. known to be poor colonists were not detected. Various ferns such as *Polystichum* spp., *Dryopteris affinis* (Lowe) Fraser-Jenk. and *Asplenium scolopendrium* were found, but are absent from the woods on clayey soils on the mainland.

A correlation matrix for all variables (Table 1) is given in Table 3. The area is not correlated with any of the other independent variables. Age is correlated with all isolation variables. Older woods are situated nearer to the mainland, more isolated from other woods and closer to the villages. The dependent variables were all correlated with each other. The number of species per wood was correlated with area, age and distance to the villages. 59% of the variation could be explained using a multiple regression model with all these variables. The total number of woodland species was correlated with area, age, distance to the villages and the distance to neighbouring woods larger than 1 ha. The best model with area and age explained 38% of the variation. The number of fern species per woodland was alone correlated with area (Fig. 2). No correlations were found with isolation and age (Table 4).

Table 2. List of woodland species in the surveyed woods on clayey soils in Flevoland. Dis. = dispersal types: An1 = dispersal by wind crossing large distances (ferns, orchids), An2 = dispersal by wind crossing restricted distances, An3 = dispersal by wind crossing short distances, B = barochorous species, En = endozoochorous species, Ep = epizoöchorous species, M = myrmecochorous species, H = hydratocchorous species. Hab. = other important habitats, s = wood banks, b = road verges. Np = frequency in polder woods (n = 53), N% = Np:53 x 100%, n = frequency in estate woods (n = 3), n% = n:3 x 100%. * = not observed during the survey, but observed previously.

| Name | Dis. | Hab. | Np | N% | n | n% |
|--|------|------|----|-----|---|-----|
| Ferns | | | | | | |
| <i>Dryopteris filix-mas</i> (L.) Schott. | An1 | - | 24 | 45 | 2 | 67 |
| <i>Dryopteris dilatata</i> (Hoffm.) A.Gray | An1 | - | 13 | 25 | 3 | 100 |
| <i>Athyrium filix-femina</i> (L.) Roth | An1 | - | 10 | 19 | 3 | 100 |
| <i>Dryopteris carthusiana</i> (Vill.) H.P.Fuchs | An1 | - | 7 | 13 | 0 | 0 |
| <i>Dryopteris affinis</i> (Lowe) Fraser-Jenks. | An1 | - | 5 | 9 | 0 | 0 |
| <i>Polystichum setiferum</i> (Forssk.) Woyn. | An1 | - | 3 | 6 | 0 | 0 |
| <i>Asplenium scolopendrium</i> L. | An1 | - | 3 | 6 | 0 | 0 |
| <i>Ophioglossum vulgatum</i> L. | An1 | - | 2 | 4 | 0 | 0 |
| <i>Polystichum aculeatum</i> (L.) Roth | An1 | - | 1 | 2 | 0 | 0 |
| <i>Polystichum lonchitis</i> (L.) Roth | An1 | - | 1 | 2 | 0 | 0 |
| <i>Polypodium vulgare</i> L. | An1 | - | 1 | 2 | 0 | 0* |
| <i>Dryopteris cristata</i> (L.) A.Gray | An1 | - | 1 | 2 | 0 | 0* |
| Other woodland species | | | | | | |
| <i>Urtica dioica</i> L. | Ep | b s | 53 | 100 | 3 | 100 |
| <i>Ribes rubrum</i> L. | En | s | 41 | 77 | 3 | 100 |
| <i>Ribes uva-crispa</i> L. | En | s | 30 | 57 | 3 | 100 |
| <i>Epilobium montanum</i> L. | An2 | - | 29 | 55 | 3 | 100 |
| <i>Alliaria petiolata</i> (M. Bieb.) Cavara & Grande | B | b s | 21 | 40 | 3 | 100 |
| <i>Geranium robertianum</i> L. | Ep | s | 21 | 40 | 3 | 100 |
| <i>Ribes nigrum</i> L. | En | - | 18 | 34 | 1 | 33 |
| <i>Rubus caesius</i> L. | En | s | 16 | 31 | 3 | 100 |
| <i>Rubus</i> section <i>Rubus</i> | En | s | 16 | 31 | 2 | 67 |
| <i>Geum urbanum</i> L. | Ep | - | 16 | 30 | 3 | 100 |
| <i>Epipactis helleborine</i> (L.) Crantz | An1 | b s | 16 | 30 | 0 | 0 |
| <i>Rubus</i> section <i>Corylifolia</i> | En | s | 15 | 28 | 1 | 33 |
| <i>Ranunculus ficaria</i> L. | B | b s | 14 | 26 | 3 | 100 |
| <i>Cardamine flexuosa</i> With. | An2 | - | 13 | 25 | 3 | 100 |
| <i>Listera ovata</i> (L.) R.Br. | An1 | - | 6 | 11 | 2 | 67 |
| <i>Veronica hederifolia</i> L. | M | s | 6 | 11 | 2 | 67 |
| <i>Silene dioica</i> (L.) Clairv. | An3 | b s | 5 | 9 | 1 | 33 |
| <i>Chelidonium majus</i> L. | M | - | 4 | 8 | 1 | 33 |
| <i>Rubus idaeus</i> L. | En | - | 4 | 8 | 1 | 33 |
| <i>Circaeaa lutetiana</i> L. | Ep | - | 3 | 6 | 3 | 100 |

| Name | Dis. | Hab. | Np | N% | n | n% |
|--|------|------|----|----|---|-----|
| <i>Stachys sylvatica</i> L. | Ep | - | 3 | 6 | 2 | 67 |
| <i>Lonicera periclymenum</i> L. | En | - | 3 | 6 | 1 | 33 |
| <i>Scrophularia nodosa</i> L. | An3 | b | 2 | 4 | 3 | 100 |
| <i>Poa nemoralis</i> L. | An3 | - | 2 | 4 | 3 | 100 |
| <i>Hedera helix</i> L. | En | - | 2 | 4 | 3 | 100 |
| <i>Carex remota</i> L. | H | - | 1 | 2 | 3 | 100 |
| <i>Fragaria vesca</i> L. | En | - | 1 | 2 | 2 | 67 |
| <i>Impatiens parviflora</i> DC | Au | - | 1 | 2 | 1 | 33 |
| <i>Chaerophyllum temulum</i> L. | Ep | - | 1 | 2 | 1 | 33 |
| <i>Deschampsia caespitosa</i> (L.) Trin. | Ep | - | 1 | 2 | 1 | 33 |
| <i>Ilex aquifolium</i> L. | En | - | 1 | 2 | 1 | 33 |
| Woodland species, characteristic for the <i>Fraxino-Ulmetum</i>, not found in the surveyed wood, found in woods on other soil types | | | | | | |
| <i>Rumex sanguineus</i> L. | B | - | 0 | 0 | 3 | 100 |
| <i>Festuca gigantea</i> (L.) Vill. | Ep | - | 0 | 0 | 3 | 100 |
| <i>Brachypodium sylvaticum</i> (Huds.) P. Beauv. | Ep | - | 0 | 0 | 2 | 67 |
| <i>Ornithogalum umbellatum</i> L. | B | - | 0 | 0 | 2 | 67 |
| <i>Impatiens noli-tangere</i> L. | Au | - | 0 | 0 | 1 | 33 |
| <i>Moehringia trinervia</i> (L.) Clairv. | B | - | 0 | 0 | 1 | 33 |
| Woodland species, not found in Flevoland | | | | | | |
| <i>Allium vineale</i> L. | B | - | 0 | 0 | 3 | 100 |
| <i>Carex sylvatica</i> Huds. | B | - | 0 | 0 | 2 | 67 |
| <i>Elymus caninus</i> (L.) L. | Ep | - | 0 | 0 | 1 | 33 |
| <i>Ranunculus auricomus</i> L. | B | - | 0 | 0 | 1 | 33 |

Multiple regressions with the five most common species explained 27 - 47% of the variation. Age and distance to villages were significant for *Ribes rubrum* and *R. uva-crispa* L. The best model for *Dryopteris filix-mas* only concerned the area (Table 5). For the species tested by chi-square analyses *Ribes uva-crispa*, *Geum urbanum* L. and *Ranunculus ficaria* L. ssp *bulbifer* Lambinon were positively correlated with the older woods, *Dryopteris dilatata* (Hoffm.) A. Gray, *Dryopteris affinis*, *Athyrium filix-femina* (L.) Roth and *Cardamine flexuosa* With. with the larger woods. No species were positively correlated with small woods or the distance to the mainland, but *Dryopteris dilatata* was correlated with the less isolated woods, situated in the vicinity of other woods, *Geum urbanum*, *Ribes uva-crispa* and *Ribes nigrum* L. with woods in the vicinity of villages.

The various habitats

The stands

The maximum number of woodland species per stand, per ha per wood (Nmax) varied from 1 to 8 species, ferns comprising 0 to 83% (Table 6). The Nmax is very low in dense and young stands, increasing when stands grow older. Stands with *Fraxinus*

Table 3. Correlations between various independent and dependent variables (for abbreviations, see table 1). * = significant $p < 0.05$, ** = significant $p < 0.01$, *** = significant $p < 0.001$. - = negative correlation.

| | 1 | lnA | d1 | d2 | ld3 | ld4 | s1 | s2 | s3 |
|-----|---|-----|-----|----|-----|------|----|----|----|
| kl | . | ** | . | . | . | . | . | . | . |
| 1 | . | . | **- | *- | * | ***- | * | * | . |
| lnA | . | . | . | . | . | . | ** | ** | ** |
| 1 | . | . | *** | *- | . | . | . | . | . |
| d2 | . | . | . | * | . | . | . | . | . |
| ld3 | . | . | . | . | . | . | . | . | . |
| ld4 | . | . | . | . | . | * | * | * | * |
| s1 | . | . | . | . | . | . | ** | ** | . |
| s2 | . | . | . | . | . | . | . | ** | . |

excelsior are relatively rich in species. *Dryopteris filix-mas* is the most common fern species. In some large woods *Pinus* has been planted on clay. These stands are the first to be colonised by *Dryopteris* spp. and *Athyrium filix-femina*, while in the same time-span in stands under other species *Dryopteris filix-mas* is found in low densities.

Trenches

Eight of the 53 surveyed woods are intersected by trenches. The majority of fern species are significantly correlated with trenches (Table 7). As trenches contain water in winter-time the ferns are restricted to the trench banks. Nine of the 11 fern species are correlated with trenches in one or more woods. Various rare species, with only a limited number of specimens, are completely correlated with trenches, such as *Polystichum lonchitis* (L.) Roth and *Polystichum aculeatum* (L.) Roth, others are growing in and outside trenches, but their densities are significantly higher on the trench banks. At one wood near Ens (Noordoostpolder) *Dryopteris filix-mas* avoided the trenches. Of the phanerogams only *Epilobium montanum* L. and *Ribes rubrum* are significantly correlated with trenches in some woods.

Other habitats

Sown grasses dominate the rides and the herb layer is poor in species. On lightly clayey soils (lutum content 5-12%) *Ophioglossum vulgatum* L. established at the edge of these rides (Bremer, 1988). When the rides are overshadowed (mostly within 30 years)

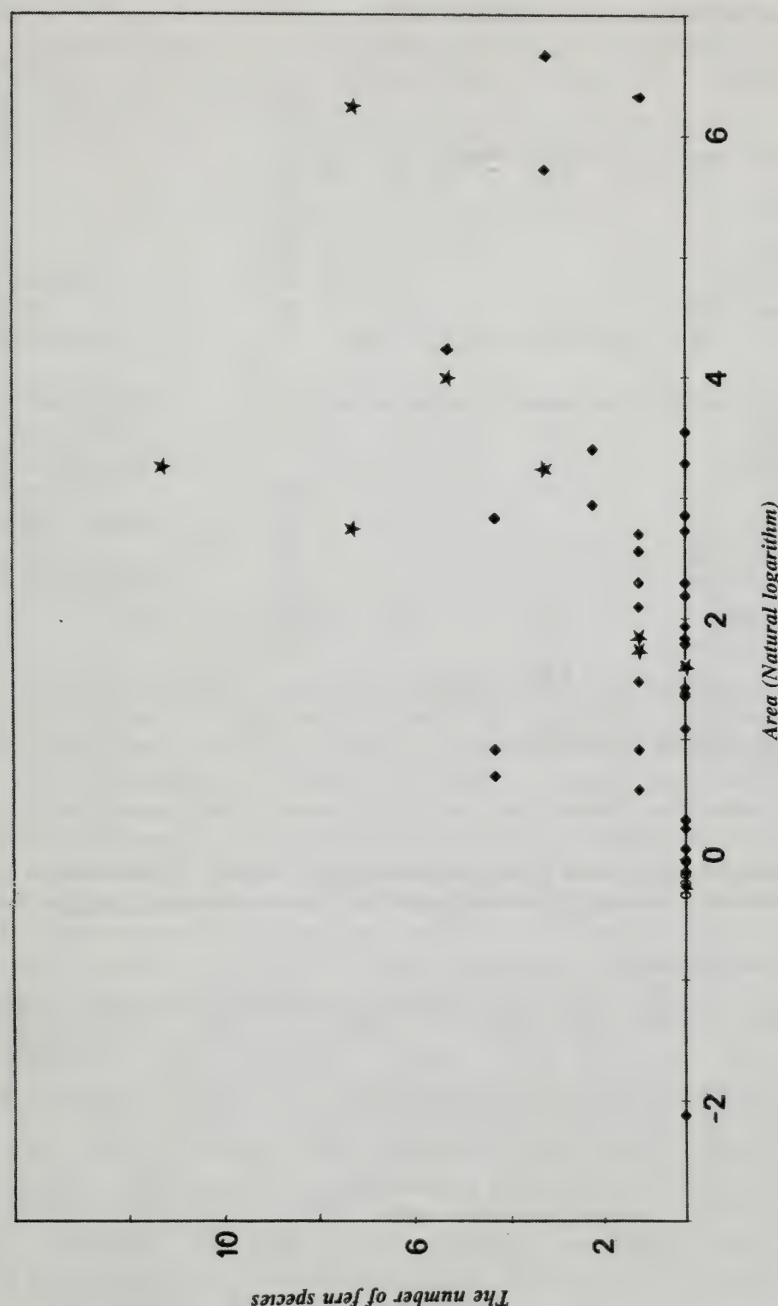


Figure 2. Relation between area (natural logarithm) and the number of fern species per wood. * = woods with trenches.

Table 4. Multiple regression models for the dependent variables (for abbreviations, see table 1). V²= explained variation.

| | V ² |
|---|---|
| <i>s1 = number of species per wood</i> | |
| 1 | 12 |
| ld4 | 17 |
| lnA | 39 |
| lnA + 1 | 54 |
| lnA + ld4 + 1 | 59 |
| | $s1 = 2.2 + 4.1 \ln A + 0.32 l - 1.4 ld4$ |
| <i>s2 = number of woodland species per wood</i> | |
| ld3 | 4 |
| ld4 | 5 |
| l | 8 |
| lnA | 26 |
| lnA + ld3 | 26 |
| lnA + ld4 | 34 |
| lnA + 1 | 36 |
| lnA + l + ld4 | 38 |
| | $s2 = -0.9 + 1.5 \ln A + 0.2 l$ |
| <i>s3 = number of ferns per wood</i> | |
| lnA | 15 |

Dryopteris filix-mas can establish itself. Various epizoochorous species are concentrated along paths and rides such as *Circaeae lutetiana* L. and *Geum urbanum*.

Colonisation

At four medium-sized young, planted woods the colonisation was monitored for at least 15 years. The Emmeloorderbos (without trenches) was planted on slightly to heavy clayey soils in the period 1949-1954. *Fraxinus excelsior* is currently the most prominent tree species. Monitoring started in 1970. The first specimens of *Dryopteris filix-mas* were established more than 20 years after planting, followed by acidophilous species on decaying wood of *Pinus* and *Picea* (e.g. *Dryopteris dilatata*). As the total number of woodland species was increasing, the number of ferns stabilised after about 1985 (Fig. 3). Other woodland species were established before the ferns (Fig. 4a). These species are anemochorous (e.g. *Epipactis helleborine* (L.) Crantz, endozoochorous (e.g. *Ribes* spp.), epizoochorous (e.g. *Geum urbanum*) and some are only able to disperse over short distances (e.g. *Impatiens parviflora* DC.). Whilst the maximum number of fern species has been realised, the number of other woodland species is still increasing. A quarter of the potential species is still absent. Most of those belong to the categories with very short distance dispersal.

Table 5. Regression and multiple regression for woodland species, growing in more than 45 % of the surveyed woods. Dfm, Em, Rr and Rc: presence per wood according to an ordinal transformed Tansley code. * = significant $p < 0,05$, ** = significant $p < 0,01$ *** = significant $p < 0,001$. The best fitting model is presented. V^2 = explained variation. For abbreviations, see Table 2.

| | k | l | lnA | d1 | d2 | ld3 | ld4 | nbos | V^2 |
|---|---|-----|-----|----|----|-----|-----|------|-------|
| Ferns | | | | | | | | | |
| <i>Dryopteris filix-mas</i> (L.) Schott. | * | . | *** | . | . | . | . | * | |
| Dfm = -1,0 + 0,4lnA | | | | | | | | | 27 |
| Other woodland species | | | | | | | | | |
| <i>Epilobium montanum</i> L. | . | ** | . | . | . | ** | *** | . | |
| Em = 0,5 - 0,3 ld4 + 0,3 ld3 | | | | | | | | | 41 |
| <i>Ribes rubrum</i> L. | . | *** | . | . | . | . | *** | . | |
| Rr = -1,0 + 0,1 l - 0,4 ld4 | | | | | | | | | 47 |
| <i>Ribes uva-crispa</i> L. | . | * | . | . | . | * | *** | . | |
| Rc = -1,1 + 0,1 l - 0,2 ld4 | | | | | | | | | 36 |

The Tollebekerbos (without trenches) was planted in 1957. The first specimen of *Dryopteris filix-mas* became established on a bank at the edge of the wood about 25 years after planting. Some years later *Dryopteris dilata* was found on decayed wood.

The Jagersveld (O.-Flevoland) was planted in 1964/66 on a slightly clayey soil. The trenches (c. 1 km in extent and on average 0.5 m deep) carry water in winter-time, but in summer-time the phreatic level can drop to more than 1.5 m below surface level. Monitoring started in 1979. The wood proved to be rich in fern-species; 11 species were found, e.g. *Polystichum aculeatum*, *Polystichum setiferum* and *Polystichum lonchitis*. *Dryopteris cristata* (L.) A.Gray was found here for the first time in Flevoland in this habitat. *Dryopteris cristata* and *D. affinis* disappeared within c. 10 years of establishment. Six species were strictly correlated with trenches. As waterlevel rose in winter some plants were inundated and died, while others were damaged by frost during severe winters.

As a comparison a young planted wood on acidified clay near Zwolle was monitored beginning in 1983. The small wood (without trenches) was planted in 1971. There were no ferns at the start of monitoring. Four species germinated, including *Dryopteris carthusiana* (Vill.) H.P.Fuchs, after heavy thinning in 1988. Other woodland species were present at that time, some of them came from the grassland present before afforestation (*Ranunculus ficaria*, *Deschampsia caespitosa* (L.) Beauv.). Since 1988 the number of fern species has failed to increase, while the number of woodland species is still increasing (Fig. 4b).

Table 6. The maximum number of woodland species per ha per wood (first line), second line: the number of fern species and the percentage. Fex = *Fraxinus excelsior* L., Fsy = *Fagus sylvatica* L., Pca = *Populus × canadensis* Moench, Aps = *Acer pseudoplatanus* L., Qro = *Quercus robur* L., Pi = *Pinus*, Cbe = *Carpinus betulus* L., Tco = *Tilia cordata* Mill., Pav = *Prunus avium* (L.) L.

| | Fex | Fsy | Pca | Aps | Qro | Pi | Cbe | Tco |
|---|------|------|------|-----|-----|------|------|------|
| Edelkarper (23 yrs) | 2 | 0 | 2 | 1 | - | - | 2 | 1 |
| | 1 50 | 0 | 0 | 0 | - | - | 1 50 | 0 |
| Larserbos (25 yrs) | 3 | 0 | 2 | 2 | 2 | - | - | 5 |
| | 1 50 | 0 | 1 50 | 0 | 0 | - | - | 2 40 |
| Wisentbos (25 yrs) | 2 | 3 | 1 | - | 2 | 6 | 3 | - |
| | 0 | 1 33 | 0 | - | 0 | 5 83 | 0 | - |
| Harderbos (25 yrs) | 3 | 1 | 3 | 2 | - | 5 | - | - |
| | 1 33 | 0 | 0 | 0 | - | 3 60 | - | - |
| Bremerbergbos (31 yrs, trenched) | 3 | 1 | 8 | - | - | - | - | - |
| | 0 | 0 | 2 25 | - | - | - | - | - |
| Emmelerbos (43 yrs) | 7 | 1 | - | 2 | - | - | - | - |
| | 1 14 | 0 | - | 0 | - | - | - | - |
| Tollebekerbos (36 yrs) | 5 | 3 | - | - | 3 | - | - | - |
| | 1 20 | 1 33 | - | - | 0 | - | - | - |
| Enserbos (40 yrs, trenched) | 7 | 6 | - | - | - | - | - | - |
| | 1 14 | 1 16 | - | - | - | - | - | - |
| Biddinghuizen (M 42) (24 yrs, trenched) | 6 | - | - | - | - | - | - | - |
| | 2 33 | - | - | - | - | - | - | - |
| minimum-maximum number of wood inhabiting species | | | | | | | | |
| | 1-7 | 0-6 | 1-8 | 1-2 | 2-3 | 5-6 | 2-3 | 1-5 |

Rare fern species

Various species were found which have not been detected in woodlands on clayey soils on the Dutch mainland. *Asplenium scolopendrium* has been found in Flevoland in seven woods, with the largest population in the Kuinderbos (currently more than 3,000 plants). The populations on clay (at four woods) have always been small. At the Jagersveld, specimens ($n=26$) were correlated with trench banks. These plants have been monitored since 1979 (Fig. 5). No plants from the first years of monitoring survived; the oldest recorded plant was 16 years old when it died. 92% of the plants lived fewer than 10 years, about 50% dying in winters with severe frosts. The maximum length of fronds (per plant) decreased as well due to severe winters (Fig. 6).

Table 7. Woodland species in trenched woods. OSw = Swifterbos-oost, OBB = Bremerbergbos, NEb = Enserbos, OHr = Houtribbos, Z7 = Biddinghuizen, OJv = Jagersveld. The trench-habitat (g) of woodfloor (r) is indicated. n = number of counted specimen.

* = species present, no preference, - = species absent, . = species not surveyed, g/r = species exclusively on trench side or woodfloor, mostly less than 10 specimen per wood. g*/r* = significant preference for trench (g) or woodfloor (r), tested bij X², * = p < 0.05

| | n | Osw | OBB | Neb | Ohr | Z7 | OJv |
|--|-----|-----|-----|-----|-----|-----|-----|
| Density trenches (km, per ha) | | 0.8 | 0.8 | 0.4 | 1.1 | 0.3 | 0.8 |
| Ferns | | | | | | | |
| <i>Dryopteris filix-mas</i> (L.) Schott | 670 | g* | g* | r* | g* | * | g* |
| <i>Dryopteris dilatata</i> (Hoffm.) A.Gray | 1 | g* | r | - | r | - | - |
| <i>Dryopteris carthusiana</i> (Vill.) H.P. Fuchs | 14 | g* | g | - | . | - | . |
| <i>Athyrium filix-femina</i> (L.) Roth | 61 | g* | * | - | . | - | . |
| <i>Polystichum setiferum</i> (Forssk.) Woyn. | 5 | g | g | - | - | - | g |
| <i>Dryopteris affinis</i> (Lowe) Fraser-Jenks. | 5 | g | g | - | - | - | g |
| <i>Asplenium scolopendrium</i> L. | 25 | - | g* | - | - | - | g* |
| <i>Polystichum lonchitis</i> (L.) Roth. | 1 | - | - | - | - | - | g |
| <i>Polystichum aculeatum</i> (L.) Roth. | 6 | - | - | - | - | - | g* |
| Other wood-inhabiting species | | | | | | | |
| <i>Epilobium montanum</i> L. | 215 | g* | . | g* | r | - | - |
| <i>Ribes uva-crispa</i> L. | 86 | * | . | . | - | . | . |
| <i>Ribus rubrum</i> L. | 100 | * | . | . | - | g* | * |

Polystichum aculeatum has been detected in Flevoland in six woods with, as in the previous species, the largest population in the Kuinderbos (currently c. 500 plants); the plants growing on calcareous sand. On clay there have been two records, in both cases correlated with trench banks. *Polystichum setiferum* has been detected in Flevoland in six woods with the largest population in the Kuinderbos (in 1993 128 specimens, Bremer, 1995). Plants are always growing on trench banks on calcareous sand, boulder clay or clay. There are three clayey woods where this species is found, with at most three specimens per wood. *Polystichum lonchitis* was recorded for the first time in the Netherlands in the Kuinderbos on calcareous sand (Bremer, 1981). A site near Lelystad, on light clayey soil, was found in 1986 (Smit, 1989). Plants are still growing in both areas.

Ophioglossum vulgatum can be found in Flevoland in grasslands and woods. In woods elliptic patches are found on boulder clay, calcareous sand and clayey soils. Bremer (1988) surveyed all the localities in woods within Flevoland (n=16), 37% occurring on clayey soils. At some localities patches occur on clay overlying pleistocene

sands with seepage. At other sites the clay layers are thicker without seepage, but predominantly at all localities the phreatic level in springtime is less than 0.5 m below the surface level. The canopy consisted in all cases of *Fraxinus excelsior*, mixed with other broad-leaved trees. For some populations during the last 15 years, patches decreased in vitality or even disappeared due to a heavier shade cast and/or the fall of slowly decomposing litter by *Quercus robur* and *Fagus sylvatica*.

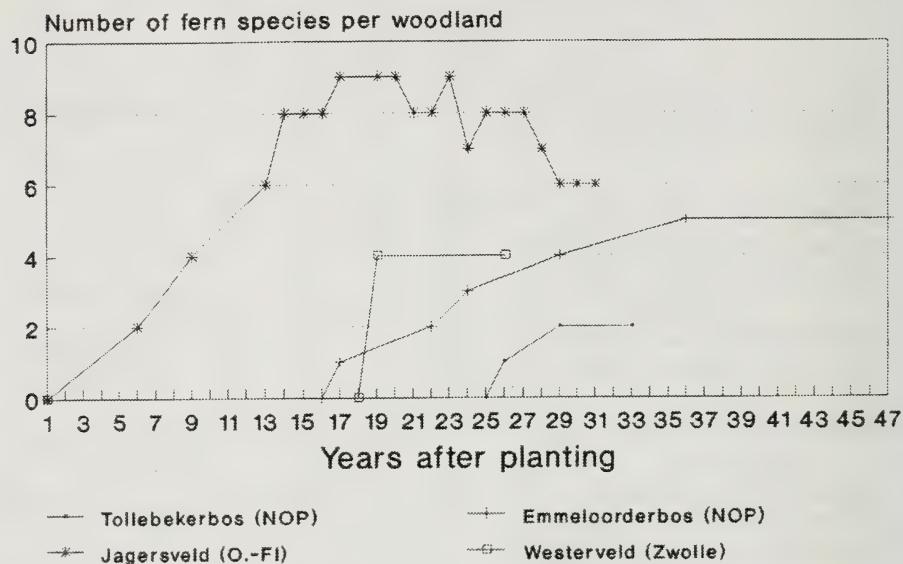


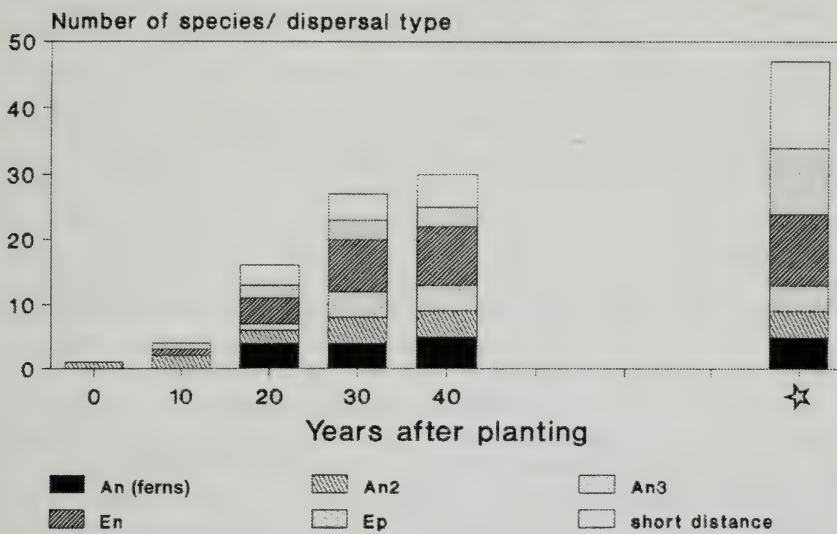
Figure 3. The number of fern species in relation to the age of the afforestation, monitored in four woods.

DISCUSSION

Habitat islands

The number of species on a site depends principally on area, an almost universal finding, which holds true for woodland species as well (Dzwonko & Loster, 1989; Peterken & Game, 1984). Grashof-Bokdam (1997) found an area effect for some fern species, a finding supported by this study. Woodland age is important because the number of species increases with age as demonstrated with monitoring (Fig. 3). We may assume that this process is still going on; older woods being richer in species than young ones (e.g Peterken & Game, 1984; Dzwonko & Loster, 1984). In the regressions the contribution of age is less than that of area. We have to take into account that the variation in area (0.15-790 ha) is much larger than the variation in age (16-43 years). Of the isolation parameters, the isolation (distance to villages) was significant, e.g for some endozoochorous species. Some species are spread from gardens by birds (e.g *Ribes* spp.), while by walking man (or dogs) will act as vector for seeds (e.g epizoochorous species, but other species as well).

4a



4b

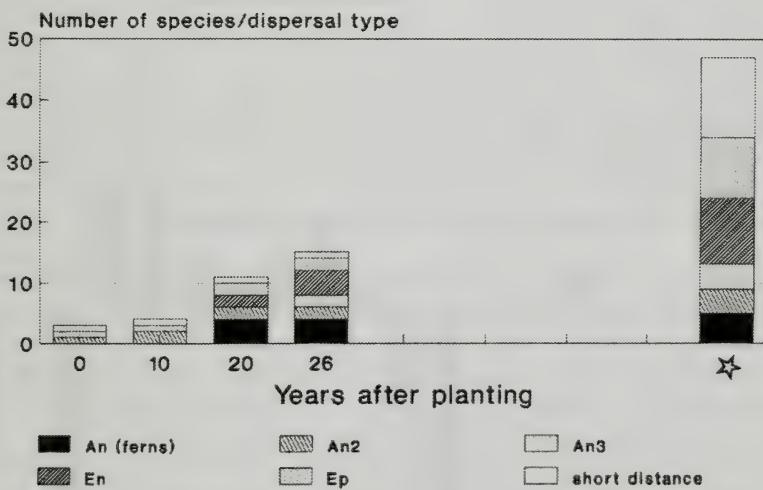


Figure 4. Changes in dispersal types since afforestation in **a.** the Emmeloorderbos (Noordoostpolder) and **b.** Westerveld (vicinity Zwolle).

An(ferns): ferns, An2 = anemochorous species, dispersal over hundreds of meters, An3 = anemochorous species; short distance dispersal, En = endozoochorous species, Ep = epizoochorous species, other = short distance dispersal (autochorous, barochorous).

* = dispersal types based on all woodland species to be expected on clayey soils; species strictly correlated with trenches omitted.

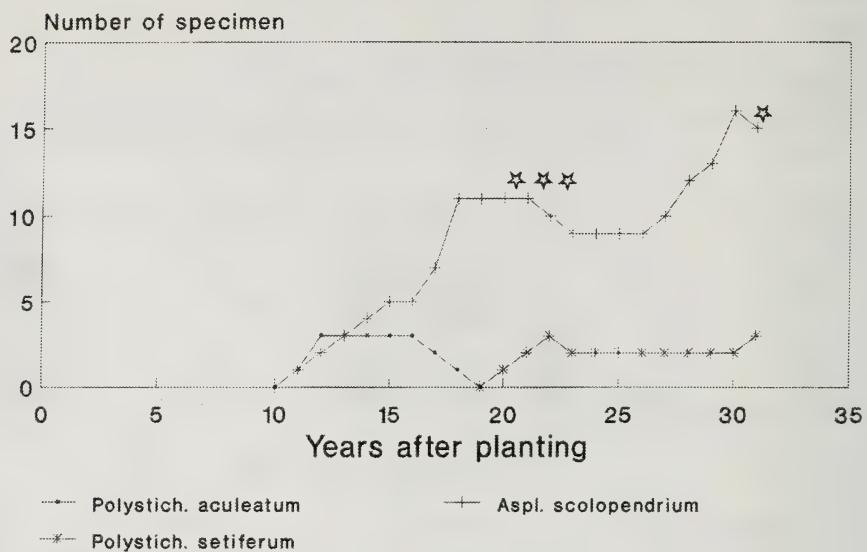


Figure 5. The number of specimens of rare ferns at the Jagersveld. * = severe winters with frost damage.

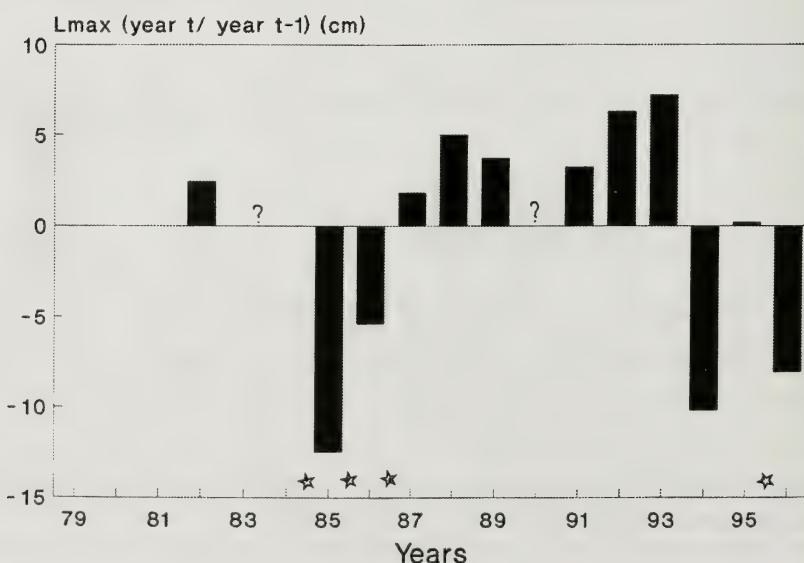


Figure 6. The change in maximum length of fronds (Lmax) of *Asplenium scolopendrium* (per specimen) as observed at the population in the Jagersveld (1979 - 1996). * = severe winters with frost damage, ? = no data collected.

The clayey woods are habitat islands, isolated by surrounding agricultural areas. Although the theory of island biogeography has been applied to habitat islands, many studies have indicated that this is not correct (Hermy, 1986). Our study confirms these conclusions, as there is no equilibrium between immigration and extinction (colonisation means that immigration is going on) and we found no correlation for the isolation with the mainland, as expected in this theory. Roadside plants showed a relation with the mainland (Nip-van der Voort *et al.*, 1979), but the verges are not isolated. In the Jagersveld the number of fern species stabilised, probably indicating an equilibrium. But this species rich woodland was one of the most isolated. Ferns have a high dispersive potential, not restricted by distances of tens of kilometers. Grashof-Bokdam (1997) however found an isolation effect (defined as connectivity) for *Dryopteris filix-mas* in forest patches belonging to the *Quercion roburi-petraea* and for *Dryopteris dilatata* in 15-20 years old woodlots and wooded banks, most of them belonging to the *Quercion roburi-petraea* as well.

In the monitored woods ferns were not the first to colonise, against expectation. Other species can be present at the time of planting, e.g. *Ranunculus ficaria*, when planting took place on grasslands (e.g. at Westerveld). These species are absent when planting took place on arable fields, as in the polders. The species colonising these recent woodlands belong to various dispersal types, including those without effective dispersal mechanisms. As indicated by multiple regression the distance to villages is of importance, suggesting that man does have a prominent impact on the colonisation of various species.

Habitat

Most ferns were found in stands with *Fraxinus excelsior* in the canopy. These stands can be assigned to the *Fraxino-Ulmetum*. Stands rich in ferns near Lelystad are composed of various broad-leaved tree species, *Fraxinus excelsior* being the most important. This wood has something in common with the Ash-Maple-Hazel woods on heavy, moderately calcareous, poorly drained soils in eastern England, which have more species of flowering plants and ferns than any other woodland of eastern England (Rackham, 1980).

Remarkably, stands of *Pinus* (not natural on clay!) provide a particularly good habitat for ferns, as the young stands have an acid ecto-organic layer, providing habitat for *Dryopteris* spp. and an appropriate humidity. Even *Asplenium scolopendrium* established in one of these stands (and was not correlated with trenches as seemed the rule for this species). These observations indicate the likelihood that spores reach the isolated woods, but are not able to germinate. Near Zwolle spores of four species germinated quickly after thinning, probably indicating a sporebank. In recent years the existence of viable fern spores in soil has been recognised (Milberg, 1991; Dyer & Lindsay, 1992).

Our study confirms trenched woods are richer in ferns than woods without this kind of drainage. Various species are completely correlated with trenches. Trench banks seem to be an appropriate habitat as there is no accumulation of litter, temperatures are less extreme and on the average humidity is higher, as after heavy rainfall and in wintertime when the bottom is filled with water (Bremer, 1980a). However, even at best, for example the locality near Lelystad, the density of specimens is low, indicating that colonisation is a process with little opportunity of success, as all species were sporulating.

The trenches on clayey soil have much in common with the situation in the Kuinderbos, where rare species are correlated with fine calcareous sand on trench banks (Bremer, 1980a, b). Trenches elsewhere in the Netherlands mostly have an acidified substrate without calcicole fern species.

Colonisation

Some fern species, recorded here, have not previously been observed in clayey woods elsewhere in the Netherlands. Long distance dispersal must have taken place for some species, such as *Polystichum lonchitis*, only present as two plants in the woods of Flevoland. Establishment of these might have taken place from the nearest naturally occurring plants, i.e. from spores belonging to British or central European populations. Similarly, *Polystichum setiferum* might have come from the rich populations of south-western England. Fern spores are capable of being carried long distances and probably are dispersed widely. Lellinger (1985) notes that sometimes spores do germinate and produce sporophytes far outside the usual range of a species. An outstanding example of an out-of-range distribution, being that of *Grammitis nimbata* (Jenman) Proctor, a Cuban species growing in North Carolina, some thousands of kilometres out of the species main range. The rarest species which established in the clayey woods had 'only' to pass hundreds of kilometres. Monitoring takes place to ascertain if this kind of establishment results in persistence.

Ecology

Asplenium scolopendrium was not observed before on clayey trench banks in the Netherlands, probably because this habitat (with calcareous substrate) is rather rare on the mainland. It mostly occurs on walls and sometimes terrestrially in the dunes (Weeda *et al.*, 1985). The mass growth in trenches was unknown till the first records in the Kuinderbos (Bremer, 1980) and the clayey woods described here. Probably the trenches imitate more natural habitats such as ravine woods in Central Europe. *Asplenium scolopendrium* is prone to frost damage. After heavy frost populations can be decimated, as observed on wall populations (personal observations by the authors in the Netherlands). In the polder woods frost can be damaging as well, as demonstrated in the Jagersveld, but it hardly influences the size of populations. The same was observed in the Kuinderbos (unpublished data).

In the Jagersveld three *Polystichum* spp. were found. The same was observed in the Kuinderbos where the three species are even growing on the same trench bank, indicating an overlap in ecology. All these species are very rare in the Netherlands. Nevertheless they were able to colonise independently the same locality. *Polystichum lonchitis* is restricted to two locations in Flevoland and at its first location has been present for more than 20 years. In Scotland plants occur chiefly at c. 600-900 m elevation, descending very locally to about c. 150 m (Page, 1982), and even c. 50 m (Gent *et al.*, 1995). In Central Europe it descends to an elevation of 300 m, preferring the montane and alpine area (Dostál *et al.*, 1984). Other plant species with a montane distribution have been found on trench banks in the polders as well (e.g. the bryophyte *Distichium capillaceum* (Hedw.) Bruch & Schimp., Bremer & Ott, 1990), possibly surviving due to the microclimate.

Ophioglossum vulgatum is a rare wood inhabiting species in the Netherlands, although not mentioned as such in the Dutch flora (Weeda *et al.*, 1985). There are some

recent observations in various types of woods such as the *Querco-Betuletum*, *Pruno-Fraxinetum* and *Stellario-Carpinetum* (Bremer, 1988). The same holds true for Britain. Page (1982) did not mention woodland as a habitat either, while Rackham (1980) mentioned the small colonisation potential, but the species has been detected in British woods as well (Tallowin & Swinscow, 1986). In Flevoland *Ophioglossum vulgatum* thrives as long as there is no drying-out by drainage, or accumulation of leaf litter.

Numerous species, not observed before in the Dutch broad-leaved clayey woods, are established in Flevoland.

The Jagersveld is shown to be the richest wood. This richness is supported by several factors such as the length of trenches, high water levels in winter, its light clayey nature, high pH (due to shells) and variation in a canopy of broad-leaved shrubs and trees. Other woods in the polders on clay are poorer in species, as there is not such a combination of habitat characteristics. Woods on the mainland do not have trenches with a calcareous substrate.

Some of the established species have been classified as indicative for ancient woodlands. Rackham (1980) mentioned *Ophioglossum vulgatum* and *Dryopteris affinis* to have some association with ancient woodland. *Polystichum aculeatum* was associated with ancient woods in central Lincolnshire. The colonisation of young planted woods in Flevoland demonstrates the opposite. *Polypodium vulgare L.* has been indicated as a slightly calcifuge species (Page, 1982). In the Kuinderbos the species is able to grow on calcareous sand (Bremer, 1990) and near Lelystad even on calcareous sandy clay. This may be an effect of the scarcity of woods on clayey soils in the Netherlands.

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