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Carbon, nitrogen and phosphorus stoichiometry controls interspecific patterns of leaf litter-derived dissolved organic matter biodegradation in subtropical plantations of China

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Leaching of leaf litter is the primary source of dissolved organic matter (DOM) in forest soils. However, the interspecific variations of litter-derived DOM characteristics and biodegradation and their controlling factors remain unclear in subtropical plantations. Using fresh leaf litter of two broadleaf trees (*Liquidambar formosana* and *Schima superba*) and two coniferous trees (*Pinus massoniana* and *P. elliottii*) in subtropical plantations of China, we assessed the effects of tree species on the amounts and properties of litter-derived DOM with a short-term leaching experiment, and examined the interspecific variation of DOM biodegradation using a 56-day laboratory incubation method. Broadleaf tree litter generally leached higher amounts of dissolved organic carbon (DOC), dissolved total nitrogen (DTN), and dissolved total phosphorus (DTP) than coniferous tree litter. Compared with coniferous trees, broadleaf trees had higher DOM aromaticity and molecular weight, but lower DOC:DTP and DTN:DTP ratios in the litter leachates. Despite greater DOM aromaticity and molecular weight, broadleaf trees had higher litter-derived DOM biodegradation than coniferous trees because of the relatively lower DOC:DTP and DTN:DTP ratios. These results indicate the distinct patterns of litter-derived DOM characteristics and biodegradation between broadleaf and coniferous trees, and also highlight the predominant role of C:N:P stoichiometry in driving the interspecific variation of litter-derived DOM biodegradation in subtropical plantations of China.

Keywords: Broadleaf Trees, Coniferous Trees, DOM Aromaticity, DOM Molecular Weight, Leaching

Introduction

Dissolved organic matter (DOM) often represents the most labile organic matter fraction in soils and plays an essential role in maintaining ecosystem services and functions in forests (Kalbitz et al. 2000, Neff & Asner 2001, Kalbitz & Kaiser 2008, Jansen et al. 2014). In forest soils, leaching of soluble compounds from plant litter is the primary source of DOM, especially in the early stage of litter decomposition (Cleveland et al. 2004, Ibrahima et al. 2008). Although the importance of litter-derived DOM has recently attracted considerable attention (Don & Kalbitz 2005, Kiikkilä et al. 2013, Chomel et al. 2020), the amounts and chemical composition (*e.g.*, aromaticity and molecular weight) of DOM leaching from different tree litter are highly variable and the controls causing these interspecific variations are elusive. Accordingly, these uncertainties about tree litter-derived DOM will limit our understanding of key ecological processes in forest ecosystems.

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In forests, litter-derived DOM is either degraded by heterotrophic organisms or absorbed by soil minerals to form stable soil organic matter or delivered directly to groundwater *via* leaching (Kalbitz & Kaiser 2008, Uselman et al. 2012, Cotrufo et al. 2015). Thus, microbial degradation is a crucial factor controlling the fate of litter-derived DOM, and knowledge about the controls on DOM biodegradation is a prerequisite for understanding DOM dynamics in forest soils. Because microbial growth and activity are often limited by energy and nutrients (Soong et al. 2020), DOM biodegradation is believed to be influenced by carbon (C) quality and stoichiometric ratios between C and nutrients. In empirical studies, however, the controls on litter-derived DOM biodegradation remain unclear in forests (Wickland et al. 2007, Kiikkilä et al. 2013, Hensgens et al. 2020). Several studies have observed that DOM biodegradation was tightly correlated with C quality such as aromaticity or humification index (Don & Kalbitz 2005, Wymore et al. 2015), while other studies have found the predominant role of C:nitrogen (N):phosphorus (P) stoichiometry in regulating DOM biodegradation (Mineau et al. 2013). Moreover, most previous studies have been performed in boreal and temperate forests, and little is

Fig. 1 - Geographical location of the study site in China.

known about the interspecific patterns of litter-derived DOM biodegradation in sub/tropical forests. Considering that leaching makes a substantial contribution to litter decomposition in sub/tropical forests (Cleveland et al. 2004, Keller & Phillips 2019), additional studies are needed to clarify the biodegradation of litter-derived DOM and its underlying mechanisms in these forest ecosystems.

To clarify the effect of tree species on litter-derived DOM dynamics, we investigated the differences in the amount, chemical composition, and biodegradation of leaf litter-derived DOM between broadleaf trees (*Liquidambar formosana* and *Schima superba*) and coniferous trees (*Pinus massoniana* and *P. elliottii*) in subtropical plantations of southern China. Considering that broadleaf trees can produce leaf litter with higher nutrient concentrations and lower lignin concentration than coniferous trees (Gholz et al. 2000, Li et al. 2016), we raised the following three hypotheses: (1) broadleaf tree litter would yield larger amounts of DOM than coniferous tree litter during leaching; (2) compared with broadleaf trees, coniferous trees would have greater DOM aromaticity and molecular weight in the litter leachates; and (3) litter-derived DOM biodegradation would be higher for broadleaf trees than for coniferous trees.

Materials and methods

Site description

The experiment was performed in the Long-term Forest Restoration Experimental Station of Jiangxi Agricultural University (26° 44′ N, 115° 04′ E) located in the Luoxi Town, Taihe County, Jiangxi Province, China (Fig. 1). The climate of the study site is a humid subtropical monsoon climate. The average annual precipitation is 1726 mm, and the average annual air temperature is 18.6 °C. The soil is red soil developed from Quaternary red clay, and is classified as Ferric Acrisols in the FAO classification system (IUSS Working Group 2006). In the study site, the soil is severely degraded due to the intensive anthropogenic activities such as grazing, firewood collection, and cultivation. Accordingly, soil organic matter content is extremely low, and the lands are sparsely covered by the drought-tolerant grasses such as *Imperata koenigii, Cymbopogon goeringii*, and *Searia viridis* (Gong et al. 2013). In 1991, the long-term forest restoration experiment was conducted on these severely degraded lands, and the main afforestation tree species included *L. formosana, S. superba, P. massoniana*, and *P. elliottii, Vernicia fordii, Paulownia fortune, Eucalyptus robusta, Lespedeza bicolor*, and *Acacia mearnsii*. The detailed information on the study site was shown in Gong et al. (2013).

Leaf litter sampling and measurement

In this study, we collected leaf litter from two broadleaf trees (*L. formosana* and *S. superba*) and two coniferous trees (*P. massoniana* and *P. elliottii*) in these plantations. For each plantation, we randomly established six plots (20 × 20 m) as replicates and set up five litter traps (1 × 1 m) in each plot in September 2018. The mean thickness of litter layer in the *L. formosana, S. superba, P. massoniana*, and *P. elliottii* plantations was about 0.4, 4.7, 1.1, and 2.4 cm, respectively. From October to November 2018, freshly fallen leaves in the litter traps were collected semimonthly, oven-dried at 65 °C, and used to determine initial chemical properties and litter-derived DOM. Litter organic C and N concentrations were measured with the dry combustion method on a TOC analyzer (multi N/C 2100s®, Analytik, Jena, Germany), total P concentration was measured colorimetrically on an AMS Alliance SmartChem® 140 spectrophotometer (AMS, Frepillon, France) after acid digestion, and total polyphenol concentration were measured by the Folin-Ciocaileu method with gallic acid as the standard (Stern et al. 1996). In this study, litter C:N, C:P, and N:P ratios were expressed as atomic ratios. The initial properties of tree leaf litter were shown in Tab. 1.

Litter-derived DOM was extracted with a short-term leaching experiment (Don & Kalbitz 2005). Oven-dried leaf litter (3 g) per plot was placed in 200 mL of deionized water in the 500 mL Mason jars and soaked in the dark at room temperature (20 °C) for 48 hours. Afterward, litter leachates were filtered through 0.7 µm Whatman GF/F glass microfiber filters and immediately used to measure DOM properties. Dissolved organic C (DOC) and dissolved total N (DTN) concentrations were measured on a TOC analyzer, and dissolved total P (DTP) concentration was measured with the peroxodisulfate oxidation method (Ebina et al. 1983). The total extractable amounts of DOC, DTN, and DTP were obtained from the respective amounts of DOC, DTN, and DTP in the litter leachates and the initial litter dry mass. In addition, the stoichiometric ratios among DOC, DTN, and DTP were expressed as atomic ratios.

The absorbances of DOM were measured from 250 nm to 700 nm on an ultraviolet-

Tab. 1 - Initial properties of tree leaf litter in subtropical plantations of China. Data are means ± standard errors (*n*=6). In the same column, different lowercase letters indicate significant differences (*p*<0.05) among the four species.

Species	Organic C (mg g^{-1})	Total N (mg g^{-1})	Total P (mg g^{-1})	Total polyphenol (mg g^{-1})	C:N ratio	C:P ratio	N:P ratio	Water holding capacity (%)
L. formosana	438 ± 3 ^{c}	9.52 ± 0.17 ^{a}	1.45 ± 0.05 ^{a}	145 ± 3 ^{a}	54 ± 1 ^{c}	785 ± 27 ^{c}	14.6 ± 0.6 ^{a}	131 ± 1 ^{a}
S. superba	457 ± 3 ^{b}	5.70 ± 0.09 ^{b}	0.85 ± 0.04 ^{c}	101 ± 3 ^{b}	94 ± 2 ^{b}	1399 ± 66 ^{b}	14.9 ± 0.6 ^{a}	94 ± 3 ^{b}
P. massoniana	481 ± 3 ^{a}	4.85 ± 0.04 ^{c}	0.96 ± 0.03 ^{b}	88 ± 2 ^{c}	116 ± 1 ^{a}	1305 ± 47 ^{b}	11.3 ± 0.4 ^{b}	72 ± 2 ^{c}
P. elliottii	441 ± 3 ^{b}	4.32 ± 0.06 ^{d}	0.66 ± 0.03 ^{c}	86 ± 2 ^{c}	119 ± 2 ^{a}	1737 ± 91 ^{a}	14.6 ± 0.9 ^{a}	72 ± 3 ^{c}

Tab. 2 - Total extractable amounts of dissolved organic C (DOC), dissolved total N (DTN), and dissolved total P (DTP) after 48-hour leaching of tree leaf litter in subtropical plantations of China. Data are means± standard errors (*n*=6). In the same column, different lowercase letters indicate significant differences (*p*<0.05) among the four species.

Tree species	DOC amount (μg C g^{-1} litter)	DTN amount (μg N g^{-1} litter)	DTP amount (μg P g^{-1} litter)	DOC:DTN ratio	DOC:DTP ratio	DTN:DTP ratio
L. formosana	13,922 ± 109 ^{a}	223 ± 5 ^{a}	66.3 ± 2.8 ^{a}	72.8 ± 1.7 ^{a}	548 ± 24 ^{c}	7.6 ± 0.4 ^{c}
S. superba	10,798 ± 199 ^{b}	170 ± 6 ^{b}	12.2 ± 0.3 ^{b}	74.6 ± 2.3 ^{a}	2302 ± 81 ^{b}	31.0 ± 1.2 ^{b}
P. massoniana	8,207 ± 90 ^{d}	151 ± 4 ^{b}	10.0 ± 0.4 ^{b}	63.6 ± 1.6 ^{b}	2139 ± 88 ^{b}	33.7 ± 1.3 ^{b}
P. elliottii	10,120 ± 85 ^{c}	158 ± 5 ^{b}	7.4 ± 0.5 ^{b}	75.1 ± 2.9 ^{a}	3622 ± 261 ^{a}	48.1 ± 2.3 ^{a}

visible dual-beam spectrophotometer (UV 600SC®, Jinghua Instruments, China) with 1-cm quartz cells. Before measurement, litter leachates were diluted when necessary. In this study, the specific ultraviolet absorbances at 254 nm ($SUVA_{254}$), 280 nm ($SUVA_{280}$), 350 nm ($SUVA_{350}$), and 370 nm ($SUVA_{370}$) were used to indicate the aromaticity of DOM, and the higher values were associated with greater aromatic content (Weishaar et al. 2003, Hansen et al. 2016); S_R was used to indicate DOM molecular weight, and higher S_R values showed lower molecular weight (Helms et al. 2008, Hansen et al. 2016). For each litter leachate, $SUVA_{254}$, $SUVA_{280}$, $SUVA_{350}$, and $SUVA_{370}$ were obtained by dividing the ultraviolet absorbances at 254, 280, 350, and 370 nm by the DOC concentration, respectively (Weishaar et al. 2003, Hansen et al. 2016). To calculate S_R values, we firstly obtained $S_{275\text{-}295}$ and $S_{350\text{-}400}$ values by fitting absorption spectrum to an exponential decay function over the wavelength range of 275-295 nm and 350-400 nm, respectively, and then calculated S_R values as the ratio of spectral slope $S_{275\text{-}295}$ to spectral slope $S_{350\text{-}400}$ (Helms et al. 2008).

Dissolved organic matter biodegradation was measured by a 56-day standard laboratory incubation method (McDowell et al. 2006). To prepare the inoculum, 40-g fresh soils (0-10 cm depth) from a mixed coniferous-broadleaf plantation were placed in 1000 mL deionized water in the dark at 20 °C for 12 hours. The inoculum suspension was filtered through 0.7 μm glass microfiber filters, and stored for the laboratory incubation experiment. In the leaf litter leachates, DOC concentration was diluted to 10-20 mg DOC L^{-1} to prevent excessive microbial growth. Afterward, 100-mL diluted litter leachate per treatment was placed in 250 mL glass jars, inoculated with 5 mL microbial inoculum, sealed, and incubated in the dark at 20 °C. Meanwhile, six glass jars containing 100 mL deionized water and 5 mL inoculum were used as blanks. There were 150 glass jars: five treatments (*L. formosana, S. superba, P. massoniana, P. elliottii*, and blank) × six replicates × five sampling times (7, 14, 28, 42, and 56 days). Following 7, 14, 28, 42, and 56 days of incubation, the water sample in six jars per treatment was collected and filtered to determine DOC concentration and S_R value. In the filters, DOC concentration and S_R value were obtained with the method mentioned above. For each litter leachate, DOM biodegradation (%) was calculated from the difference in cumulative DOC consumption between litter leachates and the blank over the incubation period, and was expressed as the percentage of the initial DOC concentration (McDowell et al. 2006).

Statistical analyses

The statistical analyses were conducted using the SPSS® statistical software (version 19.0) for Windows, and the statistically significant level of 0.05 was accepted. Before statistical analyses, the normality of the data was examined with the Levene test, and all data followed a normal distribution. One-way ANOVA was used to assess the effect of tree species on DOM properties in the litter leachates, and *post-hoc* Tukey's HSD test was adopted to compare the significant differences in DOM properties among the four tree species. Repeated measures of ANOVA were used to examine the effect of tree species on DOM biodegradation and S_R values over the incubation periods. We also used the linear regression to assess the relationship between DOM biodegradation and initial DOC:DTN, DOC:DTP, and DTN:DTP ratios in the litter leachates.

Results

Initial litter properties varied significantly with tree species (Tab. 1). Broadleaf tree (*L. formosana* and *S. superba*) leaf litter had higher total N concentration, total polyphenol concentration, and water holding capacity, but lower C:N ratio than coniferous tree (*P. massoniana* and *P. elliottii*) leaf litter (Tab. 1). Among the four tree species, *L. formosana* litter had highest total N, total P, and total polyphenol concentrations, whereas *P. elliottii* litter had lowest total N, total P, and total polyphenol concentrations (Tab. 1). Consequently, *L. formosana* litter had lowest C:N and C:P ratios, whereas *P. elliottii* litter had highest C:N and C:P ratios among the tree species (Tab. 1).

During leaching, the extractable amounts of DOC, DTN, and DTP were significantly influenced by tree species (Tab. 2). In the litter leachates, two broadleaf trees (*L. formosana* and *S. superba*) generally had higher amounts of DOC, DTN, and DTP than two coniferous trees (*P. massoniana* and *P. elliottii* – Tab. 2). For broadleaf trees, *L. formosana* litter released greater DOC amounts during leaching than *S. superba* litter, and for coniferous trees, *P. massoniana* had lower extractable DOC amounts than *P. elliottii* (Tab. 2). In addition, *L. formosana* litter produced higher amounts of DTN and DTP during leaching than the other three tree species (Tab. 2).

In the litter leachates, both DOC:DTN:DTP stoichiometry and DOM optical properties differed significantly among tree species (Tab. 2). Among the four species, *L. formosana* had lowest DOC:DTP and DTN:DTP ratios, while *P. elliottii* had highest DOC:

Tab. 3 - Absorbance optical properties of dissolved organic matter in the leachates of tree leaf litter in subtropical plantations of China. Data are means ± standard errors (*n*=6). In the same column, different lowercase letters indicate significant differences (*p*<0.05) among the four species.

Tree species	$SUVA_{254}$ (L mg-C^{-1} m^{-1})	$SUVA_{280}$ (L mg-C^{-1} m^{-1})	$SUVA_{350}$ L mg-C^{-1} m^{-1})	$SUVA_{370}$ L mg-C^{-1} m^{-1})	S_r values
L. formosana	8.26 ± 0.32 ^{a}	7.37 ± 0.36 ^{a}	1.35 ± 0.06 ^{a}	1.01 ± 0.05 ^{a}	1.14 ± 0.02 ^{b}
S. superba	8.09 ± 0.35 ^{a}	8.19 ± 0.32 ^{a}	1.44 ± 0.05 ^{a}	1.00 ± 0.04 ^{a}	1.28 ± 0.06 ^{b}
P. massoniana	1.75 ± 0.05 ^{b}	1.63 ± 0.08 ^{b}	0.35 ± 0.01 ^{b}	0.27 ± 0.01 ^{b}	2.32 ± 0.14 ^{a}
P. elliottii	1.69 ± 0.08 ^{b}	1.36 ± 0.15 ^{b}	0.20 ± 0.02 ^{b}	0.15 ± 0.02 ^{b}	2.51 ± 0.24 ^{a}

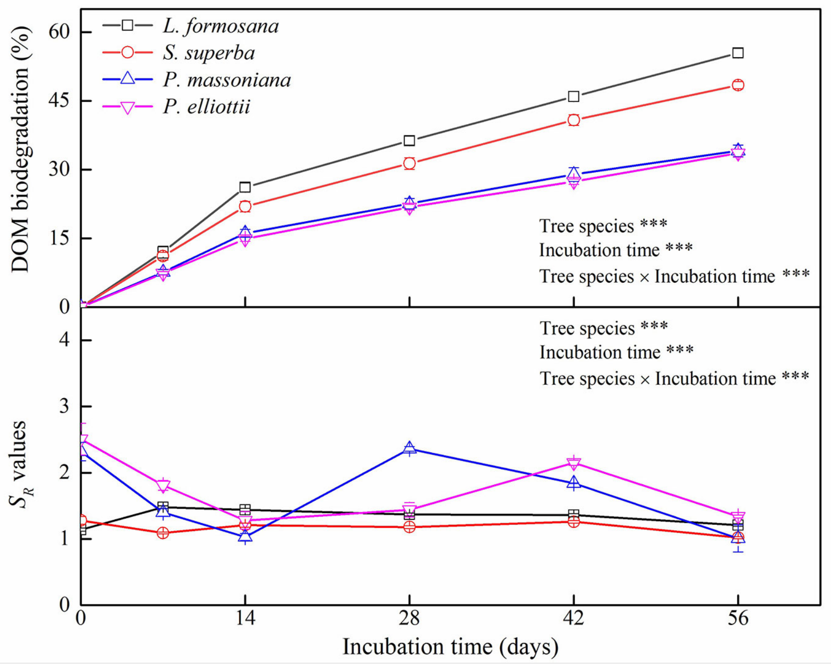

Fig. 2 - Leaf litter-leached dissolved organic matter (DOM) biodegradation and changes in S_R values during 56 days of incubation in subtropical plantations of China. (***): p<0.001.

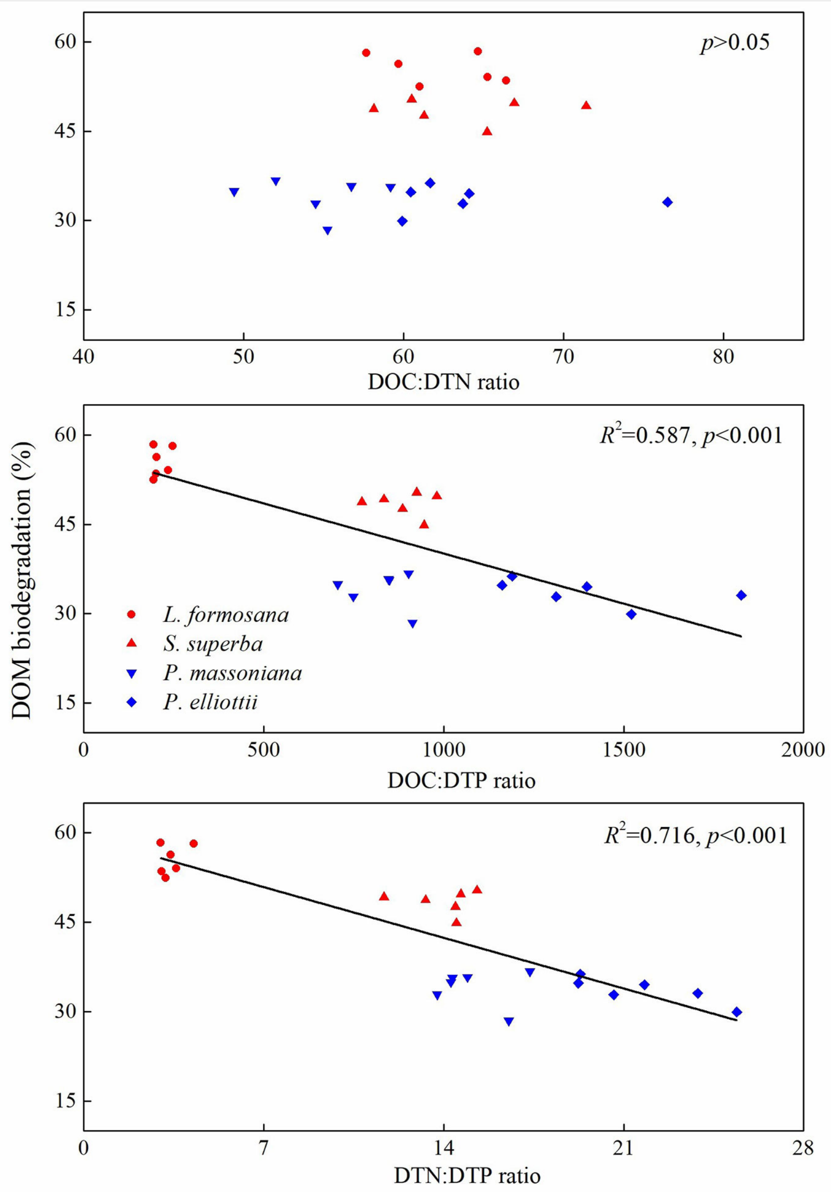

Fig. 3 - Relationship between dissolved organic matter (DOM) biodegradation and stoichiometric ratios of dissolved organic C (DOC), dissolved total N (DTN), and dissolved total P (DTP) in subtropical plantations of China.

DTP and DTN:DTP ratios (Tab. 2). In addition, *P. massoniana* had lower DOC:DTN ratio than the other three tree species (Tab. 2). In the litter leachates, broadleaf trees (*L. formosana* and *S. superba*) had greater $SUVA_{254}$, $SUVA_{280}$, $SUVA_{350}$, and $SUVA_{370}$ values, but lower S_R values than coniferous trees (*P. massoniana* and *P. elliottii* – Tab. 3). However, no significant differences in the selected absorbance optical properties were observed between *L. formosana* and *S. superba* or between *P. massoniana* and *P. elliottii* (Tab. 3).

Tree species, incubation time, and their interaction significantly affected biodegradation and S_R values of DOM during 56 days of incubation (Fig. 2). Litter-derived DOM biodegradation was greater for broadleaf trees than coniferous trees over the incubation period (Fig. 2). Moreover, litter-derived DOM biodegradation was always higher for *L. formosana* than for *S. superba*, whereas no significant difference in litter-derived DOM biodegradation was observed between *P. massoniana* and *P. elliottii* (Fig. 2). In addition, S_R values of DOM varied with tree species in the initial 42 days of incubation, but showed no significant difference among the tree species by the end of incubation (Fig. 2). After 56-day incubation, DOM biodegradation correlated negatively with DOC:DTP ratio (R^2 = 0.587, p<0.001) and DTN:DTP ratio (R^2 = 0.716, p<0.001), but did not exhibit a significant relationship with DOC:DTN ratio (Fig. 3).

Discussion

In line with the first hypothesis, *L. formosana* and *S. superba* generally yielded greater amounts of DOC, DTN, and DTP per gram of dry leaf litter than *P. massoniana* and *P. elliottii* following short-term leaching. Previous studies also observed similar patterns of litter-derived DOC or/and dissolved nutrient amounts between broadleaf and coniferous trees in boreal and temperate forests (Don & Kalbitz 2005, Kalbitz et al. 2006, Joly et al. 2016, Hensgens et al. 2020). In this study, the substantial differences in DOC quantity in the litter leachates would be explained by the distinct leaf litter physical and chemical properties among broadleaf and coniferous trees. First, broadleaf litter might contain higher amounts of soluble C and nutrient fractions such as sugar and secondary metabolic compounds than coniferous litter (Joly et al. 2016, Li et al. 2016). Second, compared with coniferous species, broadleaf species produced leaf litter with a relatively thinner epidermic and hypodermic layer, lower toughness, and flatter surface structure, which would enable leaf litter to be easily broken and leached (Don & Kalbitz 2005, Ibrahima et al. 2008, Hensgens et al. 2020). Third, relative to coniferous litter, the relatively higher water holding capacity of broadleaf litter (Tab. 1) could permit a larger amount of water to enter leaf litter, and thus enhance leaching of soluble compounds (Joly et al. 2016). Considering that most previous studies have been conducted in temperate and boreal forests, our result confirms the generality of interspecific patterns in leaf litter-derived DOM amounts between broadleaf and coniferous trees to subtropical forests.

Contrary to the second hypothesis, both *L. formosana* and *S. superba* had higher $SUVA_{254}$, $SUVA_{280}$, $SUVA_{350}$, and $SUVA_{270}$ values, but lower S_R values in the litter leachates than the selected two pine trees. Given that litter-derived DOM chemical make-up is primarily influenced by litter chemistry (Don & Kalbitz 2005, Kalbitz et al. 2006, Uselman et al. 2012, Kiikkilä et al. 2013, Joly et al. 2016), the higher litter total polyphenol concentration of broadleaf trees (Tab. 1) would account for the greater aromaticity and molecular weight of DOM in the litter leachates relative to coniferous trees in this study. In general, DOM aromaticity and molecular weight are observed to be tightly correlated with heterotrophic growth and metabolism, pollutant mobilization and transportation, and groundwater quality (Kalbitz et al. 2003, Hansen et al. 2016, Joly et al. 2016). Accordingly, these findings will help explain the spatial variations of ecosystem services between broadleaf and coniferous tree plantations in subtropical regions.

Consistent with the third hypothesis, litter-derived DOM biodegradation was greater for broadleaf trees than coniferous trees during 56-day incubation. In contrast, several studies found that leaf litter-derived DOM biodegradation showed a slight difference between broadleaf and coniferous trees in temperate and boreal forests (Kiikkilä et al. 2013, Hensgens et al. 2020). Don & Kalbitz (2005) even observed much greater DOM biodegradation in the fresh litter leachates for coniferous trees than for broadleaf trees. These inconsistent results implied that the interspecific patterns of litter-derived DOM biodegradation between broadleaf and coniferous trees in subtropical forests might be different from that in temperate and boreal forests. In general, DOM biodegradation correlated positively with nutrient availability, but negatively with DOM aromaticity and molecular weight (Kalbitz et al. 2003, Wickland et al. 2007, Mao et al. 2017). Despite greater DOM aromaticity and molecular weight, broadleaf species often had lower DOC:DTP and DTN:DTP ratios in the litter leachates than coniferous species. Considering that DOC biodegradation was limited by P availability in subtropical regions (Mao et al. 2017), broadleaf tree litter produced DOM with greater biodegradability than coniferous trees. These results suggest that C:N:P stoichiometry is an overriding factor controlling the interspecific patterns of litter-derived DOM biodegradation between broadleaf and coniferous trees in subtropical plantations.

Interestingly, the magnitudes of the changes in S_R values of DOM varied substantially with species. Over the entire incubation period, S_R values of DOM declined for *P. massoniana* and *P. elliottii*, but remained unchanged for *L. formosana* and *S. superba* (Fig. 2). Although the mechanisms causing these contrasting patterns were unclear, we speculated that the intrinsic differences in DOM chemical composition might account for the divergent shifts in molecular weight among tree species. The decreased S_R values indicated that, for coniferous species, microorganisms might predominantly utilize the labile fractions of DOM with relatively low molecular weight, resulting in the net accumulation of organic compounds with a high molecular weight in the leachates (Helms et al. 2008, Hansen et al. 2016). In contrast, S_R values of DOM did not change with incubation time, probably due to the relatively high DOM aromaticity and complexity in the litter leachates of broadleaf trees. Accordingly, S_R values of DOM did not differ between broadleaf and coniferous species by the end of incubation. These results suggest that leaf litter-derived DOM chemical composition will become convergent with microbial degradation proceeds in subtropical plantations.

Conclusions

In summary, broadleaf trees produced larger amounts of leaf litter-derived DOM with greater aromaticity and molecular weight than coniferous trees in subtropical plantations of China. Over 56 days of incubation, DOM biodegradation was higher for broadleaf trees than coniferous trees, although DOM molecular weight became convergent among tree species. Moreover, the interspecific patterns of DOM biodegradation was primarily driven by DOC:DTN:DTP stoichiometry rather than DOM aromaticity and molecular weight. These findings imply that, compared with coniferous trees, broadleaf trees can provide labile litter-derived DOM for microbial growth and metabolism, and thus facilitate soil organic matter formation and accumulation via the DOM-microbial path in subtropical plantations (Cotrufo et al. 2015). Therefore, our results will help explain and forecast the spatial patterns of C and nutrient cycles between broadleaf and coniferous tree plantations, and also suggest that broadleaf tree species are preferentially recommended for afforestation and reforestation programs in subtropical regions of China.

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References

Chomel M, Baldy V, Guittonny M, Greff S, DesRochers A (2020). Litter leachates have stronger impact than leaf litter on Folsomia candida fitness. Soil Biology and Biochemistry 147: 107850. - doi: 10.1016/j.soilbio.2020.107850

Cleveland CC, Neff JC, Townsend AR, Hood E (2004). Composition, dynamics, and fate of leached dissolved organic matter in terrestrial ecosystems: results from a decomposition experiment. Ecosystems 7: 275-285. - doi: 10.1007/s10021-003-0236-7

Cotrufo MF, Soong JL, Horton AJ, Campbell EE, Haddix ML, Wall DH, Parton WJ (2015). Formation of soil organic matter via biochemical and physical pathways of litter mass loss. Nature Geoscience 8: 776-779. - doi: 10.1038/ngeo2520

Don A, Kalbitz K (2005). Amounts and degradability of dissolved organic carbon from foliar litter at different decomposition stages. Soil Biology and Biochemistry 37: 2171-2179. - doi: 10.1016/j.soilbio.2005.03.019

Ebina J, Tsutsui T, Shirai T (1983). Simultaneous determination of total nitrogen and total phosphorus in water using peroxodisulfate oxidation. Water Research 17: 1721-1726. - doi: 10.1016/0043-1354(83)90192-6

Gholz HL, Wedin DA, Smitherman SM, Harmon ME, Parton WJ (2000). Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biology 6: 751-765. - doi: 10.1046/j.1365-2486.2000.00349.x

Gong X, Liu Y, Li Q, Wei X, Guo X, Niu D, Zhang W, Zhang J, Zhang L (2013). Sub-tropic degraded red soil restoration: Is soil organic carbon build-up limited by nutrients supply. Forest Ecology and Management 300: 77-87. - doi: 10.1016/j.foreco.2012.12.002

Hansen AM, Kraus TEC, Pellerin BA, Fleck JA, Downing BD, Bergamaschi BA (2016). Optical properties of dissolved organic matter (DOM): effects of biological and photolytic degradation. Limnology and Oceanography 61: 1015-1032. - doi: 10.1002/lno.10270

Helms JR, Stubbins A, Ritchie JD, Minor EC, Kieber DJ, Mopper K (2008). Absorption spectral slopes and slope ratios as indicators of molecular weight, source, and photobleaching of chromophoric dissolved organic matter. Limnology and Oceanography 53: 955-969. - doi: 10.4319/lo.2008.53.3.0955

Hensgens G, Laudon H, Peichl M, Gil IA, Zhou Q, Berggren M (2020). The role of the understory in litter DOC and nutrient leaching in boreal forests. Biogeochemistry 149: 87-103. - doi: 10.1007/s10533-020-00668-5

Ibrahima A, Biyanzi P, Halima M (2008). Changes in organic compounds during leaf litter leaching: laboratory experiment on eight plant species of the Sudano-guinea Savannas of Ngaoundere, Cameroon. iForest - Biogeosciences and Forestry 1 (1): 27-33. - doi: 10.3832/ifor0450-0010027

IUSS Working Group WRB (2006). World reference base for soil resources 2006. World Soil Resources Reports no. 103, FAO, Rome, Italy, pp. 128.

Jansen B, Kalbitz K, McDowell WH (2014). Dissolved organic matter: linking soils and aquatic systems. Vadose Zone Journal 13: 1-4. - doi: 10.2136/vzj2014.05.0051

Joly FX, Fromin N, Kiikkilä O, Hättenschwiler S (2016). Diversity of leaf litter leachates from temperate forest trees and its consequences for soil microbial activity. Biogeochemistry 129: 373-388. - doi: 10.1007/s10533-016-0239-z

Kalbitz K, Solinger S, Park JH, Michalzik B, Matzner E (2000). Controls on the dynamics of dissolved organic matter in soils: a review. Soil Science 165: 277-304. - doi: 10.1097/00010694-200004000-00001

Kalbitz K, Schmerwitz J, Schwesig D, Matzner E (2003). Biodegradation of soil-derived dissolved organic matter as related to its properties. Geoderma 113: 273-291. - doi: 10.1016/S0016-7061(02)00365-8

Kalbitz K, Kaiser K, Bargholz J, Dardenne P (2006). Lignin degradation controls the production of dissolved organic matter in decomposing foliar litter. European Journal of Soil Science 57: 504-516. - doi: 10.1111/j.1365-2389.2006.00797.x

Kalbitz K, Kaiser K (2008). Contribution of dissolved organic matter to carbon storage in forest mineral soils. Journal of Plant Nutrition and Soil Science 171: 52-60. - doi: 10.1002/jpln.200700043

Keller AB, Phillips RP (2019). Leaf litter decay rates differ between mycorrhizal groups in temperate, but not tropical, forests. New Phytologist 222: 556-564. - doi: 10.1111/nph.15524

Kiikkilä O, Smolander A, Kitunen V (2013). Degradability, molecular weight and adsorption properties of dissolved organic carbon and nitrogen leached from different types of decomposing litter. Plant and Soil 373: 787-798. - doi: 10.1007/s11104-013-1837-3

Li H, Wu F, Yang W, Xu L, Ni X, He J, Tan B, Hu Y, Justin MF (2016). The losses of condensed tannins in six foliar litters vary with gap position and season in an alpine forest. iForest - Biogeosciences and Forestry 9: 910-918. - doi: 10.3832/ifor1738-009

Mao R, Chen HM, Li SY (2017). Phosphorus availability as a primary control of dissolved organic carbon biodegradation in the tributaries of the Yangtze River in the Three Gorges Reservoir Region. Science of the Total Environment 574: 1472-1476. - doi: 10.1016/j.scitotenv.2016.08.132

McDowell WH, Zsolnay A, Aitkenhead-Peterson JA, Gregorich EG, Jones DL, Jodemann D, Kalbitz K, Marschner B, Schwesig D (2006). A comparison of methods to determine the biodegradable dissolved organic carbon from different terrestrial sources. Soil Biology and Biochemistry 38: 1933-1942. - doi: 10.1016/j.soilbio.2005.12.018

Mineau MM, Rigsby CM, Ely DT, Fernandez IJ, Norton SA, Ohno T, Valett HM, Simon KS (2013). Chronic catchment nitrogen enrichment and stoichiometric constraints on the bioavailability of dissolved organic matter from leaf leachate. Freshwater Biology 58: 248-260. - doi: 10.1111/fwb.12054

Neff JC, Asner GP (2001). Dissolved organic carbon in terrestrial ecosystems: synthesis and a model. Ecosystems 4: 29-48. - doi: 10.1007/s100210000058

Soong JL, Fuchslueger L, Marañon-Jimenez S, Torn MS, Janssens IA, Penuelas J, Richter A (2020). Microbial carbon limitation: the need for integrating microorganisms into our understanding of ecosystem carbon cycling. Global Change Biology 26: 1953-1961. - doi: 10.1111/gcb.14962

Stern JL, Hagerman AE, Steinberg PD, Winter FC, Estes JA (1996). A new assay for quantifying brown algal phlorotannins and comparisons to previous methods. Journal of Chemical Ecology 22: 1273-1293. - doi: 10.1007/BF02266965

Uselman SM, Qualls RG, Lilienfein J (2012). Quality of soluble organic C, N, and P produeced by different types and species of litter: root litter versus leaf litter. Soil Biology and Biochemistry 54: 57-67. - doi: 10.1016/j.soilbio.2012.03.021

Weishaar JL, Aiken GR, Bergamaschi BA, Fram MS, Fujii R, Mopper K (2003). Evaluation of specific ultraviolet absorbance as an indicator of the chemical composition and reactivity of dissolved organic carbon. Environment Science and Technology 37: 4702-4708. - doi: 10.1021/es030360x

Wickland KP, Neff JC, Aiken GR (2007). Dissolved organic carbon in Alaskan boreal forest: sources, chemical characteristics, and biodegradability. Ecosystems 10: 1323-1340. - doi: 10.1007/s10021-007-9101-4

Wymore AS, Compson ZG, McDowell WH, Potter JD, Hungate BA, Whitham TG, Marks JC (2015). Leaf-litter leachates is distinct in optical properties and bioavailability to stream heterotrophs. Freshwater Science 34: 857-866. - doi: 10.1086/682000