

VU Research Portal

The use of plant litter and soil fauna traits in a mechanistic assessment of litter decomposition under global change

Makkonen, M.A.

2012

document version

Publisher's PDF, also known as Version of record

[Link to publication in VU Research Portal](#)

citation for published version (APA)

Makkonen, M. A. (2012). *The use of plant litter and soil fauna traits in a mechanistic assessment of litter decomposition under global change*. [PhD-Thesis - Research and graduation internal, Vrije Universiteit Amsterdam]. VU University.

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

E-mail address:

vuresearchportal.ub@vu.nl

Chapter VI

General discussion

The general aim of this thesis was to improve the mechanistic understanding of the biological and environmental controls on plant litter decomposition and decomposer communities in forest ecosystems. Thereto I used trait-approaches for both plant litter and soil fauna. Litter decomposition is a key ecosystem process that supplies soil food webs with essential resources and is fundamental to important ecosystem services, such as primary productivity. Unfortunately, there are still major gaps in our knowledge on the controls on litter decomposition. This includes for example the importance of the interactions between soil biodiversity and decomposition, and the factors that control carbon sequestration during decomposition (see General introduction, Hättenschwiler *et al.* 2005; Prescott 2010). The need to fill these gaps is emphasized especially by the ongoing global climate change and loss of biodiversity that will further strengthen in the future (Meehl *et al.* 2007; Secretariat of the Convention on Biological Diversity 2010). The research questions of this thesis were presented in Figure 1 of the General Introduction and below I will discuss them consecutively. Thus, I will go from the local to the global controls of decomposer communities and/or litter decomposition.

Can trait assessments of soil fauna be used to improve the analysis of community responses to climate change?

The first research question explores whether the use of species traits could be helpful in understanding the responses of soil fauna communities to climate change. The responses of northern high latitude vegetation to climate change are already visible (Callaghan *et al.* 2011) and predicted to increase further (ACIA 2005). Therefore, it is very important to understand the general principles of how climate change will not only affect the vegetation, but also the soil fauna and how this feeds back to soil processes. Studies assessing the responses of soil fauna communities to global climate change are scarce and lack generalizations, especially with regards to species specific changes (see General Introduction). Soil fauna species are known to differ in their response to environmental changes. Some species react positively, other negatively or not at all to changes in specific environmental factors. Thus based on the scarce knowledge available, there does not seem to be any generality in community response patterns. Trait-approaches could be valuable tools for finding generalities in the responses of the soil fauna communities and investigating the mechanisms behind them (see General introduction, e.g. McGill *et al.* 2006; Suding *et al.* 2008).

By using these trait-based approaches, I found that the subarctic Collembola community responded strongly and in a predictable way to a decreased level of soil moisture under mimicked climate change (Chapter II). In a long-term subarctic Open Top Chamber (OTC) experiment, the decrease in soil moisture reduced the density and species richness of Collembola. The trait-based approach proved to be a fruitful tool in assessing the strongly varying responses of individual Collembola species to mimicked climate change. Trait assessment revealed that under enhanced drought levels the abundance of smaller, hydrophilic and deeper-dwelling species decreased more than the abundance of their counterparts, the larger, xeroreistant and surface-dwelling species. This decrease and shift in the abundance and composition of the Collembola community, corresponded to changes in litter decomposition. Previously plant litter decomposition was found to decrease in these OTC experimental plots (see Chapter II) and I hypothesized this to be partly due to the decrease in Collembola community. This is because when the OTC treatments increased either the downward shift in Collembola or their mortality,

the overall result is that the role of Collembola is decreased in plant litter decomposition, as this takes place in the soil upper layers.

The strength of the trait assessments to unravel mechanistic insight behind community responses to environmental changes in this study warrants its use in further soil fauna community response studies. This is further corroborated by a recent study by Bokhorst *et al.* (2012) where similar traits of soil Collembola and Acari were used in assessing the changes in these fauna communities induced by extreme winter warming events in subarctic Sweden, about 3 km from our study site. In the study by Bokhorst *et al.* (2012), extreme winter warming events did not affect the classical variables used in community responses, e.g. species richness, total soil fauna abundance, and biomass. However, the trait assessment showed that the Prostigmata and deeper-dwelling Collembola were the most susceptible groups to these winter warming events, which heavily increased the freeze-thaw cycles in the soil. Their study indicated that species traits, unlike taxa, play a major role in community assembly.

Furthermore, the trait approach allows linking of the changes in community structure to the functioning of ecosystems (Lavorel & Garnier 2002; Suding *et al.* 2008). Violle *et al.* (2007) have defined these functional traits as “*any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization*”. Functional traits can be used in the search for generality in the soil fauna community responses to environmental changes (using response traits) and further their effect on ecosystem processes (using effect traits). Nevertheless, the use of traits of soil fauna is hampered by the fact that both response and effect traits are not recorded systematically, except for some morphological features. More research that systematically records traits of several groups and taxa within them is highly needed.

Can traits of plant litter explain litter mixing effects?

For several decades now, we know that decomposition in single-species litters (monocultures), deviates from decomposition taking place in litter mixtures (See General Introduction, Wardle *et al.* 1997; Gartner & Cardon 2004). Despite the general notion that in ‘real life’ decomposition usually takes place in litter mixtures, most of our knowledge of litter decomposition comes from litter monoculture studies. Thus, to improve the estimates of decomposition rates in ‘real life’, we should try to understand the mechanisms controlling litter mixing effects. First I assessed the relationship between micro-arthropod community structures and plant litter diversity. More specifically I wanted to see how altering litter quality (chemical and physical traits) affects the communities of micro-arthropods inhabiting the plant litter. There appeared to be no link between litter diversity and micro-arthropod diversity or any other assessed micro-arthropod community indices (Chapter III). These results fit into a pattern of varying results that have been obtained in other studies so far. A positive connection between diversities in plant litter and decomposers has been found in some studies (Hansen & Coleman 1998; Kaneko & Salamanca 1999), while other studies have reported no connection (Schädler & Brandl 2005; Wardle *et al.* 2006; Keith *et al.* 2008). It waits to be seen whether decomposers are regulated by litter species richness and diversity per se, or whether it is more the identity, community and functional diversity of litter that drive them (Heemsbergen *et al.* 2004; Hooper *et al.* 2005; Lecerf *et al.* 2011).

In contrast to plant litter richness, litter quality, i.e. litter identity and composition, was found to control the structure of Oribatida and Collembola communities. The link between litter quality

and fauna community structure was stronger for Oribatida as their density followed mass loss of the plant litter, i.e., the density was higher in higher quality litter. A direct link between soil fauna abundance and decomposition is only seldomly recorded (Anderson 1975; Reddy 1989; Wang *et al.* 2009) and it implies a close relationship between fauna and microbial decomposers. More specifically, I found the densities of both Collembola and Oribatida to relate to plant litter quality. Although various species showed similar resource preferences with regards to litter chemical and physical traits, I also found some strong species specific responses to litter quality indicating niche partitioning. This was especially observed in the collembolan *Pogonognathellus flavescens* and the oribatid *Eupelops torulosus*. The niche partitioning is one factor leading to complementarity effects (Loreau & Hector 2001; Tilman & Lehman 2001) and thus can cause positive (synergistic) non-additive litter mixing effects in decomposition (Gessner *et al.* 2010).

In addition to investigating the link between litter traits and micro-arthropods in litter mixtures, I assessed the relationship between litter physical traits and the strength of litter mixing effects on mass loss and found a strong link between these (Chapter IV). As originally hypothesized (but not shown) by Wardle *et al.* (2003), water holding capacity of litter affected the decomposition rates of the co-occurring plant litter species. Water holding capacity does not only affect the decomposers in mixtures of litters, but it is also expected to affect the decomposers in general (Swift *et al.* 1979). Despite being often overlooked (but see Hansen 2000; Wardle *et al.* 2003), plant litter is not only a resource for the multitrophic decomposer community, but it is also their habitat and determinant of their micro-climate. Especially moisture is an important controlling factor for the structure and functioning of microbial and faunal decomposers (see General introduction). In situations where soil moisture conditions are not optimal for decomposers, and thus may limit decomposition, water holding capacity of the litter can be a strong determinant of the decomposer communities via its effects on micro-climatic conditions. In this study I have shown that water holding capacity controls litter mixing effects of vascular plants. This effect is expected to be even stronger when vascular plants are decomposed together with mosses, as mosses have a truly high water holding capacity (Dilks & Proctor 1979; Hayward & Clymo 1982). In the dry study area of the present study where the vegetation understorey is dominated by mosses, water holding capacity of the litter is most likely a strong controlling factor over plant litter decomposition and can explain non-additive effects in litter mixtures.

In addition to physical plant litter trait control over litter mixing effects, I showed that climate as such also modifies litter mixing effects (Chapter IV). Although the effect of climate on litter mixing effects has never been directly assessed prior to this study, it is logical to assume that it occurs. As climate is a strong controlling factor for all decomposers, it makes sense that climate also modifies the interactions between decomposers that control litter mixing effects. Furthermore, climate not only affects the decomposers, it also affects the trait composition that determines litter quality. I found that increased precipitation, affects directly and via the litter traits the litter mixing effects. More specifically, in conditions where moisture limits decomposition, improved moisture levels are beneficial to decomposer communities and thus lead to increased decomposition. Nevertheless, the positive effect of improved moisture conditions can be hindered by increased precipitation, which increases the leaching of inhibitory compounds of the co-occurring plant litter to their neighboring litter species. Thus, from these findings I can conclude that similarly to additive decomposition processes, the non-additive decomposition processes in litter mixtures are controlled by both litter chemical and physical traits and climate.

What are the global drivers of plant litter decomposition?

In addition to studying specific mechanisms in the subarctic, it is important to test the general applicability of the controlling factors of litter decomposition at the global scale. Due to variation in local climate, soil conditions, fauna and flora composition, the relative controls of all of these factors on plant litter decomposition may vary from site to site (Swift *et al.* 1979; Cadish & Giller 1997). Predicting decomposition rates is more than challenging if the relative roles of specific mechanisms behind the control on plant litter decomposition vary substantially among geographical areas and ecosystems. However, when the same controls prevail globally, it will become much easier to incorporate robust estimates of plant litter decomposition into global carbon cycle models.

Chapter V assessed simultaneously the global roles of plant litter quality, decomposers and environment on decomposition rates in forest ecosystems. This was done at a very large spatial scale by studying litter decomposition in four biomes ranging from the subarctic to the tropics. In this study, I discovered that plant litter identity, used as an integrative proxy for litter quality, has a strong and consistent effect on litter decomposition irrespective of the site of incubation. Furthermore, I found that a small set of plant traits was sufficient to explain variation in decomposition at a global-scale. Surprisingly, I also found that the litter traits that best explained the decomposition rates differed from the traits that are commonly considered as the best proxies for litter degradation, such as ratios between the concentrations of nitrogen, carbon and lignin in litter (see General introduction, e.g. Couteaux *et al.* 1995; Trofymow *et al.* 2002; Currie *et al.* 2009). In contrast to those traits, I found that the concentrations of magnesium, tannins and the litter physical trait, leaf water saturation capacity, correlated best with the decomposition rates across the biomes. The effect of tannins on decomposition is well known (Swift *et al.* 1979; Kraus *et al.* 2003; Coulis *et al.* 2009), but litter magnesium content and leaf water saturation capacity being among the strongest controls on decomposition is surprising.

Several explanations for these results can be given. A rather trivial explanation is that in many decomposition studies the control by cations such as magnesium has not been considered. This is surprising as for example microbes need Mg for their enzymatic activity and stabilization of ribosomes, nucleic acids and membranes (Madigan *et al.* 2009). Additionally, cations indirectly affect the pH as they are base ions and there is a link between pH and litter decomposition rates (Cornelissen *et al.* 2006). Although in the study by Cornelissen *et al.* (2006) litter pH was not the strongest controlling factor for litter decomposition, pH had significant effects on decomposition of subarctic litters. Similarly to cations, the role of litter physical traits on decomposition has been neglected in most studies (see General introduction). I found (Chapters IV and V) that water holding capacity of the leaf litter strongly affected decomposition. The physical and chemical litter traits are interlinked (Swift *et al.* 1979) and thus, it is hard and also not sensible to separate the effects of these traits on litter decomposition. Instead they should be seen as an overall trait syndrome. Increasingly higher number of studies has concentrated on capturing this trait syndrome, often labeled as the leaf economics spectrum, which classifies plant (litter) species by their different physiological strategies (Wright *et al.* 2004; Santiago 2007; Freschet *et al.* 2010; Bakker *et al.* 2011; Freschet *et al.* 2012). In the leaf economic spectrum, the variation in plant (litter) traits is seen as the result of trade-offs between e.g. either fast growth and high photosynthesis or slow growth and well protected, long-lived leaves. Nevertheless, for the prediction of plant litter decomposition, proxies of the litter quality are needed. This study

has shown that physical traits can perform equally well or even better than the chemical traits as such proxies (Chapters IV and V). These results indicate that more research should be done to link the litter physical traits with the activity and structure of the decomposer communities to improve the mechanistic understanding of the decomposition process. To put it simple: litter physical traits are important determinants of plant litter quality and thus, they should be included more into decomposition studies.

In the global decomposition assessment, I also studied the variation in litter decomposition caused by different groups of decomposers. Litter decomposition studies are heavily criticized for not assessing the process with a full set of decomposer communities, as is the case in 'real life' (Prescott 2005). This omission is due to the fact that the mesh size in the commonly used litterbags is usually too small to allow the access of all soil fauna to the litter. To improve the assessments of global plant litter decomposition, I quantified and separated the effects of the usually excluded soil macro- and mesofauna from the commonly included microbes and microfauna. Unexpectedly, I found that the composition of the decomposer community, as distinguished by their size class, had on a global scale only little effect on litter decomposition. However, although these different fauna classes caused only minor variation in litter species specific decomposition rates globally, their effect was truly strong in the tropical rain forest. Furthermore, the soil macrofauna seemed to deviate in their resource quality preferences between the tropical and temperate biome. Soil macrofauna should have the strongest effect on decomposition in areas where their abundances and body sizes are the highest. Thus finding these strong effects on tropical and temperate biomes, where both temperature and moisture conditions are favourable, is not surprising. Nevertheless, the finding that soil macrofauna had only minor effects in the Mediterranean and subarctic biomes, is surprising. Similarly, the lack of soil mesofaunal effect on decomposition, especially in the higher latitude biomes, where they play a bigger role in decomposition compared to the tropics (Kampichler & Bruckner 2009), is surprising. I hypothesized that soil meso- and macrofauna have an effect on decomposition on all the biomes, but that these effects were not always evident in the present study due to decomposition being in its early phases in some of the biomes. This hypothesis is based to the fact that mass loss was only 50% in the subarctic and Mediterranean biomes, and 80% in the temperate biome of the mass loss in the tropics. As plant litter quality (Swift *et al.* 1979; Cadish & Giller 1997), litter mixing effects (Lecerf *et al.* 2011) and decomposer communities (e.g. Anderson 1975; Berg *et al.* 1998a; Berg *et al.* 1998b; Schädler & Brandl 2005) change during the decomposition process, we can also expect that the role of larger decomposers is similarly modified by the decomposition phases. My hypothesis is further supported by another study conducted on the same locations and with the same separation of the soil fauna groups but only using the local plant litters at each site. In that study by Handa *et al.* (unpublished data) a strong difference in decomposition rates was found between the different soil fauna groups in all the biomes, including the subarctic mountain birch forest. Furthermore, in the study by Handa *et al.* (unpublished data) decomposition had on average proceeded further and was more similar among different plant litter types compared to the experiment reported in Chapter V. This study highlights the need to assess further the global roles of soil meso- and macrofauna on plant litter decomposition at different phases of decomposition.

Conclusions

This thesis focused on the mechanisms behind the controls on both decomposer communities and plant litter decomposition on a local and global scale. The trait assessments of plant litter quality and decomposers improved the understanding of the community compositional changes and their effects on soil processes. More specifically, I found traits to explain the responses of the soil Collembola community to climate change, the varying community structure of microarthropods inhabiting the heterogeneous plant litter layers and some general controls over litter decomposition that persist globally. It seems to be important to include litter physical traits into the decomposition assessments in order to improve the characterization of litter quality aspects with regards to the functioning of decomposers. Finally, this study contributes to a better understanding of the effects of global climate change and loss of biodiversity in soils.

References

- ACIA (2005). Arctic Climate Impact Assessment. Cambridge University Press, New York, NY, USA.
- Anderson J.M. (1975). Succession, diversity and trophic relationships of some soil animals in decomposing leaf litter. *Journal of Animal Ecology*, 44, 475-495.
- Bakker M.A., Carreño-Rocabado G. & Poorter L. (2011). Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. *Functional Ecology*, 25, 473-483.
- Berg M.P., Kniese J.P., Bedaux J.J.M. & Verhoef H.A. (1998a). Dynamics and stratification of functional groups of micro- and mesoarthropods in the organic layer of a Scots pine forest. *Biology and Fertility of Soils*, 26, 268-284.
- Berg M.P., Kniese J.P. & Verhoef H.A. (1998b). Dynamics and stratification of bacteria and fungi in the organic layers of a scots pine forest soil. *Biology and Fertility of Soils*, 26, 313-322.
- Bokhorst S., Phoenix G.K., Bjerke J.W., Callaghan T.V., Huyer-Brugman F. & Berg M.P. (2012). Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. *Global Change Biology*, 18, 1152-1162.
- Cadish G. & Giller K.E. (eds.) (1997). Driven by nature, plant litter quality and decomposition. CAB international, Wallingford, UK.
- Callaghan T., Tweedie C. & Webber P. (2011). Multi-decadal changes in tundra environments and ecosystems: The International Polar Year-Back to the Future Project (IPY-BTF). *AMBIO: A Journal of the Human Environment*, 40, 555-557.
- Cornelissen J.H.C., Quasted H.M., van Logtestijn R.S.P., Pérez-Harguindeguy N., Gwynn-Jones D., Díaz S., *et al.* (2006). Foliar pH as a new plant trait: can it explain variation in foliar chemistry and carbon cycling processes among subarctic plant species and types? *Oecologia*, 147, 315-326.
- Coulis M., Hättenschwiler S., Rapior S. & Coq S. (2009). The fate of condensed tannins during litter consumption by soil animals. *Soil Biology and Biochemistry*, 41, 2573-2578.
- Couteaux M.-M., Bottner P. & Berg B. (1995). Litter decomposition, climate and litter quality. *Trends in Ecology & Evolution*, 10, 63-66.
- Currie W.S., Harmon M.E., Burke I.C., Hart S.C., Parton W.J. & Silver W. (2009). Cross-biome transplants of plant litter show decomposition models extend to a broader climatic range but lose predictability at the decadal time scale. *Global Change Biology*, 16, 1744-1761.

- Dilks T.J.K. & Proctor M.C.F. (1979). Photosynthesis, respiration and water content in bryophytes. *New Phytologist*, 82, 97-114.
- Freschet G.T., Aerts R. & Cornelissen J.H.C. (2012). A plant economics spectrum of litter decomposability. *Functional Ecology*, 26, 56-65.
- Freschet G.T., Cornelissen J.H.C., van Logtestijn R.S.P. & Aerts R. (2010). Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology*, 98, 362-373.
- Gartner T.B. & Cardon Z.G. (2004). Decomposition dynamics in mixed-species leaf litter. *Oikos*, 104, 230-246.
- Gessner M.O., Swan C.M., Dang C.K., McKie B.G., Bardgett R.D., Wall D.H., *et al.* (2010). Diversity meets decomposition. *Trends in Ecology & Evolution*, 25, 372-380.
- Hansen R.A. (2000). Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology*, 81, 1120-1132.
- Hansen R.A. & Coleman D.C. (1998). Litter complexity and composition are determinants of the diversity and species composition of oribatid mites (Acari: Oribatida) in litterbags. *Applied Soil Ecology*, 9, 17-23.
- Hättenschwiler S., Tiunov A.V. & Scheu S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 36, 191-218.
- Hayward P.M. & Clymo R.S. (1982). Profiles of water content and pore size in Sphagnum and peat, and their relation to peat bog ecology. *Proceedings of the Royal Society of London Series B*, 215, 299-325.
- Heemsbergen D.A., Berg M.P., Loreau M., van Hal J.R., Faber J.H. & Verhoef H.A. (2004). Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science*, 306, 1019-1020.
- Hooper D.U., Chapin F.S., Ewel J.J., Hector A., Inchausti P., Lavorel S., *et al.* (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75, 3-35.
- Kampichler C. & Bruckner A. (2009). The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. *Biological Reviews*, 84, 375-389.
- Kaneko N. & Salamanca E. (1999). Mixed leaf litter effects on decomposition rates and soil microarthropod communities in an oak-pine stand in Japan. *Ecological Research*, 14, 131-138.
- Keith A.M., van der Wal R., Brooker R.W., Osler G.H.R., Chapman S.J., Burslem D.F.R.P., *et al.* (2008). Increasing litter species richness reduces variability in a terrestrial decomposer system. *Ecology*, 89, 2657-2664.
- Kraus T.E.C., Dahlgren R.A. & Zasoski R.J. (2003). Tannins in nutrient dynamics of forest ecosystems - a review. *Plant and Soil*, 256, 41-66.
- Lavorel S. & Garnier E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, 16, 545-556.
- Lecerf A., Marie G., Kominoski J.S., LeRoy C.J., Bernadet C. & Swan C.M. (2011). Incubation time, functional litter diversity, and habitat characteristics predict litter-mixing effects on decomposition. *Ecology*, 92, 160-169.
- Loreau M. & Hector A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72-76.
- Madigan M.T., Martinko J.M., Dunlap P.V., Clark D.P. & Brock T. (2009). *Brock biology of microorganisms*. Twelfth edn. Pearson Benjamin Cummings, San Francisco.
- McGill B.J., Enquist B.J., Weiher E. & Westoby M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178-185.
- Meehl G.A., Stocke T.F., Collins W.D., Friedlingstein P., Gaye A.T., Gregory J.M., *et al.* (2007). Global climate projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds. Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M & Miller HL). Cambridge University Press Cambridge, United Kingdom and New York, NY, USA.

- Prescott C. (2010). Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry*, 101, 133-149.
- Prescott C.E. (2005). Do rates of litter decomposition tell us anything we really need to know? *Forest Ecology and Management*, 220, 66-74.
- Reddy M. (1989). Mass loss and concentrations of nutrients in relation to microarthropod abundance, during needle decomposition in a pine plantation. *Proceedings: Animal Sciences*, 98, 285-289.
- Santiago L.S. (2007). Extending the leaf economics spectrum to decomposition: evidence from a tropical forest. *Ecology*, 88, 1126-1131.
- Schädler M. & Brandl R. (2005). Do invertebrate decomposers affect the disappearance rate of litter mixtures? *Soil Biology and Biochemistry*, 37, 329-337.
- Secretariat of the Convention on Biological Diversity (2010). *Global Biodiversity Outlook 3*, Montréal, Canada.
- Suding K.N., Lavorel S., Chapin F.S., Cornelissen J.H.C., Diaz S., Garnier E., *et al.* (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, 14, 1125-1140.
- Swift M.J., Heal O.W. & Anderson J.M. (1979). *Decomposition in terrestrial ecosystems*. Blackwell Scientific Publications, Oxford.
- Tilman D. & Lehman C. (2001). Biodiversity, composition, and ecosystem processes: theory and concepts. In: *The Functional Consequences of Biodiversity* (eds. Kinzig AP, Pacala SW & Tilman D). Princeton University Press Princeton, pp. 9-41.
- Trofymow J.A., Moore T.R., Titus B., Prescott C., Morrison I., Siltanen M., *et al.* (2002). Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. *Canadian Journal of Forest Research*, 32, 789-804.
- Violle C., Navas M.-L., Vile D., Kazakou E., Fortunel C., Hummel I., *et al.* (2007). Let the concept of trait be functional! *Oikos*, 116, 882-892.
- Wang S., Ruan H. & Wang B. (2009). Effects of soil microarthropods on plant litter decomposition across an elevation gradient in the Wuyi Mountains. *Soil Biology and Biochemistry*, 41, 891-897.
- Wardle D.A., Bonner K.I. & Nicholson K.S. (1997). Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos*, 247-258.
- Wardle D.A., Nilsson M.-C., Zackrisson O. & Gallet C. (2003). Determinants of litter mixing effects in a Swedish boreal forest. *Soil Biology and Biochemistry*, 35, 827-835.
- Wardle D.A., Yeates G.W., Barker G.M. & Bonner K.I. (2006). The influence of plant litter diversity on decomposer abundance and diversity. *Soil Biology and Biochemistry*, 38, 1052-1062.
- Wright I.J., Reich P.B., Westoby M., Ackerly D.D., Baruch Z., Bongers F., *et al.* (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821-827.