Zeitschrift: Candollea : journal international de botanique systématique = international journal of systematic botany

Herausgeber: Conservatoire et Jardin botaniques de la Ville de Genève

Band: 47 (1992)

Heft: 1

Artikel: Substrate preference of Lauraceae and ferns in the Iquios Area, Peru

Autor: Werff, Henk van der

DOI: https://doi.org/10.5169/seals-879560

Substrate preference of Lauraceae and ferns in the Iquitos Area, Peru

HENK VAN DER WERFF

ABSTRACT

WERFF, H. VAN DER (1992). Substrate preference of Lauraceae and ferns in the Iquitos Area, Peru. *Candollea* 47: 11-20. In English, English and French abstracts.

Species distribution and diversity of Lauraceae and pteridophytes were studied on several sites with different soil types in the Iquitos area, Peru. Due to difficulties of collecting and identifying Lauraceae, not many conclusions could be drawn on substrate preference of Lauraceae. A few species showed a substrate preference; only one species was found on several soil types. The data on ferns were more conclusive, with nearly all species restricted to either nutrient-poor sandy soil or nutrient-rich lateritic soil. Such substrate specificity is not postulated nor explained by the refuge theory, but shows that Beta-diversity significantly contributes to the species diversity in a given area.

RÉSUMÉ

WERFF, H. VAN DER (1992). Préférence du substrat des Lauracées et des Fougères dans la région d'Iquitos, Pérou. *Candollea* 47: 11-20. En anglais, résumés anglais et français.

On a étudié la distribution et la diversité des espèces de Lauracées et de Ptéridophytes dans plusieurs sites ayant divers types de sols dans la région d'Iquitos, Pérou. A cause des difficultés de récolte et d'identification des Lauracées, on a pas pu tirer beaucoup de conclusions quant aux préférences de cette famille pour certains types de substrat. Quelques espèces ont montré une telle préférence. Il n'y a qu'une seule espèce qu'on trouve sur plusieurs types de sols. Les Fougères ont fourni des données plus concluantes, puisque presque toutes les espèces sont limitées ou aux sols sablonneux pauvres, ou aux sols latéritiques riches. La théorie des refuges ne postule ni n'explique une telle spécificité de substrat, mais elle démontre que la diversité beta fait une contribution significative à la diversité des espèces dans une région donnée.

Introduction

The high species diversity in neotropical rain forests, as well as the observation that some areas have a higher species number than others, have long attracted the attention of biologists. Several explanations have been offered for the uneven species distribution; the most discussed of these is probably the refuge theory. This theory postulates that during the last two million years wet tropical forests have gone through several cycles of contraction and expansion (HAFFER, 1982). During the contraction periods the forests became restricted to about two dozen areas (PRANCE, 1982) with a high species diversity; during the expansion periods, forests occupied vastly greater areas, but the contraction areas retained a higher species diversity. PRANCE (1982) brought together the botanical evidence in support of the refuge theory, but he already excluded from consideration as refuges areas with a non-forest vegetation, such as savannas or montane habitats with scrub. Prance considered such areas with high species diversity and endemism as centers of endemism, areas with a habitat quite different from the surrounding rain forests, where a number of specialized species had evolved. Implicit in this view is the assumption that rain forests form a homogeneous vegetation type, which cannot be subdivided into different habitats. This assumption has lately been challenged. CAMPBELL & al. (1986) reviewed the available information on Amazonian forest

CODEN: CNDLAR
ISSN: 0373-2967
47(1) 11 (1992)

composition and concluded there is no homogeneous Amazonian forest, but rather a mosaic of forest types. BALSLEV & al. (1987) found only an 18% overlap in species between adjacent flooded and unflooded forest in lowland Ecuador, while GENTRY (1988) showed that a number of common tree species in his Tambopata tree plots were restricted to forest on a particular type of soil. Unfortunately, the number of published forest inventory studies is small. A recent forest study in Amazonian Ecuador (BALSLEV & al., 1987) suggests a reason for this. In their study, 228 and 149 tree species were found to be present in the adjacent unflooded and floodplain forests, a number which far exceeds anything found in temperate zone forests. The amount of time required for adequate collecting and identifying the trees would discourage most botanists. Even in the study by BALSLEV & al., conducted by a team of botanists with many years of experience in neotropical botany, 121 out of 333 species remained unidentified.

These studies, as well as GENTRY (1981), suggest that neotropical rain forests contain a number of distinct habitats, each with its own specialized species. Using this concept, GENTRY (1988) formulated an alternative theory for the uneven distribution of species numbers in neotropical forests. He postulated that many rainforest species are restricted to a particular habitat and that the total species number in a given area is strongly influenced by the number of habitats in that area.

This study was undertaken in order to determine if species distribution supports the refuge theory or the habitat diversity theory. The refuge theory does not make any specific predictions about species distribution, whereas the habitat diversity theory predicts that at least some species are restricted to a particular habitat. Forest on different substrates were selected as representing different habitats.

Site and vegetation description

With Iquitos as base, forests on several different soil types are easily accessible, listed in Table 1. The area, included in the East Peru-Acre refuge of PRANCE (1982), has a uniform elevation (130-140 m) and climate (3000-3500 mm rain per year, without a pronounced dry period). A common substrate close to Iquitos is relatively nutrient-poor lateritic clay; forest on this soil type has been extensively cut and this forest has not been studied. Also found near Iquitos is a terra firme forest on a substrate of white sand with a small amount of clay. The forest on this soil type has a closed canopy and is 20-25 m tall; it is locally called varillal. I collected in this forest type near Puerto Almendras, ca. 45 minutes outside Iquitos; near Mishana, ca. three hours by boat upstream on the Río Nanay; at the IIAP filed station near Alpahuayo, at Km 21 along the road Iquitos-Nauta; and near Jenaro Herrera, ca. 12 hours by boat upstream from Iquitos. Seasonally flooded forest on this substrate was studied near Mishana and Jenaro Herrera. In this flooded forest, called tahuampa, the upper centimeters of the soil consisted of clay deposited during the annual inundation by the Amazon river. At two localities (Puerto Almendras and Jenaro Herrera) small patches of pure white sand were found. In these areas the forest becomes low (5-10 m) and open, but with a denser shrub layer than in varillal; it is called chamizal. Near Jenaro Herrera another forest type

	Puerto Almendras	*Mishana*	*Alpahuayo*	*Jenaro Herrera*	*Yanamono*
Varillal = forest on sand with little clay	*	*	*	*	
Chamizal = low, open forest on pure sand	*	.	.	*	
Aguajal = Palm dominated swamp forest on sandy soil with little clay	.	.	.	*	
Tahuampa = flooded forest on rich soil	.	.	.	.	*
Tahuampa = flooded forest on sandy soil	*	.	.	*	
Forest on rich lateritic soil	.	.	.	.	*

Table 1. — Localities and vegetation types studied.

on sandy soil was sampled; it occurs along small creeks, whose drainage is stagnated during the periods of flooding by the Amazon and its larger tributaries. These small creeks inundate parts of forest and create a swamp forest dominated by palms. If the dominant palms is *Mauritia flexuosa,* this forest type is called aguajal; if it is dominated by other palms, sacha aguajal.

Although both aguajal and tahuampa are inundated forests, the two differ profoundly in structure and species composition. The main reasons explaining the differences between tahuampa and aguajal are probably that tahuampa is flooded by relatively nutrient-rich water from the Amazon (which carried a lot of silt) while aguajal is flooded by nutrient-poor water which runs off from white sand soils. Also, in tahuampa the water is probably deeper than in aguajal.

Finally, near Yanamono, about two hours downstream from Iquitos, non-inundated forest on richer, lateritic soil was studied. The trees are 30-35 m tall, but the forest is otherwise similar in structure to varillal. Inundated forest on lateritic soil was also studied near Yanamono.

Methods

Field work took place from July 26, 1988 to August 28, 1988. The limited amount of time for field work made it impossible to base the study on the entire forest composition and therefore only Lauraceae and pteridophytes were included. These two groups were selected because the author has ample experience with them in the field. An additional reason for including pteridophytes is that they are usually common and relatively easy to collect and identify.

Lists of pteridophytes and Lauraceae in the various sites were made by daily collecting. Because one of the main objectives of the field work was collecting Lauraceae, mostly medium-sized to large trees, which occur scattered throughout the forest, no quadrats were made. By making an inventory of quadrats one would obtain better data on presence and abundance of pteridophytes, but one also would get less information on Lauraceae than by simply walking through the forest and searching for these two groups. Thus, the results are based on collections (vouchers are deposited in MO) and field notes made at the end of each day. Some of the records are strictly based on sight identification and are not represented by vouchers; these refer to easily identified ferns, such as *Didymochlaena truncatula, Danaea nodosa, Adiantum pulverulentum* and *Tectaria incisa.* In some localities, common ferns, known from other sites, were not recollected, but were scored in the field notes (for instance, *Trichomanes martiusii, T. accedens* and *Cyclodium meniscioides*). No sight identifications of Lauraceae were made; in my experience identification of Lauraceae without microscopic dissection of the flowers is very difficult.

This method of collecting and scoring presence/absence does not yield reliable quantitative data. In the case of pteridophytes, only locally abundant species received a different score than rare or occasional species. Abundant implies that those species dominated and were present everywhere. Among the Lauraceae, no abundant species were found; it was, in fact, rare to find more than five individuals of a given species on a particular day.

Because the goal of this study was to investigate if pteridophytes and Lauraceae are substrate-specific, epiphytic ferns are excluded. Hemi-epiphytes, which root in the soil, but whose climbing stems are supported by trees, are included (mostly species of *Polybotrya, Lomariopsis,* and *Lomagramma*). Occasionally, epiphytic ferns show a preference for a particular vegetation type, but this is an indirect effect, when their preferred host tree is restricted to a particular substrate or habitat. An example is *Anetium citrifolium* (L.) Splitg., which was only found on the trunk of a palm growing in swampy places, or flooded forest. However, such ferns are better regarded as host-restricted than habitat-restricted and are therefore not included in this study.

Due to the skills of the Peruvian participants in recognizing Lauraceae (a quick check of the bark was sufficient for recognition), we found many sterile Lauraceae which we did not collect. Thus, the number of species we collected was only a fraction of the number of species present. Problems of identification are fewer in ferns and therefore the fern lists are more extensive and more complete than the Lauraceae lists.

Results

Lauraceae

The data on Lauraceae do not allow many conclusions in regard to habitat preference. There are two reasons for this. In the first place, many species were only found once. For instance, *Endlicheria metallica* Kostermans was found once in varillal of Puerto Almendras. Based on this observation, one cannot conclude that this species has a preference for varillal. In order to accept a substrate preference for a given species, one would require that a species occurs regularly on that substrate, preferably in different sites on the same substrate. Thus, single observations cannot be used. Secondly, identification of Lauraceae is frequently difficult, especially when material is sterile or fruiting. Undescribed species are also not uncommon and present additional problems in identification. I have refrained from using doubtful identifications and as a result the data set for Lauraceae is not large. Nevertheless, some conclusions can be drawn from the data presented in Table 2 and field notes. Firstly, no Lauraceae were found in the chamizal, low, open forest on pure white sand. This is somewhat surprising, because Lauraceae do occur elsewhere in scrub forest or shrubby savanna on white sand (for instance in southern Venezuela). Secondly, the flooded forest along the Amazon was poor in species. *Pleurothyrium parviflorum* was collected in both flooded forest sites; label data of other collections indicate this species is consistently collected in flooded forest and not in terra firme forest. The other species collected in flooded forest were only found once, but label data in MO indicate that most of these (*Endlicheria arunciflora* (Meissn.) Mez and *E. verticillata* Mez) are restricted to flooded forest. Finally, there are four species that have been found in three of the four varillal sites, in forest on sand with little clay mixed in. Of these four, *Anaueria brasiliensis* is rarely collected, while *Endlicheria citriodora* is an undescribed species. Only one species, *Licaria cannella* s.l., was collected in the forest on rich lateritic soil and in two sites with varillal. As currently accepted, *Licaria cannella* (Meissn.) Kostermans is a rather variable species with three subspecies and the collections from the Iquitos area are not homogeneous in respect to leaf characters, flower size and flower indument. The three collections may well belong to different taxa, but this cannot be determined without examination of specimens throughout the range of this species.

In general, the data on Lauraceae indicate that, with exception of *Licaria cannella* s.l., no species was found on two or more substrate types and that only a few species were collected frequently enough to suggest they are restricted to a particular substrate. The number of species for which data are available is small.

Pteridophytes

Data on presence and, to some degree, abundance of terrestrial pteridophytes are presented in Table 3. Rare species, mostly species of which only once a population was found, are included. Only ferns occurring in (more or less) undisturbed forest are taken into consideration and the few weedy species found along broad trails or similar disturbed places are excluded (*Nephrolepis* sp., *Pityrogramma calomelanos* (L.) Link). Also excluded is *Thelypteris opulenta* (Kaulf.) Fosb., which was occasionally present in flooded forest, but nearly always growing on fallen, decomposing tree trunks. *Ophioglossum nudicaule* Hook. & Grev. was probably the weediest pteridophyte encountered; it was common in part of the soccer field at the Arboretum Jenaro Herrera.

Species diversity

The sites sampled were found to differ greatly in species diversity. The lowest number of species was found in the three flooded forest sites, each with only three species present. At the Mishana tahuampa site, all *Metaxya rostrata* plants were sterile and juvenile, probably plants which started to grow after the latest flood cycle. The paucity of fern species (and also individuals) in tahuampa indicates that most ferns do not tolerate being submerged by floods for several months very well.

The chamizal at Jenaro Herrera showed also a low diversity, with only five species present. This was largely due to the small size of this stand of forest, only a fraction of the area of tahuampa

	Tahuampa	*Tahuampa*	*Varillal*	*Varillal*	*Varillal*	*Varillal*
	Jenaro Herrera	*Yanamono*	*Jenaro Herrera*	*Puerto Almendras*	*Mishana*	*Alpahuayo*
Pleurothyrium parviflorum Ducke	*	*				
Anaueria brasiliensis Kostermans			*	*		*
Aniba megaphylla Mez				*	*	*
Endlicheria citriodora van der Werff			*		*	*
Ocotea myriantha (Meissner) Mez.......			*		*	*

Table 2. — Distribution of Lauraceae.

that was investigated. The other sites on chamizal and varillal had more or less comparable species diversity. By far the richest in pteridophyte species was the Yanamono site, with 26 species present. This high diversity was not caused by collecting artifacts, such as number of collecting days or size of the area, but showed there were simply more species present. In his analysis of tree species diversity, GENTRY (1988) found that the Yanamono site was richer than forest on predominantly white sand (varillal), but the differences in diversity of trees were much smaller than found for pteridophytes.

A factor which does appear to contribute to species diversity is size of the area investigated. Although all sites were homogeneous in respect to soil type, creekbeds were present and such small-scale diversity results in microhabitats which are drier or wetter, lighter or darker than the average. Ferns do respond to drier or wetter sites and these moisture differences were more noticeable in Yanamono with lateritic clay soil than on the sites with sandy soil, where the drainage is better. Examples of ferns which were restricted to microhabitats at Yanamono are *Danaea humilis* (one group of plants found on a steep, dark, wet clay bank; I found this species in the same habitat in Ecuador) and *Bolbitis nicotianifolia* (once found in a marshy, open spot along a creek). A species of *Danaea,* probably *D. elliptica,* was only found along trails in varillal (at Jenaro Herrera and Mishana), very inconspicuous among herbs. Sometimes a species in a particular microhabitat was common in a different vegetation type, for example *Polybotrya glandulosa* was found rarely along creeks in varillal, but these plants were always depauperate and sterile. This species was common in swamp forest (aguajal); robust and fertile specimens only occurred in that habitat.

Thus, the larger a stand of a particular forest type surveyed, the greater the possibility of finding various microhabitats, which contribute to the species diversity. I did not find that distribution of Lauraceae (mostly medium to large trees) was affected by microhabitats which do influence fern distribution.

Species composition

Names and distribution of the 59 species of terrestrial pteridophytes belonging to 23 genera found in the investigated areas is presented in Table 3. This table shows two large groups of species: those that occur in Yanamono (on rather rich, lateritic soil) and in the flooded forests (tahuampa) versus those that occur in terra firme forest on sandy soil or in swamp forest. Only two species, both not common, were found in non-flooded forests on sandy and lateritic soil *(Polybotrya osmundacea* and *Saccoloma inaequale).* The flooded forest on lateritic soil sites were poor in ferns. They shared two species with unflooded forest on lateritic soil *(Thelypteris juruensis, Lomariopsis japurensis),* but *T. juruensis* was far more common in flooded than on non-flooded forst. *Adiantum latifolium* was the only species apparently restricted to flooded forest. Twenty one species were only found in the non-flooded forest on lateritic soil

The second main group of fern species is restricted to the non-flooded forests on sandy soils. The swamp forest on sandy soil (sacha aguajal) shares many ferns with this group and forms part of it. Good indicator species for these forests are *Trichomanes martiusii, T. accedens, T. bicorne,*

Table 3. — Distribution of pteridophytes: * = sight identification; ** = abundant.

	Varillal	*Varillal*	*Varillal*	*Varillal*	*Chamizal*	*Chamizal*	*Aguajal*		*Tahuampa*	*Tahuampa*
	Alpahuayo	*Mishana*	*Puerto Almendras*	*Jenaro Herrera*	*Puerto Almendras*	*Jenaro Herrera*	*Jenaro Herrera*	*Yanamono*	*Jenaro Herrera*	*Yanamono*
Trichomanes martiusii Presl.	x*	x	.	x**	x	x**	x			
Trichomanes accedens Presl.	x	x**	x	.	x	.	x			
Trichomanes bicorne Hooker	.	x	.	x**	x	x**				
Lindsaea lancea (L.) Bedd.	.	x	x*	x**	.	x				
Elaphoglossum discolor (Kuhn) C. Chr.	.	.	x**	.	x	x**				
Lindsaea divaricata Klotzsch	x	.	.	.	x	.	x			
Adiantum tomentosum Klotzsch	.	x**	x	.	.	.	x**			
Lindsaea schomburgkii Klotzsch	.	.	x	.	x*					
Metaxya rostrata (HBK.) Presl	.	x	.	.	.	.	x			
Trichomanes pinnatum Hedw.	.	.	.	x	.	.	x**			
Cyclodium meniscioides (Willd.) Presl.	x*	x	x**	x						
Selaginella producta Baker vel aff.	x	.	x**	x						
Cyathea bradei (Windisch) comb. ined.	.	x	x							
Danaea sp.	.	x	.	x						
Lindsaea hemiglossa Kramer	x	.	x							
Triplophyllum dicksonioides (Fée) Holtum	.	.	x*	x						
Cyathea pilossisima (Baker) Domin	x	.	.	x						
Selaginella lechleri Hieron.	.	.	x							
Arachnoides macrostegia (Hook. & Conant) Tryon	.	x	x							
Cyathea macrosora (Baker) Domin	.	.	x							
Polybotrya caudata Kunze	.	.	.	x						
Polybotrya pubens Martius	.	.	.	x						
Schizaea elegans (Vahl) Sw.	.	.	.	x						
Saccoloma inaequale (Kunze) Mett.	.	.	.	x	.	.	.	x		
Polybotrya osmundacea Willd.	.	.	.	x	.	.	.	x		
Trichomanes humboldtii Lellinger	.	.	.	.	x					
Trichomanes arbuscula Desv.	.	.	.	.	x					
Lindsaea arcuata Kunze	.	.	.	.	x					
Lindsaea No. 9998	.	.	.	.	.	x				
Polybotrya glandulosa Kuhn	.	.	.	.	.	.	x**			
Selaginella fragilis A. Braun	.	.	.	.	.	.	x**			
Lindsaea guianensis (Aubl.) Dry.	.	.	.	.	.	.	x			
Cyathea cf. *lastosora* (Kuhn) Domin	.	.	.	.	.	.	x			
Thelypteris juruensis (C. Chr.) Tryon & Conant	.	.	.	.	.	.	.	x	x**	x**
Lomariopsis japurensis (Mart.) J. Smith	.	.	.	.	.	.	.	x	x	x
Adiantum latifolium Lam.	.	.	.	.	.	.	.	.	x	x
Diplazium ambiguum Raddi	.	.	.	.	.	.	.	x		
Diplazium eggersii (Sodiro) C. Chr.	.	.	.	.	.	.	.	x		
Lomariopsis fendleri (Eaton) Underw.	.	.	.	.	.	.	.	x		

Table 3.

Thelypteris abrupta (Desv.) Proctor	.	.	.	.	.	.	.	x		
Thelypteris ancyriothrix (Ros.) A. R. Smith	.	.	.	.	.	.	.	x		
Thelypteris biformata (Ros.) Tryon	.	.	.	.	.	.	.	x		
Thelypteris glandulosa (Desv.) Proctor ..	.	.	.	.	.	.	.	x		
Bolbitis oligarchica (Baker) Hennipm. ..	.	.	.	.	.	.	.	x		
Bolbitis nicotianifolia (Sw.) Alston	.	.	.	.	.	.	.	x		
Didymochlaena truncatula (Sw.) J. Smith	.	.	.	.	.	.	.	x*		
Lindsaea ornithoptera Kramer, ined. ...	.	.	.	.	.	.	.	x		
Pteris altissima Poiret in Lam.	.	.	.	.	.	.	.	x		
Polybotrya crassirhizoma Lellinger	.	.	.	.	.	.	.	x		
Lomagramma guianensis (Aubl.) Ching .	.	.	.	.	.	.	.	x		
Selaginella haematodes (Kunze) Spring .	.	.	.	.	.	.	.	x		
Danaea humilis Moore	.	.	.	.	.	.	.	x		
Danaea nodosa (L.) Sm.	.	.	.	.	.	.	.	x*		
Nephelea sp.	.	.	.	.	.	.	.	x*		
Selaginella exaltata (Kunze) Spring	.	.	.	.	.	.	.	x*		
Tectaria incisa Cav.	.	.	.	.	.	.	.	x*		
Tectaria incisa "pulverulentum"	.	.	.	.	.	.	.	x		
Adiantum pulverulentum L.	.	.	.	.	.	.	.	x*		
Salpichlaena volubilis(Kaulf.) J. Smith ..	.	.	.	.	.	.	.	.	.	x
Total	7	10	13	14	10	5	10	26	3	3
Number of collecting days/site	3	2	3	6	1/2	1/2	1/2	4	1	1/2

Lindsaea lancea, Elaphoglossum discolor and *Adiantum tomentosum.* Within this group of forest types the swamp forest (sacha aguajal) at Jenaro Herrera stands apart by the presence of *Polybotrya glandulosa, Selaginella fragilis* (both common species), *Lindsaea guianensis* and *Cyathea* cf. *lasiosora* (the last two species occasional). To find *P. glandulosa* as a common species in the swamp forest was surprising; in his monograph of *Polybotrya,* MORAN (1987) listed only three collections of this species. The fact that the swamp forest is a rare forest type and that it cannot be reached by boat may have contributed to the paucity of collections of this species.

The two non-flooded forest types on white sand, varillal and chamizal, also differ in their fern floras. The chamizal, which occurs on extreme nutrient-poor soil, is an uncommon forest type and only twice were small stands of it sampled. Two *Trichomanes* species, *T. humboldtii* and *T. arbuscula* were only found in the chamizal at Puerto Almendras, the largest stand investigated. The chamizal at Jenaro Herrera covered a much smaller area and in spite of a careful search, these two *Trichomanes* species were not found there. Tho *Lindsaea* species were also found only in the chamizal, *L. arcuata* at Puerto Almendras and an unidentified species at Jenaro Herrera.

The varillal forest included several fern species not found elsewhere. These are, listed in decreasing frequency, *Cyclodium meniscioides, Selaginella producta* vel aff., *Cyathea bradei, Danaea elliptica, Lindsaea hemiglossa, Triplophyllum dicksonioides, Cyathea pilosissima* and *Arachniodes macrostegia.* In addition, *Selaginella lechleri* and *Cyathea macrosora* were found only in the varillal at Puerto Almendras and *Polybotrya caudata, P. pubens* and *Schizaea elegans* only in varillal at Jenaro Herrera.

Interestingly, the substrate in the tahuampa forest has apparently no influence on its terrestrial pteridophytes; the tahuampa at Yanamono is a rich lateritic substrate, but at Jenaro Herrera a white sand substrate. However, both tahuampas are flooded by the sediment-rich Amazon and the annual deposits of sediment are apparently more important to pteridophytes than the underlying soil types. In contrast, the swamp forest (aguajal) is inundated by nutrient-poor water from the surrounding white sand areas and its fern flora resembles those of the terra firme forest on white sand. Thus, in flooded forest the quality of the flood-water determines its fern flora, and not the underlying substrate.

The larger genera, represented by five or more species in Table 3, showed different distribution patterns. Two genera, *Polybotrya* and *Selaginella,* each with five species, had their species more or less evenly divided between sandy and lateritic substrate. One genus, *Thelypteris,* with five species, had all five species in areas with lateritic soil. *Trichomanes,* with seven species, was only found on sandy soils and *Lindsaea* showed also a preference for sandy soils (present with seven species on sand, and one, as yet undescribed, species on lateritic soil). The numbers of species involved of those genera are small and are certainly not large enough to draw a general conclusion about substrate preferences of the genera. However, I have found during earlier field work that *Lindsaea* and *Trichomanes* are better represented on nutrient-poor substrates than on nutrient-rich substrates.

In general, the ferns on the sandy substrate (dominated by *Trichomanes* and *Lindsaea*) were smaller than those on nutrient-richer soil, with genera as *Didymochlaena, Diplazium, Pteris, Tectaria, Bolbitis* and *Danaea nodosa,* the tallest of the three *Danaea* species found. I did not notice size differences in tree ferns on sandy versus lateritic soil.

Discussion

For a study like this, one would hope to have made a reasonably complete survey of the selected species groups. It is not likely that this goal was achieved for the Lauraceae. The difficulty of finding flowering specimens, without which identification is usually not possible, is the main reason for the incomplete survey. Pteridophytes, on the other hand, are easy to find, usually common, and their identification is relatively easy. One may therefore expect a more complete survey for pteridophytes than for Lauraceae. A comparison with an earlier pteridophyte collecting visit to Yanamono shows this is indeed the case. In 1984, Dr. Robbin Moran spent three days collecting ferns at Yanamono. He found 20 species of terrestrial or hemi-epiphytic ferns versus 27 species in this study (combining terra firme and flooded forest). Three of his species were not found by the author (*Poly-*

botrya caudata Kunze, *Thelypteris lugubriformis* (Ros.) Tryon and *T. opposita* (Vahl) Ching), while during this study ten species not seen by Dr. Moran were collected. This indicates that the present survey yielded a reasonably complete list of the terrestrial and hemi-epiphytic pteridophytes at Yanamono. One may assume that the surveys at the other localities were equally complete.

Few articles have been published which specifically discuss habitat preference or lack thereof among pteridophytes. In several papers, notes on habitat preference of some ferns are mentioned, but generally only those species are listed which occur on unusual substrates (KRAMER, 1974; TRYON & CONANT, 1975) or which occur in broadly defined vegetation types (TRYON, 1960; VAN DER WERFF & SMITH, 1980). More detailed notes on habitat preferences among ferns are given by GRAYUM & CHURCHILL (1987) on La Selva, Costa Rica and VAN DER WERFF (1990) on the Galapagos Islands, Ecuador, but none of these studies was aimed at documenting a substrate preference of ferns. An exception is a recent article by YOUNG & LEÓN (1989), who studied the distribution of pteridophytes in a two ha. area, partly on clay and partly on sandy loam in the Palcazu Valley, Peru, at 350 m elevation. They found 35 species of terrestrial pteridophytes (excluding weedy species), of which 21 were restricted to one of the two substrates and 14 occurred on both soil types. Thus, most pteridophytes were found to be restricted to a particular soil type and their findings aree with the results of this study. However, YOUNG & LEÓN (1989) found more species occurring on both substrates than in the present study. An explanation for this might be that the substrate types in Young & León's study differ less from each other than the substrates in the study reported here. "White sand specialists", such as *Elaphoglossum discolor, Trichomanes accedens, T. bicorne, T. arbuscula, T. humboldtii* and *T. martiusii,* were not found in their study area. In this study, forest on the most common substrate around Iquitos, nutrient-poor lateritic clay, was not studied, because much of it has been cut. Instead, forest on extreme nutrient-poor (varillal; to a lesser degree chamizal) substrate and nutrient-rich substrate (terra firme forest at Yanamono) were compared.

The data presented here show that nealy all pteridophytes and Lauraceae included in this study show some degree of substrate preference and that almost no species occurred both in varillal and in forest on nutrient-rich lateritic soil at Yanamono. Of the two competing theories to explain species diversity in neotropical forests, the refuge theory does not require nor explain substrate preference of the rain forest species, whereas the habitat diversity does demand and explain this. Although the results of this study thus do not refute the refuge theory, they clearly support the habitat diversity model. Data published earlier (e.g., GENTRY, 1981; BALSLEV & al., 1987 and YOUNG & LEÓN, 1989) and in this publication do not support the model of rain forest as a homogeneous vegetation type with randomly distributed species, but instead point to rain forest as consisting of distinct communities, each of which occurs under particular environmental conditions. The total number of species found in a given area thus depends strongly on the number of communities found in that area.

ACKNOWLEGMENTS

I sincerely thank the National Geographic Society for their support of the field work (Grant 3821-88). Dr. Robbin Moran generously made his field notes available to me. Several pteridologists (K. U. Kramer, Robbin C. Moran, Allan R. Smith and Robert G. Stolze) gave much-needed help with identification of the pteridophytes.

REFERENCES

BALSLEV, H., J. LUTEYN, B. ØLLGAARD & L. HOLM-NIELSEN (1987). Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Bot.* 92: 37-57.

CAMPBELL, D. G., D. C. DALY, G. T. PRANCE & U. N. MACIEL (1986). Quantitative ecological inventory of terra firme and varzea tropical forest on the Rio Xingu, Brazilian Amazon. *Brittonia* 38: 369-393.

GENTRY, A. H. (1981). Distributional patterns and an additional species of the Passiflora vitifolia complex: Amazonian species diversity due to edaphically differentiated communities. *Pl. Syst. Evol.* 137: 95-105.

GENTRY, A. H. (1988). Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Missouri Bot. Gard.* 75: 1-34.

GRAYUM, M. H. & H. W. CHURCHILL (1987). An introduction to the pteridophyte flora of Finca La Selva, Costa Rica. *Amer. Fern. J.* 77: 73-89.

HAFFER, J. (1982). General aspects of the refuge theory. *In:* PRANCE, G. T., ed., *Biological diversification in the Tropics:* pp. 6-24.

KRAMER, K. U. (1974). Notes on the distribution of the pteridophytes of Surinam. *Amer. Fern J.* 64: 107-117.

MORAN, R. C. (1987). Monograph of the neotropical fern genus Polybotrya (Dryopteridaceae). *Illinois Nat. Hist. Bull.* 34: 1-138.

PRANCE, G. T. (1982). Forest refuges: evidence from woody angiosperms. *In:* PRANCE, G. T., ed., *Biological diversification in the Tropics:* pp. 137-158.

TRYON, R. M. (1960). The ecology of Peruvian ferns. *Amer. Fern J.* 50: 46-55.

TRYON, R. M. & D. S. CONANT (1975). The ferns of Brazilian Amazonia. *Acta Amazonica* 5: 23-34.

WERFF, H. VAN DER & A. R. SMITH (1980). Pteridophytes of the State of Falcon, Venezuela. *Opera Bot.* 56: 1-34.

WERFF, H. VAN DER (1990). Ferns as indicators of vegetation types in the Galapagos archipelago. *In:* LAWESSON, J. E. & al., eds., *Botanical Research and managements in in Galapagos. Monogr. Syst. Bot. Missouri Bot. Gard.* 32: 79-92.

YOUNG, K. R. & B. LEÓN (1989). Pteridophyte species diversity in the central Peruvian Amazon: importance of edaphic specialization. *Brittonia* 41: 388-395.

Address of the author: Missouri Botanical Garden, P. O. Box 299, Saint Louis, Missouri 63166-0299, USA.