Notes on the ecology of the Xylariaceae of Papua New Guinea

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The geographical distribution of the xylariaceous fungi recorded from Papua New Guinea is presented. Most of the taxa are wide-spread in tropical regions with about 60% pantropical. When species richness was compared with that of other areas that have been intensively studied, the results indicated that Papua New Guinea is relatively rich in species compared to other Old World areas, but is less rich than neotropical regions. Although this result seems to be generally sound such comparisons should be interpreted with caution; a critical analysis of the apparent species richness on a local scale indicates that the results are strongly influenced by sampling intensity. Habitats in which xylariaceous fungi were collected ranged from wet, shaded virgin rain forests, to dry, sun-exposed sites. The species composition of the xylariaceous funga depended, however, strongly on habitat characteristics. Overall, *Kretzschmaria*, *Nemania* and many *Xylaria* species occurred in dense, shaded sites, whereas the genera *Biscogniauxia* and *Hypoxylon* were more abundant in relatively dry and open sites. *Daldinia* species were found in open to extremely dry, sun-exposed sites.

Keywords: ecology, Xylariaceae.

The ecology of tropical Xylariaceae has recently been reviewed by Whalley (1985, 1993). The occurrence of many taxa has been described to be strongly influenced by habitat and/or geographical region. Thus, a number of xylariaceous taxa occur in specific habitats or are endemic to particular regions.

The Xylariaceae of Papua New Guinea have been the subject of recent taxonomic studies based on extensive field collections made during two expeditions (Van der Gucht & Van der Veken, 1992; Van der Gucht, 1992; Van der Gucht, 1994). In the present study we present the ecological conclusions emerging from these field collections. This study is only based on fruiting structures found. As it is now known that xylariaceous fungi are widespread as endophytes also in many tropical plants (Petrini & Petrini, 1985; Rodrigues &

Samuels, 1990; Rodrigues & al., 1993), the distribution pattern presented here refers only to one aspect of their lifestyle, and reflects the circumstances under which they are able to produce teleomorphs.

This paper also considers the effect of sampling effort in introducing a bias with respect to conclusions on habitat quality and biodiversity. Therefore a comparison of the number of species found in the different localities investigated before and after a correction for the differences in sampling effort was undertaken in an attempt to reduce such bias. Sampling effort is judged from the number of visits to one locality, with each visit entailing about 1/2 day of intensive searching.

In addition the ecological characteristics of xylariaceous fungi from Papua New Guinea are compared with those reported from other tropical regions by Whalley (1993).

Geographical distribution

The survey of xylariaceous fungi in the world is far from complete, therefore statements on the distribution of taxa have to be interpreted carefully. From the data available, however, it is clear that the majority of taxa found in Papua New Guinea are confined to the tropics: ca. 60% can be considered pantropical, ca. 6.5% paleotropical, and for ca. 7.8% the available data indicate that they might be endemic to South-East Asia (Fig. 1).

As the neotropics are well-studied compared to the paleotropics (e. g. Dennis, 1970; Pérez-Silva, 1973; Rogers & al., 1988; Silveira & Rodrigues, 1985; Medel & al., 1989; Gonzalez & Rogers, 1993), it is probable that several of the species here treated as paleotropical indeed do not occur in the neotropics.

The number of so-called cosmopolitan species is relatively low, ca. 13%. Of these, *Hypoxylon perforatum* (Schwein.: Fr.) Fr. was found only in the highlands of Papua New Guinea (Van der Gucht, 1992; 1994). *Nemania atropurpurea* (Fr.) Pouzar, a taxon previously recorded only from North and Central Europe and Canada, has now been found in the lowland rain forest of Balek Wildlife Sanctuary, Papua New Guinea (Van der Gucht, 1994).

Taxa with their distribution limited to Papua New Guinea are those not previously described and it is probable that most of these taxa will prove not to be endemic to Papua New Guinea. *Hypoxylon retpela* Van der Gucht & Van der Veken, a new species described from Papua New Guinean material by Van der Gucht & Van der Veken (1992), also occurs in Indonesia (J. D. Rogers & Yu-M. Ju, pers. comm.). *Hypoxylon ravidoroseum* Y.-M. Ju, Van der Gucht & J. D. Rogers and

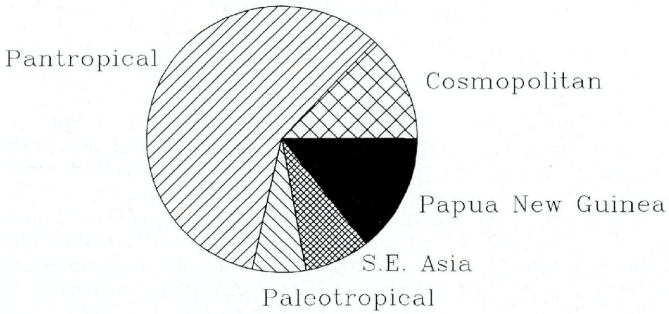

Fig. 1. – The distribution pattern of xylariaceous fungi found in Papua New Guinea.

Nemania immersidiscus Van der Gucht, Y.-M. Ju & J. D. Rogers, both new to Papua New Guinea, also occur in Hawaii (Van der Gucht & al., 1995). It seems likely that the degree of endemism is probably very low, and that the xylariaceous taxa occurring in Papua New Guinea are typical, tropical species. As such, it seems that the distribution pattern of xylariaceous fungi, reflected by presence of teleomorphs, is less limited by dispersal capacities than by ecological influences (e. g. temperature ranges; Whalley, 1993).

In common with the pattern exhibited by vascular plants (Gressitt, 1982), the xylariaceous funga[1] of Northern and Central Papua New Guinea is more related to the Asian than to the Australian one. Out of the 49 taxa reported in the study by Van der Gucht (1994) already known to occur in South-East Asia and/or Australia (including New Caledonia, New Zealand and Tasmania), 23 have not been listed for Australia, wheras only 2 (*Daldinia grande* Child and *Xylaria palmicola* G. Winter) are not known from Asia; 24 out of the 49 taxa are common to both regions.

The predominance of tropical as compared to cosmopolitan species is similar to the pattern observed by Quanten (1993) for the Polyporaceae of Papua New Guinea. Quanten (1993) also demonstrated a prevalence of Laurasian over Australian elements in the polypore funga of Papua New Guinea.

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[1] I agree with Barr (1983) that we are in need of a suitable term referring to fungi, in parallel to the terms "flora" and "fauna". However, from the two terms proposed by her, I consider "funga" as more suitable than "mycota", because the latter term is also used as a suffix for naming taxa at the Division level.

Effect of sampling intensity

An overview of the different localities sampled during the 1989 and 1992 expeditions to the northern provinces of Papua New Guinea is given in Tab. 1. In Fig. 2 the total number of taxa from the different localities investigated and the number of taxa divided by the number of visits to each locality are presented. The relatively large number of taxa (26) collected in the "Ramu region", predominantly in an alluvial flood-plain forest, contrasts with the low number of taxa collected in the highlands ("Ukarumpa": 10 taxa; "Wau": 5). As many as 21 taxa were found on Laing Island, a coralligenous island with less than 700 x 100 m surface area. This is largely the result of a high sampling effort, as the island has been repeatedly searched. When corrected for

Tab. 1. – Number of taxa recorded from the different localities sampled during the 1989 and 1992 expeditions to Papua New Guinea. Sampling effort is judged from the number of visits, with each visit entailing about 1/2 day of intensive searching. Locality: name of the village or island (Laing) or wildlife sanctuary (Balek); if cited as "...": region covering several sampling localities. "Finisterre Range": many sites along the road Madang–Lae; "Lae": several localities in the neighbourhood of Lae; "Ramu": several localities in the region around Brahman mission; "Sepik": several sites in the neighbourhood of Marienberg, Taway and Watam; "Ukarumpa": four localities in the neighbourhood of Ukarumpa; "Wau": three localities in the region around Wau. Year: expedition(s) during which the locality was visited; N° visits: total number of visits to the locality or region; N° taxa: total number of taxa found in the given locality or region.

Locality	Province	Year	N° visits	N° taxa
Alexishafen (coconut plantation)	Madang	1992	1	2
Amron (lowland rain forest)	Madang	1992	2	8
Awar (coastal rain forest)	Madang	1992	2	18
Babel (coconut plantation)	Madang	1992	1	1
Baiteta (lowland rain forest)	Madang	1989 + 1992	2	13
Balek (lowland hill forest)	Madang	1989 + 1992	3	16
Boroi (mangrove)	Madang	1989	1	1
Bunapas (lowland rain forest)	Madang	1989	3	8
"Finisterre" (largely lowland hill forest)	Madang	1989 + 1992	11	25
Kamba (disturbed lowland rain forest)	Madang	1992	1	4
Kaupena (disturbed highland rain forest)	Southern Highlands	1989	3	6
"Lae" (lowland rain forest)	Morobe	1989	5	23
Laing (coralligenous island)	Madang	1989 + 1992	5	21
Nagada (remnant woodland along coast)	Madang	1992	2	4
"Ramu" (alluvial flood-plain and hill forest)	Madang	1992	4	26
Sek (coralligenous island)	Madang	1992	1	1
Sepen (disturbed rain forest with bamboo)	Madang	1992	1	4
"Sepik" (alluvial flood-plain and hill forest)	Madang	1992	6	19
"Ukarumpa" (disturbed highland forest)	East Sepik	1989	4	10
"Wau" (highland rain forest)	East. Highlands Morobe	1989	3	5

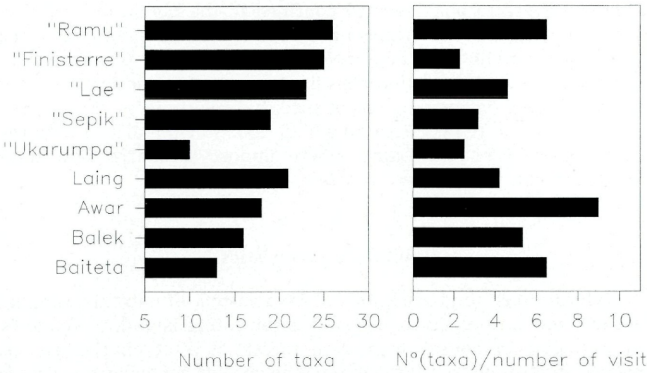

Fig. 2. – Species richness of the different localities and regions sampled during the 1989 and 1992 expeditions (see Table 2), estimated from the total number of taxa collected (left graph) and the number of taxa corrected for differences in sampling effort (number of visits; right graph).

differences resulting from sampling effort, the coastal forest near Awar stands out as the richest habitat, with the "Ramu region" (alluvial flood-plain forest), Baiteta and Balek (lowland hill forest) also being relatively rich in taxa. The forest near Awar is largely primary rain forest, although locally strongly disturbed by occasional gardens, is rich in habitat types, with sites ranging from dry to very wet, and from very shaded to sun-exposed.

Most of the habitats found to be poor in species, with less than three taxa collected per visit, proved to be highly disturbed [rain forest: Bunapas, Marienberg (Sepik region), Nagada, forest in immediate vicinity of Brahman mission (Ramu region), Sek island; coconut plantation: Alexishafen, Babel]. In addition, only a few taxa were collected in mangroves (Boroi, near Lae), although this may be due to the fact that effort was not concentrated on these habitats. In South East Asia mangroves regularly host xylariaceous taxa (Whalley & al., 1994).

Finally, high altitude localities (Kaupena, near Ukarumpa, near Wau) also proved to contain relatively few xylariaceous species. Although the highland localities provided few records, most of the species occurring at higher altitudes were only rarely present in the lowland, or not at all. Indeed, species such as *Hypoxylon bovei* var. *microsporum* J. H. Mill., *H. pilgerianum* Henn., *H. macroannulatum* S. Ito & S. Imai, *H. perforatum*, *Nemania serpens* (Pers.: Fr.) Gray, *Xylaria cranioides* (Sacc. & Paol.) Dennis, *X. gracillima* (Fr.) Fr.,

X. mellisii (Berk.) Cooke seemed confined to the highland localities. As such, the highland localities have contributed considerably to the overall species richness of Papua New Guinea (Van der Gucht, 1994).

Based on our data, differences in intensity of collecting can have a large influence on comparisons of species diversity (e. g. "Finisterre" where 11 visits were necessary to get 25 taxa, in comparison with the Ramu region, Lae and Laing where almost as many taxa were collected in half the number of visits).

Habitat characteristics

Xylariaceous fungi are known from a variety of habitats, ranging from dry and sun-exposed sites such as on Laing Island, to shadowy and wet sites in dense virgin rain forest. Habitat characteristics, however, determine to a large extent the species composition. This is especially apparent at the generic level (Fig. 3). For each taxon, it was determined whether it occurred predominantly (almost exclusively) in shadowy, dense forest, or it was more likely to be found in open and sun-exposed, often dry habitats. A third category of species occur in open as well as in shadowy sites and no preference can be deduced from the records available. There are striking differences among genera concerning the number of taxa recorded in open versus shaded habitats (Fig. 3). Most taxa belonging to the genera *Kretzschmaria* Fr. and *Nemania* Gray emend. Pouzar inhabit dense forests. A similar, but less strong, overall preference for apparently dense, undisturbed rain forest is shown by *Xylaria* Hill ex Schrank. In contrast, most species of *Biscogniauxia* Kuntze and *Hypoxylon* Bull. are frequent in open to sun-exposed sites. This preference for open habitats is strongest in *Daldinia* Ces. & De Not., with all three species having been almost exclusively found in sun-exposed sites. These observations on habitat preferences of the different genera are in overall agreement with the conclusions drawn by Whalley in his review on the ecology of tropical Xylariaceae (Whalley, 1993).

Most *Biscogniauxia* species were associated with dry and open habitats; when they occurred in rain forest, it was mainly in disturbed sites [e. g. *B. citriforme* (Whalley, Hammelev & Talig.) Van der Gucht & Whalley, *B. citriforme* var. *macrospora* Van der Gucht & Whalley, and *B. uniapiculata* (Penz. & Sacc.) Whalley & Læssøe] (Van der Gucht, 1992; 1994). There are, however, exceptions to this pattern: *B. grenadensis* var. *macrospora* (J. H. Mill.) Whalley & Læssøe and *B. uniapiculata* var. *macrospora* (J. D. Rogers) Whalley & Læssøe were occupants of relatively dense lowland rain forest.

Camillea tinctor (Berk.) Læssøe, J. D. Rogers & Whalley is a wide-spread and common species in lowland areas of Papua New

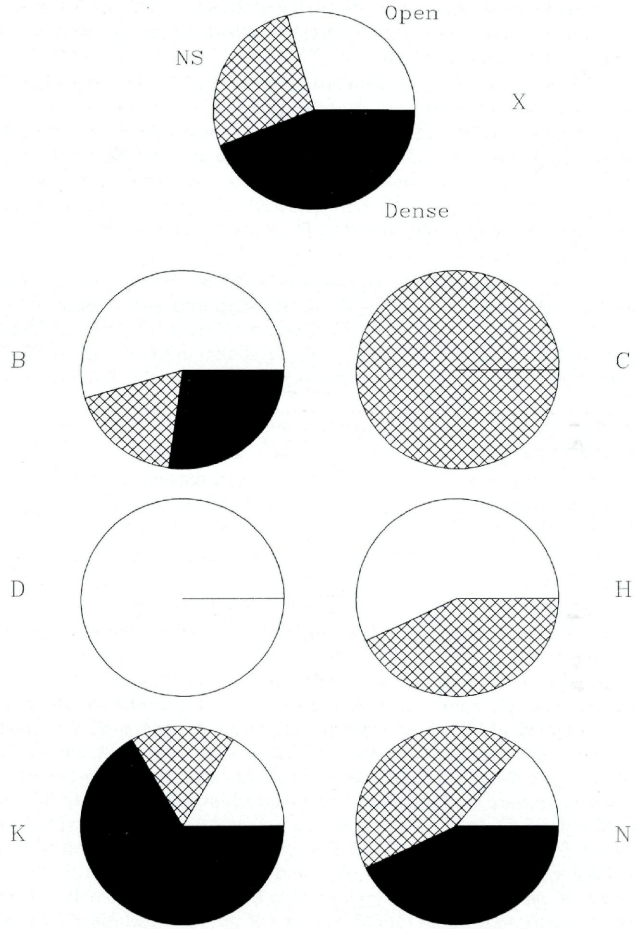

Fig. 3. – Habitat preference in xylariaceous fungi found in Papua New Guinea: proportion of taxa that were found predominantly in open and dry habitats (no hatching), in shadowy and wet sites in dense rain forest (solid), or in both types of habitats (criss-cross hatching). – NS (not specified): no apparent preference, or no clear pattern evident from the available data. Genera: X – *Xylaria* (34 taxa); B – *Biscogniauxia* (12 taxa); C – *Camillea* (1 taxon); D – *Daldinia* (3 taxa); H – *Hypoxylon* (21 taxa); K –*Kretzschmaria* (6 taxa); N – *Nemania* (7 taxa).

Guinea. It has now been recorded from a variety of habitats ranging from undisturbed primary rain forest to sun-exposed sites on Laing Island (Van der Gucht, 1992).

All three *Daldinia* species were confined to, or showed a distinct preference for, dry, open and sun-exposed sites, and developed along natural clearings, in and around native gardens, along roads and in plantations (Van der Gucht, 1994). *Daldinia eschscholzii* (Ehrenb.) Rehm, by far the most common species, also occurred in *Casuarina* forest and was abundant on Laing Island. *D. albozonata* Lloyd was only found in the lowland, whereas *D. grande* was recorded only once from a highland locality.

Although most of the *Hypoxylon* species were predominantly found in relatively dry and open to sun-exposed sites, some of the more common taxa, such as *H. dieckmannii* Theiss., *H. monticulosum* Mont. and *H. stygium* (Lév.) Sacc. occurred also in dense lowland rain forest (Van der Gucht & Van der Veken, 1992; Van der Gucht, 1994). *Hypoxylon oodes* Berk. & Broome is a common species of coastal areas, including very dry habitats such as *Casuarina* forest and remnant woodland on Laing Island.

The genus *Kretzschmaria* exhibits an apparent preference for dense lowland rain forest (Van der Gucht, 1994) but *Kretzschmaria deusta* (Hoffm.: Fr.) P. M. D. Martin is the only common species.

Similarly representatives of *Nemania* occurred mainly in dense and wet lowland rain forests, but such pattern was less clear than for *Kretzschmaria* (Van der Gucht, 1994). *Nemania serpens* was found only once, in a highland rain forest. No *Nemania* species can be considered abundant in Papua New Guinea.

In *Xylaria* an overall preference for rather dense habitats was observed but the more common species, e. g. *X. allantoidea* Berk., *X. anisopleura* (Mont.) Fr., *X. cubensis* (Mont.) Fr., *X. laevis* Lloyd, also tended to occur in more open and disturbed habitats (Van der Gucht, 1994). This preference for shaded and wet sites seems to be typical in *X. axifera* Mont., *X. eucephala* Sacc. & Paol., *X. luteostromata* Lloyd, *X. multiplex* (Kunze) Fr., *X. telfairii* (Berk.) Fr., and to a lesser extent in *X. adscendens* (Fr.) Fr., *X. curta* Fr., *X. papulis* Lloyd and *X. oligotoma* Sacc. & Paol. Most of these are taxa with small stromata, with a diameter of less than 5 mm. In contrast *X. palmicola* and *X. scruposa* (Fr.) Fr. were observed only in open, disturbed sites in lowland rain forest. Two of the three records of *X. poitei* (Lév.) Fr. were from mangroves.

Two types of stromata occurred in *X. cubensis*: relatively large, solitary stromata were the usual form in rather dense rain forest, whereas a smaller, shorter form, growing gregariously, was collected in more open and dry sites, including the coastal localities of Laing Island and Awar.

Most *Xylaria* species were only found in lowland localities but *X. anisopleura*, *X. schweinitzii* Berk. & M. A. Curtis and *X. telfairii* occurred also in highland rain forest, although they were mainly lowland species. *Xylaria cranioides*, *X. gracillima* and *X. mellisii* are apparently confined to highland rain forest.

The differences among genera in overall habitat preferences is also evident from the species composition of the xylariaceous funga from different localities. Fig. 4 shows the relative frequency of taxa in the different genera found in relatively rich localities. The alluvial flood-plain forest near Brahman (Ramu) is very rich in *Xylaria* species. The relatively wet hill forest of Balek is rich in *Xylaria*, *Kretzschmaria* and *Nemania* as compared to the more disturbed and often drier hill forest of the Finisterre Range.

A relatively large number of species were collected only in coastal areas, with Awar and Laing Island being the most intensively searched localities. Most of these taxa showed an apparent preference for sun-exposed, relatively dry sites. *Biscogniauxia mediterranea* (De Not.) Kuntze, *Hypoxylon sclerophaeum* Berk. & M. A. Curtis and *H. subgilvum* Berk. & Broome were only found on Laing Island.

Other taxa were collected only in highland localities (e. g. Ukarumpa). Several of the specimens collected in the Highlands differ slightly from typical material, e. g. *Xylaria anisopleura* collected in the highlands differs in the more robust stromata and larger ascospores (Van der Gucht, 1994). To a lesser extent, the same observation holds for the material collected in coastal areas. Thus *Hypoxylon caries* (Schwein.) Sacc. collected on Laing Island differs in its slightly sunken stromata and slightly larger ascospores (Van der Gucht, 1994).

Conclusions

There are few studies of xylariaceous fungi in the tropics for which field collections are extensive enough to draw conclusions on their ecology and preferred habitat characteristics. There is a general agreement, however, between our results and the patterns depicted by Whalley (1993), as well as with the observations on the Xylariaceae of Mexico (Gonzalez, 1992). Based on a comparison of the number of Papua New Guinean taxa of the genera *Biscogniauxia*, *Camillea*, *Daldinia*, *Hypoxylon*, *Kretzschmaria*, *Nemania* and *Xylaria* with the number of species recorded from other subtropical and tropical areas from which reasonably detailed surveys are available, as well as with the number of species recorded from Europe and South Africa it becomes clear that the neotropics are richer in taxa (Tab. 2). The most striking difference lies in the occurrence of a larger number of *Xylaria* and *Camillea* species. *Camillea* is a mainly neotropical genus, with

Tab. 2. – Species richness in Papua New Guinea compared to other regions. Number of taxa reported from the different countries are derived from the following sources: Papua New Guinea (PNG): Carroll, 1964; Shaw, 1984; Van der Gucht, 1994. – North Sulawesi (Indonesia): Rogers & al., 1987. – Venezuela: Dennis, 1970; Rogers & al., 1988. – Mexico: Pérez-Silva, 1973, 1975, 1983; Medel & al., 1989; Gonzalez & Rogers, 1993. – Zaire: Dennis, 1961, 1963. – Uganda: Taligoola & Whalley, 1976; Whalley & Taligoola, 1978. – South Africa: Martin, 1967, 1968a, 1968b, 1969a, 1969b, 1970. – Europe: Bertault, 1984; Petrini & Müller, 1986; Pouzar, 1986; Granmo & al., 1989. – NS: genus not covered by the study.

Taxon	PNG	North Sulawesi (Indonesia)	Venezuela	Mexico	Zaire	Uganda	South Africa	Europe
Biscogniauxia	12	3	7	16	3	3	9	8
Sect. *Biscogniauxia*	8	1	6	13	3	2	7	6
Sect. *Appendiculata*	4	2	1	3	0	1	2	0
Sect. *Scleraster*	0	0	0	0	0	0	0	2
Camillea	1	0	15	14	0	0	0	0
Daldinia	3	1	1	3	5	NS	2	5
Hypoxylon s. str.	22	15	28	23	12	13	26	18
Sect. *Hypoxylon*	13	8	15	13	7	8	19	15
Sect. *Papillata*	2	4	3	2	2	1	2	3
Sect. *Annulata*	7	3	4	8	3	5	5	0
Kretzschmaria	6	5	8	8	4	1	3	1
Nemania	7	0	1	1	1	0	17	12
Xylaria	43[1]	27	65	64	29	NS	23	45[2]
Total	94	51	125	129	54	(17[3])	80	88

[1] Actual status unknown for three taxa

[2] Bertault (1984): Europe and North Africa.

[3] Since not all genera are covered by this study the total number of species is placed between brackets.

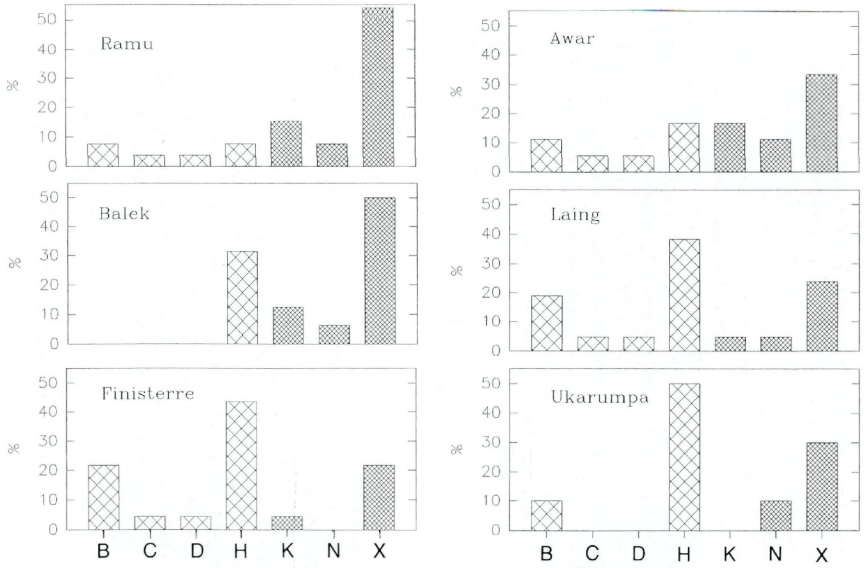

Fig. 4. – The relative frequency of taxa of the different genera in the xylariaceous funga collected in several localities. – Genera: B – *Biscogniauxia*, C – *Camillea*, D – *Daldinia*, H – *Hypoxylon*, K – *Kretzschmaria*, N – *Nemania*, X – *Xylaria*. Hatching visualizes the apparent preference of the genera for open sites (coarse hatching) or shadowy and wet sites (fine hatching). For localities, see Table 2.

only two species recorded out of the new world (Læssøe & al., 1989). A new species of *Camillea* has been very recently discovered in Malaysia (M. Whalley, pers. comm.).

Overall, our results indicate that Australasia has fewer *Xylaria* species than (sub)tropical America, although perhaps to a lesser extent than was suggested by Samuels (1990) based on the study by Rogers & al. (1987) from North Sulawesi. The tropics clearly exhibit a much greater diversity of *Xylaria* species than temperate regions. Although *Xylaria* have been intensively studied in Canada and continental U.S.A., only 22 species have been reported (Callan & Rogers, 1993), which contrasts with the large number of species described from Venezuela and Mexico. Such pattern, however, is not evident for *Hypoxylon* s. str., for which temperate and tropical regions may prove almost equally rich in species. *Kretzschmaria* on the other hand can be considered mainly a tropical genus. Regarding *Nemania* and *Biscogniauxia* section *Scleraster* Pouzar, current information suggests that temperate regions may exhibit a greater diversity.

The data presented in Tab. 2, however, should be interpreted with caution, as the sizes of the areas covered by the different studies differ substantially. For instance, whereas the flora of Venezuelan fungi by Dennis (1970) and the studies on xylariaceous fungi of Mexico (Pérez-Silva, 1973; Medel & al., 1989; Gonzalez & Rogers, 1993) cover an extensive area, the study by Rogers & al. (1987) on the xylariaceae of North Sulawesi (Indonesia) is limited to a rather small, even if intensively searched area. Similarly, the study in Papua New Guinea is based on intensive collecting, but only in the northern part of the island, and with a bias for lowland areas. The study of the xylariaceous fungi of Uganda (Taligoola & Whalley, 1976; Whalley & Taligoola, 1978) is similarly restricted to the forest area. Most of the xylariaceous records of Zaire cited by Dennis (1961, 1963) are based on material collected by investigators not specifically looking for xylariaceous fungi and is probably biased towards larger and more conspicuous species. This might also be the reason why Zaire appears to be poor in species.

To conclude, a general picture of the habitat characteristics and ecology of tropical Xylariaceae is emerging from field studies carried out in different parts of the world. Three statements seem to be generally valid: xylariaceous fungi are good dispersers; their range is set by ecological requirements more than by limits to dispersal; and their preferred habitat characteristics differ largely between genera as well as species.

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