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Fungistatic effects of purified conifer tannins against five wood-decaying fungi

Paula Thitz [a,*], Maarit Karonen [a], Aitor Barbero-López [b], Antti Haapala [b], Virpi Virjamo [c]

[a] Natural Chemistry Research Group, Department of Chemistry, University of Turku, FI-20014, Turku, Finland
[b] Department of Chemistry and Sustainable Technology, University of Eastern Finland, P.O. Box 111, Joensuu, 80101, Finland
[c] School of Forest Sciences, University of Eastern Finland, PO Box 111, FI-80101, Joensuu, Finland

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ABSTRACT

Success of saprotrophic fungi in wood requires resilience against plant defenses such as condensed tannins, but few studies quantify the variability in fungal tolerance while using well-characterized defence compounds purified from authentic sources. To investigate the antifungal activity of condensed tannins, we quantified the bioactivity of conifer tannins from Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) against five saprotrophs. Condensed tannins from conifer barks and from Scots pine needles showed moderate antifungal activities despite their low contents, and tannin structure affected their efficacy against the fungi. Fungal sensitivity to condensed tannins was species-specific but did not vary systematically between rot types, indicating that specialization of brown-rot fungi on conifers does not imply better or worse tolerance to conifer tannins compared to non-specialized white-rot fungi. Despite the resilience of some saprotrophs, our analysis suggests generalized antifungal activity of condensed tannins against wood-decaying fungi.

1. Introduction

Besides the mycorrhizal, endophytic, or pathogenic fungi capable of colonizing compatible plant tissues (e.g., Zeilinger et al., 2016), a range of variably host-exclusive wood-decaying fungi (also known as saprotrophic or saproxylic fungi) thrive on woody plants (Zhou and Hyde, 2001; Boddy and Hiscox, 2016). Biodiversity of wood-decaying fungi is particularly high in unmanaged forests where dead wood is not removed (e.g., Juutilainen et al., 2014; Kutszegi et al., 2021). Although the activity (e.g., Lindahl et al., 2007; Eastwood et al., 2011) and identity (Fukasawa, 2021) of these fungal decomposers is paramount for the circulation of organic carbon and nutrients in forest ecosystems, their activity on materials harvested from forests constrains the lifetime and use of wood products, unless toxic wood preservatives or some form of material modification are used (Freeman and McIntyre, 2008; Zelinka et al., 2022).

Most plants produce a wide array of specialized (earlier term: secondary) metabolites to regulate the biotic interactions they are involved in (Whitehead et al., 2021). These metabolites can, for example, restrict the colonization by fungal pathogens (Deytieux-Belleau et al., 2009), limit the growth of hyphae within plant tissues (Jersch et al., 1989) or indicate suitable host species for mutualistic fungi (Steinkellner et al., 2007). Although these compounds mainly play roles in biotic interactions, many of them persist in dead and decomposing wood and photosynthetic tissues (Venugopal et al., 2016; Paaso et al., 2017; Shay et al., 2018), forcing the wood-decaying fungi to interact with them. High amounts of extractable compounds have traditionally been correlated with good decay resistance for example in larch (*Larix decidua* Mill.) and Scots pine (*Pinus sylvestris* L.) heartwood (Windeisen et al., 2002; Harju and Venäläinen, 2006; Bopenga et al., 2020).

Condensed tannins (also known as proanthocyanidins) are specialized plant metabolites that commonly occur in woody species (Porter, 1989). These oligo- and polymeric phenolic compounds are composed of flavonoid subunits, and are often associated with antiherbivore (e.g., Barbehenn and Constabel, 2011) or antifungal properties (Jersch et al., 1989; Holeski et al., 2009; Morey et al., 2016). The bioactivity of condensed tannins relies mainly on their capacity to bind and precipitate proteins, nitrogenous compounds or metal ions (potentially decreasing resource availability), or on their oxidative properties (e.g., Lattanzio et al., 2006; Adamczyk et al., 2017) which can lead to enzyme inactivation. Both mechanisms are affected by the structure of condensed tannins (Barbehenn et al., 2006; Ropiak et al., 2017), which is known to

* Corresponding author. Research Centre for Ecological Change, Organismal & Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, PO Box 65, FI-00014, Finland.
E-mail address: paula.thitz@helsinki.fi (P. Thitz).

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vary between plant species or structures, or may even change in response to environmental conditions (Mueller-Harvey et al., 2019; Thitz et al., 2021).

Multiple bioassays have indicated fungistatic (growth-decreasing) activity of polyphenol (Hart and Hilllis, 1974) or tannin-containing extracts (Hart and Hillis, 1972; Anttila et al., 2013; Özgenç et al., 2017; Barbero-López et al., 2020), and bioassays with purified hydrolyzable tannins or other non-tannin polyphenols, such as lignins or their degradation products, have been conducted (Davidson et al., 1938; Hintikka, 1971; Scalbert, 1991; Nickerson et al., 2023). Despite the earlier work suggesting that condensed tannin-containing conifer extracts may have variable antifungal activity against fungi from different rot types (Anttila et al., 2013), we were not able to find earlier studies with well-characterized condensed tannins purified from ecologically relevant sources (needed for inferring how condensed tannin structure may affect their antifungal activity). Although the structure-activity relationships for the antiherbivore activity of condensed tannins have been studied (Ayres et al., 1997), we found no earlier studies that would combine the structural aspects of condensed tannins on their antifungal properties. Since wood-decaying fungi are adapted to live on substrates rich in specialized metabolites, it is not surprising that some of them have evolved ways to circumvent plant defences (e.g., Morel-Rouhier, 2021). This underlines the need to test the effects of purified condensed tannins with variable structures on multiple ecologically relevant fungal strains with variable specialization to the substrate from which the condensed tannins originated.

In nature, the fungal hyphae exploring plant tissues face typically not only one, but a mixture of different phytochemicals with different bioactivities (Routa et al., 2017). Depending on the chemical properties of individual compounds or their mode of activity against the specific fungi, mixtures of specialized metabolites can have synergistic (Schultz and Nicholas, 2000; Mattos et al., 2019) or antagonistic effects on the exploring hyphae. Reactions between the components of a mixture may influence the total reactivity or bioactivity, as has been observed in tannin mixtures (Barbehenn et al., 2006) or in combinations of specific alkaloids and phenolic compounds (Stermitz et al., 2000). Although condensed tannins can be expected to react with nitrogen-containing alkaloids (Hagerman, 2012) and coniferous tree species are known to produce bioactive piperidine alkaloid compounds (Tawara et al., 1993), the combined bioactivity of naturally occurring tannin-alkaloid mixtures against wood-decaying saprotrophs is unknown. Quantifying these interactive effects is relevant for assessing the ecosystem-wide impacts of plant material containing both compounds (such as Norway spruce litter) for fungal decomposition in comparison to systems where only one of these compound types occurs in significant amounts (such as in Scots pine-dominated forests; Virjamo et al., 2013; Virjamo and Julkunen-Tiitto, 2014, 2018).

To explore how the structures of condensed tannins relate to their ability to inhibit the growth of wood-decaying fungi, we conducted bioassays with purified condensed tannins against five wood-decaying fungi (conifer specialist brown-rot fungi *Coniophora puteana*, *Gloeophyllum trabeum* and *Rhodonia placenta*, and generalist white-rot fungi *Pleurotus ostreatus* and *Trametes versicolor*), many of which frequently occur both in natural and constructed settings (Kubart et al., 2016; Gabriel and Švec, 2017; Song et al., 2017; Cline et al., 2018) and are capable of causing substantial decay (Worrall et al., 1997). Conducting bioassays with condensed tannins purified from needles and bark of two ecologically and economically important boreal conifers, Norway spruce (*Picea abies* L. Karsten) and Scots pine, allowed us to make the first systematic comparisons of their fungistatic activities. Condensed tannin content in heartwood of these conifer species is not known, as most studies either did not separate wood from bark or only focused on the latter, although some records suggest Norway spruce wood is missing these compounds (Kemppainen et al., 2014). Hereafter, condensed tannins from these sources are referred to simply as 'conifer tannins' since gymnosperms lack other tannin groups such as hydrolyzable tannins (e.g., Kraus et al., 2004) that are based on tannic or gallic acid and common in angiosperms such as oaks (Barbehenn et al., 2006). Bioactivity of conifer tannins was compared to a commercially available condensed tannin mixture from quebracho (*Schinopsis lorentzii* Engl.). Additionally, we explored whether the condensed tannins extracted from Norway spruce had interactive effects with a piperidine alkaloid fraction extracted from Norway spruce (needles/bark) on one of the studied conifer specialists (low alkaloid availability limited this bioassay to a single species).

We expected to find fungistatic activity of conifer tannins on at least some of the studied fungi. Adaptations and counter-adaptations produced by evolutionary arms-race between plants and their antagonists (arms-race hypothesis, e.g. Whitehead et al., 2021) could be expected to either increase the efficacy of plant defenses against their specialized antagonists (in this case, boosting the conifer defenses against brown rot fungi specialized on them) or to increase the tolerance of specialized antagonists on those defenses (in this case, increasing the brown rot fungal tolerance to conifer defenses; Simpson et al., 2024) depending on whether plants or fungi are leading on the evolutionary tug-of-war. We expected that the growth of unadapted fungi will be inhibited by conifer condensed tannins, whereas the fungi that have already developed tolerance for this particular plant defense (i.e., are adapted on conifer materials) will not change their growth due to the presence of conifer condensed tannins. In some cases, the adapted fungi may even increase their growth in response to condensed tannin presence, since dietary specialization can be expected to provide them an evolutionary benefit for quickly colonizing condensed tannin containing wood materials. Due to the fundamental role of bark in protecting woody tissues against wood-decaying fungi (Pearce, 1996; Dossa et al., 2018; Chang et al., 2020), we expected bark tannins to have higher activity than needle tannins against the studied wood-decaying fungi, even if they are not specialized on using bark or needles as a carbon source. Further, we expected that *G. trabeum* (selected for the interaction tests due to its stable growth rate on malt agar) responds to the mixture of Norway spruce tannins and alkaloids in a non-additive manner, i.e., that these compounds have an interactive effect on this brown-rot causing fungi.

2. Materials and methods

2.1. Purification of potentially bioactive compounds

2.1.1. Condensed tannin fractions

Freeze-dried and homogenized needles and bark from 2–5-year-old seed-originated field-grown Norway spruce and Scots pine, collected annually during 2016–2019, were extracted at +4 °C by shaking in 80 % aqueous acetone. The soluble extract was collected, and the extraction of the residue with 80 % acetone repeated at least 3 times or until the extract obtained was nearly colourless. The ratio of plant dry weight (DW) to the total extraction volume was ca. 0.016 g/mL (0.014–0.018 g/mL), which resulted in similar extraction efficiencies within plant structures (Table S1). Acetone was removed from pooled extracts by rotary evaporation, and the aqueous extracts were freeze-dried. Chromatographic separation of extracts was done with the Sephadex LH-20 method modified from Salminen and Karonen (2011), which effectively removed the free sugars and majority of non-tannin low-molecular weight phenolics from the samples. The extracts were dissolved in 10 mL H_2O, filtrated (0.45 μm PTFE), and applicated on top of the equilibrated column, and the eluents specified in Table S1 were pumped at 5 mL/min through the column to separate the extract components into six fractions. Well-mixed fractions were sampled, organic solvents were removed by rotatory evaporation and the remaining aqueous phases were freeze-dried (Table S1). Sephadex column was balanced with 500 mL aqueous methanol and rinsed with at least 800 mL of H_2O between each fractionation.

Samples of Sephadex LH-20 fractions were filtered through 0.2 μm PTFE filter and analysed by UHPLC-DAD-MS/MS according to Engström

et al. (2014) to determine the concentrations, procyanidin content (PC %) and mean degree of polymerization (mDP) of condensed tannins in fractions. Purity of the tannins in the fractions was defined based on the absorbance at 280 nm in UHPLC-DAD, as the proportion of area that could be attributed to condensed tannins compared to the total peak area. Polymeric condensed tannins were separated mainly into Sep6 fractions obtained with 80 % acetone (Table S1). Molar concentrations of fractions were calculated based on average structure (PC/PD share and mDP) and mass concentration.

2.1.2. Alkaloid fractions

Alkaloids were purified from needles and bark of 3–5-year-old field-grown Norway spruce (collected annually during 2017–2019) using the solid-phase partitioning as described in Virjamo et al. (2013). Shortly, plant material homogenized in liquid N_2 was incubated in 0.5M HCl, after which pH of the filtrate was adjusted to at least 11 using 6M NaOH, and alkaloid fractions were chromatographically separated in Extrelut® NT20 column that was eluted with CH_2Cl_2. Alkaloid fraction was analysed with GC–MS (with EI ionization) as described in Virjamo et al. (2013), and total alkaloid concentration (as epihydropinidine equivalents) were defined as the sum of individual compounds (Table S2). After GC-MS analyses the organic solvent was evaporated with rotary evaporator, and the remaining alkaloids were redissolved in ultrapure H_2O and stored in −20 °C.

2.2. Fungal bioactivity tests

2.2.1. Fungal strains

The wood-decaying basidiomycetes used in this experiment were the brown-rot fungi *C. puteana* (strain BAM 112; order Boletales), *R. placenta* (also known as *Oligoporus placentus* or *Postia placenta*; strain BAM 113; order Polyporales) and *G. trabeum* (strain BAM 115; order Gloeophyllales), and the white-rot fungi *P. ostreatus* (strain BAM 96; order Agaricales) and *T. versicolor* (also known as *Coriolus versicolor* or *Polyporus versicolor*; strain BAM 116; order Polyporales), all purchased from the Federal Institute for Materials Research and Testing (BAM, Berlin, Germany).

2.2.2. Antifungal tests

The control growth medium in the antifungal tests was prepared by mixing 35 mg/mL malt extract and 20 mg/mL bacteriological agar in mQ-water and autoclaving the mixtures. To prepare the malt agar mixtures amended with tannins to test their antifungal activity (Table S3), the commercial water-soluble extract Colatan GT 10 (Unitán, Argentina), extracted from tannin-rich quebracho bark, and the four purified conifer tannin fractions (Sep6) were dissolved in 10 mL of water, sterilized by filtering through 0.2 μm PE-filter and mixed to sterile agar solutions. The final agar mixture contained 0.7 mg/mL of quebracho tannin (pH 5.498) or Sep6 fractions, the latter corresponding to 0.44–0.70 mg of pure conifer tannins per mL (or 0.18–0.22 mmol/L; Table 1) depending on the tannin source. Adding 0.7 mg/ml conifer tannin extracts did not affect the pH of the agar mixed with conifer tannins (Table 1) compared to the control medium (pH 5.388). For testing the synergetic or antagonistic effect of tannins and alkaloids (Table S3), concentrated Norway spruce alkaloid fractions (45 μg/μL for bark and 35 μg/μL for needle alkaloids) were diluted, and the volume leading to 25 μg alkaloids/mL was filtered and added to the mixtures. Since variable fungal growth responses could prevent detection of the potential interactive effects, and the quantity of purified alkaloid fraction limited the testing to a single fungal strain, we selected the conifer-adapted brown-rot species *G. trabeum* which grew at a more consistent rate compared to other species in our previous tests. The contents used for conifer tannins and alkaloids correspond to ca. 8 % of the average soluble condensed tannins (0.66–0.79 % of FW) and to ca. 8 % of the alkaloids (0.029–0.032 % of FW) in the corresponding plant structures, measured with UHPLC-DAD-MS/MS (Engström et al., 2014) or GC-MS (Virjamo et al., 2013), respectively. Equal volumes of malt agar mixture were pipetted on petri dishes (diameter 5.5 cm) stored in +4 °C until the beginning of the experiment.

Table 1
Tannin concentrations in conifer tannin treatments, and pH measured from corresponding media with unfiltered condensed tannin solutions. Mass and molar concentrations corresponding to 0.7 mg/mL of fraction concentration on agar were calculated based on purity and average molar mass of fractions (Table S1).

Plant material	mg tannin/mL	mmol/L	pH
Scots pine bark	0.44	0.22	5.381
Scots pine needle	0.70	0.18	5.346
Norway spruce bark	0.52	0.18	5.373
Norway spruce needle	0.66	0.22	5.376

The growth experiment was started by transferring a fungal plug with 5.5 mm diameter from an existing colony to Petri dishes with one of the control or treatment agar mixtures. The five fungi were used to test the fungistatic activity of Colatan GT10 and conifer tannins (5–6 replicates per fungi and growth medium, Table S3), while *G. trabeum* was used for testing the synergistic or antagonistic effect of tannins and alkaloids (5–7 replicates per growth medium, Table S3). Whenever not measured, petri dishes were kept in stable conditions (22 °C, 65 % relative humidity, no light). Growth of the fungal hyphae was followed daily by measuring the radius of fungal growth (r) at three representable directions until one day before the petri dishes were full, and the area overgrown by hyphae (A, as cm^2) was estimated as $A = \pi r^2_{mean}$. Each plate was carefully observed against a white light source to measure r based on the edge of fine hyphal extensions that advanced beyond the edge of profuse aerial mycelium that was easily observable on plates. The plates containing each fungi were followed until the first Petri dish (in any treatment with the same fungi) was fully covered with hyphae, and areas overgrown by hyphae one day before this were used for calculating the growth inhibition (%) as $(A_i - \bar{A}_{control})/\bar{A}_{control}$ and log-response ratios (Hedges et al., 1999), as $\ln(RR) = \ln(A_i) - \ln(\bar{A}_{control})$, where A_i is area overgrown by hyphae in observation i and $\bar{A}_{control}$ is the mean of areas in the corresponding control treatment. $\ln(RR)$ values below 0 indicate inhibited growth compared to control treatment.

Photos of all agar plates were taken 0–1 day after the first plate (per fungi) were full (Fig. S3; all photos available at https://doi.org/10.6084/m9.figshare.31150192). Within each fungal line, there were minor differences in colour between different treatments but the differences in fluffiness (which would have indicated an altered density or thickness of the hyphal layer due to tannin treatments, leading to different fungal biomasses) were relatively rare, allowing for the estimation of fungal growth rates based on hyphal extension compared to the corresponding control treatment.

Some fungi have complex enzymatic pathways to degrade organic compounds (Akhtar and Mannan, 2020), resulting in compounds produced and released to the growth substrate to degrade or cope with the harmful chemicals. The presence of a halo (a colored zone around the fungus without visible hyphae; Fig. S4) was recorded after 2–3 days of growth. These halos indicate that some change happened in the growth media around the fungi due to the treatments, probably caused by the enzymes released by fungi to cope with the antifungal agent.

2.3. Statistical analyses

Areas overgrown by fungi were analysed to determine whether the treatments (four different conifer tannins and quebracho tannins) had an overall effect on wood-decaying white- or brown-rot fungi based on the responses of the five fungi we studied (Table S4A; mixed model with fungi as random), and which of the tested tannin extracts affected growth in these specific fungi (Table S4B; non-mixed model with fungi as fixed, and interactive effect of fungi and treatment). Fungi-specific random intercepts in the approach with mixed models treat the

studied fungal species as a random sample from the population of wood-decaying fungi (e.g., Abrego and Ovaskainen, 2020). These random intercepts represent the average area overgrown by fungi over all treatments (e.g., Gelman, 2005).

We investigated the effects of plant structure and conifer species on fungal responses (areas overgrown with hyphae) with a mixed effect model specified in Table S5. The initial model included main and interactive effects for the plant structure and species, but since the interactive term did not improve model fit (likelihood-ratio tests, $p = 0.892$) it was removed, and inference was based on the corresponding main effects model (Table S5). The potential effect of different purity (content or concentration) of tannin fractions originating from different plant materials on area overgrown by hyphae on individual agar plates (models in Tables S4 and S5) was assessed by checking the correlations of residuals with fraction purity. No such correlations were found which indicates that fraction purity did not affect results in Table S4 or S5.

Structural data obtained from four conifer tannin fractions was combined with average areas overgrown by hyphae in five fungi exposed to the corresponding tannin fraction. The simultaneous main effects of PC% and mDP were analysed with mixed effect models specified in Table S6 (with random intercepts for each fungi) based on these 20 fungi- and treatment specific average area responses. These models included fraction purity (as tannin content or concentration, respectively shown in Table S6A or S6B) as a covariate, to ensure that its variability between different tannin fractions (Table S1) did not interfere with interpreting effects of tannin structure from these models.

Interactive effects of condensed tannins and alkaloids from Norway spruce on the area overgrown by *G. trabeum* hyphae were studied with full factorial models specified in Table S7 including interactive effects of tannin and alkaloid addition. Models were separately fit for needle and stem compounds (26 and 23 observations in Table S7A and S7B including the control treatments, respectively). Since no interactive effect of tannins and alkaloids was found, main effects were inferred from a corresponding main effect model.

In addition to area-based analysis described above, we performed the corresponding analyses using log-response ratios as the response variable in all models, but this had only minor effects on fungi-specific results (Fig. S1). All models were fit in R using the functions lm() in package stats (for non-mixed models; R Core Team, 2021) and lmer() in lmerTest (for mixed models; Kuznetsova et al., 2017). Research data and scripts related to this manuscript are available on Figshare (https://doi.org/10.6084/m9.figshare.31150192).

3. Results

3.1. Bioactivity of condensed tannins against wood-decaying fungi

The tannin content of purified fractions ranged from 63 % (Scots pine

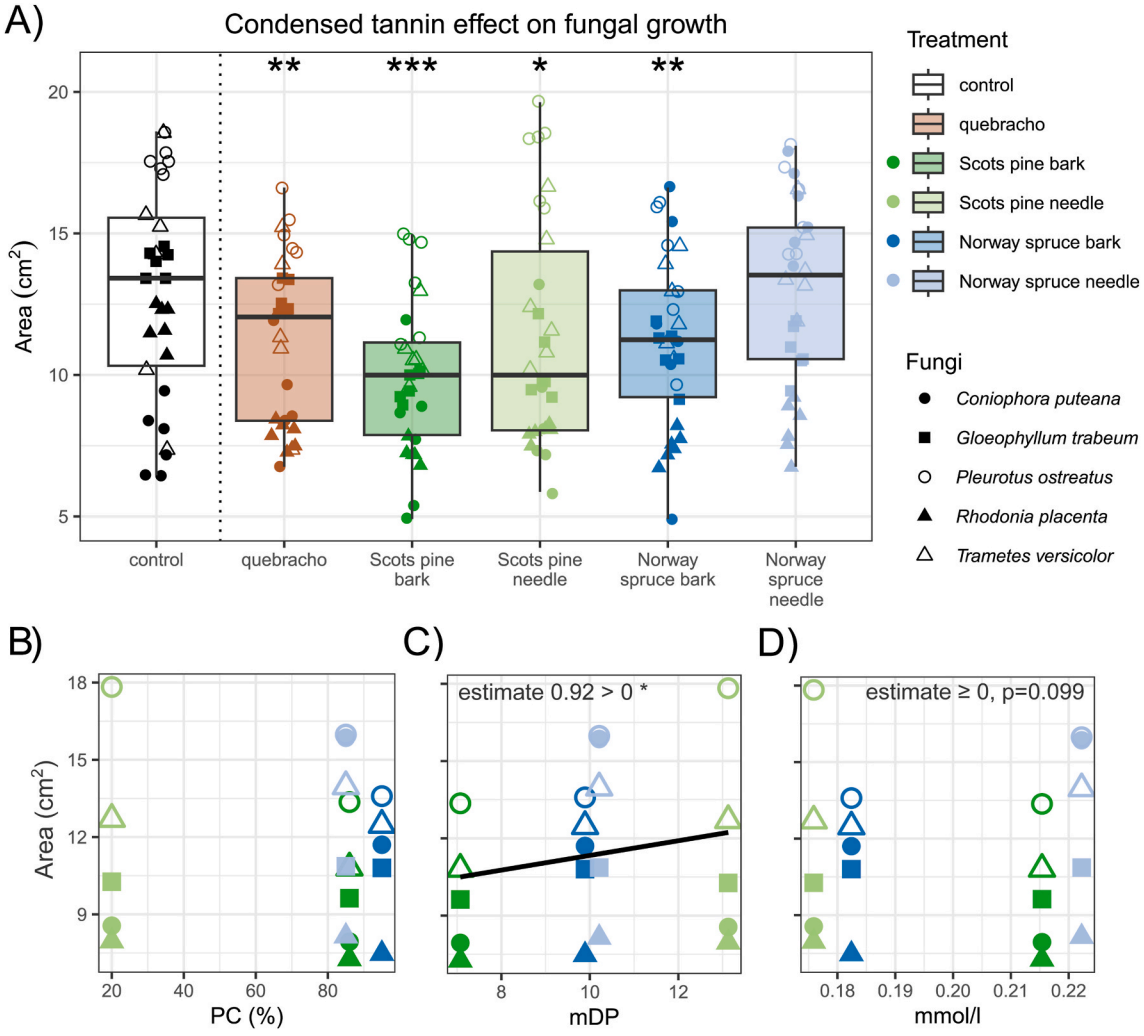

Fig. 1. A) Bioactivity of studied tannin fractions against saprotrophic fungi, shows as area overgrown by hyphae. Stars indicate treatments where fungal growth was inhibited compared to control treatment (fungi treated as random) with $0.01<p<0.05$ (*) or $p<0.001$ (***). B–C) The effects of tannin structure (PC or mDP) on the mean area overgrown by hyphae in different fungi, when molar concentrations of tannins (D) were used as a covariate.

bark) to 99 % (Scots pine needle; Table S1), but this variability did not affect fungal growth (covariate non-significant in Fig. 1D, Fig. S2C, and Table S6). There was within-strain variability in fungal growth rates, despite carefully preparing similar mediums and keeping all plates in equal conditions in the growth cabinet so that the only difference between the agar plates were different fungi and tannin treatments. For example within the control treatment, the area overgrown by fungi ranged between 84 % and 123 % (*C. puteana*), 91 %–106 % (*R. placenta*), 96 %–104 % (*G. trabeum*), 97 %–105 % (*P. ostreatus*) and 54 %–137 % (*T. versicolor*) compared to the mean on control plates with corresponding fungi.

Adding commercially available quebracho extracts or purified conifer tannins to malt agar decreased the growth of fungi relative to the control treatment ($F = 8.3$, $P < 0.001$; Table S4A). Average inhibition ranged from 8 to 22 % in the presence of quebracho and all conifer tannin treatments except for Norway spruce needle tannins, which had no overall effects on studied wood-decaying fungi (Fig. 1A). Sensitivity of fungi for the tannin treatments varied, with *R. placenta* and *G. trabeum* among the most and *C. puteana* the least sensitive (Table 2). On average, the studied brown-rot fungi (5.6 ± 13.1 % inhibition; mean and standard error) were nearly equally sensitive to conifer tannin treatments as the studied white-rot fungi (11. 1 ± 0.1 % inhibition; note that the means and standard errors overlap). The fungi-specific growth responses to condensed tannin treatments varied according to fungi and treatment ($F = 6.36$, $P < 0.001$; Table S4B). Responses of individual fungi varied from inhibited growth in some or all of the tannin treatments (*R. placenta*, *G. trabeum*, *P. ostreatus* and *T. versicolor*) to even enhanced growth in the presence of some tannin fractions (*C. puteana*; Fig. 2).

Transparent or slightly tan zone around the growing hyphae ('halo') was observed in the early days of the experiment regardless of the treatment in the brown-rot fungi *R. placenta* and *C. puteana*. No halo was found in any of the treatments in the brown-rot *Gloeophyllum trabeum*. In case of the white-rot fungus *T. versicolor*, yellowish and red halos occurred only in the treatments with quebracho or conifer tannins, but not in the control samples (Fig. 2). In the white-rot *P. ostreatus*, only the presence of Norway spruce tannins caused a yellowish halo (Fig. 2).

3.2. Comparison of different conifer tannins and the effect of structure on fungistatic activity

Plant structure ($F = 18.9$, $P < 0.001$) and species ($F = 13.8$, $P < 0.001$) from which conifer tannins were purified affected the fungal growth responses (Table S5). Tannin fractions from Scots pine were 17 % more inhibitory than the fractions from Norway spruce ($P < 0.001$; average inhibitions were 16.1 % and −0.8 %, respectively) while the fractions extracted from bark were 13 % more inhibitory than fractions from needles ($P < 0.001$; average inhibitions were 17.1 % and 4.0 %, respectively).

Procyanidin contents (PC%) varied between 20 % and 95 % and the mean degree of polymerization (mDP) between 7 and 13 subunits in conifer tannins fractions, while their purity ranged from 62 % to 99 %. Taken together, these results strongly suggest that the differences in tannin structure or composition in these conifer structures resulted in different fungistatic activity. However, none of the easily measurable traits of tannin structure or fraction quality were significantly related to average fungal responses when the mass concentration of tannins in the fraction (linearly related to purity) was used as a covariate (Fig. S1; Table S6A), but using molar concentration as a covariate revealed a significant positive relationship between fungal growth and mDP (Fig. 1B–D; Table S6B), indicating stronger antifungal activity on smaller tannin polymers.

Table 2
Average growth inhibitions (decrease in relative area of the agar plate covered by hyphae) caused by conifer tannin treatments per fungi. Mean and standard error (SE; n = 5–6) are shown and fungi belonging to different rot types are sorted from most to least sensitive to conifer tannins. Please note that the negative inhibition value indicates an increased hyphal area when conifer tannins are present compared to control.

Rot type	Fungi	Inhibition (%; mean ± SE)
brown	*Rhodonia placenta*	34.8 ± 2.5
brown	*Gloeophyllum trabeum*	25.8 ± 2.9
white	*Pleurotus ostreatus*	14.1 ± 5.9
white	*Trametes versicolor*	7.9 ± 6.1
brown	*Coniophora puteana*	−43.7 ± 22.2

3.3. Fungistatic effects of Norway spruce alkaloids and condensed tannins against Gloeophyllum trabeum

Growth of *G. trabeum* was inhibited by both condensed tannin fractions and alkaloid extracts from Norway spruce (Table S7A and B; Fig. 3), but no interactive effects between these two groups of plant defense compounds were found (non-significant interaction terms within needle and bark models; $F_{needle} = 1.33$, $P_{needle} = 0.261$ and $F_{bark} = 0.97$, $P_{bark} = 0.336$), indicating no synergistic or antagonistic effects of these bioactive compounds. Growth inhibition of *G. trabeum* by Norway spruce tannins (irrespective of plant structure) and Norway spruce bark alkaloids were approximately equal (inhibition was 22 % for both needle tannins and bark compounds), while needle alkaloids reduced growth only by 10 % compared to the control treatment without added defense compounds (Fig. 3).

4. Discussion

4.1. Condensed tannins have fungistatic effects against most tested saprotrophs

Despite the low condensed tannin amounts (0.4–0.7 mg/g or 0.18–0.22 mmol/L) in this study, most tested conifer tannin treatments showed fungistatic activity against wood-decaying fungi (Fig. 1A), agreeing with earlier studies indicating that extracts from Norway spruce and Scots pine can have antifungal activity at condensed tannin contents as low as 0.25 mg/ml in liquid media (Anttila et al., 2013). Conifer tannins reduced fungal growth by 12–24 % *in vitro*, which makes their fungistatic activity low compared to industrial antifungal agents (e.g., Barbero-López, 2020). Due to the time and logistic constraints in purifying large amounts of condensed tannins from plant material, the condensed tannin contents we were able to use in our *in vitro* experiment were only about 8 % of typical contents in needles and barks of Norway spruce and Scots pine (Matthews et al., 1997; Maie et al., 2003; Kanerva et al., 2008; Kemppainen et al., 2014; Virjamo et al., 2014; Tegelberg et al., 2018). Considering that antifungal assays typically observe positive dose-response relationships (Hintikka, 1996; Anttila et al., 2013; Tascioglu et al., 2013; Özgenç et al., 2017; but see Hart and Hilllis, 1974), our findings strongly suggest that the tannin concentrations in intact conifer materials are sufficient for slowing down the wood or needle colonization by wood-decaying fungi. Colonization is a natural part of the life cycle of most saprotrophs, and thus bark chemical composition would be expected to exert an evolutionary pressure for fungal adaptation similar to heartwood chemistry, even if bark defences against saprotrophs are not impermeable (Gilmartin et al., 2022). Thus, our data is consistent with the similar antifungal role of condensed tannins against wood-decaying fungi in conifers as in deciduous species (Ullah et al., 2017). This antifungal effect on saprotrophs is similar to condensed tannin effect on non-saprotrophic endophytes (Bailey et al., 2005) and pathogens (Hammerbacher et al., 2014).

Considering the importance of dead wood and fungal decomposition for carbon storage in forests (between 8 and 20 % of total carbon stocks; Cornwell et al., 2009; Fukasawa, 2021; Martin et al., 2021), the antifungal role of conifer condensed tannins may affect the carbon stored in forest biomass. Further, if conifer tannins have similar fungistatic effects also on free-living saprotrophs (i.e., decomposer fungi that live on soils

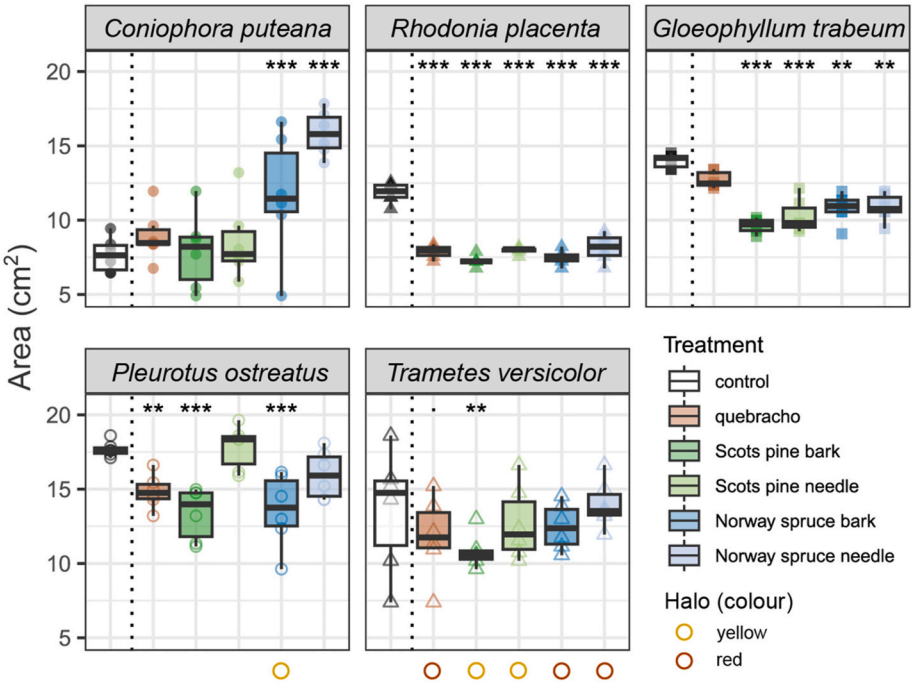

Fig. 2. Area overgrown by hyphae of the studied saprotrophs in different tannin treatments, with stars indicating the treatments where growth was inhibited compared to the control treatment (fungi treated as fixed), as $0.001<p<0.01$ (**), or $p<0.001$ (***). Colored halos early on the experiment are indicated by colored rings below the specific combinations of fungi and treatments where they systematically occurred.

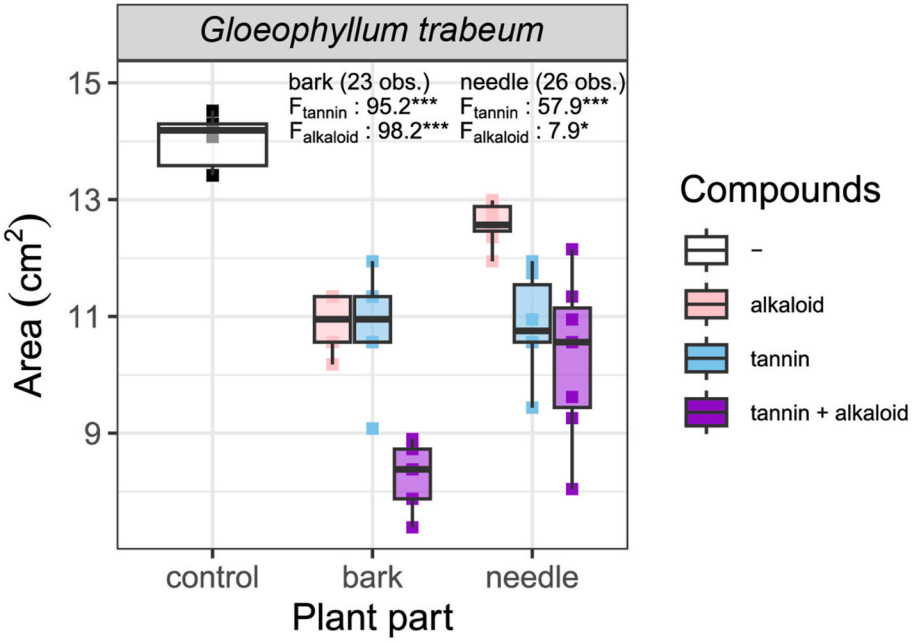

Fig. 3. Effects of Norway spruce tannins and alkaloids on the area overgrown by hyphae in *Gloeophyllum trabeum*. No interactive effects of tannins and alkaloids were found, so F-values and stars refer to the corresponding main effect models built separately for bark and needles. $0.01<p<0.05$ (*), $0.001<p<0.01$ (**), or $p<0.001$ (***).

and decompose plant litter or woody materials there), their tannin-containing litter may also influence the nitrogen dynamics in ecosystems dominated by ectomycorrhizal species, since these fungi may partly rely on saprotrophs to mobilize organic nitrogen from tannin-protein complexes in forest soils (Bending and Read, 1997; Wu et al., 2003). It is important to note that conifer tannin concentrations may respond to environmental changes (e.g., Julkunen-Tiitto et al., 2015), suggesting that the plant tannin content (and its potential ecosystem effects) may change with climate. Dose response studies using ecologically relevant and well-characterized tannins and several different study organisms will be needed to determine the condensed tannins effects on ecosystems.

Wood-decaying saprotrophs are at least partially limited to certain substrates by their decay processes (Goodell et al., 2008) and specialized endophytes have been shown to have higher tolerance for host defenses (Nickerson et al., 2023). White-rot fungi depolymerize both lignin and

cellulose enzymatically, while the brown-rot lineages descended from them have replaced ligninolytic enzymes with non-enzymatic processes (Hibbett and Donoghue, 2001; Eastwood et al., 2011). Broadly speaking, brown rot is the dominant rot-type in conifers (Simpson et al., 2024), even though comparison of Basidiomycete genomes suggests that different wood degradation systems fall on a continuum rather than strict rot-type categories (Riley et al., 2014). In an assay using hydrolysable tannins and 2 white and 2 brown-rot species, Tomak and Gonultas (2018) found the brown-rot spp. to be more susceptible. Other authors suggest a higher susceptibility in brown rot species specifically for the condensed tannins (Bopenga et al., 2020) or condensed tannins originating in conifers (Anttila et al., 2013; but see contrasting results of Özgenç et al., 2017). Our data with only marginally higher mean sensitivity of white compared to brown rot fungi and large variability within rot type categories did not support either of these conclusions (Fig. 2, Table 2) – instead, different fungal species had different tolerances to the tested conifer condensed tannins, suggesting that they are an active plant defence against a broad range of saprotrophs, in addition to their antiherbivore roles. Variable responses of conifer-specific brown rot fungi could support the arms-race hypothesis (Whitehead et al., 2021), as fungi frequently exposed to plant defences sometimes develop a resistance against them. The fungi-specific growth responses detected here (Fig. 2) would suggest that *C. puteana* is adapted on condensed tannin-containing conifers and specialized on growing on Norway spruce, and *R. placenta* and *G. trabeum* are non-adapted to either all or specifically to conifer bark condensed tannins (see also Table 2). Less frequent occurrence of the studied white-rot fungi (*P. ostreatus* and *T. versicolor*) on conifers may not allow for coevolutionary development between fungal resilience and condensed tannins. However, to fully disentangle the effects of rot type from host specificity, future experiments should include white-rot fungi specialized on conifers or brown-rot fungi specialized on hardwood trees (e.g., Simpson et al., 2024).

Alternatively, variable fungal responses could be related to some other evolutionary or ecological aspects. Different evolutionary history between species from Boletales (*C. puteana* increased growth in presence of spruce tannins) and from Polyporales and Gloeophyllales (*R. placenta* and *G. trabeum* decreased growth when at least conifer tannins were present) could relate to distinct brown rot responses to condensed tannins, even if the brown rot Polyporales *R. placenta* and white rot Polyporales *T. versicolor* did not respond to condensed tannins similarly (Fig. 2). Brown rot fungi are generally considered tolerant to oxidative stress or high temperature (Garcia et al., 2020; Castaño et al., 2021) and they have been suggested to be more tolerant to lignin degradation products (Hintikka, 1971), but despite the higher ROS tolerance of enzymes secreted by *R. placenta* compared *T. versicolor* (Castaño et al., 2021), these two species exhibited an opposite pattern for their tannin tolerance (Fig. 2).

Growth amelioration of the tannin-resilient brown-rot species *Coniophora puteana* in the presence of Norway spruce tannins (Fig. 2) may indicate that this generalist species (Kubart et al., 2016) which is also resilient to Scots pine terpenoids (Nerg et al., 2004) utilized either polymeric tannins or low-molecular weight phenolics of the extracts as a carbon source. The low-molecular weight phenolics could include dihydroflavonols (taxifolin or ampelopsin), which are structurally so similar to flavan-3-ols and condensed tannins that they cannot be removed with our chromatographic tannin purification method (Karonen et al., 2004), although it effectively removes free sugars or other low-molecular weight phenolics (Salminen and Karonen, 2011). The alternative carbon source for *C. puteana* could be condensed tannins themselves. Both condensed and hydrolysable tannins can in some cases increase microbial activity (Kraus et al., 2004; Mason et al., 2016; Prigione et al., 2018), although the specific responses depended on tannin origin and presumably structure similar to our results. Despite the early findings that certain filamentous fungi can sustain themselves on condensed tannins from wattle (*Acacia* sp.; Lewis and Starkey, 1969; see also Scalbert, 1991), microbial degradation of condensed tannins is poorly known compared to that of hydrolysable tannins, which can be degraded by tannases or gallic acid decarboxylases (e.g., Bhat et al., 1998; Prigione et al., 2018). Condensed tannins or their monomers could be inactivated either by degrading fungal enzymes (catechin oxygenases; Sambandam and Mahadevan, 1993; polyphenol oxidases, tyrosinases or peroxidases; Nichols-Orians, 1991; Gnanamani et al., 2001; Adamczyk et al., 2009) or by fungal laccases which could initiate polymerization leading to precipitation (see references in Prigione et al., 2018). Tannin degradation by certain soft-rot fungi has been observed (Vane et al., 2005), and specific enzymatic mechanisms in tannin-tolerant fungi including *Trametes versicolor* (which also has the capacity of tannin degradation in the presence of glucose, see Lewis and Starkey, 1969) have been elucidated (Archambault et al., 1996; Lorusso et al., 1996; Contreras-Domínguez et al., 2006). The relative resilience of *T. versicolor* to condensed tannins compared to *P. ostreatus* (sensitive to bark tannins) or *G. trabeum* (sensitive to all conifer tannins; Table 2, Fig. 2) matches the order of decreasing minimum inhibitory concentrations to unspecified tannins reported by Hintikka (1996) for closely related species. *T. versicolor* resilience could be related to frequent occurrence of this species on tannin-rich oaks (*Quercus* sp.; e.g., Hart and Hillis, 1972).

The halos observed around the white-rot fungi during the first days of fungal exposure to tannins (not observed in controls), show that the fungal exudation profile to the media changed in response to tannins. Corresponding colored halos (so called Bavendamm reaction) commonly occurring in white-rot and occasionally in brown-rot fungi exposed to tannic or gallic acids (Davidson et al., 1938) are commonly interpreted as quinone compounds caused by fungal polyphenol oxidases (e.g., Giltrap, 1982; So et al., 2017; Lee et al., 2020). However, we cannot fully exclude the possibility that halos observed in our experiment could have been fungal proteins precipitated by condensed tannins in the medium. To our best knowledge, this is the first study to report halo production in response to condensed tannins. However, it is worth noting that in this experiment two of the three studied brown rot fungi produced transparent halos also in control agar where the tannins were not present (Fig. 2, Fig. S4).

Discrepancies between results from different studies (compare our results to Anttila et al., 2013; Tomak and Gonultas, 2018) highlight the importance of knowing the chemical composition of studied extracts and calls the attention to how little is known of the resistance and vulnerability of wood-decaying fungi to different plant metabolites that persist in decomposing wood and needles (Venugopal et al., 2016; Paaso et al., 2017; Shay et al., 2018). In any case, the species-specific differences in the sensitivity of fungi to conifer tannins that were visible in our data (Fig. 2) as well as in earlier studies using multiple fungal strains (Anttila et al., 2013) underline the need for caution when drawing conclusions from studies using single fungal species.

Correspondingly, using single fungal strain per species and few fungal species can increase the probability that the effects observed in our study do not represent other strains or species. Future studies with purified condensed tannins from ecologically relevant sources and a wider selection of fungi will be needed to confirm our findings. In the case of our study, selecting the studied fungi from different rot types and from different brown-rot clades should increase the probability that the five studied fungi represent the variability of fungal responses to condensed tannins in general, supporting our conclusion that condensed tannins from Norway spruce and Scots pine bark and Norway spruce needles (Fig. 1A, Table S4A) may have a generalized antifungal effect on fungal saprotrophs. Future studies on antifungal activity of purified compounds should consider recording also other morphological responses of fungi than area overgrown by hyphae, such as hyphal density or biomass which may vary independently of the area-based growth responses, as may have occurred in *P. ostreatus*. Combining these approaches with enzyme assays done on malt agar or quantifying the lignin or cellulose degradation either from malt agar or from wood could

provide further insights into the mechanism of tannin toxicity or tolerance of saprotrophic fungi.

4.2. Origin and structure of conifer tannins affects their antifungal activity

Despite the relatively similar molar concentrations in conifer tannin treatments (Table 1), bark condensed tannins inhibited fungal growth more strongly than needle tannins (Fig. 1A). High bioactivity of bark tannins in Norway spruce was also noted by Anttila et al. (2013) who measured relatively similar bioactivities for enriched tannin fractions from bark and cone, despite a much lower acid butanol yield (indicating either lower condensed tannin content or different structure) in the former. The higher fungistatic activity of bark compared to needle tannins probably relates to the critical role of this organ in preventing saprotrophic fungi from accessing woody tissues including functionally important sapwood and cambium, which, in the absence of injuries, are thoroughly protected by bark (Pearce, 1996; Ulyshen, 2016; Chang et al., 2020). This forces the majority of wood-decaying fungi and herbivore or saproxylic fauna to by-pass the defences on plant's surface (Virjamo et al., 2013; Hammerbacher et al., 2014; Schmidt et al., 2010) before establishing on wood, even if some non-specialist fungal saprotrophs were frequently detected in sapwood of healthy *Fagus sylvatica* (Gilmartin et al., 2022). The competitive advantage that the wood-decaying fungi would get from early establishment (Boddy and Hiscox, 2016) probably explains their frequent occurrence within the endophyte communities of trees (Song et al., 2017; Cline et al., 2018; Gilmartin et al., 2022), which highlights the role of bark defences against saprotrophs already in living trees.

Compared to relatively few studies comparing extracts or compounds from different plant structures, bioactivity studies comparing extracts from different species are much more common (Broda, 2020). Species-specific differences we found in the antifungal capacity of tannins align well with earlier studies where both extracts and commercially available tannins were used (Tascioglu et al., 2013; Tomak and Gonultas, 2018). Contrasting the results from decay tests with wood blocks (Tascioglu et al., 2013), we found antifungal activity of conifer tannins *in vitro* also in some cases where quebracho tannin extracts were not active (Fig. 2), highlighting the impact of wood-retention capacity (largely determined by tannin structure) on the concentrations of water-soluble bioactive compounds remaining in leached wood.

Both the plant structure and species-specific differences in tannin bioactivity (higher when polymer fractions were purified from Scots pine compared to Norway spruce, and higher from bark compared to needles) should reflect differences in tannin structure (Ayres et al., 1997; Zeller, 2019), which is known to vary between species (Leppä et al., 2018) and plant structures (Hernes and Hedges, 2004). Despite the complexity hidden behind the commonly measured structural traits such as mDP or the proportion of dihydroxylated (PC%) to trihydroxylated flavan-3-ol subunits (PD%) in the tannin mixture (e.g., Kennedy and Taylor, 2003; Naumann et al., 2018; Zeller, 2019), we found a significant relationship between mDP of condensed tannins isolated from conifers and their antifungal activity. Surprisingly, the highest activity was found in fractions with lowest mDP of condensed tannins (Fig. 1C), contrasting some earlier findings (Ayres et al., 1997; Tavendale et al., 2005; Naumann et al., 2018) but supporting others (Jersch et al., 1989; see ref. in Patra and Saxena, 2011). We are not aware of earlier structure-activity studies specific to fungi, but at least for some modes of tannin bioactivity, there is evidence of an upper limit for polymer size that can interact with macromolecules (Hagerman, 2012; Vazquez-Flores et al., 2018). Higher antifungal activity of smaller tannin polymers (Fig. 1C) could be linked to the suggested role of fungal laccases as initiators of polymerization in tannin-tolerant fungi (Prigione et al., 2018) which could provide a mechanistic explanation for the tolerance of *T. versicolor*, which is capable of producing these enzymes (e.g., Hart and Hillis, 1972; Boddy and Hiscox, 2016). Despite the earlier suggestions that flavan-3-ol trihydroxylation would increase their inhibitory activity against micro-organisms (Scalbert, 1991), we found no such pattern for saprotrophic fungi (Fig. 1B).

Importantly, the effect of tannin structure on bioactivity became visible only when the analysis accounted for the molar concentration of fractions. Molar concentrations reflect the interactions between individual molecules more accurately than the corresponding mass concentrations or contents (mg/g), which may give misleading results especially when there are large size differences in the studied molecules. Since earlier bioactivity or structure-activity studies mostly use mass-based measures, our recommendation would be to include both molar and mass concentrations in the statistical analyses and publications when they are available (molar concentrations cannot be calculated if the average molar mass of the tannin mixture is not known).

Polymer size of condensed tannins may also affect practical applications where tannin-containing extracts are imbued in wood to increase its resilience to decay – too large a polymer size may inhibit tannin retention in fine-grained wood, leading to leaching and reduced antifungal properties of the processed wood (Tascioglu et al., 2013). Leaching from wood is a common problem in bio-based wood preservatives, which commonly happens for water-soluble compounds such as caffeine (Kwaśniewska-Sip et al., 2019). While tannins and tannin-rich extracts are considered potential wood preservatives, their high leachability from wood hinders their use in this field (Barbero-López et al., 2021), which highlights the relevance of understanding the role of the polymer size in tannin fixation to wood. Another practical aspect arising from working with high polymers is their tendency to self-aggregate (Kennedy and Taylor, 2003).

4.3. No evidence for interclass synergies or antagonistic effects between conifer defense compounds

Intra- or interclass synergies between secondary metabolites could explain the relatively modest bioactivities of individual compounds (Richards et al., 2016; Virjamo et al., 2020), although this may not be the main driver for phytochemical diversity (Whitehead et al., 2021). Despite the demonstrated synergistic antibacterial activities of certain alkaloids and polyphenols isolated from *Berberis fremontii* (Stermitz et al., 2000) and the predicted reactivity of alkaloids with condensed tannins (Adamczyk et al., 2017), we found no evidence of non-additive (synergistic or antagonistic) interactions between tannins and alkaloids from Norway spruce against the tested tannin-sensitive wood-decaying fungus *G. trabeum* (Fig. 3).

Assuming that the interactions between tannins and alkaloids did not remain undetected in this study simply due to kinetic constraints (too short time from mixing the alkaloid and tannin fractions to agar to the beginning of antifungal assays), the accumulation of two compound classes with additive antifungal activities in Norway spruce (Fig. 3) could explain the lower growth-reducing activity of its tannin fractions compared to Scots pine (Fig. 1A and results in 3.2) which nearly lacks alkaloids (Virjamo et al., 2013; Virjamo and Julkunen-Tiitto, 2014, 2018). Thus, our overall results comply with the costs of defense (Stamp, 2003) pushing the two boreal conifer species with similar exposure to fungal antagonists to investing in either two different types of antifungal compounds or maximizing the defensive capacity of the chosen class of antifungal compounds. Future studies on the topic should also consider the influence of other conifer specialized metabolites such as terpenes (Nerg et al., 2004), alone and in combination with conifer phenolics and alkaloids.

4.4. Applied perspectives and conclusions

Conifer tannins show potential for developing less-toxic wood-preservatives although their ecotoxicological properties remain to be assessed similar to what has been started for tannic acids (Libralato et al., 2011). The high tannin-tolerance of *Coniophora puteana*, which

can also degrade polyaromatic hydrocarbons (Memić et al., 2020), could lead to interesting potential in bioremediation. Low retention or high leachability of conifer-originating tannins from wood blocks (Tascioglu et al., 2013; Tomak and Gonultas, 2018) still needs to be overcome for practical wood-protection applications. Condensed tannins purified from Scots pine bark (with the smallest mean degree of polymerization) inhibited fungal growth most efficiently, affecting all but one tannin-resilient fungi. The highest antifungal activity in smallest studied conifer tannins opens interesting venues for development of less-toxic wood preservative solutions, as low degree of polymerization may alleviate the leaching problems.

Climate change-related changes in condensed tannin contents of conifers could have implications for fungi that decompose wood and for carbon-sink capacity of natural and managed forests. Understanding the implications of antifungal capacity of condensed tannins for the ecological roles that fungal saprotrophs play in boreal forests will require combining results from approaches using purified compounds in controlled conditions, applied both singly and as ecologically relevant mixtures, and from experimental setups that account for the naturally occurring spatial heterogeneity in different wood defensive compounds.

To conclude, condensed tannins from Norway spruce and Scots pine had generalized antifungal activity against the studied wood-decomposing fungi, but the antifungal activity was unrelated to fungal specialization on conifers (rot type). Higher bioactivity of bark compared to needle condensed tannins can be related to bark's protective function against fungal decomposers or herbivores that might otherwise attack sapwood and cambium critical for tree functioning. Bioassays with the conifer specialist *G. trabeum* did not reveal synergism or antagonism between Norway spruce alkaloids and condensed tannins, but structural features of conifer tannins were related to their antifungal activity, with consequences for their applied wood protection potential.

CRediT authorship contribution statement

Paula Thitz: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Maarit Karonen:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Aitor Barbero-López:** Writing – review & editing, Methodology, Investigation, Funding acquisition. **Antti Haapala:** Writing – review & editing, Resources, Methodology. **Virpi Virjamo:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funeco.2026.101499.

Data availability

Research data and scripts related to this manuscript are available on Figshare dataset (doi-link to published data repository).

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