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# Bark controls tree branch-leached dissolved organic matter production and bioavailability in a subtropical forest

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**Abstract** Bark is an essential component of tree branches, yet its role in controlling branch-leached dissolved organic matter (DOM) characteristics remains unknown in forests. Here, we collected branches (about 1.5 cm in diameter) of two evergreen coniferous trees, two deciduous broadleaf trees, and three evergreen broadleaf trees from a subtropical forest in southern China, and subsequently used a bark removal experiment to determine the effects of bark on branch-derived DOM quantity and bioavailability. Regardless of tree type, the presence of bark reduced tree branch-leached dissolved organic carbon (DOC), dissolved total nitrogen (DTN), and dissolved total phosphorus (DTP) productions. Moreover, DOC, DTN, and DTP productions leached from the branches containing bark were always much lower than the expected values summed from barks and the branches without bark. The presence of bark increased DOM aromaticity in the broadleaf tree branch leachates but reduced DOM aromaticity in the coniferous tree branch leachates. During 42 days of incubation, the presence of bark decreased broadleaf tree branch-leached DOM bioavailability and the relative increments of aromaticity, whereas the opposite trends were observed for the coniferous tree branch-leached DOM. Tree branch-derived DOM bioavailability correlated negatively with $SUVA_{254}$ values, but exhibited no relationship with either DOC:DTN ratio or DOC:DTP ratio. These observations highlight that tree bark can prevent DOM leaching from branches and regulate branch-leached DOM bioavailability via its effect on DOM aromaticity in subtropical forests.

**Keywords** Bark function · DOM aromaticity · Leaching · Stoichiometry · Tree type

## Introduction

Dissolved organic matter (DOM) represents a small but crucial fraction of soil organic matter in forests due to its relatively high mobility and bioavailability (Neff and Asner 2001; Kindler et al. 2011). Generally, DOM acts as fuel for heterotrophic microorganisms (Kalbitz et al. 2003; Joly et al. 2016), and thus plays a critical role in microbial-mediated ecological

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processes (Gunnenberger and Kaiser 2003; Kalbitz et al. 2003; Cotrufo et al. 2015). As most plant biomass returns to soils as plant litter, plant litter-leached soluble organic matter during decomposition is regarded as an essential source of DOM in forest soils (Guggenberger and Kaiser 2003; Schreeg et al. 2013). Although the importance of litter-leached DOM has been widely acknowledged (Bantle et al. 2014; Soong et al. 2014; Hensgens et al. 2020), the underlying mechanisms controlling litter-leached DOM amounts and bioavailability are still unclear in forests. To address these knowledge gaps, it is necessary to clarify how litter physical and chemical traits affect litter-leached DOM characteristics in forests.

Wood litter is an essential component of carbon (C) stock in forests (Russell et al. 2015; Magnússon et al. 2016), accounting for about 8% of glocal forest C stock (Pan et al. 2011). Thus, wood litter decomposition plays a pivotal part in regulating C and nutrient cycles (Russell et al. 2015; Harmon et al. 2021). In general, woody tissue is covered by bark, which contributes to about 14% of aboveground woody biomass in forests (Schepaschenko et al. 2017). However, bark and inside wood (i.e., wood without bark) are often considered as a whole plant organ, and the bark effect on wood litter decomposition has been overlooked in forests. Recently, Dossa et al. (2018) have pointed out that bark acts as a physical barrier to soil decomposers, decelerating early-stage wood litter decomposition. In addition to biota-mediated decomposition, leaching is also a key process controlling wood litter decomposition, especially in the early stage (Park and Matzner 2003; Russell et al. 2015). During leaching, bark may influence litter-derived DOM production via its effect on wood litter physical traits such as litter surface roughness and specific surface area (Kammer and Hagedorn 2011; Soong et al. 2014). However, it is unclear whether bark could physically prevent the leaching of DOM from wood litter. In forests, wood litter-leached DOM is crucial to regulate greenhouse gas emission, nutrient availability, and soil organic matter formation and stabilization (Cotrufo et al. 2015; Magnússon et al. 2016; Harmon et al. 2021). Accordingly, additional studies are urgently needed to uncover the role of tree bark in controlling wood litter-leached DOM production.

Litter-derived DOM bioavailability is often influenced by the initial C quality and nutrient availability, both of which are determined by litter chemistry (Don and Kalbitz, 2005; Bantle et al. 2014; Kim et al. 2014). In the wood tissues, bark includes the layer of cells outside the vascular cambium and is often divided into inner and outer parts (Rosell et al. 2014). In general, the inner bark consists primarily of living phloem, phelloderm, and cork cambium, and thus stores and transfers carbohydrates and nutrients, whereas the outer bark is predominantly comprised of rhytidome, and thus acts as a protective layer against herbivores, pathogens, and fire (Franceschi et al. 2005; Rosell et al. 2014). In contrast, inside wood in the wood tissue is mainly composed of xylem, and thus acts as the mechanical support. Due to the contrasting functions, bark generally has greater concentrations of nutrients and defensive compounds (e.g., condensed tannins and phenolic compounds) (Ganjegunte et al. 2004; Harmon et al., 2021) but lower lignin (Ganjegunte et al. 2004; Feng et al. 2013) and hemicelluloses (Schädel et al. 2010) concentrations than the inside wood. Therefore, the presence of bark may exert a substantial influence on wood litter-derived DOM bioavailability through its effects on C quality and nutrient availability in forests.

In this study, we collected tree branches of two evergreen coniferous trees (*Pinus massoniana* and *Pinus elliottii*), two deciduous broadleaf trees (*Liquidambar formosana* and *Quercus fabri*), and three evergreen broadleaf trees (*Cyclobalanopsis glauca*, *Machilus pauhoi*, and *Michelia macclurei*) from a subtropical forest in southern China and performed a bark removal experiment to assess the impact of bark on branch-leached DOM quantity and bioavailability. We used the amounts of dissolved organic carbon (DOC), total nitrogen (DTN), and total phosphorus (DTP) to represent DOM production and used the specific ultraviolet absorbance at 254 nm ($SUVA_{254}$) to indicate DOM aromaticity (Weishaar et al. 2003). Afterward, we conducted a 42-day standard incubation experiment to assess branch-leached DOM bioavailability. The main aim of this study was to reveal how tree bark affects branch-derived DOM production and bioavailability in a subtropical forest of southern China. We hypothesized that: (1) the presence of bark would reduce branch-leached DOM production due to its physical protection, and (2) the presence of bark would enhance DOM bioavailability because of the greater nutrient concentrations and associated higher nutrient availability in the tree branch leachates.

## Materials and methods

### Study site

In this study, tree branches were collected from a subtropical forest located in the long-term Forest Restoration Experimental Station of Jiangxi Agricultural University (26°55′16″ N, 114°48′14″ E), Taihe County, Jiangxi Province, southern China. This forest was established in 1991 to control soil erosion and restore degraded land. The study site belongs to the subtropical monsoon climate zone with the annual mean temperature and precipitation of 18.6 °C and 1726 mm, respectively. In this forest, mean stand density, tree height, and tree diameter at breast height are about 1120 tree ha$^{-1}$, 10.1 m, and 16.7 cm, respectively. The main tree species include *Liquidambar formosana*, *Cyclobalanopsis glauca*, *Pinus massoniana*, *Pinus elliottii*, *Michelia macclurei*, and *Machilus pauhoi*, and the understory species are ferns such as *Dryopteris championii*, *Woodwardia japonica*, and *Dicranopteris pedata*. The detailed information about the study site is shown in Xu et al. (2021).

### Litter sampling and measurement

In this study, we selected two evergreen coniferous trees (*P. massoniana* and *P. elliottii*), two deciduous broadleaf trees (*L. formosana* and *Q. fabri*), and three evergreen broadleaf trees (*C. glauca*, *M. pauhoi*, and *M. macclurei*) to assess the effect of bark on tree branch-leached DOM quantity and bioavailability. For each tree species, we randomly chose six target individuals with similar tree height and diameter at breast height as replicates in April 2020. Fresh branches with about 1.5 cm in diameter were collected from four directions of every target tree with pruning shears, cut into sections of 4 cm in length, and mixed. Subsequently, we used a knife to remove bark from half of the branches. In this study, bark was defined as all tissues outside the vascular cambium in the tree branch (Rosell et al. 2014). In the whole branch, the initial mass proportion of inside wood and bark is shown in Table S1. Bark, the branches without bark, and the branches with bark were divided into two subsamples. The first subsample was used to measure the initial physical and chemical properties, and another subsample was used for the leaching experiment.

For each litter type, litter density and dry matter content were measured according to the procedures of Pérez-Harguindeguy et al. (2013). Fresh plant organs were weighed, oven-dried at 65 °C to the constant weight, and re-weighed to determine the initial moisture content. Subsequently, the oven-dried plant materials per litter type were milled to pass through a 0.15-mm sieve and stored for measuring initial litter properties. Organic C and total N concentrations were measured on a FlashSmart CHNS/O Elemental Analyzer (Thermo Fisher Scientific, Bremen, Germany), total P concentration was measured colorimetrically on an Auto Discrete Chemical Analyzer (Smartchem 140, AMS Alliance, Italy) after acid digestion, and total polyphenols concentration was determined with the Folin–Ciocalteau method (Yu and Dahlgren 2000). For each tree type, the initial litter properties were the mean values of tree species within the same type. The initial litter properties are shown in Table 1.

Litter-leached DOM was obtained with a soaking experiment (Schreeg et al. 2013). Three pieces of whole branches, three pieces of branches without bark, and two grams of bark were used in this leaching experiment. Litter samples were soaked in deionized water (1:50 mass:volume ratio) in 500-mL jars at 20 °C in the dark for 24 h. Litter leachates were filtered through 0.7 µm Whatman™ GF/F glass microfiber filters (Little Chalfont, Buckinghamshire, UK) and used to measure DOM properties. In the leachates, DOC and DTN concentrations were determined with the dry combustion method on a total organic carbon analyzer (multi N/C 2100S, Analytik Jena, Germany), DTP concentration was determined colorimetrically after peroxodisulfate oxidation (Ebina et al. 1983), and the absorbances of DOM at 254 nm were determined with an ultraviolet–visible spectrophotometer (UV600SC, Jinghua Instruments, Shanghai, China). Dissolved organic C, DTN, and DTP productions were calculated from the amounts of DOC, DTN, and DTP in the leachates and litter dry mass, respectively, and SUVA$_{254}$ value was quantified by dividing the absorbances at 254 nm by DOC concentration (Weishaar et al. 2003).

Dissolved organic matter bioavailability was assessed with the standard laboratory incubation

**Table 1** Initial tree litter properties in a subtropical forest of southern China

| Organ type | Organic C (mg g$^{-1}$) | Total N (mg g$^{-1}$) | Total P (μg g$^{-1}$) | C:N ratio | C:P ratio | Polyphenols (mg g$^{-1}$) | Litter density (g cm$^{-3}$) | Leaf dry matter content (%) |
|---|---|---|---|---|---|---|---|---|
| Evergreen coniferous tree | | | | | | | | |
| Branch with bark | 454(2)c | 2.75(0.05)b | 442(6)b | 165(3)b | 1030(15)b | 18.9(0.4)b | 0.426(0.002)b | 438(4)b |
| Branch without bark | 482(3)a | 1.73(0.06)c | 377(7)c | 281(11)a | 1282(23)a | 6.9(0.2)c | 0.447(0.003)a | 474(4)a |
| Bark | 469(3)b | 4.47(0.11)a | 553(8)a | 105(3)c | 851(15)c | 38.8(0.6)a | 0.400(0.002)c | 270(2)c |
| Deciduous broadleaf tree | | | | | | | | |
| Branch with bark | 460(2)ab | 3.33(0.05)b | 410(5)b | 138(2)b | 1125(12)b | 26.6(0.5)b | 0.509(0.003)b | 585(2)b |
| Branch without bark | 464(3)a | 2.07(0.05)c | 360(5)c | 224(6)a | 1289(22)a | 9.1(0.2)c | 0.538(0.003)a | 616(1)a |
| Bark | 451(4)b | 6.55(0.07)a | 537(5)a | 69(1)c | 840(7)c | 68.2(1.2)a | 0.457(0.002)c | 329(2)c |
| Evergreen broadleaf tree | | | | | | | | |
| Branch with bark | 454(4)a | 6.10(0.03)a | 431(4)b | 146(2)b | 1055(17)b | 25.4(0.3)b | 0.515(0.002)b | 623(1)b |
| Branch without bark | 455(5)a | 2.10(0.05)c | 392(2)c | 218(4)a | 1162(10)a | 11.2(0.6)c | 0.550(0.003)a | 647(3)a |
| Bark | 452(3)a | 5.70(0.07)b | 524(4)a | 79(2)c | 863(5)c | 62.0(1.1)a | 0.461(0.003)c | 347(2)c |

The standard errors of the means ($n=6$) are shown in the parentheses. At each tree type, different letters in the same column indicate significant differences among plant organs ($P<0.05$)

experiment (Don and Kalbitz 2005). Before incubation, we obtained microbial inoculum by soaking 30-g fresh forest soils (0–10 cm depth) in 750 mL deionized water in the dark at about 20 °C for 12 h. When necessary, DOC concentration in the litter leachates was diluted to about 20 mg L$^{-1}$ to avoid excessive growth of microorganisms. For each litter treatment, 50 mL diluted litter leachates and 5 mL microbial inoculum were placed in 500 mL glass bottles. In addition, we established 12 glass bottles containing 50 mL deionized water and 5 mL microbial inoculum as blanks. All glass bottles were aerobically incubated in the dark at 20 °C. After 14 and 42 days of incubation, the waters in the glass bottles were sampled, filtered, and used to measure DOC concentration and SUVA$_{254}$ values. In total, there were 252 glass bottles (seven tree species × three organ types × six replicates × two sampling dates). Litter-derived DOM bioavailability (%) was obtained by the proportional losses of DOC concentration during incubation, and the relative change of SUVA$_{254}$ (%) was expressed as the proportion of the initial SUVA$_{254}$ value.

## Calculation and statistical analyses

The statistical analyses were performed with R version 3.6.1 (R Development Core Team 2019), and the significant level was $\alpha=0.05$. First, linear mixed models were performed to assess the responses of litter-derived DOM variables to tree type and organ type using the 'nlme' package. Similarly, the responses of DOM bioavailability and the relative changes of SUVA$_{254}$ value to incubation time, tree type, and organ type were also assessed with the linear mixed models. Second, Tukey's HSD was used to test the differences in DOM properties among the organ types in the 'agricolae' package. Last, a nonlinear regression analysis was used to examine the relationship between DOM bioavailability and the initial DOM properties.

In this study, we calculated the expected DOC (or DTN or DTP) production using the following function:

$$P_{expected} = Bark_p \times P_{bark} + Inside\ wood_p \times P_{wood},$$

where $P_{expected}$ was the expected DOC (or DTN or DTP) production of the whole branches including bark and inside wood, $Bark_p$ was the mass proportion of bark in the whole branches, $P_{bark}$ was bark-leached DOC (or DTN or DTP) production, $Inside\ wood_p$ was the mass proportion of inside wood in the whole branches, and $P_{wood}$ was inside wood-leached DOC (or DTN or DTP) production. To test the effect of bark on DOM productions, a paired *t*-test was conducted to compare the difference in observed and expected values with the 'stats' package.

## Results

Tree type, organ type, and their interaction significantly influenced DOC production, DTN production, DTP production, DOC:DTN ratio, DOC:DTP ratio, and $\mathrm{SUVA}_{254}$ value (all $P < 0.001$, Table 2). Regardless of tree type, DOC, DTN, and DTP productions were greatest for bark, but lowest for the branches with bark among three organ types ($P < 0.05$, Table 3). Within each tree type, the expected branch-leached DOC, DTN, and DTP productions were higher than the observed values, respectively (all $P < 0.001$, Fig. 1). Among the three organ types, DOC:DTN ratio, DOC:DTP ratio, and $\mathrm{SUVA}_{254}$ value were highest for bark within broadleaf trees, but were often lowest for bark within evergreen coniferous trees (Table 3).

Incubation time, tree type, organ type, and their interactions significantly affected DOM bioavailability and the relative changes of $\mathrm{SUVA}_{254}$ value (Table S2). For evergreen coniferous trees, DOM bioavailability and the relative changes of $\mathrm{SUVA}_{254}$

**Table 2** Results (*F* values) of linear mixed models on the effects of tree type (T), organ type (O), and their interaction on litter-derived dissolved organic matter variables in a subtropical forest of southern China

| | DOC production | DTN production | DTP production | DOC:DTN ratio | DOC:DTP ratio | $\mathrm{SUVA}_{254}$ |
|---|---|---|---|---|---|---|
| T | 1505*** | 191*** | 416*** | 1082*** | 352*** | 1584*** |
| O | 8669*** | 1849*** | 2713*** | 1306*** | 1709*** | 957*** |
| T×O | 1011*** | 179*** | 274*** | 362*** | 731*** | 916*** |

*DOC* dissolved organic carbon, *DTN* dissolved total nitrogen, *DTP* dissolved total phosphorus, $SUVA_{254}$ the specific UV absorbance at 254 nm

*$P < 0.05$

**$P < 0.01$

***$P < 0.001$

**Table 3** Tree litter-derived dissolved organic matter characteristics in a subtropical forest of southern China

| Organ type | DOC production mg $g^{-1}$ | DTN production μg $g^{-1}$ | DTP production μg $g^{-1}$ | DOC:DTN ratio | DOC:DTP ratio | $\mathrm{SUVA}_{254}$ L mg $C^{-1}$ $m^{-1}$ |
|---|---|---|---|---|---|---|
| Evergreen coniferous tree | | | | | | |
| Branch with bark | 0.51(0.01)c | 13.7(0.2)c | 2.5(0.1)b | 37.0(0.7)a | 207(8)a | 1.77(0.03)b |
| Branch without bark | 0.72(0.01)b | 24.7(0.5)b | 3.5(0.1)b | 29.1(0.6)b | 204(7)a | 2.01(0.02)a |
| Bark | 3.77(0.07)a | 123.6(3.1)a | 27.3(0.5)a | 30.6(1.0)b | 139(4)b | 1.15(0.02)c |
| Deciduous broadleaf tree | | | | | | |
| Branch with bark | 1.10(0.02)c | 31.9(0.7)c | 7.5(0.2)c | 34.5(1.3)b | 147(6)b | 2.65(0.04)b |
| Branch without bark | 1.83(0.03)b | 63.4(1.7)b | 15.5(0.4)b | 29.0(1.1)b | 118(3)c | 1.95(0.02)c |
| Bark | 13.90(0.21)a | 83.4(2.9)a | 18.4(0.3)a | 167.0(4.0)a | 754(11)a | 3.93(0.04)a |
| Evergreen broadleaf tree | | | | | | |
| Branch with bark | 0.84(0.02)c | 12.2(0.2)c | 8.1(0.2)c | 69.1(2.0)c | 105(5)b | 2.23(0.02)b |
| Branch without bark | 1.73(0.04)b | 18.7(0.3)b | 16.8(0.4)b | 92.5(2.0)b | 103(4)b | 1.18(0.02)c |
| Bark | 15.10(0.20)a | 75.4(1.4)a | 32.1(0.6)a | 201.0(4.0)a | 472(14)a | 2.88(0.04)a |

The standard errors of the means ($n = 6$) are shown in the parentheses. At each tree type, different letters in the same column indicate significant differences among plant organs ($P < 0.05$)

*DOC* dissolved organic carbon, *DTN* dissolved total nitrogen, *DTP* dissolved total phosphorus, $SUVA_{254}$ the specific UV absorbance at 254 nm

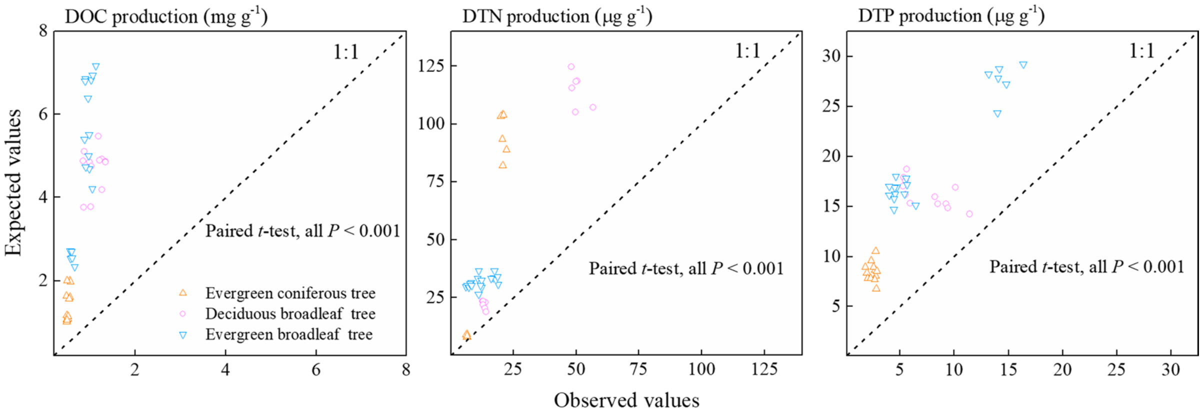

**Fig. 1** Observed and expected branch-leached DOC, DTN, and DTP productions during 24-h leaching in a subtropical forest of southern China. *DOC* dissolved organic carbon, *DTN* dissolved total nitrogen, *DTP* dissolved total phosphorus

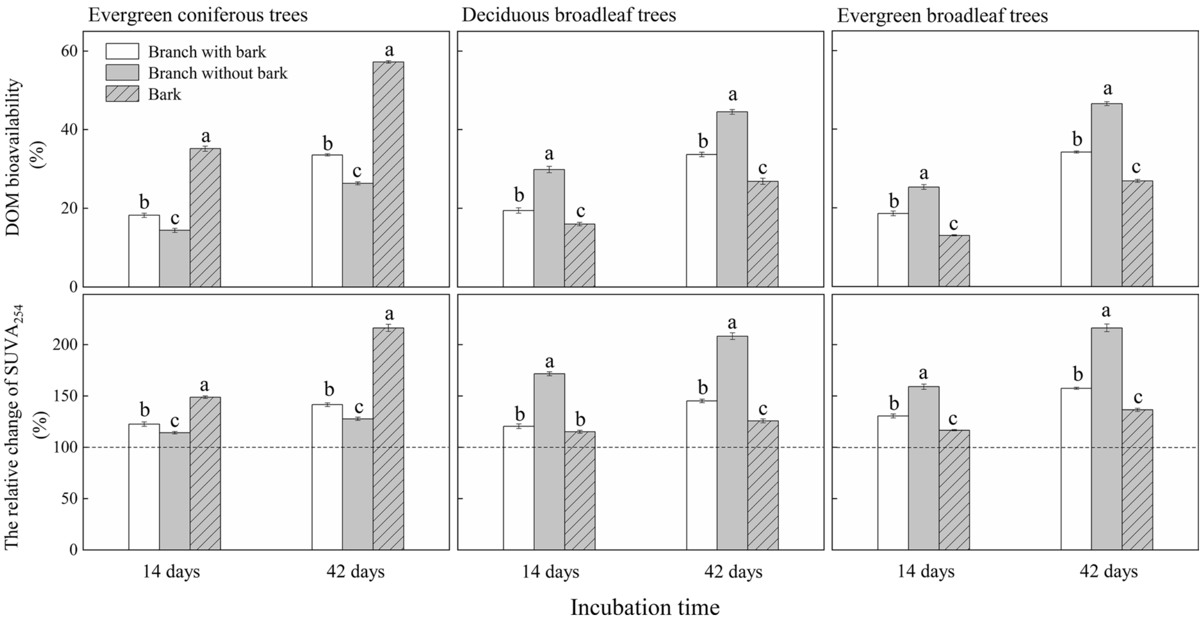

**Fig. 2** Litter-leached DOM bioavailability and the relative change of $SUVA_{254}$ during 42-day incubation in a subtropical forest of southern China. The error bars are the standard error of the means ($n = 6$). Different letters indicate the significant differences ($P < 0.05$) among three organ types after 14 and 42 days of incubation. *DOM* dissolved organic matter, *$SUVA_{254}$* the specific UV absorbance at 254 nm

value were greatest for bark, but were lowest for branches without bark among the three organs across 42 days of incubation ($P < 0.05$, Fig. 2). For both evergreen and deciduous broadleaf trees, DOM bioavailability and the relative changes of $SUVA_{254}$ value were lowest for bark, but were highest for branches without bark among the three organs across 42 days of incubation ($P < 0.05$, Fig. 2). After 14 and 42 days of incubation, DOM bioavailability showed a negative exponential relationship with the initial $SUVA_{254}$ values ($P < 0.001$, Fig. 3), but did not correlate significantly with either DOC:DTN ratio or DOC:DTP ratio ($P > 0.05$, Fig. 3). In addition, there was a positive relationship

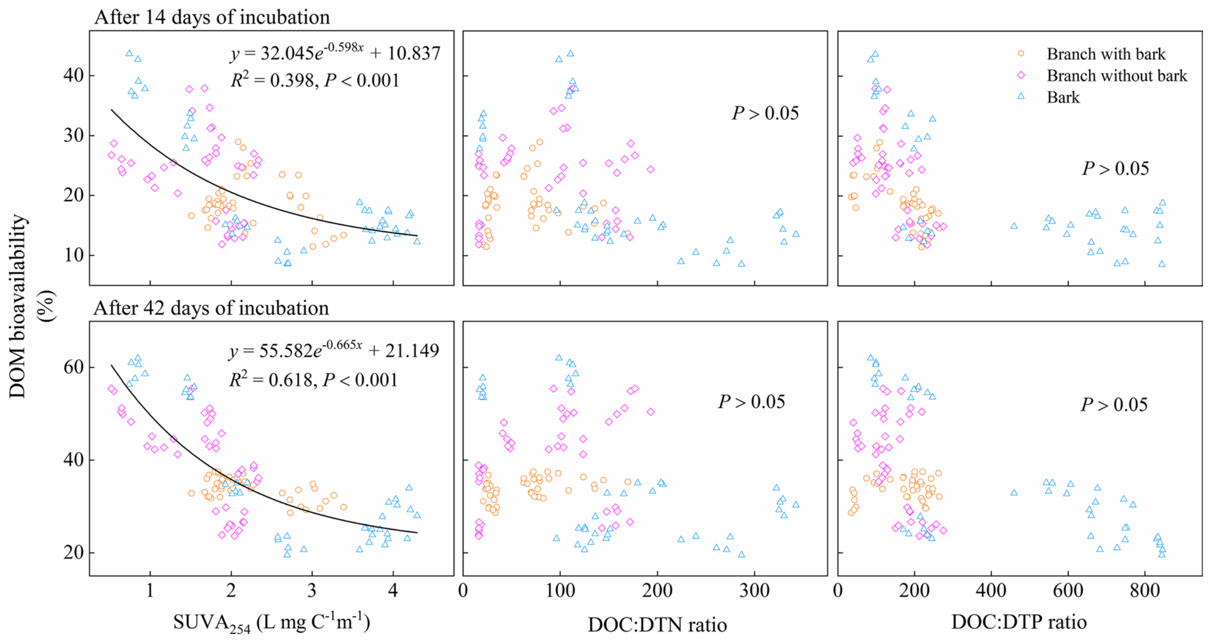

**Fig. 3** Relationships between DOM bioavailability and the initial properties in a subtropical forest of southern China. *DOM* dissolved organic matter, *$SUVA_{254}$* the specific UV absorbance at 254 nm, *DOC* dissolved organic carbon, *DTN* dissolved total nitrogen, *DTP* dissolved total phosphorus

between DOM bioavailability and the relative changes of $SUVA_{254}$ after 14 and 42 days of incubation ($P < 0.001$, Fig. S1).

## Discussion

### Tree bark effect on branch-leached DOM production and characteristics

Consistent with the first hypothesis, tree branches with bark leached lower amounts of DOC, DTN, and DTP than tree branches without bark (Table 3). Moreover, the observed DOC, DTN, and DTP productions of the whole branch were much lower than the corresponding expected values calculated from tree bark and the branch without bark (Fig. 1). These results indicate that the presence of bark can prevent the leaching of soluble organic C and nutrients from tree branches via physical protection. In this study, the inhibiting effect of bark on DOM production during leaching would be explained by the following mechanisms. First, the wrapping effect of tree bark reduced the exposed surface area of tree branches to contact the waters (Jones et al. 2020), and thus decreased DOM leaching from tree branches. Second, the suberin layer of tree bark might prevent water from entering the branches during leaching (Kolattukudy 2011). In previous studies, tree bark has often been regarded as a physical barrier to decomposer and thus decelerated wood litter decomposition in both terrestrial and aquatic ecosystems (Dossa et al. 2016, 2018; Jones et al. 2020). The negative effect of bark on DOM production in this study suggests that tree bark can also inhibit wood litter decomposition by reducing leaching in subtropical forests.

Regardless of tree species, tree bark always leached the greatest amounts of DOC, DTN, and DTP among the three organ types (Table 3), indicating that bark could be a potent source of litter-leached DOM in forest soils. Compared with the whole branch (i.e., tree branch including bark) and inside wood, the relatively lower tissue density and dry matter content of tree bark (Table 1) could permit the entrance of water into the litter, enhancing the leaching of soluble organic compounds (Joly et al. 2016). Moreover, tree bark, particularly the inner layer of the bark, often includes the living phloem, phelloderm, and cork cambium, whereas the inside wood is primarily composed of dead xylem that provides mechanical support for trees. Thus, bark, especially the living parts in the inner layer, stores greater amounts of carbohydrates and nutrients than inside wood (Feng et al. 2013; Harmon 2021). In addition, the wrapping effect of the outer bark in the whole branch could physically protect the inner bark and inside wood against leaching (Rosell et al. 2014), although the whole tree branch contained bark. In contrast, the exposure of inner bark to water would enhance leaching of soluble organic C and nutrients. Therefore, tree bark produced a higher amount of DOM than both whole branch and inside wood during leaching. Considering that bark and inside wood are often treated as a whole organ, these results imply that bark and inside wood should be separated in further studies.

Interestingly, tree bark effect on DOC:DTN and DOC:DTP ratios in the branch leachates was highly dependent on tree type (Table 3). Both DOC:DTN ratio of evergreen coniferous trees and DOC:DTP ratio of deciduous broadleaf trees were increased, whereas DOC:DTN ratio of evergreen broadleaf trees was reduced by the presence of tree bark. In this study, the contrasting interspecific patterns of C:N:P stoichiometric ratios between tree litter and tree litter leachates reflected that the initial litter nutrient concentrations could not be an effective indicator of nutrient availability in the litter leachates. Previous studies have observed that organic C compounds such as cellulose and lignin, rather than nutrient concentrations, determined litter-leached DOM production in forests (Don and Kalbitz 2005; Hagedorn and Machwitz 2007; Hensgens et al. 2020). Accordingly, the interspecific variations of DOC:DTN:DTP ratios in the leachates would be predominantly explained by the differential releases of soluble organic compounds varying in nutrient concentrations during the leaching processes of plant litter (Kim et al. 2014). In this study, tree bark could act as a filter for DOM fractions during leaching due to the relatively low tissue density and dry matter content (Pérez-Harguindeguy et al. 2013; Dossa et al. 2018). Therefore, tree bark can exert substantial influences on C:N:P stoichiometry in the leachates through its filter effect on soluble organic matter in forests.

In the litter leachates, the $SUVA_{254}$ value reflects the aromatic degree of DOM, and the higher $SUVA_{254}$ value indicates the greater aromatic degree of DOM (Weishaar et al. 2003). In this study, the presence of tree bark reduced DOM aromaticity (i.e., lower $SUVA_{254}$ values) in the leachates of coniferous trees, but increased DOM aromaticity (i.e., higher $SUVA_{254}$ values) in the leachates of broadleaf trees (Table 3). These inconsistent patterns would be explained by the substantial differences in bark-derived DOM aromatic content between coniferous and broadleaf trees. For coniferous trees, the bark would prevent the resins with complex molecular structures from leaching via the wrapping effect (Dossa et al. 2018), and thus, the presence of bark lowered $SUVA_{254}$ values in the leachates. However, in order to protect branches from herbivores and pathogens, broadleaf tree bark often produces a great number of defense compounds such as polyphenol and condensed tannins (Paine et al. 2010). In this study, we also found much higher polyphenols concentration in the broadleaf tree bark than in the broadleaf tree branches without bark (Table 1). Given that litter-derived DOM aromatic degree is often influenced by the initial litter C quality (Hagedorn and Machwitz 2007; Bantle et al. 2014), the presence of bark increased DOM aromaticity in the litter leachates of broadleaf trees. These results highlight that the tree bark effect on branch-leached DOM chemical composition depends on tree type in subtropical forests.

## Tree bark effect on branch-derived DOM bioavailability

Over 42 days of incubation, the presence of bark increased branch-leached DOM bioavailability of coniferous trees, but reduced branch-derived leached DOM bioavailability of broadleaf trees. Thus, our results partly supported the second hypothesis. In general, microbial degradation of DOM is limited by nutrient availability and DOC quality (Kalbitz et al. 2003; Don and Kalbitz 2005; Hensgens et al. 2020; Xu et al. 2021). In this study, DOM bioavailability showed no significant relationship with either DOC:DTN ratio or DOC:DTP ratio, but negatively correlated with the initial $SUVA_{254}$ value (Fig. 3), indicating the predominance of DOM aromaticity in driving the variations of branch-derived DOM bioavailability in this subtropical forest. Accordingly, the opposite effects of tree bark on branch-derived DOM bioavailability between coniferous and broadleaf trees would be attributed to the differences in aromatic C content in the leachates (Xu et al. 2021). In this subtropical forest, the tree bark effect on DOM bioavailability was positive for coniferous trees because of the lowered aromaticity, but was negative for broadleaf trees due to the increased aromaticity. These results clearly show that the tree bark effect on DOM bioavailability is species-specific and highlight that the presence of tree bark regulates branch-derived DOM bioavailability primarily by altering C quality in subtropical forests.

The relative changes of $SUVA_{254}$ values exceeded 100% during the incubation periods (Fig. 2), indicating an increase in DOM aromaticity in the leachates (Weishaar et al. 2003). In general, heterotrophic microorganisms preferentially use the labile DOM fractions with low molecular weight, leading to the net accumulation of aromatic and humic substances (Cory and Kaplan 2012). This assumption was further supported by the positive relationship between the relative changes of $SUVA_{254}$ value and DOM bioavailability over 42 days of incubation (Fig. S1). Thus, $SUVA_{254}$ values increased when microbial degradation of DOM proceeded, and the magnitude of this change often increased with incubation time. Because tree bark effect on branch-derived DOM bioavailability depends on tree type, the presence of bark increased the relative changes of $SUVA_{254}$ value for coniferous trees, but decreased the relative changes of $SUVA_{254}$ value for both deciduous and evergreen broadleaf trees.

Considering the substantial contribution of wood litter to ecosystem C stock in forests (Pan et al. 2011; Russell et al. 2015; Magnússon et al. 2016), our findings have important implications for organic matter decomposition and forest C budget. First, the presence of bark often inhibits biota-mediated wood litter decomposition in forests (Dossa et al. 2016, 2018). In this study, tree bark was observed to physically retard wood litter decomposition by preventing DOM from leaching. These results further highlight the critical role of bark in promoting organic C accumulation in wood litter in forests. Moreover, wood litter-leached DOM can be easily diverted into microbial biomass due to the relatively high lability (Magnússon et al. 2016), which would enhance the formation of stable soil C pool via microbial C pump (Cotrufo et al. 2015; Liang et al. 2020). In this study, the contrasting bark effects on wood litter-leached DOM bioavailability between broadleaf and coniferous trees would partly help explain the spatial variations of soil organic C stock and stabilization in subtropical forests.

## Conclusion

For both coniferous and broadleaf trees, the presence of bark substantially reduced tree branch-leached DOC, DTN, and DTP productions in this subtropical forest. However, the tree bark effect of branch-derived DOM bioavailability varied with tree type. The presence of bark decreased broadleaf tree branch-derived DOM bioavailability, but increased coniferous tree branch-derived DOM bioavailability. The negative relationship between DOM bioavailability and initial $SUVA_{254}$ values indicates that tree bark alters branch-derived DOM bioavailability primarily through its effect on DOM aromaticity. Because of the substantial contribution of leaching to litter decomposition in warm and humid regions, these observations will help us understand the role of bark in regulating C and nutrient cycles in subtropical forests.

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**Data availability** All data generated or analysed during this study are included as electronic supplementary material.

### Declarations

**Conflict of interest** We declare that we do not have any commercial or associative interest that represents a conflict of interest in connection with the work submitted.

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