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Lillian Holmer · Jan Stenlid

Diffuse competition for heterogeneous substrate in soil among six species of wood-decomposing basidiomycetes

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Abstract Competition among six wood decay fungi was studied using 15×15 mm wood blocks placed in 250×250 mm plastic trays filled with unsterilized sand or clay. The wood blocks were preinoculated with *Heterobasidion annosum* (Fr.) Bref., *Resinicium bicolor* (Alb. & Schw. ex Fr.) Parm., *Phanerochaete sanguinea* (Fr.) Hjortstam, *Coniophora* sp. DC. ex Me"rat, *Armillaria borealis* Marxmuller and Korhonen and *Hypholoma capnoides* (Fr.) Kummer before they were combined in all possible combinations in the trays. Two methods were used, one with all wood blocks inoculated, and one with sterilized non-inoculated wood blocks distributed between the inoculated ones. Wood blocks preinoculated with the six species were also used in a pairwise competition test. Following incubation for 9 months in darkness at 21°C, mycelia were reisolated and identified. *R. bicolor* was most successful at invading through the soil and replacing other species in the wood blocks. *P. sanguinea*, *Coniophora* sp. and *H. capnoides* also had some success.

Key words Secondary resource capture · Fungal competition · *Heterobasidion annosum* · *Resinicium bicolor* · *Hypholoma capnoides*

Introduction

Competition among fungal mycelia for substrates can be divided into two distinct stages – primary and secondary resource capture (Rayner and Boddy 1988). Primary resource capture occurs when a fungus is gaining initial access to a food resource. Such resources are rare and will typically be available after disturbance. Secondary resource capture is the result of replacement of the primary invader by a subsequent mycelium. Many pathogenic species, such as the root rotting basidiomycete *Heterobasidion annosum*, rely on the former mode of competition, whereas saprotrophic species may exhibit both types of resource capture.

In saprotrophic decay fungi, the mode of arrival and establishment is of great importance for the outcome of the competition. Long-distance dispersal and initial population establishment is typically accomplished by spores, while enlargement of individual mycelia is through vegetative growth of hyphae. Colonization via hyphal aggregates or cords is more effective in catching substrates than spores, since the former allows an input of nutrients and water via translocation from old food bases (Redfern and Filip 1991; Dowson et al 1989; Thompson and Rayner 1982). Secondary resource capture, in particular, is facilitated by mycelial cords as the mode of dispersal.

Field studies have suggested that the strong ability for secondary resource capture shown by some cord-forming basidiomycetes might be useful in biological control of root pathogens such as *Armillaria* species (Rayner 1979; Rayner and Todd 1979; Thompson and Boddy 1983; Pearce and Malajczuk 1990; Kirby et al. 1990; Holmer and Stenlid 1993).

In this laboratory study we used *Heterobasidion annosum* and *Armillaria borealis*, two pathogenic root rotting basidiomycetes with primary resource capture strategy, and four primarily saprotrophic wood decaying species that form mycelial cords and that might have secondary resource capture ability. The aim of the study was to investigate the outcome of competitive interactions among wood decay fungi. By varying the experimental set-up and by excluding the species one-by-one, we were able to assess the contribution of the individual species to interactions in the system as a whole and to compare that with predictions from pairwise interactions. By placing empty wood blocks between the inoculated ones, we simulated the spatial discontinuity in food resources and competitor distribution characteristic of natural habitats. The results should help in finding suitable candidates for biological control of root pathogens as well as providing new information on the dynamics of fungal communities in woodlands.

L. Holmer · J. Stenlid (✉)
Department of Forest Mycology and Pathology,
Swedish University of Agricultural Sciences, Box 7026,
S-750 07 Uppsala, Sweden

								Ha		Rb		Ps					
Ps		Rb		Hc			Ab		Csp		Hc						
	Csp		Ab					Hc		Ab		Csp					
Ha		Ps		Rb			Rb		Ps		Ha						
	Hc		Csp					Csp		Hc		Ab					
Csp		Ab		Ps			Ha		Rb		Ps						
	Rb		Hc					Ps		Ha		Rb					
Hc		Csp		Ab			Hc		Ab		Csp						
	Ps		Rb					Rb		Ps		Ha					
Rb		Hc		Csp			Csp		Hc		Ab						
	Ab		Ps					Ab		Csp		Hc					
								Ps		Ha		Rb					
a							b										

Fig. 1 Matrix from method 1: **a** with five species and **b** with six species. *Ha Heterobasidion annosum; Rb Resinicium bicolor; Ps Phanerochaete sanguinea; Hc Hypholoma capnoides; Ab Armillaria borealis; Csp Coniophora* sp

Material and methods

Fungal strains

The six species in the study, *Heterobasidion annosum* (Fr.) Bref., *Resinicium bicolor* (Alb. & Schw. ex Fr.) Parm., *Phanerochaete sanguinea* (Fr.) Hjortstam, *Coniophora* sp. DC. ex Mérat, *Armillaria borealis* Marxmuller and Korhonen and *Hypholoma capnoides* (Fr.) Kummer were each represented by one strain. All strains were isolated from stumps of Norway spruce (*Picea abies*) close to Uppsala and stored on Hagem agar (HA; Stenlid 1985) at 5°C until used in the study.

Preparation of wood blocks

Cubes, 15×15 mm, were cut from fresh wood of Norway spruce and autoclaved twice with a 24-h interval at 12°C. The wood blocks were thereafter transferred under sterile conditions to 2-week-old cultures of the fungi grown on HA in 250 ml Erlenmeyer-flasks and incubated at room temperature in darkness for 1 month.

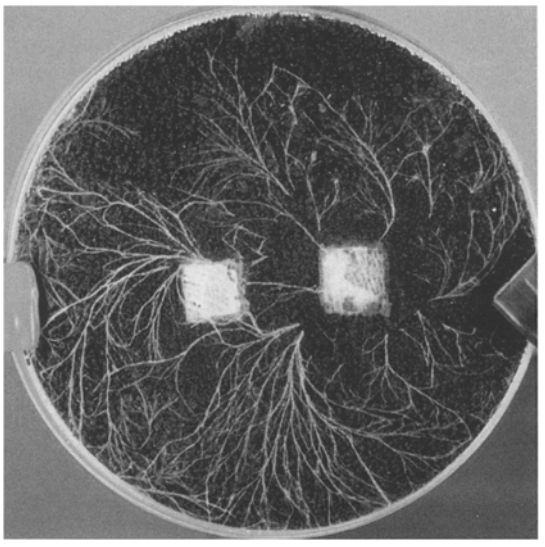

Fig. 3 Experimental set-up in method 3. *Heterobasidion annosum* versus *Resinicium bicolor*

Experimental procedures

Three different methods were used in the experiment. In two of them five or six species were combined in large plastic trays; in one of the methods all wood blocks in the tray were inoculated; in the other sterilized wood blocks were placed between the inoculated ones (Figs. 1a,b, 2a,b). In the third method, species were confronted pairwise in large petri dishes (Fig. 3).

Method 1

The inoculated wood blocks were placed in 240×240 mm plastic trays (NUNC), which were filled with unsterilized soil. The species were combined in seven different ways. In tray 1, all six species were present, and in trays 2–7 one species at a time was removed. When present in the trays, each species was represented by five wood blocks except in tray 1 where all species were represented by six wood blocks each. The inoculated wood blocks were placed so that the neighbours were of different species in all possible combinations. The distance between the wood blocks was 33 mm (Fig. 1a,b).

During the experiment the trays were placed in darkness at 21°C. The moisture content was kept constant by weighing the trays regularly and adding sterile water if necessary. Photographs were taken of the trays from below once a month. After 9 months all wood blocks were cut in three slices; from all of them samples were taken from the wood, placed on HA plates and incubated for 2 weeks at room temperature. The mycelia were identified based on their typical characteristics. The experiment was conducted once.

Rb	X	Ps	X	Ab			Rb	X	Csp	X	Hc	X					
X	Csp	X	Hc	X			X	Ab	X	Ha	X	Ps					
Ab	X	Rb	X	Ps			Hc	X	Rb	X	Csp	X					
X	Hc	X	Csp	X			X	Ps	X	Ab	X	Ha					
Ps	X	Ab	X	Rb			Csp	X	Hc	X	Ps	X					
X	Csp	X	Hc	X			X	Ab	X	Ha	X	Rb					
a							b										

Fig. 2 Matrix from method 2: **a** with five species, **b** with six species. *Crosses* represent empty wood blocks. *Ha Heterobasidion annosum; Rb Resinicium bicolor; Ps Phanerochaete sanguinea; Hc Hypholoma capnoides; Ab Armillaria borealis; Csp Coniophora* sp

Method 2

In this method, "empty" sterilized wood blocks were placed in between the inoculated ones. The seven different combinations of species used in method 1 were also used in this method, but each species was here represented by three wood blocks when present in the trays. The distance between two inoculated wood blocks was 27 mm, but the distance between one inoculated and one "empty" wood block was 20 mm (Fig. 2a,b). Each of the seven combinations of species in this method was replicated once.

Apart from the changes described above, the experimental procedures for method 2 were identical to those in method 1.

Method 3

Here the species were inoculated pairwise in 140-mm petri dishes by using the same type of colonized wood blocks as described above. The petri dishes were filled with unsterilized soil, either sand or clay. The six species were paired in all possible combinations, one set on clay and one on sand. The plates were kept at 21°C in darkness for 9 months during which time photographs were taken. Fungi were thereafter isolated as described for the other two methods.

Results

Method 1

All fungal species in the experiment except for *H. annosum* were chosen for their ability to form rhizomorphs or mycelial cords. *R. bicolor* and *H. capnoides* foraged by forming extensive cord systems between the wood blocks in this non-sterile system. *P. sanguinea* and *Coniophora* sp. did so to a lesser degree. When substrate units originally occupied by another fungal species were reached, these were frequently captured by the arriving fungus (Fig. 4a,b). Of the species in this experiment, *R. bicolor* was the strongest competitor, suppressing the foraging activity of the other species (Fig. 6b-g). The only time any of the other species was able to capture more than two resource units in a tray was when *R. bicolor* was omitted from the experimental set-up. In the absence of *R. bicolor*, *H. capnoides* took the lead in terms of capturing wood blocks (Fig. 6a). *H.*

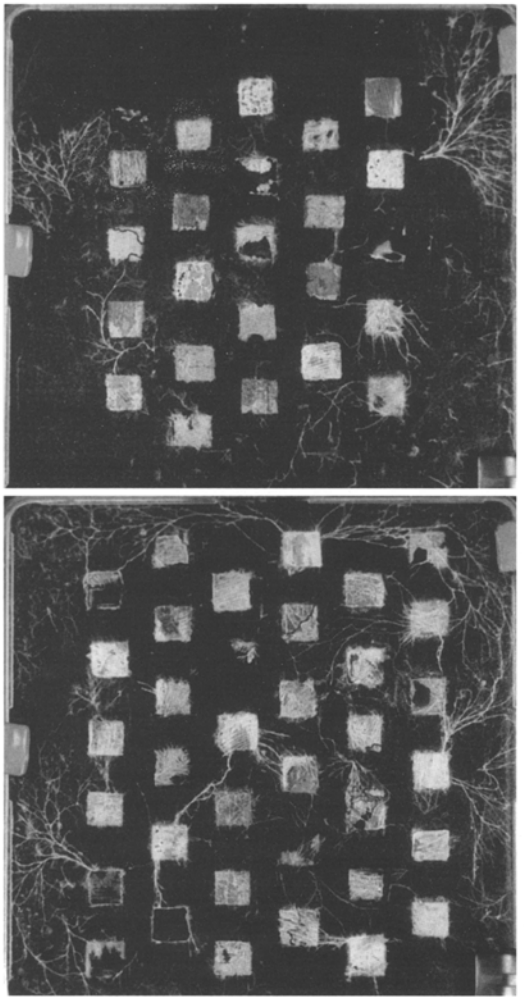

Fig. 4 Method 1 after 6 months: **a** all species except *Heterobasidion annosum*, **b** all six species

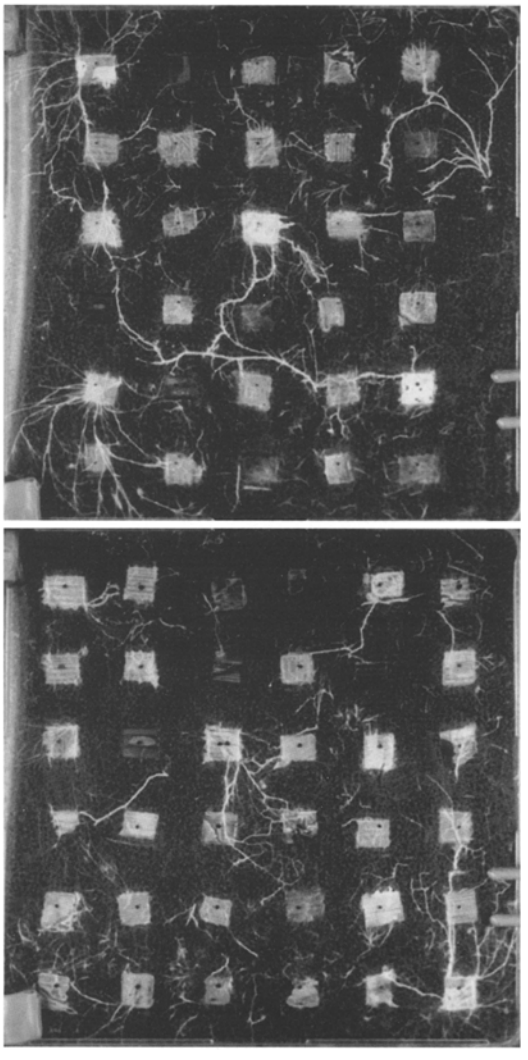

Fig. 5 Method 2 after 6 months: **a** all species except *Heterobasidion annosum*, **b** all six species

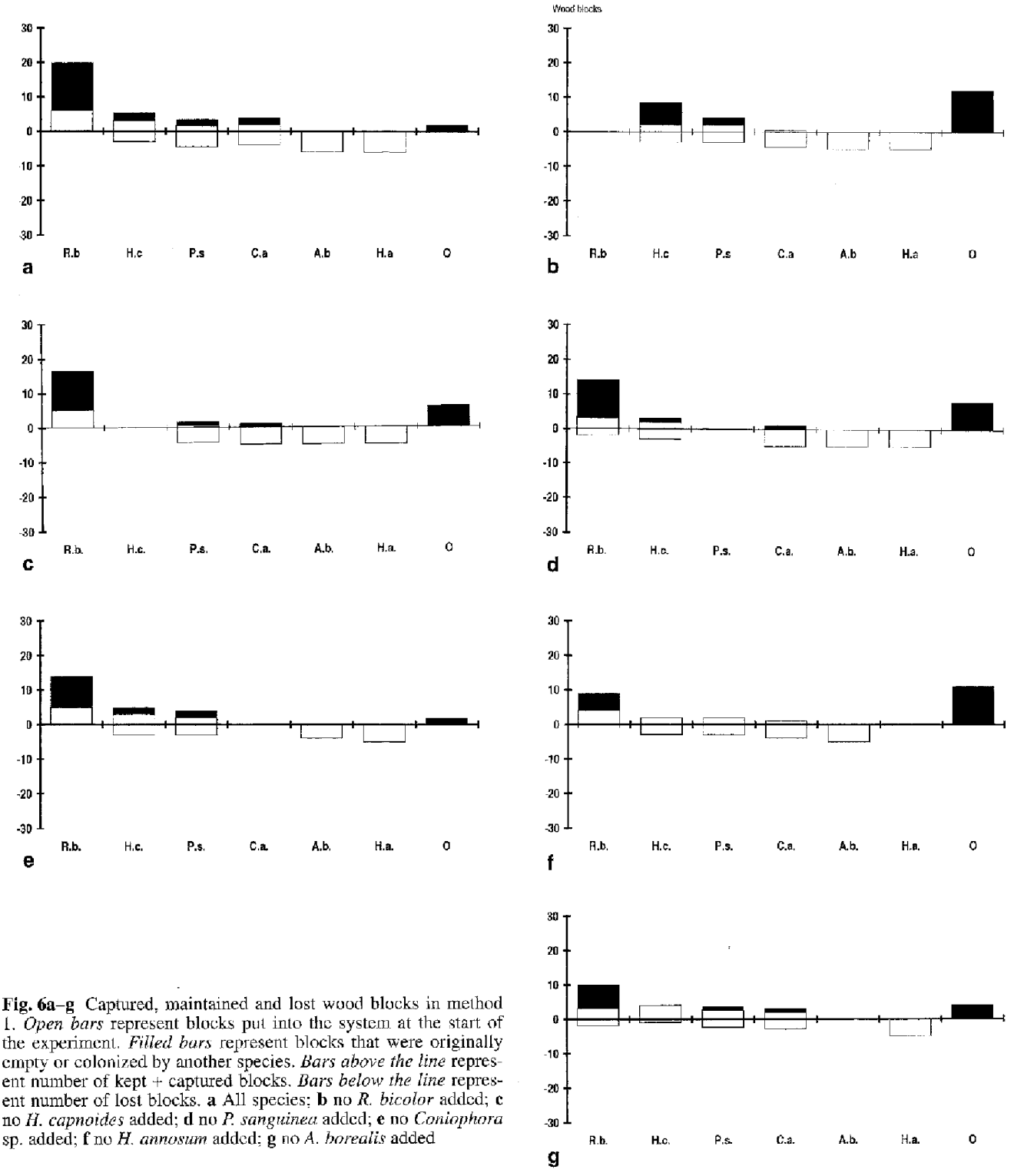

Fig. 6a–g Captured, maintained and lost wood blocks in method 1. *Open bars* represent blocks put into the system at the start of the experiment. *Filled bars* represent blocks that were originally empty or colonized by another species. *Bars above the line* represent number of kept + captured blocks. *Bars below the line* represent number of lost blocks. **a** All species; **b** no *R. bicolor* added; **c** no *H. capnoides* added; **d** no *P. sanguinea* added; **e** no *Coniophora* sp. added; **f** no *H. annosum* added; **g** no *A. borealis* added

annosum and *A. borealis* had not been isolated from any resource unit at the time the experiment was terminated (Fig. 6a-g).

Of the original colonizers of the wood blocks, only *R. bicolor* was able to maintain most of its original resource units (90%). The three cord-formers *H. capnoides*, *P. sanguinea* and *Coniophora* sp. also maintained some of their original blocks but to a lower and variable degree (on average 47%, 37%, and 18%, respectively). *H. annosum* and *A. borealis* were absent from the blocks at the time of harvest (Table 1).

R. bicolor was the strongest fungus in terms of capturing resource units from other species. By means of mycelial cords it was able to penetrate the soil, and establish in, and exclude other species from, wood blocks. By the end of the experiment, *R. bicolor* had become es-

Table 1 Results from method 1; number of units put into the system, units gained, units kept, units lost, units at the end of the experiment, percentage of units captured from other species at the end of the experiment and percentage of units held at the end of the experiment. (*R.b., Resinicium bicolor; H.c., Hypholoma capnoides; P.s., Phanerochaete sanguinea; C.a., Coniophora* sp.; *A.b., Armillaria borealis; H.a., Heterobasidion annosum*)

Species	Units put into system	Units gained		Units kept	Units lost			Units at the end of experiment	% of units at end of experiment captured from other species	% of units kept at end of experiment
		From other species	From empty blocks		To R.b.	To other species	Empty			
R.b.	30	65	–	26	–	1	3	91	71	90
H.c.	30	12	–	14	6	1	9	26	46	47
P.s.	30	7	–	11	11.5	2	5.5	18	39	37
C.a.	30	4	–	5.5	11.5	3	10	9.5	42	18
A.b.	30	0	–	0	18	4	8	0	–	0
H.a.	30	0	–	0	18	10	2	0	–	0

Table 2 Results from method 2; number of units put into the system, units gained, units kept, units lost, units at the end of the experiment, percentage of units captured from other species at the end of the experiment and percentage of units held at the end of the experiment. (Abbreviations as in Table 1)

Species	Units put into system	Units gained		Units kept	Units lost			Units at the end of experiment	% of units at end of experiment captured from other species	% of units kept at end of experiment
		From other species	From empty blocks		To R.b.	To other species	Empty			
R.b.	36	47	67.5	33	–	1	3	147.5	32	92
H.c.	36	8	26	22	8.5	1.5	4	56	14	61
P.s.	36	5	17	23	7	1	5	45	11	64
C.a.	36	1	11.5	11	14	4	7	23.5	4	31
A.b.	36	0	0	0	11	1	24	0	–	0
H.a.	36	0	0	0	6.5	5.5	24	0	–	0
Empty	216	68	–	96	67.5	54.5	–	163	42	–

tablished in 65 resource units previously occupied by another species. *H. capnoides, P. sanguinea* and *Coniophora* sp. also captured wood blocks but to a lesser extent; 12, 7 and 4 units, respectively (Table 1).

The quotient between the number of resource units captured during experiment 1 and the total number of units occupied by a species at the end of the experiment reflects its disposition for foraging for resources. A high quotient indicates high foraging tendency. *R. bicolor* had the highest score (71%) followed by *H. capnoides, Coniophora* sp. and *P. sanguinea* (46%, 42%, and 39%, respectively; Table 1).

As regards a species losing a block to another species, most were lost by *H. annosum* (93% of the original number of blocks) followed by *A. borealis, Coniophora* sp., *P. sanguinea, H. capnoides* and *R. bicolor* (3% of the original number). That is, the ranking order was reversed compared with that for the capturing capacity. On average, 48% of blocks were lost to another species (Table 1).

Empty resource units (from which none of the original fungi was isolated by the end of the experiment) originated most frequently from blocks inoculated with *Coniophora sp.* (33% of the number of original blocks) followed by *A. borealis, H. capnoides, P. sanguinea, R. bicolor* and *H. annosum* (7% of original number). On average, 21% of the blocks were empty by the end of the experiment.

Method 2

Generally, the behaviour of the six species resembled that in experiment 1. The main differences were firstly, the many empty wood blocks that were interspersed between those inoculated with fungi enhanced the capture of new resource units; secondly, there were fewer resource units captured from other fungi; the difference was significant for *R. bicolor* and *H. capnoides* ($P = 0.01$, chi-squared test) but not for *P. sanguinea* and *Coniophora* sp; and thirdly there was a difference between the experiments in the fate of resource units inoculated with *H. annosum, A. borealis* and *P. sanguinea* as indicated by a chi-squared test ($P = 0.05$). In the first two species, a significantly higher proportion of the wood blocks became empty of colonizers, while *P. sanguinea* showed a significantly higher proportion of maintenance of its resources (Figs. 6a–g, 7a–g).

The survival of the original colonizers was enhanced as compared with experiment 1. *R. bicolor* maintained, on average, 92% of its original resource units. For *H. capnoides, P. sanguinea* and *Coniophora* sp. the corresponding frequencies were 61%, 64%, and 31%, respectively. *H. annosum* and *A. borealis* were absent from the blocks at the time of harvest. On average, 41% of the wood blocks hosted the same fungal species throughout the experiment (Table 2).

Capture of resource units inoculated by another fungus was decreased compared with experiment 1. *R. bi-*

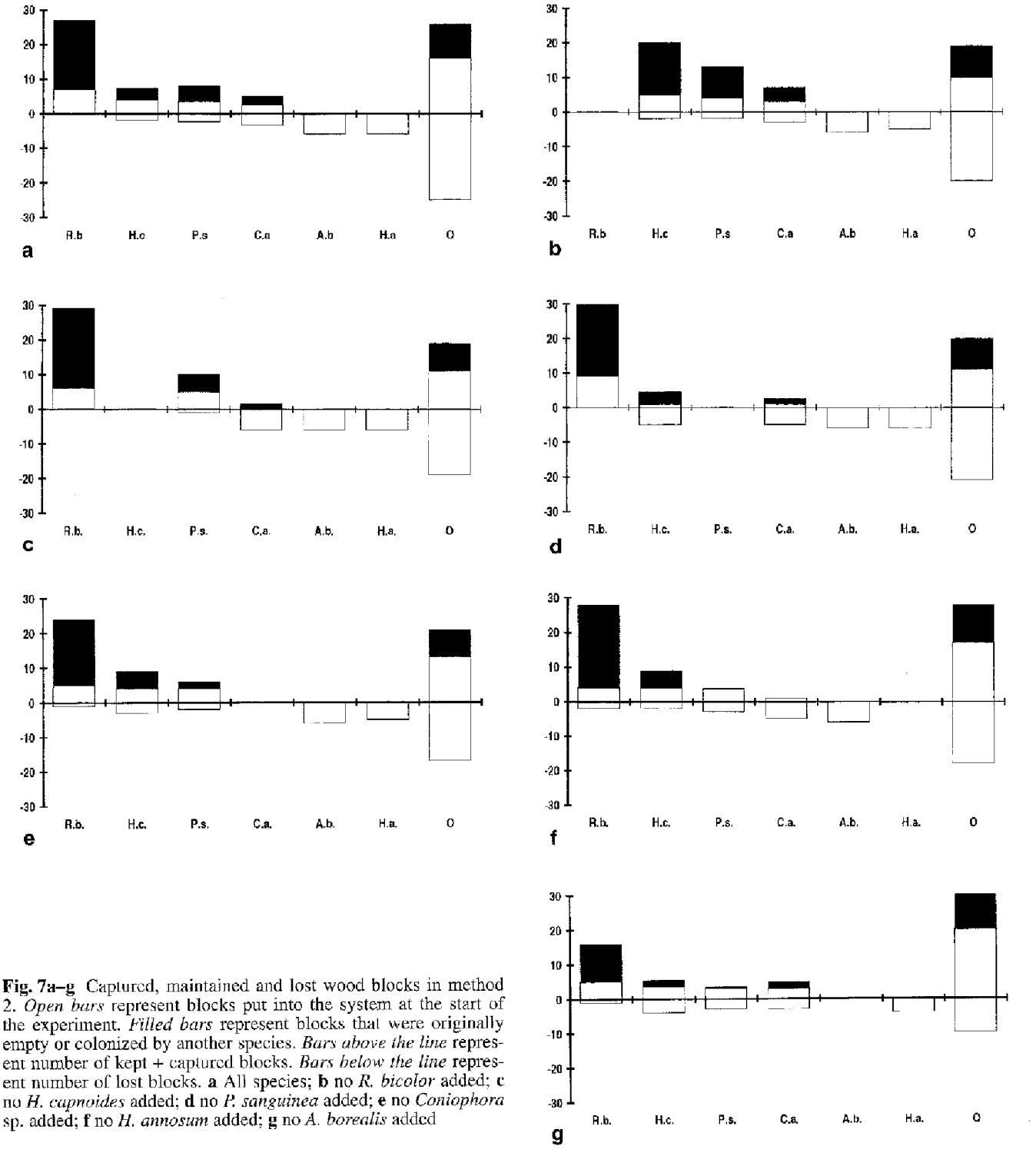

Fig. 7a–g Captured, maintained and lost wood blocks in method 2. *Open bars* represent blocks put into the system at the start of the experiment. *Filled bars* represent blocks that were originally empty or colonized by another species. *Bars above the line* represent number of kept + captured blocks. *Bars below the line* represent number of lost blocks. **a** All species; **b** no *R. bicolor* added; **c** no *H. capnoides* added; **d** no *P. sanguinea* added; **e** no *Coniophora* sp. added; **f** no *H. annosum* added; **g** no *A. borealis* added

color was again the strongest fungus in terms of capturing resource units from other species. By the end of experiment 2, *R. bicolor* har become established in 47 such resource units. *H. capnoides, P. sanguinea* and *Coniophora* sp. also captured wood blocks but to a lesser extent; 8 units, 5 units, and 1 unit, respectively (Table 2).

The quotient between the number of resource units captured during the experiment and the total number of units occupied by a species at the end of the experiment was lower in experiment 2. *R. bicolor* had the highest score (78%) followed by *H. capnoides, Coniophora* sp. and *P. sanguinea* (61%, 53%, and 49%, respectively). However, if only wood blocks inoculated with fungi at the beginning of the experiment are included in the calculations, the corresponding figures were 32%, 14%, 4%, and 11%, respectively (Table 2).

Most blocks were lost to another species by *Coniophora* sp. in this experiment (50% of the original number of

Table 3 Results from method 3; number of units put into the system, units gained, units kept, units lost, units at the end of the experiment, percentage of units captured from other species at the end of the experiment and percentage of units held at the end of the experiment. (*s* sand, *c* clay; other abbreviations as in Table 1)

Species	Units put into system	Units gained		Units kept	Units lost			Units at the end of experiment	% of units at end of experiment captured from other species	% of units kept at end of experiment
		From other species	From other blocks		To R.b.	To other species	Empty			
R.b.; c	4	4	–	4	–	0	0	8	50	100
R.b.; s	5	5	–	5	–	0	0	10	50	100
H.c.; c	5	2	–	5	0	0	0	7	29	100
H.c.; s	5	4	–	5	0	0	0	9	44	100
P.s.; c	5	0	–	4	1	0	0	4	0	80
P.s.; s	5	0	–	3	1	1	0	3	0	60
C.a.; c	5	0	–	0	1	1	3	0	0	0
C.a.; s	5	0	–	0	1	1	3	0	0	0
A.b.; c	4	0	–	0	–	1	3	0	0	0
A.c.; s	5	0	–	0	1	1	3	0	0	0
H.a.; c	5	0	–	0	1	0	4	0	0	0
H.a.; s	5	0	–	0	1	1	3	0	0	0

blocks), followed by *H. annosum*, *A. borealis*, *H. capnoides*, *P. sanguinea* and *R. bicolor* (3% of the original number). In experiment 2, the ranking order was almost, but not fully, reversed compared with that for capturing capacity. On average, 29% of the wood blocks were lost to another species (Table 2).

Previously inoculated resource units empty at the end of experiment 2 originated most frequently from blocks inoculated with *A. borealis* and *H. annosum* (67% of the number of original blocks) followed by *Coniophora* sp., *P. sanguinea*, *H. capnoides* and *R. bicolor* (8% of the original number). On average, 31% of the blocks inoculated with fungi at the start were empty at the end of the experiment.

Of the originally empty wood blocks, 56% were colonized at the end of the experiment. Of these, 67.5 were colonized by *R. bicolor*, 26 by *H. capnoides*, 17 by *P. sanguinea* and 11.5 by *Coniophora* sp. (Table 2).

Method 3

R. bicolor was also the strongest species in this method, followed by *H. capnoides*. In clay, *R. bicolor* managed to capture all wood blocks and replace the previously inoculated species. The result was the same in sand. *R. bicolor* maintained 100% of its original resource units both in sand and clay. *H. capnoides* captured 40% of the wood blocks in clay and 80% in sand. It maintained 100% of its own domains in both types of soil. *P. sanguinea* did not manage to capture any wood blocks, but was able to defend 80% of its own domain in clay and 60% in sand. *A. borealis*, *H. annosum* and *Coniophora* sp. were not found in any resource unit at the end of the experiment (Table 3).

Discussion

Overall, the species studied could be ranked in combative order as follows: *R. bicolor* > *H. capnoides* > *P. sanguinea* > *Coniophora* sp. > *A. borealis* = *H. annosum*. *R. bicolor* was the most competitive species under the conditions used in the experiments. This agrees with earlier results from pairwise competition experiments with a similar set of species (Holmer and Stenlid 1994) and observations in the field (Kirby et al. 1990). In the experimental set-ups where *R. bicolor* was absent, *H. capnoides* in particular, but also *Coniophora* sp. and *P. sanguinea* were able to expand to a much larger extent. *R. bicolor* apparently is able to suppress other fungi, a quality that may partly explain its widespread appearance in nature.

Wood blocks of Norway spruce were used in all three experimental methods. It could be hypothesized that some of the fungi involved might have a closer affinity for other types of wood than from spruce and that the outcome of the interactions would have been different if wood blocks from other tree species had been used.

The differences among species may be related to their ecological strategies. Dowson et al. (1988) suggested that those with the least specialized resource relationships also possess the most aggressive combative strategies, while those with more specialized relationships are less combative or more defensive. Furthermore, Rypácek (1966) concluded that pathogenic fungi were less competitive than saprotrophs. The very low competitive ability of the two pathogenic species (*H. annosum* and *A. borealis*) in the present work supports both hypotheses.

One interesting point is whether the cost of foraging reduces the ability of a species to defend its original resources. The findings indicate that the increased capture of wood blocks in experiment 2 compared with experiment 1 did not adversely affect survival in the original blocks. On the contrary, survival was higher. That might partly be explained by the reduced competitive pressure due to the increased distance to neighbouring competitors. The significantly higher proportion of empty blocks among those originally colonized by *H. annosum* and *A. borealis* indicates that the colonizing ability was lower outside the originally empty blocks. If experiment 2 had

been extended for a longer time period this situation might have been changed. The survival rate of *P. sanguinea* in particular was positively affected by the addition of empty blocks and the possible alleviation of competitive pressure.

One of the objectives of adding all species to one part of the experiment and excluding the species one-by-one from the others was to study species interactions from a holistic angle rather than just building up the experimental communities piece-by-piece. However, with this particular set of fungi, the difference was marginal between the two approaches. By using variable mycelial sizes grown in wood disc sectors (Holmer and Stenlid 1994), similar relative competitive strengths between *R. bicolor, P. sanguinea, Coniophora* sp. and *H. annosum* were shown.

Limited differences were detected between the relative frequency of the various species in their ability to colonize the wood blocks irrespective of whether they were colonized by other species or were empty before the experiment. This indicates that specific competitive interactions probably were not a major interacting factor. Adding empty wood blocks to the experimental trays reduced the ability to attack wood blocks originally inhabited by another species.

The competitive pressure in our experiments with added empty wood blocks indicates that a constant input of uncolonized woody debris would reduce competition and thus lead to a richer community compared with a situation when empty resources are lacking. However, studies in plant communities (Goldberg and Barton 1992; Reader and Best 1989) seem to support the theory proposed by Grime (1977, 1979) that competition should be more intense and have larger effects on species composition on productive sites.

Competition interactions in plant communities may be divided into competitive effect (ability to suppress resource levels for other species) and competitive response (the ability to tolerate suppression or low resource levels; Goldberg 1990). These two components correspond to two ways in which individual plants can be good competitors; the latter, containing species with good competitive response, are often referred to as stress tolerators. The experimental set-up used in our experiments may be employed to interpret the competitive effects and responses for wood decomposers in a soil environment. Judging from our results, there is a clear correlation between the two modes of competition. However, it is possible that if the number of species was extended there might be other taxa with a more marked profile for one or other mode. For example, antibiotic production may be a good trait for killing and replacing other species but may be of limited value when defending resources against invaders resistant to the substance.

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