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. 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

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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. elliotii) 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 Experiments Station of Jiangxi Agricultural University (26° 44' N, 115° 04' E) located in the Luxi Town, Taihe County, Jiangxi Province, China (Fig. 1). The climate of the study site is 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, Gymnopogon goeringii, and Searia viridis (Gong et al. 2015). 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. elliotii, 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. elliotii) 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. elliotii 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 was measured by the Folin-Ciocalteu 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 DOC were expressed as atomic ratios. The absorbances of DOC were expressed as atomic ratios. The absorbances of DOC were expressed as atomic ratios. The absorbances of DOC were expressed as atomic ratios. The absorbances of DOC were expressed as atomic ratios. The absorbances of DOC were expressed as atomic ratios. The absorbances of DOC were expressed as atomic ratios. The absorbances of DOC were expressed as atomic ratios. The absorbances of DOC were expressed as atomic ratios. The absorbances of DOC were expressed as atomic ratios. The absorbances of DOC were expressed as atomic ratios. The absorbances of DOC were expressed as atomic ratios. The absorbances of DOC were expressed as atomic ratios.

**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 a         | 9.52 ± 0.17 a   | 1.45 ± 0.05 a   | 145 ± 3 a                | 54 ± 1 a   | 785 ± 27 c | 14.6 ± 0.6 a | 131 ± 4 b                 |
| S. superba      | 457 ± 3 b         | 5.70 ± 0.09 b   | 0.85 ± 0.04 b   | 101 ± 3 b                | 94 ± 2 b   | 1399 ± 66 b | 14.9 ± 0.6 a | 94 ± 3 b                  |
| P. massoniana   | 481 ± 3 c         | 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. elliotii     | 441 ± 3 d         | 4.32 ± 0.06 d   | 0.66 ± 0.03 c   | 86 ± 2 c                 | 119 ± 2 a  | 1717 ± 91 a | 14.6 ± 0.9 a | 72 ± 3 c                  |
visible dual-beam spectrophotometer (UV 6000SC®, Jihhua Instruments, China) with 1-cm quartz cells. Before measurement, litter leaches were diluted when necessary. In this study, the specific ultraviolet absorbances at 254 nm (SUVA254), 280 nm (SUVA280), 350 nm (SUVA350), and 370 nm (SUVA370) 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); Sn was used to indicate DOM molecular weight, and higher Sn values showed lower molecular weight (Helms et al. 2008, Hansen et al. 2016). For each litter leachate, SUVA254, SUVA280, SUVA350, and SUVA370 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 Sn values, we firstly obtained SUVA254 and SUVA370 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 Sn values as the ratio of spectral slope SUVA254 to spectral slope SUVA370 (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 conifer plantation were placed in 250 mL glass jars, inoculated with 100 mL deionized water in the dark at 20 °C for 12 hours. The inoculum suspension was prepared by the DOC concentration, respectively (Hansen et al. 2016). Afterward, 100-mL microbial growth. Afterward, 100-mL
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Fig. 2 - Leaf litter-leached dissolved organic matter (DOM) biodegradation and changes in $S_8$ 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 (Table 2). In addition, *P. massoniana* had lower DOC:DTP ra-
tio than the other three tree species (Table 2). In the litter leachates, broadleaf trees (L. *formosana* and *S. superba*) had greater SUVA254, SUVA340, SUVA465, and SUVA300 val-
ues, but lower Sr values than coniferous trees (*P. massoniana* and *P.elliottii* – Tab. 3). Tree species, incubation time, and their interaction significantly affected biodegra-
dation and Sr 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 al-
ways higher for *L. formosana* than for *S. su-
perba*, whereas no significant difference in litter-derived DOM biodegradation was ob-
erved between *P. massoniana* and *P.elliottii* (Fig. 2). In addition, Sr values of DOM varied with tree species in the initial 42 days of incubation, but showed no signifi-
cant difference among the tree species by the end of incubation (Fig. 2). After 56-day cor-
related, DOM biodegradation correlated negatively with DOC:DTP ratio (R² = 0.587, p<0.001) and DNT:DTP ratio (R² = 0.716, p<0.001), but did not exhibit a signifi-
cant relationship with DOC:CDT ratio (Fig. 3).

Discussion

In line with the first hypothesis, *L. for-
mosana* and *S. superba* generally yielded greater amounts of DOC, DNT, and DTP per gram of dry leaf litter than *P. massoniana* and *P. elliottii* following short-term leach-
ing. Previous studies also observed similar patterns of litter-derived DOC or/and dis-
solved nutrient amounts between broad-
leaf 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 substan-
tial differences in DOC quantity in the litter leachates would be explained by the dis-
tinct leaf litter physical and chemical prop-
erties among broadleaf and coniferous trees. First, broadleaf litter might contain higher amounts of soluble C and nutrient fractions such as sugar and secondary met-
abolic compounds than coniferous litter (Joly et al. 2016, Li et al. 2016). Second, compared with coniferous species, broad-
leaf species produced leaf litter with a rela-
tively thinner epidermic and hypodermic layer, lower toughness, and flatter surface structure, which would enable leaf litter to be easily broken and leached (Don & Kalb-
itz 2005, Ibrahimia 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 com-
ounds (Joly et al. 2016). Considering that most previous studies have been con-
ducted in temperate and boreal forests, the result confirms the generality of inter-
specific patterns in leaf litter-derived DOM amounts between broadleaf and conifer-
ous trees to tropical forests.

Contrary to the second hypothesis, both *L. formosana* and *S. superba* had higher SUVA254, SUVA340, SUVA465, and SUVA300 val-
ues, but lower Sr values in the litter leachates than the selected two pine trees. Given that litter-derived DOM chemical make-up was determined by litter chemistry (Don & Kalbitz 2005, Kalbitz et al. 2006, Uselman et al. 2012, Kikkilä 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, pollu-
tant mobilization and transportation, and groundwater quality (Kalbitz et al. 2003, Hansen et al. 2016, Joly et al. 2016). Accord-
ingly, these findings will help explain the spatial variations of ecosystem services be-
tween broadleaf and coniferous tree plan-
tations in subtropical regions.

Consistent with the third hypothesis, lit-
ter-derived DOM biodegradation was great 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 conifer-
ous trees in temperate and boreal forests (Kikkilä 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 re-
sults implied that the interspecific patterns of litter-derived DOM biodegradation be-
tween 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, Wick-
land et al. 2007, Mao et al. 2017). Despite greater DOM aromaticity and molecular weight, broadleaf species often had lower DOC:DTP and DNT:DTP ratios in the litter leachates than coniferous species. Consider-
ing that DOC biodegradation was limited by P availability in subtropical regions (Mao et al. 2017), broadleaf third 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 be-
tween broadleaf and coniferous trees in subtropical plantations.

Interestingly, the magnitudes of the changes in Sr values of DOM varied sub-
stantially with species. Over the entire incu-
bation period, Sr values of DOM declined for *P. massoniana* and *P. elliottii*, but re-
mained 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 Sr values indicated that, for coniferous species, microorganisms might predominantly utilize the labile fractions of DOM originating from relatively low molecular weight, resulting in the net accumulation of or-
ganic compounds with a high molecular weight in the leachates (Helms et al. 2008, Hansen et al. 2016). In contrast, Sr 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, Sr 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 com-
position will become convergent with mi-
crobial degradation proceeds in subtropi-
cal 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 incub-
bation, 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 bio-
degradation was primarily driven by DOC: DNT:DTP stoichiometry rather than DOM aromaticity and molecular weight. These findings imply that, compared with conifer-
ous trees, broadleaf trees can provide labile litter-derived DOM for microbial growth and metabolism, and thus facilitate soil organic matter formation and accumu-
lation via the DOM-microbial path in sub-
tropical plantations (Cotrufo et al. 2015).

Therefore, our results will help explain and forecast the spatial patterns of C and nutri-
ent cycles between broadleaf and conifer-
ous tree plantations, and also suggest that broadleaf tree species are preferentially re-
commended for afforestation and refor-
estation programs in subtropical regions of China.

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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): 27-53. - 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, Kikklüa 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/s11053-016-0239-2

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: 10.1002/(SICI)1080-6295(200004)100:3<277::AID-SSA>3.0.CO;2-3

Kalbitz K, Schmerwitz J, Schwenig 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

Kikklüa O, Smolandera A, Kittenven 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: 785-798. - 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/ifi01738-009

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, Atkenhead-Peterson JA, Gregorich EG, Jones DL, Jodemann D, Kalbitz K, Marschner B, Schwesig D (2006). A comparison of methods to determine the biodegradability of 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 UJ, 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/s10021-0000-0958

Soong JL, Fuchsleguer L, Marañon-Jimenez S, Tom MS, Janssens IA, Penuelas J, Richter A (2002). Microbial carbon limitation: the need for integrating microorganisms into our understanding of ecosystem carbon cycling. Global Change Biology 26: 1953-1961. - doi: 10.1111/j.1466-4071.2001.00196.x

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 produced by different types and species of litter: root litter versus leaf litter. Soil Biology and Biochemistry 44: 57-67. - doi: 10.1016/j.soilbio.2010.03.011

Weishaar JL, Alken GR, Bergamaschi BA, Fram MS, Fuji 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, Alken GR (2007). Dissolved organic carbon in Alaskan boreal forest: sources, chemical characteristics, and biodegradability. Ecosystems 10: 1523-1540. - 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