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Short Communication

Condensed tannin effects on decomposition of very fine roots among temperate tree species

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ABSTRACT

Below-ground litter is the dominant soil carbon and nutrient input in many ecosystems, yet the general functional traits underlying below-ground decomposition remain elusive. As defensive compounds, condensed tannin (CT) might be expected to be abundant in very fine roots (<0.5 mm) and are associated with decomposition dynamics. Here, we quantified the interspecific variation in fine root CT concentrations and examined the functional significance of CT for fine root decomposition over four years among 15 Chinese temperate tree species. Concentrations of CT varied between 5.82% and 16.02% among species. After four years of decomposition, initial litter nutrients explained no interspecific variation in fine root decomposition rates in this relatively nutrient-rich temperate forest. In contrast, substrate carbon compounds strongly control the process of fine root decomposition and CT was important for predicating fine root decomposition rates. Our results imply that the strong negative effects of CT on fine root decomposition can have great impacts on soil biological processes.

Decomposition of plant litter regulates the rate at which carbon and nutrients cycle in ecosystems, and is an important first step for the formation of soil humus. Although root litter is the dominant soil C and nutrients input in many ecosystems (Gill and Jackson, 2000), few established principles have been quantified for the factors that control root decomposition (Silver and Miya, 2001; Berg and McClaugherty, 2014).

Tannins are one of the most widely distributed plant secondary metabolites, and may have different ecological effects from other plant phenolics because of their ability to precipitate numerous proteins and peptides (Hartzfeld et al., 2002). Tannins have long been recognized as defensive compounds, which may play an important role in biological processes including plant–herbivore interactions (Coulis et al., 2009; Coq et al., 2010) and UV radiation-protection (Close and McArthur, 2002). Some recent evidence showed that condensed tannin (CT) in leaf litter could interfere with the process of decomposition (Coq et al., 2010; Hättenschwiler et al., 2011). This might be expected to be particularly true for fine root decomposition, given fine roots may have relatively high CT concentration (Gallet and Lebreton, 1995; Hättenschwiler and Vitousek, 2000; Kraus et al., 2003). However, CT has rarely been studied in root decomposition studies. Here we examined the functional significance of litter CT for fine root decomposition among 16 temperate tree species.

In April 2009, we harvested root samples from 11 temperate tree species at the Fenglin Nature Reserve in Heilongjiang Province, northeastern China (128 °58′–129 °15′E, 48 °02′–48 °12′N). The decomposition rate of an additional four tree species (*Pinus koraiensis*, *Larix gmelinii*, *Betula platyphylla* and *Populus davidiana*) were used in our analysis by using data from Sun et al. (2013). Detailed descriptions regarding the study site can be found in Sun et al. (2012, 2013). Approximately 2.0 g of fine root (<0.5 mm) material was sealed into 20 × 20 cm litter bags (nylon, mesh size 120 μm). The fine mesh width was used to avoid losses of root fragments that are decomposing and prevent fine roots of trees growing into the litterbags, but still allowed the passage of fungal hyphae (Langley and Hungate, 2003). Litterbags were installed in May 2009 at a depth of 10 cm below the mineral-organic boundary in each of three replicate plots, and harvested in August and October 2009 and in October 2010–2012. It is important to note that the present study was done exactly in parallel with the Sun et al. (2013). At each harvest date, four replicate bags per species were recovered. Harvested root samples were cleaned of adhering soil, oven-dried and weighed. Details about trait measurements of

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Table 1
Dominant mycorrhizal (Myc) type and initial litter chemistry parameters (mg/g root dry mass) of the 15 studied species (all values are mean ± SE, $n = 3$).

Species	Myc	N	P	K	Ca	Mg	C:N	Extractives	AHF	AUF	Soluble phenolics	Total phenolics	Condensed tannins
Abies nephrolepis	EM	18.4 (1.5)	1.2 (0.0)	5.5 (0.2)	8.2 (0.5)	0.8 (0.1)	25.8 (1.8)	177.3 (17.0)	425.0 (15.8)	397.2 (26.4)	33.9 (3.7)	275.3 (26.7)	120.7 (19.0)
Picea koraiensis	EM	16.9 (0.9)	1.6 (0.1)	7.0 (0.1)	5.5 (0.4)	1.0 (0.2)	29.3 (3.0)	305.5 (19.2)	280.9 (9.7)	413.9 (47.1)	70.3 (3.2)	238.8 (16.2)	103.6 (8.8)
Fraxinus mandshurica	AM	23.8 (1.2)	2.5 (0.1)	3.2 (0.3)	10.3 (0.9)	2.6 (0.5)	22.6 (4.4)	326.3 (22.5)	386.5 (30.1)	286.2 (29.0)	26.0 (2.8)	380.5 (25.4)	75.4 (5.0)
Betula costata	EM	16.5 (0.6)	2.8 (0.3)	3.9 (0.1)	9.1 (0.6)	0.9 (0.1)	31.9 (3.8)	256.8 (10.4)	394.2 (25.8)	350.6 (36.2)	39.7 (3.5)	229.2 (17.3)	69.5 (6.4)
Ulmus pumila	AM	23.7 (1.1)	3.0 (0.2)	4.1 (0.3)	15.8 (0.8)	1.7 (0.3)	19.7 (2.5)	426.4 (16.0)	213.1 (17.9)	361.4 (33.8)	49.5 (2.6)	270.9 (21.8)	125.3 (11.7)
Phellodendron amurense	AM	20.2 (1.3)	1.4 (0.0)	5.5 (0.7)	8.1 (0.5)	1.9 (0.2)	25.4 (4.6)	382.1 (35.1)	380.0 (22.6)	237.3 (17.0)	18.4 (1.2)	329.4 (27.6)	58.2 (3.7)
Acer mono	EM	13.0 (1.7)	3.9 (0.1)	3.0 (0.2)	14.4 (0.7)	1.3 (0.2)	36.9 (2.0)	402.3 (25.7)	307.6 (16.1)	290.8 (22.4)	25.1 (3.7)	295.1 (15.2)	88.1 (7.4)
Quercus mongolica	EM	20.1 (0.5)	2.8 (0.2)	3.9 (0.2)	6.0 (0.4)	1.8 (0.3)	25.3 (1.6)	279.3 (20.2)	335.7 (32.5)	386.1 (36.6)	56.3 (6.4)	219.6 (19.3)	160.2 (14.5)
Euonymus sacrosancta	AM	24.3 (1.6)	2.1 (0.3)	3.7 (0.3)	10.2 (0.4)	2.5 (0.3)	18.0 (2.7)	441.9 (39.3)	275.0 (18.7)	283.6 (24.7)	23.6 (4.1)	96.0 (10.4)	69.3 (5.1)
Alnus sibirica	EM	15.4 (0.8)	3.6 (0.1)	2.2 (0.2)	14.7 (0.9)	1.9 (0.1)	34.1 (1.1)	414.7 (26.3)	232.1 (9.2)	354.0 (33.1)	30.8 (3.9)	318.2 (16.7)	87.8 (5.5)
Acer tegmentosum	AM	18.2 (1.2)	1.9 (0.1)	4.6 (0.4)	6.8 (0.3)	2.0 (0.4)	29.8 (3.5)	225.3 (19.6)	394.2 (27.0)	380.2 (29.5)	64.3 (4.3)	223.7 (25.8)	138.3 (10.4)
*Pinus koraiensis**	EM	15.7 (0.7)	1.5 (0.2)	2.2 (0.1)	12.1 (1.3)	2.1 (0.1)	32.1 (0.9)	349.4 (38.7)	208.5 (12.8)	443.2 (35.4)	28.7 (3.0)	261.3 (19.2)	150.1 (10.3)
*Larix gmelinii**	EM	19.6 (0.8)	2.3 (0.3)	4.1 (0.2)	5.8 (0.4)	2.3 (0.1)	26.3 (1.5)	268.3 (16.9)	275.0 (10.4)	457.5 (43.6)	34.2 (2.4)	275.2 (21.5)	138.7 (9.5)
*Betula platyphylla**	EM	21.8 (1.2)	1.8 (0.1)	6.8 (0.3)	4.9 (0.4)	2.8 (0.3)	20.3 (2.5)	346.9 (30.6)	250.1 (25.3)	403.5 (41.9)	33.6 (1.9)	340.4 (26.0)	86.9 (5.8)
*Populus davidiana**	EM[a]	25.3 (1.3)	2.0 (0.2)	3.9 (0.1)	7.9 (0.7)	1.7 (0.1)	18.6 (1.7)	358.0 (29.6)	261.2 (9.2)	382.1 (12.5)	59.4 (4.1)	363.8 (30.1)	107.3 (12.6)

Key to abbreviations: AM, arbuscular mycorrhizas; EM, ectomycorrhizas; AHF, acid-hydrolyzable fraction; AUF, acid-unhydrolyzable fraction.
* Values of litter quality parameters from Sun et al. (2013).

C, N, P, K, Ca, Mg, extractives, acid-hydrolyzable fraction (AHF) and acid-unhydrolyzable fraction (AUF) are presented in Sun et al. (2013). It is important to note that this so-called 'AUF' is an operationally defined C-fraction of litter material that is not degraded by strong acid treatment. Besides true molecular lignin, this concept AUF also captures some waxes and other organic

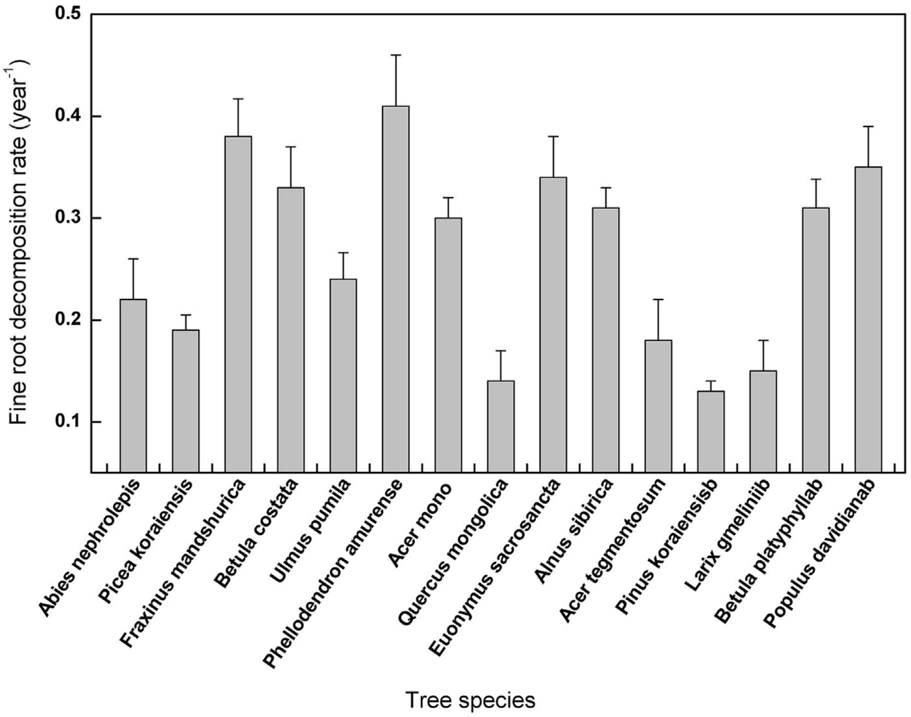

Fig. 1. Fine root decomposition rates (mean + SE, $n = 3$) of the 15 studied species over 4 years of decomposition in the field. Decomposition rates of *Pinus koraiensis*, *Larix gmelinii*, *Betula platyphylla* and *Populus davidiana* were calculated using data from Sun et al. (2013).