THE FERN GAZETTE

Edited by
J.A. Crabbe

THE BRITISH PTERIDIOLOGICAL SOCIETY

Volume 13 Part 7 1990
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(THE FERN GAZETTE Volume 13 Part 6 was published on 18th June 1990)
MODULAR GROWTH OF **HUPERZIA SELAGO** (**LYCOPODIACEAE**: **PTERIDOPHYTA**)

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**ABSTRACT**

*Huperzia selago* is an evergreen perennial of arctic and alpine environments. It demonstrates modular growth as it consists of a series of annually produced segments which can be aged.

*H. selago* demonstrates a very deterministic* pattern of growth with early dichotomous branching followed by infrequent branching as the lower parts of branches become decumbent. Relative growth rates are very low and characteristic of species of stressed environments in which it is found.

*H. selago* has a high vegetative reproductive capacity through the production of bulbils, which are readily established in relatively closed vegetation. The bulbils are more successful as a means of vegetative spread in extremely patchy environments than the stoloniferous habit. This form of reproduction is opportunistic in relatively closed vegetation compared to sexual reproduction. The species relies on spore production for long distance transport and opportunistic establishment in early successional habitats generated by disturbance and erosion on the tops and steep slopes of mountains.

**INTRODUCTION**

The sporophyte of *Huperzia selago* (L.) Bernh. ex Schrank is a widespread perennial of the stressed environments of arctic and alpine areas. It shows an annual cycle in which sporophyll and microphyll production by the apical meristem alternate (Case 1943). As a consequence, all segments of the plant can be aged (Headley 1986). This means that the modular concept (Prevost 1978) can be used to describe the age-related growth, fecundity, death and survival of branches (Callaghan et al. 1986a; 1986b; 1990).

The application of the modular concept to the growth and physiology of the closely related stoloniferous plant, *Lycopodium annotinum* L., has been used to describe its foraging habit and response to spatially patchy environments (Callaghan et al. 1986a). Also it has been shown that this species has potentially indefinite growth (Callaghan et al. 1990). However, *H. selago* is a decumbent perennial that reproduces vegetatively by bulbils and despite having potentially indefinite growth, it is a short-lived perennial with a very different growth and reproductive strategy from that of *L. annotinum*.

This paper described in detail the modular growth of *H. selago* growing in three contrasting environments, one a temperate upland oceanic site in Snowdonia, North Wales, another an alpine subarctic site in northern Sweden and a third high arctic site in Svalbard.

**Sites**

Material was collected from three sites: one below Carnedd Dafydd in North Wales (53° 09' N, 3° 58' W); one on Mount Njulla in the Abisko National Park in Swedish Lapland (68° 24' N, 18° 42' E) and one on Svalbard (78° 15' N, 16° 30' E). The site in Snowdonia is an acid grassland at 580 m a.s.l. on a stabilised talus slope. The vegetation is dominated by *Nardus stricta* L. and *Festuca ovina* L. with *Vaccinium myrtillus* L., *Galium saxatile* L., *Anthoxanthum odoratum* L., *Cryptogramma crispa* (L.) R.Br. ex Hooker, *Campylopus paradoxus* Wils., *Hypnum cupressiforme* Hedw., *Polytrichum alpinum* Hedw.

*n.b. The terms deterministic and opportunistic are used in the sense of plasticity in growth and reproductive strategies of the plant, and not used in a morphogenetic sense.*
and *Rhytidiadelphus loreus* (Hedw.) Warnst, also present. The site at Abisko is close to the summit of Mount Njulla (1160 m a.s.l.) which supports a dry mountain heath vegetation. This is dominated by *Salix herbacea* L. and *Cassiope tetragona* (L.) D. Don, with *Festuca ovina*, *Vaccinium vitis-idaea* L., *V. myrtillus*, *Salix polaris* Wg., *Silene acaulis* (L.) Jacq., *Carex bigelowii* Torr. ex Schwein. and *Polytrichum alpinum* also present in the vegetation (see Headley 1986 for further details). The site on Svalbard is on a south-facing snow-free ridge at 200-250 m a.s.l. and the vegetation is dominated by *Salix polaris*, *Cassiope tetragona*, *Polygonum viviparum* L. and *Carex rupestris* All.

**Material**

Branches of *H. selago* only grow apically and branch by true iso-dichotomy (Ølgaard 1979). Senescence proceeds distally with the microphylls and sporophylls remaining in situ. There is an annual alternation in the production of sporophylls and microphylls. Sporophylls are initiated at the beginning of the growing season and the apical meristem changes to initiating microphylls at the end of the growing season (Case 1943). The sporangia require over a year to mature, but they do not normally dehisce and release the spores until the winter after they have matured. Bulbils are generally initiated with the microphylls and are supported by specialised structures (bulbil bases) which persist like the microphylls. The bulbils and microphylls take a year to mature and bulbils are released in the autumn and winter following initiation (Case 1943). This pattern of growth means that annual segments of plant can be aged by counting back sequences of sporophylls and microphylls from an active meristem (Fig. 1).

![FIGURE 1. A branch of *Huperzia selago* showing four annual segments of growth.](image-url)
Over the first 2 to 4 years of the life of a *H. selago* plant, bulbils and sporophylls are not produced. The segments of annual growth can still be identified however, by the slight reduction in the size of microphylls produced at the end of the growing season. The development of a plant of *H. selago* therefore enables the determination of overall plant age, as well as the ages of all segments, and the sequence of production of all segments within the plant (Fig. 2).

Roots are initiated just behind the apical meristem and grow down through the cortex (Saxelby 1908). They emerge from the base of the branches where they contact the soil and as a consequence they cannot be aged in contrast to the root system of *Lycopodium annotinum* (Headley et al. 1985).

FIGURE 2. Schematic diagram of two typical *Huperzia selago* plants (one 7 years old and the other 4 years old) with the sequence of segment ages and segment position shown.

**Methods**

On 25th March 1982, 19 plants of *H. selago* were collected from the Snowdonia site and stored at -15°C until they were analysed. The plants were divided into their annual segments and classified according to their age and position (see Fig. 2). The number of bulbil bases on each segment was counted and the number of dichotomies was also recorded. The segments were dried at 105°C for 12 hours before being weighed individually. On 2nd August 1982, 18 plants of *H. selago* were collected from the Abisko site. They were dried and pressed before being analysed as above. Thirty seven plants were collected at random from Adventdalen, Svalbard in July 1987 and stored at -20°C prior to analysis.

A further 20 plants of *H. selago* were collected from the Snowdonia site complete with the soil in which they were rooted. The soil was carefully washed from their roots. The plants were aged and separated into roots and branches, before being dried and weighed. Ten fresh plants of *H. selago* were collected from the Snowdonia site on 10th October 1982 and the mature undehisced sporangia carefully removed and counted from each of 35 one year old segments. The one-year-old segments, spores and sporangial wall material
were dried and weighed as above. The number of spores per sporangia was estimated by suspending the spores dehisced from a known number of sporangia in 1 cm³ water containing a wetting agent and counting the number of spores in 0.1 mm³ of the suspension using a haemocytometer slide. Four separate counts were made for each of 3 separate suspensions, each containing the spores from 38 or more sporangia.

![Graph showing changes in branch fecundity with increasing distance from the base of *Huperzia selago* plants, i.e. segment position, from Snowdonia (circles), Abisko (triangles) and Svalbard (squares). Means with S.E. bars shown.](image)

FIGURE 3. Changes in branch fecundity with increasing distance from the base of *Huperzia selago* plants, i.e. segment position, from Snowdonia (circles), Abisko (triangles) and Svalbard (squares). Means with S.E. bars shown.

The viability of spores from fresh branches was estimated by opening a fresh mature sporangium in a drop of lactophenol cotton blue (cytoplasmic stain) on a microscope slide. The numbers of stained and unstained spores were counted for transects across the slide until a total of 600 or more spores had been counted. This was repeated for a total of 9 sporangia.

**RESULTS**

**Branch fecundity and mortality**
The frequency of branching, or dichotomy, declines with increasing segment position, which is equivalent to increasing age of the whole plant, in all three populations. This results in the opposite of a tree-like structure (Fig. 3). There is a much lower frequency of branching in the Svalbard population in the first year. The Snowdonia population has a significantly higher dichotomy frequency than the Abisko and Svalbard populations in the fourth and fifth years. Overall the population which has much the lowest dichotomy frequency of the three populations is that from Abisko.

The mortality of branches is generally below 10% in the first five years of growth (Fig. 4). After this period mortality is generally highest in the Abisko population.
FIGURE 4. Changes in mean branch mortality (%) with increasing distance from the base of Huperzia selago plants from Snowdonia (circles), Abisko (triangles) and Svalbard (squares).

FIGURE 5. Changes in mature segment weight with increasing distance from the base of Huperzia selago plants from Snowdonia (circles), Abisko (triangles) and Svalbard (squares). Means with S.E. bars shown.
Growth of branches
The weight of segments is affected by a) the population they belong to, b) their position, c) their age and d) if they have dichotomised. Segments of material from Abisko weigh less than those from the other two sites (Fig. 5), while the segments of the Snowdonia population are by far the heaviest. In general, the basal segments are heavier than those higher up the plant (Fig. 5). As they age, dry weight is accumulated over one year in material from Snowdonia, whereas segments increase in dry weight over a 1-8 year period in material from Abisko and Svalbard (Fig. 6).

Larger segments are associated with dichotomies and segments with a dichotomy in material from Snowdonia were 72% heavier (55 mg segment$^{-1}$) than those without (32 mg segment$^{-1}$). There is however, an interaction between segment position, and age, and dichotomy which has not been quantified here.

Allocation of dry weight to roots
The proportion of total plant weight allocated to roots declines significantly from 24.6% ± 1.7% in one year old plants to 9.8% ± 0.8% in two or more year old plants from Snowdonia (t=8.879, d.f.=18, p < 0.001). There is no significant effect of plant age on the percentage biomass in the roots of 2 or more year old plants (r=0.058, d.f.=11, p >0.05).

Total plant weight
There appears to be a biphasic growth pattern in total dry weight of plants for the Snowdonia and Svalbard populations (Fig. 6). The initially more rapid increase in dry weight (RGR
MODULAR GROWTH OF HUPERZIA SELAGO

= 2.23 and 1.76 g g\(^{-1}\) y\(^{-1}\), calculated from data in Fig. 7, for the Snowdonia and Svalbard populations, respectively) is in the first two years of growth. The slower RGR after this is very low (0.375 and 0.136 g g\(^{-1}\) y\(^{-1}\)). The total dry weight of the *H. selago* plants from Abisko showed no significant correlation with age.

**Vegetative reproduction**

As branches of *H. selago* grow apically, the basal segments become decumbent and as a result the plant spreads out either centrifugally on flat terrain or downhill on a slope. Fragmentation of a large plant in theory is possible, but large clones of *H. selago* are rare, with clones 1-2 metres across having only been reported from the undisturbed coniferous forests of Russia (Syelivanova-Gorodkova 1968).

The normal mode of reproduction is by bulbils, as all plants harvested or examined possessed the distinctively shaped leaves of the bulbil at the very base of the plant. The

![Figure 7](image)

**Figure 7.** Relationship between whole plant weight (expressed on a logarithmic scale) and age of *Huperzia selago* plants from Snowdonia (solid circles and line) and Svalbard (open circles and dashed line). Means with S.E. bars shown for three or more replicates.
production of bulbils does not normally start until the third or fourth year of the plant's life (Fig. 8) and they are therefore, not released until the fourth or fifth year. The number of bulbils produced per segment increases with the age of the plant (Fig. 8). Despite the branch segments of the Abisko populations being lighter and hence smaller, the number of bulbils produced per segment is greater than that produced by the branch segments of the Snowdonia population over the first 8 years (Fig. 7). There is however, a much higher bulbil production per segment in the Snowdonia population later in the life of the plant (Fig. 8).

The mean weight of bulbis produced by the \textit{H. selago} plants from Svalbard is intermediate (1.04 ± 0.06 mg) between those of the Abisko population (0.69 ± 0.04 mg) and the Snowdonia population (1.88 ± 0.10 mg).

![Figure 8](image_url)

\textbf{FIGURE 8.} Changes in bulbil production with increasing distance from the base of \textit{Huperzia selago} plants from Snowdonia (circles) and Abisko (triangles). Means with S.E. bars shown.

\textbf{Spore production}

Larger segments, which naturally weigh more, produce more sporangia (Fig. 9). The allocation to spores is 7.0% ± 1.2% of the dry weight of the one-year-old segment which produces them. The number of spores in each sporangium is 19,000 ± 2,000. This means that a plant from Snowdonia, will produce on average 0.97 x 10⁶ spores segment⁻¹. However the viability of spores is only 6.7% ± 2.2%.

\textbf{DISCUSSION}

\textit{H. selago} is very widespread and frequently a component of montane, boreal and tundra environments, although it is never dominant in the communities in which it occurs (Headley 1986). It is a plant of very low relative growth rate and is consequently found growing in infertile habitats or niches within these environments (Headley 1986).
There is a very strong pattern of basal (positional) branching in *H. selago*, which does not differ very greatly between the populations sampled in this study or elsewhere (Turmel 1982). As *H. selago* does not have secondary thickening the basal branching which is the opposite to a tree-like structure, maximises the support of higher branches. However, the support is inefficient and individual branches gradually become decumbent at the base as the weight of a growing branch exceeds the capacity of the lower part of the stem to support it (Niklas & O‘Rourke 1982). This pattern of basal branching is also observed in the vertical branch systems of the stoloniferous members of the *Lycopodiaceae; L. annotinum* and *L. clavatum* (Callaghan et al. 1986a).

The annual weight increments of individual branches are generally very low, and are very similar to those of other evergreen tundra plants (4 to 62 mg y⁻¹) at Eagle Summit, Alaska (Miller 1982). The climatic conditions experienced on the top of Mount Njulla, are more severe than those in Snowdonia and mean segment weight is on average 77% ± 3% lower in plants from Njulla compared to that of Snowdonia plants. Although climatic conditions affect segment weight, and age also affects the weight of developing segments, the position of the segment on the plant is the most important determinant of segment weight within any one plant.

*H. selago* differs from *L. annotinum* in not having a foraging strategy, but a tolerance of very stressed climatic and edaphic environments. *H. selago* is found as far north as Ellesmere Island and northern Greenland (82°N) and is found in soils that are naturally impoverished of major plant nutrients (0.4-18.2 ppm N; 4.4-5.8 ppm P). This is one reason for the very low RGR. The plant can respond to low phosphorus supply by increasing the rates of phosphate uptake (Headley 1986). However the plant can maintain much of its annual nutrient requirements by efficient internal recycling of the elements from basal segments to apical segments (50-80% for nitrogen and 40-60% for phosphorus) (Headley 1986). The immobility of *H. selago* compared to that of *L. annotinum* means that the plant has to be more efficient at capturing and utilising nutrients as root growth is restricted spatially. As a consequence, there is a much larger allocation of dry weight to roots in *H. selago* (10% of total plant weight) than in *L. annotinum* (5% of total plant weight).

Very old plants can become well established and have potentially indefinite growth in sheltered undisturbed forest habitats in Russia (Syelivanova-Gorodkova 1968). *H. selago* is however normally short lived (6-16 years) in the open habitats in Europe due to the premature death of the branches. As this species, like all the temperate members of the *Lycopodiaceae*, very rarely produces adventitious shoots, the removal of the branch tips by grazing or burning, as often happens in upland Britain, kills the plant. The plant may also show signs of premature death due to an inability to produce new roots as a consequence of being rooted in small crevices in rocks.

*H. selago* overcomes the problems of a limited life-span and immobility through successful reproduction by bulbils. *H. selago* plants may produce large quantities of bulbils over their whole life span, for example a plant from Snowdonia produced a total of 1166 bulbils over its 13 year growing period, which represented an investment of 18% of its dry weight to this form of reproduction. The allocation of this amount of dry weight to vegetative reproduction by bulbils is very similar to that observed for *Saxifraga cernua* and *Polygonum viviparum* (Wehrmeister & Bonde 1977; Petersen 1981). Reproduction by bulbils is particularly successful in the sparse vegetation of severely stressed and disturbed environments in the arctic (Bell & Bliss 1980; Callaghan & Emanuelsson 1985).

There is normally 100% germination of fresh bulbils which readily established on a wide range of substrata, including raw humus, peat, moss cushions, cracks in rocks, sand and rankers. This is typical for other species that reproduce by bulbils and plantlets (Harmer & Lee 1978b). This mode of reproduction is adequate for maintaining a viable population and spreading it within a particular site, especially a moderately closed community. The
large nutrient reserves within the bulbils (Smith 1920; Harmer & Lee 1978a; Headley 1986) are sufficient to enable the plant to grow up through competing grasses in the uplands of North Wales, the Lake District and Scotland, while opportunistic germination maximises the use of short growing seasons.

The distance between safe microsites are too great for *L. annotinum* to cross by means of subsidised growth of the stolon system in the extremely patchy environments of fellfields, screes and mountain tops, and rhizomatous/stoloniferous plants cannot generally tolerate the disturbance associated with some of these habitats. It is here however, that *H. selago* and other bulbiferous/viviparous species have an advantage. The bulbils can successfully be transported by wind and water. This is a more opportunistic method of vegetation reproduction.

![Figure 9](image-url)

**FIGURE 9.** Relationship between the number of sporangia per segment and segment dry weight in *Huperzia selago* plants from Snowdonia. $r = 0.718$, $P = 0.001$.

The low allocation of dry weight to sexual reproduction (7.0%) and the absence of genets in closed vegetation is similar to that for *L. annotinum* and other perennials of the tundra (Chester & Shaver 1982; Callaghan & Emmanuelsson 1985). *H. selago* can only successfully spread any significant distance by the numerous spores produced in the large sporangia. A single 13 year old plant, which had 248 spore bearing annual segments over its whole life will have produced approximately $2.4 \times 10^8$ spores. This also therefore, means that the probability of observing sexual reproduction (i.e. the gametophyte stage) is very low. For this reason and the fact that gametophytes of temperate *Lycopodium* species
(sensu lato) are generally subterannean, few collections of gametophytes, including \textit{H. selago}, have been made. Those gametophytes which have been found, invariably occurred in open or disturbed habitats (Oinonen 1968; Bruce & Beitel 1979). Sexual reproduction is therefore more opportunistic than vegetative reproduction and has a similar function to that observed in \textit{Viola} species (Newell 1983). The success of the widespread species \textit{H. selago} in its stressed environment, depends therefore, on a balance between a strongly deterministic growth pattern and an opportunistic vegetative and sexual reproductive strategy.

ACKNOWLEDGEMENTS

One of us (A.D.H.) wishes to thank the Natural Environmental Research Council for the generous funding of part of the work carried out described in this paper. Both of us wish to thank Professor Mats Sonesson of the Abisko Research Station for support there, and T.V.C. wishes to thank N.J.C. Tyler and Professor A.S. Blix of the Department of Arctic Biology, University of Tromsø for financial and logistic support on Svalbard.

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REVIEW


This is a welcomed book of a standard work, now at a reasonable price, and especially so because many of the more outrageous mistakes of the 1987 hardback 3rd edition have been corrected, e.g. Asplenium cuneifolium Viv. is no longer included as a British species. This work when originally written by Clapham, Tutin and Warburg (the latter was responsible for ferns) contained many gems of observation or opinion which, although often not substantiated, were stimulating. I notice that Huperzia selago spores are said to be ‘non-functional’, the plant reproducing by bulbils. I suspect this is not so and work carried out in North America by Joe Beitel suggests there is a complex of sexual species here and hybrids are common. There is an indication that European plants, including material from Britain, may also show some hybridity and contain more than one species. Notes are given on the morphology of the hybrid ferns in the British Isles which will be useful to many. Two nomenclatural corrections need to be made: unfortunate as it may seem to those that grow the pinnate-pinnatisect cultivar form of Polypodium cambricum, that name should be accepted for the plant we have hitherto called P. australe Fée. The plant that was originally called Asplenium lanceolatum Hudson and latterly A. billotii F.W. Schultz should now be called A. obovatum Viv. subsp. lanceolatum P. Silva.

For British botanists this Flora is now within grasp.

A.C. JERMY
LYCOPODIELLA INUNDATA (LYCOPODIACEAE: PTERIDOPHYTA)
ON CHINA-CLAY AT LEE MOOR, S. DEVON*

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ABSTRACT
Records are presented from fieldwork in 1980-81 of density and distribution of Lycopodiella inundata in the disused south china-clay pit (SX 577593) at Smallhanger Down, Lee Moor, S. Devon, v-c 3. There were about 3000 plants in three main habitats: humus-covered wet quartz sand, damp mounds of peat which are derived allochthonously from the surrounding moorland, and bare, saturated china-clay. It was in close proximity with Drosera rotundifolia, suggesting some association between the two species.

The substratum is nutrient poor, particularly in nitrogen (N) and phosphorus (P); as D. rotundifolia is insectivorous and obtains supplementary N and P supplies, the levels of these nutrients were analysed. The N content of L. inundata plants did not appear to vary with substratum, although the concentration of N increased slightly with an increase in humic matter. The N concentration in the substratum was correlated with the joint occurrence of L. inundata and D. rotundifolia.

INTRODUCTION
Following the report (Wigston et al. 1981) of Lycopodiella inundata (L.) Holub in abundance on old (1860-1955) china-clay working at Smallhanger, in 1980-81 visits were made to the site where an unusually high abundance of about 3000 plants of L. inundata in the south pit (SX 577593) and about 1500 in the north pit (SX 576595) were found growing in association with Calluna vulgaris, Drosera rotundifolia, Juncus, Molinia caerulea, Potamogeton, Rhododendron ponticum, Rhynchospora alba, Salix atrocinerea, S. caprea, Sphagnum and Ulex gallii.

L. inundata is a sub-Atlantic species, widely distributed throughout Western and Central Europe (Jalas & Suominen 1972), in Asia (Kuvaev & Rudskii 1973) and N. America (Hulten 1958). Its distribution in Britain shown by the Atlas of ferns of the British Isles (Jermy et al. 1978) indicates that its occurrence has declined since 1950, attributed (Jermy et al. 1978) to the drainage of acid wetland sites.

Despite its apparent decline in semi-natural sites there have been recent reports of it in man-made sites. Five plants have been recorded on quartz sand waste at Fox Tor Mires, S. Devon, v-c 3 (Wigston 1979), a maximum of seventeen plants at the base of a disused sand pit of Ling Common, W. Norfolk, v-c 28 (Petch 1980), and an estimate of at least 2000 plants at the base of a disused china-clay pit at Smallhanger, S. Devon (Wigston, Pickering & Jones 1981). This present study reports an investigation of the population of L. inundata at Smallhanger Down south clay pit, Lee Moor, S. Devon, v-c 3 (SX 577593).

THE HABITAT
Smallhanger south clay pit SX 577593 is situated on the south-west edge of the Lee Moor china-clay complex. The pit was worked in a small way from about 1860, until being abandoned in about 1955. The southern pit now has four quarry faces and one open side.

*Submitted to The Fern Gazette in December 1986. This unfortunate delay is regretted. EDITOR.
The faces have slopes of 30-60 degrees declining in slope towards the base. Erosion has caused a series of gullies and ridges which run perpendicular from some of the quarry faces.

The base of the pit is gently undulating, with substrata of acidic quartz sand and china-clay. The sand is free draining, but the fine china-clay is waterlogged where it has settled in hollows. The pit is at an altitude of 200 metres.

METHODS
An initial visual survey of the site showed that *L. inundata* grew abundantly in several vegetation types, but at different densities. An area was chosen for detailed investigation banded by four points: SX 57735929, 57785929, 57765925, 57735925 (Fig. 1).

![Figure 1. Smallhanger China Clay Pits (scale in metres).](image)

This area included the main population of *L. inundata* in the clay pit, and also all the vegetation types delimited in the visual survey. Species lists were compiled for each vegetation type. Microtopographical and vegetation maps (Figs. 2 and 3) of the area were prepared using standard surveying techniques.

The survey established the boundaries of each vegetation type, contours at 25 cm intervals, and recorded each occurrence of *L. inundata* and *Drosera rotundifolia*. Quadrats were located in appropriate areas to record the density of *L. inundata* in each vegetation type in which it occurred within the mapped area. A 1m square quadrat divided by a wire grid into 10cm squares was used. For each quadrat details were drawn of every *L. inundata* plant, with an arrow used to indicate horizontal shoots and a dot to show vertical shoots. A typical quadrat is illustrated in Fig. 4.

VEGETATION TYPES
Twelve vegetation types were delimited (Fig. 3) in the initial survey:

I A heath community dominated by *Calluna vulgaris*, with heath mosses and lichens, and some *Juncus*. There is much bare ground. This community was elevated slightly above the base of the pit, and the ground is damp, though not waterlogged,
Figure 2. South Pit – microtopography (scale in metres).

Figure 3. South Pit – vegetation types (scale in metres).
II Elevated dry mounds, again dominated by heath species such as *C. vulgaris* and *Ulex gallii*, with *L. inundata* at the base of the mound,

III *Sphagnum* spp. with acidophile grasses and *D. rotundifolia*,

IV A damp hollow community with *Juncus* spp and *D. rotundifolia*,

V Waterlogged china-clay waste, with *Sphagnum* spp. and some *D. rotundifolia*,

Va The same as V but with *L. inundata* within *Rhynchospora alba*,

VI A *Sphagnum* dominated community, similar to III above, but without *D. rotundifolia*,

VII *Sphagnum* spp. with *Juncus* spp.,

VIII Open water with acidophile grass clumps,

IX Well drained quartz sand and gravel, with occasional mosses,

X *Sphagnum* spp., *Juncus* spp., and *Potamogeton* spp. growing on wet or waterlogged ground,

XI Vegetation dominated by *L. inundata* on slightly humic clay in association with *R. alba* and much *D. rotundifolia*; *Molinia caerulea* also present,

XII China-clay waste covered by open water (this may be a more waterlogged variant of V).

Figure 4. Quadrat 13 with transect line.
Figure 5. Transect across quadrat 13.

**POPULATION ENUMERATION**

The numbers of plants in each quadrat were counted (Tab. 1). One plant was counted for each vertical shoot and/or where one or more horizontal shoots appeared to originate. These numbers were converted to an average number of plants per quadrat of a particular vegetation type (Tab. 2). These density figures were multiplied by the number of estimated 1m² of *L. inundata* in that vegetation type to give the total number of plants of *L. inundata* in that vegetation type (Tab. 3). These totals were summed to produce the estimated total of 2979 plants, which is very large in comparison with other records in the South West (vice-counties 1, 2, 3). The importance of the china-clay habitat was increased by the discovery in March 1981 of a population of 1500+ plants in Smallhanger north clay pit, SX 57635953.

**TABLE 1**

<table>
<thead>
<tr>
<th>Quadrat number</th>
<th>Vegetation type</th>
<th>Number of <em>L. inundata</em> plants in quadrat</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>II</td>
<td>6</td>
</tr>
<tr>
<td>2</td>
<td>XI</td>
<td>290</td>
</tr>
<tr>
<td>3</td>
<td>XI</td>
<td>220</td>
</tr>
<tr>
<td>4</td>
<td>Va</td>
<td>4</td>
</tr>
<tr>
<td>5</td>
<td>Va</td>
<td>24</td>
</tr>
<tr>
<td>6</td>
<td>Va</td>
<td>121</td>
</tr>
<tr>
<td>7</td>
<td>XI</td>
<td>94</td>
</tr>
<tr>
<td>11</td>
<td>XI</td>
<td>68</td>
</tr>
<tr>
<td>13</td>
<td>XI</td>
<td>118</td>
</tr>
</tbody>
</table>

*L. inundata* did occur in quadrats 8, 9, 10 & 12, but an accurate count was not undertaken due to time limitations and an already abundant amount of population data for this vegetation type (XI).
TABLE 2
Average number of \textit{L. inundata} plants per quadrat in each vegetation type

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Number of quadrats with \textit{L. inundata}</th>
<th>Total number of \textit{L. inundata} plants</th>
<th>Average number of \textit{L. inundata} per quadrat</th>
</tr>
</thead>
<tbody>
<tr>
<td>II</td>
<td>1</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Va</td>
<td>3</td>
<td>149</td>
<td>49.6</td>
</tr>
<tr>
<td>XI</td>
<td>5</td>
<td>790</td>
<td>158</td>
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</tbody>
</table>

TABLE 3
Total population of \textit{L. inundata} in mapped area

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Average number of \textit{L. inundata} in vegetation type</th>
<th>Number of areas of \textit{L. inundata} in that veg. type</th>
<th>Total number of \textit{L. inundata} plants in that veg. type</th>
</tr>
</thead>
<tbody>
<tr>
<td>II</td>
<td>6</td>
<td>25</td>
<td>150</td>
</tr>
<tr>
<td>Va</td>
<td>49.6</td>
<td>22</td>
<td>1091</td>
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<tr>
<td>XI</td>
<td>158</td>
<td>11</td>
<td>1738</td>
</tr>
</tbody>
</table>

Estimated total number of \textit{L. inundata} plants in mapped area 2979

DISTRIBUTION

The southern Smallhanger pit contained three habitats in which \textit{L. inundata} grew. These were:

(a) waterlogged china-clay waste with \textit{L. inundata} within \textit{R. alba} (vegetation type Va),
(b) \textit{L. inundata} growing on damp humus-covered china-clay with \textit{R. alba}, \textit{D. rotundifolia} and \textit{M. caerulea} (vegetation type XI),
(c) elevated drier peaty moulds with \textit{L. inundata} growing near the base (vegetation type II).

The vegetation boundaries were not always distinct; for example types Va - XI - II tended to occur in a transition from bare china-clay to peat substratum, and from waterlogged to damp, occasionally flooded, ground. Such transitions mean that vegetation types recorded in Fig. 3 are a general guide; specific local vegetation types are assigned for each quadrat (Tab. 1).

At Smallhanger, \textit{L. inundata} will grow on a range of habitats, although it is apparent from its density figures (Tab. 2) that the favoured habitat is vegetation type XI, with an average of 158 plants per quadrat. Secondary habitats are vegetation type Va and II with an average of 50 and 6 plants per quadrat respectively. At Smallhanger the optimum habitat of \textit{L. inundata} is a damp humus-covered clay waste, in association with \textit{D. rotundifolia}. This finding is similar to that reached by Brunerye (1971) following work at Correze, France, he concluded that the optimum ecological conditions for the growth of the species was saturated peaty sands, with some gravel; he also concluded that sub-optimum habitats were:

(i) On the edge of peaty moors, in particular on the steep sides of hollows with peaty bottoms. The soil was mainly peat, but not as wet as the bottom of the hollows, which are normally saturated,
(ii) When peaty sands are progressively covered with silt or mud; under these conditions \textit{L. inundata} can only survive if it is regularly flooded, and as long as the density of other vegetation is not too great,
(iii) On wet sand paths, where \textit{L. inundata} was found to establish itself with \textit{Juncetum silvatici}. 
It seems that Brunerye's sub-optimum habitat (i) is analogous to the Smallhanger vegetation type II, and sub-optimum habitat (ii) to vegetation type Va.

The *Atlas of ferns of the British Isles* (Jermy et al. 1978) indicates that *L. inundata* currently occurs at few sites and at low population densities. Our work, and that of Brunerye (1971) suggests that the decline of *L. inundata* is not so much due to the drainage of acid wetland sites (Jermy et al. 1978) with a peat or bog soil (as this may only be a secondary habitat), but due to the rarity of the optimum habitat. Where wet humus-covered clay waste has occurred at Smallhanger it is able to flourish, particularly in association with *D. rotundifolia*.

**NITROGEN (N) AND PHOSPHORUS (P) LEVELS**

Work by Bradshaw *et al.* (1975) has shown that the nutrient levels in sand and mica waste are very low. The low levels of the most limiting nutrients, N and P, prevent the growth of many species on china-clay waste. Stone & Thorp (1971) investigated the growth of four species of the genus *Lycopodium* growing in circular clumps; they found that readily soluble N increased sharply at the point where the rhizoids first developed along the advancing Lycopod rhizomes.

To investigate the possible relationship between the growth of *L. inundata, D. rotundifolia* and the nutrient levels in the clay substratum at Smallhanger south pit, the total N concentration and available P of the soil was determined across a transect, traversing a circle of *L. inundata* growth. The transect analysed was located across quadrat 13 (Fig. 4) and crossed a circular growth of *L. inundata*, associated with *D. rotundifolia* on humus-covered china-clay, vegetation type XI. The ring of *L. inundata* was surrounded by bare china-clay, vegetation type XII.

A 1.8m transect line was laid across the area, and substratum samples were taken at 20 cm intervals. Field analysis of the substratum indicated a pH range of 4.2 - 4.7, the reading of lower pH occurring within the humus-covered china-clay, and the higher pH reading from the bare clay. The collected samples were dried and digested by the Kjeldahl technique (Brookes 1976); following digestion the solutions were diluted with deionised water, then analysed for N and P concentrations using a Technicon automatic-analyser. The results (Fig. 5) from this instrument gave relative (not absolute) N levels (due to the acid nature of the digest) and quantitative P levels. The N is illustrated according to the % N recorded rather than actual concentrations. The concentration of N in the substratum across the transect is shown to be low in areas of bare clay, but increased across the area of *L. inundata* growing on humus-covered clay waste in association of *D. rotundifolia*. In contrast the concentration of P in the substratum across the transect fell very slightly across the area containing *L. inundata*.

**DISCUSSION**

The marked increase in the concentration of N in the substratum across the transect is unlikely to be caused by the deposition of animal faeces, because there is no corresponding increase in the P concentration. It is possible that the lowering of soil P concentration across the area is due to its uptake by the vegetation. The large increase in the soil N concentration across the area with *L. inundata* may be due to either an input of N from *D. rotundifolia*, or to mycorrhiza on the subterranean part of *L. inundata*, or a combination of both. Further work needs to be undertaken to establish if there is any casual relationship between the occurrence of *L. inundata* and *D. rotundifolia*.

**CONCLUSION**

The Smallhanger south clay pit has a population of ± 3000 plants of *L. inundata*. This population occurs over three habitats: the optimum was humus-covered clay waste subject to flooding, and the sub-optimum were waterlogged china-clay and damp peat mounds.
Perhaps the main reason for the rarity of the species now in the British Isles is due to the scarcity of its optimum habitat, rather than a reduction in its secondary habitats due to drainage.

The increase of N concentration in the soil along the transect suggests that *L. inundata* has the ability to either produce or exploit reserves of N which gives it an advantage over other plants to grow abundantly in a normally nutrient-poor inhospitable habitat. However, growth with its associated vegetation undoubtedly improves the soil by increasing the available N enabling other species to invade the habitat. At Smallhanger there is currently a gradual invasion of herbaceous, shrub and tree species in the base of the pit (Wigston *et al.* 1981). *L. inundata* appears to act as a pioneer species of inorganic acid wetland.

**ACKNOWLEDGMENTS**

We would like to thank Mr Roger Davies, who first drew our attention to the site; English China Clay Lovering Pochin and Co. Ltd for permission to use the site, and particularly Mr J.V. Silverlock who supplied the history of the site; Susan Jones who gave invaluable help with fieldwork; and Chris Preston of the BRC, Monks Wood who supplied records of *L. inundata* in Vice-Counties 1, 2 and 3.

**REFERENCES**


THE UPTAKE AND TRANSLOCATION OF CAESIUM 134 AND STRONTIUM 85 IN BRACKEN PTERIDUM AQUILINUM (DENNSTAEDTIACEAE: PTERIDOPHYTA)

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Department of Cell and Structural Biology, The University, Oxford Road, Manchester M13 9PL, England

*Department of Chemistry, Manchester University.
**Institute of Terrestrial Ecology, Merlewood, Grange over Sands, Cumbria LA11 6JU England

ABSTRACT

This is a report of preliminary research in which the study of the morphology and physiology of bracken (Pteridium aquilinum) is combined with the investigation of uptake of radionuclides from accidental nuclear release. Monitoring the uptake and translocation of artificially applied radioactive caesium and radioactive strontium in bracken plants should help to indicate how these radionuclides with contrasting behaviour enter and cycle through a long lived element of an important ecosystem.

THE CHERNOBYL INCIDENT

The highest yield nuclear accident to date, on 26th April 1986 at a nuclear power station at Chernobyl, near Kiev, Russia, resulted in widespread contamination of the northern hemisphere. Caesium (Cs) 137 (radioactive half life 29.7 years) and 134 (radioactive half life 2.1 years), released in the ratio 2:1, were the most important radionuclides released, together with some strontium (Sr) 90 (half life 28 years). Radionuclide deposition was greatest in areas of high rainfall (Allen 1986).

INTERCEPTION AND RETENTION OF RADIONUCLIDES BY VEGETATION AND SOILS

Models had predicted that radioactive caesium would rapidly become unavailable to plants because it would bind to clay minerals in the soil. However, these models were based on lowland agricultural systems where soils are predominantly mineral (Howard & Livens 1987). The British areas most affected by Chernobyl deposition were permanent pastures on organic soils, which had 2-4 times higher Cs134 and 137 activity than improved pastures in the same areas. These areas are also areas of abundant growth of bracken Pteridium aquilinum (L) Kuhn. The high organic to low clay content of these soils ensured that the Cs 134 and 137 remained mobile (Howard & Livens 1987; Barber 1964) and available for transfer along the food chain ultimately to man. This will pertain for the foreseeable future, possibly for the entire half life of Cs 137, because Chernobyl caesium is moving down the soil profile very slowly (Eggleton & Sandalls 1988).

The large surface area offered by bracken both above and below ground may intercept and then cycle radionuclides through these organic soils. Cs is cited by some workers as being an analogue of potassium (K) (Rickard 1966). As K is accumulated in the meristems of bracken it may be expected that Cs may be also concentrated there. Its long half life means that this could lead to genetic damage in the plant. Sr is known to be a good analogue of Ca. Sr85 may be found concentrated in the older parts of the plant like Ca (Russell 1963). An experiment over two seasons should show the long term seasonal translocation patterns of the two radionuclides. This will also help to illustrate nutrient allocation in this clonal plant. A short term experiment will contrast short term translocation patterns at different times of the year.

†One of the contributions to the BPS Autumn Indoor Meeting on 14 October 1989 at Whitelands College, London (see Bulletin 3 number 6), based on a poster entitled ‘Radionuclide uptake, transport and effect on bracken’ presented at the international conference ‘Bracken 89’, University of Sydney, 18-21 July 1989.
MOVEMENT OF RADIOACTIVE CAESIUM IN BRACKEN PLANTS

Two pilot experiments using Cs134 alone have been completed to develop the best method. In the first experiment mature roots, the rhizome shoot tip and pinna tip of 3 plants grown in perlite were immersed in 7,400 Bq/ml Cs134 in distilled water. 20 μl droplets of distilled water containing 185,000 Bq/ml Cs134 were applied to the frond of another plant. After 24 hours the samples were washed for 15 minutes to remove radionuclide from the apoplast.

The fronds were subjected to autoradiography. The rhizomes were cut up into their component parts i.e. rhizome shoots, frond primordia, rhizome pieces etc., fixed, and then counted for gamma emissions on a sodium iodide detector. The parts giving sufficient counts were then sectioned and subjected to microautoradiography.

Evidence of translocation (mainly in the phloem) was indicated when the radionuclide was applied to the rhizome shoot but not to anywhere else. If further experiments confirm this, an important nutrient uptake role for the rhizome tip is indicated by this. The second smaller experiment involved a plant being left for 7 weeks in situ after removal of the radionuclide solution from the root. Widespread translocation of the radionuclide was observed.

DISTRIBUTION OF STABLE CAESIUM AND STRONTIUM IN BRACKEN TISSUES

An analysis of stable caesium and strontium in different parts of plants should indicate where radioactive Cs and Sr will accumulate in bracken. Rubidium (Rb) and potassium are alkali metals like Cs so should similarly indicate its distribution. The analysis of K and calcium (Ca) also offers a way of comparing how these major plant nutrients are distributed relative to Cs and Sr. Samples have been taken from:- fronds, frond primordia, shoot tips, rhizome, roots and soil, with pure sucrose as a control. Cs and Rb were analysed by neutron activation and gamma spectrometry. Ca, Sr and K were measured by atomic emission spectrometry.

Results for 4 mature plants show that levels of the elements vary between sites and between tissues of the same plant. Rb and K appear to be preferentially accumulated in the rhizome meristem and frond primordia. However, Cs is not accumulated in any specific part of the plant. Ca and to a lesser extent Sr were concentrated in the senescing fronds. The concentration factors (quantitative expressions of the amount of element transferred from soil to plant parts) for 19 plants show Ca and Sr transfer from the soil to the senescent fronds is much greater than for any other plant part.

Ca is preferentially accumulated in the senescent fronds because it is a component of cell walls as calcium pectate. It also takes part in the control mechanism for growth and developmental processes and therefore is more abundant in active tissues like the frond rather than inactive tissues such as the rhizome; being immobile it concentrates in old woody tissue as more mobile elements are moved out. Sr acts similarly due to its analogy. Where photosynthetic fronds are present there were similar amounts of Sr and Ca to senescent fronds. Radioactive Sr therefore would be expected to be found in the leaf litter from where recycling to plants could take place. Although no firm conclusions can be drawn from the data for Cs, it appears that no analogy to K seems to exist for bracken. More data from neutron activation analysis should help clarify this.

THE POTENTIAL ROLE OF MYCORRIZAS IN RADIOACTIVE UPTAKE

Mycorrhizas are known to increase the uptake of certain nutrients by plants. It may be possible to link greater uptake of Cs134 and Sr85 with the presence of mycorrhizas. Percentage infection was estimated (after Jones & Sheffield 1988) for random samples of roots from all the plants sampled. A correlation analysis was carried out between the amount of mycorrhizal infection and Sr, Ca and K contents in the plants and soil. No correlation was found. A similar investigation will be carried out for Rb and Cs.
CAESIUM 134 & STRONTIUM 85 IN PTERIDIUM AQUILINUM

THE POTENTIAL EFFECT OF ACID RAIN ON RADIONUCLIDE UPTAKE
The influence of acid rain on cuticle thickness and hence efficiency of radionuclide uptake is being investigated. If there is a cline in the thickness of the frond cuticle on plants taken from a transect between a “clean” and polluted area a radionuclide uptake experiment is planned.

CONCLUSIONS
This is preliminary research leading to short and long term experiments. The results from the pilot radionuclide application experiment show that Cs134 may be translocated in the phloem, but the stable element analysis indicates that it may not be preferentially accumulated in rhizome meristems. The latter may mean that the genetic material of bracken may not be damaged in the event of a nuclear accident. A previously unknown uptake role may be indicated for the rhizome shoot tip.

ACKNOWLEDGEMENTS
We would like to thank Frank Barnett, Dave Robson and Mike Earnshaw for their invaluable technical and other help, and The Natural Environment Research Council for funding the project.

REFERENCES

ADIEU PROFESSOR
With the greatest sense of loss and sorrow we have to report the death of RICHARD ERIC HOLTTUM aged ninety-five.

His later years were affected by the death of his wife, his total deafness and, two years ago, severe bodily weakness with mental black-out and permanent loss of memory, all of which he bore with his characteristic dignity and fortitude. On the Fourteenth of October he was admitted to hospital with pneumonia and died resignedly and peacefully on the Eighteenth.

An Obituary is planned for The Bulletin.
REVIEWS


This is a definitive account of the ferns and allied plants of Canada by two professional botanists that have made pteridophytes their speciality. It has been a long time in the making and the authors have kept abreast of current thinking and referred to the latest paper on each species if it occurs. The 'Remarks' under each species make very interesting reading. The book is written however, for the interested layman and the initial chapters put topics like cytology, the role of hybrids, choice of latin names etc. into context.

I was pleased to see, after so much recourse to the alphabet in many recent regional accounts of ferns, that this book is arranged systematically, 12 families being included, the most interesting being the Adiantoid ferns being put with Dennstaedtia and Pteridium, a relationship not generally accepted now. At the generic level the names Phyllitis and Camptosorus are maintained and so, thankfully, is the name Asplenium viride Huds.; Athyrium alpestre (Hoppe) Rylands is retained for A. distentifolium Tausch, perhaps correctly so. It is interesting to see the differences between the North American taxon (subsp. americana) and our European plant. The evolutionary relationships of complex genera like Dryopteris (11 spp.) and Polystichum (11 spp.) are explained in detail. The correct name for Azolla caroliniana Willd. should be A. filiculoides Michx.

Each taxon is illustrated; the detailed drawings are good but some of the whole plant figures could have been treated with more care, or have too obviously been drawn from herbarium specimens. In such cases the 'jiz' of the plant is lost. The book ends with 159 detailed maps showing the distribution of all taxa in Canada, a really very useful adjunct. All in all, this is a good book and should be on the shelves of all interested in Northern hemisphere ferns.

A.C. JERMY


This is an expensive book, but one, once seen, that all fern-lovers will want to possess. It covers 184 species of fern and 22 fern allies, including those introduced to New Zealand and now part of the flora. 216 of these are illustrated in beautiful colour pictures from which all species can be easily identified and most are elaborated in some 198 line drawings or black-and-white photos. I find the latter sometimes overprinted and quite dark, however. There are keys to the genera and, in the text, keys to the species. The descriptions are concise and details of distribution are given generally or more precisely for the rarer species. A map of the two islands is given at the back of the book with localities mentioned in the text. Common English, and Maori names, where available are given. The ecological notes give a good idea of the garden requirements of the species should the plant become available in Spore Exchange banks.

A.C. JERMY
CYTOTAXONOMIC NOTES ON THE PTERIDOPHYTES OF COSTA RICA 1. GLEICHENIACEAE

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ABSTRACT

Eight species of *Gleichenia* from Costa Rica have been cytologically investigated. Six of these represent new chromosome counts for the genus.

INTRODUCTION

The programme of research on the cytotaxonomy of the pteridophyte floras of two contrasting islands at opposite ends of the Caribbean was effectively brought to a close by the publication of the results for Jamaica (Walker 1962, 1966, 1973) and for Trinidad (Jermy 1985, Walker 1985, Jermy & Walker 1985). These surveys had raised a whole series of questions which made it desirable to extend the work to the mainland of tropical America and this culminated in a visit to Costa Rica in 1986 by A.C. Jermy and myself.

Costa Rica has an exceedingly rich fern flora whose individual species cover the entire spectrum from being narrow endemics to those which are widespread throughout tropical America or even beyond. Many genera are either not, or only very poorly represented in the Caribbean region whilst others are common there. Such a situation was ideal for the purpose of the present programme. Identification of the plants has been made infinitely easier by the publication by David Lellinger of the first part of his monumental *The ferns and fern-allies of Costa Rica, Panama, and the Chocó* in 1989.

MATERIALS AND METHODS

Meiotic fixations were made in 3 parts absolute alcohol to 1 part glacial acetic acid either directly in the field or a few hours later at base. Before leaving Costa Rica the acetic alcohol was replaced by 70% ethanol for storage until examination at Newcastle. Voucher specimens were routinely taken, together with additional ripe sporing material.

Living plants were sent to the Royal Botanic Gardens, Kew and to Moorbank Garden at Newcastle University. Spores were also collected and these have provided a valuable source of additional plants. Cytological work is still continuing on most families as new plants raised from spores become fertile. However, two families in particular neither transplant successfully without very special conditions nor can be raised easily from spores. These are Gleicheniaceae and the filmy ferns Hymenophyllaceae and the cytological results have been wholly dependent on field-fixed material. Work on these two families has now been completed and form the first two parts in the present series of reports.

RESULTS

The cytological results are given in Table 1.

<table>
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<tr>
<th>Taxon</th>
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G. costaricensis (Underwood) C.Chr.

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G. intermedia Bak.

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G. nitidula Rosenst.

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G. aff. nitidula

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G. retroflexa Bomm. & Christ

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<th>Chromosome Number</th>
<th>Ploidy</th>
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<td>T14044</td>
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<td>n = 34</td>
<td>2x</td>
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</table>

G. strictissima Christ

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<th>Location</th>
<th>Chromosome Number</th>
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</thead>
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<td>Taucito, Pcia. Cartago, 1600m</td>
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<td>T14057</td>
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FIGURE 1: a) Metaphase 1 in *G. bancroftii*, x 1000. b) Explanatory diagram showing 56 bivalents.

FIGURE 2: a) Metaphase 1 in *G. costaricensis*, x 1000. b) Explanatory diagram showing 68 bivalents.

FIGURE 3: a) Metaphase 1 in *G. bifida*, x 1000. b) Explanatory diagram showing 34 bivalents.
NOTES ON SOME INDIVIDUAL SPECIES

G. bancroftii
This large handsome species is very distinctive, being the only member of the genus in the New World with one (up to 3) bipinnate primary branches which are not dichotomously forked. This is related to a small number of Old World species.

Although having a wide range from Mexico to Venezuela and including much of the Greater and Lesser Antilles this species is considered to be rather rare in Costa Rica. Lellinger (1989) noting the presence of only three specimens, two from Pcia.Heredia and one unlocalized. My cytologically worked specimen was from a new locality, namely the Cerro de la Muerte in Pcia.San José. I also photographed this unmistakable species in the Zona Protectora, Pcia.Heredia. The addition of two further localities in only a few weeks of random collecting suggests that G. bancroftii may be much more widespread in Costa Rica than had been realised.

Like the specimens from Jamaica (Walker 1966, 1973) and from Mexico (Mickel, Wagner & Chen 1966) the Costa Rican material showed \( n = 56 \). This agrees with the only other member of the subgenus which has been cytologically examined, namely G. glauca Hook. Further comments on the chromosomes of G. bancroftii will be found in the Discussion.

G. bifida.
This is one of the most widespread and abundant members of the tropical American gleichenias, ranging from Mexico to Brazil and throughout the Caribbean. It is a very characteristic plant of roadside banks and open clearings where it often forms dense thickets, frequently intermixed with other species of Gleichenia. The underside of the segments is covered by a dense tomentum of brown hairs which is rather variable as regards its density.

G. bifida has proved to be diploid with \( n = 34 \) wherever it has been examined, namely Jamaica, Puerto Rico, and Trinidad among the Caribbean islands and Mexico and now Costa Rica on the mainland (see Table 2 for references).

In Trinidad G. bifida was a member of a small complex of species and backcross hybrids involving G. remota (Kauf.) Spreng. and G. interjecta Jermy and T. Walker, the latter being the fertile allotetraploid derivative of the cross G. remota × G. bifida, followed by chromosome doubling. There relatively high proportions of hybrid plants were discovered in the course of random sampling of populations. Bearing these facts in mind a search was made in Costa Rica for hybrids involving G. bifida but none were found, although this may have been due to insufficient sampling in the time available or to the apparent absence of G. interjecta. It would be worth while to carry out a systematic search for this latter species as it may be formed de novo, independently of a Trinidadian source, since both parental species G. bifida and G. remota are present in Costa Rica and may be found growing together e.g. on a roadside bank west of Mogos, Pcia. Puntarenas at c. 100m altitude.

G. costaricensis
One of the three plants for which chromosome counts were obtained was gathered from the type locality of the species on a roadside bank on Volcan Poás, Pcia. Alajuela at c.2500m. The other two plants were from the Cerro de la Muerte, Pcia.San José at 2500m and 3100m respectively. All three showed \( n = 68 \) and hence were tetraploid, the only species to be so in this survey of Costa Rican taxa. The bivalents are more or less uniform in appearance (fig. 2) and lack the marked bimodal size distribution seen in those of G. interjecta in Trinidad (Walker 1985).
G. nitidula
Two specimens from Tausito, Picia, Cartago, were diploid with $n = 34$, as was also a third one from the same locality. However, this third plant whilst initially being identified as *G. nitidula* on closer examination was found to differ from this species in some important features such as details of the bud scale morphology. This is probably a new taxon which will have to be described and named but in the meantime it is recorded in Table 1 as *G. aff. nitidula*.

![Silhouette of frond of *G. retroflexa* c. half natural size.](image)

**FIGURE 4:**

![Explanatory diagrams showing 34 bivalents in each cell.](image)

**FIGURE 5:**

a) Metaphase 1 in two cells of *G. retroflexa*, x 1000.
b) Explanatory diagrams showing 34 bivalents in each cell.

**FIGURE 4:**

Silhouette of frond of *G. retroflexa* c. half natural size.

**FIGURE 5:**

a) Metaphase 1 in two cells of *G. retroflexa*, x 1000.
b) Explanatory diagrams showing 34 bivalents in each cell.

G. retroflexa
This species is highly distinctive with its small stature and strongly reflexed widely spaced segments borne on axes having a characteristic zig-zag formation (fig. 4). Despite its anomalous appearance it is a member of subgenus *Mertensia* and is a diploid with $n = 34$ (figs. 5a, 5b). Luis Gomez (quoted in Lellinger 1989) considers that this species hybridizes with *G. intermedia*, the offspring being *G. orthoclada* Christ. It would be of great interest to examine this latter taxon cytologically to determine its alleged hybrid status, and if this is confirmed to see if it is a diploid hybrid between the two presumed parental species or if chromosome doubling has taken place to produce a fertile allotetraploid. It appears to be not uncommon in the Cordillera Central; if it is a diploid hybrid this suggests that it has been formed repeatedly.
DISCUSSION

Holttum’s treatment (1957) of *Gleichenia s.l.* recognised the two genera *Gleichenia* and *Dicranopteris*, the former consisting of the three subgenera *Gleichenia*, *Diplopterygium* and *Mertensia* and the latter of two subgenera, namely *Dicranopteris* and *Acropterygium*. Each subgenus characteristically has its own distinctive basic chromosome number (Walker 1966). Although both subgenera of *Dicranopteris* are represented in Costa Rica no cytological results were obtained and as a consequence they will not be considered further here.

In *Gleichenia*, subgenus *Gleichenia* is absent from the New World in contrast to *Diplopterygium* and *Mertensia* which are present in both the eastern and western hemispheres. *Diplopterygium* consists of only a few species of which *G. bancroftii* is the sole American representative. As noted earlier the two species of *Diplopterygium* that have been examined, namely *G. bancroftii* in tropical America and *G. glauca* in India, both have \( n = 56 \) and in the lack of further information this has always been assumed to be the diploid state. The chromosome morphology of *G. bancroftii* is very distinctive, the bivalents appearing to be smaller and more attenuated than those of the other subgenera, particularly *Mertensia* (compare figures 1, 2 and 3). Whilst meiotic chromosomes cannot be used for karyotype analysis, nevertheless the difference in appearance between such chromosomes in these two subgenera suggests that karyotypic analysis of somatic cells may be very rewarding. Such an analysis in *Diplopterygium* may make possible a judgement as to whether the \( n = 56 \) represents a diploid level of ploidy on a base number of \( x = 56 \) or a tetraploid level on a base of \( x = 28 \), the latter figure fitting somewhat more easily into the known basic chromosome number series in the genus *Gleichenia*, namely \( x = 20, 22, (28) \) and 34.

By contrast *Mertensia* is a sizeable subgenus containing some 90 species in total of which c.40 occur in the American tropics and in southern South America (Tryon and Tryon 1982). The basic chromosome number, \( x = 34 \), is typical of all members throughout the world that have been counted (for records of the extra-American species see Löve, Löve and Pichi Sermolli 1977). In the New World a total of 6 species and 2 hybrids had been cytologically examined prior to the present communication (Table 2).

### TABLE 2

Cytology of New World taxa of *Gleichenia* subgenus *Mertensia* prior to present communication.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Country</th>
<th>Reference</th>
<th>Chromosome Number</th>
<th>Ploidy</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. bifida</em> (Willd.) Spreng.</td>
<td>Jamaica</td>
<td>Walker (1966, 1973)</td>
<td>( n = 34 )</td>
<td>2x</td>
</tr>
<tr>
<td></td>
<td>Trinidad</td>
<td>Walker (1985)</td>
<td>( n = 34 )</td>
<td>2x</td>
</tr>
<tr>
<td></td>
<td>Mexico</td>
<td>Smith &amp; Mickel (1977)</td>
<td>( n = 34 )</td>
<td>2x</td>
</tr>
<tr>
<td></td>
<td>Puerto Rico</td>
<td>Sorsa (1968)</td>
<td>( n = 34 )</td>
<td>2x</td>
</tr>
<tr>
<td></td>
<td>(Costa Rica)</td>
<td>pres. comm.</td>
<td>( n = 34 )</td>
<td>2x</td>
</tr>
<tr>
<td><em>G. brittonii</em> (Maxon) C.Chr.</td>
<td>Trinidad</td>
<td>Walker (1985)</td>
<td>( n = 34 )</td>
<td>2x</td>
</tr>
<tr>
<td><em>G. interjecta</em> Jermy &amp; T. Walker</td>
<td>Jamaica</td>
<td>Walker (1966)</td>
<td>( n = 68 )</td>
<td>4x</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>( 2n = 136 )</td>
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The present work adds a further 6 species (Table 1) which, together with G. bifida represents about half the Costa Rican taxa of Mertensia. These new records consist of 5 diploid and one tetraploid species, bringing the total of New World taxa so far examined to 9 diploid and 3 tetraploid species, together with 2 triploid interspecific hybrids.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the help given in Costa Rica by numerous people and organisations, especially by the Director and staff of the Museo Nacional and Dr Luis Gomez for his invaluable help and knowledge, the staff of Servicio de Parques Nacionales, Dr Gary Hartshorn and the Organization for Tropical Studies and Miss Angela Heaney. Living plants were carefully cultivated at the Royal Botanic Gardens, Kew, and by Miss A.T. Pickering and staff at Moorbank Garden, Newcastle University. Miss A. Paul and Miss Josephine Camus at the BM provided much help. I am most grateful to Clive Jermy for his assistance in innumerable ways.

Financial support by the Royal Society and the R.B. Cooke Travel Fund is gratefully acknowledged.

REFERENCES


NEW RECORDS AND NEW CYTOLOGICAL RESULTS FOR THE FERN FLORA OF MADEIRA

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&
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ABSTRACT
Two taxa, Asplenium adiantum-nigrum and A. x ticinense, are recorded for Madeira for the first time. For these and for two other species (A. septentrionale and Cheilanthes tinaei for which no cytological data were given in the survey of the cytology of indigenous Madeiran ferns compiled by Manton et al. 1986) the chromosome numbers are reported. The rare Hymenophyllum wilsonii was found at two new localities; its identity was cytologically confirmed.

INTRODUCTION
In a study concerning the cytology of the fern flora of Madeira, chromosome numbers and/or meiotic pairing behaviour of chromosomes were reported for almost all indigenous species of the island (Manton et al. 1986). In subsequent publications, the chromosome number of Anogramma leptophylla from Madeira was documented (Gibby 1986) and three new endemic taxa whose cytology was already shown in the publication by Manton et al. (1986) were formally described and named (Gibby & Lovis 1989). The cytology of some fern species from Madeira that were known only from herbarium collections were not included in these papers.

Stimulated by the work of Manton et al. (1986), the authors of this contribution were able, during an excursion to Madeira in August 1988, to record two ferns as new to Madeira and to collect material for chromosome counts of two further species that had not yet been checked cytologically from this island.

MATERIALS AND METHODS
For examination and measurements of spores in the field a small portable microscope with calibrated eyepiece was used. This method (Bennert et al. 1990) allows identification of hybrids by their aborted spores directly in the field. Furthermore, different cytotypes of aggregate species (like Asplenium trichomanes) or diploid and tetraploid taxa belonging to closely related and morphologically very similar species complexes (like Asplenium adiantum-nigrum and A. onopteris) can be separated by spore measurements, provided that their size is sufficiently distinct. More exact measurements of spore size was done later using preparations mounted in balsam (Euparal) (see Bennert et al. 1989). For cytological investigations premature sporangia were fixed in the field using a mixture of acetic acid and ethanol (1:3). Preparations were made following the classical method of Manton (1950:293). Some plants were collected living and cultivated in Glottertal or in the greenhouse of the Botanical Garden at Bochum for further investigations. For documentation, herbarium specimens of all new recorded taxa were collected (Ras = herbarium Rasbach; WB = herbarium Bennert).

RESULTS
A new endemic Dryopteris hybrid (most likely D. aitoniana × D. maderensis) will be described separately (Bennert et al., in prep.). We here present the new records and new cytological results:
Asplenium adiantum-nigrum L.

This species was hitherto unknown from Madeira although Manton et al. (1986) already suspected its occurrence on the island. *A. adiantum-nigrum* is known from the Azores, the Canary Islands and the Cape Verde Islands (Fernandes 1984, Hansen & Sunding 1985, Manton et al. 1986). On 15 August 1988, climbing uphill from the hydro-electric plant “Faja da Nogueira” (above Porto da Cruz) to the “Levada da Serra”, we saw repeatedly plants whose morphology (see fig. 1a) and spore size were indicative of *A. adiantum-nigrum*.

Figure 1. Silhouettes of fronds: a) *Asplenium adiantum-nigrum* (Ras-660), b) *A. × ticinense* (WB SP-27/88), c) *A. septentrionale* (Ras-638), d) *Cheilanthes tinaei* (Ras-652), e) *Hymenophyllum wilsonii* (Ras-650).
The spore size (exospore without perispore) of several plants was measured and was in the range of (33) 36-40 (44) µm. This agrees well with the figures given by Reichstein (1984) for this species in Central Europe (in spite of slightly different methods applied for measurements). *A. adiantum-nigrum* grows between 600 and 900 m alt. preferring open situations and rocky outcrops in a laurel forest vegetation being rather heavily degraded by woodcutting and grazing. These sites are often dominated by seedlings of *Erica* spec. and several composites of which *Helichrysum foetidum* is the most notable one. Additional fern species noted include *Asplenium anceps, A. × ticinense* (see below), *A. onopteris, A. trichomanes* subsp. *quadrivalens, Polystichum setiferum* and *Pteridium aquilinum*.

One sample of *A. adiantum-nigrum* was fixed in the field (Ras-660); several specimens (Ras-655, 658, 660; WB 162/88, 164/88) and one living plant (SP 29/88) were collected. Cytological examination of Ras-660 showed that the plant was tetraploid with n = 72 at meiosis (fig. 2 a, 2b). For comparison, spores of *A. onopteris* were measured and a range of (25) 28-30 (33) µm was obtained. One plant (Ras-657) was checked cytologically; it was diploid and gave n = 36 at meiosis.

![Figure 2. Cytology (spore mother cells in meiosis) of some Madeiran ferns. a) and b) Asplenium adiantum-nigrum (Ras-660), a) photograph, b) explanatory diagram showing 72 bivalents; c) and d) A. × ticinense (WB SP-27/88), c) photograph, d) explanatory diagram showing 36 univalents and 36 bivalents, pairs black, univalents outlined; e) and f) Cheilanthes tinaei (Ras-652), e) photograph, f) explanatory diagram showing 60 bivalents.](image-url)
Although occurring on all larger archipelagos of the Macaronesian Islands, *A. adiantum-nigrum* is, in contrast to *A. onopteris*, a rare plant with the exception of certain parts of the Azores (Fernandes 1984, Manton et al. 1986) where the climate tends to be cooler and moister than on most of the other islands. A chromosome count of a plant from the Azores by Queirós & Ormonde (1987) showed that it was indeed tetraploid thus confirming its identity with *A. adiantum-nigrum*. On Tenerife (Canary Islands) this species is obviously restricted to the highest parts of the island. It was found in the “Las Cañadas” at an elevation of ca. 2160 m in March 1979 by one of us (W.B.) and identified on the basis of spore size and perispore micromorphology (Bennert et al. 1982). A living plant from the same area (“Montaña Mostaza”) was collected by D. Ludwig in November 1983 and since then cultivated in Bochum. It was checked cytologically by H.R. in September 1987 and found to be tetraploid.

**Asplenium × ticinense** D.E. Meyer

Asplenium × ticinense, the hybrid between *A. adiantum-nigrum* and *A. onopteris*, was first described by Meyer (1960) based on a plant from Ticino (Switzerland). For the Macaronesian Islands this hybrid has, to our knowledge, only been mentioned by Fernandes (1984) who surveyed herbarium material of the *A. adiantum-nigrum* complex from the Azores and found several specimens with aborted spores.

On the way to the “Levada da Serra” where *A. adiantum-nigrum* and *A. onopteris* grew together (see above) several plants with intermediate morphology (see fig. 1b) and aborted spores were discovered. One living plant was collected (WB SP 27/88); it was found rather close to the “Levada da Serra” at an altitude of ca. 950 m. Two plants (Ras-659 and WB SP 27/88) were checked cytologically; as expected, they were triploid and showed \( n = 36^{11} \) and \( 36^1 \) at meiosis (fig. 2c and 2d). This result agrees fully with earlier cytological investigations of *A. × ticinense* (see Reichstein 1981). It corresponds with the genome formula Cu On On with Cu representing one genome of *A. cuneifolium* and On one of *A. onopteris*. Asplenium adiantum-nigrum is an allotetraploid plant (Cu Cu On On) being derived from the two diploids, *A. cuneifolium* and *A. onopteris*. Thus, in *A. × ticinense* two genomes originating from *A. adiantum-nigrum* (Cu On) and one of *A. onopteris* (On) are combined with the two On genomes forming bivalents (in this case of allosyndetic origin) and the single Cu genome remaining unpaired.

**Asplenium septentrionale** (L.) Hoffm.

Hansen & Sunding (1985) list this species for Madeira and the Canary Islands. Manton et al. (1986) mention a herbarium specimen from Madeira collected at “Passada da Vacas”; its cytology could not be checked. On 29 July 1988 we searched the area around the “Pico do Arieiro” (1818 m) and the “Pico do Juncal” (1800 m) for ferns. At an altitude of about 1760 m a colony of *Asplenium septentrionale* was found growing on steep NE exposed not shaded rocks. The following fern species were recorded in the vicinity: Asplenium obovatum subsp. lanceolatum = *A. billotii* (rare), *A. onopteris* (rare, only dwarfed plants), *A. trichomanes*, Cystopteris spec. and *Polystichum falcinellum* (dwarfed). Most plants of *A. septentrionale* were relatively small (see fig. 1c), the habitat was obviously rather dry. One plant (Ras-638) was fixed in the field (1 August 1988) and checked cytologically. It was tetraploid with \( n = 72^{11} \). This result corresponds with earlier cytological investigations reported for this species in Europe and the Canary Islands (see Benl 1967 and Manton et al. 1986).

**Cheilanthes tinaei** Tod.

Nardi et al. (1978) as well as Rasbach et al. (1982) report on herbarium specimens of this species from Madeira. The locality “São Roque” near Funchal, mentioned by Rasbach et al. (1982), had been visited by H.R. and K.R. in June 1980. A fixation of young sporangia
for cytological investigations gave no countable stages. On 4 August 1988 this colony growing on a wall of basaltic rocks just beside the road was revisited. The plants were completely dried out and blackened by exhaust gases and dust. One living plant was collected and has been cultivated since then as Ras-652 in Glottertal. The plant produced new growth (see fig. 1d) and could be checked cytologically. As expected, it was tetraploid and showed $n = 60^{ll}$ at meiosis (fig. 2e and 2f). Not far away from the station of *Ch. tinaei* the occurrence of *Ch. maderensis* Lowe could be confirmed. Cytological control of a plant that was taken into cultivation showed $n = 30^{ll}$, as it was already reported by Manton et al. (1986) for this species. *Cheilanthes guanichica* Bolle, another species reported to occur in the vicinity of Funchal (Rasbach et al. 1982), could not be found. Heavy traffic and intensive house building activities in Funchal are probably responsible for a strong reduction of the vegetation colonizing wall sides and will continue to affect these habitats adversely. So far, none of these *Cheilanthes* species have been found growing on natural rocks.

**Hymenophyllum wilsonii** Hook.

Manton et al. (1986) list a single station of this species in the western part of the island. In August 1988 we succeeded in discovering two new localities: 1) W of the “Boca da Encumeada” on a steep slope above rocks at the “Levada do Norte” at 1100 m alt., 2) E of the “Boca da Encumeada” at 1100 m alt., epiphytic on *Erica arborea*. A plant from one population (Ras-650, see fig. 1e) was controlled cytologically; it showed $n = 18^{ll}$ at meiosis confirming its identity with *Hymenophyllum wilsonii*.

**ACKNOWLEDGEMENTS**

We thank Dipl.-Biol. D. Ludwig, Bochum, for providing us with several living ferns that he collected on Tenerife in November 1983, and Dr M. Gibby, London, for checking and improving the text.

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