

Sains Malaysiana 45(7)(2016): 1041–1047

Leaching and Freeze-Thaw Events Contribute to Litter Decomposition - A Review (Kejadian Larut Lesap dan Beku-Cair Menyumbang kepada Penguraian Sampah - Suatu Ulasan)

LIPING JIANG, KAI YUE, YULIAN YANG & QINGGUI WU*

ABSTRACT

Litter decomposition is vital for carbon and nutrient turnover in terrestrial ecosystems, and this process has now been thoroughly demonstrated to be regulated by various mechanisms. The total environment has been continuously changing in recent decades, especially in high-latitude regions; these alterations, however, profoundly contribute to the decomposition process, but a comprehensive recognition has not available. Here we reviewed the empirical observations and current knowledge regarding how hydrological leaching and freeze-thaw events modulate early decomposition of plant litter. Leaching contributes a considerable percentage of mass loss and carbon and nutrient release in early stage of decomposition, but the magnitudes are different between species levels depending on the chemical traits. Frequent freezing and thawing events could positively influence decomposition rate in cold biomes but also hamper soil decomposer and there is no general and predictable pattern has been emerged. Further experiments should be manipulated to estimate how the altered freezing and thawing effect on carbon and nutrient release from plant litter to better understanding the changing environment on litter decomposition.

Keywords: cold biomes; freeze-thaw; leaching; litter decomposition

ABSTRAK

Penguraian sampah adalah penting untuk pusing ganti karbon dan nutrien dalam ekosistem daratan dan proses ini kini telah dibuktikan secara terperinci dikawal oleh pelbagai mekanisme. Persekitaran secara keseluruhan berterusan berubah sejak beberapa dekad kebelakangan ini terutamanya di kawasan berlatitud tinggi; perubahan ini, walau bagaimanapun menyumbang secara mendalam kepada proses penguraian, tetapi tidak terdapat suatu pengiktirafan yang komprehensif. Di sini kami mengkaji cerapan empirik dan pengetahuan semasa tentang bagaimana kejadian hidrologi larut lesap dan beku-cair memodulatkan proses awal pereputan sampah loji. Larut lesap menyumbang kepada peratusan kehilangan jisim dan karbon serta pelepasan nutrien yang agak besar pada peringkat awal pereputan, tetapi magnitud tersebut berbeza antara tahap spesies bergantung kepada sifat kimia. Kekerapan kejadian larut lesap dan beku-cair boleh secara positif mempengaruhi kadar penguraian dalam biom sejuk tetapi juga menghalang tanah diurai serta tidak terdapat pola umum dan boleh diramal yang muncul. Uji kaji susulan harus dimanipulasi untuk menganggarkan bagaimanakah kesan pengubahsuaian larut lesap dan beku-cair ke atas pembebasan karbon dan nutrien dari loji sampah untuk memahami dengan lebih baik persekitaran yang berubah-ubah kepada penguraian sampah.

Kata kunci: Beku-cair; biom sejuk; larut lesap; penguraian sampah

INTRODUCTION

Decomposition of plant litter is one of the most fundamental processes for global carbon budgets, as approximately half of the ecosystem productivity is returned to the soil via litter decay in terrestrial ecosystems (Wardle et al. 2004). Multiple factors are responsible for regulating decomposition rate, but in a given ecosystem, the ambient environment can considerably modulate this process. Alterations of environmental conditions greatly impact on soil decomposer and thereby change the chemical compositions (Aerts 1997; Wardle et al. 2004). This has received increasing interest in the past two decades because many scientists paid their attention to climate warming (Prescott 2010). However, increasing temperature is expected to be amplified in cold biomes (Copper 2014),

which are important accumulators of soil organic carbon (Arctic Climate Impact Assessment 2005; Davidson & Janssens 2006) and where litter decomposition is strongly limited by low temperature (Hobbie et al. 2002; Robinson 2002).

Contemporary literatures have mostly focused on the effects of chemical and biological agents on litter decomposition (Preston et al. 2009), while studies investigating physical factors, such as leaching and freeze-thaw events, in litter breakdown were scanty. The amounts of water soluble substances in fresh litter decrease considerably in early stage of decomposition owing to leaching and freeze-thaw cycle was considered to be a significant environmental factors regulating litter decomposition in cold biomes (Zhu et al. 2012). Increasing

evidence has demonstrated that freeze-thaw events directly modify carbon release from foliar litter (Wu et al. 2014) and contribute to decomposition rates (Yang et al. 2014). Such results have indicated that changes in freeze-thaw cycles may lead to changes in litter decomposition and elemental cycles in terrestrial ecosystems and the effect of leaching on water soluble substances could also be affected as well because of altered hydrological condition accompanying by soil freezing and thawing. However, there have been only a few studies that investigated the effects of leaching and freeze-thaw events on litter decomposition and the potential mechanisms underlying were still unclear.

In order to get a general understanding of the roles of leaching and freeze-thaw events on litter decomposition, it would be fundamental for getting a comprehensive mechanism of these physical processes in cold biomes. Hence, we reviewed some empirical observations on the contribution of leaching and freeze-thaw cycles to litter decomposition in cold biomes to provide general insight and highlighted in challenges and opportunities of systematic research in future.

LEACHING AND LITTER DECOMPOSITION

At early stage of decomposition, the large amounts of dissolved materials in fresh litter could be leached (Schreeg et al. 2013). This labile leachate could trigger the carbon use efficiency of microorganisms and thereby further promote decomposition (Cotrufo et al. 2015, 2013).

THE EFFECTS OF LEACHING ON MASS LOSS

As early as in 1878, Müller emphasized that water soluble substances are of great importance for soil formation and these substances derive chiefly from litter during decomposition. Previous investigations have shown a positive correlation between the amount of water soluble substances in the litter and the decomposition rate during the first months and this mainly due to the effect of leaching. It was reported that mass loss from fresh litter was equal to the loss of soluble compounds during the first weeks of *in situ* decomposition (Bernhard-Reversat 1993) and this study emphasized the dependence of early decomposition process on the release of soluble compounds. Nykvist (1963, 1962; 1961a; 1961b, 1959a; 1959b) conducted a series of experiments in laboratory to investigate the factors that may affect the leaching of litter and concluded that: the total amount of water soluble organic and inorganic substances leached from ground litter after one day ranged from 8-25% of the dry mass among six experimented litter types; the amount of water soluble substances was greater when leaching took place under anaerobic conditions than under aerobic; this was due to a greater decomposition rate of water soluble substances under aerobic environment; the pH value raised under aerobic environment, but fallen under anaerobic condition, and this may be related to the formation of aliphatic acids during decomposition; and the influence of temperature on leaching of water soluble

substances was greater in oak litter and large amounts were leached from needle litter of pine and spruce at high temperatures. These results indicated that leaching was not only modulated by abiotic factors such as pH value and temperature, but also affected by the functional traits of plant litter, which have been proved to be a predominant factor controlling on litter decomposition within a given ecosystem worldwide (Cornwell et al. 2008; Makkonen et al. 2012).

Many other researchers have also reported the effects of leaching on early stage of litter decomposition (Table 1) and the results were similar to that reported by Nykvist. We can see from Table 1 that mean litter mass loss of foliar litter ranged from 1.5% to 11.4% for one day of leaching and from 6.0% to as much as 47.2% for more than one day of treatment. Generally, leaching is largely completed within the first 24-48 h after immersed in water and the loss up to 30% of the original mass, depending on litter species. However, it is noteworthy that, although the mass loss in the first day may account for a large amount of the whole losing mass, the period of leaching is a prolonged process developing over weeks (France et al. 1997).

THE EFFECTS OF LEACHING ON CARBON RELEASE

Dissolved organic matter (DOM) leached from decomposing litter is the most important carrier for the flux of nutrients, eluviation of metals and transport of hydrophobic pollutants. Natural DOM is composed of components that have widely difference in physicochemical properties and may also be consisted of mixtures of labile and refractory to microbial decomposition (Qualls 2005), but the most studied counterparts were dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) in published citations. In a leaching experiment using the needle and fine root of spruce litter, leaching rate of DOC tended to decrease with time for both litter types and was most pronounced for fresh root from mineral soil and senesced needle from litter layer, which had the highest DOC leaching on the first measurement occasion (Hansson et al. 2010). The fraction of carbon leached as DOC decreased with time for all litter types except for the fresh needle litter and almost all litter types stabilized at approximately 20%. Using microcosms, initial carbon mineralization and leaching rates of DOC from litter of eight tree species in CO₂ enrichment conditions were measured by Hagedorn and Machwitz (2007) in a broadleaf forest. Over 11 weeks of leaching, between 2.5% (*Pinus uncinata* and *Fagus sylvatica*) and 15% (*Carpinus betulus*) of litter carbon were leached as DOC, corresponding to 9-36% of the total mass loss. The results suggested that elevated CO₂ decreased lignin degradation but accelerated both carbon mineralization and DOC leaching from the litter and DOC was less biodegradable when its parent litter was incubated under elevated CO₂. Using ¹⁴C labeled leaf litter of *Populus fremontii* that had decomposed for one year, the fractions of dissolved organic matters that was extracted in water were, in this order: hydrophilic acid (30.5%), fulvic acid

TABLE 1. Mass loss of some foliar litters attributed by leaching

Species	Mass loss (%)		References
	1 day	>1 day	
<i>Annona senegalensis</i>	6.5	15.7	Ibrahima et al. 2007
<i>Acacia mangium</i>	--	27.9	Yang et al. 2012
<i>Berzelia lanuginosa</i>	11.4	14.7	Raubenheimer & Day 1991
<i>Betula papyrifera</i>	--	15.7	France et al. 1997
<i>Castanea sativa</i>	6.0	13.8	Ibrahima et al. 1995
<i>Cistus monspeliensis</i>	3.5	11.2	Ibrahima et al. 1995
<i>Eucalyptus urophylla</i>	--	47.2	Yang et al. 2012
<i>Elegia thyrsoifera</i>	2.5	8.5	Raubenheimer & Day 1991
<i>Fagus sylvatica</i>	3.1	6.5	Ibrahima et al. 1995
<i>Lophira lanceolata</i>	2.3	9.8	Ibrahima et al. 2007
<i>Nothofagus solandri</i> var. <i>cliffortioides</i>	1.5	7.3	McCammon 1980
<i>Populus tremuloides</i>	--	12.4	France et al. 1997
<i>Picea mariana</i>	--	15.1	France et al. 1997
<i>Pinus banksiana</i>	--	5.7	France et al. 1997
<i>Pinus massoniana</i>	--	30.8	Yang et al. 2012
<i>Pinus halepensis</i>	2.9	8.0	Ibrahima et al. 1995
<i>Quercus pubescens</i>	4.8	11.7	Ibrahima et al. 1995
<i>Quercus coccifera</i>	4.8	12.4	Ibrahima et al. 1995
<i>Quercus ilex</i>	3.9	13.8	Ibrahima et al. 1995
<i>Quercus robur</i>	--	6.0	Tietema & Wessel 1994
<i>Syzygium guineense</i> var. <i>guineense</i>	4.4	14.1	Ibrahima et al. 2007
<i>Syzygium guineense</i> var. <i>macrocarpum</i>	3.1	11.7	Ibrahima et al. 2007
<i>Vitellaria paradoxa</i>	8.6	14.2	Ibrahima et al. 2007
<i>Vitex doniana</i>	9.1	15.5	Ibrahima et al. 2007
<i>Vitex madiensis</i>	15.0	19.0	Ibrahima et al. 2007
<i>Ximenia americana</i>	18.8	34.0	Ibrahima et al. 2007

(33.8%), humic acid (39.0%), unfractionated DOC (43.5%), unseparated hydrophilic acid and neutral phenolic (63.3%), glucose (66.4%) and hydrophilic neutral (70.2%) (Qualls 2005).

THE EFFECTS OF LEACHING ON NUTRIENT RELEASE

Nutrient leaching from freshly senesced litter could provide essential materials available for plant and microbial uptake, such as orthophosphate, inorganic and organic nitrogen (Sinsabaugh et al. 2002). It was reported that grazed pastures lost large amounts of nitrogen as DON through leaching and these amounts were estimated to be 4-120 kg N ha⁻¹ year⁻¹ in some New Zealand pasture soils (Ghani et al. 2010). In a laboratory study, the concentration of DON in the leachates declined to less than 1 mg N L⁻¹ within 7-14 days of incubation; this consistent with the observation that extractable DON in water ranged between 2 and 63 mg N L⁻¹ (Ghani et al. 2013). Within the first 21 days of incubation, DON concentration was decreased to near zero without any significant change in the concentration of NO₃⁻ or NH₄⁺, indicating that microbes could utilized organic nitrogen preferentially. Phosphorus leached from both fresh and aged leaves was mostly free of orthophosphate and therefore was readily available (Baldwin 1999). Hafner et al. (2005) measured the concentrations of DOC, DON, NH₄⁺, NO₃⁻, dissolved organic sulfur, SO₄²⁻, Cl⁻, Al, Ca, K, Mg,

Na and P of through fall and leachates of litter and coarse woody debris *in situ* at a young mixed lowland forest in New York. Their results suggested that concentrations of DOC were much higher in coarse woody debris leachate (15 mM) than in through fall (0.7 mM) or litter leachate (1.6 mM). Concentrations of some elements correlated with DOC concentrations, highlighting the possibility of elemental complexation reaction with DOM. At microsite scale, the fluxes of DOC from coarse woody debris were higher relative to through fall and litter leachate. Including DOC, some solute concentrations through fall showed positive correlations to mean air temperature and fewer showed positive correlations in litter leachate, while negative correlations were observed to precipitation. These results suggested that both biological and hydrologic factors controlling leaching.

Collectively, the solubility of different elements during leaching varied markedly. On average 100% of total potassium, 35% of total phosphorus, 28% of total sodium, 5% of total nitrogen, 4% of total calcium and 3% of total carbon could be soluble (Schreeg et al. 2013). Elemental solubility was linked within a species: when a species ranked high in the soluble fraction of one element, it also ranked high in the solubility of other elements. Overall nutrient-specific patterns of solubility from freshly senesced litter emphasized that litter elements cannot be treated equally in conceptual models of decomposition.

DOES TEMPERATURE COUNT IN LEACHING?

Temperature is one of the most important environmental factors affecting litter decomposition and its effect would be more distinct in cold biomes. In a laboratory leaching experiment, temperature was proven to be an important factor affecting DOC leaching obviously after 1-36 days of incubation (Andersson & Nilsson 2001; Andersson et al. 2000), indicating that temperature must be taken into consideration while assessing the effect of leaching on litter decomposition. However, literature about this was rare and the available data were not all-inclusive. What the contribution of leaching to litter decomposition across different temperatures looks like and how to compare the leaching contribution visually across a range of temperatures, will be interesting questions for scientists.

FREEZE-THAW EVENTS AND DECOMPOSITION

Increasing evidence has indicated that decomposition rate during freeze-thaw season accounted for a large proportion (Christenson et al. 2010; Wu et al. 2010) and the altered spatial and temporal patterns of soil freezing conditions have significant implications for nutrient cycling in cold biomes. Freeze-thaw events could alter chemical compositions, nutrient availability and transportation in soils by various mechanisms and generally promote mineralization (Deluca et al. 1992), thus litter decomposition may be affected by a complex range of chemical, biological and physical factors induced by freeze-thaw.

THE ROLES OF FREEZE-THAW EVENTS ON LITTER DECOMPOSITION

Soil freeze-thaw event is an alternately process of freezing and thawing in topsoil as a consequence of temperature fluctuation, accompanying by other physical processes such as cryoturbation and leaching (Henry 2007). The main effect of freeze-thaw cycle was the influence on soil physical characteristics. The volumetric change in ice water conversion (expansion and contraction) could damage soil aggregate structure with the occurrence of leaching of snowmelt during this process. Alternate freezing and thawing can change the physical structures of litter, increase litter infiltration rate and decrease the stability of soil aggregates. The magnitude depends on temperature, soil moisture, soil aggregates and frequency of freeze-thaw cycles (Edwards et al. 2007). Moreover, high water content and continuous freeze-thaw cycles during early spring could show a greater destructive impact on macromolecular substances in leaf litter (Austin & Ballaré 2010). In addition, the changes of chemical compounds in litter during wintertime inevitably affect the subsequent decomposition in growing season. However, most of the current studies reporting freeze-thaw events were carried out in agricultural or forested soil; little research was manipulated on litter decomposition. Due to methods

limitation and low activity of soil organisms, measurements of litter decomposition in cold biomes during winter and early spring were limited (Uchida et al. 2005).

THE EFFECTS OF FREEZE-THAW EVENTS ON MASS LOSS

In the past, it was generally assumed that litter decomposition during winter could be ignored (Campbell et al. 2005). However, in the last decade, an increasing numbers of studies reported that microbial activity, which is crucial to litter decomposition, does not cease in winter (Robinson 2001; Schimel & Mikan 2005). Significant mass loss and nutrient release from litter during winter in low temperature forests and other cold biomes have been reported (Hobbie & Chapin 1996; Melillo et al. 1982). Simulated laboratory experiments have indicated that frequent freeze-thaw cycles show considerable effect on the physical structure of litter and therefore on decomposition rate (Freppaz et al. 2007; Taylor & Parkinson 1988). Our previous studies conducted litterbags during freeze-thaw season in subalpine forests region (Wu et al. 2010; Zhu et al. 2012) have suggested that decomposition rates during this period contributed significantly to the first year of decomposition that about 18% and 20% of mass lost from fir (*Abies faxoniana*) and birch (*Betula albosinensis*) litter, respectively. Mass loss and nutrient release during freeze-thaw season were attributed to physical destruction, hydraulic leaching and the related microbial activity.

THE EFFECTS OF FREEZE-THAW EVENTS ON SOIL DECOMPOSER

The effect of freeze-thaw events on soil fauna and microorganism could also have great influences on litter decomposition rate. Sjurset al. (2005) reported that there was no conclusive evidence that recurring freeze-thaw events had a negative effect on soil fauna community and such treatment even seemed to stimulate the abundance of Acaridida. Yanai et al. (2004) investigated the effects of soil freeze-thaw cycles on soil microbial biomass and found that freeze-thaw cycles led to a significant 6% of increase in chitin decomposition and a 7% of decrease in rice decomposition, indicating that the partial sterilization associated with the soil freeze-thaw cycles might disturb soil microbial functions. Freeze-thaw cycles, in seasonally snow covered soils, were likely to have a selective effect on the microbial biomass (Freppaz et al. 2007). Freezing and thawing resulted in a change of ammonification and release of DON, which represent an important influence upon nitrogen cycling in cold biomes (Figure 1). Xia et al. (2012) quantified the contribution of soil fauna to the decomposition of birch leaf litter in a subalpine forest during freeze-thaw season using different mesh sizes (0.02, 0.125, 1 and 3 mm) of litterbags. Over the freeze-thaw season, about 11.8%, 13.2%, 15.4% and 19.5% of the mass losses were detected in the litterbags with 0.02, 0.125, 1 and 3 mm mesh sizes, respectively. The total contribution of soil fauna to litter decomposition accounted for 39.5%

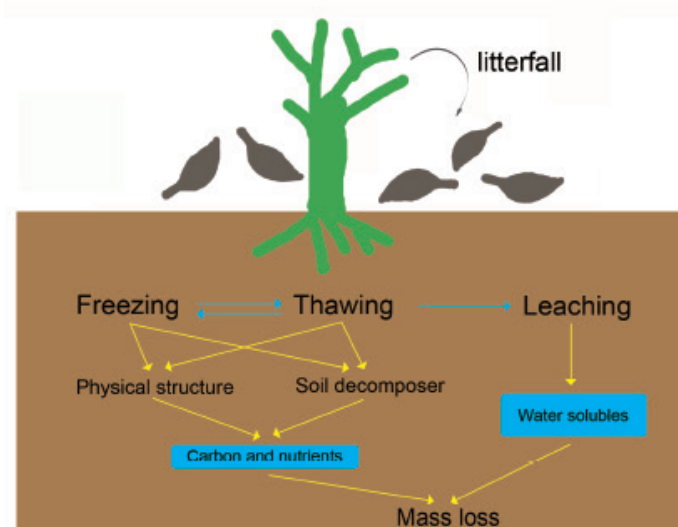


FIGURE 1. A diagram explaining leaching and freeze-thaw events affecting litter decomposition

of the mass loss and showed the order of micro- < meso- < macro-fauna. Moreover, the highest contribution of micro-fauna (7.9%), meso-fauna (11.9%) and macro-fauna (22.7%) occurred at the onset of freezing stage, deep frozen stage and thawing stage, respectively. All these results demonstrated that soil fauna play an important role in litter decomposition during freeze-thaw season.

THE EFFECTS OF FREEZE-THAW EVENTS ACCOMPANIED WITH OTHER FACTORS

A study has suggested that most of mass in fresh litter during cold season loss in autumn before the onset of winter and the decomposition during the 'true' wintertime is almost non-existent (Bokhorst et al. 2010). Both the repeated warming and freezing treatments in their laboratory incubation and the simulated winter warming in field had no effect on total mass loss. So they suggested that freeze-thaw events do not affect fresh litter decomposition. However, according to our previous investigations and the available literatures, we propose that freeze-thaw cycles do affect litter decomposition significantly and the potential mechanisms can be summarized as follows: biological decomposition might be responsible for a majority of mass loss and release of carbon and nutrient during the cold season, as microbial activity did not completely cease in the frozen period (Brooks et al. 1997); Thawing events, accompanied with the increase of moisture and temperature during the early spring, can increase microbial activity and the concomitant leaching can induce great release of nutrients (Lemma et al. 2007); and freezing may have a destructive effect on the physical structure of litter, breaking down the recalcitrant components such as resin and 'lignin' in litter (Groffman et al. 2001) and consequently promote mass loss and nutrient release.

POTENTIAL PROBLEMS IN STUDYING FREEZE-THAW CYCLES ON LITTER DECOMPOSITION

Physical disruptions, such as frequent freezing and thawing, did not generate feedbacks during litter decomposition. Freeze-thaw events were likely to affect litter decomposition through mechanical disruption and thus expose new surfaces on where enzymes could act. Physical disruption may even be more important to formation of soil organic matter because a mixture could promote the aggregation of organic and mineral materials. Thus studies on freeze-thaw events effect on litter decomposition should not be restricted to fresh litter only. Another problem was about how to quantify the freeze-thaw cycle. Some inappropriate methods may result in misleading quantification of the frequency of freeze-thaw cycles and made it hard to establish a causal connection between litter decomposition and effects of freeze-thaw events. Accompanying with the alternate freezing and thawing, the amount of water available for leaching seems to be important for the release of water soluble substances. How to distinguish such confounding factors and the effect of freeze-thaw itself is of great importance. Controlled experiments may be useful in further investigations.

ACKNOWLEDGEMENTS

This study was financially supported by the Open Project from the Ecological Security and Protection Key Laboratory of Sichuan Province (ESP1404), the Project of Mianyang Normal University (QD2015B07 & 2015A01), the Project of the Education Department of Sichuan Province (162A0322) and National Natural Science Foundation of China (31270498 & 31570445). We would like to give personnel thanks to Dr. Krishna Prasad Oli for his valuable comments and inputs.

REFERENCES

- Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79: 439-449.
- Andersson, S. & Nilsson, S.I. 2001. Influence of pH and temperature on microbial activity, substrate availability of soil-solution bacteria and leaching of dissolved organic carbon in a mor humus. *Soil Biology and Biochemistry* 33: 1181-1191.
- Andersson, S., Nilsson, S.I. & Saetre, P. 2000. Leaching of dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) in mor humus as affected by temperature and pH. *Soil Biology and Biochemistry* 32: 1-10.
- Arctic Climate Impact Assessment. 2005. *Arctic Climate Impact Assessment-Scientific Report*. Cambridge: Cambridge University Press.
- Austin, A.T. & Ballaré, C.L. 2010. Dual role of lignin in plant litter decomposition in terrestrial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 107: 4618-4622.
- Baldwin, D.S. 1999. Dissolved organic matter and phosphorus leached from fresh and 'terrestrially' aged river red gum leaves: implications for assessing river-floodplain interactions. *Freshwater Biology* 41: 675-685.
- Bernhard-Reversat, F. 1993. Dynamics of litter and organic matter at the soil-litter interface in fast-growing tree plantations on sandy ferralitic soils (Congo). *Acta Oecologica* 14: 179-195.
- Bokhorst, S., Bjerke, J.W., Melillo, J., Callaghan, T.V. & Phoenix, G.K. 2010. Impacts of extreme winter warming events on litter decomposition in a sub-Arctic heathland. *Soil Biology and Biochemistry* 42(4): 611-617.
- Brooks, P.D., Schmidt, S.K. & Williams, M.W. 1997. Winter production of CO₂ and N₂O from alpine tundra: environmental controls and relationship to inter-system C and N fluxes. *Oecologia* 110: 403-413.
- Campbell, J.L., Mitchell, M.J. & Groffman, P.M., Christenson, L.M. & Hardy, J.P. 2005. Winter in northeastern North America: a critical period for ecological processes. *Frontiers in Ecology and the Environment* 3: 314-322.
- Christenson, L.M., Mitchell, M.J. & Groffman, P.M. & Lovett, G.M. 2010. Winter climate change implications for decomposition in northeastern forests: comparisons of sugar maple litter with herbivore fecal inputs. *Global Change Biology* 16: 2589-2601.
- Copper, E.J. 2014. Warmer shorter winters disrupt arctic terrestrial ecosystems. *Annual Review of Ecology, Evolution and Systems* 45: 271-295.
- Cornwell, W.K., Cornelissen, J.H.C. Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V. & Westoby, M. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11: 1065-1071.
- Cotrufo, M.F., Wallenstein, M.W., Boot, C.M., Deneff, K. & Paul, E. 2013. The microbial efficiency-matrix stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Global Change Biology* 19: 988-995.
- Cotrufo, M.F., Soong, J.L., Horton, A.J., Campbell, E.E., Haddix, M.L., Wall, D.H. & Parton, W.J. 2015. Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience* 8: 776-779.
- Davidson, E.A. & Janssens, I.A. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440: 165-173.
- Deluca, T.H., Keeney, D.R. & McCarty, G.W. 1992. Effect of freeze-thaw events on mineralization of soil nitrogen. *Biology and Fertility of Soils* 14: 116-120.
- Edwards, A.C., Scalenghe, R. & Freppaz, M. 2007. Changes in the seasonal snow cover of alpine regions and its effect on soil processes: a review. *Quaternary International* 162-163: 172-181.
- France, R., Culbert, H., Freeborough, C. & Peters, R. 1997. Leaching and early mass loss of boreal leaves and wood in oligotrophic water. *Hydrobiologia* 345: 209-214.
- Freppaz, M., Williams, B.L. & Edwards, A.C., Scalenghe, R. & Zanini, E. 2007. Simulating soil freeze/thaw cycles typical of winter alpine conditions: Implications for N and P availability. *Applied Soil Ecology* 35(1): 247-255.
- Ghani, A., Müller, K., Dodd, M. & Mackay, A. 2010. Dissolved organic matter leaching in some contrasting New Zealand pasture soils. *European Journal of Soil Science* 61: 525-538.
- Ghani, A., Sarathchandra, U., Ledgard, S., Dexter, M. & Lindsey, S. 2013. Microbial decomposition of leached or extracted dissolved organic carbon and nitrogen from pasture soils. *Biology and Fertility of Soils* 49: 747-755.
- Groffman, P.M., Driscoll, C.T., Fahey, T.J., Hardy, J.P., Fitzhugh, R.D. & Tierney, G.L. 2001. Colder soils in a warmer world: a snow manipulation study in a northern hardwood forest ecosystem. *Biogeochemistry* 56: 135-150.
- Hafner, S.D., Groffman, P.M. & Mitchell, M.J. 2005. Leaching of dissolved organic carbon, dissolved organic nitrogen, and other solutes from coarse woody debris and litter in a mixed forest in New York State. *Biogeochemistry* 74: 257-282.
- Hagedorn, F. & Machwitz, M. 2007. Controls on dissolved organic matter leaching from forest litter grown under elevated atmospheric. *Soil Biology and Biochemistry* 39: 1759-1769.
- Hansson, K., Kleja, D.B., Kalbitz, K. & Larsson, H. 2010. Amounts of carbon mineralised and leached as DOC during decomposition of Norway spruce needles and fine roots. *Soil Biology and Biochemistry* 42: 178-185.
- Henry, H.A.L. 2007. Soil freeze-thaw cycle experiments: trends, methodological weaknesses and suggested improvements. *Soil Biology and Biochemistry* 39: 977-986.
- Hobbie, S., Nadelhoffer, K. & Höglberg, P. 2002. A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions. *Plant and Soil* 242: 163-170.
- Hobbie, S. & Chapin III, F.S. 1996. Winter regulation of tundra litter carbon and nitrogen dynamics. *Biogeochemistry* 35: 327-338.
- Lemma, B., Nilsson, I., Kleja, D.B., Olsson, M. & Knicker, H. 2007. Decomposition and substrate quality of leaf litters and fine roots from three exotic plantations and a native forest in the southwestern highlands of Ethiopia. *Soil Biology and Biochemistry* 39: 2317-2328.
- Makkonen, M., Berg, M.P., Handa, I.T., Hättenschwiler, S., van Ruijven, J., van Bodegom, P.M. & Aerts, R. 2012. Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. *Ecology Letters* 15: 1033-1041.

- Melillo, J.M., Aber, J.D. & Muratore, J.F. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63: 621-626.
- Nykvist, N. 1963. Leaching and decomposition of water-soluble organic substances from different types of leaf and needle litter. *Studia Forestalia Suecica* 3: 1-31.
- Nykvist, N. 1962. Leaching and decomposition of litter V. Experiments on leaf litter of *Alnus glutinosa*, *Fagus sylvatica* and *Quercus robur*. *Oikos* 13: 232-248.
- Nykvist, N. 1961a. Leaching and decomposition of litter. III. Experiments on leaf litter of *Betula verrucosa*. *Oikos* 12: 249-263.
- Nykvist, N. 1961b. Leaching and decomposition of litter. IV. Experiments on needle litter of *Picea abies*. *Oikos* 12: 264-279.
- Nykvist, N. 1959a. Leaching and decomposition of litter I. Experiments on leaf litter of *Fraxinus excelsior*. *Oikos* 10: 190-211.
- Nykvist, N. 1959b. Leaching and decomposition of litter II. Experiments on needle litter of *Pinus silvestris*. *Oikos* 10: 212-224.
- Prescott, C.E. 2005. Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry* 101: 133-149.
- Preston, C.M., Nault, J.R., Trofymow, J.A. & Smyth, C.E. 2009. Chemical changes during 6 years of decomposition of 11 sites in some Canadian forest sites. Part 1. Elemental composition, tanins, phenolics, and proximate fractions. *Ecosystems* 12: 1053-1077.
- Qualls, R.G. 2005. Biodegradability of fractions of dissolved organic carbon leached from decomposing leaf litter. *Environmental Science and Technology* 39: 1616-1622.
- Robinson, C. 2002. Controls on decomposition and soil nitrogen availability at high latitudes. *Plant and Soil* 242: 65-81.
- Robinson, C.H. 2001. Cold adaptation in Arctic and Antarctic fungi. *New Phytologist* 151: 341-353.
- Schimel, J.P. & Mikan, C. 2005. Changing microbial substrate use in Arctic tundra soils through a freeze-thaw cycle. *Soil Biology and Biochemistry* 37: 1411-1418.
- Schreeg, L.A., Mack, M.C. & Turner, B.L. 2013. Nutrient-specific solubility patterns of leaf litter across 41 lowland tropical woody species. *Ecology* 94: 94-105.
- Sinsabaugh, R.L., Carreiro, M.M. & Repert, D.A. 2002. Allocation of extracellular enzymatic activity in relation to litter composition, N deposition, and mass loss. *Biogeochemistry* 60: 1-24.
- Sjursen, H., Michelsen, A. & Holmstrup, M. 2005. Effects of freeze-thaw cycles on microarthropods and nutrient availability in a sub-Arctic soil. *Applied Soil Ecology* 28: 79-93.
- Taylor, B.R. & Parkinson, D. 1988. Does repeated freezing and thawing accelerate decay of leaf litter? *Soil Biology and Biochemistry* 20: 657-665.
- Uchida, M., Mo, W., Nakatsubo, T., Tsuchiya, Y., Horikoshi, T. & Koizumi, H. 2005. Microbial activity and litter decomposition under snow cover in a cool-temperate broad-leaved deciduous forest. *Agricultural and Forest Meteorology* 134: 102-109.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. & Wall, D.H. 2004. Ecological linkages between aboveground and belowground biota. *Science* 304: 1629-1633.
- Wu, F., Peng, C., Zhu, J., Jian, Z., Tan, B. & Wanqin, Y. 2014. Impact of changes in freezing and thawing on foliar litter carbon release in alpine/subalpine forests along an altitudinal gradient in the eastern Tibetan Plateau. *Biogeosciences* 11: 9539-9564.
- Wu, F., Yang, W., Zhang, J. & Deng, R. 2010. Litter decomposition in two subalpine forests during the freeze-thaw season. *Acta Oecologica* 36: 135-140.
- Xia, L., Wu, F.Z., Yang, W.Q. & Tan, B. 2012. Contribution of soil fauna to the mass loss of *Betula albosinensis* leaf litter at early decomposition stage of subalpine forest litter in western Sichuan. *Acta Ecologica Sinica* 23: 301-306.
- Yanai, Y., Toyota, K. & Okazaki, M. 2004. Effects of successive soil freeze-thaw cycles on soil microbial biomass and organic matter decomposition potential of soils. *Soil Science and Plant Nutrition* 50: 821-829.
- Yang, G.R., Zhang, X.Q., Cai, D.S., Shi, X.H., Zhang, H. & Huang, C.B. 2012. Litter decomposition of dominant plantations in Guangxi and its effects on leachate quality. *Chinese Journal of Applied Ecology* 23: 9-16 (in Chinese with English abstract).
- Yang, Q., Xu, M., Chi, Y., Zheng, Y., Shen, R. & Wang, S. 2014. Effects of freeze damage on litter production, quality and decomposition in a loblolly pine forest in central China. *Plant and Soil* 374: 449-458.
- Zhu, J., He, X., Wu, F., Yang, W. & Tan, B. 2012. Decomposition of *Abies faxoniana* litter varies with freeze-thaw stages and altitudes in subalpine/alpine forests of southwest China. *Scandinavian Journal of Forest Research* 27: 586-596.

Liping Jiang, Yulian Yang & Qinggui Wu*
 Ecological Security and Protection
 Key Laboratory of Sichuan Province
 Mianyang Normal University
 166, West Mianxing Road
 Gaoxin District, Sichuan Province
 Mianyang 621000
 P.R. China

Liping Jiang & Kai Yue
 Long-term Research Station of Alpine Forest Ecosystems
 Key Laboratory of Ecological Forestry Engineering
 Institute of Ecology and Forestry
 Sichuan Agricultural University
 Chengdu 611130
 P.R. China

*Corresponding author; email: qgwu30@163.com

Received: 6 November 2015

Accepted: 30 January 2016