



Increased CO₂ evolution caused by heat treatment in wood-decaying fungi

Fredrik Carlsson¹  · Mattias Edman¹ · Bengt Gunnar Jonsson¹

Received: 10 October 2016 / Revised: 7 February 2017 / Accepted: 8 February 2017
© The Author(s) 2017. This article is published with open access at Springerlink.com

Abstract Wood-decaying fungi are regarded as the main decomposers of woody debris in boreal forests. Given that fungal respiration makes a significant contribution to terrestrial carbon flows, it is important to understand how the wood-decaying fungal metabolism is regulated in relation to different environmental conditions and disturbances. In the present study, we investigated the effect of temperature stress on wood decomposition rate in 18 species of wood-decaying fungi, representing a broad range of species–habitat associations. Heat shock duration and temperature were calibrated to match the conditions of a forest fire. We found a general increase in fungal decay rate after heat shock; the response was more pronounced in species associated with fire-prone forests. The underlying mechanism is unclear, but possibly relates to an up-regulation at the cellular level in response to heat shock. Our results show that the decomposition rate of dead wood can be strongly affected by environmental triggers.

Keywords Decomposition · Saproxylic fungi · CO₂ · Heat treatment · Wood decay · Carbon cycling

Introduction

Saprotrophic fungi are regarded as the main decayers of woody debris in boreal forests; together with bacteria and insects, they decompose dead or dying trees. In this respect, saprotrophic fungi play an important role in the turnover of carbon and nutrients in boreal forests (Stokland et al. 2012). Even small woody debris, such as needles and twigs, contain fungal mycelia (Juutilainen et al. 2014), and it seems likely that at least some wood-decaying species are present in all dead wood at any time (Boddy et al. 2008). In boreal forests, up to 30% of the total biomass (Stokland 2001) may be present in the form of coarse or fine woody debris (CWD, FWD; Delaney et al. 1998; Houghton et al. 2001; Siitonen 2001). On a global scale, evidence indicates that up to 10% of total CO₂ emissions come from decaying wood (Pan et al. 2011). Due to the abundance and importance of wood-decaying fungi in dead wood, any factor or process affecting the fungal decay rate will influence total carbon release on a larger (ecosystem) scale (Venugopal et al. 2016).

Tolerance to stress and disturbance is clearly important for many boreal species, shaping ecosystems and affecting community dynamics (Esseen et al. 1997; Hunter 1999). In particular, forest fires have played a major role in shaping boreal forest dynamics (Harrison 1958; Niklasson and Granström 2000; Ryan 2002; Zackrisson 1977). Over time, many boreal forest species, including wood-decaying fungi, have had to deal with repeated fires. Hence, it is likely that tolerance to extreme temperatures in some wood-decaying fungal species may have evolved as an adaptation to forest fires. Consequently, some species of wood-decaying fungi are able to survive elevated temperatures relative to their growth optima (Maswaka and Magan 1999; Ramsfield et al. 2010; Schmidt 2006). Although it can be argued that this is a pattern widely spread across the whole organism group (Miric and Willeitner 1984; Schmidt and Huckfeldt 2005; Törnqvist et al. 1987; Viitanen and Ritshkoff 1991), it has

Section Editor: Dominik Begerow

Electronic supplementary material The online version of this article (doi:10.1007/s11557-017-1281-5) contains supplementary material, which is available to authorized users.

✉ Fredrik Carlsson
Fredrik.carlsson@miun.se

¹ Department of Natural Sciences, Mid Sweden University, Sundsvall, Sweden

been shown that species present in fire-prone forests can tolerate heat shock to a greater extent than species without such an association (Carlsson et al. 2012, 2014). However, it is still unknown whether the increased heat tolerance is an adaptation to forest fires or to dry exposed conditions, since several of the species found after a forest fire also occur in open, sun-exposed forests.

In this context, it is important to understand the regulation of decomposition by wood-decaying fungi. The metabolism of such fungi involves a range of enzymes and acids to degrade hemicelluloses, celluloses and, for some species, lignin (Baldrian et al. 2005; Baldrian 2008; Hatakka 2001). There is evidence that carbon supply and the availability of inorganic nitrogen play a role in the up-regulation of polysaccharide-degrading enzymes (Rineau et al. 2013). During decomposition, most CO₂ is released into the surrounding air, while some is used in the synthesis of tissue and released when the mycelia are subsequently consumed or degraded (Boddy and Watkinson 1995; Hiscox et al. 2015).

In this laboratory study, we examined the CO₂ evolution of 18 species of wood-decaying fungi before and after heat treatment. Here, we use the term CO₂ evolution only as a direct measure of released CO₂ gas in the containers used in the experiments. First, we evaluated the normal CO₂ evolution over a period of 2 months after inoculation. Second, we subjected fungi to temperature stress similar to the conditions inside a log during a forest fire. The primary goal with this approach was to evaluate what effect forest fires have on a wide range of wood-decaying fungal species with respect to CO₂ evolution. The results would indicate the extent to which changed environmental conditions can influence CO₂ turnover in forest ecosystems as regards the physiological response of an organism group.

Materials and methods

Species characterization

To increase general applicability, we included a broad spectrum of species representing different functional traits and habitat requirements (Table 1). We chose both white and brown rot fungi as well as species with different decay stage preferences (Renvall 1995). The chosen species also have different relationships to forest fires. Eight of the species can be considered to be associated with forest fires. These are mainly found in natural forests with a history of fire influence; most of these species are rare in managed forests (Berg et al. 2002; Gärdenfors 2010; Hallingbäck and Aronsson 1998; Larsson 1997; Niemelä 2005; Ryvarden and Melo 2014). Four of the species (*Dichomitus squalens*, *Gleophyllum carbonarium*, *Antrodia xantha* and *Antrodia sinuosa*) are clearly more frequent on pine logs associated with recent forest fires (Junninen and Komonen 2011; Olsson and Jonsson 2010). *Oligoporus sericeomollis* is found frequently on charred wood (Zhou and Dai 2012). *Gleophyllum protractum*, *Junghuhnia luteoalba*, and *Antrodia infirma* are not associated

with recent fires, but still seem to prefer pine forests with a history of fire influence (personal observation). We also included two species, *Phlebiopsis gigantea* and *Gleophyllum sepiarium*, which are predominantly found in warm, dry and open habitats which resemble the microclimatic situation in forests subjected to fire (Hallingbäck and Aronsson 1998; Niemelä 2005). Finally, as a contrast to the above species, we included eight species without any specific relationship to forest fires, or warm dry habitats; the group includes species with a variety of habitat requirements (Table 1). Eleven of the species (*G. protractum*, *P. gigantea*, *D. squalens*, *A. sinuosa*, *J. luteoalba*, *A. infirma*, *O. sericeomollis*, *G. sepiarium*, *S. amorphia*, *Ischnoderma benzoinum* and *Fomitopsis pinicola*) were previously tested for maximum heat tolerance and all are known to survive the treatment used in this study (Carlsson et al. 2012).

Collection and inoculation

Three strains of all species were collected in Sweden in the autumns of 2007, 2008 and 2010, with the exception of two of the *D. squalens* strains which were collected in eastern Finland in 2010. For the rare *G. carbonarium*, we were only able to obtain one strain. However, we still decided to include it because of its strong relationship with charred dead wood (Hallingbäck and Aronsson 1998). All species are part of the Mid Sweden University Fungi Collection. The selected strains were subcultured in 9-cm vented Petri dishes with 2% malt agar (MEA) prior to experimental use. At the start of inoculation, 0.5 cm³ agar with mycelium was taken from the dishes and inoculated onto sterilized pine wood cylinders (2 cm diameter × 2 cm height); all wood cylinders came from the same tree. The wood cylinders were soaked in sterilized water for 2 h, and autoclaved for 20 min prior to inoculation.

The wood cylinders were placed in 3.5 × 6 cm autoclaved glass containers with resealable lids. To maintain humidity during the experiment, these containers were supplemented with a 0.5-cm layer of water agar. In total, we used 162 wood cylinders for the experiment, i.e. three strains of each species replicated three times. All containers were kept in a laminar flow cabinet at 20 °C temperature during the whole experiment and remained free from contamination throughout, while the caps on the containers were closed with loose lids to allow for some gas flow. Throughout the time of the experiment, the containers were controlled so that the water agar did not desiccate, allowing continuous hydration of the wood cylinders.

Measurements

To measure CO₂ evolution, we used an EGM-4 Environmental CO₂ gas monitor (PP systems®). We started measuring the day after inoculation, then measurements were made once a week. At the start of a measurement, the container was cleared of accumulated CO₂ by opening the lid and waiting for 30 s. All measurements were carried

Table 1 Species included in the study

Species	Fire association	Decay stage	Type of rot	Substrate
<i>Antrodia infirma</i>	A	3	Brown	Pine, (Spruce)
<i>A. sinuosa</i>	A	2.8	Brown	Pine, Spruce
<i>A. xantha</i>	A	2.6	Brown	Pine, Spruce
<i>Dichomitus squalens</i>	A	1	White	Pine, (Spruce)
<i>Fomitopsis pinicola</i>	NA	2.6	Brown	Pine, Spruce
<i>Gloeophyllum carbonarium</i>	A	3	Brown	Pine
<i>G. protractum</i>	A	2.6	Brown	Pine, (Spruce)
<i>G. sepiarium</i>	A	1	Brown	Pine, Spruce
<i>Gloeoporus taxicola</i>	NA	2.5	White	Pine, Spruce
<i>Heterobasidion parviporum</i>	NA	1	White	(Pine), Spruce
<i>Ischnoderma benzoinum</i>	NA	3	White	Pine, Spruce
<i>Junghunia luteoalba</i>	A	2.8	white	Pine, (Spruce)
<i>Leptoporus mollis</i>	NA	2.3	Brown	(Pine), Spruce
<i>Oligoporus sericiomollis</i>	A	3.5	Brown	Pine, Spruce
<i>Phellinus nigrolimitatus</i>	NA	3.8	White	(Pine), Spruce
<i>P. viticola</i>	NA	3	White	(Pine), Spruce
<i>Phlebiopsis gigantea</i>	A	1.2	White	Pine, (Spruce)
<i>Skeletocutis amorphia</i>	NA	2	White	Pine, Spruce

Succession data (average decay stage) are based on Renvall (1995); Fire association (A associated with forest fires, NA not associated with forest fire), type of rot and substrate preference are based on information from Swedish Species Information Center (2015), Hallingbäck and Aronsson (1998); Larsson (1997); Niemelä (2005); Ryvarden and Melo (2014) and confirmed by personal observations. Parentheses indicate that the species can also be found on this substrate, although it is mainly found on the other one

out in the laminar flow cabinet, allowing for continuous removal of accumulated CO₂. A syringe mounted on a lid with a connection to the detector was then used to close the container. The CO₂ accumulation was then measured for 1 min, using automatic suction, and the initial and final values were taken, giving the CO₂ accumulation for each species during 1 min, i.e. the ppm CO₂ per minute, at that specific time.

After 7 weeks of measurements, 108 samples were heat-treated. All samples were enclosed in sterilized packages of tin foil. These packages were then placed in a Memmert© 500 oven. The temperature was set to 100 °C and samples were treated for 25 min. This treatment roughly corresponds to the temperature regime inside a burning log during a forest fire (Carlsson et al. 2014). The glass containers were cleaned and autoclaved and new water agar was added before the wood cylinders were replaced (ensuring that each wood cylinder was returned to its original container). The lids were sterilized with 70% EtOH. Measurements were resumed on the same day as the heat treatment, and continued for 7 weeks (one measurement per week). A total of 54 samples were used as control and allowed to grow continuously without heat treatment on the same water agar footing.

Moisture content

In order to estimate the water loss due to heat treatment, ten wood discs were weighed and then soaked in sterilized water for 2 h. The wood discs were treated with heat as described in

the previous section. The weight of the wood discs were recorded before and after soaking in water (dry and wet weight) as well as after heat treatment.

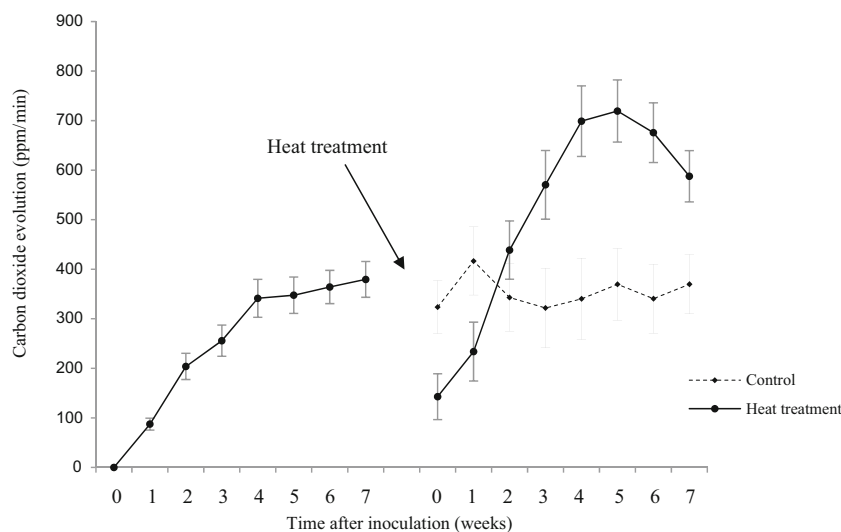
Results

The initial CO₂ evolution varied greatly between species; however, it increased over time in all species until a “plateau” had been reached, at approximately 7 weeks (Fig. 1). All species exhibited significantly increased CO₂ evolution after heat treatment (Fig. 2). CO₂ evolution peaked around 4–6 weeks after heat treatment and then started to decline (Fig. 1). Moisture content in the wood discs decreased from 43% (SE ± 1.3%) to 26% (SE ± 1.5%) during heat treatment.

There was a difference in maximum CO₂ evolution after heat treatment when comparing the fire-associated species and the non-fire-associated species, with a tendency for the former species to be ranked higher when sorted based on the difference between pre- and post-heat treatment CO₂ evolution; a Mann–Withney test was carried out and showed a significant rank order difference between the two groups (Fig. 1b). Another difference was the drop in CO₂ evolution after heat treatment, which was generally larger among the non-fire-associated species.

Decay stage preference seemed related to CO₂ evolution before heat treatment, with a tendency that species associated with early decay stages had a higher CO₂ evolution (Fig. 2),

Fig. 1 Average CO₂ evolution (±SE) of wood-decaying fungi during the decomposition experiment. Total replicates are $n = 162$ until week 8, then $n = 108$ for heat treatment and $n = 54$ (control). Error bars SE values calculated from mean values across all species where the replicates of each individual have been pooled ($n = 18$)



although *I. benzoinum* was an exception. This pattern disappeared after heat treatment. The fungal rot type did not affect the CO₂ evolution as tested in this study.

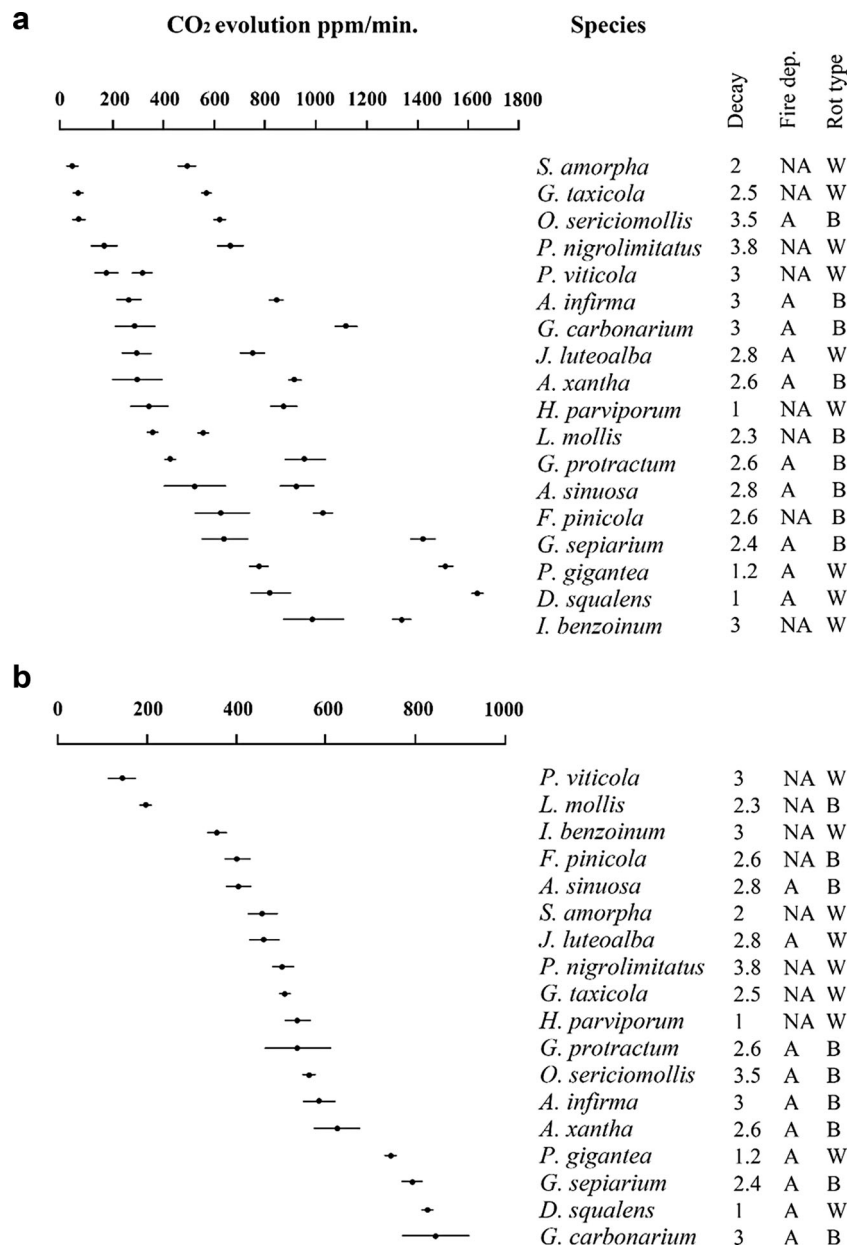
Discussion

CO₂ evolution in the 18 studied species of wood-decaying fungi seems to follow a general pattern after colonization/inoculation: CO₂ evolution increases with time until a plateau is reached. This is probably linked to colonization of the substrate, i.e. as the fungi colonize the substrate and expand, more wood begins to be decomposed. This continues until the whole substrate is colonized, at which point the increase in CO₂ evolution levels out and a plateau is reached for that specific substrate–species combination. Different species reach this plateau at different times, indicating that the colonization of the substrate takes different lengths of time for different species. This kind of species-specific colonization has been described previously (Boddy et al. 2008) and relates to the strategy and mycelial expansion rate of individual species. For some species, the plateau is not as distinct; however, the linearity of CO₂ evolution increase before heat treatment is also present in these species. All species significantly increased their CO₂ evolution after heat treatment, in comparison to the control, indicating that heat treatment induces some form of increase in fungal metabolism. The result is less pronounced in some species, but the mean for all species shows a strong response. The increase was found to be greater in fire-associated fungi, which at the same time had a lower drop in CO₂ evolution directly after heat treatment (Fig. 2), suggesting that their physiology may be adapted to heat disturbance. Furthermore, wood became considerably dryer after heat treatment, and it is likely that the fire-adapted species can withstand desiccation better than non-fire-associated species. Several of the fire-associated species are also found in dry, sun-exposed wood (e.g. Ryvarden and Melo 2014) which could explain their increased viability after heat

treatment. Earlier data (Schmidt 2006) indicate that the desiccation of wood after heat treatment brings the wood down to a critically low moisture content for some of the species. It is likely that rehydration of the substrate through direct contact with water agar is imperative for some of the fungi to resume growth. It also needs to be pointed out that the measurements were performed using non-hermetically closed containers and some surrounding air from the laminar flow cabinet may have entered the containers and caused a slight underestimation of CO₂ accumulation.

The physiological reason for the increase in CO₂ evolution after heat treatment cannot be deduced from the experiments, but may relate to several factors. One possibility is the potential availability of new resources after heat treatment. This is supported by the fact that CO₂ evolution started to decline following a peak 4–6 weeks after heat treatment, indicating that a pulse of resources became available after heat treatment. The decline in CO₂ evolution would then indicate that those resources had been depleted. A possible resource that becomes available after heat treatment is dead mycelia. Dead or degrading mycelia contain nitrogen, in which the fungi are deficient under normal conditions (Boddy et al. 2008; Moore et al. 2011). Such a readily available nitrogen source could generate an increase in fungal metabolism since regulation of fungi nitrogen metabolism allows for utilization of many different sources (Marzulf 1997). Although this could contribute somewhat to the observed patterns, we consider it unlikely that degrading mycelia have a major influence on CO₂ levels beyond the first week after heat treatment. The thermal modification of wood in the experiment may also have affected CO₂ evolution. Although strong heat treatment of the wood reduces fungal growth, moderate heat treatment may have the opposite effect. Antifungals such as monoterpenes evaporate when temperatures are moderately elevated, which makes the wood more accessible to fungi (Mattson et al. 1988; Englund and Nussbaum 2000). Another possible reason for the increased CO₂ evolution is an up-regulation at the cellular

Fig. 2 **a** Average maximum CO₂ evolution (±SE) before and after heat shock; species are listed from slowest to fastest decomposers before heat shock. There was a significant difference (paired *t* test; *p* < 0.05) in decomposition rate before and after heat treatment for all species. **b** Species sorted by the difference between maximum CO₂ evolution before and after heat shock. Decay stage (decay given in *numbers*), Fire dependency (*fire dep.* where *A* fire-associated, *NA* non-fire-associated) and rot type (*B* causing *brown* rot, *W* causing *white* rot) are listed after the species name



level, as a response to heat shock, due to increased laccase production (Ritossa 1996; Smith et al. 1998).

Changes in carbon flux following forest fire (Kashian et al. 2006) are important, since fire frequency on a global scale is predicted to increase (IPCC 2014). The response to heat treatment found in the present study may have effects on the carbon cycling and thus on CO₂ emissions of an ecosystem following a forest fire, as fungal species already present in dead wood will be subjected to a heat treatment similar to that in the present study. Our results suggest that most species will, at least initially, cause increased CO₂ evolution. How long the effect persists is not clear and merits further study. The burst in CO₂ evolution found in most of the species studied could have an additive effect on the carbon release after a forest fire, adding to the CO₂ released by the fire itself. A forest fire produces variable amounts of charred wood (Eriksson

et al. 2013). It is known that charred wood decomposes very slowly (Hatakka 2001). Over longer periods of time, burnt stumps of pine wood decompose at a slower rate than unburnt stumps (Shorohova et al. 2008), indicating that the burst in CO₂ evolution directly after a fire may later be cancelled out by other factors. Hence, the combined effects of forest fire on wood decomposition are complex. In addition, competitive outcomes between wood-decaying fungi may differ in burnt and unburnt wood, suggesting that wood chemical modifications from heating influence species differently (Edman and Eriksson 2016). The success of an individual and the development of the community structure is largely dependent on the wood properties, assemblage history and facilitative interactions (Edman and Fällström 2013; Tiunov and Scheu 2005; Fukami et al. 2010; Dickie et al. 2012). However, in fire-prone forests, an increase in decomposition rate (indicated

by increased CO₂ evolution) after fire disturbance may also help some species to expand and ultimately change the structure of the community. Possibly, the effect of such a change could influence carbon release, since wood decomposition rates can be strongly influenced by fungal species composition (Setälä and McLean 2004; Fukami et al. 2010; Van der Wal et al. 2015).

Conclusions

Our laboratory experiment allows enhanced functional understanding of fungal decay in relation to environmental factors such as changes in temperature and discrete disturbance events. The results also highlight the complexity of the fungal community in boreal forests with implications for both changes in species composition and CO₂ evolution.

Acknowledgements We would like to thank Miriam Matheis, Torborg Jonsson and Håkan Noberg for help in the laboratory and Per-Erik Mukka for collecting some of the fungal strains. We would also like to thank Jacob Heilmann Clausen and Björn Lindahl for valuable comments on an earlier draft of the manuscript. This research was supported by The Swedish Research Council Formas (project no. 2007–464)

Open Access This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

References

- Baldrian P (2008) Enzymes of saprotrophic basidiomycetes. In: Boddy L, Frankland J, Van Weist P (eds) Ecology of saprotrophic basidiomycetes. Academic, Amsterdam, pp 19–41
- Baldrian P, Valášková V, Merhautová V, Gabriel J (2005) Degradation of lignocellulose by *Pleurotus ostreatus* in the presence of copper, manganese, lead and zinc. Res Microbiol 156(5):670–676
- Berg Å, Gärdenfors U, Hallingbäck T, Norén M (2002) Habitat preferences of red-listed fungi and bryophytes in woodland key habitats in southern Sweden - analyses of data from a national survey. Biodivers Conserv 11:1479–1503
- Boddy L, Watkinson SC (1995) Wood decomposition, higher fungi and their role in nutrient cycling. Can J Bot 73:1377–1383
- Boddy L, Frankland JC, Van West P (eds) (2008) Ecology of saprotrophic basidiomycetes. Academic, Amsterdam
- Carlsson F, Edman M, Holm S, Eriksson AM, Jonsson BG (2012) Increased heat resistance in mycelia from wood decaying fungi prevalent in forests characterized by fire: a possible adaptation to forest fire. Fungal Biol 116:1025–1031
- Carlsson F, Edman M, Holm S, Jonsson BG (2014) Effect of heat on interspecific competition in saprotrophic wood decaying fungi. Fungal Ecol 11:100–106
- Delaney M, Brown S, Lugo AE, Torres-Lezama A, Quintero NB (1998) The quantity and turnover of dead wood in permanent forest plots in six life zones of Venezuela. Biotropica 30:2–11
- Dickie I, Fukami T, Wilkie JP, Allen RB, Buchanan PK (2012) Do assembly history effects attenuate from species to ecosystem properties? A field test with wood-inhabiting fungi. Ecol Lett 15:133–141
- Edman M, Eriksson AM (2016) Competitive outcomes between wood decaying fungi are altered in burnt wood. FEMS Microbiol Ecol 92: 1–7
- Edman M, Fällström I (2013) An introduced tree species alters the assemblage structure and functional composition of wood decaying fungi in microcosms. For Ecol Manag 306:9–14
- Englund F, Nussbaum R (2000) Monoterpenes in Scots Pine and Norway Spruce and their emission during Kiln drying. Holzforschung 54: 449–456
- Eriksson AM, Olsson J, Jonsson BG, Toivonen S, Edman M (2013) Effects of restoration fire on dead wood heterogeneity and availability in three *Pinus sylvestris* forests in Sweden. Silva Fenn 47:954
- Esseen PA, Ehnström B, Ericson L, Sjöberg K (1997) Boreal forests. Ecol Bull 46:16–47
- Fukami T, Dickie IA, Paula Wilkie J, Paulus BC, Park D, Roberts A, Buchanan PK, Allen RB (2010) Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. Ecol Lett 13:675–684
- Gärdenfors U (ed) (2010) Rödlistade arter i Sverige ArtDatabanken, Uppsala
- Hallingbäck T, Aronsson G (eds) (1998) Ekologisk katalog över storsvampar och Myxomyceter. [Macrofungi and Myxomycetes of Sweden and their ecology.] ArtDatabanken, SLU, Uppsala. 2nd revised and extended printing
- Harrison TM (1958) Forest fire in the Mesozoic. J Ecol 46(2):447–453
- Hatakka A (2001) Biopolymers. Biology, chemistry, biotechnology, applications. In: Hofrichter M, Steinbüchel A (eds) Lignin, humic substances and coal, vol 1. Wiley-VCH, Weinheim, pp 129–180
- Hiscox J, Savoury M, Vaughan IP, Muller CT, Boddy L (2015) Antagonistic fungal interactions influence carbon dioxide evolution from decomposing wood. Fungal Ecol 14:24–32
- Houghton RA, Lawrence KT, Hackler JT, Brown S (2001) The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. Glob Change Biol 7:731–746
- Hunter M (1999) Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge
- IPCC Climate Change (2014) Synthesis Report. In: Team Core Writing, Pachauri RK, Meyer LA (eds) Synthesis report. Contribution of Working Groups 1, 2 and 3 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC Geneva, Switzerland, p 155
- Junninen K, Komonen A (2011) Conservation ecology of boreal polypores: a review. Biol Conserv 144:11–20
- Juutilainen K, Mönkkönen M, Kotiranta H, Halme P (2014) The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions. For Ecol Manag 313:283–291
- Kashian D, Romme W, Tinker D, Turner M, Ryan M (2006) Carbon storage on landscapes with stand replacing fires. Bioscience 56: 598–606
- Larsson KH (ed) (1997) Rödlistade svampar i Sverige – Artfakta. ArtDatabanken, SLU, Uppsala
- Marzulf GA (1997) Genetic regulation of nitrogen metabolism in the fungi. Microbiol Mol Biol Rev 61:17–32
- Maswaka AY, Magan N (1999) Temperature and water potential relations of tropical *Trametes* and other wood-decay fungi from the indigenous forests of Zimbabwe. Mycol Res 103:1309–1317
- Mattson W, Levieux J, Bernard-Dagan C (1988) Mechanism of woody plant defence against insects. Springer, New York
- Miric M, Willeitner H (1984) Lethal temperature for some wood-destroying fungi with respect to eradication by heat treatment. International Research Group on Wood Preservation, Doc. Nr. IRG/WP/1229, 8

- Moore D, Robson GD, Trinci APJ (2011) 21st Century Guidebook to Fungi. Cambridge University Press, New York
- Niemelä T (2005) Käväät, puiden sienet, Norrlinna. 13, Helsinki Museum of Natural History. Helsinki University Press, Helsinki
- Niklasson M, Granström A (2000) Numbers and size of fires: long term trends in a Swedish boreal landscape. *Ecology* 81:1496–1499
- Olsson J, Jonsson BG (2010) Restoration fire and wood-inhabiting fungi in a Swedish *Pinus sylvestris* forest. *For Ecol Manag* 259:1971–1980
- Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao S, Rautiainen A, Sitch S, Hayes D (2011) A large persistent carbon sink in the world's forests. *Science* 333:988–993
- Ramsfield TD, Ball RD, Gardner JF, Dick MA (2010) Temperature and time combinations required to cause mortality of a range of fungi colonizing wood. *Can J Plant Pathol* 32:368–375
- Renvall P (1995) Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia* 35:1–51
- Rineau F, Shah F, Smiths MM, Persson P, Johansson T, Carleer R, Troein C, Tunlid A (2013) Carbon availability triggers the decomposition of plant litter and assimilation of nitrogen by an ectomycorrhizal fungus. *ISME J* 10:2010–2022
- Ritossa F (1996) Discovery of the heat shock response. *Cell Stress Chaperones* 1:97–98
- Ryan KC (2002) Dynamic interactions between forest structure and fire behavior in boreal ecosystems. *Silva Fenn* 36:13–39
- Ryvarden L, Melo I (2014) Poroid fungi of Europe. Institute of Biological Sciences, Oslo
- Schmidt O (2006) Wood and tree fungi biology, protection, damage and use. Springer, Berlin
- Schmidt O, Huckfeldt T (2005) Gebäudeplize. In: Müller J (ed) *Holzschutz im Hochbau*. Fraunhofer IRG, Stuttgart, pp 44–72
- Setälä H, McLean MA (2004) Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. *Oecologia* 139:98–107
- Shorohova E, Kapitsa E, Vanha-Majamaa I (2008) Decomposition of stumps in a chronosequence after clear-felling vs. clear-felling with prescribed burning in a southern boreal forest in Finland. *For Ecol Manag* 255:3606–3612
- Siitonen J (2001) Forest management coarse woody debris and saproxylic organisms. Fennoscandian forests as an example. *Ecol Bull* 49: 11–41
- Smith M, Shnyreva A, Wood DA, Thurston CF (1998) Tandem organization and highly disparate expression of the two laccase genes *lcc1* and *lcc2* in the cultivated mushroom *Agaricus bisporus*. *Microbiology* 144:1063–1069
- Stokland JN (2001) The coarse wood debris profile: an archive of recent forest history and an important biodiversity indicator. *Ecol Bull* 71–83
- Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in dead wood. Cambridge University Press, New York
- Swedish Species Information Center (1/10/2015) <http://www.slu.se/en/collaborative-centres-and-projects/artdatabanken/>
- Tiunov AV, Scheu S (2005) Facilitative interactions rather than resource partitioning drive diversity-functioning relationships in laboratory fungal communities. *Ecol Lett* 8:618–625
- Törnqvist T, Kärenlampi P, Lundström H, Milberg P, Tamminen Z (1987) Vedegenskaper och mikrobiella angrepp i och på byggnadsvirke. Swed. Univ. Agricultural Science, Uppsala, p 10
- Van der Wal A, Ottosson E, de Boer W (2015) Neglected role of fungal community composition in explaining variation in wood decay rates. *Ecology* 96:124–133
- Venugopal P, Junninen K, Linnakoski R, Edman M, Kouki J (2016) Climate and wood quality have decayer-specific effects on fungal wood decomposition. *For Ecol Manag* 360:341–351
- Viitanen H, Ritshkoff AC (1991) Mold growth in pine and sapwood in relation to air humidity and temperature. Swedish University Agricultural Department of Forest Production 221
- Zackrisson O (1977) Influence of forest fire on the North Swedish boreal forest. *Oikos* 29:22
- Zhou LW, Dai YC (2012) Phylogeny and taxonomy of Phylloporia (Hymenochaetales) with the description of five new species and a key to worldwide species. *Mycologia* 104:211–222