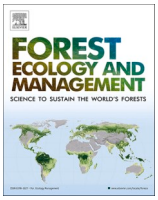
Forest Ecology and Management 571 (2024) 122240

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Disentangling how the opportunistic parasitic fungus *Armillaria* affects the flammability of coarse deadwood in exotic pine plantations

Shudong Zhang [a,*], Bas van Spronsen [a,b], Myrthe Fonck [c], Richard S.P. van Logtestijn [a], Nadia A. Soudzilovskaia [d,e], Krijn Trimbos [e], Johannes H.C. Cornelissen [a]

[a] *Amsterdam Institute for Life and Environment (A-LIFE), Systems Ecology Section, Vrije Universiteit Amsterdam, De Boelelaan 1108, Amsterdam 1081 HZ, the Netherlands*
[b] *Biodiversity and Natural Systems, Water & Maritime, Royal Haskoning DHV, Laan 1914 no 35, Amersfoort 3818 EX, the Netherlands*
[c] *PWN, Visitor Centre De Hoep, Johannisweg 2, Box. 1, Castricum 1901 NX, the Netherlands*
[d] *Center for Environmental Sciences, Hasselt University, Hasselt, Belgium*
[e] *Department of Environmental Biology, Institute of Environmental Sciences, Leiden University, Einsteinweg 2, Leiden 2333 CC, the Netherlands*

ARTICLE INFO

Keywords:
Black pine
Honey fungus
Plant flammability
Coarse deadwood
Wildfire
Plant–pathogen interactions

ABSTRACT

Parasitic wood fungi are important to forest carbon cycles globally. However, whether or how they affect the flammability of coarse deadwood is poorly understood. Given the predicted climate-driven increase in wildfires and associated carbon emissions into the atmosphere, potentially amplifying climate warming, filling this knowledge gap should have high priority. We thereto investigated coastal plantations of the exotic black pine, *Pinus nigra* J.F. Arnold, in the Netherlands, which are widely suffering from *Armillaria* infection. We hypothesized that branches from forest stands with a visible *Armillaria* infection will burn differently compared with branches from stands without a visible *Armillaria* infection, due to *Armillaria* infection having an additional effect on the branch traits. We tested this hypothesis by burning coarse *Pinus nigra* branches across a range of densities from infected and uninfected forest patches under standardized conditions in a fire lab and by measuring *Armillaria* biomass (via ddPCR), deadwood traits and key flammability parameters. *Armillaria* infection did enhance the flammability of *Pinus nigra* branches (e.g. more ignitable, longer flame duration and higher percentage mass loss). This higher flammability originated from both direct *Armillaria* influences, e.g. via changing wood structure (before and/or after wood death), and indirect influences, e.g. by facilitating nitrogen fixation in wood, thereby increasing wood decomposability and consequently reducing wood density. Our findings also have important implications for understanding the role of pathogens in fire regimes more broadly.

1. Introduction

Parasitic and saprotrophic wood fungi break down wood of both living and dead trees, thereby playing an important role in the nutrient and carbon cycles associated with trees (Harmon et al., 1986; Jakuš 1998; Schmidt, 2006; Bradford et al., 2014; Baldrian, 2016). Parasitic wood fungi obtain their carbon mostly from living trees. Their infestation could eventually cause mortality of the host tree, especially when it is subject to stress under extreme climatic conditions (Schmidt, 2006); this is beneficial for saprophytic decay fungi but could be detrimental for a forest ecosystem (Rosso and Hansen, 1998; Cherubini et al., 2002). When the host tree dies, its dead biomass (leaves, fine stems and coarse deadwood) accumulates at the soil surface, acting as the fuel for surface fire. Among these dead materials, the coarse deadwood has a long residence time due to its lower decomposition rate compared with fine litters (Weedon et al., 2009; Cornelissen et al., 2017). This accumulated surface deadwood unit plays an important role in facilitating wildfire spread (Zhao et al., 2018). It can also start a crown fire through fuel ladders or heating soil through smoldering combustion, thereby intensifying wildfire damage for instance to tree roots (Kauffman and Martin, 1989; Blauw et al., 2017).

Apart from fuel loads, fuel traits (representing its structure and chemical concentrations) also constitute important factor that strongly influences the wildfire regime (Cornelissen et al., 2017; Pausas and Keeley, 2021). These traits of deadwood could also be influenced by wood parasitic fungi. For example, parasitic fungi can stimulate wood

* Corresponding author.
E-mail address: zhangshudong1120@163.com (S. Zhang).

https://doi.org/10.1016/j.foreco.2024.122240
Received 20 January 2024; Received in revised form 21 August 2024; Accepted 22 August 2024
Available online 26 August 2024

break-down directly. Furthermore, by promoting bark beetle and subsequent detritivore attacks (Jakuš 1998; Zuo et al., 2016; Kandasamy et al., 2023), along with saprophytic fungi-induced wood decay, the internal wood density is also reduced. This in turn creates more internal ventilation which in its turn increases flammability (Hyde et al., 2011; Hyde, Smith and Ottmar, 2012; Zhao et al., 2018). Meanwhile, as white rot fungi, some parasitic fungi are known for targeting lignin in deadwood and reducing its concentration. This reduces the heat content (i.e. fire intensity) during a fire (Demirbaş 2001; Schmidt, 2006). While low-lignin wood may have a low volatilization temperature and a tendency to char, the reduced lignin concentration may increase mass loss during fire (Cornwell et al., 2009).

The widespread black pine, *Pinus nigra* J.F. Arnold; native to the Mediterranean region, is known to suffer from honey fungus (*Armillaria mellea* (Vahl.) P. Kumm. complex) infection, probably as a consequence of recurring soil drought stress. *Armillaria* is a widespread genus of white rot fungi known to be one of the most destructive root rot pathogens in forest ecosystems (Hood, Redfern and Kile, 1991; Schmidt, 2006). By disrupting the upward movement of water and nutrition through the xylem, *Armillaria* infections result in the mortality of cambium, wood cells and bark, which leads to growth reduction and possible death (Cherubini et al., 2002; Devkota and Hammerschmidt, 2020). *Armillaria* can kill or weaken trees as a primary pathogen (Rosso and Hansen, 1998; Kubiak et al., 2017) but also as a secondary pathogen where it attacks trees that are stressed, weakened or wounded by abiotic conditions, insect activity or diseases (Piercey-Normore and Bérubé 2000; Cherubini et al., 2002; Sierota, Grodzki and Szczepkowski, 2019). Moreover, *Armillaria* can also function as a saprotrophic fungus, generating mycelial fans on deceased trees. These observations suggest that an infection with *Armillaria* could affect forest surface fires by the following pathways: (1) intensifying surface fire by increasing standing and down dead wood quantity; (2) at single wood piece scale, altering flammability by influencing deadwood qualities (structure and chemical concentrations).

Although *Armillaria* is known as a root pathogen, their rhizomorphs and mycelial fans that develop under the bark may actually reach high up in the trunk. However, we do not know whether these rhizomorphs and mycelial fans could reach the living branches and then pass on their effects to the coarse deadwood by changing its density and chemical quality (especially lignin content); and thereby its flammability. If not, after the tree dies, we also do not know whether these opportunistic parasitic fungi will become saprotrophic fungi and subsequently influence coarse deadwood flammability. These specific influences of *Armillaria* may manifest by differences in the chemical quality and flammability between coarse wood with and without an *Armillaria* infection. Given the globally widespread occurrence of parasitic wood fungi and the predicted climate-driven increase in wildfires and associated carbon emissions into the atmosphere, potentially amplifying climate warming (IPCC, 2021), addressing this question is a high priority.

Like many other conifer species, *Pinus nigra* is susceptible to *Armillaria* (Mesanza, Patten and Iturritxa, 2017), especially when it has already been weakened by recurring local soil drought stress. The increasing infection rates of trees by *Armillaria* in the area in recent years, has raised a debate among the local forest managers regarding the potential necessity of replacing these exotic pines. This debate has arisen due to the potential for these pines to pose a greater risk of forest fires in the future, which has been a significant concern for forest management in the region. This situation has made these *Pinus nigra* stands an ideal host for *Armillaria* and a suitable model species for our experiments, while our case study has broader relevance for wildfire in forests affected by climate-induced pathogens. In this study, we aimed to single out the effects of *Armillaria* on the flammability of coarse wood of *Pinus nigra* in coastal plantations of the exotic black pine in the Netherlands. These plantations are particularly fire-prone during drought periods and several large stands have burnt in recent decades. We hypothesized that branches from forest stands with a visible *Armillaria* infection will burn differently during a surface fire compared with branches from stands without a visible *Armillaria* infection, due to *Armillaria* infection having an additional effect on the branch (fuel) traits. The additional effect is expected because, based on our observations and the literature (e.g. Cherubini et al., 2002) observations, not the density but also the internal wood anatomy and chemistry may be affected by pathogens such as *Armillaria*. We have tested this hypothesis by collecting coarse (5 cm diameter) *Pinus nigra* branches within a range of wood densities from the soil surface of infected and uninfected coastal forest patches in the Netherlands, and then burning them under standardized conditions in a fire lab and measuring *Armillaria* biomass, wood traits and key parameters representing flammability.

2. Materials and methods

2.1. Collection of plant materials

The branches used in this experiment were collected from *Pinus nigra* in forest plantations near Castricum in the Netherlands (52°33'26 N, 4°37'20 E) on the 14th of February, 2019. The *P. nigra* trees in the sample sites seemed to had reached maturity without any visible symptoms of fire damage, so we assumed these sites had been fire-free for at least five decades. This forest area is located in the coastal sand dunes and the most common tree species are *Pinus nigra*, *Acer pseudoplatanus* L. and *Quercus robur* L. *Pinus nigra* is an exotic species which was planted after the Second World War for dune stabilization and timber production. It has been widely introduced into other parts of Europe as well. It is vulnerable to fluctuating water levels including recurring drought, which weakens the tree. *Armillaria* is a widespread parasitic fungus that occurs on all continents except Antarctica. A wide range of plant species, particularly trees and shrubs in boreal and temperate forests, may be susceptible to *Armillaria* infection. Due to abiotic stress weakening the resistance of trees, *Armillaria* can infect these weakened trees more easily. Especially in this study, *Pinus nigra* trees were planted closely within stands, which benefits the spread of *Armillaria*.

There were two types of patches within the same forest area: healthy *Pinus nigra* patches and infected *Pinus nigra* patches; see Fig. S1 for the visible features of *Armillaria* infection at the forest patch scale. We randomly collected dead branches that, together, visually represented the entire range of decay stages from freshly senesced to strongly decomposed, both from three *Armillaria* infected patches and three nearby uninfected patches. The healthy patches were located 3.5 kilometers north of the infected patches. This made sure that the *Pinus nigra* trees in healthy patches were under the minimum effect of *Armillaria* spread. The distance between healthy patches varied from 50 to 100 m, and the distance between infected patches varies from 100 to 600 m. All patches were 1.5–2.0 kilometers away from the sea. Based on these and our field observations, all environmental parameters in these patches appeared the same, except that one patch type showed no sign of an infection while the other type showed visible, severe *Armillaria* infection symptoms. The patches which had irregular shapes, measured around 0.01 km^2. Based on previous knowledge, wood density will influence deadwood flammability as a structural trait. To disentangle the wood density effect from other trait effects that are potentially altered by *Armillaria* infection on deadwood flammability, we needed to check if and how *Armillaria* infection influences wood flammability at given wood density. Whether or not a piece of deadwood will burn may often depend on subtle differences in flammability around a threshold for ignition and subsequent combustion. Therefore, even a relatively small additional contribution of pathogenic fungi to flammability may have a large impact if it can determine the start of a surface fire that may subsequently turn into a stand-scale wildfire. In this way we could compare the flammability of branches with similar wood densities and soil properties but with different causes of death (pathogen-mediated senescence vs. branch senescence without pathogens). All branches

were collected according to the following standards: with diameter of 5 cm, more than 30 cm long and no clear damage on the branch surface. Any side-branches were removed during collection by a handsaw. In each patch, at least 15 branches were collected from different downed deadwood units on the ground. After collection, the branches were transported to the Vrije Universiteit Amsterdam where they were stored in a cold room at 7 ℃ to retain their humidity until preparation for the experimental burns. Before processing, branches from infected and uninfected patches were each pooled and then sorted by visually estimated decay stage.

2.2. Armillaria biomass estimation

Since we wanted to specifically investigate the effect of *Armillaria* on the flammability of coarse wood of *Pinus nigra*, we needed to show whether the fungus was actually physically in the wood and in what quantities. To address this question we employed a droplet digital PCR (ddPCR) technique allowing unambiguous quantification of microorganism biomass (Barceló et al. 2020). To avoid cross-contamination in the storage room, samples from infected and uninfected patches in each decay stage were sealed in plastic bags separately. Within a week after collection, branches were further selected and a subsample of the branch was cut to measure *Armillaria* biomass (see Subsample in Fig. S2a). In total 60 branches with a broad range of wood densities (30 from healthy and 30 from infected patches) provided subsamples for *Armillaria* biomass estimation.

Multiple holes were drilled into the subsample and the collected sawdust was then pulverized in a ball mill (Retsch MM400, Haan, Germany) to obtain a fine, homogeneous mixture. DNA was extracted from this mixture with the use of a Dneasy PowerSoil Kit (Qiagen) following the standard protocols from the manufacturer. The forward ITS3 and reverse Armi2R primers followed Guglielmo et al. (2007). DNA was extracted at Vrije Universiteit Amsterdam while the dd-PCR analysis was performed at Leiden University. For PCR protocol optimization (selecting the appropriate annealing temperature) we used the steps as described in the Bio-Rad Droplet Digital PCR Applications Guide. Each ddPCR reaction mixture (22 μL) contained 3 μL of DNA template, 1 μL of each primer (10 μM), 7 μL of Milli-Q and 10 μL of Bio-Rad EvaGreen Supermix (Bio-Rad, Hercules, CA, USA). Of this 22 μl PCR mixture, 20 μl was transferred onto a DG8 Bio-Rad cartridge containing 8 wells and covered with a DG8 rubber gasket, in which it was mixed with Bio-Rad droplet generator oil and partitioned into 6000–20,000 droplets by using the Bio-Rad QX-100 droplet generator (Bio-Rad). Additionally, negative controls were run in every plate containing 3 μl Milli-Q to check and correct for potential contamination.

The droplet of the individual sample was applied to a 96-well PCR reaction plate. PCR was performed in the 96-well plate sealed with pierceable sealing foil by using the PX1 PCR plate sealer (Bio-rad). PCR conditions were 10 min at 95 °C, 40 cycles of denaturation for 30 s at 95 °C and extension for 60 s at 56 °C with ramp rate of 2 °C s^{-1}, followed by 10 min at 90 °C and a hold at 12 °C. After PCR amplification, the plate was transferred to the Bio-Rad QX-100 droplet reader (Bio-Rad). Bio-Rad's QuantaSoft software version 1.3.2.0 was used to quantify the copies of target DNA in μL^{-1}. The threshold for a positive signal was determined according to the QuantaSoft instructions: in short, by using the separation value between the threshold and the centre of the negative droplet band from the positive control sample, we subsequently determined threshold values in the test samples. Droplets above the threshold were counted as positive events. Count estimates for each sample were compared to the maximum confidence interval (95 %) of the negative controls to determine if DNA concentrations were statistically different from zero.

The resulting concentration measurements in molecules/μl were used for further statistical analyses. Extra samples were added with known *Armillaria* biomasses from a fruiting body we collected to construct a calibration line. These calibration samples contained concentrations of *Armillaria* biomass from 0 % to 100 %, with 10 % intervals (see Table S1). Because our samples from the experiment all contained relatively more wood, we adjusted the calibration and excluded the measurements with low wood and high *Armillaria* concentrations (80–100 %). *Armillaria* biomass of all the samples was then calculated with the use of the calibration line per gram dry weight of the subsample (Fig. S3).

2.3. Wood properties

After DNA extraction, all samples were air-dried for two months in a greenhouse at room temperature at the Vrije Universiteit Amsterdam to stop fungal growth until equilibrium mass. This mimicked a dry period in the field (representing realistic wildfire likelihood) in a standardized manner. Then, in total 110 samples, including 60 branches providing subsamples for *Armillaria* biomass estimation, that were used for the fire experiment were cut in 20 cm long sections (Fig. S2b). The diameter was measured with digital calipers in three places, i.e. at both ends and in the middle of this section. The average branch diameter was used in calculations. The mean average diameter of healthy and infected branches were 50.29 ± 5.37 mm and 48.89 ± 5.72 mm (Mean ± SD).

Two subsamples (at least 2 cm thick), cut from both ends of the fire sample (subsample 1 and 2, see Fig. S2b), were measured for wood density. Wood density was determined with the water replacement method (Williamson and Wiemann, 2010). First the air-dry mass of the subsample was measured and then the subsample was saturated in demineralized water for one week before the volume measurement. After that, the subsample was dried at 70 ℃ for one week. Wood density (g/cm^3) was defined as oven-dried mass per volume. The mean value of wood densities of two subsamples was then calculated as the wood density of the fire sample. Subsample 3 was cut from the end of subsample 2 (Fig. S2b). Subsample 3 was first weighted and then dried at 70 ℃ for one week. Wood moisture (%) was defined as ((air-dried mass - oven-dried mass)/air-dried mass) * 100 %. After drying, homogeneous ground material collected from subsample 3 was used for measurement of wood chemical traits. Carbon and nitrogen content was measured by dry combustion on a Flash EA 1112 elemental analyzer (Thermo Scientific, Rondana, Italy). Then the C to N ratio was calculated. Lignin was determined following Poorter and Villar (1997): in short, after several extraction steps to ensure that only cellulose and lignin made up the composition of the residue of the sample, the C and N concentrations of this residue were used to calculate the lignin concentration, based upon the known difference in carbon content between cellulose and lignin. In order to compare the overall chemical profiles of branches from infected and uninfected forest patches, Fourier Transform Infrared (FTIR) signals of wood samples were also identified using a FTIR spectrophotometer (ABB, model MB300, Canada). The spectra were measured in the absorbance range from 4000 to 600 cm^{-1} over 32 scans per sample, at a resolution of 4 cm^{-1}. Each sample was scanned twice and we took the mean value as the final result. For comparing FTIR signals between branches from healthy and infected patches, the mean values of spectra in each groups were then calculated.

2.4. Fire experiment

Experimental burns were conducted in the Fire Laboratory of Amsterdam for Research in Ecology (FLARE) located at Vrije Universiteit Amsterdam. The methodology was adjusted from that used in Zhao et al. (2018). Prior to the flammability experiment, branches (see fire sample in Fig. S2b) were dried in the oven (35 ℃) for five days before they were burned, to reduce the potential influence of air humidity fluctuations in the greenhouse on the sample moisture content among different experimental days. Before being transferred to the oven, samples were weighed and then corrected by the moisture content (via the subsample; see wood properties section) to give the sample dry mass just before the burn. The branches were burned in a block order with one

block a day. In each block 6 or 10 samples, i.e. 3 healthy and 3 infected samples or 5 healthy and 5 infected samples, each from a wide range of wood densities, were randomly chosen. Within one block, each sample was burned in a random order separately. The experimental burns were carried out over 15 days. All burns where conducted in a fume hood on a solid fire resistant plate and room temperature was 23 ± 4 ℃. The fume hood was ventilated at a constant moderate speed (0.4 m/s). To mimic the natural spread of surface wildfires we built a fuel bed that consisted of a first layer of thin, highly flammable wood wools and a second layer of beech chippings, which had been dried in the oven at 35 ℃ and burned slower than the first layer. The first layer was chosen to spread the fire around the branch while the second layer was chosen to generate enough heat and burn sufficiently slowly to ignite the branch. This fuel bed mimicked a forest surface litter layer composed of dead leaves and twigs. To standardize the fuel beds in all fires the mass was set at 50 g for the first layer and 200 g for the second layer. The branch was placed exactly in the middle and on top of the fuel bed. All fires were ignited with two cotton disks, which were injected with 1 ml of 70 % ethanol and placed at the front and back (Fig. 1a). The temperature was measured each second with four thermocouples (1 mm thick type K thermocouple, TC Direct, Uxbridge, UK), which could measure temperatures accurately up to 1100 ℃. The temperature data was recorded with TC Meas, a program that transforms the thermocouple signal into temperature, written by the Electronic Engineering Group Bèta VU at Vrije Universiteit Amsterdam in Labview. The four thermocouples were placed 2 cm above the branch (Fig. 1a). As the experimental burns would cause a minor increase in air temperature in the fume hood, at the beginning of each burning day a reference burn was done with only the litter bed in order to reduce the temperature differences between the first sample and other samples.

Fuel flammability can be categorized into four components: ignitability (ease of plant ignition), combustibility (the intensity or speed at which a fire burns), sustainability (how long the fuel burns) and consumability (proportion of biomass combusted; Anderson, 1970; Martin et al., 1993). Accordingly, several flammability parameters were measured as follows: (1) Ignitability: Time until ignition was determined as the time (s) from the fire reaching the branch until the first flames came out of the branch itself and lasted longer than two seconds (Fig. 1b). (2) Sustainability: Flame duration was determined as the time (s) from ignition of the branch until extinction of the fire (Fig. 1c). (3) Sustainability: Smoldering time (Fig. 1d) was determined as the time in seconds from the extinction of the fire until the branch temperature was below 50 ℃. The branch was removed from the litter bed to smolder further on its own 20 minutes after the extinction to prevent influences of the smoldering litter bed and to get better measurements of the remaining mass after the fire (Fig. 1e). During smoldering, a thermocouple was used to measure the branch temperature. For branches with low density, the thermocouple was inserted into the smoldering part of the branch. For branches with high density (thermocouple could not be inserted), the thermocouple was attached to the smoldering surface of the branch. (4) Combustibility: Mean maximum temperature (T_{max}; ℃) was measured by the thermocouples 1–4 (Fig. 1a). (5) Consumability: Percentage mass loss was calculated with the mass (g) of the branch before and after the fire and was also corrected for moisture content. It was calculated as ((Mass $_{before}$ – Mass $_{after}$) / Mass $_{before}$) * 100 %. While these five fire variables represent different aspects of flammability and fire behavior, it is important to acknowledge that they are likely to partly covary.

2.5. Data analysis

Due to large differences in density within the branch (Fig. S4), which would not give representative data, one sample was completely removed from the data set. One measurement was also excluded from the *Armillaria* biomass calculation result because it had a distinctive amount of *Armillaria* biomass. Thus, only 58 samples, 30 healthy branches and

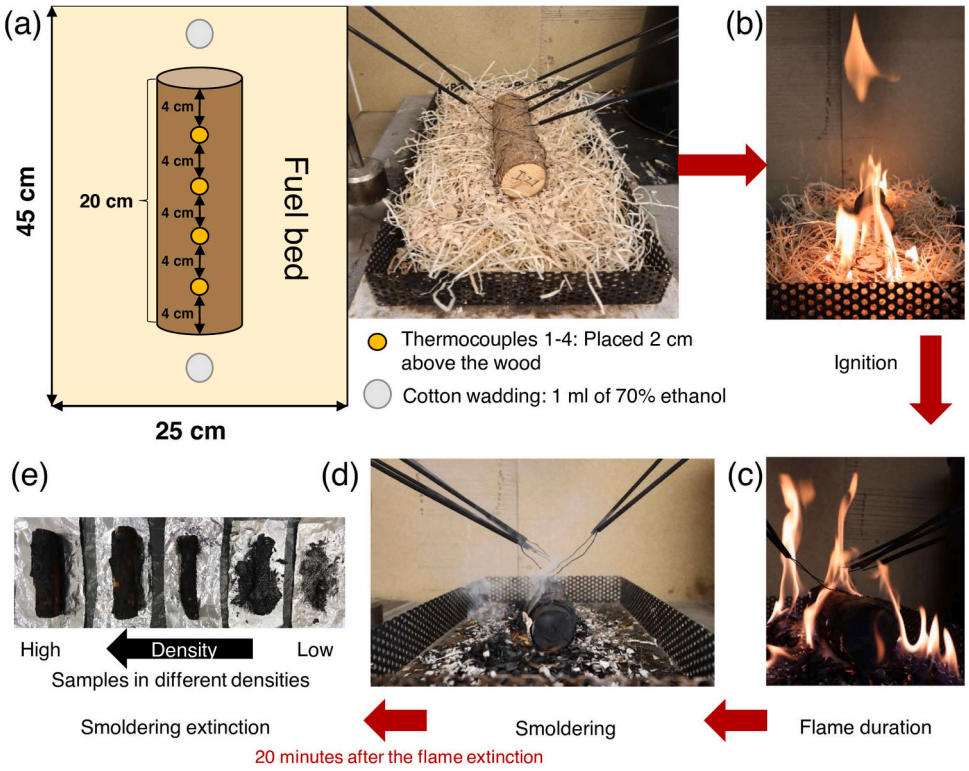


Fig. 1. Protocol of experimental burns. (a) Setup for the burning experiment. In each experimental burn one branch sample was burned in the middle of the fuel bed. (b) Example showing the ignition of a sample. (c) Example of flame duration measurement. (d) Example of sample smoldering. Branch has been removed from fuel bed 20 minutes after the flame extinction until its temperature drops below 50 ℃. (e) Example of the remaining part of samples (with different initial wood densities before fire experimental burns) when smoldering extinction.

28 infected branches, were used for the *Armillaria* biomass estimation and 109 samples, 55 healthy branches and 54 infected branches, for the wood traits and flammability analysis. All data were processed in R (v4.0.3; R Core Team, 2020). Healthy and infected patches were not paired with each other in this study and each branch was collected with different density and from different downed deadwood units. Therefore, we decided to treat branches as independent samples from either infected or healthy patches.

Wilcoxon tests were performed for differences in wood properties and *Armillaria* biomass between branches from healthy versus infected forest patches. ANCOVAs were used to analyse the effect of *Armillaria* infection on flammability parameters, with Eq. (1) by the "car" package (Fox and Weisberg, 2019):

$$y \sim Armillaria\ effect \times Wood\ density + \varepsilon \quad (1)$$

where, y represents different flammability parameters. *Armillaria effect* is the main effect and *Wood density* is used as a covariate. ε is the random error term.

Linear regressions were used to check the relations of wood density with *Armillaria* biomass, other wood properties and each of the flammability parameters with Eq. (2):

$$y \sim b + ax + \varepsilon \quad (2)$$

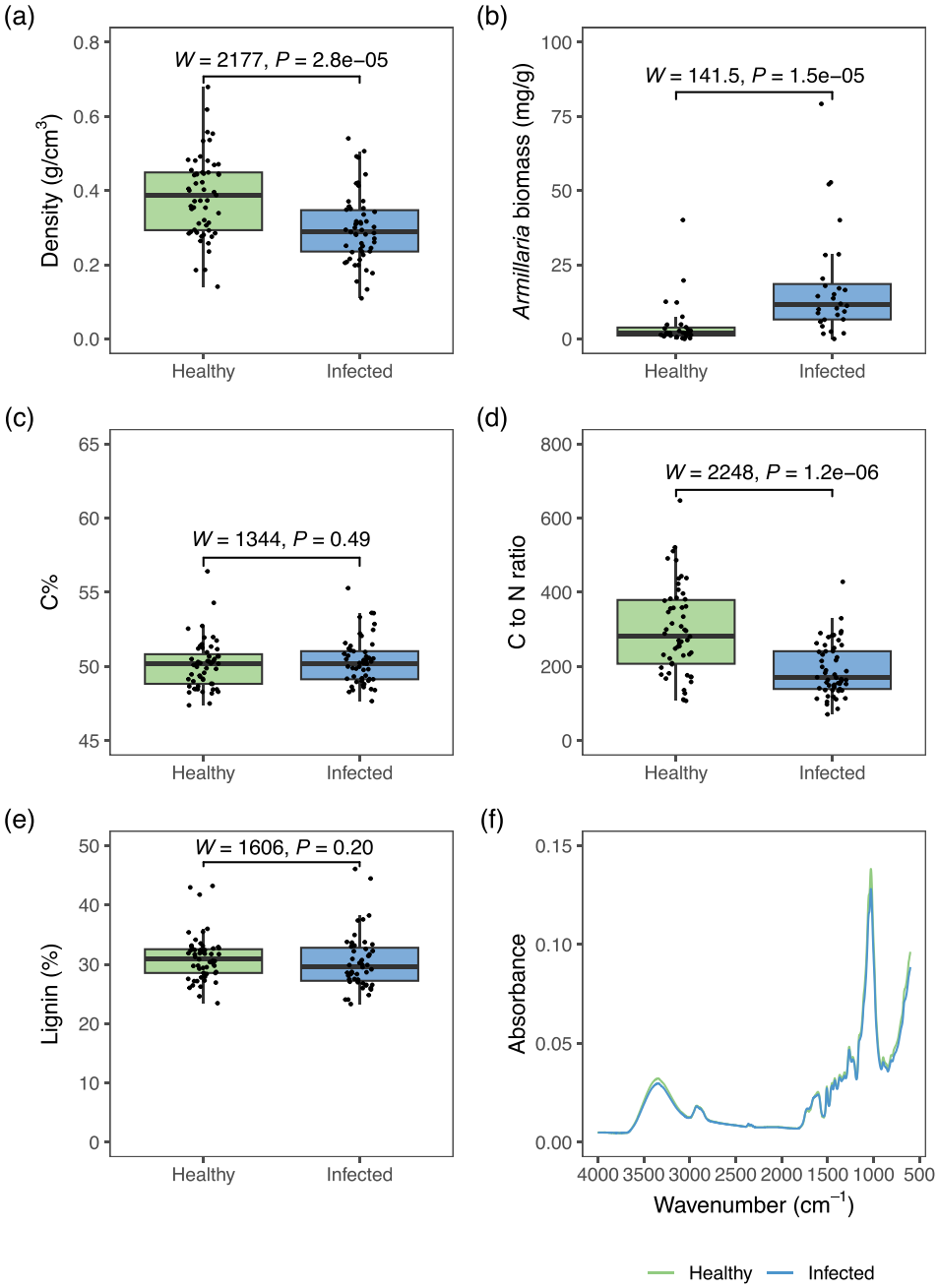


Fig. 2. Wood traits and *Armillaria* biomass in *Pinus nigra* branches collected from *Armillaria* infected patches and healthy patches. (a) Wood density, (b) Biomass of *Armillaria* per gram wood, (c) Carbon (C) content, (d) C to N ratio, (e) Lignin content, and (f) Fourier Transform Infrared (FTIR) signals. The box represents the interquartile range (IQR), with the median value indicated by the horizontal line inside the box. The whiskers extend to 1.5 times the IQR. Wilcoxon tests were performed to look for differences in wood properties and *Armillaria* biomass between branches (infected vs uninfected) of the two forest stand types (healthy and infected). W and P values of the test results are given (see Table S2).

where, y is the wood flammability parameter or wood property, x is wood density. The slope of the line is a and b is the intercept. ε is the random error term.

All data was tested for normality and homogeneity of residual variance by visual inspection of residual and probability plots. Time until ignition, flame duration, smoldering time and T_{max} were log_{10}-transformed; and percentage of mass loss was ln(x+1)-transformed to best fit the assumption of ANCOVA. *Armillaria* biomass and C to N ratio were also transformed accordingly. A Principal Component Analysis (PCA) was used to combine all the flammability parameters and the difference in overall flammability between healthy and infected branches was compared with the PCA plot.

3. Results

3.1. Dd-PCR and Armillaria biomass

The final calibration line for the estimation of *Armillaria* biomass had an R-squared of 0.96 (Fig. S3). Branches from the healthy patches contained significantly less *Armillaria* biomass per gram wood than branches from infected patches ($P < 0.001$, Fig. 2b). *Armillaria* biomass per gram wood was not significantly correlated with wood density in branches from infected patches ($P = 0.07$) and healthy patches ($P = 0.05$; Fig. S5a).

3.2. Wood properties

Wood density and C to N ratio of branches from infected patches were significantly lower than those from healthy patches ($P < 0.001$; Fig. 2a, d). The C to N ratio was significant positively correlated with wood density in both healthy and infected branches ($P < 0.001$; Fig. S5b). There were no differences in C and lignin content between branches from healthy and infected patches (Fig. 2c, e). Also, the mean FTIR spectra showed no clear difference in patterns between healthy and infected branches (Fig. 2f).

3.3. Flammability

The results of ANCOVA showed that *Armillaria* infection had significant effects on time until ignition, flame duration and percentage mass loss, but no significant effects on smoldering time and T_{max} (Table 1). Wood density had a significant positive or negative correlation with all flammability parameters, and there were significant interactive effects (density × *Armillaria* infection) on time until ignition and flame duration (Table 1, Fig. 3). This means that *Armillaria* partly had different effects on the flammability parameters that could not be explained by differences in wood density. Although there were significant interactive effects (density × *Armillaria* infection) on time until ignition and flame duration, the infected and healthy branches shared the same trends (both increased or decreased with the density changes). Their trend lines only crossed at very low or high density (Fig. 3a, b). Based on this, we suggest that the main effects are still meaningful. The PCA result also showed that the flammabilities of healthy and infected branches were potentially different (Fig. 4). Overall, our results showed that branches from infected patches were more flammable compared with branches from healthy patches.

4. Discussion

To our knowledge, this is the first experimental study to disentangle the effects of *Armillaria*, as the opportunistic parasitic fungus, from the effects of other saprophytic fungi on the flammability of coarse deadwood. The general results from our experimental burns showed that infection by *Armillaria* does influence flammability of coarse dead black pine branches (see Fig. 4). However, wood density is known to be the most influential determinant of wood flammability (de Souza Costa and Sandberg, 2004; Hyde et al., 2011; Hyde, Smith and Ottmar, 2012; Zhao et al., 2014, 2018), and this is confirmed by our results from regressions of flammability parameters on wood density (Fig. 3). We also found that *Armillaria* affected flammability when controlling for wood density (which was lower on average in infected patches; see above). Indeed, three out of five flammability parameters (time until ignition, flame duration and percentage mass loss) were significantly influenced by *Armillaria* infection at given wood density (Table 1). Below, we will first discuss the *Armillaria* biomass found in the branches, followed by a focus on the question of mechanism: 'how does *Armillaria* infection affect coarse deadwood flammability?', and then the limitations of our fire experimental setup. Finally, we will discuss the implications of our study for future forest management.

4.1. Armillaria biomass found in the black pine branches

The dd-PCR results showed that branches collected from infected forest patches indeed contained substantial *Armillaria* biomass while branches from apparently uninfected patches had at most very low biomass (Fig. 2b) significantly less than infected branches. Although we did not have direct evidence to prove that *Armillaria* can attack live branches of *Pinus nigra*, the significant amount of *Armillaria* biomass

Table 1
Results of ANCOVAs for the effects of *Armillaria* infection on flammability parameters. Branch density was taken as a covariate. Fungi represents the *Armillaria* effects.

	Model		df	*F*	*P*
Time until ignition (s)	Log_{10}(Time until ignition) ~ Density × Fungi	Density	1	16.86	<0.001
		Fungi	1	10.71	0.001
		Interaction (Density × Fungi)	1	6.70	0.011
		Residuals	105		
Flame duration (s)	Log_{10}(Flame duration) ~ Density × Fungi	Density	1	5.07	0.026
		Fungi	1	6.20	0.014
		Interaction (Density × Fungi)	1	4.09	0.046
		Residuals	105		
Smoldering time (s)	Log_{10}(Smoldering time) ~ Density × Fungi	Density	1	37.82	<0.001
		Fungi	1	3.20	0.076
		Interaction (Density × Fungi)	1	2.94	0.089
		Residuals	105		
Mean maximum temperature (℃)	Log_{10}(Mean maximum temperature) ~ Density × Fungi	Density	1	32.83	<0.001
		Fungi	1	1.16	0.283
		Interaction (Density × Fungi)	1	1.53	0.219
		Residuals	105		
Percentage of mass loss (%)	Ln(Percentage of mass loss+1) ~ Density × Fungi	Density	1	104.43	<0.001
		Fungi	1	4.62	0.034
		Interaction (Density × Fungi)	1	0.01	0.915
		Residuals	105		

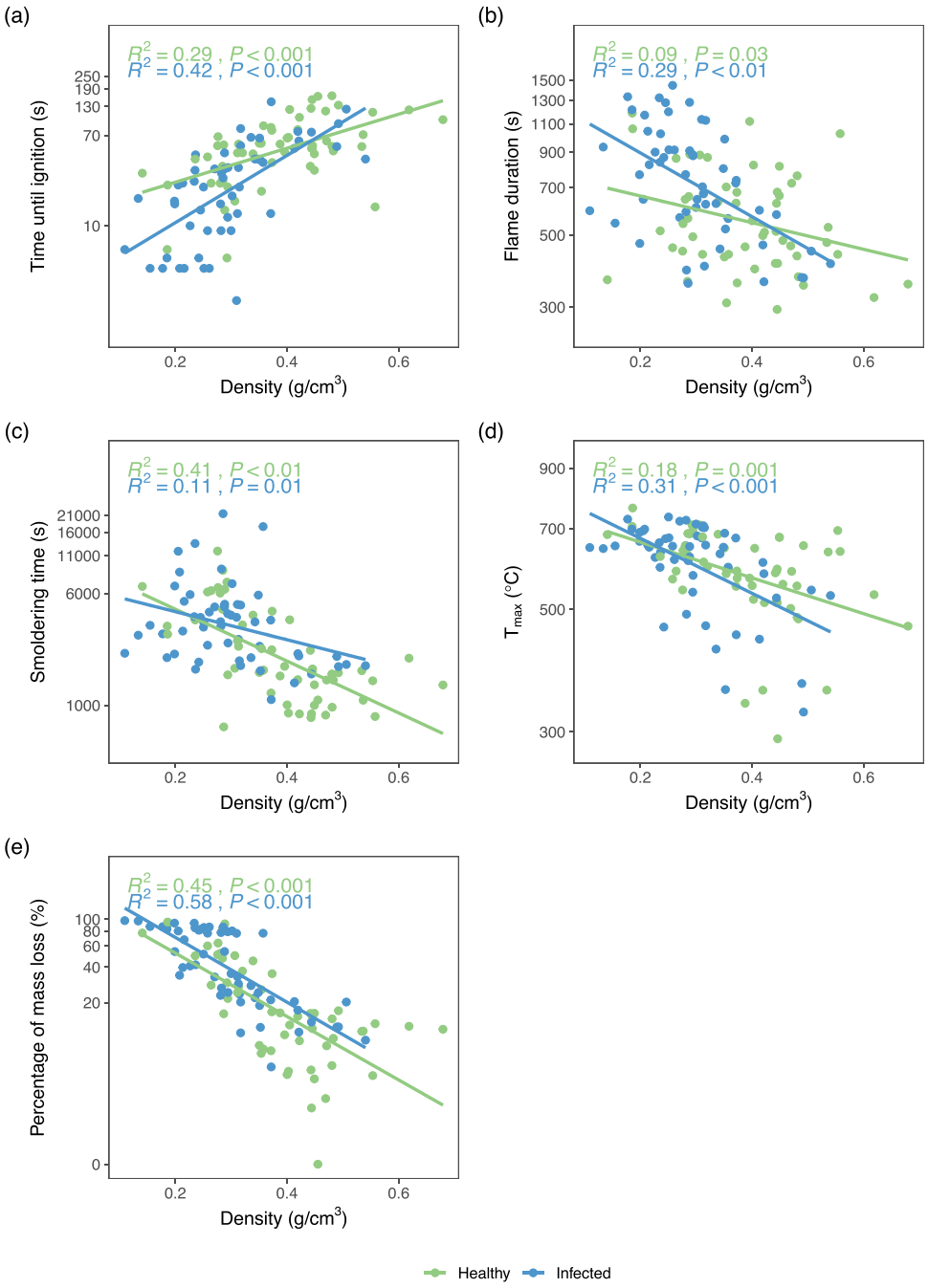


Fig. 3. Relationships among density with five flammability parameters. Blue represent the *Pinus nigra* branch collected in the *Armillaria* infected and green the healthy branch collected in uninfected patches. R^2 and P values of regression lines are given. T_{max}, Mean maximum temperature. The y axis of a, b, c and d shows on the $\log_{10}(y)$ scale and e on the $\ln(y+1)$ scale.

found in the infected dead branches from various stages of decomposition (Fig. S5a) indicates that *Armillaria* can indeed attack these branches at some point either as a pathogen or a saprotroph, or both. Thus, the substantial presence of *Armillaria* biomass in the branches from infected patches suggests that *Armillaria*, functioning as an opportunistic parasitic fungus, are present in the *Pinus nigra* coarse wood and may potentially impact the traits of these wood.

4.2. How does Armillaria infection affect coarse deadwood flammability?

Armillaria infection did not affect wood C and lignin content of coarse branches (Fig. 2c, e) in *Pinus nigra* plantations. The mean FTIR spectra of branches also showed that branches of infected and uninfected patches did not have clear differences in chemical composition (Fig. 2f). The only significant difference was the C to N ratio which was lower in infected patches (Fig. 2d). C to N ratio is an important trait that reflects the litter and wood decomposability: lower C to N ratio means faster litter turn over (Aerts, 1997; Cornwell et al., 2009; Weedon et al., 2009; García-Palacios et al., 2016; Hu et al., 2017; Liao et al., 2022). Our result is consistent with this relationship (Fig. S5b), as the lower wood densities on average imply faster decomposition rates in infected patches (see above).

As the ANCOVA results demonstrated that, at a given wood density, infected branches burnt better (see above), we deduce that *Armillaria*

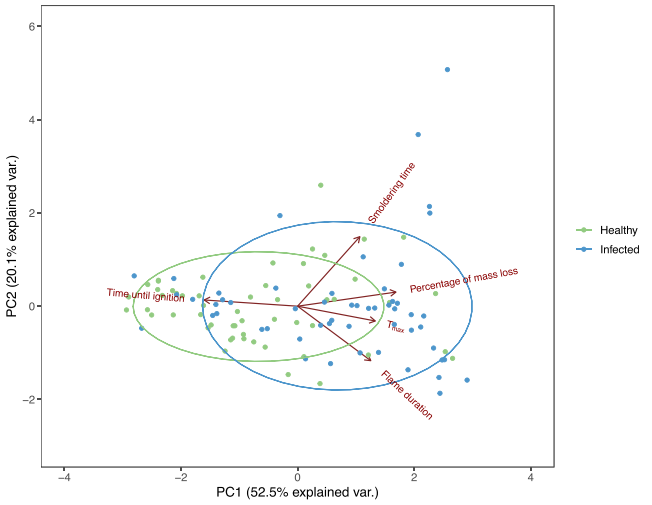


Fig. 4. Principle component analysis (PCA) for five flammability parameters. Blue dots represent the *Pinus nigra* branches collected in the *Armillaria* infected patches and green dots the healthy branches collected in uninfected patches. T_{max}, Mean maximum temperature.

infection has a direct influence on deadwood quality, which subsequently affects wood flammability. There is empirical evidence that *Armillaria* spp. have the ability to form tubular air channels in wood through hyphae that radially penetrate from the cambium into xylem rays, and with the growth of *Armillaria* an increasing number of hyphae will break down wood cells, thereby causing more perforations in the xylem (Metzler and Hecht, 2004). This suggests that *Armillaria* growth may bring more air deep into the wood. As oxygen is a key factor determining wood flammability, *Armillaria* growth changing oxygen availability at the wood cell scale may explain why wood was more flammable after *Armillaria* infection.

Indirectly, *Armillaria* growth may also be the reason that wood N content increased, as fungi are known to import N into wood to aid them in breaking down carbon sources (Holub, Spears and Lajtha, 2001; Stenlid, Penttilä and Dahlberg, 2008; Bebber et al., 2011; Philpott et al., 2014; Rinne et al., 2017). And this growth may subsequently facilitate activity by the microbial community in the wood. Together, these factors may increase the decomposability of the wood; and thereby, via lower wood density, its flammability. However, further study should reveal whether and how anatomical changes in the wood due to *Armillaria* affect wood flammability. Future studies should also test the role of wood pathogens such as *Armillaria* in even coarser wood, i.e. tree trunks, as they represent an important fraction of the aboveground carbon in forests. Such studies will have to overcome practical challenges of scaling up experimental burns to larger dimensions while retaining standardised conditions.

4.3. Limitations of our experimental setup

Wildfires are more likely to happen under drought, thus the branches were first air-dried in a greenhouse for 2 months, then dried in the oven (35 ℃) for five days before they were burned to mimic a dry period. Also, environmental factors like wind may greatly influence wood fire behaviour (Nelson and Ralph, 2002; Plucinski and Anderson, 2008; Ellis, 2015; Abouali, Viegas and Raposo, 2021; Finney et al., 2021), and might therefore mask any '*Armillaria* effect'. Thus, our idea for this experiment was to first check if the '*Armillaria* effect' will influence wood flammability under standardised environmental conditions (equilibrium air-dry fuel and constant wind speed). However, in the field condition, fire hazards could be more complex. Thus, future tests should also focus on the interaction of the '*Armillaria* effect' with fuel moistures or with windy weather. The wood density of branches in infected patches was significantly lower than that in healthy patches (Fig. 2a). However, the way we collected branches may have caused a slight bias in comparing wood density between healthy and infected patches. Branches were first collected in a range of different densities by estimating the density by eye, and we could not know the actual time period that each branch had decomposed on the forest floor. This could have led to differences in the range of densities between the "infected" and the "uninfected" branches. Still, during our collection, the availability of branches with low densities was a lot higher in infected patches, which suggests that our general result of lower densities in infected patches is a reflection of the real situation in the field, with faster decomposition of branches in infected patches.

4.4. Implications for the future forest management

The non-native species *Pinus nigra* that we studied was planted widely after the Second World War (see Methods). In the West Atlantic coastal dune areas, it is vulnerable to the climate extremes, such as prolonged droughts, compared to the native species. In the near future, with warming climate and more frequent and intense drought periods, vulnerable species such as this may more easily be affected by tree pathogens such as *Armillaria* and insect pests (e.g. bark beetles). Our study system is not a traditional fire prone system. As far as we know, most wildfires here start as a small-scale surface fire which are ignited by human sources (e.g. cigarettes, campfires) during hot and dry periods (Stoof et al., 2024). They often subsequently develop into stand-level crown fires. As we demonstrated that pathogens like *Armillaria* would make the deadwood more flammable, these weakened exotic plantations will face more wildfire problems, making the system more fire prone. That is first by killing more host trees, increasing the amount of fuel loads on the soil surface, and then at the single wood unit scale making deadwood more flammable, especially increasing the combustibility, i.e. percentage of mass loss during fire. Although the relatively fast decomposition in the infected plantations will consume accumulated fuel, the overall amount of fuel load is increased given the fact that *Armillaria* increases the mortality of trees. As decomposition and wildfire are two predominant pathways that return the organic carbon of the accumulated dead plant biomass to the atmosphere, the fast decomposition and high percentage of mass loss during fire of infected deadwoods means that more carbon will be released eventually. This will threaten the forest carbon storing function at the landscape scale.

In conclusion, our study has provided empirical support that at a given wood density, branches from forest stands with a visible *Armillaria* infection will ignite faster and burn with a higher intensity than uninfected branches. These changes in flammability likely originated from both direct influences of *Armillaria* infection, e.g. via changing wood structure (before and/or after wood death), and indirect influences, for instance by driving nitrogen import into in wood, thereby increasing wood decomposability and consequently reducing wood density. While we focused on *Pinus nigra* here, our findings have broader relevance for wildfire in forests affected by climate-induced pathogens, as such pathogen attacks are a globally widespread and increasing phenomenon (La Porta et al., 2008; Jactel et al., 2012; Seidl et al., 2017; McDowell et al., 2020; Venäläinen et al., 2020). Future tests should be applied to more *Armillaria* susceptible coniferous species to check whether this positive effect of *Armillaria* infection on deadwood flammability is consistent across species. This will be important for forest management in an increasingly fire-prone world.

CRediT authorship contribution statement

Nadia A. Soudzilovskaia: Resources, Investigation. **Richard S.P. van Logtestijn:** Writing – review & editing, Investigation, Conceptualization. **Myrthe Fonck:** Investigation, Conceptualization. **Bas van Spronsen:** Methodology, Investigation, Conceptualization. **Shudong Zhang:** Writing – review & editing, Writing – original draft, Project

administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Johannes H.C. Cornelissen:** Writing – review & editing, Supervision, Resources, Investigation, Conceptualization. **Krijn Trimbos:** Resources, Investigation.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Shudong Zhang reports financial support was provided by China Scholarship Council. Shudong Zhang reports a relationship with China Scholarship Council that includes: funding grants. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data used in this study are publicly available via Figshare: https://doi.org/10.6084/m9.figshare.26819557.

Acknowledgements

Shudong Zhang received a PhD grant (201804910633) from the China Scholarship Council. We would like to thank Emily Didaskalou, Tycho Hoogstrate, Luke Blauw and Dr. James Weedon for their help during the experimental design and field work. We also want to thank PWN for enabling access to their forest plantations.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122240.

References

Abouali, A., Viegas, D.X., Raposo, J.R., 2021. Analysis of the wind flow and fire spread dynamics over a sloped–ridgeline hill. Combust. Flame 234, 111724.
Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79, 439.
Anderson, H.E., 1970. Forest fuel ignitibility. Fire Technol. 6, 312–319.
Baldrian, P., 2016. Forest microbiome: diversity, complexity and dynamics. FEMS Microbiol. Rev. 41, 109–130.
Barceló, M., van Bodegom, P.M., Tedersoo, L., den Haan, N., Veen, G.F., Ostonen, I., Trimbos, K., Soudzilovskaia, N.A., 2020. The abundance of arbuscular mycorrhiza in soils is linked to the total length of roots colonized at ecosystem level. PloS One 15, e0237256.
Bebber, D.P., Watkinson, S.C., Boddy, L., Darrah, P.R., 2011. Simulated nitrogen deposition affects wood decomposition by cord-forming fungi. Oecologia 167, 1177–1184.
Blauw, L.G., van Logtestijn, R.S.P., Broekman, R., Aerts, R., Cornelissen, J.H.C., 2017. Tree species identity in high-latitude forests determines fire spread through fuel ladders from branches to soil and vice versa. For. Ecol. Manag. 400, 475–484.
Bradford, M.A., Warren Ii, R.J., Baldrian, P., Crowther, T.W., Maynard, D.S., Oldfield, E. E., Wieder, W.R., Wood, S.A., King, J.R., 2014. Climate fails to predict wood decomposition at regional scales. Nat. Clim. Change 4, 625–630.
Cherubini, P., Fontana, G., Rigling, D., Dobbertin, M., Brang, P., Innes, J.L., 2002. Tree-life history prior to death: two fungal root pathogens affect tree-ring growth differently. J. Ecol. 90, 839–850.
R. Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Cornelissen, J.H.C., Grootemaat, S., Verheijen, L.M., Cornwell, W.K., van Bodegom, P.M., van der Wal, R., Aerts, R., 2017. Are litter decomposition and fire linked through plant species traits? N. Phytol. 216, 653–669.
Cornwell, W.K., Cornelissen, J.H.C., Allison, S.D., Bauhus, J., Eggleton, P., Preston, C.M., Scarff, F., Weedon, J.T., Wirth, C., Zanne, A.E., 2009. Plant traits and wood fates across the globe: rotted, burned, or consumed? Glob. Change Biol. 15, 2431–2449.
Demirbaş, A., 2001. Relationships between lignin contents and heating values of biomass. Energy Convers. Manag. 42, 183–188.
Devkota, P., Hammerschmidt, R., 2020. The infection process of *Armillaria mellea* and *Armillaria solidipes*. Physiol. Mol. Plant Pathol. 112, 101543.
Ellis, P.F.M., 2015. The likelihood of ignition of dry-eucalypt forest litter by firebrands. Int. J. Wildland Fire 24, 225–235.
Finney, M.A., McAllister, S.S., Grumstrup, T.P. & Forthofer, J.M. (2021) Wildland fire behaviour: Dynamics, principles and processes. CSIRO Publishing, Melbourne.
Fox, J., Weisberg, S., 2019. Third edition. An R Companion to Applied Regression. Sage, Thousand Oaks CA.
García-Palacios, P., McKie, B.G., Handa, I.T., Frainer, A., Hättenschwiler, S., 2016. The importance of litter traits and decomposers for litter decomposition: a comparison of aquatic and terrestrial ecosystems within and across biomes. Funct. Ecol. 30, 819–829.
Guglielmo, F., Bergemann, S.E., Gonthier, P., Nicolotti, G., Garbelotto, M., 2007. A multiplex PCR-based method for the detection and early identification of wood rotting fungi in standing trees. J. Appl. Microbiol. 103, 1490–1507.
Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. In: MacFadyen, A., Ford, E.D. (Eds.), Advances in Ecological Research. Academic Press, pp. 133–302.
Holub, S.M., Spears, J.D., Lajtha, K., 2001. A reanalysis of nutrient dynamics in coniferous coarse woody debris. Can. J. For. Res. 31, 1894–1902.
Hood, I., Redfern, D.B., Kile, G.A., 1991. In: Shaw, C.G., Kile, G.A. (Eds.), Armillaria in Planted Hosts. Armillaria Root Diaeases. Forest Service, US Department of Agriculture, Washington D.C, pp. 122–149.
Hu, Z., Xu, C., McDowell, N.G., Johnson, D.J., Wang, M., Luo, Y., Zhou, X., Huang, Z., 2017. Linking microbial community composition to C loss rates during wood decomposition. Soil Biol. Biochem. 104, 108–116.
Hyde, J.C., Smith, A.M.S., Ottmar, R.D., 2012. Properties affecting the consumption of sound and rotten coarse woody debris in northern Idaho: a preliminary investigation using laboratory fires. Int. J. Wildland Fire 21, 596–608.
Hyde, J.C., Smith, A.M.S., Ottmar, R.D., Alvarado, E.C., Morgan, P., 2011. The combustion of sound and rotten coarse woody debris: a review. Int. J. Wildland Fire 20, 163–174.
IPCC, 2021. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, R., Zhou)., B. (Eds.), The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK & New York, NY, USA.
Jactel, H., Petit, J., Desprez-Loustau, M.-L., Delzon, S., Piou, D., Battisti, A., Koricheva, J., 2012. Drought effects on damage by forest insects and pathogens: a meta-analysis. Glob. Change Biol. 18, 267–276.
Jakuš, R., 1998. Types of bark beetle (Coleoptera: Scolytidae) infestation in spruce forest stands affected by air pollution, bark beetle outbreak and honey fungus (*Armillaria mellea*). Anz. Sch. ädlingskunde, Pflanzenschutz, Umweltschutz 71, 41.
Kandasamy, D., Zaman, R., Nakamura, Y., Zhao, T., Hartmann, H., Andersson, M.N., Hammerbacher, A., Gershenzon, J., 2023. Conifer-killing bark beetles locate fungal symbionts by detecting volatile fungal metabolites of host tree resin monoterpenes. PLoS Biol. 21, e3001887.
Kauffman, J.B., Martin, R.E., 1989. Fire behavior, fuel consumption, and forest-floor changes following prescribed understory fires in Sierra Nevada mixed conifer forests. Can. J. For. Res. 19, 455–462.
Kubiak, K., Żółciak, A., Damszel, M., Lech, P., Sierota, Z., 2017. *Armillaria* pathogenesis under climate changes. Forests 8, 100.
La Porta, N., Capretti, P., Thomsen, I.M., Kasanen, R., Hietala, A.M., Von Weissenberg, K., 2008. Forest pathogens with higher damage potential due to climate change in Europe. Can. J. Plant Pathol. 30, 177–195.
Liao, C., Long, C., Zhang, Q., Cheng, X., 2022. Stronger effect of litter quality than microorganisms on leaf and root litter C and N loss at different decomposition stages following a subtropical land use change. Funct. Ecol. 36, 896–907.
Martin, R.E., Gordon, D.A., Gutierrez, M.E., Lee, D.S., Molina, D.M., Schroeder, R.A., Sapsis, D.B., Stephens, S.L., Chambers, M., 1993. Assessing the flammability of domestic and wildland vegetation, 94-02 Proceedings of the 12th International Conference on Fire and Forest Meteorology. Society of American Foresters Publication, Bethesda, MD, USA, pp. 130–137.
McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G.C., Jackson, R.B., Johnson, D.J., Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B., Pugh, T.A.M., Seidl, R., Turner, M.G., Uriarte, M., Walker, A.P., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. Science 368 eaaz9463.
Mesanza, N., Patten, C.L., Iturritxa, E., 2017. Distribution and characterization of *Armillaria* complex in Atlantic forest ecosystems of Spain. Forests 8, 235.
Metzler, B., Hecht, U., 2004. Three-dimensional structure of tubular air channels formed by Armillaria spp. in water-saturated logs of silver fir and Norway spruce. Can. J. Bot. 82, 1338–1345.
Nelson, J., Ralph, M., 2002. An effective wind speed for models of fire spread. Int. J. Wildland Fire 11, 153–161.
Pausas, J.G., Keeley, J.E., 2021. Wildfires and global change. Front. Ecol. Environ. 19, 387–395.
Philpott, T.J., Prescott, C.E., Chapman, W.K., Grayston, S.J., 2014. Nitrogen translocation and accumulation by a cord-forming fungus (*Hypholoma fasciculare*) into simulated woody debris. For. Ecol. Manag. 315, 121–128.
Piercey-Normore, M.D., Bérubé, J.A., 2000. Artificial inoculation with *Armillaria ostoyae* in established conifers stressed by defoliation, planting, and thinning in Newfoundland. Can. J. For. Res. 30, 1758–1765.
Plucinski, M.P., Anderson, W.R., 2008. Laboratory determination of factors influencing successful point ignition in the litter layer of shrubland vegetation. Int. J. Wildland Fire 17, 628–637.
Poorter, H., Villar, R., 1997. The fate of acquired carbon in plants: chemical composition and construction costs. In: Bazzaz, F.A., Grace, J. (Eds.), Plant resource allocation. Academic Press, San Diego, pp. 39–72.

Rinne, K.T., Rajala, T., Peltoniemi, K., Chen, J., Smolander, A., Mäkipää, R., 2017. Accumulation rates and sources of external nitrogen in decaying wood in a Norway spruce dominated forest. Funct. Ecol. 31, 530–541.
Rosso, P., Hansen, E., 1998. Tree vigour and the susceptibility of Douglas fir to *Armillaria* root disease. Eur. J. For. Pathol. 28, 43–52.
Schmidt, O., 2006. Wood and Tree Fungi: Biology, Damage, Protection, and Use. Springer-Verlag, Berlin Heidelberg, Germany.
Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyer, C.P.O., 2017. Forest disturbances under climate change. Nat. Clim. Change 7, 395–402.
Sierota, Z., Grodzki, W., Szczepkowski, A., 2019. Abiotic and biotic disturbances affecting forest health in Poland over the past 30 years: Impacts of climate and forest management. Forests 10, 75.
de Souza Costa, F., Sandberg, D., 2004. Mathematical model of a smoldering log. Combust. Flame 139, 227–238.
Stenlid, J., Penttilä, R., Dahlberg, A., 2008. Chapter 13 Wood-decay basidiomycetes in boreal forests: Distribution and community development. In: Boddy, L., Frankland, J. C., van West, P. (Eds.), British Mycological Society Symposia Series. Academic Press, UK, pp. 239–262.
Stoof, C.R., Kok, E., Cardil Forradellas, A., van Marle, M.J.E., 2024. In temperate Europe, fire is already here: The case of The Netherlands. Ambio 53, 604–623.
Venäläinen, A., Lehtonen, I., Laapas, M., Ruosteenoja, K., Tikkanen, O.-P., Viiri, H., Ikonen, V.-P., Peltola, H., 2020. Climate change induces multiple risks to boreal forests and forestry in Finland: A literature review. Glob. Change Biol. 26, 4178–4196.
Weedon, J.T., Cornwell, W.K., Cornelissen, J.H.C., Zanne, A.E., Wirth, C., Coomes, D.A., 2009. Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? Ecol. Lett. 12, 45–56.
Williamson, G.B., Wiemann, M.C., 2010. Measuring wood specific gravity … Correctly. Am. J. Bot. 97, 519–524.
Zhao, W., Blauw, L.G., van Logtestijn, R.S.P., Cornwell, W.K., Cornelissen, J.H.C., 2014. Interactions between fine wood decomposition and flammability. Forests 5, 827–846.
Zhao, W., van Logtestijn, R.S.P., van der Werf, G.R., van Hal, J.R., Cornelissen, J.H.C., 2018. Disentangling effects of key coarse woody debris fuel properties on its combustion, consumption and carbon gas emissions during experimental laboratory fire. For. Ecol. Manag. 427, 275–288.
Zuo, J., Cornelissen, J.H.C., Hefting, M.M., Sass-Klaassen, U., van Logtestijn, R.S.P., van Hal, J., Goudzwaard, L., Liu, J.C., Berg, M.P., 2016. The (w)hole story: facilitation of dead wood fauna by bark beetles? Soil Biol. Biochem. 95, 70–77.