

Effect of vegetation type on decomposition rates of wood in Drenthe, The Netherlands

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SUMMARY

The effect of vegetation type on decomposition rates of wood was studied. Wood of *Juniperus communis* was laid down in 11 different habitats, and wood of *Quercus robur*, *Pinus sylvestris*, and *Juniperus communis* was laid down together in six different habitats. There were large differences in the decomposition constant and mycofloristic composition between different vegetation types. Species diversity of secondary opportunistic fungal species is positively correlated with decomposition of juniper-wood, whereas no significant correlation was found between diversity of basidiomycetes and decomposition of juniper-wood. All vegetation types possessed two or more characteristic species. Only very few species showed substrate specificity.

Key-words: decomposition, mycofloristic composition, *Juniperus communis*, *Pinus sylvestris*, *Quercus robur*.

INTRODUCTION

The rate of decomposition of litter and wood is determined by many variables, among which the most important are the chemical and physical quality of the substrate, the climate, and the species composition of the decomposer community.

In decomposition studies, often, only the overall decay is considered. Necessary for the understanding of decomposition processes is a synecological approach in which attention is directed towards species composition of fungal communities.

The study of macrofungi on decomposing wood has so far been largely descriptive, i.e. the accurate recording of sequential occupation by sporocarps on the same site. It is often difficult to interpret such series of sequential occupation as a succession, both for practical and conceptual reasons (cf. Frankland 1981; Cooke & Rayner 1984). Such studies record the presence only of sporocarps, not the presence of their mycelia. It might well be possible that these processes are not parallel.

A critical survey of publications dealing with fungal communities on wood clarifies that the category of macromycetes has been applied rather restrictively. Most species of resupinate corticioid fungi are conspicuously absent from such inventories, although their actual species number often exceeds that of polypores and agarics taken together.

The present study was undertaken to answer the following questions: (i) how is decomposition rate determined by vegetation type? (ii) How is decomposition rate determined by mycofloristic composition of different substrates in different habitats? (iii) Is mycofloristic composition primarily determined by the available fungi in the local habitat or by substrate characteristics?

The present study discriminates between the effects of habitat differences and substrate differences (cf. Meentemeyer & Berg 1986). The second and third questions are not only important from a mycofloristic point of view, but also provide insight into the structure of fungal communities and niches of fungal species.

DESCRIPTION OF EXPERIMENTAL SITES

The habitat types selected for this investigation are all located within a few kilometres from Wijster, Drenthe, Province in The Netherlands. Macroclimatically, the region is characterized by an Atlantic climate, but the province of Drenthe has comparatively high annual precipitation and cold winters (Barkman & Westhoff 1969).

Two separate experiments were carried out. In the first experiment branches of juniper (*Juniperus communis* L.) were deposited in 11 different habitats, namely D, S, N, Q, P, O, C, B, F, M and R. In the second experiment branches of oak (*Quercus robur* L.), Scots Pine (*Pinus sylvestris* L.), and juniper were deposited in six different habitats, namely S, N, Q, P, O and F.

The D habitat consisted of a bare layer of juniper needles within dense juniper scrub. The S habitat consisted of a bare layer of juniper needles situated at the south side of an isolated juniper shrub. The N habitat consisted of mossy vegetation at the north side of a juniper scrub.

The Q habitat was situated in an oakwood without understorey and with a dense layer of oak leaves. Both the P and O habitats were pinewoods, but the P habitat had a dense understorey of *Empetrum nigrum* L., whereas the O habitat had an undergrowth with *Oxalis acetosella* L. and *Rubus fruticosus* coll.

The B habitat is located at the south side of a birchwood (*Betula pubescens* Ehrh.) without undergrowth and the soil is covered with raw humus. The C habitat is a very dry vegetation with *Calluna vulgaris* L. and the M habitat is moister and *Molinia coerulea* (L.) Moench is the dominant species. The F habitat is located in a fen with *Sphagnum apiculatum* Lindb. and *Polytrichum commune* Hedw. on very moist soil. The R habitat is a rather ruderal vegetation with *Holcus lanatus* L., *Rubus fruticosus* coll., and scattered juvenile oaks and birches.

METHODS

Early in 1976 freshly cut branches of oak, pine and juniper were collected. Branches were approximately 40 cm long and 5–10 cm thick. The air dried weight of these branches was determined at the beginning of the experiment. Relative density of different branches of the same wood was also determined, and exhibited only small intraspecific variation indicating that all fragments of the same wood were in a comparable state of decay.

All pieces were sterilized by γ -radiation (1000 kW) at the ITAL, Wageningen, sealed and unpacked in the experimental plots. However, due to differences in fungal colonization of the living branches (cf. Swift *et al.* 1976), nutrient availability between branches of the same wood might be different.

The woody fragments were laid down for recolonization in different microhabitats and they were deposited in the moss or litter layer (see description of experimental sites). Once a year, usually in the second half of November, the fragments were brought to the laboratory, examined carefully with the aid of a hand-lens, and returned to the field afterwards in

Table 1. Weight loss (%), decomposition constant ($\text{year}^{-1} k$) and half-time (years, HT) for juniper-wood in various habitats

	Weight-loss (%)	k	HT
O Pinewood with <i>Oxalis</i>	38	0.060	12
F Fen	35	0.055	13
R Ruderal vegetation	32	0.047	15
M <i>Molinia</i> vegetation	31	0.047	15
Q Oakwood	30	0.044	16
N North side of juniper scrub	19	0.027	26
D Inside dense juniper scrub	19	0.026	27
P Pinewood with <i>Empetrum</i>	18	0.025	28
C <i>Calluna</i> heath	18	0.025	28
B Birchwood	10	0.013	53
S South side of juniper shrub	6	0.008	87

exactly the same position. Small parts of fungal sporocarps were removed for identification purposes. This sampling of fungi could influence the decay process as the wood is partly exposed again, but we consider this effect of sampling as negligible.

At the end of the experiments, in 1983, air-dried weight of the woody fragments was determined again.

Nomenclature of the fungi follows Arnolds *et al.* (1984).

RESULTS

In the first experiment weight loss of juniper-wood after 8 years varied between 6 and 38%. Decomposition was fastest in O and F, and slowest in B and S.

Under the assumption that a constant fraction of the wood decomposes each time-unit, the decomposition constant and the half-time (Swift *et al.* 1979) are indicated in Table 1.

Species composition of the different pieces of juniper-wood is indicated in Table 2. There is not much similarity in species composition between the different habitats, indicating a large effect of vegetation type and/or random colonization processes. Decomposition rate is correlated with total taxonomic diversity ($r=0.61$, $P<0.05$) and with diversity of ascomycete taxa ($r=0.75$, $P<0.01$). There is no significant correlation between decay rate and diversity of basidiomycete taxa, which are almost exclusively responsible for the degradation of lignin ($r=0.14$, not significant).

Table 3 shows the decomposition constants of wood of oak, pine and juniper in different habitats. Inspection of that table indicates a large variation both between different substrates and different vegetation types. Oak-wood was decomposed fastest and juniper-wood slowest. A comparison between habitats shows that decay is always slowest in S.

The mycofloristic observations indicate that only a few fungi are substrate specific (Table 4). Of 52 species listed, two (*Mollisia cinerea* and *Phlebia radiata*) prefer oak-wood, and two (*Ascocorticium anomalum* and possibly *Mycena galopoda*) seem to prefer juniper-wood. No preferent species for pine-wood were encountered. On the other hand, all microhabitats show at least two preferent species.

Species number on the different substrates did not differ significantly. No correlation between the decomposition rate and species diversity ($r=-0.03$, not significant) was found.

Table 2. Fungi on juniper-wood in 11 different habitats

Habitat	O	F	R	M	Q	N	D	P	C	B	S
Decomposition constant	0.060	0.055	0.047	0.047	0.044	0.027	0.026	0.025	0.025	0.013	0.008
Number of species	10	7	9	10	10	9	8	8	11	5	2
Number of basidiom. species	5	1	4	7	6	6	6	6	6	2	2
<i>Ascocorticium anomalum</i>	+	+	+	+	+	.	+	+	.	+	.
<i>Ascocoryne cylichnium</i>	+	+	+	+	+
<i>Basidiodendron cinereum</i>	.	.	+	+	.	.	+	+	.	.	.
<i>Botryobasidium subcornatum</i>	+	.	.	+	+	.	.
<i>Cistella pinicola</i>	+	+	+	.	+	+	+	.	+	+	.
<i>Dacrymyces stillatus</i>	+	+	+	.	+	.	.
<i>Hyaloscypha hyalina</i>	+	+	+	.	+	+	.	+	+	.	.
<i>Marasmius androsaceus</i>	.	.	.	+	.	+	.	.	+	.	.
<i>Mycena galopoda</i>	+	+	.	+	.	.	.
<i>Stypella papillata</i>	+	.	+	+	.	.

Additional species:

O: *Phaeohelotium* sp.; *Gymnopilus penetrans*; *Gloeocystidiellum furfuraceum*; *Trechispora mollusca*; F: *Claussenomyces atrovirens*; *Galerina* sp.; *Pezizella* sp.; R: *Gymnopilus penetrans*; *Orbilbia luteorubella*; *Tricholomopsis rutilans*; M: *Bisporella* sp.; *Mycena sanguinolenta*; *Sistotrema brinkmannii*; *Trechispora vaga*; *Tulasnella violea*; Q: *Lactarius* spec.; *Schizopora paradoxa*; *Tyromyces caesi*; N: *Galerina allospora*; *Hyphoderma praetermissum*; *Hyphoderma puberum*; *Phaeohelotium* sp.; D: *Coniophora arida*; *Basidiodendron caesiocinereum*; *Sistotrema commune* var. *efibulatum*; *Trechispora microspora*; P: *Galerina stylifera*; *Hypochnicium geogenium*; *Tomentellopsis echinospora*; *Xenasma filicinum*; C: *Ceratobasidium cornigerum*; *Hypocrea aureoviridis*; *Orbilbia berberidis*; *Sebacina calospora*; *Zignoella ovoidea*; S: *Athelia arachnoidea*; *Athelia salicum*.

Table 3. Decomposition constant (year⁻¹) of wood of *Quercus*, *Pinus* and *Juniperus* in different habitats

	<i>Quercus</i>	<i>Pinus</i>	<i>Juniperus</i>
S South side of juniper scrub	0.066	0.022	0.008
N North side of juniper scrub	0.273	0.134	0.027
Q Oakwood	0.489	0.054	0.044
P Pinewood with <i>Empetrum</i>	0.253	0.042	0.025
O Pinewood with <i>Oxalis</i>	0.151	0.113	0.060
F Fen	0.175	0.109	0.055

DISCUSSION

The correlation between the decomposition rate of juniper-wood and species diversity is distinctly depressed when only the Basidiomycetes (except for *Coniophora arida* all species are white-rotters) are considered. Assuming that the number of fungal species forming basidiocarps provides a suitable measure for actual Basidiomycete species diversity, we conclude that species composition exerts only a weak influence on decay rates. Käärik (1975) has suggested that the action of different fungi simultaneously and in succession retards the decomposition process.

Table 4. Fungi on Oak-wood (Q), Pine-wood (P), and Juniper-wood (J), in different microhabitats

Habitat	S			N			Q			P			O			F		
Wood type	Q	P	J	Q	P	J	Q	P	J	Q	P	J	Q	P	J	Q	P	J
Number of species	6	3	2	9	10	9	4	6	10	8	6	8	6	10	10	7	1	7
<i>Athelia arachnoidea</i>	+	+	+															
<i>Athelia salicum</i>	+	+	+															
<i>Hyphoderma praetermissum</i>					+	+												
<i>Hyphoderma puberum</i>					+	+												
<i>Marasmius androsaceus</i>					+	+												
<i>Orbilia luteorubella</i>					+	+												
<i>Mycena galopoda</i>						+	+	+	+	+								
<i>Stropharia aeruginosa</i>							+	+	+									
<i>Hypochnicium geogenium</i>										+	+	+						
<i>Basidiodendron cinereum</i>										+	+							
<i>Tomentellopsis echinospora</i>										+	+							
<i>Gloeocystidiellum furfuraceum</i>													+	+				
<i>Gymnopilus penetrans</i>													+	+				
<i>Claussenomyces atrovirens</i>																+		+
<i>Ascocoryne cylichnium</i>																+		+
<i>Ascocorticium anomalum</i>								+			+		+	+				+
<i>Mollisia cinerea</i>	+	+		+												+		
<i>Phlebia radiata</i>				+	+		+	+		+			+					
<i>Ascocoryne sarcoides</i>				+	+		+	+	+				+	+	+	+		
<i>Botryobasidium subcoronatum</i>				+									+	+				
<i>Cistella pinicola</i>				+	+			+					+	+				+
<i>Hyaloscypha hyalina</i>	+			+	+		+	+	+	+	+	+	+	+	+	+	+	+
<i>Stypella papillata</i>										+			+	+				
<i>Trechispora mollusca</i>							+						+	+				

Incidental species:

S(Q): *Peniophora incarnata*, *Sphaerobolus stellatus*; N(Q): *Arachnoscypha* sp., *Bisporella* sp., *Chaetosphaeria myriocarpa*; N(P): *Calocera cornea*, *Merulius tremellosus*, *Achroomyces peniophorae*; N(J): *Dacrymyces stillatus*, *Galerina allospora*, *Phaeohelotium* sp.; Q(J): *Dacrymyces stillatus*, *Lactarius* sp., *Schizopora paradoxa*, *Tyromyces caesius*; P(Q): *Calocera cornea*, *Hypocrea rufa*, *Hypomyces rosellus*, *Psathyrella hydrophila*; P(P): *Ascocorticium vermiferum*; P(J): *Galerina stylifera*, *Xenasma filicinum*; O(Q): *Mycocacia uda*, *Zignoella ovoidea*; O(P): *Orbilia berberidis*, *Sebacina calospora*; O(J): *Phaeohelotium* sp.; F(Q): *Hypochnicium eichleri*, *Zignoella ovoidea*; F(J): *Galerina* sp., *Pezizella* sp.

There is a very clear correlation between the decay rate of juniper-wood and ascomycete species diversity (mostly secondary opportunistic species). These species exploit rather simple carbohydrates that are released when the more refractory substances are degraded, and it is, therefore, not surprising that their species number increases with the larger decomposition rates (Meredith 1960; Montgomery 1982). The same pattern was noted for pine-wood, but because of the smaller sample size this correlation ($r=0.54$) was not significant. No relationship between the decay rate of oak-wood and ascomycete species diversity was found ($r=-0.20$, not significant).

Differences in decomposition rates of different substrates, noted in the second experiment, can be explained by a number of physical and chemical factors, e.g. anatomy of the wood (Hintikka 1973), presence of terpenes and phenols (Hintikka 1970), and lignin content and structural complexity of the lignins (Kirk & Fenn 1982).

Categorizing of species with a preference for a certain substrate type should be done with caution. *Phlebia radiata* is said to occur mostly on deciduous wood, but rarely on spruce in humid localities (Eriksson *et al.* 1981). *Mycena galopoda* seems to prefer leaf and needle litter, although it is not infrequently found on small woody components (Frankland 1984). Growth of the mycelium has been shown to be inhibited by tannins (Harrison 1971) and this inhibitory effect might explain its preference for certain types of wood.

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REFERENCES

- Arnolds, E.J.M., Creveld, M., Jansen, E. & Kuiper, Th.W. (1984): Standaardlijst van Nederlandse macrofungi. *Coolia* **26** (Suppl.): 1–362.
- Barkman, J.J. & Westhoff, V. (1969): Botanical evaluation of the Drenthian district. *Vegetatio* **19**: 330–388.
- Cooke, R.C. & Rayner, A.D.M. (1984): *Ecology of Saprotrophic Fungi*. XIV, 415 Longman, London.
- Eriksson, J., Hjortstam, K. & Ryvarden, L. (1981): *The Corticiaceae of North Europe* **6**, 1051–1276. Fungiflora, Oslo.
- Frankland, J.C. (1981): Mechanisms in fungal succession. In: Wicklow D.T. & Carrol G.C. (eds): *The Fungal Community*. 403–426, Marcel Dekker, New York.
- (1984): Autecology and the mycelium of a woodland litter decomposer. In: Jennings D.H. & Rayner A.D.M. (eds): *The Ecology and Physiology of the Fungal Mycelium*. 241–260, Cambridge University Press, Cambridge.
- Harrison, A.F. (1971): The inhibitory effect of oak leaf litter tannins on the growth of fungi in relation to litter decomposition. *Soil Biol. Biochem* **3**: 167–172.
- Hintikka, V. (1970): Selective effect of terpenes on wood-decomposing Hymenomycetes. *Karstenia* **11**: 28–32.
- (1973): Passive entry of spores into wood. *Karstenia* **13**: 5–8.
- Käärik, A.A. (1975): Decomposition of wood. In: Dickinson C.H. & Pugh, G.J.F. (eds): *Biology of Plant Litter Decomposition* **1**: 129–174. Academic Press, London.
- Kirk, T.K. & Fenn, P. (1982): Formation and action of the ligninolytic system in basidiomycetes. In: Frankland J.C., Hedger J.N. & Swift M.J. (eds): *Decomposer Basidiomycetes*. 67–90. Cambridge University Press, Cambridge.
- Meentemeyer, V. & Berg, B. (1986): Regional variation in rate of mass loss of *Pinus sylvestris* needle litter in Swedish pine forests as influenced by climate and litter quality. *Scand. J. For. Res.* **1**: 167–180.
- Meredith, D.S. (1960): Further observations on fungi inhabiting pine stumps. *Ann. Bot.* **24**: 63–78.
- Montgomery, R.A.P. (1982): The rôle of polysaccharidase enzymes in the decay of wood by Basidiomycetes. In: Frankland J.C., Hedger J.N. & Swift M.J. (eds): *Decomposer Basidiomycetes*. 51–65. Cambridge University Press, Cambridge.
- Swift, M.J., Heal, O.W. & Anderson, J.M. (1979): *Decomposition in Terrestrial Ecosystems*. 340 pp. Blackwell, Oxford.
- , Healy, I.N., Hibberd, J.K., Sykes, J.M., Bampoe, V. & Nesbitt, M.E. (1976): The decomposition of branch-wood in the canopy and floor of a mixed deciduous woodland. *Oecologia* **26**: 138–149.