Fungal Diversity

Fungal succession on fronds of *Phoenix hanceana* in Hong Kong

Yanna, W.H. Ho* and Kevin D. Hyde

Centre for Research in Fungal Diversity, Department of Ecology and Biodiversity, The University of Hong Kong, Pokfulam Road, Hong Kong SAR; e-mail: whhob@hkucc.hku.hk

Yanna, Ho, W.H. and Hyde, K.D. (2002). Fungal succession on fronds of *Phoenix hanceana* in Hong Kong. In: *Fungal Succession* (eds. K.D. Hyde and E.B.G. Jones). Fungal Diversity 10: 185-211.

Seventy-three fungal taxa were identified during the decomposition process of frond baits of *Phoenix hanceana*, comprising leaves, rachis-tips, mid-rachides and rachis-bases. Pioneer, mature and impoverished communities were observed in sequence on the frond baits. Fungal communities on different frond parts reached pioneer, mature and impoverished communities at different rates. Fungal communities on leaves and rachis-tips matured more slowly than other parts, but became impoverished rapidly thereafter, and samples were completely decayed at month 13. On the contrary, fungal communities on mid-rachides and rachis-bases matured earlier at month 1, but became impoverished at month 13. Naturally occurring fronds were also examined at the same time. Only half of the fungi were common to baits and naturally occurring fronds. Thus, examination of both frond baits at different stages of decomposition and naturally occurring fronds is recommended to obtain a better estimation of biodiversity.

Key words: fungal distribution, fungal ecology, palm, plant decomposition.

Introduction

Succession has been defined as "the sequential occupation of the same site by thalli (normally mycelia) either of different fungi, or of different associations of fungi" (Rayner and Todd, 1979).

There have been numerous studies on substratum succession involving a variety of substrata, for example, cellulose film (Tribe, 1957, 1961), plant litter (Webster, 1956; Tokumasu, 1998) and wool (Ghawana *et al.*, 1997). There have also been several studies of succession of fungi on degrading cellulosic substrates (Kuester, 1979; Gorska, 1982)

In succession, biotic communities change over time and the complete sequence of change is called a sere. Seres are made up of recognizable units (seral stages) (Luczkovich and Knowles, 2000). In general, fungal communities go through the following three stages (Dix and Webster, 1985; Gessner *et al.*, 1993):

* Corresponding author: W.H. Ho; email: whhob@hkucc.hku.hk

Pioneer community

This community consists of pioneer species which have low percentages of abundance (Dix and Webster, 1985; Gessner *et al.*, 1993). Pioneer species tend to be fast growing, short-lived, and capable of rapid and wide dispersal (Luczkovich and Knowles, 2000). This community type usually has low species diversity, while a few species have high abundance (Dix and Webster, 1985; Gessner *et al.*, 1993).

Mature community

The species diversity in mature communities is high and has peaked, while a number of species occur with a low percentages of abundance. However, several species may have a high level of abundance. The dominant species have extremely high levels of abundance. During the later stages of the mature community, the number of dominant species declines, but species diversity is still high (Dix and Webster, 1985; Gessner *et al.*, 1993).

The highest species diversity is likely to correspond with the highest rates of decomposition because greater genetic diversity is likely to correspond with greater enzyme diversity. There is also a greater likelihood that mutualistic associations and synergistic interactions can develop that can promote decay (Dix and Webster, 1985). Bärlocher and Kendrick (1974) found that five aquatic hyphomycete species growing together decomposed leaves faster than a single species.

Impoverished community

The species diversity declines towards an impoverished community. The community is dominated by a few species with extrememly high levels of abundance (Dix and Webster, 1985; Gessner *et al.*, 1993). These dominant species tend to be persistent and longer-lived species (Luczkovich and Knowles, 2000). However, there are still some species with low levels of abundance. The community will be in climax when it is dominated by one or two highly antagonistic species (Dix and Webster, 1985).

The present study was initiated to investigate the sequential occurrence of sporulating fungi on frond baits of *Phoenix hanceana*, and also to address the question, "Where are the undescribed fungi?", with the following objectives:

1. To investigate the fungal communities occurring on palm fronds during different stages of decay on different frond parts until complete decomposition.
2. To compare fungal communities from the succession study and with those of naturally occurring samples.

Materials and methods

Study sites

Hong Kong SAR (22°N 114°E) is located at the south-eastern coast of China, east of Guang Dong Province, some 100 km (1° latitude) south of the Tropic of Cancer. The study site was located in Tai Mo Shan (22°25'N 114°05'E) at around 600 m attitude. The climate in Hong Kong SAR is subtropical, tending towards temperate for nearly half of the year (Dudgeon 1994). During April to September, there is a wet and hot season, due to the prevalent south-western monsoon, and during October to the following March, there is a dry and cooler season due to the prevalent north-eastern monsoon (Dudgeon 1994). In general, January and August are the driest and wettest months respectively. The mean daily temperature ranges from 15.8 C in January to 28.8 C in July. It is not uncommon for temperatures to drop below 10 C during January and February (Dudgeon 1994).

Sample collection

Samples of succession study

Twelve *Phoenix hanceana* trees that were higher than 3 m and bearing more than 30 green, mature fronds were selected in a forest at Twisk, Tai Mo Shan, Hong Kong SAR on 16 July 1998. Ten random palm trees were used in this experiment and the remaining two trees were set as backup. Eleven green and mature fronds were cut from each of the ten individual palm trees. One of each of the eleven fronds was randomly collected at day 0. The other fronds were tied by nylon string to the host to prevent the fronds being removed. The position and location of the experimental fronds (frond baits) were similar to the adjacent naturally fallen fronds on the ground. At each sampling time, one decaying frond bait was randomly collected from each selected palm tree. It was planned to collect decaying fronds at week 1, months 1, 2, 4, 6, 12, 18, 24, 30 and 36. However, at month 13, leaves and rachis-tips were found completely decayed and at month 18, mid-rachides and rachis-bases were completely decayed. Therefore, frond baits were only collected on 16 July 1998 (day 0), 23 July 1998 (week 1), 17 August 1998 (month 1), 19 September 1998 (month 2), 17 November 1998 (month 4), 21 January 1999 (month 6) and 8 September 1999 (month 13). Collection of frond baits was more frequent at the early part of this study because fungal communities on palm (*Livistona chinensis*) were recorded to change rapidly at the earlier stages of decay (Yanna *et al.*, 2001b) and a dramatic increase of activities of saprobic fungi was also observed on newly dead leaves of the monocotyledon, *Pisum* sp. (Dickinson, 1967).

Ten samples were retrieved at each sampling time. Thirty centimeter long tip, middle and basal parts of rachis and a ten pieces of leaves were cut and placed individually in separate snap-locked plastic bags in the forest and brought back to the laboratory. Sterile moist tissue was added in the plastic bags to create a damp chamber within the bags. All samples were examined under a microscope within one month, except for the samples collected at day 0. In the latter case, microscopic examination was completed within 2 days in order to prevent growth of fungi that were not sporulating on the living fronds when they were cut. Squash mounts of sporulating fungi were made in water for examination with differential interference contrast microscopy. Fungi were isolated by staff of The University of Hong Kong Culture Collection (HKUCC) and the cultures are cryo-preserved at -140 C in HKUCC. Palm samples were also air-dried in an oven at 35-40 C and deposited in the University of Hong Kong Herbarium [HKU(M)]. Details of the fungi (specimens and cultures) are stored in the databases of HKUCC and HKU(M).

Naturally occurring samples

During the experimental period, naturally occurring fronds of *Phoenix hanceana* were collected on 17 August 1998, 21 January 1999 and 8 September 1999 for comparison with the frond baits. At each sampling time, a frond which had been decaying for a long time (later stages of decay) and a frond which was recently dead (the early stages of decay) were collected from each palm tree selected for the successional study. Samples were examined and stored as described for the frond baits.

Statistical analysis and simple calculation

A 3-dimensional correspondence analysis was performed to examine the differences in fungal communities at different times of decay. The fungi recorded on the palm frond parts were also compared with those from naturally occurring samples by correspondence analysis (Booth and Kenkel, 1986; Anonymous, 1995).

The fungi found in this study are presented in terms of percentage abundance. Fungal taxa with a percentage abundance equal to or higher than ten are regarded as dominant species. These fungal taxa are plotted to illustrate changes in the dominant species throughout the experimental period. Shannon indices (H') are used to express species diversity of a community (Shannon and Weaver, 1949), whereas species area curves are used to determine the adequacy of the sampling size.

$$\text{Percentage abundance of taxon A} = \frac{\text{occurrence of taxon A}}{\text{occurrence of all taxa}} \times 100\%$$

Shannon index (H') = $-\Sigma P_i \log_2 P_i$
where P_i is the probability of finding each taxon in a collection

Results

Determination of adequacy of sampling size

The species area curves for each frond part almost reached asymptote because the slopes of the curves were declining with the increase number of sample and at about 10 samples the slopes were near zero (Figs. 1-7). Although the curve did not completely level off, the number of samples was large enough to obtain highly representative results.

Colonisation patterns on different frond parts

Correspondence analyses of fungal communities at different times throughout the decay process are presented in Figs. 8-15. Shannon indices for different frond parts are plotted in Fig. 16 to illustrate changes of fungal diversity throughout the study period. Dominant species at different stages of decay are given in Figs. 17-20. The percentages of abundance for each species are listed in Table 1.

The values of Shannon index increased from 1.4-2 at the beginning of the study and reached peaks of about 3.7-4.1 at 120-200 days (Fig. 16). Fungal communities on leaves peaked first (at about 120 days) and were followed by rachis-tips (at about 150 days), and mid-rachides and rachis-bases (at about 200 days). Fungal diversity subsequently gradually declined. The changes of fungal communities on different frond parts were as follows.

Leaves

There were 44 fungal taxa found on the palm leaves over the experimental period, while three-dimensional correspondence analysis of fungal communities showed that there were at least three distinct communities (day 0, week 1-month 1, months 2-6) (Figs. 8, 9). The fungal community composition was distinct at each stage of succession, while dominant species at each sampling time were distinct (Fig. 17, Table 1).

Actinopelte sp., *Asterina clasterosporium*, *Everhartia phoenicis*, *Graphiola* sp., and an unidentified discomycete were recorded on green leaves at day 0. *Everhartia phoenicis* was associated with yellow spots on leaves (Yanna *et al.*, 2000), while *Graphiola* sp. was associated with brown spots. Fruiting bodies of *Actinopelte* sp., *Asterina clasterosporium*, and the unidentified discomycete, were formed on thin mycelial mats on the leaf

Table 1. Percentage of abundance of fungi found on samples of *Phoenix hanceana* during succession process in Hong Kong SAR (10 sub-samples per sampling time).

Species	day 0				week 1				month 1				month 2				month 4				month 6				month 13	
	l*	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt
Actinopelte sp.	33	42	43	33	6	8	33	30			4															
Antipodium arecae Matsush.						8			3	15	23	29		4	13	15		8	12	9			3	6		
Asterina clasterosporium S. Hughes	33	47	43	33	13	23	53	50																		
Astrosphaeriella nypae K.D. Hyde										3							2	5			6	9				
Beltrania africana S. Hughes												5											3			
Beltrania rhombica Penz.									3														3			
Blennoria buxi Fr.								10																		
Camposporium antennatum Harkn.																	5									
Capsulospora brunneispora K.D. Hyde									6															3		
Chaetopsina hongkongensis Goh & K.D. Hyde					6						4			4	22	15			5	6			8	8		
Circinotrichum palmicola J.E. Taylor, K.D. Hyde & E.B.G. Jones									3																	
Codinaea intermedia Rambelli													15	7			9	3	5	3	11	12	11	8		
Costantinella clavata Hol.-Jech																						3	3			
Cryptophiale udagawae Piroz. & Ichinoe									3		4							3								
Cylindrocladiella elegans Crous & M.J. Wingf.					6																					
Cylindrocladium brasiliense (Bat. & Cif.) Peerally					13	31	7		6	10	27	14	3	11	22	7		10	19	6		12	14	14		
Cylindrocladium quinqueseptatum Boedijn & Reitsma					6	8						5														
Cylindrocladium scoparium Morgan													6	11			2									
Dactylaria fusiformis Shearer & J.L. Crane														4				3								

* l = leaves; rt = rachis-tips; mr = mid-rachides; rb = rachis-bases.

Table 1 continued.

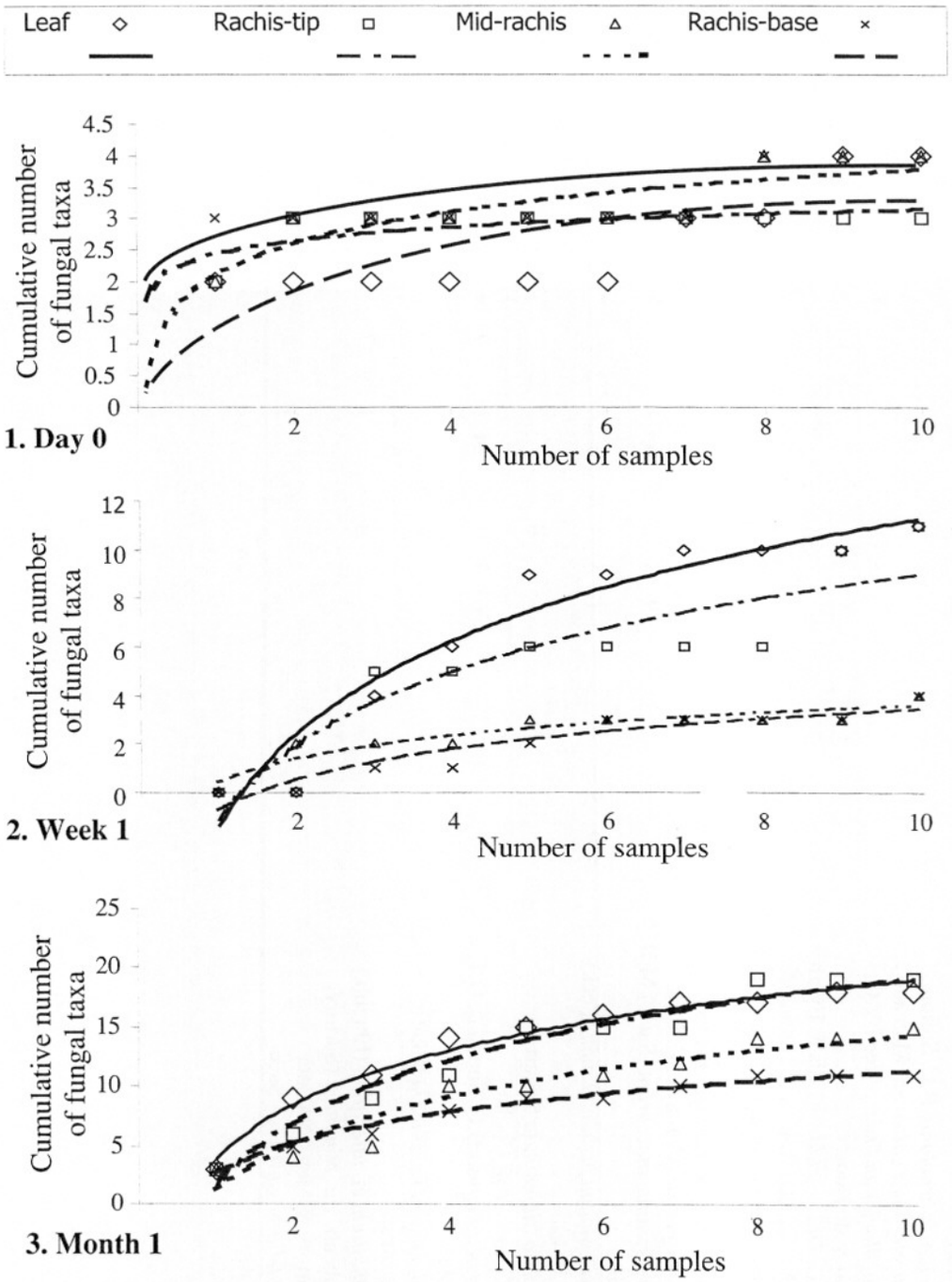
Species	day 0				week 1				month 1				month 2				month 4				month 6				month 13	
	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt
Diaporthe phoenicis Pat.									9				15				2	8		6		3		3		
Dictyochaeta menisporoides Hol.-Jech.									3	3																
Dictyochaeta simplex (S. Hughes & W.B. Kendr.) Hol.-Jech.									3	3								8	2		6	9				
Dictyosporium elegans Corda																							3			
Dictyosporium tetraseriale Goh, Yanna & K.D. Hyde																						3				
Didymosphaeria calamicola Aptroot, J. Fröhl. & K.D. Hyde																							3			
Dinemasporium lanatum Nag Raj & R.F. Castañeda													9	4				3								
Diplococcium stoveri (M.B. Ellis) R.C. Sinclair, Eicker & Bhat		11	5	29		8		10		3							5	3		3	6	3	3			
Discomycete	7				6																					
Domingoella-like species										3																
Endocalyx cinctus Petch										10	4	9	3	19	9	19		15	17	26		18	14	19		
Endomelanconium phoenicicola Yanna, K.D. Hyde & Goh					13				3	5																
Everhartia phoenicis Yanna, W.H. Ho & K.D. Hyde	20					8																				
Exserticlava vasiformis (Matsush.) S. Hughes																									25	25
Fasciatispora petrakii (Mhaskar & V.G. Rao) K.D. Hyde																	2									
Gliocladium sp.					6																					
Graphiola sp.	7																									

Table 1 continued.

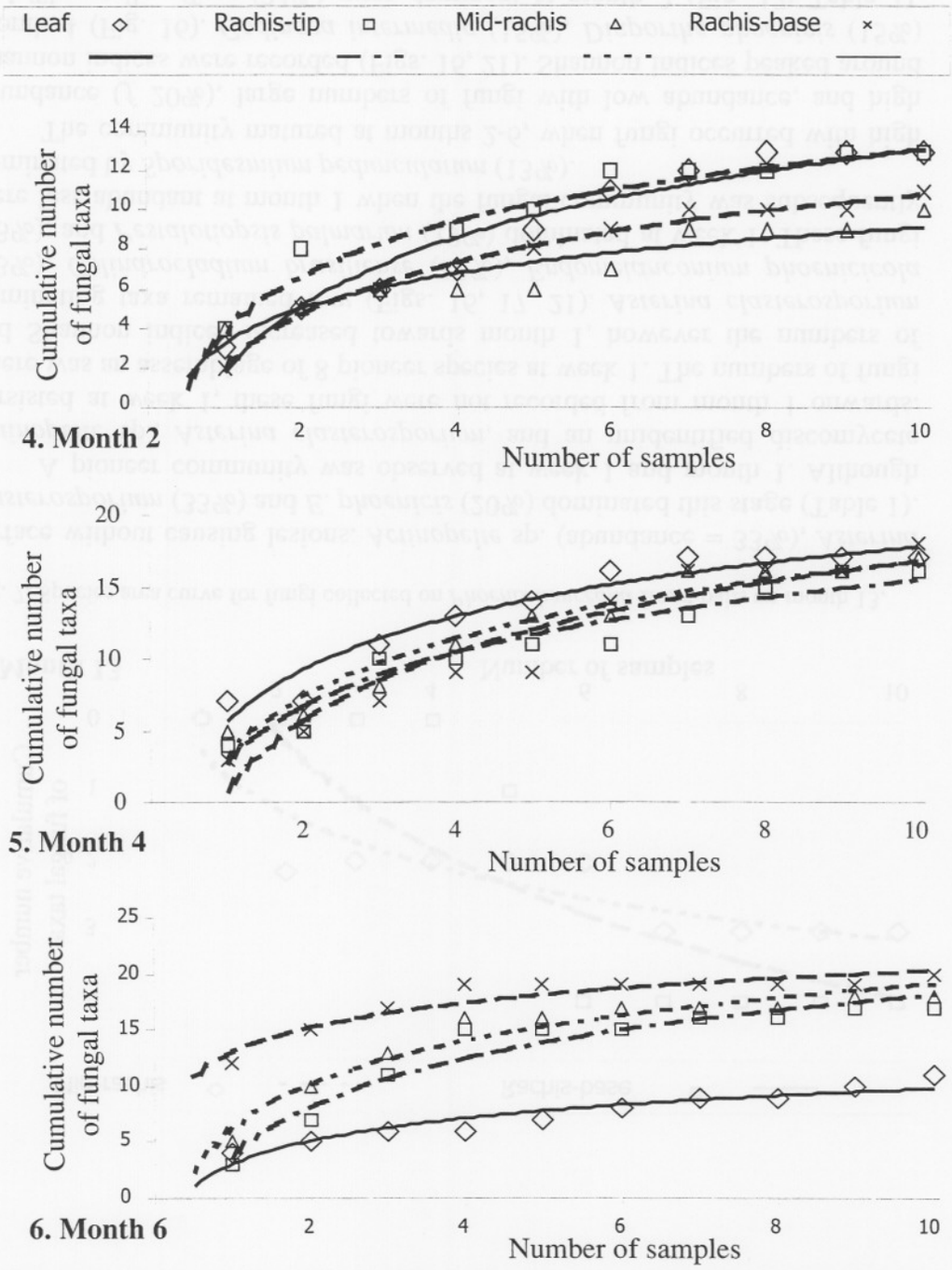
Species	day 0				week 1				month 1				month 2				month 4				month 6				month 13	
	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt
Guignardia manokwaria K.D. Hyde																		5	7	3		6	3			
Harknessia globosa B.C. Sutton										4			3	4		4		8	5	14		6	11	14		
Herpotrichia macrotricha (Berk. & Broome) Sacc.																			2			3	8	3		
Lasiodiplodia theobromae (Pat.) Griff. & Maubl.																4										
Linocarpon pandani (Syd. P. Syd.) Syd. & P. Syd.										3																
Melanographium palmicola Goh & K.D. Hyde																		3								
Monodictys putredinis (Wallr.) Hughes																			2							
Montagnula stromatosus J.E. Taylor, K.D. Hyde & E.B.G. Jones																			2	3						
Nectria chaetopsinae Samuels										4				4	19	11			10			3	5	3		
Oxydothis parvula (Syd.) Petr.									3	8	4	5														
Papulaspora sepedonioides Preuss																					11					
Penzigomyces nodipes (Penz. & Sacc.) Subram.										3	4	5												3	50	
Periconia minutssima Corda																	5									
Pestalotiopsis palmarum (Cooke) Steyaert					19	8			9	8	4															
Phaeosphaeria eustomoides (Sacc.) Shoemaker & C.E. Babc.									3																	
Phoma putaminum Speg.									9	3												3	8			
Phoma sp.							7																			
Phoma sp.															7											
Phomatospora berkeleyi Sacc.																	2				6					

Table 1 continued.

Species	day 0				week 1				month 1				month 2				month 4				month 6				month 13	
	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt	mr	rb	l	rt
Phomatospora sp.																				3						
Phomopsis archeri (S.A. Archer) B.C. Sutton									3	3																
Phomopsis arnoldiae B.C. Sutton																				3						
Polytretophora calcarata Mercado													3				2									
Ramichloridium fasciculatum V.G. Rao & de Hoog										3							7	3				3				
Roussoëlla pustulans (Ellis & Everh.) Y.M. Ju, J.D. Rogers & Huhndorf																			2							
Selenosporella curvispora Mac Garvie														4						3						
Serenomyces shearii Petr.										10	8	19				4				3				3		
Sporidesmiella hyalosperma var. *hyalosperma* (Corda) P.M. Kirk																	2				6				25	25
Sporidesmium macrurum (Sacc.) M.B. Ellis									9	3		5	6	4			5	5	2	3	11			3		
Sporidesmium pedunculatum (Peck) M.B. Ellis		9	5						13	5			6	4	3		7	5	2	3		3				25
Stilbella albominuta Seifert											4				3											
Tetraploa ellisii Cooke																	12				6			3		
Thozetella effusa B.C. Sutton & G.T. Cole				6					6	3			24	11		7	9	8	5		11	6	5			
Trichoderma harzianum Rifae												5								3						25
Tubakia sp.													6				21				22					
Verticillium cf. *lateritium* (Ehrenb.) Rabenh. var. *minimum* (Sartory, Sartory & Mey.) Valenta											4			4	9	7				3						
Volutella gilva (Pers.) Sacc.														4												



Figs. 1-3. Species area curves for fungi collected on *Phoenix hanceana* frond baits at different stages of succession.



4. Month 2

5. Month 4

6. Month 6

Figs. 4-6. Species area curves for fungi collected on *Phoenix hanceana* frond baits at different stages of succession.

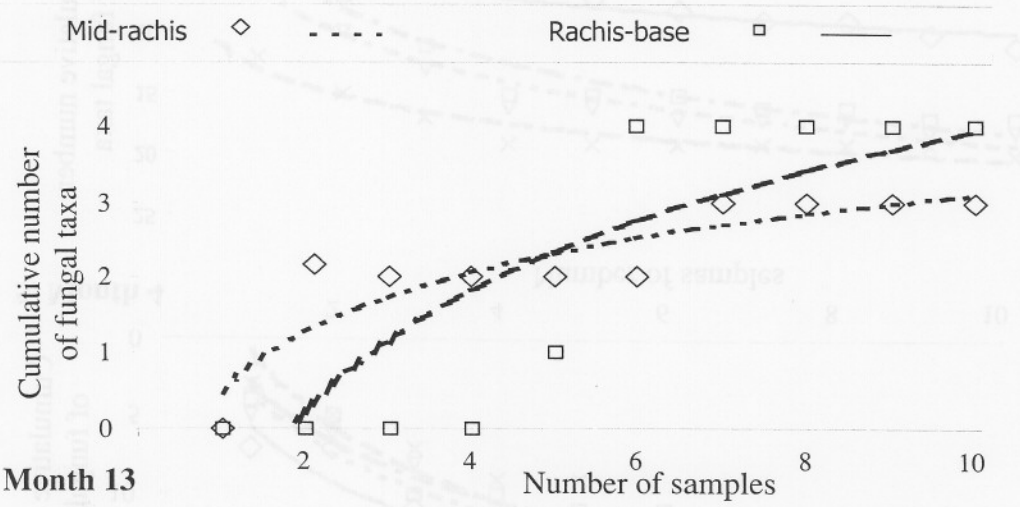


Fig. 7. Species area curve for fungi collected on *Phoenix hanceana* frond baits on month 13.

surface without causing lesions. *Actinopelte* sp. (abundance = 33%), *Asterina clasterosporium* (33%) and *E. phoenicis* (20%) dominated this stage (Table 1).

A pioneer community was observed at week 1 and month 1. Although *Actinopelte* sp., *Asterina clasterosporium*, and an unidentified discomycete persisted at week 1, these fungi were not recorded from month 1 onwards. There was an assemblage of 8 pioneer species at week 1. The numbers of fungi and Shannon indices increased towards month 1, however the numbers of dominating taxa remained low (Figs. 16, 17, 21). *Asterina clasterosporium* (13%), *Cylindrocladium brasiliense* (13%), *Endomelanconium phoenicicola* (13%), and *Pestalotiopsis palmarum* (19%) dominated at week 1. These fungi were less abundant at month 1 when the fungal community was subsequently dominated by *Sporidesmium pedunculatum* (13%).

The community matured at months 2-6, when fungi occurred with high abundance (*f* 20%), large numbers of fungi with low abundance, and high Shannon indices were recorded (Figs. 16, 21). Shannon indices peaked around month 4 (Fig. 16). *Codinaea intermedia* (15%), *Diaporthe phoenicis* (15%) and *Thozetella effusa* (24%) were dominant at month 2 (Fig. 17; Table 1). These fungi became less abundant at months 4 and 6 when the community was dominated by *Tubakia* sp. (21-22%) (Fig. 17; Table 1).

At month 13, leaves were found to be completely decayed, and an impoverished community was not observed and would have appeared between month 6 and 13.

Rachis-tips

There were 41 fungal taxa found on the rachis-tips, while three-dimensional correspondence analysis showed that there were at least three distinct communities (day 0, week 1-month 1 and months 2-6) (Figs. 10, 11). Months 2, 4 and 6 clustered in the analyses, indicating similar fungal communities were found.

Low numbers of fungi were recorded on green rachis-tips. These included *Diplococcium stoveri* associated with brown spots, and *Actinopelte* sp. and *Asterina clasterosporium* found on the surface of healthy parts (Fig. 18; Table 1). *Actinopelte* sp. (42%) and *Asterina clasterosporium* (47%) and *Diplococcium stoveri* (11%) dominated this stage.

The number of fungal taxa and Shannon index increased from week 1 to month 1 (Figs. 16, 22). Of the species recorded at day 0, the abundance of *Actinopelte* sp. and *Asterina clasterosporium* dropped drastically at week 1 and these fungi were not found at the later stages, while *Diplococcium stoveri* persisted (Fig. 18; Table 1). Twenty pioneer species were found at week 1 and month 1. *Cylindrocladium brasiliense* dominated the fungal community at week 1 (31%), but its abundance declined thereafter to 10-12% at months 1-6. *Antipodium arecae* (15%) and *Serenomyces shearii* (10%) dominated the fungal communities at month 1 (Fig. 18; Table 1).

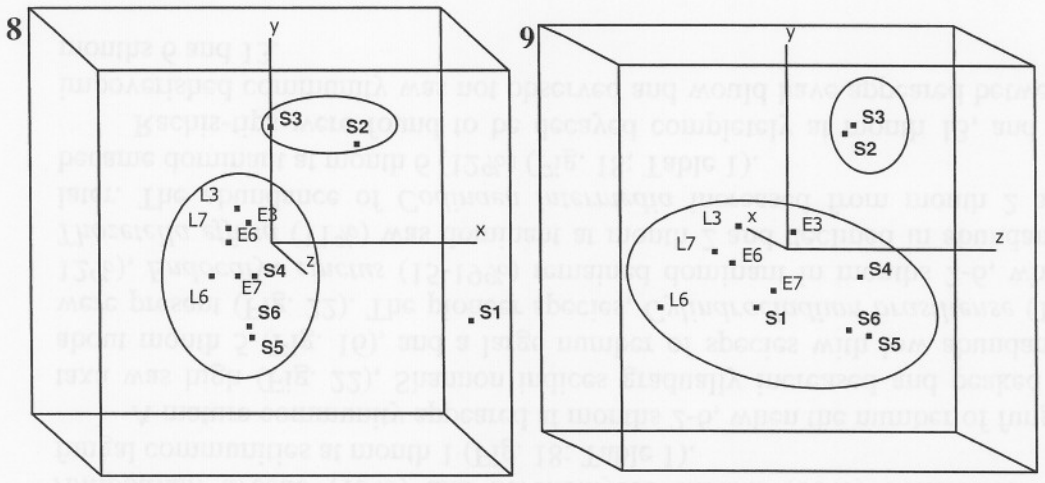
A mature community appeared at months 2-6, when the number of fungal taxa was high (Fig. 22), Shannon indices gradually increased and peaked at about month 5 (Fig. 16), and a large number of species with low abundance were present (Fig. 22). The pioneer species, *Cylindrocladium brasiliense* (10-12%), *Endocalyx cinctus* (15-19%) remained dominant in months 2-6, while *Thozetella effusa* (11%) was dominant at month 2 and declined in abundance later. The abundance of *Codinaea intermedia* increased from month 2 and became dominant at month 6 (12%) (Fig. 18; Table 1).

Rachis-tips were found to be decayed completely at month 13, and an impoverished community was not observed and would have appeared between months 6 and 13.

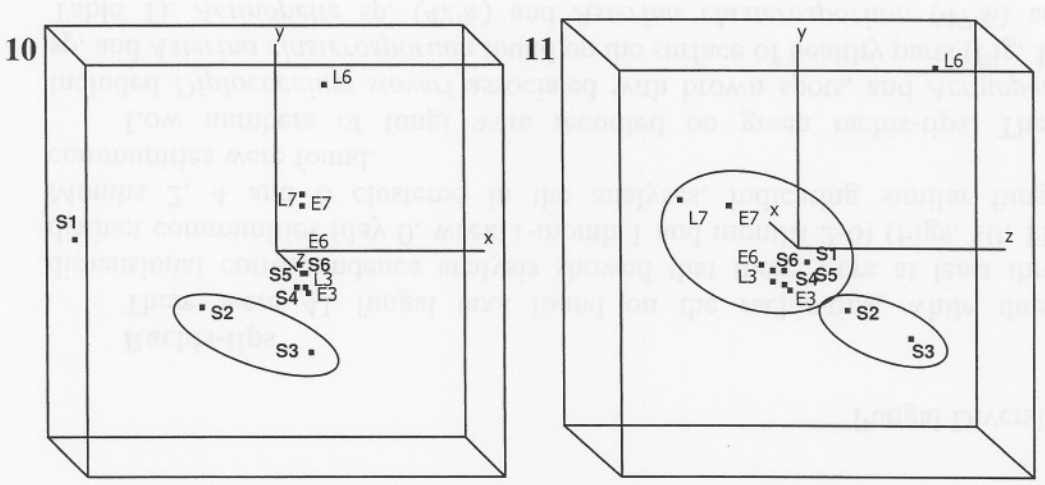
Mid-rachides

There were 35 fungal taxa found, with 3 distinct succession stages comprising distinct fungal communities on the mid-rachides throughout the decay process (day 0-week 1, months 1-6 and month 13) (Fig. 14). The fungal communities at day 0 and week 1, and those at months 1, 2, 4 and 6 form two coherent clusters in the analyses.

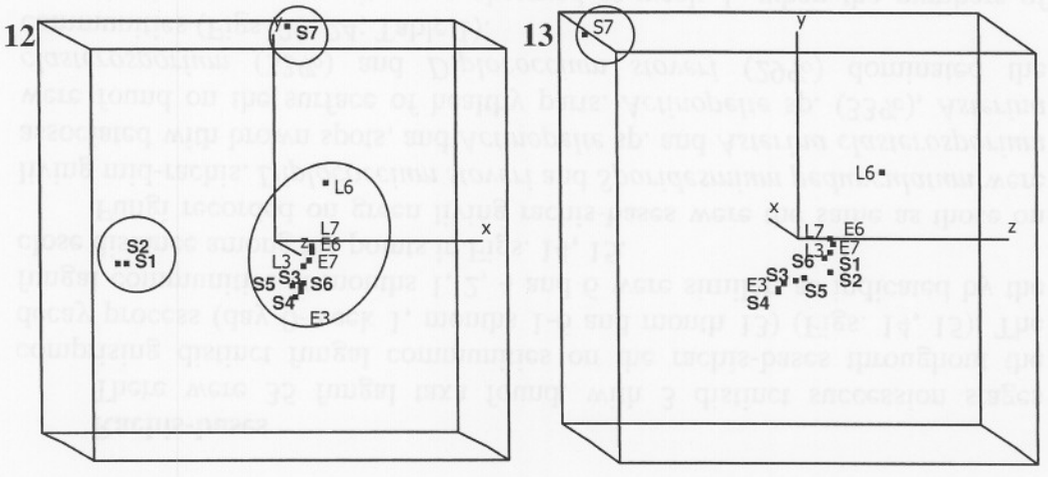
Low numbers of fungi were recorded on green living mid-rachides. These included *Diplococcium stoveri* and *Sporidesmium pedunculatum*



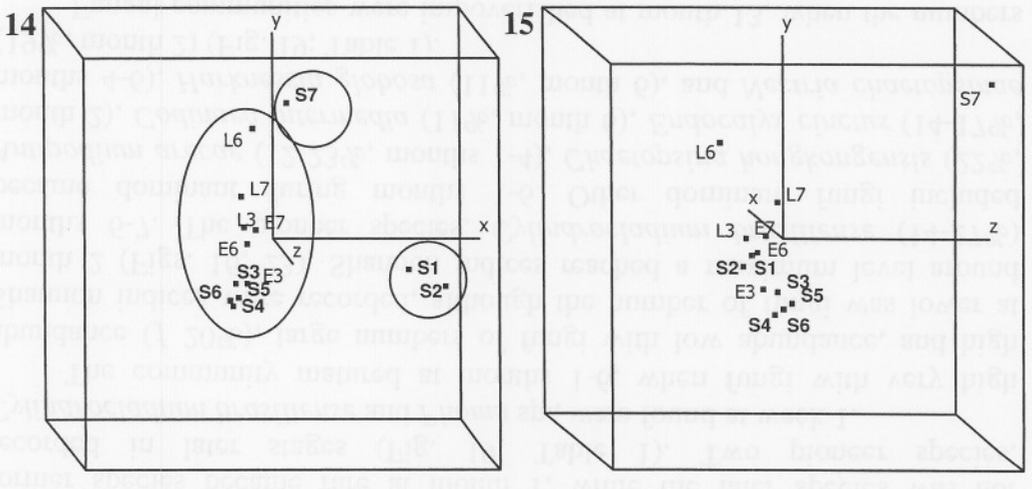
Figs. 8, 9. Three-dimensional correspondence analysis of fungi on leaves of *Phoenix hanceana*. **8.** Diagram oriented at x- and y-axes. **9.** Diagram oriented at y- and z-axes. Percentage of total variance explained by model is 52.21%. E: naturally occurring fronds at early stages of decay. L: naturally occurring fronds at later stages of decay. S: frond baits. 1-7: sampling times and stages of succession [16 July 1998 (day 0), 23 July 1998 (week 1), 17 August 1998 (month 1), 19 September 1998 (month 2), 17 November 1998 (month 4), 21 January 1999 (month 6) and 8 September 1999 (month 13) respectively]. Remarks: Leaves were completely decayed before month 13 and no sample from this part could be collected.



Figs. 10, 11. Three-dimensional correspondence analysis of fungi on rachis-tips of *Phoenix hanceana*. **10.** Diagram oriented at x- and y-axes. **11.** Diagram oriented at y- and z-axes. Percentage of total variance explained by model is 58.36%. For abbreviations see Figs. 8-9. Remarks: Rachis-tips were completely decayed before month 13 and no sample from this part could be collected.



Figs. 12, 13. Three-dimensional correspondence analysis of fungi on mid-rachides of *Phoenix hanceana*. **12.** Diagram oriented at x- and y-axes. **13.** Diagram oriented at y- and z-axes. Percentage of total variance explained by model is 51.13%. For abbreviations see Figs. 8-9.



Figs. 14, 15. Three-dimensional correspondence analysis of fungi on rachis-bases of *Phoenix hanceana*. **14.** Diagram oriented at x- and y-axes. **15.** Diagram oriented at y- and z-axes. Percentage of total variance explained by model is 51.58%. For abbreviations see Figs. 8-9.

associated with brown spots, and *Actinopelte* sp. and *Asterina clasterosporium* found on the surface of healthy parts (Fig. 19; Table 1). As on leaves and rachis-tips, *Actinopelte* sp. (43%) and *Asterina clasterosporium* (43%) dominated this stage.

A pioneer community was observed at week 1, when the numbers of fungal taxa and the Shannon indices were low (Figs. 16, 23). *Actinopelte* sp.

(33%) and *Asterina clasterosporium* (53%) remained dominant at week 1. The former species became rare at month 1, while the later species was not recorded in later stages (Fig. 19; Table 1). Two pioneer species, *Cylindrocladium brasiliense* and *Phoma* sp., were found at week 1.

The community matured at months 1-6, when fungi with very high abundance (*f* 20%), large numbers of fungi with low abundance, and high Shannon indices were recorded, although the number of fungi was lower at month 2 (Figs. 16, 23). Shannon indices reached a maximum level around months 6-7. The pioneer species, *Cylindrocladium brasiliense* (14-27%) became dominant during months 1-6. Other dominant fungi included *Antipodium arecae* (12-23%, months 1-4), *Chaetopsina hongkongensis* (22%, month 2), *Codinaea intermedia* (11%, month 6), *Endocalyx cinctus* (14-17%, months 4-6), *Harknessia globosa* (11%, month 6), and *Nectria chaetopsinae* (19%, month 2) (Fig. 19; Table 1).

Fungal communities were impoverished at month 13, when the numbers of fungal taxa and the Shannon indices decreased drastically (Figs. 16, 23). The community comprised three highly abundant fungi, i.e. *Exserticlava vasiformis* (25%), *Penzigomyces nodipes* (50%) and *Sporidesmiella hyalosperma* var. *hyalosperma* (25%) (Fig. 19; Table 1).

Rachis-bases

There were 35 fungal taxa found, with 3 distinct succession stages comprising distinct fungal communities on the rachis-bases throughout the decay process (day 0-week 1, months 1-6 and month 13) (Figs. 14, 15). The fungal communities at months 1, 2, 4 and 6 were similar, as indicated by the close distance among the points in Figs. 14, 15.

Fungi recorded on green living rachis-bases were the same as those on living mid-rachis. *Diplococcium stoveri* and *Sporidesmium pedunculatum* were associated with brown spots, and *Actinopelte* sp. and *Asterina clasterosporium* were found on the surface of healthy parts. *Actinopelte* sp. (33%), *Asterina clasterosporium* (33%) and *Diplococcium stoveri* (29%) dominated the communities (Figs. 20, 24; Table 1).

A pioneer community was observed at week 1, when the numbers of fungal taxa and the Shannon indices were low (Figs. 16, 24). The abundance of *Actinopelte* sp. and *Diplococcium stoveri* declined from 33 to 30%, and from 29 to 10%, respectively. *Asterina clasterosporium* (50%) remained dominant, while one pioneer species, *Blennoria buxi*, was recorded. This indicates that the fungal community was changing from the stage of living rachis-bases to a pioneer community.

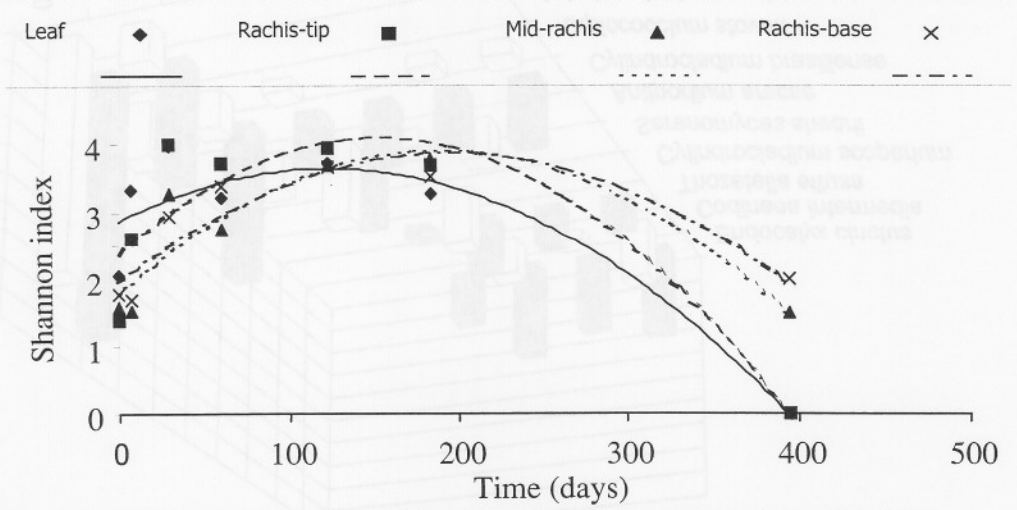


Fig. 16. Shannon indices for diffferent frond parts throughout the experimental period.

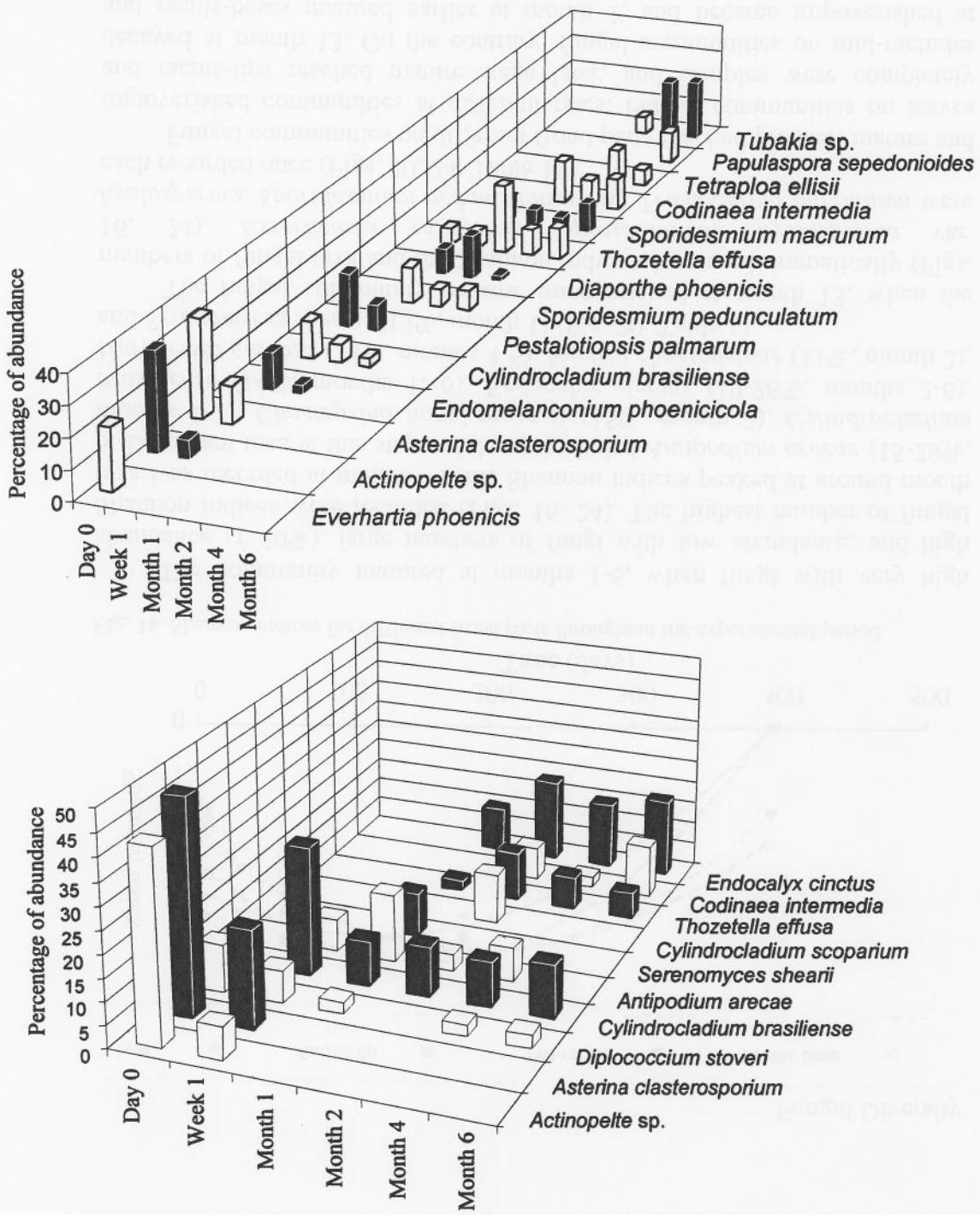
The community matured at months 1-6, when fungi with very high abundance (*f* 20%), large numbers of fungi with low abundance, and high Shannon indices were recorded (Figs. 16, 24). The highest number of fungal taxa was recorded at month 4 while Shannon indices peaked at around month 6. Dominant taxa at this stage of decay included *Antipodium arecae* (15-29%, months 1-2), *Chaetopsina hongkongensis* (15%, month 2), *Cylindrocladium brasiliense* (14%, months 1, 6), *Endocalyx cinctus* (19-26%, months 2-6), *Harknessia globosa* (14%, months 4-6), *Nectria chaetopsinae* (11%, month 2), and *Serenomyces shearii* (19%, month 1) (Fig. 20; Table 1).

The fungal community became impoverished at month 13, when the numbers of fungal taxa and the Shannon indices decreased dramatically (Figs. 16, 24). *Exserticlava vasiformis*, *Sporidesmiella hyalosperma* var. *hyalosperma*, *Sporidesmium pedunculatum* and *Trichoderma harzianum* were each recorded once (Figs. 20, 24; Table 1).

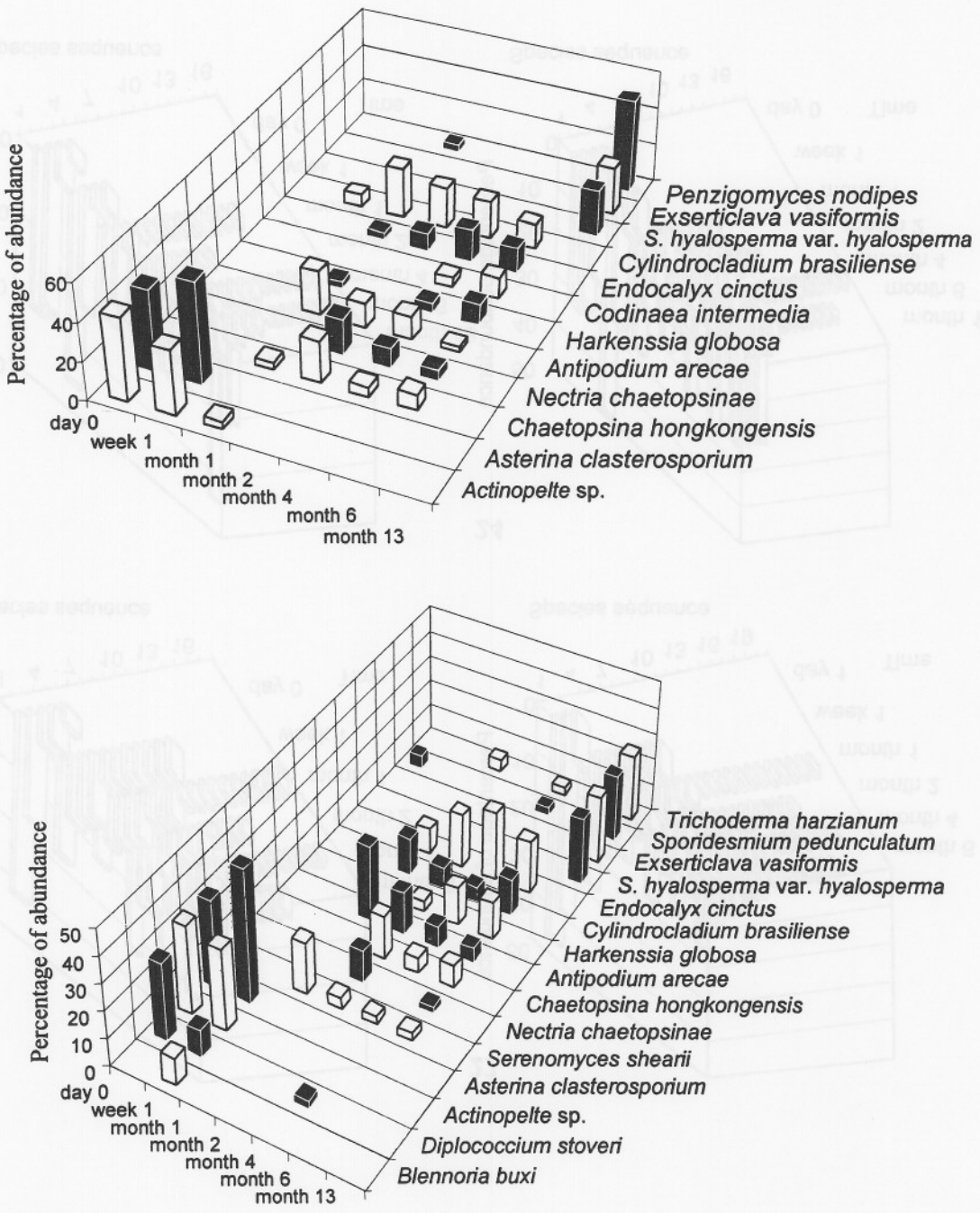
Fungal communities on different frond parts reached pioneer, mature and impoverished communities at different rates. Fungal communities on leaves and rachis-tips reached mature stage later, and samples were completely decayed at month 13. On the contrary, fungal communities on mid-rachides and rachis-bases matured earlier at month 1, and became impoverished at month 13. The development of the different stages of fungal communities on different frond parts is summarized in Table 2.

Comparison between fungal communities on naturally occurring fronds and the frond baits

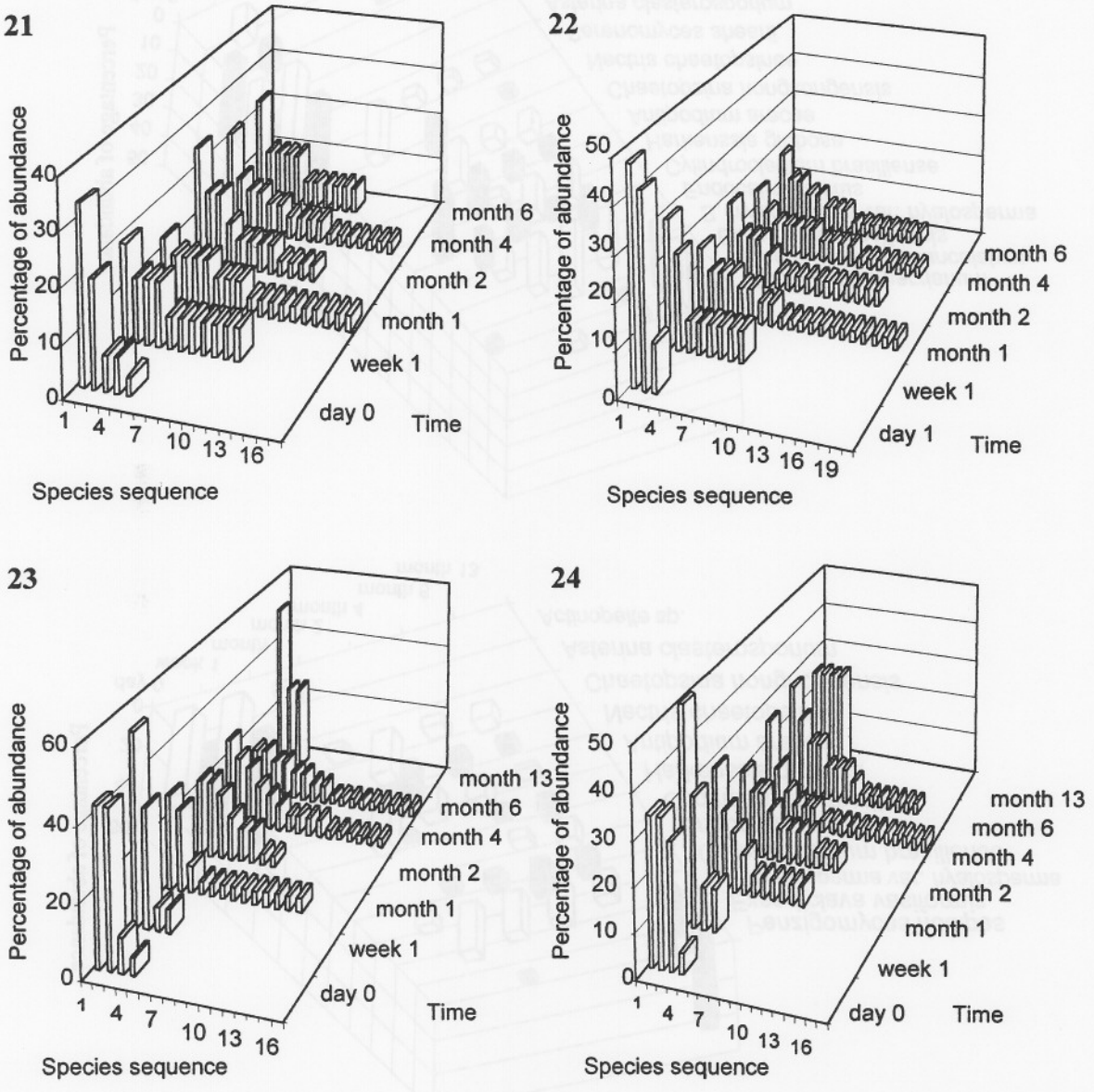
There were 73 fungal taxa recorded from seven collections of frond baits during the fungal succession study (Table 1), while 73 fungal taxa were found



Figs. 17, 18. Percentage abundance of dominant fungi on **17.** Leaves (top). **18.** Rachis-tip (bottom).



Figs. 19, 20. Percentage abundance of dominant fungi on **19.** Mid-rachides (top). **20.** Rachis-bases (bottom).



Figs. 21-24. Fungal species-abundance distributions on different frond parts. Species in each sampling time are ordered with most abundant at the left to the least abundant at the right.

from three collections of naturally occurring fronds (Yanna *et al.*, 2001a) during the same experimental period of the succession study. A high proportion of fungi (56 out of 101 taxa) only occurred on either naturally occurring fronds or frond baits.

Table 2. The development of different stages by fungi on different frond parts.

	week 1	month 1	month 2	month 4	month 6	month 13
Leaves	← Pioneer →		←	Mature	→	
Rachis-tips	← Pioneer →		←	Mature	→	
Mid-rachides	◄ Pioneer ►	◄		Mature	→ ◄	Impoverished ►
Rachis-bases	◄ Pioneer ►	◄		Mature	→ ◄	Impoverished ►

In this succession study, the fungal communities of leaves and rachis-tips at months 2-6 were relatively similar to those on naturally occurring fronds (Figs. 8-11). Similarly, fungal communities of mid-rachides and rachis-bases at months 1-6 (Figs. 12-15) were more similar to the fungal communities on respective naturally occurring frond parts. The fungal communities on the naturally occurring fronds were more similar to each other than to the fungal communities on succession samples (Figs. 8-15).

Discussion

Saprobic fungal succession could be classified as seral succession or substratum succession (Cooke, 1979; Frankland, 1992). Seral succession refers to the succession associated with the vegetation seres of a developing ecosystem; for example, a forest or sand dune system, in which the supply of resources changes progressively. Changes in the plant community regulate the decomposer community. Reactions between the two are reciprocal, but the accumulation of organic matter tends to "drag" the decomposer succession in the wake of the higher-plant succession (McNaughton and Wolf, 1973). Substratum succession refers to the succession of species that occurs on any colonisable plant, animal or man-made material (Cooke, 1979; Frankland, 1992), for example, the occurrence of different fungal taxa at different stages of decomposition on petioles of *Pteridium aquilinum* (Frankland, 1966, 1969, 1976).

Fungal successions are also classified as primary or secondary. Primary succession occurs on sites that have not previously been occupied. Such sites exist on newly formed soils, such as exposed sandbars and volcanic ash. The colonisation of a sunken ship by coral reef organisms is an example of primary succession (Luczkovich and Knowles, 2000). Secondary succession occurs when a biotic community has been disturbed, then becomes reestablished. Remnants of the previous biotic community still exist at the site and contribute to recolonisation. Secondary succession is much more common than primary succession; much of the landscape is in a stage of secondary succession. One common example of secondary succession is the reestablishment of a forest vegetation after an area has been logged. When a forest is logged, only the

merchantable timber is removed, undesirable tree species, shrubs, saplings, and seeds remain and constitute the coloniser pool (Luczkovich and Knowles, 2000).

Succession of fungal fruiting bodies on herbivore dung was well documented before 1900 (Hudson, 1968). Succession of fungi on plant litter has also been studied by Chesters (1950) and Mangenot (1952) and on wood by Carre (1964). Subsequently studies on succession of fungi on leaf litter have also been carried out. There have been extensive studies of fungal succession on leaf litter of dicotyledon trees (e.g. Saito, 1956; Hering, 1965; Hogg and Hudson, 1966; Pasqualetti *et al.*, 1999) and pine trees (e.g. Kendrick and Burges, 1962; Tokumasu *et al.*, 1994). Similar studies have also been made on ferns (Frankland, 1966; Yasmeen, 1999).

Successional studies of saprobic fungi on temperate terrestrial monocotyledons have been carried out on culms of the cocksfoot (*Dactylis glomerata*) by Webster (1956, 1957), on stems of couch grass (*Agropyron repens*) by Hudson and Webster (1958), on leaves of sedge (*Carex paniculata*) by Pugh (1958), on leaves of pea (*Pisum sativum*) by Dickinson (1967), and on leaves of grasses (*Festuca contracta* and *Poa flabellata*) by Hurst *et al.* (1983). Studies of succession of fungi on tropical terrestrial monocotyledons have been carried out on sugarcane (*Saccharum* spp.) by Hudson (1962), Sandhu and Sidhu (1980), and Srivastava *et al.* (1989), on decaying banana leaves (*Musa sapientum*) by Meredith (1962), on leaves of grass (*Loudetia simplex*) by Puppi *et al.* (1978), on root surface of millet (*Pennisetum typhoides*) by Kanaujia (1981, 1982), on stems of wheat (*Triticum aestivum*) by Srivastava *et al.* (1983) and on leaf and root litter of pineapple (*Ananas comosus*) by Tiwari *et al.* (1994). The only succession study on dead palm material was conducted on fronds of *Livistona chinensis* (Yanna *et al.*, 2001b).

Changes of species composition throughout the decay process have been observed in this study (Figs. 8-15, 17-20) and also in previous succession studies on monocotyledons. Banana leaves, for instance, were first colonised by primary colonisers, such as *Deightoniella torulosa*, *Nigrospora* spp. and *Verticillium theobromae*, and were replaced by species of *Aspergillus*, *Alternaria*, *Cephalosporium*, *Cladosporium*, *Fusarium*, *Paecilomyces*, and *Penicillium* with time (Meredith, 1962).

Changes of fungal composition in each succession study were unique and depended on the substratum and the environment (Frankland, 1992). This is also true in fungal succession on palms. Among the 91 fungi recorded during the succession study of *Livistona chinensis* in Hong Kong, SAR (Yanna *et al.*, 2001b), only *Dictyosporium elegans*, *D. tetraseriale* and *Pestalotiopsis palmarum* were also recorded on *Phoenix hanceana* in this study (Table 1).

Dictyosporium elegans was found on all frond parts of *Livistona chinensis* at month 10, with a higher abundance on mid-rachis and rachis-bases (abundance up to 16.75%) (Yanna *et al.*, 2001b), however, it was only found on mid-rachides of *Phoenix hanceana* at month 6 with low abundance (2.7%) (Table 1). *Dictyosporium tetraseriale* was found on rachis-tips of *Livistona chinensis* and *Phoenix hanceana* at months 2 and 6 respectively with low abundance. *Pestalotiopsis palmarum* was found early on fronds of both hosts, and dominated mid-rachides of *Livistona chinensis* and leaves of *Phoenix hanceana*. It occurred on all frond parts of *Livistona chinensis* during week 2 to month 2 (abundance 3.1-15%), and on leaves, rachis-tips and mid-rachides of *Phoenix hanceana* during week 1 to month 1 (abundance 3.8-19%).

All fungi found in succession studies on *Livistona chinensis* and *Phoenix hanceana* were unique in comparison with other studies on monocotyledons (Webster, 1956, 1957; Hudson and Webster, 1958; Pugh, 1958; Hudson, 1962; Meredith, 1962; Dickinson, 1967; Puppi *et al.*, 1978; Sandhu and Sidhu, 1980; Kanaujia, 1981, 1982; Hurst *et al.*, 1983; Srivastava *et al.*, 1989; Tiwari *et al.*, 1994).

The time period of fungal decomposition of leaf litter varies enormously. For instance, in cool temperate pine forests, it may take ten years to fully decompose pine needles, one year for decomposition of leaves in ash and sycamore woods, and only a few weeks in tropical forests (Hudson, 1980). The time for decomposition of monocotyledons in the tropical region is generally short, e.g. 14 months for leaves of sugarcane (Hudson, 1962), 19 months for stems of couch grass (Hudson and Webster, 1958) and 2 years for litter of pineapple (Tiwari *et al.*, 1994). The decomposition of fronds of *Phoenix hanceana* in this study was rapid. Leaves and rachis-tips of *Phoenix hanceana* were completely decayed within one year, while mid-rachides and rachis-bases were decayed within 18 months.

The time for fungal communities to reach the peak of species diversity or fungal activities also varied among different studies. For example, complete decomposition of sugarcane bagasse needed 20 weeks and maximum colony counts were recorded during the 6-13 weeks (Sandhu and Sidhu, 1980). In the two-year decomposition of leaf and root litter of pineapple, the number of species, the number of viable propagules associated with the litter and the rate of weight loss were maximum during the middle phase of the litter decomposition (Tiwari *et al.*, 1994). In this study, species diversity also peaked at the middle phase of decomposition (120 days for leaves, 150 days for rachis-tips, 200 days for mid-rachides and rachis-bases).

There have been several methods employed in succession studies. In this study, baits were periodically retrieved from the natural environments followed

by direct visual examination after incubation in moist chambers. This method is most widely used in succession studies of plant litter (Webster, 1956; Srivastava *et al.*, 1983; Hyde, 1991; Ho *et al.*, 2002). Others methods include culture plating (Pugh, 1958; Srivastava *et al.*, 1983) and leaf disk washing (Sandhu and Sidhu, 1980; Hurst *et al.*, 1983). Direct visual examination would exclude non-sporulating species, while the culture plate method and leaf washing would exclude fungi that grow slowly or cannot grow at all on agar plates. It would also encourage the growth of fast growing ubiquitous species, such as *Penicillium* and the results would be unrepresentative. Employing different methods might give a more accurate result.

The high species diversity recorded in the present study prevented the use of additional methods. In the case of sugarcane bagasse where only nine species were isolated during the succession study (Sandhu and Sidhu, 1980), a combination of the three study methods would have been recommended.

Examination of fungi on naturally occurring samples is likely to result in finding fungi that only occur during certain stages of decay. For instance fungal communities on naturally occurring decaying leaves and rachis-tips, and mid-rachides and rachis-bases were similar to the ones at months 2-6 and months 1-6 respectively (Figs. 8-15). Fungal communities which changed rapidly or taxa that were present for a relatively short period of time may be easily excluded from the collections of naturally occurring samples, especially those that appeared during the pioneer and impoverished stages (Table 1). For instance, *Actinopelte* sp. (abundance up to 43%), *Asterina clasterosporium* (53%), *Blennoria buxi* (10%), *Cylindrocladium scoparium* (11%), *Everhartia phoenicis* (20%), and *Pestalotiopsis palmarum* (19%) were dominant only for a short period of time during the early succession study, but were absent on the naturally occurring fronds. In addition, *Dactylaria parvispora* (abundance up to 14%), *Oxydothis elaeicola* (17%), *Pleurophragmium acutum* (20%), and *Pseudospiropes simplex* (50%) were dominant on naturally occurring fronds, but not found on frond baits. The similarity between naturally occurring samples and succession samples was low at 0.68, with over 48% fungi being recorded either only from naturally occurring fronds or the frond baits. This study has demonstrated that examination of naturally occurring fronds and frond baits from initial senescence to complete decomposition are essential to obtain a better estimation of fungal diversity on palm frond litter.

Acknowledgments

We would like to thank Agriculture, Fisheries and Conservation Department, Hong Kong SAR Government for the permission of conducting this study in Tai Mo Shan. We would also like to express our thanks to T.K. Goh and E.H.C. McKenzie for identification of some anamorphic fungi. The University of Hong Kong is thanked for the award of postgraduate studentship to Yanna.

References

Anonymous. (1995). *JMP® Statistics and graphics guide. Version 3.1 of JMP*. SAS Institute Inc., Cary, NC.

Bärlocher, F. and Kendrick, B. (1974). Dynamics of the fungal population on leaves in a stream. Journal of Ecology 62: 761-791.

Booth, T. and Kenkel, N. (1986). Ecological studies of lignicolous marine fungi: a distribution model based on ordination and classification. In: *The Biology of Marine Fungi* (ed. S.T. Moss). Cambridge University Press, Cambridge: 297-310.

Carre, C.G. (1964). Fungus decomposition of beech cupules. Transactions of the British Mycological Society 47: 437-442.

Chesters, C.G.C. (1950). On the succession of micro-fungi associated with the decay of logs and branches. Lincolnshire Naturalists' Union Transactions 12: 129-135.

Cooke, W.B. (1979). *The Ecology of Fungi*. CRC Press Inc., Florida.

Dickinson, C.H. (1967). Fungal colonization of *Pisum* leaves. Canadian Journal of Botany 45: 915-927.

Dix, N.J. and Webster, J. (1985). *Fungal Ecology*. Chapman & Hall, London.

Dudgeon, D. (1994). *Hills and Streams: An Ecology of Hong Kong* (eds. Dudgeon, D. and Corlett, R.). Hong Kong University Press, Hong Kong SAR.

Frankland, J.C. (1966). Succession of fungi on decaying petioles of *Pteridium aquilinum*. Journal of Ecology 54: 41-63.

Frankland, J.C. (1969). Fungal decomposition of bracken petioles. Journal of Ecology 57: 25-36.

Frankland, J.C. (1976). Decomposition of bracken litter. Botanical Journal of the Linnean Society 73: 133-143.

Frankland, J.C. (1992). Mechanisms in fungal succession. In: *The Fungal Community: Its Organization and Role in the Ecosystem* (eds. D.T. Wicklow and G.C. Carroll). 2nd edn. Marcel Dekker Press, New York: 383-401.

Gessner, M.O., Thomas M., Jean-Louis, A.M. and Chauvet, E. (1993). Stable successional patterns of aquatic hyphomycetes on leaves decaying in a summer cool stream. Mycological Research 97: 163-172.

Ghawana, V.K., Shrivastava, J.N. and Kushwaha, R.K.S. (1997). Some observations on fungal succession during decomposition of wool in soil. Mycoscience 38: 79-81.

Gorska, B. (1982). Changes of microfungi during decomposition of plant material in two different woodland associations. Prace Naukowe Uniwersytetu Slaskiego w Katowicach: 99-117.

Hering, T.F. (1965). Succession of fungi in the litter of a Lake Distric oakwood. Transactions of the British Mycological Society 48: 391-408.

Ho, W.H., Yanna, Hyde, K.D. and Hodgkiss, I.J. (2002). Seasonality and sequential occurrence of fungi on wood submerged in Tai Po Kau Forest Stream, Hong Kong. In: *Fungal Succession* (eds. K.D. Hyde and E.B.G. Jones). Fungal Diversity 10: 21-43.

Hogg, B.M. and Hudson, H.J. (1966). Microfungi on leaves of *Fagus sylvatica*. I. The microfungal succession. Transactions of the British Mycological Society 49: 185-192.

Hudson, H.J. (1962). Succession of micro-fungi on ageing leaves of *Saccharum officinarum*. Transactions of the British Mycological Society 45: 395-423.

Hudson, H.J. (1968). The ecology of fungi on plant remains above the soil. New Phytologist 67: 837-874.

Hudson, H.J. (1980). *Fungal Saprophytism*. The Camelot Press Ltd, London.

Hudson, H.J. and Webster, J. (1958). Succession of fungi on decaying stems of *Agropyron repens*. Transactions of the British Mycological Society 41: 165-177.

Hurst, J.L., Pugh, G.J.F. and Walton, D.W.H. (1983). Fungal succession and substrate utilization on the leaves of three South Georgia (South Atlantic) phanerogams. British Antarctic Survey Bulletin: 89-100.

Hyde, K.D. (1991). Fungal colonization of *Rhizophora apiculata* and *Xylocarpus granatum* poles in Kampong Kapok mangrove, Brunei. Sydowia 43: 31-38.

Kanaujia, R.S. (1981). Studies on certain aspects of root surface fungi: 2. Succession of fungi on decomposing *Pennisetum typhoides*. Acta Mycologica 17: 27-40.

Kanaujia, R.S. (1982). Studies on certain aspects of root surface fungi: IV. Succession of fungi on *Pennisetum typhoides* in fertilized soils. Acta Mycologica 18: 131-144.

Kendrick, W.B. and Burges, A. (1962). Biological aspects of decay of *Pinus sylvestris* leaf litter. Nova Hedwigia 4: 313-342.

Kuester, E. (1979). Importance of actinomycetes for the decomposition of cellulose, lignin and humic substances in soil. Zeitschrift fuer Pflanzenernaehrung und Bodenkunde 142: 365-374.

Luczkovich, J.J. and Knowles, D.B. (2000). Successional and restoration: how ecosystems respond to disturbance. *http://drjoe.biology.ecu.edu/ch09/ch09.htm*.

Mangenot, M.F. (1952). Recherches methodiques sur les champignons de certains bois en decomposition. Revue Genevale de Botanique 59. 702: 381-399.

McNaughton, S.J. and Wolf, L.L. (1973). *General Ecology*. Holt, Rinehart and Winston, New York.

Meredith, D.S. (1962). Some fungi on decaying banana leaves in Jamaica. Transactions of the British Mycological Society 45: 335-347.

Pasqualetti, M., Mulas, B., Zucconi, L. and Rambelli, A. (1999). Succession of microfungal communities on *Myrtus communis* leaf litter in a Sardinian Mediterranean maquis ecosystem. Mycological Research 103: 724-728.

Pugh, G.J.F. (1958). Leaf litter fungi found on *Carex paniculata* L. Transactions of the British Mycological Society 41: 185-195.

Puppi, G., Rambelli, A., Bartoli, A. and Maggi, O. (1978). Observations on the mycoflora of green and senescent leaves of *Loudetia simplex*. Giornale Botanico Italiano 112: 361-371.

Rayner, A.D.M. and Todd, N.K. (1979). Population and community structure and dynamics of fungi in decaying wood. Advances in Botanical Research 7: 333-420.

Saito, T. (1956). Microbiological decomposition of beech litter. Ecological Review, Sendai 14: 141-147.

Sandhu, D.K. and Sidhu, M.S. (1980). Fungal succession on decomposing sugarcane bagasse. Transactions of the British Mycological Society 75: 281-286.

Shannon, C.E. and Weaver, W. (1949). *The Mathematical Theory of Communication*. University of Illinois Press, Urbana.

Srivastava, S.K., Raizada, B.B.S. and Gupta, S.C. (1983). Succession of microfungi on decaying stems of *Triticum aestivum*. Proceedings of the National Academy of Sciences India Section B (Biological Sciences) 53: 231-246.

Srivastava, S.K., Singh, L. and Raychaudhuri, S.P. (1989). Comparison of decomposer mycoflora of red-rot infected and non-infected leaf litter of sugarcane. International Journal of Tropical Plant Diseases 7: 71-80.

Tiwari, S.C., Tiwari, B.K. and Mishra, R.R. (1994). Succession of microfungi associated with the decomposing litter of pineapple (*Ananas comosus*). Pedobiologia 38: 185-192.

Tokumasu, S. (1998). Fungal successions on pine needles fallen at different seasons: the succession of interior colonizers. Mycoscience 39: 409-416.

Tokumasu, S., Aoki, T. and Oberwinkler, F. (1994). Fungal succession on pine needles in Germany. Mycoscience 35: 29-37.

Tribe, H.T. (1957). Ecology of micro-organisms in soils as observed during their development upon buried cellulose film. In: *Microbial Ecology* (eds. R.E.O. Williams and C.C. Spicer). Cambridge University Press, Cambridge: 287-298.

Tribe, H.T. (1961). Microbiology of cellulose decomposition in soil. Soil Science 92: 61-77.

Webster, J. (1956). Succession of fungi on decaying cocksfoot culms. Journal of Ecology 44: 517-544.

Webster, J. (1957). Succession of fungi on decaying cocksfoot culms. Journal of Ecology 45: 1-30.

Yanna, Ho, W.H., Goh, T.K. and Hyde, K.D. (2000). A new species of *Everhartia*, associated with leaf spots of *Phoenix hanceana* from Hong Kong. Botanical Journal of the Linnean Society 134: 465-470.

Yanna, Ho, W.H. and Hyde, K.D. (2001a). Fungal communities on decaying palm fronds in Australia, Brunei and Hong Kong. Mycological Research 105: 1458-1471.

Yanna, Ho, W.H., Hyde, K.D. and Goh, T.K. (2001b). Occurrence of fungi on tissues of *Livistona chinensis*. Fungal Diversity 6: 167-180.

Yasmeen. (1999). Mycoflora associated with fern leaf litter. Proceedings of the National Academy of Sciences India Section B (Biological Sciences) 69: 75-77.

(Received 22 December 2001; accepted 3 May 2002)