Fungal ecology and succession on *Phragmites australis* in a brackish tidal marsh. II. Stems

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Fungal succession and community development has been studied by direct observation for twenty-four months on stems of *Phragmites australis* in a brackish tidal marsh of the river Scheldt (The Netherlands). In total 49 taxa were found of which 26 taxa (53%) were ascomycetes, 16 taxa (33%) coelomycetes, four taxa (8%) hyphomycetes and only three taxa (6%) basidiomycetes. Fungal sporulation on standing stems started only after a minimum of three months in a standing dead position and showed different fungal assemblages along the vertical axis of the shoots. Cluster analysis and detrended correspondence analysis showed that all investigated microhabitats (middle canopy, basal canopy and litter layer) showed a different species composition that changed during decay. This successional sporulation was described by a three-staged pattern in each microhabitat. For all of the different microhabitats and for the groups recognized by cluster analysis, indicator taxa were pointed. Gradient analysis indicated that cellulose is the controlling factor for fungal sporulation on the stems.

Key words: ascomycetes, coelomycetes, common reed, cellulose, fungal community, hyphomycetes, indicator species analysis, vertical distribution.

Introduction

Tidal wetlands and other wetlands dominated by *Phragmites australis* (Cav.) Trin. ex Steud. are among the most productive ecosystems in the world (e.g. Mitsch and Gosselink, 2000). Most of this produced biomass exists out of recalcitrant, woody stem tissue accounting for about 50% of the total mass (Granéli, 1990; Meganck, 1998; Gessner, 2000). This huge amount of dead plant matter enters the detritial system and becomes available for fungal saprotrophic colonization first in a standing decay phase of variable length and subsequently in the litter layer (Haslam, 1972; Pieczyńska, 1972; Granéli, 1990). Both of these habitats are characterized by a different mycota (Apinis *et al*. 1972a, b, 1975; Luo *et al*., 2004; Van Ryckegem and Verbeken, 2005a, b)

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and a vertical distribution of taxa is noticed on the standing shoots (Apinis *et al*., 1975; Poon and Hyde, 1998; Van Ryckegem and Verbeken, 2005a, b).

Little is known about the factors causing changes in microbial species composition or dominance during decay (Gessner *et al*., 1997). Studies attempting to establish relationships between breakdown rates, litter characteristics and fungal performance generally conclude that concentrations of nutrients, lignin, phenolic compounds or a combination of these constituents are critical in determining litter decomposability (Kjøller and Struwe, 1982; Melillo *et al*., 1982, 1984; Enriquez *et al*., 1993; Gessner and Chauvet, 1994). However, different ecosystems seem to vary broadly according to the relative impact and interactions of a range of controlling factors, including both external ones related to specific environment inclusive site-specific invertebrate mycophagy and factors intrinsic to the decomposing plant material (Enriquez *et al*., 1993; Gessner *et al*., 1997; Graça *et al*., 2000).

This paper is a second part of a study (see Van Ryckegem and Verbeken, 2005b) which aims to describe the fungal sporulation sequence (succession) on *P. australis* and focuses on the stems in different microhabitats naturally available in a reed stand. For each of the groups identified by cluster analysis and for the different microhabitats, indicator taxa are provided. In addition, gradient analysis was used to elucidate possible factors influencing fungal sporulation during the decay of reed stems in the litter layer.

Materials and methods

For a description of the study site, field and laboratorial procedures and data processing, the reader is referred to Van Ryckegem and Verbeken (2005b). Stems were collected every 4 weeks from May 2000 till May 2002 (Cohort, 2000) and from May 2001 till May 2003 (Cohort, 2001). Both cohorts were sampled from adjacent sites to check for between year variations. The mycota were followed in the middle and basal regions of standing shoots from the start of the growing season (May) during 19 and 21 months respectively, and for 18 months in the litter layer (see also Table 3). No top stem collections were included because the top section of stems is very thin as the upper part of the culm consists mainly of tightly packed leaf sheaths. Moreover, the upper parts of standing shoots soon enter the litter layer as they are fragile and more susceptible to snapping due to gusts of wind, especially if they carry a panicle. Ten replicate stem pieces were collected at two heights in the canopy and fifteen replicates in the litter layer (see Van Ryckegem and Verbeken, 2005b) resulting in a relative occurrence of the fungal taxa on a scale of 10 for the standing stems while a relative abundance on a scale of 15 for the litter stems

were obtained. Before data analysis the latter scores were transformed to a scale of 10 as a matter of conformation.

Multivariate ordination techniques were applied to analyse the species data set in combination with measured environmental data from Van Ryckegem *et al*. (2005). This way we investigated dominant parameters characterizing the fungal sporulation sequence in the litter layer.

The species data set was reduced by including only those taxa found more than three times in the litter layer during the period of study. This criterion was met by 13 taxa (Table 1). Taxonomic descriptions and illustrations of all those taxa are available at http://biology.ugent.be/reedfungi.

Because gradient length determined by detrended correspondence analysis (DCA), an indirect or unconstrained gradient analysis, exceeded two units of standard deviation, unimodal species response curves could be expected (McCune and Grace, 2002). Consequently, a direct ordination technique, canonical correspondence analysis (CCA), was applied (Palmer, 1993). In this technique the axes are constrained by linear combinations of environmental variables. The ordination was used in combination with multiple regression to investigate the relationship between potentially explanatory variables and the observed succession of fungal sporulation during substrate decay.

The environmental matrix initially contained all measured internal substrate quality characteristics (N, P, cellulose and lignin) (Van Ryckegem *et al*., 2005), external variables (mean monthly temperature and precipitation, flooding water NO_3^-, PO_4^{-3} and salinity) and one variable (Shannon's diversity index) as a measure for fungal diversity. Each variable was tested separately in a CCA for individual explanatory power (marginal effects). The forward selection procedure in CANOCO version 4.5 (ter Braak and Smilauer, 2002) was followed to reduce the constraining matrix to a minimal set of environmental variables. They independently (avoiding multicollinearity; conditional effects) and significantly explain variation in the species data just as well as the full set of environmental variables. Significance was tested by a Monte Carlo permutation test (1000 permutations) with *P* set at 0.05 and use of a Bonferroni correction (Rice, 1990). Additionally, the first DCA-axis was interpreted indirectly in environmental terms. This technique was used to verify direct ordination results. If ordination diagrams of direct and indirect ordination look similar and identical environmental variables are selected in both procedures we have additional indications that important environmental variables are included in CCA (Jongman *et al*., 1987). This was evaluated by determining the Pearson correlation of environmental variables with the DCA-axes. Subsequently, multiple regression was applied to evaluate the complex

structures of ecological gradients expressed along the DCA-axis. Backward elimination (Zar, 1996) was used to evaluate which variables should be selected at $P < 0.05$ for the multiple regression (SYSTAT, version 10.2). Ordination graphs were prepared in PC-ORD version 4.26 (McCune and Mefford, 1999).

Results

In total 49 fungal taxa were found on stems during growth and decomposition of the common reed. For analyses the two data sets were pooled, this seemed justified because of the high similarity between the two cohorts based on species composition (Jaccard similarity: 61%) and considering species records (Bray-Curtis similarity: 78%). Both cohorts proved to have the same distribution as tested with a Mann-Whitney U test ($P = 0.63$). Furthermore, the results of the cluster analysis showed that 90% of all stem samples compared with a one year interval, clustered in the same group identified.

Fungal diversity

In total 26 taxa (53%) ascomycetes, 16 taxa (33%) in the coelomycetes, four taxa (8%) belonging to the hyphomycetes and three (6%) basidiomycetes were discovered on the stems. Comparing the distributions of the two dominant groups – ascomycetes and coelomycetes – in Fig. 1 shows the overall higher occurrence of sexual fruit bodies compared to conidiomata in the litter layer. Although overall species richness was highest in the litter layer for the two dominant groups, the average sporulation of taxa was proportionally low – especially for the coelomycetes. The asexual coelomycetes perform generally better on the aerial parts of the reed culms (Fig. 1). Standing middle portions of stems showed overall low sporulation of fungi, especially of ascomycetes. Moreover, the suggested vertical differences in species compositions presented in Fig. 1b are confirmed by cluster analysis and ordination results of the dataset.

Spatial and temporal characterization of the subcommunities

Before further analysis the dataset was reduced by removing some outliers in the given sequence. First species which were only found once or twice during the entire study were eliminated. In addition, all samples with only one or two records were removed from the dataset. Thirdly, outlier samples were identified by means of detrended correspondence analysis and

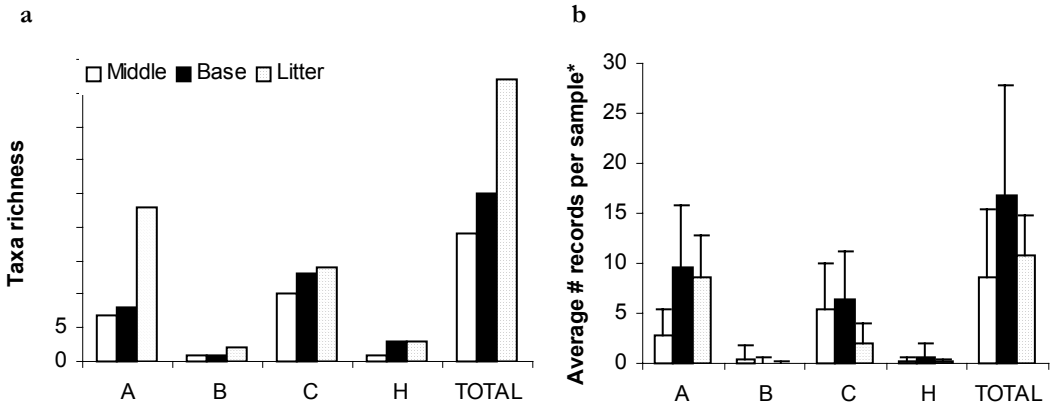


Fig. 1a. Taxa richness and distribution of the major pseudo-systematic groups on stems of *Phragmites australis* in the different microhabitats investigated. **b.** Average number of records per sample occasion* in the different microhabitats investigated. The same column coding for both panels.

* The initial samples without fungal records for the basal and middle section of standing shoots were not included for the proportional calculation of the frequency of occurrence (see Table 3).

eliminated (108STX; 207STX; 111ST0; 111ST1). All outlier samples contained initially colonized stem parts with a species poor assemblage with few records. Such outliers mask the potential information in ordination by compressing the remaining ordination output (McCune and Mefford, 1999). Eventually this resulted in a reduced dataset matrix of 66 samples and 31 taxa.

Cluster analysis (CA)

Figure 2 of the stem samples shows several interpretable groups well separated from each other by spatial and temporal species characteristics. Group 1 – clusters all samples comprising initial species assemblages from the basal stem sections and from the litter layer. Group 1 can be divided in two subgroups 1a – clusters all samples with stems that recently fell into the litter layer; 1b – clusters all samples from initially colonized basal stem collections. Group 2 – is a cluster of the basal stem collections in a later stadium of decay. Group 3 – comprises the litter layer stem samples in a further decay phase, the two final collections which are characterized by an impoverished community, are included in this group, a decision supported by ordination outcome. Group 4 – is the outgroup in the cluster analysis and groups all stem collections from middle height canopy.

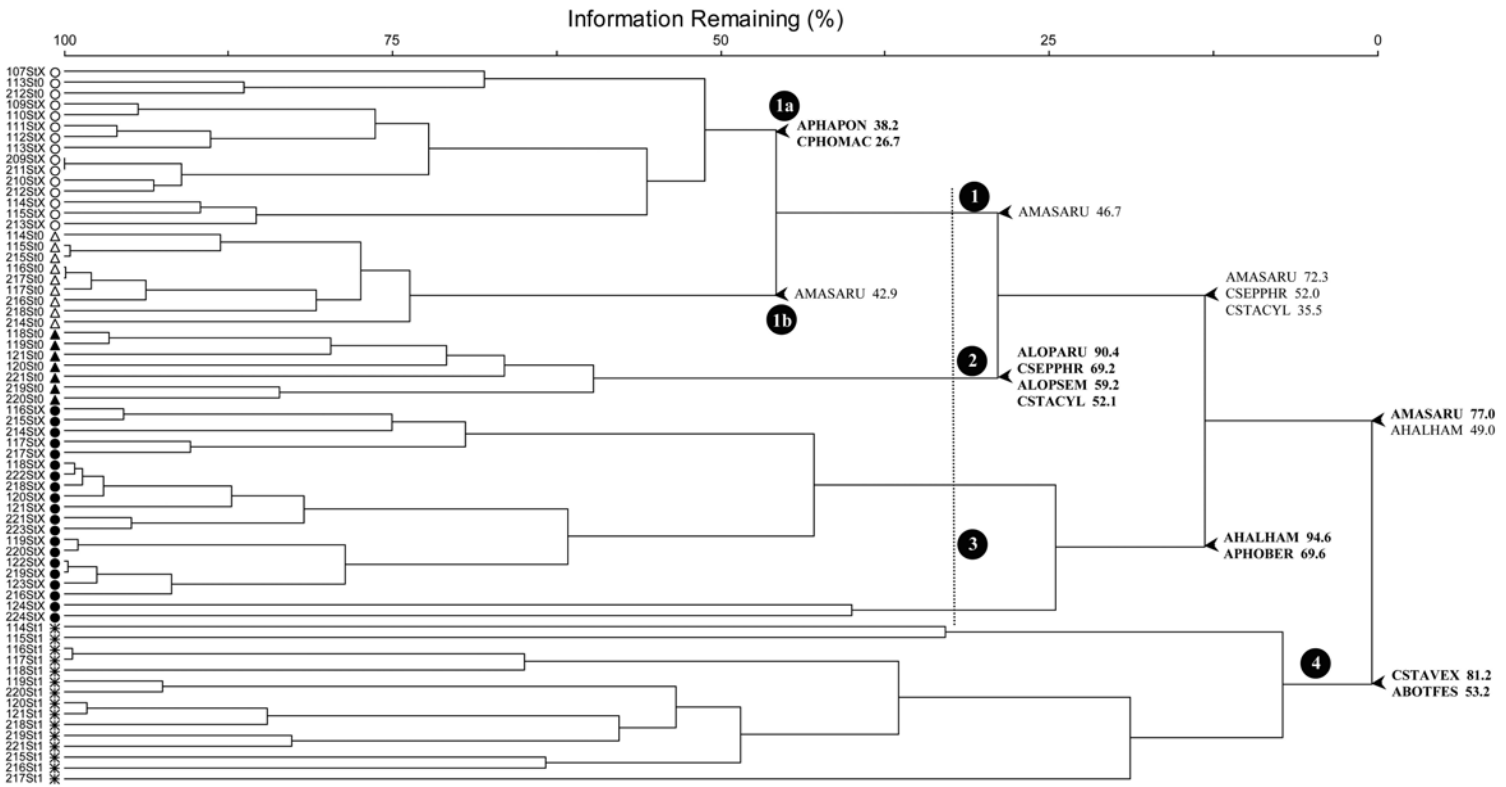


Fig. 2. Dendrogram from cluster analysis of the pooled data from cohorts 2000 and 2001 with 66 samples and 31 taxa included. Sample code exists of four character states. The first figure indicates the cohort number being 1 or 2; the second number stands for month of collection (between 7-24), (see Table 3); the letter code 'st' stands for stem sample and the last figure indicates the microhabitat (0 = basal canopy, 1 = middle canopy and X = litter layer). Indicator species with indicator values are shown for the groups generated by cluster analysis. All species with indicator value > 25 and Monte-Carlo *P*-values < 0.01 are included. The maximum indicator values for a species are printed in bold. Acronym abbreviations are found in Table 1. Dendrogram is scaled with the percentage of information remaining in the branches.

Table 1. Taxa list and frequency distribution of all taxa found on stems of *Phragmites australis* during growth and decomposition. Data for the two successive cohorts pooled. Total % frequency of occurrence (% oc.) is the proportion of records of a taxon on the number of stem sections screened with fungal presence*. % abundance (% ab.) is the proportion of records of a taxon on the total number of records. Taxa acronyms code for taxa names in Figure 2. The first letter of the acronym codes for the pseudo-systematic position of a taxon: A = ascomycetes; B = basidiomycetes; C = coelomycetes; H = hyphomycetes.

Taxa	Acronyms	# rec.	% oc.	% ab.
Massarina arundinacea (Sowerby: Fr.) Leuchtm.£	AMASARU	241	25.4	30.1
Halosphaeria hamata (Höhnk) Kohlm.£	AHALHAM	116	12.2	14.5
Septoriella phragmitis Oudem.£	CSEPPHR	86	9.1	10.8
Stagonospora vexata Sacc.£	CSTAVEX	85	9.0	10.6
Lophiostoma arundinis (Pers.) Ces. & De Not.£	ALOPARU	61	6.4	7.6
Botryosphaeria festucae (Lib.) Arx & E. Müll.£	ABOTFES	43	4.5	5.4
Phomatospora berkeleyi Sacc.£	APHOBER	28	3.0	3.5
Stagonospora cylindrica Cunnell	CSTACYL	25	2.6	3.1
Lophiostoma semiliberum (Desm.) Ces. & De Not.£	ALOPSEM	24	2.5	3.0
Stagonospora incertae sedis I£	CSTAINA	22	2.3	2.8
Phoma sp. II		21	2.2	2.6
Phoma sp. IIa		20	2.1	2.5
Phaeosphaeria pontiformis (Fuckel) Leuchtm.£	APHAPON	18	1.9	2.3
Stagonospora sp. II£	CSTAINB	16	1.7	2.0
Phoma sp. III£	CPHOMAC	13	1.4	1.6
Keissleriella linearis E. Müll.		12	1.3	1.5
Aposphaeria sp.		11	1.2	1.4
Arthrinium phaeospermum (Corda) M.B. Ellis		10	1.1	1.3
Tremella cf. *spicifera* Van Ryck., Van de Put & P. Roberts		10	1.1	1.3
Septoriella sp(p).		9	< 1	1.1
Stagonospora elegans (Berk.) Sacc. & Traverso		9		1.1
Dictyosporium oblongum (Fuckel) S. Hughes		6		< 1
Phoma sp. I		6		
Mollisia retincola (Rabenh.) P. Karst.£	AMOLRET	5		
Morenoina phragmitidis J.P. Ellis		5		
Bactrodesmium atrum M.B. Ellis		4		
Neottiosporina australiensis B. Sutton & Alcorn		4		
Maireina monacha (Speg.) W.B. Cooke		3		
Mycosphaerella lineolata (Roberge ex Desm.) J. Schröt.		3		
Phaeosphaeria luctuosa (Niessl) Otani & Mikawa		3		
Phaeosphaeria sp. III		3		
Phomatospora sp. III		3		
Asco sp. *Dothideales* incertae sedis II		2		
Cytoplacosphaeria rimosa (Oudem.) Petrak s.l.		2		
Didymella glacialis Rehm		2		
Massarina fluviatilis Aptroot & Van Ryck.		2		

Table 1 continued.

Taxa	Acronyms	# rec.	% oc.	% ab.
Phialophorophoma sp.		2		
Asco sp. *Dothideales* incertae sedis I		1		
Basidiomycete, (sterile mycelium)		1		
Camarosporium sp.		1		
Cistella fugiens (Pholl. ex Bucknall) Matheis		1		
Fusarium sp. III		1		
Gibberella zeae (Schwein.) Petch		1		
Haligena spartinae E.B.G. Jones		1		
Lophodermium arundinaceum (Schrad.) Chevall.		1		
Massariosphaeria sp.		1		
Phaeosphaeria eustoma (Fuckel) L. Holm s.l.		1		
Phomatospora dinemasporium J. Webster		1		
Phomatospora sp. II		1		
Total # records		947		
Total # samples*			800	

* Total number of 30 cm long stem section screened for fungal presence was 1160, however up till February there was no fungal sporulation on stems in a standing position. Those 360 initial samples (see Table 3) were excluded to calculate total % of frequency of occurrence (% oc.).
£ Taxa included in the gradient analysis dataset which were recorded more than three times on stems in the litter layer during the study period.

Detrended correspondence analysis (DCA)

Figures 3, 4 shows two interpretable axes with a high eigenvalue (axis 1: 0.70; axis 2: 0.32). The high eigenvalue and a large length of gradient (axis 1: 5.021; axis 2: 2.530) indicate a distinct β-diversity along both axes and a high explanatory power. An after-the-fact evaluation of the variation explained by the axes by relative Euclidean correlation (McCune and Mefford, 1999) showed 57% explanatory power for axis 1 and 5% by axis 2. DCA groupings are concurrent with the clusters identified by CA. The two samples split up in group 3 in CA, don't show extremely different in DCA and were included in group 3 for further analysis. Axis 1 represents a spatial pattern, splitting up the different microhabitats sampled and is negatively correlated (Kendall rank correlation) with a temporal factor in the litter layer samples (Fig. 4). Axis 2 shows a negative correlation with a temporal factor for the standing samples (Fig. 4).

Indicator species analysis (ISA)

ISA for the groups generated by the cluster analysis shows 10 selected indicator species plotted on the CA-diagram (Fig. 2). Species selected at the highest hierarchical level of the community dendrogram show two specific

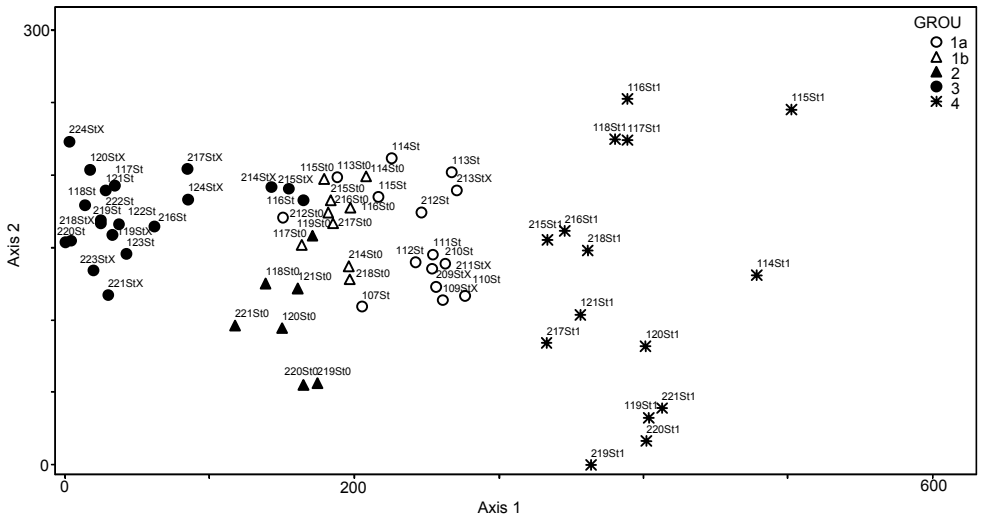


Fig. 3. First two ordination axes of a DCA based on species occurrences on stems of *Phragmites australis* with 31 taxa (raw data) and 66 samples included. Sample grouping symbols and acronyms are the same as in the cluster analysis (Fig. 2). Axes are scaled in SD units (× 100).

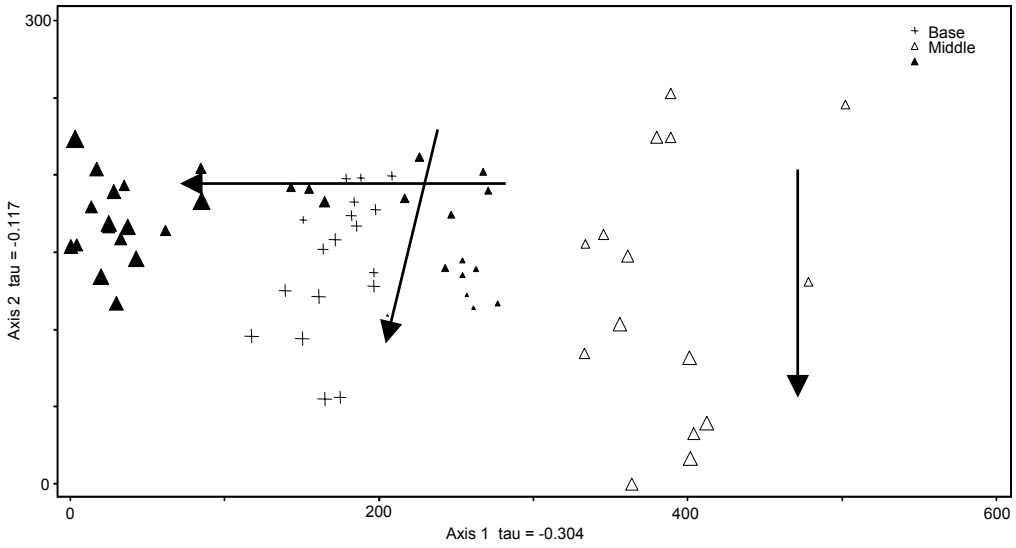


Fig. 4. DCA plot (see Fig. 3) with stem samples from *Phragmites australis* showing the temporal correlation of the first two ordination axes with Kendall rank correlation (tau) indicated. Smallest symbols indicate earliest samples in the successional community development. Axes are scaled in SD units (× 100).

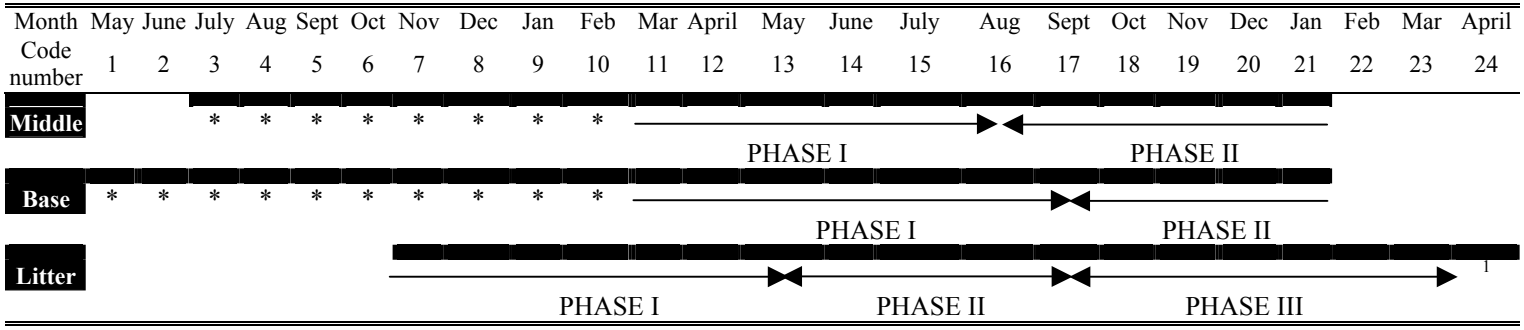
Table 2. Sequence in fungal sporulation on stems of *Phragmites australis* during decomposition in three different microhabitats (middle and basal height of standing stems and litter layer samples). Only taxa with more than 3 records (27 taxa) during the entire study are shown with their number of records, percentages abundance (calculation base on all taxa records per microhabitat), percentage recurrence and percentages occurrence in each month sampled starting from November (see Table 3) (no sporulation during the first six months of monitoring). Data from the two cohorts are pooled, 20 stem sections per month per microhabitat. 'Gr' codes for the pseudo-systematic group a taxon belongs: A = ascomycetes; B = basidiomycetes; C = coelomycetes; H = hyphomycetes.

Gr	Species	Micro-	∑	% ab.	% rec.	% occurrence (months)																
		Habitat	records			N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A
C	*Phoma* sp. III	middle	1	1	8					5													
		base	2	1	15					5		5											
		litter	10	3	77	20	10	10	5	5													
A	*Massarina arundinacea*	middle	8	5	3									10	20		5	5					
		base	131	35	53					15	15	40	85	80	95	100	75	45	30	75			
		litter	102	27	43	20	5	40	45	45	60	60	55	55	45	35	5	5			15	15	5
C	*Stagonospora vexata*	middle	68	38	80							10	15	20	55	35	40	45	55	65			
		litter	17	5	20	5	5	10	20	20	15	10											
C	*Septoriella phragmitis*	middle	11	6	13												10	15	15	15			
		base	61	17	71					5			15	5	25	35	60	60	50	50			
		litter	14	4	16	5	5	5	10	15	10	5	0	10	5								
C	*Stagonospora elegans*	base	8	2	89								10					20	10				
		litter	1	0	11	5																	
A	*Phaeosphaeria pontiformis*	middle	4	2	22									5	0	5			10				
		litter	14	4	78		5	20	20	10	5	5			5								
C	*Septoriella* sp(p).	middle	3	2	33					10						5							
		base	4	1	44								5							15			
		litter	2	1	22		5		5														
C	*Stagonospora* sp. II	middle	2	1	13									10									
		base	9	3	56					5			25	0	5	0	10						
		litter	5	1	31				5	5	5	5	0	5									
C	*Neottiosporina australiensis*	middle	1	1	25										5								
		litter	3	1	75					5	5	5											
A	*Phomatospora berkeleyi*	litter	28	7	100					5			15	10	10	25	20	10	25	0	10	0	10
C	*Stagonospora* incertae sedis I	base	9	3	41						5						5	10	0	25			
		litter	13	4	59								5	5	5	0	5	20	15	0	5	5	
A	*Botryosphaeria festucae*	middle	30	17	70									10	45	40	50	5					
		base	1	0	2												5						
		litter	12	3	28							25	10	15	10								

Table 2 continued.

Gr	Species	Micro-Habitat	∑ records	% ab.	% rec.	% occurrence (months)																
						N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A
A	*Morenoina phragmitidis*	middle	5	3	100							25											
A	*Mollisia retincola*	litter	5	1	100							5	20										
A	*Keissleriella linearis*	middle	8	5	67													20	10	10			
		base	1	0	8															5			
		litter	3	1	25							5	5	5									
A	*Halosphaeria hamata*	base	9	3	8										5	5	10	5	0	20			
		litter	107	28	92								15	10	45	40	85	50	80	85	60	55	10
C	*Stagonospora cylindrica*	base	25	7	100								5	10	15	40	20	25	5	5			
C	*Phoma* sp. IIa	middle	14	8	70										30	25	10			5			
		base	3	1	15										5			10					
		litter	3	1	15								5						5	5			
C	*Phoma* sp. II	middle	15	9	71										5	20	0	40	0	10			
		base	4	1	19													10	10				
		litter	2	1	10								5							5			
C	*Phoma* sp. I	middle	1	1	17											5							
		base	4	1	67												10			10			
		litter	1	0	17								5										
A	*Lophiostoma semiliberum*	base	16	5	67											5	15	15	15	30			
		litter	8	2	33									5	5	0	5	10	0	5	5	5	
H	*Bactrodesmium atrum*	base	4	1	100									5				5	5	5			
H	*Arthrinium phaeospermum*	middle	3	2	30												15						
		base	5	1	50										5	5	0	10	5				
		litter	2	1	20									5				5					
C	*Aposphaeria* sp.	base	10	3	91						15			15					20				
		litter	1	0	9										5								
A	*Lophiostoma arundinis*	base	52	15	85										5	15	40	45	75	80			
		litter	9	2	15										5	0	10			15	5	10	
H	*Dictyosporium oblongum*	base	5	1	83														10	15			
		litter	1	0	17										5								
B	*Tremella* cf. *spicifera*	middle	10	6	100												10	20	20				

Table 3. Sampling design and the different stages in fungal succession on stems of *Phragmites australis* recognized in our study. The complete dataset exists out two successional cohorts with one year interval, cohort 2000 started in May 2000 and cohort 2001 in May 2001.



[1] Collections from month 24 suggest that a fourth phase starts.
[*] No fungal records on the samples.

Table 4. Summary of DCA on fungal sporulation records, and summary of CCA on fungal data and environmental data during decay for stems of *Phragmites australis* in the litter layer of a tidal brackish marsh.

	Axis 1	**Axis 2**	**Axis 3**	**Total inertia**
DCA gradient length	3.211	0.892	0.857	1.32
DCA eigenvalues (unconstrained)	0.70	0.04	0.01	
CCA eigenvalues (constrained)[*] (*P*- value)[$]	0.610 (0.005)	0.289 (NS)	0.159 (NS)	1.32
Cumulative % of species variance explained by CCA	46.1	--	--	
Pearson correlation between spp. and environment (*P*-value)[$]	1 (0.005)	--	--	

[*] Constrained by 'Cellulose', the environmental variable selected after forward selection
[$] Determined by Monte Carlo test (1000 permutations)

Table 5. Pearson correlation between variables included in the stem environmental data set.

	N	**P**	**Lignin**	**Cellulose**	**Prec**	**Temp**	**Shannon**	**N water**	
N	1.00000								
P	0.90977***	1.00000							
Lignin	0.82917*	0.69737	1.00000						
Cellulose	-0.94855***	-0.89279***	-0.80257*	1.00000					
Prec	-0.05705	-0.17581	0.06140	0.03843	1.00000				
Temp	-0.64161	-0.44463	-0.57435	0.51981	0.24996	1.00000			
Shannon	-0.36272	-0.31823	-0.36646	0.52345	0.18232	0.28955	1.00000		
N Water	-0.21177	-0.25567	-0.46068	0.23330	-0.27599	-0.14722	-0.34633	1.00000	
Salinity	-0.19090	0.09621	-0.22634	0.18283	0.31021	0.66110	0.41120	-0.41743	

***$P < 0.001$; ** $P < 0.01$; * $P < 0.05$. With Bonferroni correction.

Table 6. Pearson correlation between variables and first DCA axis for stems of *Phragmites australis* in the litter layer of a tidal brackish marsh.

Stems	**DCA1**
N	-0.92629***
P	-0.83377*
LIGNIN	-0.83205*
CELLUL	0.94525***
PREC	0.19545
TEMP	0.69833
SHANNON	0.61043
NWATER	0.08211
SAL	0.39340

***$P < 0.001$; ** $P < 0.01$; * $P < 0.05$. With Bonferroni correction.

Table 7. Results of CCA with Monte Carlo simulation (1000 permutations) testing for marginal and conditional effects of environmental variables for the stem fungal community data set (see methods).

Environmental variable	Marginal effects		Conditional effects	
	Eigenvalue	*P*	Eigenvalue	*P*
Cellulose	0.61	0.001*	0.61	0.001*
Total N	0.57	0.001*	0.04	0.538 (NS)
Total P	0.53	0.004	--	
Lignin	0.53	0.001*	0.11	0.072 (NS)
Temperature	0.42	0.005	--	
Salinity	0.24	0.076	--	
NO_3^- water	0.20	0.128	--	
Shannon index	0.14	0.230	--	
Precipitation	0.10	0.410	--	
PO_4^{-3} water	not enough variation			

* Significant at $P < 0.05$ after Bonferroni correction

Table 8. The Jaccard similarity (%) matrix, based on presence-absence data of fungal taxa occurring on *Phragmites australis* stems used as a qualitative measurement for β-diversity among the microhabitats.

	Middle	Base	Litter layer
Middle	0		
Base	38	0	
Litter	37	54	0

Table 9. Indicator taxa with indicator value (IV) on *Phragmites australis* stems identified for the three different subcommunities sampled: middle and basal height stems and litter layer stems.

Middle		Base		Litter layer	
Taxa	IV	Taxa	IV	Taxa	IV
Stagonospora vexata	78.4	*Massarina arundinacea*	66.1	*Phomatospora berkeleyi*	54.5
Botryosphaeria festucae	49.6	*Septoriella phragmitis*	62.3	*Halosphaeria hamata*	52.5
		Stagonospora cylindrica	61.1		
		Lophiostoma arundinis	55.8		

colonizers for middle height stems (see also Table 5): *Stagonospora vexata* and *Botryosphaeria festucae*. The more eurytopic species, *Massarina arundinacea* and *Halosphaeria hamata* show indicator power for all basal and litter layer stem collections. *Halosphaeria hamata* and *Phomatospora berkeleyi* show the highest indicative power for the litter layer stems in a further state of decay. Characteristic species found on the basal stem part in a further stage of decay are *Lophiostoma arundinis*, *L. semiliberum*, *Septoriella phragmitis* and *Stagonospora cylindrica*. One of the first colonizers of *P. australis* stems is *M.*

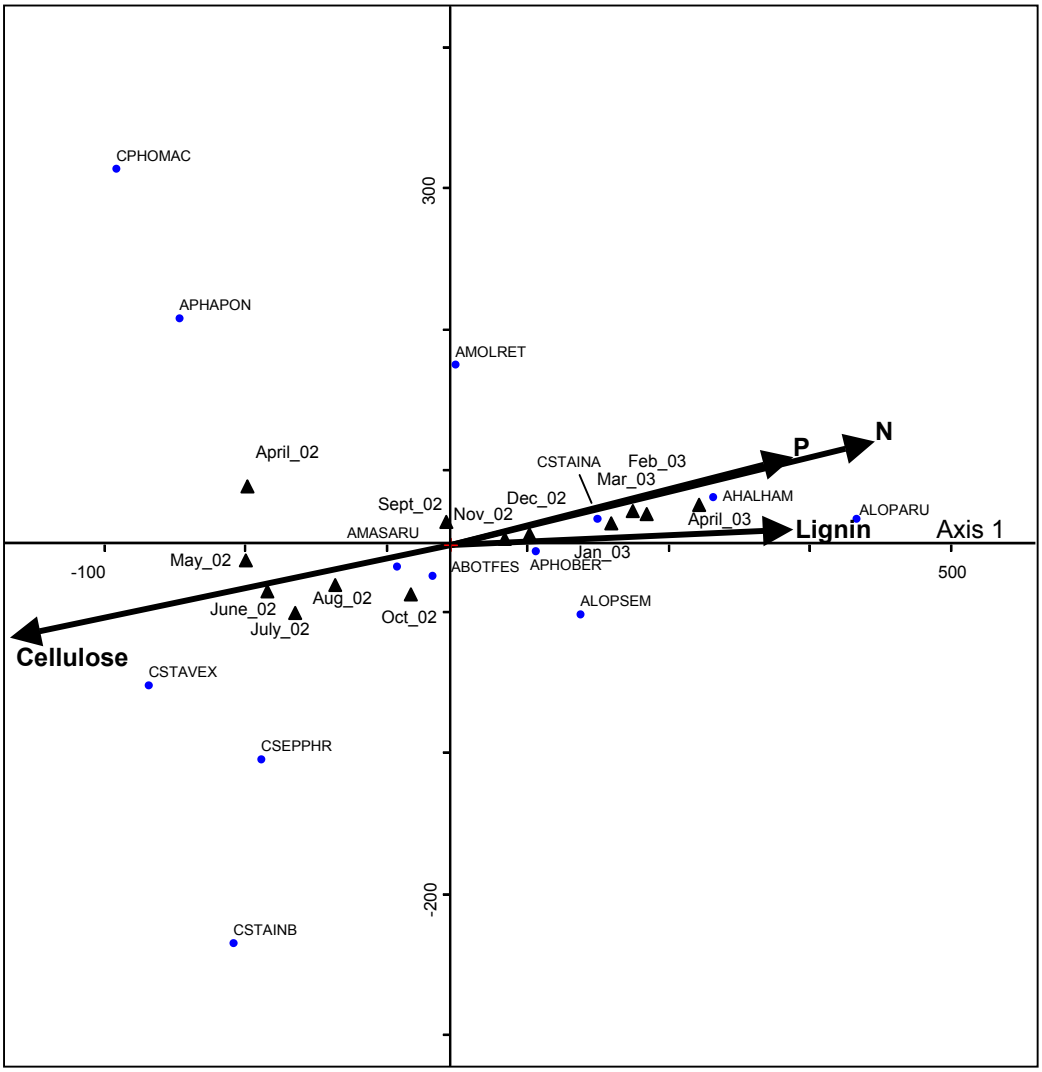


Fig. 5. Detrended correspondence analysis (DCA) joint plots (Axis 1 and 2) of stem fungal data with the most important marginal variables (arrows, Table 7) as passive variables included on the plot. ▲ indicates the position of monthly samples in ordination space screened for fungal sporulation structures; ● indicates the distribution of fungal taxa in ordination space. Acronyms of species are according to Table 1. Axes are scaled in SD units × 100.

arundinacea which is also the indicator species for group 1 and more typically one of the first species to sporulate on the basal stem sections (group 1b). However, *M. arundinacea* is a generalist as shown by its higher indicator value (IV) on a higher hierarchical level in the CA-diagram (Fig. 2). Group 1b is more negatively characterized by the absence of typical taxa. Litter layer stems freshly fallen on the sediment (group 1a) are characterized by *Phaeosphaeria pontiformis* and *Phoma* sp. III.

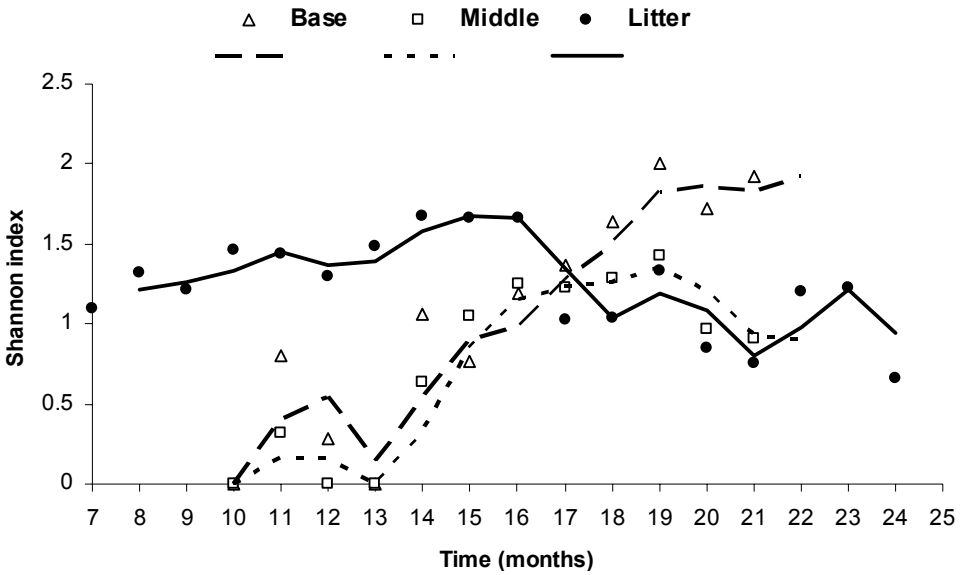


Fig. 6. Shannon diversity indices for the different microhabitats – subcommunities – sampled during the experimental period on stems of *Phragmites australis*. The line is a moving average fit with a period of two.

Gradient analysis

Eigenvalue reductions between the indirect and direct ordination technique were small, indicating that relatively little species information was lost by constraining the analysis by environmental variables (Table 4). Tables 5 shows correlation coefficients between the investigated variables. Internal variables describing substrate quality show the highest significant correlation. Pearson correlations between the first DCA axis and the litter variables are described in Table 6. All significant correlations with the first DCA axis are variables describing the internal substrate quality mainly cellulose, nitrogen and less phosphorus (Table 6, Fig. 5).

Testing for marginal effects in the CCA identified three significant variables for stem data: cellulose, N and lignin concentration (Table 7). However, only cellulose was retained after testing for conditional effects. In the final CCA models (Table 7), constrained by one significant (P set at 0.05) variable, only the first axis was significant and explained 46% of the taxa variance.

Multiple linear regression of the first DCA-axis sample scores against the selected significant environmental factors leads to a similar conclusion (cellulose retained in model, corrected $r^2 = 0.88$, $P < 0.001$).

Discussion

Diversity

Stem mycoflora showed almost the same proportions of taxa within the major taxonomic groups as leaf sheaths (Van Ryckegem and Verbeken, 2005b) with 96% of the records belonging to either ascomycetes or coelomycetes. However, on stems ascomycetes were better represented with 62% of the total fungal records (versus 37% on leaf sheaths). In general most of the taxa on reed were rare (Table 1). This kind of frequency distribution with few abundant and a long tail of rare taxa is often observed during fungal succession sequences (e.g. Apinis *et al*., 1972a, b; Zhou and Hyde, 2002).

If we compare our species list (Table 1) with previous studies describing fungal diversity on stems (Apinis *et al*., 1972b, 1975; Taligoola *et al*., 1972; Poon and Hyde, 1998; Luo *et al*., 2004) we find little similarity in species composition. This is due to different sample intensity, different methods used, different environmental conditions and taxonomic confusion which all make a comparison of results difficult (Van Ryckegem and Verbeken, 2005a; Van Ryckegem, 2005). In general a higher number of hyphomycetes and the lower number of ascomycetes were found. This may be due to the moist chamber incubation used in the other studies (l.c.) while we screened samples without incubation (see Van Ryckegem and Verbeken, 2005a). Similar to our results, Poon and Hyde (1998) found the basal part of standing stems to be the most species rich.

Vertical distribution

Vertical distribution patterns of saprotrophic fungi have been observed on standing stems of *P. australis* (Apinis *et al*., 1975; Poon and Hyde, 1998; Van Ryckegem and Verbeken, 2005a, b) and were observed on standing shoots in this study. The different microhabitats investigated (litter layer, basal and middle canopy) showed a differential species composition (MRPP overall $P < 0.0001$; all three comparisons were highly significant $P < 0.0001$, Bonferroni corrected). Based on presence-absence data (Jaccard similarity) a low resemblance was noticed between the different microhabitats (Table 8). Although eleven taxa sporulated in all the three microhabitats on stems screened, each of those taxa (Table 2) showed a higher recurrence in one of the microhabitats (see also Poon and Hyde, 1998). In Table 9 indicator taxa for each of the investigated microhabitats are presented. The species pointed as the most typical taxon for the middle height stems is *Stagonospora vexata*. However if we consider the whole fungal community on reed this species will

score lower as it is also common on leaf sheaths (Van Ryckegem and Verbeken, 2005b). On the contrary, *Botryosphaeria festucae* is typical, although not abundant, on the middle canopy stem sections. The basal stem parts are characterized by four species of which the first is also common in the litter layer: *Massarina arundinacea*. The other taxa are less common, with a shorter fructification period and sporulate within, or just above the stem region flooded by tidal exchange water. *Stagonospora elegans* was mentioned by Apinis *et al*. (1972b) as a typical colonizer of basal stem sections. However, besides being typical in the lower canopy (Table 2), the species was also found on upper leaf sheaths (Van Ryckegem and Verbeken, 2005b). *Stagonospora cylindrica* a species resembling *S. elegans* (Sutton, 1980; http://intramar.ugent.be/nemys/fungi/web/Phragmiticolous%20fungi.asp) appeared to be typical on the basal stem parts. Most characteristic colonizers of litter stems were *Phomatospora berkeleyi* and *Halosphaeria hamata* two species pointed also as indicator taxa for leaf sheaths (Van Ryckegem and Verbeken, 2005b) and considered to be the dominant species in a later phase of reed decay in our study site.

Successional sequence

A consequent successional appearance of fungal sporulation structures with comparable abundance and taxa composition was observed between two successive years in the same tidal marsh. Succession of the most dominant taxa is shown in Table 2 and phasing of species sporulation in the different microhabitats is further illustrated in Table 3 and Fig. 4 and shows comparable stages as delimitated in Van Ryckegem and Verbeken (2005b) for reed leaf sheaths. No fungal species were found sporulating on the green, living stems which agrees with the observations of Apinis *et al*. (1972b). The species colonizing dead stems are slowly developing. *M. arundinacea*, one of the first taxa to develop on the standing bases of stems, has ascomata already visible during January and February (winter) but most fruit bodies are mature during late spring and in summer. The slowest appearance of fungal fruit bodies was noticed on the middle height sections of stems with only sporadic sporulation structures formed till July, six months after senescence of the shoots (Table 2). Overall sporulation on those middle stem sections was poor (Fig. 1) and between month variation in species community was rather large (Fig. 3) because of the many rare species, resulting in an unclear successional pattern for this subcommunity. However, similar to the basal stem section, diversity gradually increases (Phase I) and reaches a peak for the middle height section in the sixteenth month (Fig. 7; Table 3) and maintains high (Phase II), with only a slight decrease to the end of the study period. The basal subcommunity

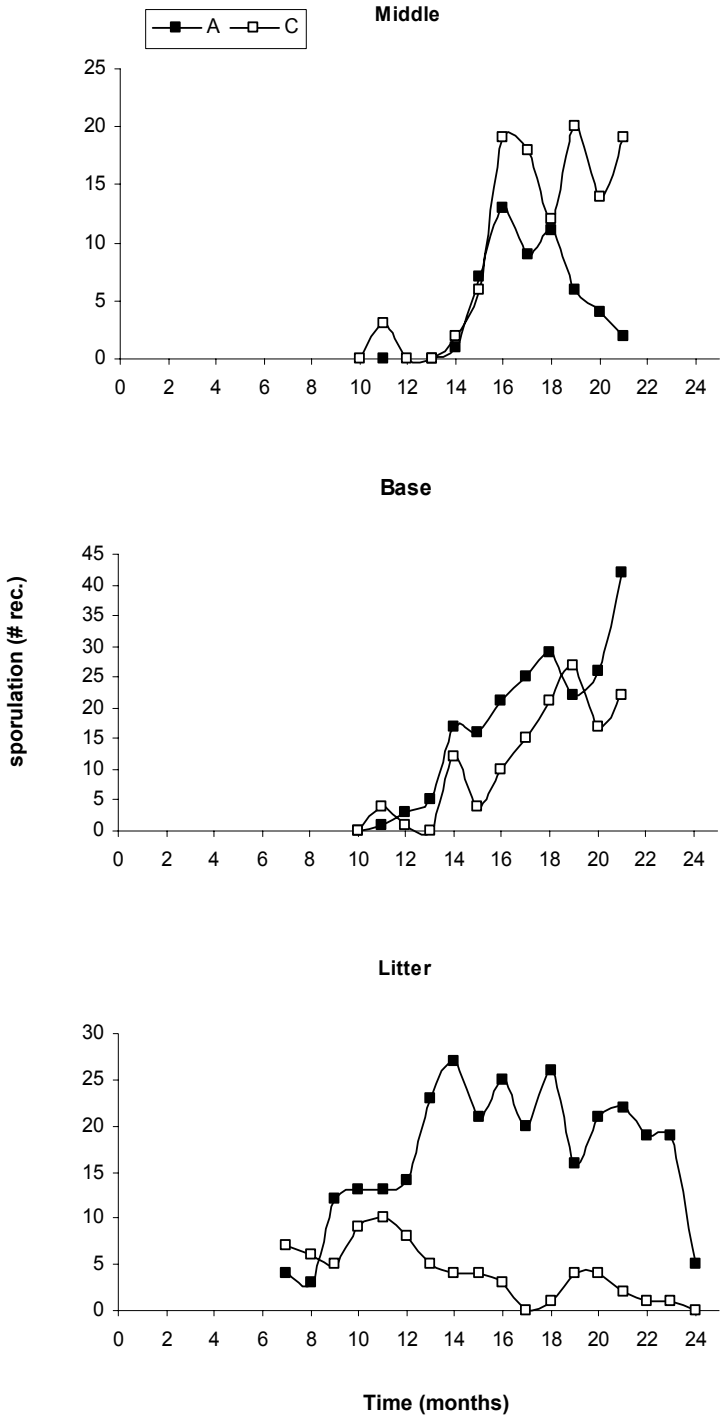


Fig. 7. Sporulation records in de different microhabitats on stems of *Phragmites australis* for the two dominant groups: A = ascomycetes; C = coelomycetes.

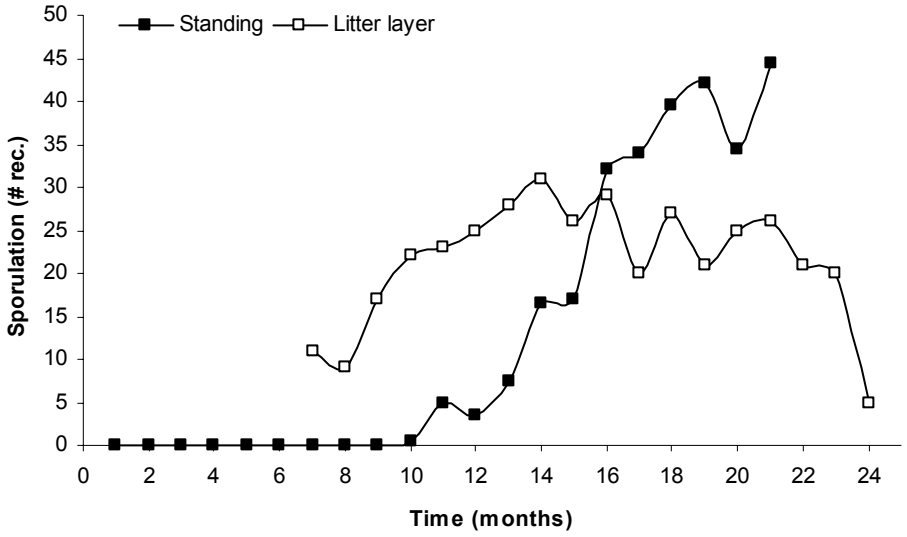


Fig. 8. Comparing fungal sporulation on standing stems and litter layer stems of *Phragmites australis*. The standing sporulation records were divided by two as two microhabitats (basal and middle height section) were sampled during the study.

seems to mature later (Fig. 7; Table 3), which could be related to the natural top-down senescence of *P. australis* stems (Granéli, 1990) and no impoverished community was observed in the canopy, probably because the sampling time was too short. Additional observations (but not replicated sufficiently and only for one year) of fungal sporulation structures on the few standing stems remaining, showed that an impoverished community established on basal stem sections characterized by *Halosphaeria hamata* being hypersaprotrophical on *M. arundinacea* and *Lophiostoma* spp. In the middle canopy, *Keissleriella linearis* becomes the dominant species during the next summer, seemingly a characteristic species for the impoverished community as it was nearly the only species seen to form fruit bodies in the middle canopy during this period. The litter layer subcommunity which was an initially divers mixture of culms fallen from the canopy on the sediment, shows a slight increase in diversity with a short period characterized as a mature community (Table 3). The three stages in litter layer sporulation are discerned in the ordination diagram (Figs. 3, 4) as separated groups. Phase I for the litter layer stems is considered as an initial fungal community establishment conform to the successional sequence described by Dix and Webster (1995) but different from the Phase X described for leaf sheaths entering the litter layer (Van Ryckegem and Verbeken, 2005b). The first phase of fungal sporulation in the litter layer is not considered to be a real transition phase because very few

species were found to be present on the stems before falling into the litter layer. However, it is possible that some endophytic taxa were present (Wirsel *et al*., 2001) and replaced by other species once fallen down (cf. Van Ryckegem and Verbeken, 2005b).

In contrast to the prompt sporulation observed on standing leaf sheaths (Van Ryckegem and Verbeken, 2005b), the standing stems show a lag period in appearance of sporulation structures with the first fungal sporulation structures on standing stems noticed in March, about three months after senescence (Fig. 8). However, it took about six months before sporulation started to become vigorous. Possibly the more recalcitrant stems are less susceptible in fungal colonization because of fewer stomata, more sclerenchymatous tissue and thicker cuticle compared to leaf sheaths (Rodewald and Rudescu, 1974). Furthermore, they are surrounded by the leaf sheaths which lower the inoculum potential by air-spora and probably create less favourable conditions for stem mycota because of the lower water availability. The latter point could be important as fungi colonizing plants in a standing dead position mainly depend on periodical (nightly) dew wetting for their activities (Newell *et al*.,1985, 1996; Kuehn *et al*. 1998; Kuehn and Suberkropp, 1998). Sporulation on stems surrounded by leaf sheaths started when nearly 50% of the leaf sheath tissue was decomposed (unpublished data). At this point probably better water condition prevails as leaf sheaths are softened, retain more water and pass this it to the stem tissue. Furthermore, at this stage, stems have proportionally more aerial contact making them more vulnerable to fungal colonization. This free aerial contact could also induce the development of fungal sporulation structures.

The observed sequential sporulation on litter layer culms is only one of the possible natural decay patterns present in a reed stand. We described the successional pattern for culms entering the litter layer mainly during late autumn and probably some of the culms had fallen in the litter layer after storms during the growth season (pers. obs.). The eventual impact of falling in the litter layer on the present community will depend on the duration of their standing decay (ie. extend a canopy community is already developed) and the season in which they snap. Especially the establishment and duration of phase I [which could become more a transition phase as found for leaf sheaths (Van Ryckegem and Verbeken, 2005b)] and phase II of the succession could be altered, while phase III and the presumed phase IV will probably be alike for all stems entering the litter layer.

Factors related to fungal succession in the litter layer

Cellulose seems to be a controlling factor for sporulation (Tables 7, 8). Nutrients (N, P) were indicated to be the driving forces behind fungal growth and productivity if carbon is not limiting (e.g. Newell *et al*., 1996). Perhaps carbon availability is a variable that is more important in regulating fungal life history and eventually succession. Depletion of carbon resources and/or changes in the proportions of the different carbon substrates (mainly cellulose, lignin, tannins and chitin) may trigger fungal reproduction. Furthermore, carbon depletion will increase niche overlap and hence increases competition between species. This will possibly favour species with high antibiotic activity and the widest range of enzymatic capabilities (Swift, 1976). Illustrative for this changed carbon availability is the appearance of hypersaprotrophic species. Such a species is *Halosphaeria hamata* (Kohlmeyer and Kohlmeyer, 1979) which becomes more dominant as decay proceeds (Table 2, Van Ryckegem and Verbeken, 2005b). These species use the luxurious amount of dead fungal tissues (mainly chitin) in the depleted litter as carbon source. This dead fungal mass is probably substantial and may be 2-fold that of living mass (e.g. Newell, 1992; Newell *et al*., 1995).

Consequences of fungal colonization on standing shoots

The results show an extensive sporulation on standing shoots both on leaf sheaths (Van Ryckegem and Verbeken, 2005b) and stems. The shoots could stay upright for longer periods than monitored here (e.g. 3-4 years, Haslam, 1972), meaning that a substantial decay could happen in an upright position possibly significantly altering the amount of necromass entering the litter layer (Kuehn *et al*. 2004), a point which should be incorporated in organic matter dynamics of wetland ecosystems (e.g. Pieczyńska, 1972; Gessner *et al*., 1996). All dominant taxa found on standing dead stems have the potential to weaken the standing shoots and being involved in the collapse of the culms. Apinis *et al*. (1972b) identified '*Septoria arundinacea*', *Stagonospora elegans* and *Massarina arundinacea* as responsible species for the collapse of standing shoots. Although *S. arundinacea* Sacc. is also found on *P. australis* (but on leaves) (Jorstad, 1967), it is thought that Apinis *et al*. (l.c.) meant *Septoriella phragmitis* with it, a species also characterized by multiseptate, long conidia of comparable size and an indicator taxon frequently found on basal stem sections of *P. australis* (Table 5). Weeda *et al*. (1994) mention *Ustilago grandis* Fr. as potential actor in reducing culm strength. However, this species was not found during this study and seems only dominant within restricted patches in the Scheldt estuary. At these locations *U. grandis* could play a role in weakening

the middle and upper parts of standing stems because of its vigorous growth and sporulation.

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