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Original Article

Initial contents of residue quality parameters predict effects of larger soil fauna on decomposition of contrasting quality residues

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ABSTRACT

A 52-week decomposition study employing the soil larger fauna exclusion technique through litter bags of two mesh sizes (20 and 0.135 mm) was conducted in a long-term (18 yr) field experiment. Organic residues of contrasting quality of N, lignin (L), polyphenols (PP) and cellulose (CL) all in grams per kilogram: rice straw (RS: 4.5N, 22.2L, 3.9PP, 449CL), groundnut stover (GN: 21.2N, 71.4L, 8.1PP, 361CL), dipterocarp leaf litter (DP: 5.1N, 303L, 68.9PP, 271CL) and tamarind leaf litter (TM: 11.6N, 190L, 27.7PP, 212CL) were applied to soil annually to assess and predict soil larger fauna effects (LFE) on decomposition based on the initial contents of the residue chemical constituents. Mass losses in all residues were not different under soil fauna inclusion and exclusion treatments during the early stage (up to week 4 after residue incorporation) but became significantly higher under the inclusion than the exclusion treatments during the later stage (week 8 onwards). LFE were highest (2–51%) under the resistant DP at most decomposition stages. During the early stage (weeks 1–4), both the initial contents of labile (N and CL) and recalcitrant C, and recalcitrant C interaction with labile constituents of residues showed significant correlations ($r = 0.64–0.90$) with LFE. In the middle stage (week 16), LFE under resistant DP and TM had significant positive correlations with L, L + PP and L/CL. They were also affected by these quality parameters as shown by the multiple regression analysis. In the later stages (weeks 26–52), the L/CL ratio was the most prominent quality parameter affecting LFE.

Introduction

Decomposition is a process by which energy and nutrients are transferred from plant residues to the decomposer organisms (Berg and Laskowski, 2006; Whalen and Sampedro, 2010). Larger sized fauna (mesofauna and macrofauna) have been shown to accelerate rates of decomposition in their presence over those of microorganisms working in conjunction with smaller-sized fauna (microfauna) alone (Irmler, 2000; Hunter et al., 2003; Yang and Chen, 2009; Whalen and Sampedro, 2010; Carrillo et al., 2012; Slade and Riutta, 2012). Detritivorous larger fauna contribute directly to decomposition through comminuting plant litter into smaller pieces which opens up new surfaces of litter for microbial attack (Lavelle, 1988; Persson, 1989; Swift and Anderson, 1989; Scheu and Wolters, 1991). Predator larger fauna also contribute indirectly to decomposition rates though their grazing on decomposer microorganisms (for example, Hunter et al., 2003). Quality or chemical composition is another important controlling factor of decomposition (Swift et al., 1979). There are interactions between these two factors (decomposers × chemical quality interaction) in controlling decomposition, for examples those shown by Yang and Chen (2009). Much evidence from both temperate (Slade and Riutta, 2012) and tropical (Yang and Chen, 2009) conditions has shown that the influence of larger fauna on decomposition varies with litter types possessing various chemical compositions. In addition, its influence is stronger in recalcitrant plant litter than more easily-decomposable counterparts. For example, in two studies employing a fauna exclusion technique through the use of different mesh-sized litter bags, lower litter quality in a rain forest ecosystem had a higher decomposition rate in fauna accessible conditions (litter bag of mesh size 2 mm) than higher quality litter under two

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humid forest ecosystems, i.e. secondary and broad-leaf forests (Yang and Chen, 2009). Under temperate conditions, Slade and Riutta (2012) reported that macrofauna had higher effects on more recalcitrant litter (oak and beech leaf litter) than more easily decomposable litter (ash and sycamore leaf litter).

The chemical quality parameters of plant litter which have been used as robust indicators of decomposition are: C, N, the ratio of C/N, lignin, and polyphenols as defined by Palm and Rowland (1997). More recently, it has been proposed that cellulose should be included as another chemical quality parameter indicating decomposition (Loranger et al., 2002; Puttaso et al., 2011; Kunlanit et al., 2014). The interactions of larger fauna and chemical quality factors have been found to be different at different stages of decomposition because the concentrations of litter chemical constituents change as decomposition proceeds which has a bearing on the assemblages and activities of decomposers (Hunter et al., 2003). The influence of the larger fauna on the decomposition of recalcitrant litter has been found to be more pronounced during the later stages of decomposition (Gonzalez and Seastedt, 2001; Hättenschwiler and Gasser, 2005; Riutta et al., 2012; Slade and Riutta, 2012). The initial concentrations of litter chemical constituents have been used to associate them with decomposition as represented by mass loss or mass remaining of residues, (for example, Loranger et al., 2002; Puttaso et al., 2011). The initial concentrations of litter chemical constituents can serve as predictors of decomposition at various decomposition stages in question. However, there is no known study using initial concentrations of litter chemical constituents to predict effects of larger fauna on decomposition.

In Northeast Thailand, serious problems of soil fertility degradation in coarse-textured soils have justified research into the use of different quality, locally available, organic residues to restore soil fertility through increasing the contents of soil organic matter (SOM), (Vityakon et al., 2000; Puttaso et al., 2011). It was found that these different residues restored SOM to different degrees after annual application for 1 yr (Vityakon et al., 2000), 10 yr (Samahadthai et al., 2010) and 13 yr (Puttaso et al., 2011). Lignin, polyphenols and cellulose and the ratios of the recalcitrant constituents to N were identified as the prominent chemical parameters that had significant relations to decomposition at the later stages of decomposition of these residues (Puttaso et al., 2011). The decomposition was described by functions of the flora and fauna of size smaller than 2 mm. However, this earlier study did not distinguish the effects of the larger fauna from the rest of the decomposers. The present study focused on the effects of larger fauna on the decomposition of contrasting quality organic residues. The hypothesis was that the initial concentrations of residue recalcitrant chemical constituents, notably lignin, and the interactions between lignin and labile constituents of residue (the ratio of lignin to labile constituents) can predict the decomposition stage at which larger fauna have their most pronounced decomposition function in different types of organic residues. The objective of this study was to identify the most prominent initial chemical parameters that can predict larger fauna effects on the decomposition of contrasting quality organic residues.

Materials and methods

Study site and soil

The study site was located on the research station of the Office of Agriculture and Co-operatives of the Northeast in Tha Phra subdistrict, Khon Kaen province, Thailand (16°20.685′N; 102°49.499′E). The soil is a Khorat sandy loam (Typic Kandiustult), which is a coarse-textured soil representative of approximately 21% of soils of Northeast Thailand and the topsoil (0–15 cm depth) has proportions of sand, silt and clay of 934 g/kg, 45 g/kg and 21 g/kg, respectively (Vityakon et al., 2000). The initial chemical characteristics of the topsoil were: pH (H_2O) 5.5, cation exchange capacity (CEC) 3.5 cmol/kg, organic C 2.1 g/kg and bulk density 1.45 g/cm^3 (Vityakon et al., 2000). The climatic conditions during the experimental year 2012 are shown in Fig. 1.

Experimental design of the long-term field experiment and treatments

The long-term field experiment was established in 1995 (Vityakon et al., 2000). The experiment had a plot size of 4 × 4 m^2 with a track width between plots of 1 m. A randomized complete block design (RCBD) with three replications was employed. The data collection for this paper was done in year 18 during May 2012–April 2013. There were four residues plus a control (no residue applied) employed as treatments. The residues with contrasting biochemical composition had been applied annually and those of year 18 are shown in Table 1. The residue materials which could be obtained locally in farming systems of Northeast Thailand included: rice (*Oryza sativa*) straw (RS), groundnut (*Arachis hypogeae*) stover (aboveground parts and depodded pulled roots) (GN), dipterocarp (*Dipterocarpus tuberculatus*) leaf litter (DP), and tamarind (*Tamarindus indica*) leaf and petiole litter (TM; dry weight ratio of leaves to petioles = 8/1). All organic residues were air dried. RS and GN residues were cut into pieces of 5–10 cm, and DP leaf litter was cut into a rectangular shape of an approximate size of 5 × 10 cm^2, whereas TM residues were not modified. These residue treatments were applied annually in early May at 10 t dry matter/ha into the soil at 20 cm depth in a 4 × 4 m^2 plot.

Litter bag experiment to study organic residue decomposition as affected by larger soil fauna

A litter bag experiment was superimposed on the long-term field experiment at the beginning of the year 18 cycle starting in early May 2012 when the residue application was being conducted. The litterbag technique was employed in order to study decomposition (Bradford et al., 2002; Coleman et al., 2004; Coyne and Thompson, 2006), and the effect of larger fauna—soil mesofauna and macrofauna—on decomposition. Two types of polyethylene litter bags (20 × 20 cm^2) were used. One was designated as coarse mesh (20 mm) which was to allow all sizes of soil fauna (micro-, meso- and macro-fauna) and microorganisms to enter, and the other as fine mesh (0.135 mm) which was to exclude larger fauna. These two mesh sizes allowed the larger fauna effect (LFE) to be determined. A sample of 40 g (dry weight equivalent; DW) of each single residue (equivalent to 10 t DW/ha) was placed in separate bags for both mesh sizes.

Litter bags with their contents of each residue type were placed in the field plots corresponding to their residue treatments. A total of 384 litter bags (four residues, three replications, two mesh sizes bag, two bags/mesh size and eight sampling dates) were deployed. Litterbags were buried at 15 cm depth at approximately 40 cm from the edge of the plot outside the center (2 × 2 m^2 area) of the plot. Two bags of each mesh size from each plot were retrieved at week 1, 2, 4, 8, 16, 26, 39 and 52 after residue incorporation (WAI). The experiment was conducted for 1 yr (52 wk) during May 2012–April 2013.

Litter remaining was manually cleaned using a brush after soil fauna and extraneous materials, such as plant roots and gravel were removed. Subsequently, each cleaned litter sample was oven dried at 60 °C until constant weight for determining the remaining dry mass. Subsamples of 0.5–1.0 g were ashed at 550 °C for 6 h (Sluiter

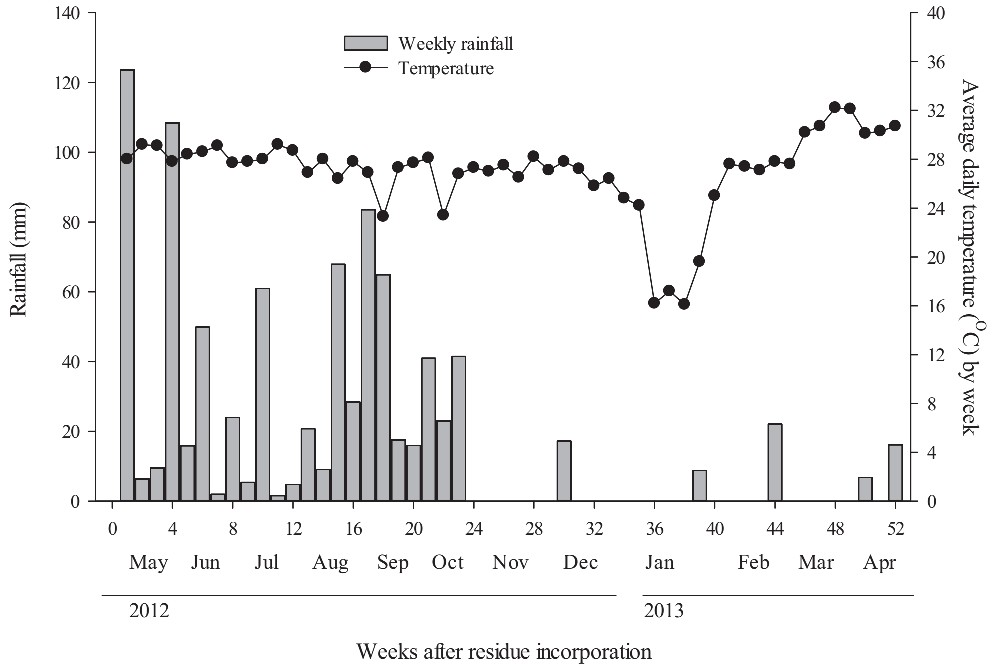

Fig. 1. Climatic conditions after residue incorporation during year 18 (May 2012–April 2013) of field experiment.

Table 1
Initial chemical characteristics (g/kg) of organic residues applied in year 18 of the long-term experiment*.

Residues	C	N	L	PP	CL	C/N	L/N	L/CL	PP/N	(L + PP)/N
RS	389.3^{d}	4.5^{d}	22.2^{d}	3.9^{d}	449.3^{a}	86.5^{a}	4.9^{c}	0.05^{d}	0.9^{c}	5.8^{c}
GN	390.6^{c}	21.2^{a}	71.4^{c}	8.1^{c}	361.3^{b}	18.4^{c}	3.4^{d}	0.2^{c}	0.4^{d}	3.8^{d}
DP	455.2^{a}	5.4^{c}	303.2^{a}	68.9^{a}	270.7^{c}	84.3^{a}	56.1^{a}	1.1^{a}	12.8^{a}	68.9^{a}
TM	410.0^{b}	11.6^{b}	190.1^{b}	27.7^{b}	211.9^{d}	35.3^{b}	16.4^{b}	0.9^{b}	2.4^{b}	18.8^{b}

RS = rice straw; GN = groundnut stover; DP = dipterocarp leaf litter; TM = tamarind leaf and petiole litter; C = carbon; N = nitrogen; L = lignin; PP = polyphenols; CL = cellulose.
* Means in the same column followed by the same lowercase letter are not significantly different at the 0.05 test level.

et al., 2008) for determining the content of ash (signifying mineral or inorganic matter) the weight of which was subtracted from the litter dry weight to obtain an ash-free basis signifying a condition free of mineral contamination.

The remaining litter mass (R) in each bag was calculated using Equation 1:

$$R(\%) = (W_t/W_0) \times 100 \quad (1)$$

where W_0 is the litter initial mass and W_t is the litter mass remaining at time *t*. The litter mass loss in two mesh-sized litter bags was used to determine the soil larger fauna effect (LFE) (Irmler, 2000; Seastedt, 1984) employing Equation 2:

$$LFE(\%) = [(A - B)/A] \times 100 \quad (2)$$

where A is litter mass loss in 20 mm mesh-sized litter bags and B is the litter mass loss (% original mass) of 0.135 mm mesh sized litter bags, both as a percentage of the original mass.

Residue analysis

Dry plant materials were finely (1 mm) ground before performing chemical analysis. Total carbon (C) was determined using a dry combustion method (Nelson and Sommers, 1982) with an organic elemental analyzer (FLASH 2000 NCS; Thermo Scientific; Paisley, England) and total nitrogen (N) using the micro-Kjeldahl method (Bremner and Mulvaney, 1982). Lignin (L) and cellulose (CL) were analyzed by sequential digestion of fiber (Van Soest, 1963). Lignocellulose was obtained after extraction with acid detergent (acid detergent fiber; ADF) using a fiber analyzer (ANKOM 200/220; Macedon; New York, NY, USA). Lignin was obtained after hydrolysis with 72% H_2SO_4 (acid detergent lignin; ADL). Cellulose was determined from the difference between ADF and ADL. Total extractable polyphenols (PP) were determined after fine plant residues were extracted with 50% methanol then measured colorimetrically using the Folin-Denis method (Anderson and Ingram, 1993).

Statistical analysis

Analysis of variance was used with a randomized complete block design (RCBD). Mean comparisons among treatments were assessed by the least significant difference (LSD), and standard error of the means (SEM). Paired *t*-test analysis was employed to test for differences in the mass remaining between mesh sizes at each sampling date.

Pearson's correlation coefficient analysis (*r*) was conducted to study relationships between initial concentrations of chemical constituents of the residues and soil larger fauna effect. Multiple regression analysis was used to determine influences of various initial chemical quality parameters that interacted with each other on decomposition as influenced by soil larger fauna. All statistical analyses were performed using the statistical package Statistics 8.0 (Analytical Software, 2003). Significant differences in all analyses were tested as indicated by asterisks used in the text (* = significant at $p \leq 0.05$; ** = significant at $p \leq 0.01$; *** = significant at $p \leq 0.001$).

Results and discussion

Residue decomposition: difference between larger fauna excluded and included treatments

During the early stages of decomposition (first 4 weeks), mass loss of all residues was more rapid than at later stages (after week 4) in both soil larger fauna excluded (fine mesh bags) and included (coarse mesh bags) treatments, (Fig. 2). During the early stages, there were no significant differences in mass loss between the larger fauna excluded and included treatments in all residues indicating that the larger fauna did not exert a dominant role in decomposition in relation to microorganisms and microfauna. Mass loss during the early stages has been found to be positively related to degradation of initial soluble components of litter, such as sugars, starch and low molecular weight compounds (Hammel et al., 1993). These readily available substrates are used by both microflora and fauna. In contrast, recalcitrant constituents of litter, including phenolics (especially insoluble phenolics) and lignin, could exert inhibitive effects to microbial activities in decomposition during the initial stage (first 2 d) according to Bernhard-Reversat (1998). The two easily decomposable residues (GN and RS) showed more rapid mass losses than the recalcitrant residues (DP and TM). GN had the largest mass loss (67% and 65% of original) in larger fauna included and excluded treatments, respectively, followed by RS (45% and 44%) and tamarind (38% and 37%), while the lowest mass loss was found in DP (22% and 19% of original) as shown in Fig. 2. The easily decomposable residues contained higher contents of labile substances readily used by decomposers than the recalcitrant residues as reflected in significantly higher CL contents in the former than the latter residues (Table 1). Mass losses were significantly higher in treatments with fauna included than excluded at the later stages of decomposition starting in week 8

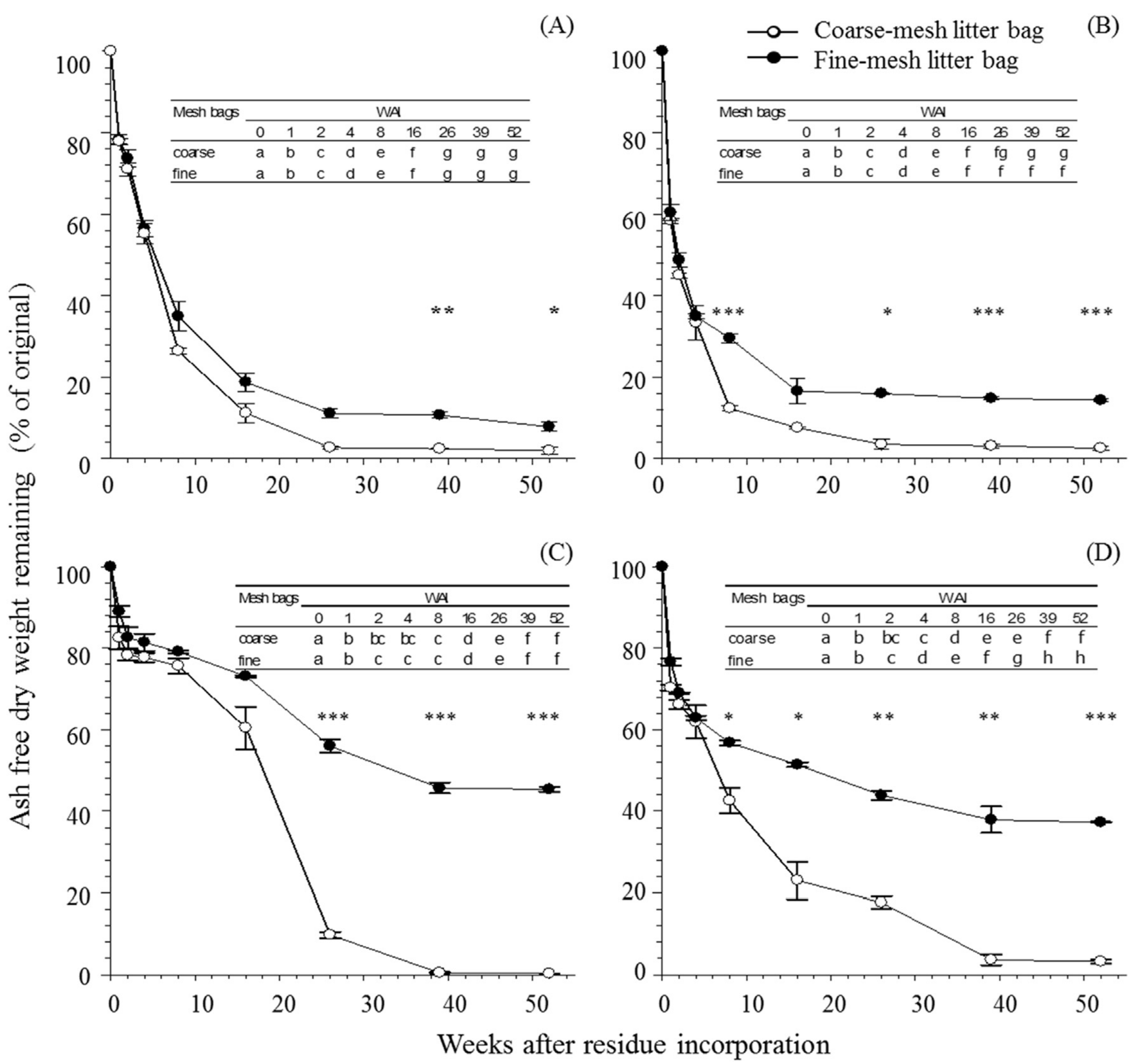

Fig. 2. Ash free dry weight remaining (% of original) in coarse-mesh sized and fine-mesh sized litter bags at various weeks after residue incorporation (WAI) of: (A) rice straw; (B) groundnut stover; (C) dipterocarp leaf litter; (D) tamarind leaf and petiole litter, where lowercase letters denote comparisons among sampling dates in each mesh-sized litter bags; means in the same row accompanied by a common letter are not statistically different ($p \leq 0.05$; least significant difference); asterisks represent statistically significant difference (* = significant at $p \leq 0.05$; ** = significant at $p \leq 0.01$; *** = significant at $p \leq 0.001$) of mean comparisons between mesh sized litter bags (paired *t*-test) at each sampling date; vertical bars represent standard error of the mean.

under GN and TM (Fig. 2B and D) and in week 26 and 39 in DP and RS, respectively (Fig. 2A and C). The higher N content residues appeared to show effects of soil larger fauna on their decomposition earlier than the lower N counterparts. The lowest L residue (RS) had larger fauna effects much later than its higher-L counterparts. Precipitous mass losses under fauna were notable, including treatment of resistant residues, (DP) during weeks 8–26 and TM during weeks 4–16 (Fig. 2C and D, respectively). At the end of the decomposition period (week 52), all residues remained less than 4% of original mass remaining in the fauna-included treatment. Significantly less mass losses were found in fauna-excluded treatments of all residues, with 8% and 14% in easily decomposable residues, RS, and GN, respectively, and 45% and 37% of original mass remaining in resistant residues, DP, and TM, respectively.

Soil larger fauna effects on decomposition in relations to residue chemical composition.

The effects of soil larger fauna (LFE) on decomposition of contrasting quality residues during the first week of decomposition were significantly different among residues, with DP showing significantly higher effects over all other residues. This was followed by TM, and GN, while RS showed the lowest effect which was significantly lower than that of TM (Fig. 3). In this initial period, there were plentiful labile compounds which could be used as sources of energy and nutrients for decomposers among which microorganisms appeared to play dominant roles. Bacteria and fungi are the two main decomposer microorganisms that degrade and utilize soluble components at a relatively high rate (Berg and Laskowski, 2006). This was shown clearly in the results of the lowest soil LFE, implying high microbial effects, under RS and GN. A significant positive correlation was found between soil LFE and the initial C contents of residues during week 1 ($r = 0.899^{***}$) of decomposition (Table 2). Higher invertase (the microbial enzyme that degrades simple sugars) activities were found under RS and GN than for the DP and TM treatments during the initial stage (3 h after these residues were added to the control soil) in an incubation experiment using the unamended soil from the same long-term experiment as in this study (Kamolmanit et al., 2013). These results showed that larger fauna, similar to microorganisms, made use of the labile compound constituents of residues as their substrates during the initial phase of decomposition. Not only soil microflora but also fauna make use of labile compounds as their substrates during the initial stage of decomposition (Vos et al., 2011; Slade and Riutta, 2012) through the following interactions. Microorganisms can produce necessary enzymes to digest recalcitrant substances (Berg and Laskowski, 2006). They then compete with soil fauna for these easily accessible substrates (Scheu and Schaefer, 1998). In the case of the cell wall component of plant litter (Takeda and Abe, 2001), soil fauna rely on microorganisms to biochemically degrade L and CL components to simple molecules before they can make use of them, while soil fauna contribute to microbial decomposition through comminuting the highly resistant litter. However, although the more labile compounds, as represented by N and CL, were used as substrates by both microflora and fauna, the more recalcitrant counterparts were used more effectively by larger fauna. This contention was supported by the negative correlation between the initial CL content and LFE ($r = -0.614^{*}$). In addition, during week 1 there were significant positive correlations between soil LFE and the initial contents of recalcitrant C constituents, that is L, PP and L + PP (Table 2). These results showed that soil larger fauna could make use of recalcitrant substances as their substrate, especially from the resistant residues, notably DP, immediately after residue incorporation. This is supported by the highest LFE being found in DP followed by TM (Fig. 3). Higher abundance and diversity of soil fauna, especially detritivores, have been found under more recalcitrant litter than more easily decomposable counterparts (Yang and Chen, 2009; Moco

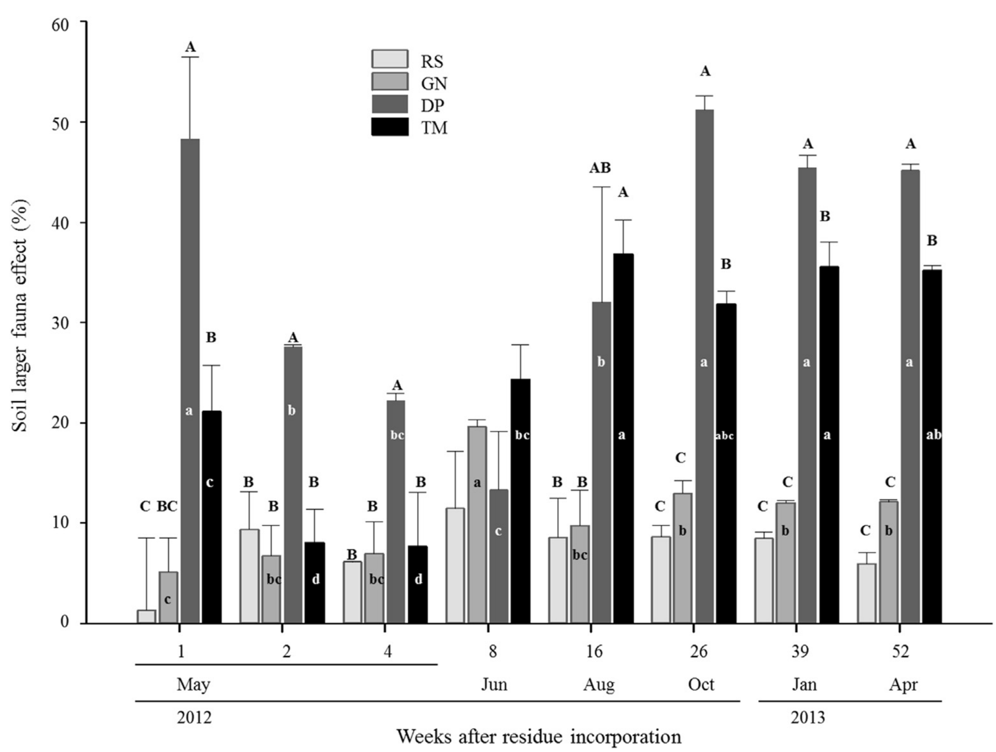

Fig. 3. Soil larger fauna effect on decomposition of different quality organic residues (RS, rice straw; GN, groundnut stover; DP, dipterocarp leaf litter; TM, tamarind leaf and petiole litter) at different stages of decomposition during year 18 of study period, where means of larger fauna effect in the same week accompanied by a common uppercase letter are not statistically different ($p \leq 0.05$; least significant difference); means of larger fauna effect across decomposition phases accompanied by a common lowercase letter are not statistically different ($p \leq 0.05$; least significant difference); vertical bars represent standard error of the mean.

Table 2
Pearson's correlation coefficients (r) between initial residue chemical compositions (g/kg) and soil larger fauna effect (%).

Period(wk)	Initial residue chemical compositions (g/kg)										
	C	N	L	PP	CL	L + PP	C/N	L/N	PP/N	L/CL	(L + PP)/N
1	0.899^{***}	-0.349^{ns}	0.891^{***}	0.901^{***}	-0.614^{*}	0.897^{***}	0.320^{ns}	0.888^{***}	0.863^{***}	0.850^{***}	0.884^{***}
2	0.848^{***}	-0.494^{ns}	0.722^{**}	0.831^{***}	-0.266^{ns}	0.746^{**}	0.562^{ns}	0.869^{***}	0.886^{***}	0.619^{*}	0.873^{***}
4	0.805^{**}	-0.351^{ns}	0.729^{**}	0.795^{**}	-0.352^{ns}	0.745^{**}	0.409^{ns}	0.819^{***}	0.821^{***}	0.636^{*}	0.821^{***}
8	-0.119^{ns}	0.407^{ns}	0.074^{ns}	-0.082^{ns}	-0.426^{ns}	0.044^{ns}	-0.540^{ns}	-0.165^{ns}	-0.216^{ns}	0.170^{ns}	-0.175^{ns}
16	0.517^{ns}	-0.169^{ns}	0.665^{*}	0.540^{ns}	-0.772^{**}	0.644^{*}	-0.030^{ns}	0.479^{ns}	0.407^{ns}	0.755^{**}	0.466^{ns}
26	0.967^{***}	-0.349^{ns}	0.990^{***}	0.976^{***}	-0.759^{**}	0.992^{***}	0.273^{ns}	0.943^{***}	0.911^{***}	0.963^{***}	0.937^{***}
39	0.903^{***}	-0.316^{ns}	0.975^{***}	0.921^{***}	-0.851^{***}	0.969^{***}	0.182^{ns}	0.867^{***}	0.820^{***}	0.985^{***}	0.859^{***}
52	0.905^{***}	-0.267^{ns}	0.986^{***}	0.925^{***}	-0.874^{***}	0.979^{***}	0.136^{ns}	0.866^{***}	0.818^{***}	0.996^{***}	0.858^{***}

C = carbon; N = nitrogen; L = lignin; PP = polyphenols; CL = cellulose; * = significant at $p \leq 0.05$; ** = significant at $p \leq 0.01$; *** = significant at $p \leq 0.001$; ns = non significant ($p > 0.05$).

et al., 2010; Vos et al., 2011). In week 2, the comparative LFE among various contrasting residues followed a similar trend to week 1, that is they were most pronounced in DP, while those of RS, GN and TM were comparable (Fig. 3). However, soil LFE under DP and TM significantly decreased relative to week 1. This showed that after week 1 soil LFE became less prominent relative to microbial effects as L was partly degraded at the initial decomposition stage (week 1) which allowed higher accessibility of more labile substrates for microbial decomposers. Additionally, residues with low N and high recalcitrant substances tended to have higher soil LFE than those with high N and low recalcitrant substances. Huhta (2007) reviewed much evidence which showed that in "N limited systems", the soil fauna role in decomposition was enhanced, whereas in "N excess systems" it was negligible. Furthermore, a high N content in residues induced more microbial decomposition than larger fauna decomposition as found under GN. A highly significant negative correlation between the LFE and microbial activities as indicated by CO_2−C evolution during the initial period (week 2) of decomposition ($r = -0.86^{***}$; data not shown) appeared to support this. This reflected increases in microbial activities in decomposition through more available substrates after comminution action of larger fauna on resistant residues during week 1 which provided increased surface areas for microbial decomposition (Lavelle, 1988; Persson, 1989; Swift and Anderson, 1989; Scheu and Wolters, 1991) or through resistant substances gradually degraded by larger fauna or both, rendering labile substances more accessible to microorganisms (Hättenschwiler and Vitousek, 2000). From week 4 to week 16, TM showed significant increases in LFE, while DP showed a significant increase from week 8 to week 16 (8 weeks later than TM) and both became comparable in week 16, LFE values in both were significantly higher than those of the more easily decomposable residues (RS and GN) in week 16 (Fig. 3). These were likely stimulated by increasing contents of recalcitrant substances, notably L, proportional to decreasing contents of more labile substances, such as sugars and simple carbohydrates. Generally, as decomposition proceeds, more easily decomposable substances are degraded early, whereas lignin remains relatively less degraded leading to its increasing content in decomposing plant residues until the later stages of decomposition (Couteaux et al., 1995; Berg and Laskowski, 2006). In week 16, significant positive correlations were found between soil LFE with recalcitrant residue constituents—L ($r = 0.665^{*}$), and L + PP ($r = 0.644^{*}$), and with the ratio of recalcitrant to labile constituents (L/CL) ($r = 0.755^{**}$) (Table 2), whereas a significant negative correlation was the case between soil LFE and CL ($r = -0.772^{***}$). These results showed that L and CL were prominent chemical parameters related to soil fauna decomposition. While L singly, or in combination with PP, enhanced larger fauna effects, CL depressed them. Lignin and CL are components of the plant cell wall structure (Talbot et al., 2012). These substances have been proposed to shape the organization of soil fauna in temperate and tropical forest ecosystems (Takeda and Abe, 2001). In addition, under DP, soil LFE showed a continuously decreasing trend from week 1 to week 8 which was significant during weeks 1–2 and weeks 2–8 (Fig. 3). This corresponded to decreases in positive r (correlation coefficient) values relating the soil LFE and L content from week 1 to week 8 (Table 2). This showed that after week 1, soil larger fauna effects became less prominent relative to microbial effects as L was partly degraded at the initial decomposition stage (week 1) which allowed higher accessibility of more labile substrates for microbial decomposers.

During the later stages of decomposition (week 26 onwards), LFE under DP significantly increased over those of earlier weeks, with the exception of week 1, to become the highest followed by TM (Fig. 3). The LFE values under DP and TM were significantly higher than those under the two easily decomposable residues (RS and GN) during the later stages (weeks 26–52). These results were similar to those reported in the literature indicating that soil larger fauna had a stronger influence on recalcitrant plant litter than on easily decomposable ones (Tian et al., 1995; Gonzalez and Seastedt, 2001; Hättenschwiler and Gasser, 2005; Riutta et al., 2012). In addition, the effects were found to be more pronounced during the later stages of decomposition (Tian et al., 1995; Yang and Chen, 2009; Slade and Riutta, 2012). Linear correlation analysis during the later stages (weeks 26, 39 and 52) showed highly significant positive correlations between soil LFE with the following residue chemical parameters: C, L, PP, the ratios of the recalcitrant parameters to N and CL, that is L/N, PP/N, (L + PP)/N and L/CL (Table 2). These results showed that in the later stages of decomposition, residue quality was dominated by recalcitrant constituents, whereas labile ones, notably N, had been exhausted. This would have created an N-limited environment in the studied coarse-textured low fertility soil which favored the soil LFE on decomposition (Huhta, 2007). In addition, the high contents of recalcitrant substances, notably L, would have induced the decomposition by soil larger fauna (Yang and Chen, 2009; Moco et al., 2010; Vos et al., 2011). Furthermore, the low soil moisture content prevailing during the dry season period (weeks 26–52) at the study site (Fig. 1) was less favorable to microbial than soil fauna decomposition. This was supported by significantly lower microbial activities as indicated by soil CO_2−C evolution (data not shown) during this later period than the earlier decomposition period. In contrast to recalcitrant substances, significant negative correlations were found between the soil LFE and CL contents ($r = -0.759^{**}$– -0.874^{***}) (Table 2) during the later stage of decomposition, which showed that CL, similar to other labile constituents of decomposing organic residues, would have been exhausted which contributed to high-L conditions (Couteaux et al., 1995; Berg and Laskowski, 2006) conducive to the high soil LFE on decomposition (Gonzalez and Seastedt, 2001; Hättenschwiler and Gasser, 2005; Riutta et al., 2012).

Influence of residue chemical composition on soil larger fauna effects

Multiple regression analysis was used to show the interactions of the multiple chemical quality parameters that influence decomposition by larger fauna during various stages of decomposition (Table 3). During the initial stage of decomposition (week 1), the levels C and N contents of residues were high and had significant influence on LFE as indicated by their respective regression coefficients. The influence of the recalcitrant substance (PP) was lower than those of C and N, while the ratio of C/N and PP/N had an influence with PP/N being highest ($b_{PP/N} = -216.83^*$) as shown by Equation (1), Table 3. Both labile and recalcitrant constituents of residues could exert effects on larger fauna decomposition as indicated by the significant influence of C (representing both labile and recalcitrant residue C pools) and N (representing the labile pool). Labile and recalcitrant compounds are both used by soil fauna as their substrates (Scheu and Schaefer, 1998). In addition, N interacted with recalcitrant C (PP) in bringing about decomposition by larger fauna. Polyphenols form complexes with N which deters microbial N mineralization (Vityakon and Dangthaisong, 2005) and, hence, decomposition. However, some larger fauna, notably earthworms and termites, have been found to be able to break down these complexes through resident microorganisms in their guts, and to utilize the released N (Hättenschwiler and Vitousek, 2000). In week 2, the C content still remained influential in soil larger fauna decomposition, while N no longer exerted its influence (Equation (2)). The influence of the C/N ratio in week 2 was much lower ($b_{C/N} = -0.66^*$) than for C ($b_C = 18^*$) in relation to week 1. In addition, the influence of PP/N ratio that had been high and significant in week 1 disappeared in week 2. These results appeared to indicate that in week 2 soil LFE in resistant residues significantly decreased (Fig. 3) due to increases in microbial decomposition. However, the soil fauna still utilized both labile and recalcitrant substance constituents of organic residues (as indicated by C) as their substrates. In week 4, the influences of the recalcitrant constituents of residues (L, PP, and L + PP) on LFE became prominent. This reflected the higher contents of recalcitrant substances proportional to the lower contents of labile constituents of organic residues at this stage. In addition, the influence of the L/CL ratio was highest ($b_{L/CL} = -112.9^*$) on LFE (Equation (3)) . During the middle stage (week 8 and week 16) of decomposition, the ratios of recalcitrant substances to N, that is L/N and (L + PP)/N, became prominent factors influencing LFE; however the ratio of L/CL continued to be the most prominent one—Equations (4) and (5). At this stage, N could have been limited which stimulated the decomposition of recalcitrant substances, notably L, by larger soil fauna (Huhta, 2007). The interactions of L and CL had significant influence on larger fauna decomposition as they are components of the plant residue cell wall which are resistant to decomposition. During the later stage of decomposition (weeks 26, 39 and 52), the L/CL ratio continued to be the most prominent chemical quality factor influencing soil LFE, while the L/N ratio no longer exerted influence at this later stage—Equations (6)–(8). This may have indicated that N was exhausted at this later decomposition stage to the point that it did not influence LFE. This is shown in the non-linear relationship between the ratio of L/N and soil LFE in which at the critical L/N value of 43 the highest soil LFE was reached beyond which the effect declined (Fig. 4A). The prominent influence of the L/CL ratio during the later stages indicated that cell wall component of plant residues consisting mainly of L and CL, influenced the organization of larger soil fauna through their control on the fauna habitat structure. However, once the cell walls were degraded, the interior cytoplasm became food resources for fauna decomposers and exerted its influence on fauna organization (Takeda and Abe, 2001). This argument is supported by the significant positive linear relationship between the ratio of L/CL and soil LFE (Fig. 4B) which showed that the cell wall component of recalcitrant residues continued to be degraded by larger soil fauna at the later stages of decomposition.

In conclusion, the L/N and L/CL ratios were identified as the most prominent initial chemical parameters for the middle (8–16 weeks) and the later (26–52 weeks) decomposition stage, respectively, which could predict soil larger fauna effects (LFE) on the decomposition of contrasting quality organic residues. This highlighted the interactions of the recalcitrant constituents of residues, notably L, with labile constituents, N and CL, in controlling soil LFE during the middle to later stages which brought about significantly higher soil LFE in more resistant residues than easily decomposable counterparts. Regarding the early stage (weeks 1–4) of decomposition, both labile (C and N) and recalcitrant (L and PP), as constituents of the residues, had influence on decomposition. This was different from the middle and later stages. However, at the end of the early stage (week 4), recalcitrant constituents became prominent. Nitrogen interaction with PP appeared to strongly control LFE during the initial stage (week 1) which brought about significant soil LFE in more resistant residues than in easily decomposable counterparts. These results have partly proved the hypothesis that the initial concentration of L and the interactions of L and the labile compounds of residues, notably N and CL, as indicated by L/N and L/CL ratios, were the major predictors of the effects of larger soil fauna on decomposition of different type of organic residues; that is, resistant residues like DP and TM were more strongly affected and the stages of decomposition, that is the later part of the early stage (4 wk after residue incorporation) for L, at the middle stage (8–16 wk) for the L/N ratio, and at the later stage (26–52 wk) for the L/CL ratio, at which larger fauna have their most pronounced decomposition function. However, during the initial stage of decomposition (1–2 wk), the results did not conform to the hypothesis, as L and the interactions of L and labile compound constituents of residues, notably N and CL, did not have any significant influence on LFE. Further research should be conducted to identify

Table 3
Multiple regression analysis of soil larger fauna effect (%; $= A + (b_C \times C) + (b_N \times N) + \ldots + (b_{(L+PP)/N} \times (L + PP)/N)$ and initial concentrations of quality parameters of organic residues over various periods of decomposition.

Period(week)	A	b_C	b_N	b_L	b_{PP}	b_{CL}	b_{L+PP}	$b_{C/N}$	$b_{L/N}$	$b_{PP/N}$	$b_{(L+PP)/N}$	$b_{L/CL}$	R^2_{adj}	Equation number
1	−22413.30	52.96*	69.04*	–	16.29*	–	–	20.73*	-32.96^{ns}	−216.83*	–	-224.18^{ns}	0.93**	(1)
2	−6850.85	18.00*	–	−1.97*	–	–	–	−0.66*	–	-51.59^{ns}	–	–	0.84**	(2)
4	5633.78	−14.66*	−1.86*	−87.14*	−89.62*	–	88.91*	–	–	–	10.23*	−112.91*	0.92**	(3)
8	2.54	–	–	−9.52*	–	–	9.04*	–	86.42**	–	−74.17**	−182.51**	0.74*	(4)
16	−16.11	–	–	−7.65*	–	–	7.28*	–	126.88***	–	−104.81***	−215.97**	0.93***	(5)
26	7.01	–	−0.93*	-37.59^{ns}	-39.32^{ns}	–	38.22^{ns}	–	–	–	–	−61.57*	0.99***	(6)
39	−2107.72	5.51*	–	–	–	–	-0.28^{ns}	–	-5.05^{ns}	–	–	29.68*	0.98***	(7)
52	6.70	–	−0.74**	–	–	–	0.40**	–	–	–	−0.94**	−35.76*	1.00***	(8)

a = y-intercept; b = regression coefficient; C = carbon; N = nitrogen; L = lignin; PP = polyphenols; CL = cellulose; R^2_{adj} = coefficient of determination (adjusted); * = significant at $p \leq 0.05$; ** = significant at $p \leq 0.01$; *** = significant at $p \leq 0.001$; ns = non significant ($p > 0.05$).

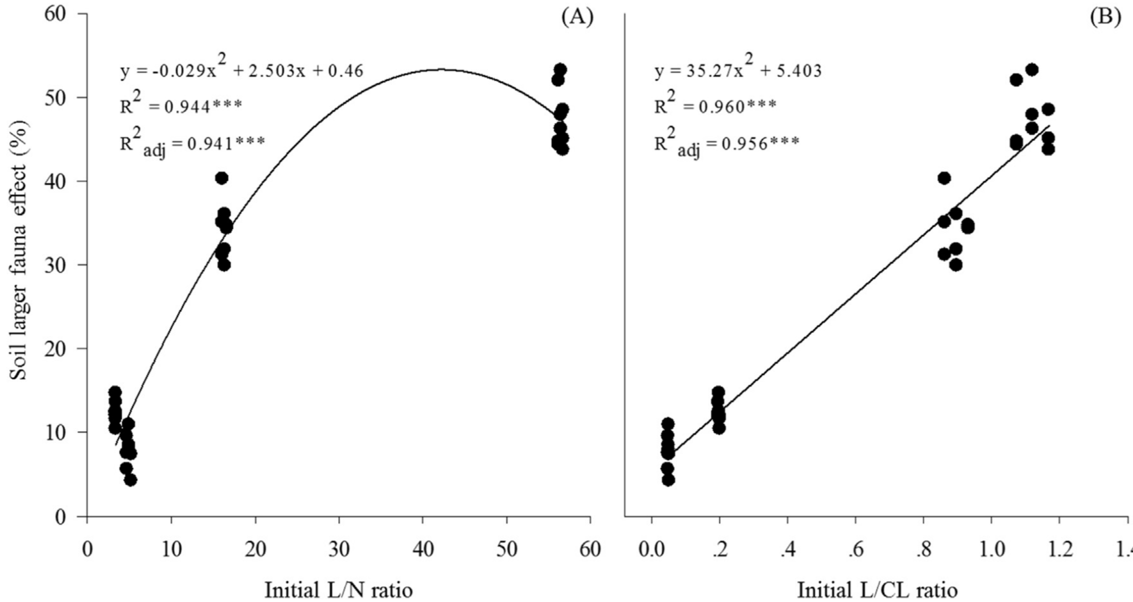

Fig. 4. Relationships between ratios of the residue initial chemical composition and larger fauna effect: (A) non-linear regression of the lignin/nitrogen (L/N) ratio and soil larger fauna effect (LFE); (B) linear regression of the lignin/cellulose (L/CL) ratio and LFE, where *** = significant at $p \leq 0.001$ and R^2_{adj} = adjusted R squared.

soil larger fauna communities (the taxonomic types and abundance) that are affected by changes in the chemical composition of the decomposing organic residues which have a bearing on the assemblages and activities of decomposers.

Conflict of interest

The authors declare that there are no conflicts of interest.

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