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Analyzing aquatic fungal communities in Australia: impacts of sample incubation and geographic distance of streams

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Fungal colonization of *Eucalyptus viminalis* exposed in three streams (two sites each) near Armidale (NSW Tablelands, Australia) was characterized by measuring reproduction from recovered leaves in aerated and static water. Spore production for zoosporic and mitosporic fungi increased by up to 220 % and 310 %, respectively, in aerated water. Percentage similarities of aquatic hyphomycete communities between pairs of aerated and static samples from the same stream averaged 67.5 %; similarities among samples from different streams averaged 50.3 %. Canonical Analysis of Principal Coordinates (CAP) revealed no significant difference between fungal communities of aerated vs. static treatments summarized over all sites. The fungal communities of substrates from an additional nine streams, primarily from the coast, were characterized in September, 2010. They were compared to those on *E. viminalis* leaves incubated for four weeks at the original six sites. CAP revealed a significant difference between tableland and coastal fungal communities. Percentage similarities correlated significantly with geographic distance of the streams ($R^2 = 0.13$), their temperature ($R^2 = 0.46$) and their altitude ($R^2 = 0.65$).

Key words: aquatic hyphomycetes, zoosporic fungi, spore production, aeration vs. static incubation, temperature, geographic distance.

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Studie se zabývá společenstvy zoosporických a mitosporických hub na opadu *Eucalyptus viminalis* ve vodě tří potoků poblíž Armidale v Austrálii.

INTRODUCTION

Autumn-shed leaves from riparian trees are a major source of food and energy for stream communities (Webster & Benfield 1986, Allan & Castillo 2007). Many studies, primarily in the northern hemisphere, have established that this

Dedicated to Ludmila Marvanová on the occasion of her 80th birthday.

allochthonous detritus becomes more palatable to stream invertebrates after being colonized by fungi (Canhoto & Graça 2008). Total fungal biomass on leaves is generally estimated by measuring levels of ergosterol, whose occurrence is largely restricted to membranes of living fungal cells (Gessner et al. 2003). Traditionally, the analysis of fungal community composition has relied on inducing a reproductive phase in (generally unidentifiable) mycelia on and in the leaves. Incubating leaves collected from stream water typically results in the formation of numerous multiradiate or sigmoid conidia. They belong to the polyphyletic, ecologically defined group of aquatic hyphomycetes (Krauss et al. 2011). Aerating the water greatly increases the rate of conidium production of pure cultures due to turbulence (Webster & Towfik 1972, Webster 1975), and increased streamflow/turbulence due to snowmelt correlated with higher numbers of aquatic hyphomycete spores in the water column of a Canadian stream (Bärlocher 2000). It has therefore become customary to submerge leaves collected from streams in agitated water, achieved by forced aeration or by shaking the container with the submerged leaves (Bärlocher 1981, Baldy et al. 1995). This selectively stimulates release of conidia of aquatic hyphomycetes; these fungi are therefore assumed to be the main agents of leaf decomposition in streams. However, we recently recovered large numbers of propagules, tentatively assigned to zoosporic fungi, during decomposition of *Eucalyptus viminalis* leaves in Australian streams. The term "fungi" is used here to encompass all fungus-like organisms, and includes members of the kingdoms Fungi and Chromista, as well as various slime moulds (Alexopoulos et al. 1996; for illustrations of the spores, see Bärlocher et al. 2011).

It is known from work with pure cultures that increasing the rate of aeration does not favour sporulation of all species to the same extent (Webster & Towfik 1972, Webster 1975). The degree of turbulence to which we expose our field samples may therefore affect our perception of community composition.

Fungal colonization has been reported to be influenced by organic and inorganic nutrients (e.g., Suberkropp & Chauvet 1995, Raviraja et al. 1998, Sridhar & Bärlocher 2000), by land-use practices (e.g., Laitung et al. 2002, Bärlocher et al. 2010) and by factors associated with alkalinity/pH and their effects on aluminium solubility (Wood-Eggenschwiler & Bärlocher 1983, Bärlocher 1987, Baudoin et al. 2008). When reviewing the geographical distribution of aquatic hyphomycete communities, Wood-Eggenschwiler & Bärlocher (1985) concluded that climate (temperature?) was the primary predictive factor. Higher similarities were found among geographically distant tropical or among temperate locations than between tropical and temperate or between tropical and subtropical regions on the same continent. Even within the same stream, distinct winter and summer assemblages can be distinguished (Suberkropp 1984) and species-specific seasonal preferences can override substrate preferences (Nikolcheva & Bärlocher 2005). Within the same climatic zone, the water chemistry can play a major role (e.g., nutrients, Suberkropp &

Chauvet 1995; Suberkropp 2001; or factors associated with alkalinity, Wood-Eggenschwiler & Bärlocher 1983; Bärlocher 1987; Baudoin et al. 2008).

The primary objective of this study was to characterize fungal colonization of eucalypt leaves in three circumneutral streams (two sites each) near Armidale (New South Wales tablelands), some with and some without riparian vegetation. We were also interested in whether the absence of induced turbulence (no aeration) during incubation of leaves recovered from streams significantly changed the total numbers of released spores (zoosporic, or aquatic hyphomycetes) or the contributions of individual species of aquatic hyphomycetes to total spore production, and therefore our evaluation of fungal community composition. Finally, we included several sites from alluvial meandering gravel bed coastal rivers (east of the Dorrigo plateau) to establish a distance-decay relationship for aquatic hyphomycetes. This measures similarities in community composition at different sites and how it changes with geographic distance separating the sites. Our goal was to determine if geographic distance among streams or local conditions (water temperatures, different riparian vegetation or geology) were more useful predictors. Due to higher altitudes, tableland streams in this region are generally colder than coastal streams (Banens 1987, Hadwen et al. 2010), and generally drain highly erodible red granitic podzols or granitic duplex soils, while the geology of nearby sub-tropical coastal rivers is dominated by basalt intrusions and alluvial deposits (Barrow & Spencer 1971, Kingham 1998). If the mechanisms described by Wood-Eggenschwiler & Bärlocher (1985) apply to Australian streams, fungal communities of tableland streams should be more similar to each other than to coastal streams and vice versa, regardless of geographic distance.

Materials and methods

Leaf collection and exposure are described in Bärlocher et al. (2011). Briefly, we collected leaves from several *Eucalyptus viminalis* trees from an urban remnant population in Armidale, Australia. After drying to constant mass, they were placed in litter bags (15 cm × 12 cm; 5 mm mesh) and exposed in 3 streams (2 sites each, Tab. 1). The three streams are tributaries of the upper Gwydir River catchment, located in northern New South Wales (NSW), Australia. The catchment is dominated by agriculture which has led to the removal of much of the native riparian vegetation (Lunt et al. 2007, Rogers & Ralph 2010). Roumalla Creek and Moredun Creek are second order streams and consisted of an upstream non-vegetated site and downstream vegetated site separated by at least 10 river km. Booralong Creek consisted of an upstream and downstream vegetated site. Each site was approximately 100 m in length and the dominant riparian vegetation included *Casuarina cunninghamiana* and *Eucalyptus* spp. at the vegetated sites.

Tab. 1. Sites for field experiments with coordinates and altitude (m).

Stream	Symbol	Coordinates	River banks	Altitude
Roumalla 1	Ro1	S 30° 25.639; E 151° 11.863	vegetated	694
Roumalla 2	Ro2	S 30° 27.162; E 151° 10.064	non-vegetated	698
Moredun 1	Mo1	S 30° 08.744; E 151° 07.037	non-vegetated	657
Moredun 2	Mo2	S 30° 08.963; E 151° 05.454	vegetated	655
Booralong 1	Bo1	S 30° 28.908; E 151° 25.561	vegetated	800
Booralong 2	Bo2	S 30° 28.746; E 151° 26.275	vegetated	793

Tab. 2. Sampling schedule in six streams. Start indicates time of immersion of a set of leaf bags. On dates marked with X, samples were recovered and analyzed.

Stream	Set	10 Aug	17 Aug	24 Aug	7 Sep	21 Sep	30 Sep	5 Oct
Roumalla 1	1	Start	X		X	X		X
	2			Start	X	X		X
Roumalla 2	1	Start	X		X	X		X
	2			Start	X			
Moredun 1	1	Start	X			X	X	X
	2			Start	X	X		X
Moredun 2	1	Start	X		X	X		X
	2			Start		X		X
Booralong 1	1	Start	X		X	X		X
	2			Start	X	X		X
Booralong 2	1	Start	X		X	X		X
	2			Start	X	X		X

The first field experiment started on August 10, 2010 (Tab. 2). Groups of five bags were placed approximately 20 m apart. Discharge during the experimental period was unusually high. Compared to the previous year, total discharge measured at the Gwydir River gauging station located downstream of all three streams, increased by a factor of 391 (August), 1758 (September) and 49,223 (October) (unpubl. obs., M. Stewart). We therefore started a second field experiment on August 24. The timing of sample collection is summarized in Tab. 2. Recovered leaves were analyzed for mass loss and ergosterol levels, and temperature and several water parameters were monitored throughout the experimental period. These results are given in Bärlocher et al. (2011).

Additional leaf material (generally around 50–80 mg) was placed in 150 ml of distilled sterile water in a 250 ml Erlenmeyer flask, and aerated for 48 h to induce fungal reproduction (airflow was approx. 1.5 ml per sec.). The supernatant was filtered through a 5 µm membrane filter, which was stained with cotton blue in lactophenol. Fungal spores trapped on the filter were counted; conidia of aquatic hyphomycetes were identified. The leaf material was dried and ashed, and spore

numbers per mg ash-free dry mass were calculated. An equal number of flasks with water and leaves were incubated without aeration and the supernatant filtered and analyzed for spores.

In addition to *E. viminalis* leaves from our field experiment, we collected leaves and needles from 9 other streams, all with riparian vegetation (Tab. 3). We selected brownish, moderately decayed material (neither green, indicating recent immersion in stream, nor black, indicating anoxic conditions). This material was incubated under aeration and evaluated as described above. Distances among the 15 sites were calculated online by the haversine formula, based on latitude/longitude data (http://www.movable-type.co.uk/scripts/latlong.html). They are listed in Tab. 4.

Tab. 3. Additional field sites for fungal collections with coordinates, altitude (m) and temperature (°C) on sampling day (September 15, 2010).

Stream	Symbol	Coordinates	Altitude	Temperature
Little Murphy	LiM	S 30° 23.000; E 152° 33.929	1069	14.3
Rocky Creek	RoC	S 30° 21.362; E 152° 43.333	744	14.8
Never Never 1	NN1	S 30° 23.232; E 152° 53.063	38	18.0
Never Never 2	NN2	S 30° 22.084; E 152°53.491	50	17.5
Never Never 3	NN3	S 30° 21.628; E 152° 54.255	76	17.0
Bellinger River 1	Be1	S 30° 25.725; E 152° 46.230	41	18.0
Bellinger River 2	Be2	S 30° 25.561; E 152° 44.870	48	17.5
Bellinger River 3	Be3	S 30° 25.985; E 152° 43.396	58	17.5
Hastings River	HaR	S 31° 26.335; E 152° 27.625	57	18.0

Tab. 4. Distances in km among collection sites. Symbols as in Tabs. 1, 3.

	Ro2	Mo1	Mo2	Bo1	Bo2	LM	NN1	NN2	NN3	Be1	Be2	Be3	HR	RoC
Ro1	4.0	32.3	32.6	23.7	23.7	131.3	161.9	162.6	163.8	150.8	148.6	146.3	164.8	146.4
Ro2		34.5	34.5	24.9	26.1	134.3	164.8	165.6	166.8	153.7	151.5	149.1	165	149.5
Mo1			2.6	47.7	48.2	141.6	171.8	172.2	173.3	161.8	159.6	157.5	192.7	155.9
Mo2				49	49.5	144	174.3	174.6	175.7	164.2	162	159.9	194.1	158.4
Bo1					1.2	109.8	140.2	141.1	141.2	129	126.9	124.5	145.1	125.1
Bo2						108.6	139.1	139.9	141.2	127.9	125.7	123.3	144.6	123.9
LM							30.6	31.3	32.6	20.3	18.1	16.1	117.8	117.8
NN1								2.2	3.5	11.9	13.8	16.3	123.7	15.9
NN2									1.5	13.4	15.2	17.7	126	16.3
NN3										14.9	16.7	19.1	127.2	17.4
Be1											2.2	4.5	116.2	9.3
Be2												2.5	115.9	8.1
Be3													114.6	8.5
HR														122.9

RESULTS

Numbers of aquatic hyphomycete conidia and zoosporic propagules released during 48 h in static water are shown in Figs. 1 and 2. In both field experiments, these numbers were significantly lower than corresponding values from aerated treatments ($p < 0.0001$ and $p = 0.007$ for aquatic hyphomycetes and zoosporic propagules, respectively; paired t-tests; values for aerated treatments in Bärlocher et al. 2011). On average, aerated leaves released 461 more conidia $mg^{-1} \cdot d^{-1}$ than leaves in stagnant water (average increase of 310 %); for zoosporic propagules the increase was 910 $mg^{-1} \cdot d^{-1}$ (220 %).

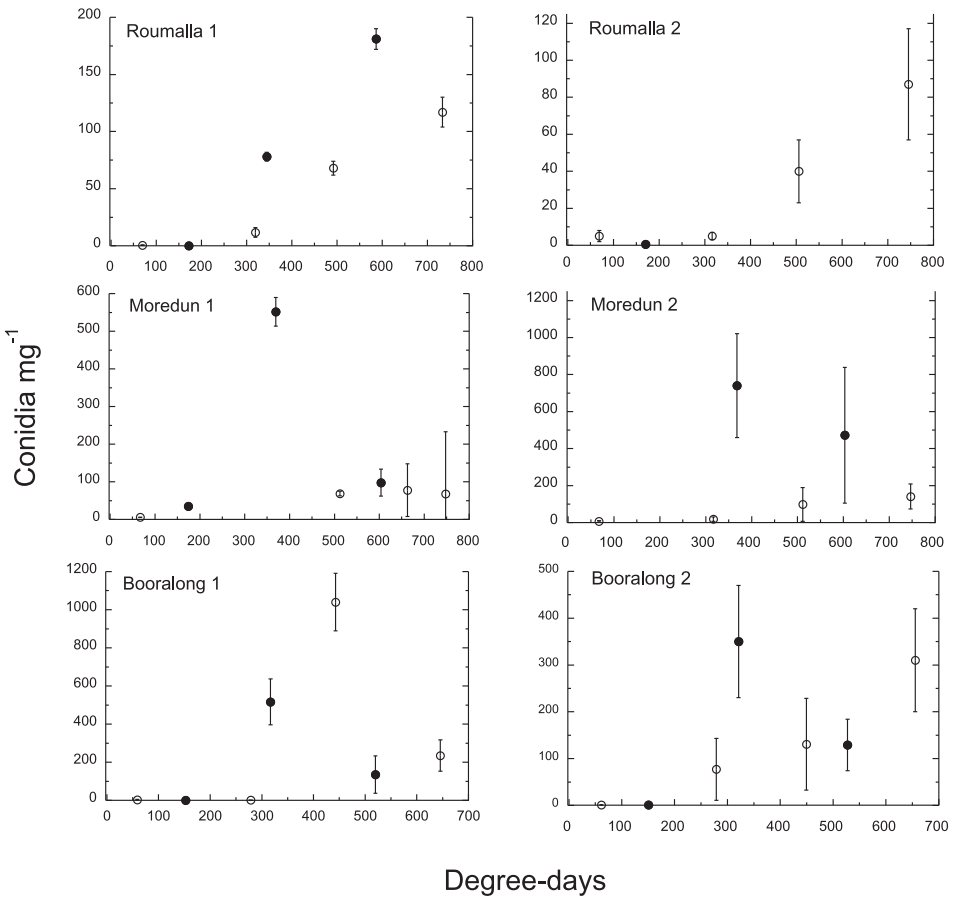

Fig. 1. Conidia of aquatic hyphomycetes released from *E. viminalis* leaves after 48 hours in static water (average, n = 4, ±SEM). ○ first experiment; ● second experiment.

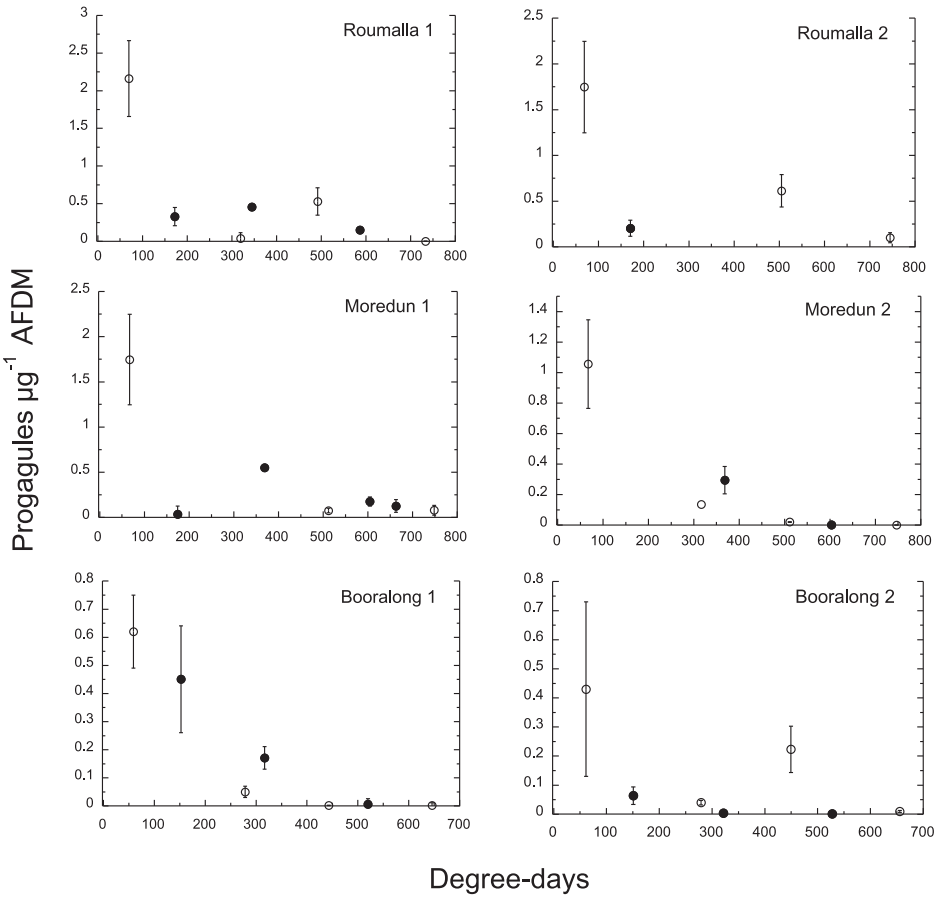

Fig. 2. Zoosporic propagules released from *E. viminalis* leaves after 48 hours in static water (average, n = 4, ±SEM). ○ first experiment; • second experiment.

The data from the first experiment were analyzed by a nested ANOVA (Stream, Location: Upstream vs. Downstream nested in streams; Time) after log(x+1) transformation. For aquatic hyphomycete conidia, Time ($p < 0.001$) and Stream ($p = 0.034$) significantly influenced the number of spores released ($p < 0.0001$), while Location did not ($p = 0.75$). The same result was found for zoosporic propagules (Time: $p = 0.011$; Stream: $p < 0.0001$).

The percentage contributions of identified aquatic hyphomycete species to total spore production during Experiment 1 (samples on 17 August, 21 September and 5 October) with and without aeration are listed in Tab. 5 (only species contributing ≥ 0.1 % of total are listed). The Bray-Curtis dissimilarities of square-root transformed data were used as basis for Principal Coordinate Analysis (Anderson

Tab. 5. Percentage contributions of aquatic hyphomycete species to cumulative spore production during Experiment 1, with (+) or without (–) aeration.

	Roumalla 1		**Roumalla 2**		**Moredun 1**		**Moredun 2**		**Booralong 1**		**Booralong 2**	
	+	**–**	**+**	**–**	**+**	**–**	**+**	**–**	**+**	**–**	**+**	**–**
Alatospora acuminata	1.3		0.1		0.1	0.1	4.5		27.8	15.2	5.3	1.4
Alatospora pulchella	0.4						1.2	0.8		0.5		
Anguillospora crassa	0.1	0.5			0.1	0.1				0.1		
Anguillospora filiformis	0.6	0.2	1.0	2.1		0.1	4.5	1.1	2.5	3.9	2.2	3.1
Anguillospora gigantea		0.1										
Anguillospora longissima	8.7	12.5	1.5	2.5	9.3	25.1	4.5	11.8	7.8	12.5	10.2	9.5
Articulospora tetracladia							3.5		0.1			
Campylospora chaetocladia	0.1	0.2										
Clavatospora longibrachiata	1.5	3.5	4.0	3.5			0.1		1.5			
Clavariopsis aquatica	5.6	6.8	2.9	6.2	7.3	12.6	2.3	8.5	12.4		14.5	14.2
Culicidospora gravida	1.0	1.3				0.1	0.3	2.5				
Dimorphospora foliicola	22.2	12.9	42.1	46.4	21.9	35.5	5.5	14.2	15.1	16.5	17.1	24.6
Flagellospora curta	15.0	5.8	15.1	1.1	12.9	0.5	7.8				5.5	3.6
Flagellospora curvula	15.5	9.0	10.3		40.3	16.5	47.2	35.5	8.1	2.3	17.0	4.2
Fusarium spp.	11.0	13.1	22.7	32.1	0.1	2.2	3.2	12.5	2.3	15.2	23.1	35.1
Heliscus lugdunensis	0.5							0.5			0.1	
Isthmotricladia sp.	0.1											
Lateriramulosa uni-inflata		0.1										
Lemonniera aquatica	5.0	3.6	0.1	0.3	4.3	4.3	2.3	2.3	1.5	0.1	1.5	0.1
Lemonniera terrestris	0.1	0.3										
Lunulospora curvula	6.5	6.8			3.5	1.2	6.3		18.3	27.1	3.4	4.1
Mycofalcella calcarata	1.2	6.7					3.2	5.9				
Tetrachaetum elegans	2.1	7.6		0.5			0.1		1.5	2.3		
Tetracladium marchalianum	0.8	1.2			0.1	1.2	2.3	1.4			0.1	
Tetracladium maxilliforme	0.1											
Tetracladium setigerum	0.1				0.1							
Tricladium chaetocladium	0.1	4.2				0.5		0.5	0.3	1.5		0.1
Tricladium sp.	0.1	3.0										
Trinacrium sp.		0.1										
Tripospermum camelopardus	0.1	0.5							0.1			
Tripospermum myrtii	0.2											
Triscelophorus acuminatus		0.1	0.1	2.3					0.7			
Triscelophorus monosporus			0.1				1.2	2.5				
Varicosporium elodeae		0.4						0.2		0.1		0.1
# species	**28**	**24**	**12**	**10**	**12**	**14**	**17**	**13**	**15**	**14**	**12**	**11**

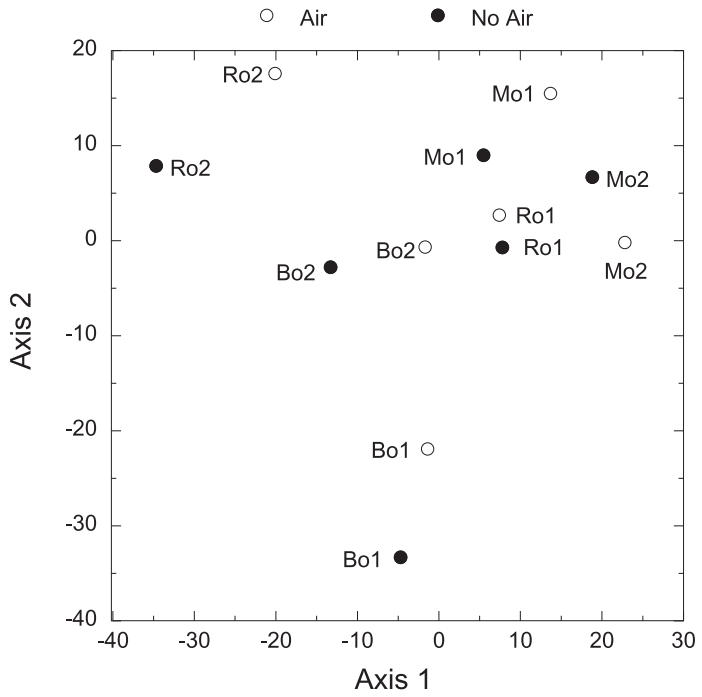

Fig. 3. Principal coordinate analysis of aquatic hyphomycete community data in Tab. 5 based on Bray-Curtis dissimilarities of square-root transformed data. Air: leaves were aerated; No Air: leaves were not aerated. Axis 1 explained 32.2 and Axis 2 25.0 % of the variation.

2003a, Krebs 1999). Axis 1 explained 32.2 % and axis 2 25.0 % of the variation. They clearly separated aerated and non-aerated treatment within each stream (Fig. 3), but average percentage similarities were higher within pairs of aerated and non-aerated communities of the same stream (67.5, SEM = 3.3) than among different streams (50.3, SEM = 1.6). Aerated vs. non-aerated communities were tested for significance by Canonical Analysis of Principal Coordinates (Anderson 2003b, Anderson and Willis 2003). No significant differences between the two groups was detected (9999 permutations, $p = 0.12$ for trace statistic and first squared canonical distribution). Total number of species in aerated vs. static incubations were tested with Wilcoxon's matched pair signed ranks test. There was no significant difference ($p = 0.16$).

The percentage contributions of aquatic hyphomycete species to total spore production on samples from the first experiment collected on 7 September (after 4 weeks of stream exposure) and samples from 9 additional stream on 15 September (Tab. 3) are listed in Tab. 6. The Bray-Curtis dissimilarities of square-root transformed data were used for Principal Coordinate Analysis (Anderson 2003a).

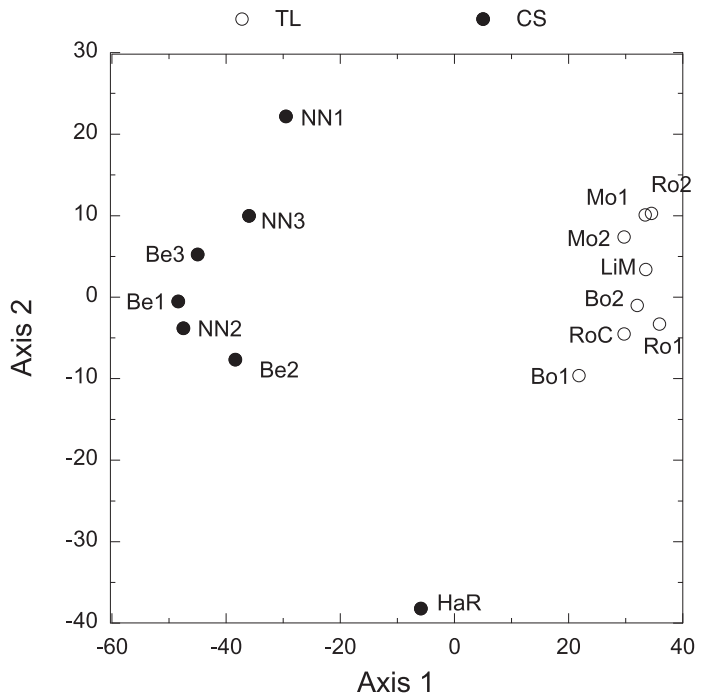

Fig. 4. Principal coordinate analysis of aquatic hyphomycete community data in Tab. 6 based on Bray-Curtis dissimilarities of square-root transformed data. Axis 1 explained 72.8 and Axis 2 10.2 % of the variation. TL, tableland streams; CS, coastal streams. Symbols as in Tabs. 1, 3.

Axis 1 explained 72.8 % and Axis 2 10.2 % of the variation. They clearly separated the majority of tableland and coastal streams, with one site (Hastings River, coastal stream) intermediate between the two groups (Fig. 4). Tableland vs. coastal stream communities were tested for significance by Canonical Analysis of Principal Coordinates (Anderson 2003b, Anderson and Willis 2003). The difference between the two groups was highly significant (9999 permutations, $p < 0.0001$ for trace statistic and first squared canonical distribution).

There was a significant, negative linear regression of percentage similarities of fungal communities vs. geographical distance (Fig. 5A). However, only a small portion of the variability is accounted for by this regression ($R^2 = 0.13$).

Fungal community similarities were also significantly correlated with differences in altitude and temperature (Figs. 5B, C). A greater portion of the variability was accounted for by differences in altitude ($R^2 = 0.65$) than in temperature ($R^2 = 0.45$). As expected, there was a significant, negative correlation between altitude and temperature ($Y = 17.1–0.0055\ X$; $R^2 = 0.81$, $p < 0.0001$).

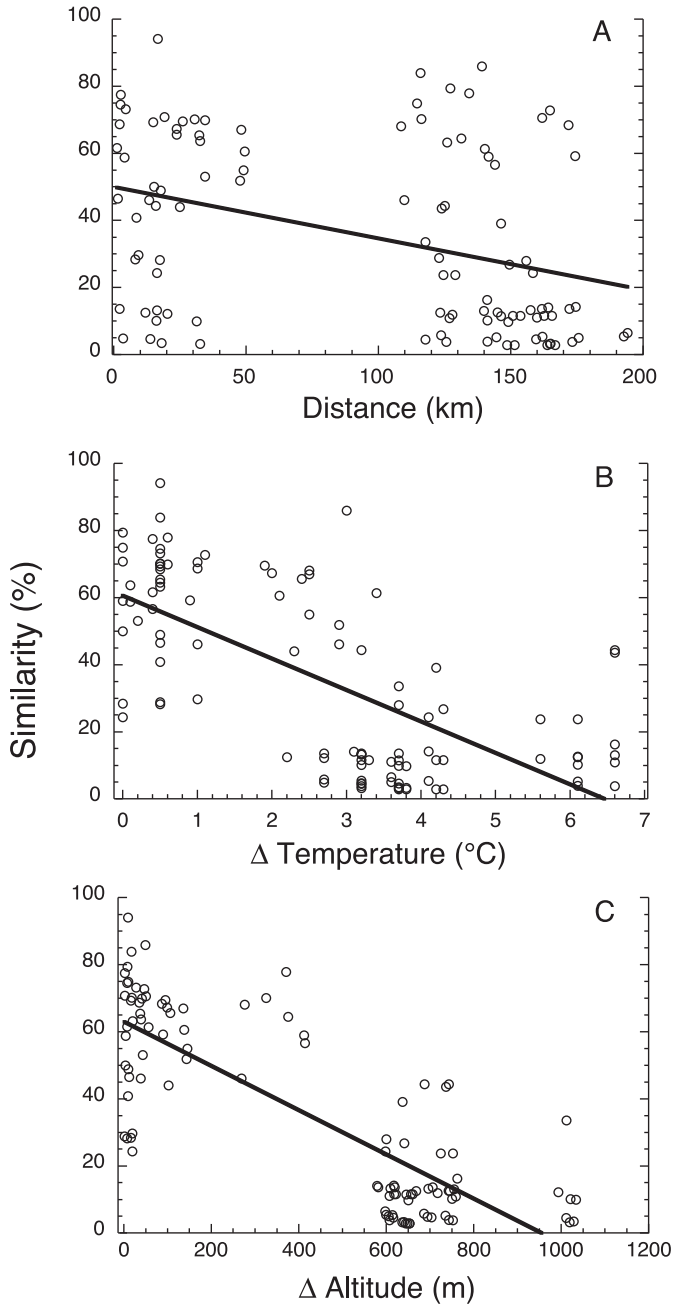

Fig. 5. Percentage fungal community similarities of Tab. 6 vs. **A.** Distance of sites; **B.** Temperature differences among sites; **C.** Altitude differences among sites. Linear regressions were all significant ($p < 0.0001$): **A.** $Y = 50.0–0.15\ x$; $R^2 = 0.13$; **B.** $Y = 60.6–9.38\ X$; $R^2 = 0.46$; **C.** $Y = 63.1–0.066\ X$; $R^2 = 0.65$.

Tab. 6. Percentage contributions of aquatic hyphomycete species to cumulative spore production from Experiment 1 samples collected on 7 September and samples collected on 15 September in 9 additional streams. Stream symbols as in Tables 1, 3. Temperature (°C) on sampling day; substrates: E. v., *Eucalyptus viminalis*; E. g., *Eucalyptus grandis*; E. sp., unidentified *Eucalyptus* leaves; C. c., needles of *Casuarina cunninghamii*; Cl, camphor laurel leaves, *Cinnamomum camphora*.

	Ro1	**Ro2**	**Mo1**	**Mo2**	**Bo1**	**Bo2**	**LiM**	**RoC**	**NN1**	**NN2**	**NN3**	**Be1**	**Be2**	**Be3**	**HR**
Temperature	13.8	13.7	14.3	13.9	11.4	11.8	14.3	14.8	18.0	17.5	17.0	18.0	17.5	17.5	18.0
Substrate	E. v.	E. v.	E. v.	E. v.	E. v.	E. v.	E. sp	E. sp	Cl	E. sp.	C. c.	E. g.	E. g.	E. g.	E. sp.
Alatospora acuminata	7.8	0.8		5.4	23.4		3.6	2.3		0.4		0.3	0.1		1.5
A. pulchella				0.1											
Anguillospora crassa														0.1	
A. filiformis	0.9	1.1	1.3	6.9	3.3	6.3	2.6	1.9	0.3	0.3	0.3	0.3	0.4	1.6	
A. longissima	15.0	2.4	6.8	5.0	5.8	8.8	11.1	7.5		0.2		0.1			8.2
Articulospora tetracladia				1.8	1.1	0.1		0.5							
Clavatospora longibrachiata	2.3	4.3		0.2	2.2	2.2	0.4	1.8		0.7				0.1	
Clavariopsis aquatica	17.8	7.8	10.6	6.6	16.1	16.9	9.0	16.0	0.1			0.9	9.4	0.6	20.9
Condylospora spumigena									0.1						
Culicidospora aquatica														0.1	3.0
Dimorphospora foliicola	12.1	29.1	27.1	12.1	13.1	18.1	17.3	19.7	1.0		9.8		0.1		
Flagellospora curta	18.7	15.7	15.7	14.1		7.3	21.3	11.9			0.1			0.1	
F. curvula	10.7	8.7	27.8	36.5	10.5	15.5	6.7	11.7	8.0						
Fusarium spp.	6.8	28.8	5.8	5.8	6.6	20.6	25.6	18.5	0.9		0.1		0.1	0.1	14.7
Geniculospora grandis															1.7
Heliscus lugdunensis	0.7														
Lemonniera aquatica	3.6		1.5	1.6	2.3	0.3		0.5						0.1	11.3
L. terrestris			0.1												
Lunulospora curvula	1.3	1.3	3.3	3.3	13.3	1.3	2.3	0.1	4.7	7.2	16.9	8.1	12.5	8.8	9.9
L. cymbiformis				0.5				1.8	39.6	86.3	59.9	84.1	60.5	69.1	16.2
Mycofalcella calcarata								2.1							
Tetrachaetum elegans									0.3	1.6	12.6	0.1		0.7	3.5
Tetracladium marchalianum				0.1	1.1	1.4	0.1	2.4	0.2	0.2				0.1	1.3
Titaeela capnophila (?)															1.5
Tricladium chaetocladium					1.2	1.2		1.2	44.6	1.3	0.3	5.2	3.9	17.9	1.7
Trinacrium sp.								0.1							
Tripospermum camelopardus	2.3												0.1		
T. myrtii										0.5					
Triscelophorus acuminatus										0.9		0.6	9.9	0.4	3.4
T. monosporus									0.1	0.2		0.3	0.2	0.1	1.2
Triscelophorus sp.									0.1	0.2			2.8	0.1	
Varicosporium elodeae									0.3						1.6
Total # species	**13**	**10**	**10**	**15**	**13**	**13**	**11**	**17**	**14**	**13**	**8**	**10**	**12**	**16**	**16**

Discussion

Despite the demonstrated impact of turbulence on sporulation by aquatic hyphomycetes (Webster & Towfik 1972, Webster 1975), remarkably little attention been paid on how varying the incubation of field samples may affect our perception of fungal communities and successions on plant litter. In fact, we are aware of only one study addressing this issue. Thomas (1992) compared ranks of the ten top fungi on *Eucalyptus viminalis* leaves and *Acacia melanoxylon* phyllodes in static and aerated flasks. In summer/autumn, nine of the ten most abundant species were identical in the two groups, and there were only minor shifts in ranks. In winter/spring, the same species were the top six of both treatments, but different species appeared in the 7th to 10th ranks; there was also substantial reordering among ranks. We observed some reordering of ranks as well, and several species appeared in only one of the treatments. Overall, however, there was no significant difference between community compositions in static and aerated treatments (based on proportions in Tab. 1; Wilcoxon matched-pairs signed ranks test, run separately for each site; p varied between 0.28, Ro1 and 0.93, Mo2). Average percentage similarities of fungal communities between aerated and static treatments of the six sites dropped to 67.5 % (no change would result in 100 %), and principal coordinate analysis clearly illustrates these shifts (Fig. 3). Compared to site differences, however, these shifts were generally small, and there was no consistent, significant difference between static and aerated treatments (CAP, p = 0.12).

Looking at individual aquatic hyphomycete species, we compared relative frequencies in the two treatments across sites whenever a species was present at all six sites in at least one treatment. Of six species, *Flagellospora curvula* increased significantly in aerated, and *Fusarium* spp. significantly increased in static conditions (Wilcoxon matched-pairs signed rank test, p = 0.03). Various *Fusarium* spp. are equally common on land as in water, while *F. curvula* is known as one of the more prolific species and is more common in the mainstem rather than in floodplain wetlands (Baldy et al. 2002, Nikolcheva & Bärlocher 2005). Sanders & Webster (1980) observed a less pronounced response to aeration in some 'aquatic' species that often occur in terrestrial situations. Generally, the tableland streams in the study region have a lower gradient and substrate particle size than the coastal streams, which increases the potential for turbulent flow in the latter. Turbulence has been shown to positively influence the composition of fungal communities through improved in situ aeration (Webster & Descals 1981, Thomas et al. 1989) but may also reduce colonization and conidia formation through physical fragmentation associated with turbulent flow (Fabre 1997). Both aquatic hyphomycete diversity and fungal biomass were reduced in the floodplain pond of a large river compared to the mainstem (Baldy et al. 2002). The lack of significant differences in our experiments is therefore surprising since pure cultures respond

strongly and selectively to changing aeration. For example, sporulation of *Anguillospora longissima*, *Tricladium splendens* and *Tetrachaetum elegans* increased by factors of 2.1, 11.7 and 20.7, respectively, when aeration rate was increased from 100 to 1000 ml·min^{-1} (Webster 1975). At the higher rate, the large spores of *Varicosporium elodeae* produced significantly fewer branches. In addition, the delivery of air can be crucial: when introduced via hypodermic needle rather than via sintered glass aerators, sporulation rate increased to higher levels (Webster & Towfik 1972). Clearly, our study with a rate of approx. 90 ml·min^{-1} has covered only a small section of possible turbulence conditions in streams.

Due to lack of morphological details, we were unable to subdivide zoosporic propagules into distinct taxa. Our study nevertheless showed that aeration dramatically increased their production (increase of 220 %) as it did with aquatic hyphomycete conidia (310 %). Assuming that this behaviour is subject to natural selection, it suggests that spore production is more beneficial to the fungi in the presence of turbulence, presumably by ensuring more efficient dispersal to new substrates. It is also clearly relevant when working out fungal allocations to mycelial growth vs. reproduction. Such budgets will only approximate reality when conditions for growth and reproduction are identical and when we collect the entire reproductive output (e.g., Suberkropp 1991, Maharning & Bärlocher 1996, Suberkropp & Chauvet 1998, Sridhar & Bärlocher 2000). Under these conditions, ≥ 50 % of acquired net energy is generally invested in producing conidia, but this percentage can fluctuate depending on, among other factors, temperature and inorganic nutrients. More typically, leaves are periodically recovered from a field site and incubated under conditions favouring reproduction (Gessner et al. 2003, Krauss et al. 2011). Extrapolating the reproductive rate under these favourable conditions to the field may overestimate fungal investment in conidia, especially when fungal-colonized leaves are buried in sediments (Cornut et al. 2010). We need to revisit the assumption that any fungal biomass will immediately and continuously be converted into reproductive propagules (Bärlocher 2009). It is a common observation that leaves continue to carry high levels of fungal biomass at later stages of decay, when conidium production has already dropped off considerably. A bet-hedging life history may dictate that rather than expending the entire biomass in instantaneous reproduction, some may be invested more profitably over a longer period of time, or even diverted to sexual reproduction (though this is more common on wood than on leaves; Webster 1992).

In total, we assigned 30 taxa to described species and 4 to genera based on conidium morphology; in addition, we observed 15 forms that may have belonged to undescribed species. Unequivocal identification often requires pure cultures and increasingly molecular data (Marvanová & Bärlocher 2001, Bärlocher 2010), which was beyond the scope of this study. To minimize errors, especially with unusual species, we consulted the original literature, e.g., Webster (1993) for

Flagellospora curta, Marvanová et al. (1993) for *Mycofalcella calcarata* and Marvanová et al. (2003) for *Titaeella capnophila*. We are aware of four other surveys of Australian stream fungi. Cowling (1963) recorded 54 species (33 previously described) from eight sites in New South Wales and one in Queensland. Price (1964) found 21 species plus 22 unidentified forms in four creeks near Adelaide, though several of her species are generally considered terrestrial or semi-terrestrial. In a survey of 23 streams in south-eastern Australia, northern New South Wales and the Northern Territory, Thomas (1992) recovered a total of 60 species, 36 of which were assigned to described species, 11 to genus and 13 were entirely unknown. Finally, Suter et al. (2011) distinguished 11 taxa in a stream in the Victorian Alpine National Park. Tab. 7 compares identified species and genera in the current and the four earlier studies.

While many species remain to be described from Australian streams, most of the more common species have been reported from many other parts of the world, and some show the same seasonal or temperature preferences. In our study, *Lunulospora curvula*, *L. cymbiformis*, *Triscelophorus acuminatus*, *T. monosporus*, *Tetrachaetum elegans* and *Tricladium chaetocladium* all appeared in later samples of the six tableland sites (when water temperatures were rising) and were more common in the low-lying, warmer coastal streams. Thomas (1992) lists *L. curvula*, *L. cymbiformis*, and T. *chaetocladium* as summer species (along with *Flagellospora penicillioides*, not found in the current study). None of these were found in the relatively cool Australian alpine streams studied by Suter et al. (2011). The same species have been mentioned world-wide as common in summer in temperate streams or year round in subtropical/tropical streams (Wood-Eggenschwiler & Bärlocher 1985, Bärlocher et al. 2010). This suggests that many species (defined by morphology) are indeed cosmopolitan, and their occurrence is strongly influenced by local conditions.

Our comparison of tableland and coastal streams (Tab. 6, Fig. 4) clearly subdivided the two groups, with one outlier in the Hastings River. Geographic distance accounted for a small portion of the variability, while temperature and altitude had a more pronounced impact (Fig. 5). Both temperature and altitude might to some extent be correlated with different geological substrata of the sites, with red granitic podzols at higher and basalt intrusions and alluvial deposits at lower altitudes (Barrow & Spencer 1971, Banens 1987, Kingham 1998). However, there is considerable local variation in both regions. The limited information of the water chemistry of individual streams available (Tab. 8, from unpubl. data D. Ryder) suggests that the coastal streams have higher N values and lower turbidity and conductivity than the tableland streams (Bärlocher et al. 2011), with the most pronounced differences occurring in the Hastings River, which has higher P, pH, and conductivity values than other coastal streams. Its fungal community was intermediate between tableland and coastal streams (Fig. 4).

Tab. 7. List of species found in the current study but absent in Cowling (1963), Price (1964), Thomas (1992) or Suter et al. (2011)

	Cowling	Price	Thomas	Suter
Alatospora acuminata				x
A. pulchella	x	x		x
Anguillospora crassa		x		x
A. filiformis	x	x		x
A. gigantea			x	x
A. longissima				x
Campylospora chaetocladia				x
Clavatospora longibrachiata	x	x		x
Condylospora spumigena	x	x		x
Culicidospora aquatica	x	x		x
C. gravida	x	x	x	x
Dimorphospora foliicola	x	x		x
Flagellospora curta	x	x	x	x
F. curvula	x	x	x	x
Geniculospora grandis	x	x	x	x
Isthmotricladia sp.	x	x		x
Lateriramulosa uni-inflata	x	x		x
Lemonniera aquatica				?
L. terrestris	x	x	x	x
Lunulospora curvula				x
L. cymbiformis	x	x		x
Mycofalcella calcarata	x	x	x	x
Tetrachaetum elegans	x			x
Tetracladium marchalianum				?
T. maxilliforme	x	x		?
T. setigerum				?
Titaeela capnophila	x	x	x	x
Tricladium chaetocladium	x	x		x
Tripospermum camelopardus	x	x	x	x
T. myrtii	x	x		x
Triscelophorus acuminatus	x	x		x
T. monosporus				x

Tab. 8. Selected stream parameters of Bellinger River and Never Never Creek (n = 12 ± SD; January to December 2010) and Hastings River (n = 5, ± SD; December 2010 to April 2011).

Stream	N_{tot} $\mu g \cdot ml^{-1}$	P_{tot} $\mu g \cdot ml^{-1}$	Turbidity NTU	pH	Conductivity µS	O_2 $mg \cdot l^{-1}$
Never Never	1.56±0.24	0.13±0.01	0.9±0.4	7.07±0.38	38±6.5	7.7±2.6
Bellinger River	1.13±0.33	0.09±0.01	1.2±0.2	6.89±0.88	33±4.9	7.9±1.3
Hastings River	1.74±0.13	0.18±0.02	4.4±0.9	7.61±0.32	119±6.0	8.2±0.9

The significance of temperature is supported by the pronounced shift in fungal communities coinciding with the warmer season in tableland streams. In three Pyrenean streams, Fabre (1966) also found significant correlations between environmental conditions summarized by elevations and fungal communities. In addition to temperature, changing riparian vegetation may play a role, though in our study, fungal communities were remarkably similar on different substrates including leaves from several native *Eucalyptus* species and the introduced *Cinnamomum camphora*, and needles of *Casuarina cunninghamii*. In Iberian streams, where the allochthonous input is often dominated by the introduced *Eucalyptus globulus*, fungal diversity depends crucially on inorganic nutrients (Pozo et al. 1998, Bärlocher & Graça 2002, Ferreira et al. 2006, Mesquita et al. 2007)

The vast majority of studies on the distribution of aquatic hyphomycetes relies on a morphologically defined species concept. This can be misleading due to convergent evolution of conidium shape by selection for dispersal in flowing water, potentially resulting in cryptic species which can only be distinguished with molecular analyses (Bärlocher 2010). Information on molecular variability within morphospecies is very limited. Laitung et al. (2004) investigated the genetic diversity in 97 isolates of *Tetrachaetum elegans* with AFLP (amplified fragment length polymorphism). Out of 247 fragments, 32 were polymorphic. Twenty percent of the observed genetic variation was the result of differences between streams. Genetic and geographical distances were not correlated but a few multilocus genotypes were observed in different locations, suggesting that environmental barriers or historical contingencies (accidental introductions via animals or humans) played some role in the population structure of this species. No clear-cut effect of leaf litter composition on genetic variation could be demonstrated.

Anderson & Shearer (2011) genotyped 391 isolates of *Tetracladium marchalianum* over two years from seven sites. Diversity at eight polymorphic microsatellite loci was high, and allele frequency remained stable over time despite lack of evidence of sexual reproduction. Genetic differentiation was only observed between the most distant rivers (450 km), suggesting large, interconnected populations of *T. marchalianum* and the absence of cryptic species. The same conclusion was reached by Letourneau et al. (2010) based on the constancy of the ITS region in the same species. Clearly, many more molecular studies incorporating isolates from large numbers of distant locations are needed, but current knowledge supports the hypothesis that many aquatic hyphomycete species are cosmopolitan, and one of the primary predictors of their occurrence in any given stream is water temperature or associated factors such as altitude or geographic proximity.

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