Mycol Progress (2017) 16:513–519
DOI 10.1007/s11557-017-1281-5

ORIGINAL ARTICLE

Increased CO_2 evolution caused by heat treatment in wood-decaying fungi

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Received: 10 October 2016 / Revised: 7 February 2017 / Accepted: 8 February 2017 / Published online: 27 February 2017

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 · CO_2 · Heat treatment · Wood decay · Carbon cycling

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.

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Introduction

Saptrotrophic 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 CO_2 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

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 CO_2 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 CO_2 evolution of 18 species of wood-decaying fungi before and after heat treatment. Here, we use the term CO_2 evolution only as a direct measure of released CO_2 gas in the containers used in the experiments. First, we evaluated the normal CO_2 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 CO_2 evolution. The results would indicate the extent to which changed environmental conditions can influence CO_2 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). *Gloeophyllum 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 *Gloeophyllum 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. amorpha*, *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 cm^3 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 CO_2 evolution, we used an EGM-4 Environmental CO_2 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 CO_2 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
Antrodia infirma	A	3	Brown	Pine, (Spruce)
A. sinuosa	A	2.8	Brown	Pine, Spruce
A. xantha	A	2.6	Brown	Pine, Spruce
Dichomitus squalens	A	1	White	Pine, (Spruce)
Fomitopsis pinicola	NA	2.6	Brown	Pine, Spruce
Gloeophyllum carbonarium	A	3	Brown	Pine
G. protractum	A	2.6	Brown	Pine, (Spruce)
G. sepiarium	A	1	Brown	Pine, Spruce
Gloeoporus taxicola	NA	2.5	White	Pine, Spruce
Heterobasidion parviporum	NA	1	White	Pine), Spruce
Ischnoderma benzoinum	NA	3	White	Pine, Spruce
Junghunia luteoalba	A	2.8	white	Pine, (Spruce)
Leptoporus mollis	NA	2.3	Brown	Pine), Spruce
Oligoporus sericiomollis	A	3.5	Brown	Pine, Spruce
Phellinus nigrolimitatus	NA	3.8	White	Pine), Spruce
P. viticola	NA	3	White	Pine), Spruce
Phlebiopsis gigantea	A	1.2	White	Pine, (Spruce)
Skeletocutis amorpha	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 CO_2. A syringe mounted on a lid with a connection to the detector was then used to close the container. The CO_2 accumulation was then measured for 1 min, using automatic suction, and the initial and final values were taken, giving the CO_2 accumulation for each species during 1 min, i.e. the ppm CO_2 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 CO_2 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 CO_2 evolution after heat treatment (Fig. 2). CO_2 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 CO_2 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 CO_2 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 CO_2 evolution after heat treatment, which was generally larger among the non-fire-associated species.

Decay stage preference seemed related to CO_2 evolution before heat treatment, with a tendency that species associated with early decay stages had a higher CO_2 evolution (Fig. 2),

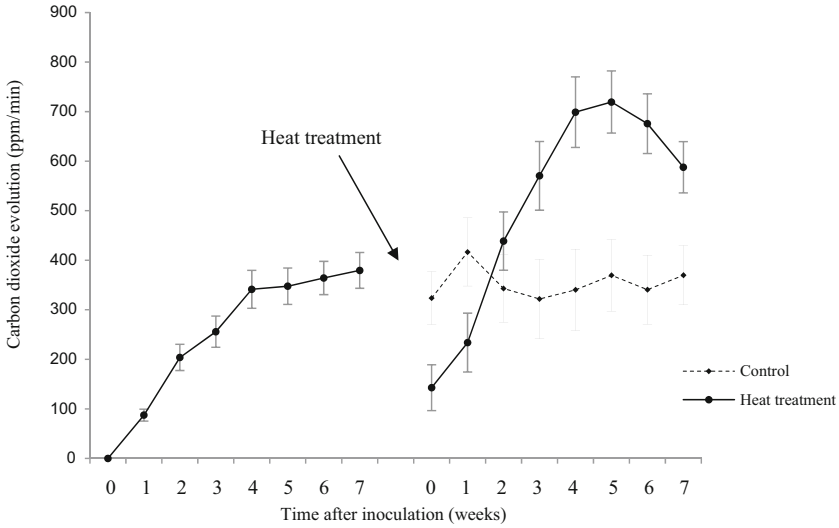

Fig. 1 Average CO_2 evolution (±SE) of wood-decaying fungi during the decomposition experiment. Total replicates are $n = 162$ until week 8, then $n = 108$ for heat treatment and $n = 54$ (control). *Error bars* SE values calculated from mean values across all species where the replicates of each individual 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 CO_2 evolution as tested in this study.

Discussion

CO_2 evolution in the 18 studied species of wood-decaying fungi seems to follow a general pattern after colonization/inoculation: CO_2 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 CO_2 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 CO_2 evolution increase before heat treatment is also present in these species. All species significantly increased their CO_2 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 CO_2 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 CO_2 accumulation.

The physiological reason for the increase in CO_2 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 CO_2 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 CO_2 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 CO_2 levels beyond the first week after heat treatment. The thermal modification of wood in the experiment may also have affected CO_2 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 CO_2 evolution is an up-regulation at the cellular

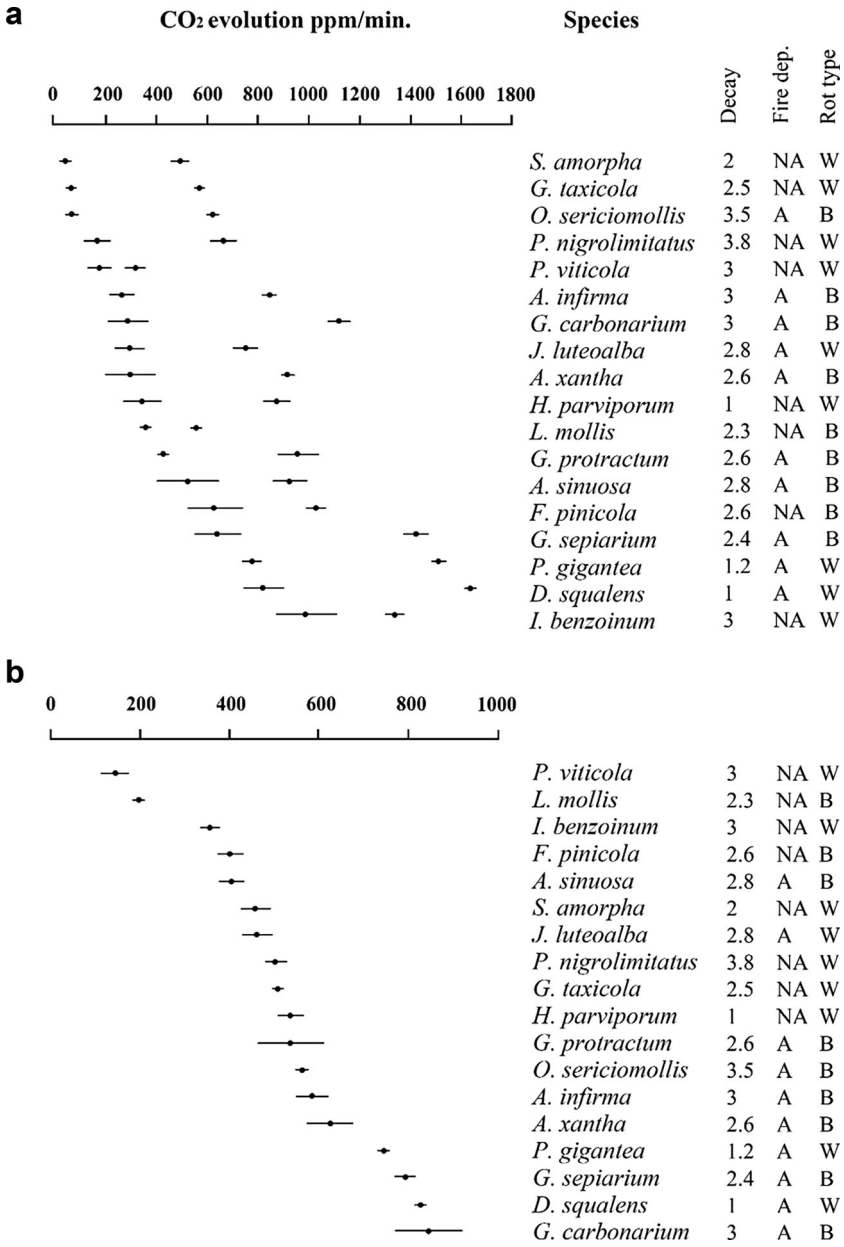

Fig. 2 **a** Average maximum CO_2 evolution (±SE) before and after heat shock; species are listed from slowest to fastest decomposers before heat shock. There was a significant difference (paired *t* test; $p < 0.05$) in decomposition rate before and after heat treatment for all species. **b** Species sorted by the difference between maximum CO_2 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 CO_2 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 CO_2 evolution. How long the effect persists is not clear and merits further study. The burst in CO_2 evolution found in most of the species studied could have an additive effect on the carbon release after a forest fire, adding to the CO_2 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 unburned stumps (Shorohova et al. 2008), indicating that the burst in CO_2 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 CO_2 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 CO_2 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)

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