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Význam ekologické stechiometrie pro vývoj půd
Importance of ecological stoichiometry in soil development

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Doctoral thesis

Supervisor: prof. Mgr. Ing. Jan Frouz, CSc.

Prague, 2019

Prohlášení:

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V Praze, 15.7.2019

Declaration:

I declare that I have prepared this thesis individually, using only information sources and literature cited. This thesis or its substantial portion has not been submitted for the award of the same or any other academic degree.

In Prague, 15.7.2019

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2. Abstract

Ecological stoichiometry is a useful tool for understanding of ecological dynamics and related processes. There are only rare informations about nutrient cycling and nutrient dynamics in plant-soil system in restoration areas after coal mining. Different plant species have developed own strategies and treat differently with nutrients which can influence nutrient cycling and consequent nutrient return to the soil. In thesis, I investigated ecological stoichiometry as one of key factors which controls soil development in post mining sites. In general introduction, known facts are summarized about e.g. plant traits, decomposition process, nutrient cycling and consequences for soil development and restoration practices. But still, relationship between leaves, plant litter, and soil is poorly understood in restoration areas. The results of a doctoral thesis are presented in five papers, out of which three have been published, one has been already submitted and one manuscript is prepared for publication in an international journal with impact factor. In the first presented publication, the influence of soil fauna was studied (especially earthworms) on soil development. Soil development differed significantly between sites afforested with different tree species and it is strongly influenced by the presence and activity of soil fauna, especially by earthworm bioturbation. Second publication examines the life cycle of *Penthetria holoserica* and its correlation with C:N ratio of alder litter fall. The life cycle of *P. holosericea* is not dependent on seasonal changes in the quality and quantity of food. Third publication focused on nutrient competition strategy of *Calamagrostis epigejos*. *C. epigejos* reabsorbed most nutrients before the senescence of leaves at older sites while reabsorbing much less at the younger sites in spontaneous succession. *C. epigejos* reduced the availability of N for other plant species especially at the beginning of the growing season in spring especially at younger nutrient poor sites, when *C. epigejos* can use N stored during the previous season. In fourth publication was studied if the addition of N into the system have negative effects on soil development which seems to be important especially in poor nutrient conditions. In the reclaimed sites, the higher amount of N released from plant litter caused a higher loss of nutrients (Ca, Mg, K, P) from the ecosystem which can lead to earlier depletion of nutrients in these sites. And last publication focused on seasonal changes in tree foliage and litter fall composition. Different foliage composition was found between individual tree species and between sites, especially in concentration of N, Ca, Mg, K and content of lignin. This thesis provides broader insight into the ecological stoichiometry and its influence on plant-soil and soil fauna development at restoration areas. The thesis also summarizes the consequences of

the influence of plant for soil development and possible recommendation for restoration practices.

3. List of publications and manuscripts included in the doctoral thesis

Publication 1: Frouz J., Livečková M., Albrechtová J., Chroňáková A., Cajthaml T., Pižl V., Háněl L., Starý J., Baldrian P., Lhotáková Z., **Šimáčková H.**, Cepáková Š. (2013). Is the effect of trees on soil properties mediated by soil fauna? A case study from post-mining sites. *Forest Ecology and Management* 309/1:87-95.

Publication 2: Frouz J., Jedlička P., **Šimáčková H.**, Lhotáková Z. (2015). The life cycle, population dynamics, and contribution to litter decomposition of *Penthetria holosericea* (Diptera: Bibionidae) in an alder forest. *European Journal of Soil Biology* 71:21-27.

Publication 3: **Veselá H.**, Mudrák O., Frouz J. (2018). The role of dead standing biomass of *Calamagrostis epigejos* in nutrient turnover during spontaneous succession. *Science of The Total Environment*, 644, 717-724.

Publication 4: **Veselá H.**, Veselá M., Cejpek J., Frouz J. (submitted). Reclaimed alder plantation in post mining sites have more open nutrient turnover causing loss of nutrients from the soil in comparison unreclaimed woody regrowth.

Publication 5: **Veselá H.**, Lhotáková Z., Albrechtová J., Frouz J. (prepared manuscript). Seasonal changes in Foliage and Litterfall bio-chemistry at reclaimed and unreclaimed sites.

Contribution of the student

Publication 1: Hana Veselá performed the preparation and chemical analysis of all soil and plant samples and commented on manuscripts drafts.

Publication 2: Hana Veselá performed the preparation and chemical analysis of all soil and plant samples and commented on manuscripts drafts.

Publication 3: Hana Veselá performed the preparation and chemical analysis of all plant samples, contributed new field complementary experiment, performed the statistical analyses and led the writing of the manuscript and prepared figures for the manuscript as well.

Publication 4: Hana Veselá performed the preparation and chemical analysis of all soil and plant samples, performed the statistical analyses and led the writing of the manuscript and prepared figures for the manuscript as well.

Publication 5: Hana Veselá performed the preparation and chemical analysis of all plant samples, performed the statistical analyses and led the writing of the manuscript and prepared figures for the manuscript as well.

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Prof. Mgr. Ing. Jan Frouz, CSc.

4. Importance of ecological stoichiometry in soil development

4.1. Introduction

Study of ecological stoichiometry allows us to understand ecological dynamics and processes in the ecosystems. Most studies are focused on carbon:nitrogen:phosphorus (C:N:P) ratio, but stoichiometry can be used for any of limiting element in terrestrial ecosystems. C, N, and P are the most basic elements in organisms which play crucial roles in their activities (Sterner and Elser 2002). The relationship between living and dead organic matter provides us knowledge about plant and soil dynamics which can help to anticipate future soil and ecosystem development (Carnol and Bazgir 2013). Dead organic plant matter represent 80 % of nutrient input into the soil (Cape et al. 1991; Knops et al. 2002). Decomposition of plant biomass is influenced by many factors such as the chemical composition of plant litter, soil moisture, temperature, and presence and composition of soil community (Aerts 1997). Understanding the dynamics of ecological stoichiometry during soil development is crucial in disturbed areas where provides a tool for better decision making about restoration practices. Publications included in the doctoral thesis (in bold) and also other papers with contributions of the author (underlined) are included in a broader context in general introduction „Importance of ecological stoichiometry in soil development“ of doctoral thesis.

4.2. Ecological stoichiometry and plant traits

4.2.1. Ecological stoichiometry

Ecological stoichiometry is a useful tool which allows us to describe an elemental composition of the ecosystem and examines how the nutrient content of organisms shapes their ecology (Sterner and Elser 2002).

The origin of stoichiometry is rooted in agricultural studies involving Liebig's law of the minimum (Hessen et al. 2004; Paris 2006). First mention of ecological stoichiometry dates to 1958 when famous oceanographer Alfred Redfield stated that the plankton of the world's oceans, as well as the solutes at the site, from the upper layers to their cool, dark depths, retain approximately the same atomic ratio of C, N, and P, which is: 106:16:1 and has been referred to as the Redfield ratio (Redfield 1958). Since then, Redfield ratio has prompted ecologists to search for similar patterns and relationships in terrestrial ecosystems. Ecological stoichiometry has been one of the most powerful and useful principles in

biogeochemistry useful principles in biogeochemistry (Reiners 1986; Cleveland and Liptzin 2007), although recent studies have shown, that Redfield ratio concept is not longer supported (Graneli et al. 1990; Giovannoni and Stingl 2005; Martiny et al. 2013) because the ratio of the biogenic elements dramatically changes locally in the ocean (Martiny et al. 2013). Ecological stoichiometry can provide new perspectives for studying terrestrial ecosystems processes at different levels from leaf physiology to ecosystem productivity (Sterner and Elser 2002; Hessen et al. 2004). However, most studies have been devoted to the relationships between living and dead organic matter, or between plants and soil. Compared to marine systems, C:N:P ratio in terrestrial ecosystems is highly variable (Sardans et al. 2016b; Zhang et al. 2017).

Most of the studies in terrestrial ecosystems concern only the above-mentioned C, N, and P (e.g. Gusewell 2004; McGroddy et al. 2004; Elser et al. 2007; Sinsabaugh et al. 2008; Manzoni et al. 2010; Zechmeister-Boltenstern et al. 2015), even though the theories and tools can be applied to any of the other limiting elements such as C, H, O, N, P, Ca, Fe, Mg, or K (Sterner and Elser 2002), but ecological stoichiometry of plant is important for the growth and dynamics of species, but stoichiometric relationships (especially of other nutrients such as Ca, Mg, K) among leaves, plant litter, and soil are still poorly understood (Carnol and Bazgir 2013; Zhang et al. 2017), especially in plant-soil system in restoration areas after coal mining.

Plants often display a wide range of variation in C:N:P ratios according to conditions of light, nutrients, and growth rate, as well as across different species and functional groups. Under severe nutrient limitation, plants produce biomass with extremely low nutrient content (high C: nutrient ratio). Most studies of plant stoichiometry have considered only N and P which are the main elements limiting plant growth and affecting plant productivity, the photosynthetic rate, and other ecosystem functions. The N and P status and the N:P stoichiometry in plant tissues, especially in leaves, have been therefore studied intensively to determine how these factors limit plant growth (e.g. Cornelissen et al. 1997; Cunningham et al. 1999; Gusewell, S & Koerselman 2002; Ackerly 2004; Wright et al. 2004; Elser et al. 2007). Species with low foliar N:P ratio tend to grow rapidly and are more competitive for soil resources than species with higher N:P ratio, especially where nutrient availability is high (Elser et al. 1996; Sardans et al. 2016b). Foliar N:P ratio has been shown to correlate with the growth rate of plants and with the structure and function of plant communities (Elser et al. 1996; Sardans et al. 2016a). However, K is the most abundant nutrient in leaves after N, and

considerably more abundant than P. Together with N and P, K plays an important role in the physiology of terrestrial plants. It is already known that the interaction of different mineral elements in plant tissues and their balance are of great importance in tree growth and survival under stress conditions (Ingestad 1981; Kuznetsova et al. 2011). The concentration of K is especially significant in dry ecosystems because of its role in physiological responses of the plant to varying water availability and shifts in foliar N:P:K ratio is related to the change in response of plants to drought (Sardans et al. 2016b). For example according to Ingestad (1981), the optimum N:P:K ratio for grey alder (*Alnus incana*) is 100:50:18, for silver birch (*Betula pendula*) is 100:13:65 and for Scots pine (*Pinus sylvestris*) is 100:14:45.

In terrestrial ecosystems, local soil conditions, canopy development, and water supply interact to affect plant C:N:P stoichiometric ratios (Vitousek et al. 1993; Zechmeister-Boltenstern et al. 2015). Plants also react to an increased level of CO₂ and atmospheric N deposition by changing their C:N:P ratio. For example, a doubling of CO₂ concentration reduces plant N content of plant biomass by about 16 %, on average (Field et al. 2016). There are also significant differences in plant stoichiometry due to phylogenetic affiliation – legumes with symbioses of N₂ fixing bacteria have higher N:P ratios than other species. N:P stoichiometry of plants is also an effective tool for exploring allocation strategies of limiting elements (Zhang et al. 2018). According to the biogeochemical niche hypothesis, coexisting plant species tend to use the main nutrients N, P, K (and other essential nutrients such as Ca, Mg and S) in different proportions (Sardans et al. 2016a). Besides in terrestrial ecosystems, stoichiometric ratios of plant biomass of different species display a wide range of C:N:P ratios which has a strong impact on litter decomposition, soil detritus and consequent nutrient cycling in the ecosystem (Sturner and Elser 2002).

4.2.2. Biogenic elements in plant biomass

Biogenic elements are present in all living organisms and beside the elements forming the basics of organics substances (C, H, O), they are important mineral elements, which are found in nature mainly in the form of inorganic compounds (Begon et al. 1996). Macrobiogenic elements are present in biomass in the amount of more than 1000 mg kg⁻¹ of dry matter and include C, H, O, N, K, Ca, Mg, P and S, and have specific tasks in metabolic processes or form functional structures in plants (Reiners 1986; Brady and Weil 1996). C, N, P are available to plants in the form of simple organic molecules or ions in the atmosphere, or ions dissolved in water (e.g. nitrates, phosphates). These substances can then be incorporated into more complex organic compounds in the biomass. After oxidation of these compounds

and conversion of the bound C back to CO₂, the mineral nutrients are again released in a simple inorganic form and are thus available to other plants. Most nutrients are taken up by roots from the soil, but plants are also able to absorb minerals throughout their body surface (Brady and Weil 1996).

Dynamics of individual elemental cycles cannot be studied in isolation, because C, N and P interact closely in terrestrial ecosystems (Chapin et al. 1986, 2000; Shaver and Chapin 1991; Vitousek et al. 1993). The **Publication 5** showed that even foliage quality and composition (especially N, Ca, Mg, K, lignin) differed between individual tree species and between nutrient poor and rich sites. The highest nutrient concentration (Ca, Mg, K) was found in foliage and litter at spontaneous succession. The amount of nutrients needed for producing a unit of aboveground biomass is significantly different between plant species (Uri et al. 2002). Nutrient accumulation in aboveground tree biomass is usually in the order N > Ca > K > Mg > P (e.g. *Populus tremuloides* - Wang et al. 1995) and increases with stand age, similar result was found at **Publication 4**. Stembark and branches have usually the highest concentrations of K, Ca, and Mg (Wang et al. 1995; **Publication 4**). In a study in afforested abandoned land with grey alder (*Alnus incana*) (Uri et al. 2002), most of accumulated N and K (38,9 % and 37,9 %) was located in the leaves and most of P (61 %) in the wood. Also, in **Publication 4** were found the highest concentration of nutrient in leaves, the lowest in branches and roots and intermediate in trunks. Deficiencies of essential macronutrients (N, P, K, Mg) result in an accumulation of carbohydrates in leaves and roots, which modify the shoot-to-root biomass ratio (Hermans et al. 2006). Plant litter of N₂ fixing plants (e.g. *Alnus*) with low C:N ratio is also more palatable and attractive for herbivore feeding (Ritchie et al. 1998; Kurokawa et al. 2010) than that of non-fixers. But in **Publication 2** were found that life cycle of *Penthetria holoserica* is not so dependent on seasonal changes in the quality and quantity of food.

4.2.2.1. Carbon

The living matter of organisms is largely made up of water, the rest being C compounds. The available form of C to plants is CO₂ and HCO₃⁻, with atmospheric CO₂ being the essential C source contained in terrestrial communities (Begon et al. 1996, Slavíková 1986). CO₂ reacts in the soil to produce carbonic acid (H₂CO₃) and the carbonates and bicarbonates of Ca, K, Mg, and Na. The bicarbonates are readily soluble and may be removed during leaching (Brady and Weil 1996). CO₂ is produced by the decomposition of organic matter of plant and animal origin, breathing of plants, animals, and microorganisms, it also comes from volcanic

activity or is released from water sources, where it comes from treasure rocks. Human activities also contribute significantly to the CO₂ flux into the atmosphere via burning of fossil fuels and land use change (Begon et al. 1996).

The uptake of CO₂ by plants from the atmosphere occurs through photosynthesis which is important for plant growth and metabolism. Reduced C compounds store energy which can be later released by breathing to drive all biological processes. CO₂ is also released back into the atmosphere by microorganisms through decomposition of organic matter (Reekie and Bazzaz 1987; Begon et al. 1996). The balance between C fixation by photosynthesis and its release by oxidation processes is the basis of the global C cycle. The C cycle is closely related to nutrients such as N and P and they interact together in the ecosystem functioning. C uptake and sequestration depend primarily on the balance between the availability and demand for these key elements (Vitousek 1984; Reekie and Bazzaz 1987; Shaver and Chapin 1991; Aerts and Chapin 1999; Hessen et al. 2004a; Zhang et al. 2017). The C content of typical plant dry matter is about 45 to 48 % and in the soil is less than 5 % of organic C (Brady and Weil 1996). The plant contributes organic matter to soil C pools either via litterfall or via belowground root turnover and exudation which significantly support the activity and growth of microbial communities and their input can lead to priming effect and microbial loop formation (Knops et al. 2002). The bulk of C in plant litter occurs in the form of cellulose, hemicellulose, and lignin, which are poorly available to microorganisms. For their decomposition, specialized enzymes are needed, which can be produced mainly by fungi and by some bacteria (Cusack et al. 2018).

4.2.2.2. Nitrogen

N is the fourth most abundant element in living organisms, and in comparison to C the cycle of N is quite complex. It is mainly found in the atmosphere where it accounts for 78 % of the volume, in the form of N₂ or N oxides. N is absolutely essential for biomass production and cell function. In plants, N is part of many organic compounds, such as amino acids, proteins, or nucleic acids which control virtually all biological processes. It is also part of RNA and DNA, chlorophylls, chitin and peptidoglycans which constitute cells and enzymes. Plants respond quickly to an increased availability of N, turning dark green in color and increasing the protein content of their seeds and foliage (Rastetter et al. 1991; Brady and Weil 1996).

N is the nutrient most frequently limiting plant growth mostly in younger temperate and higher latitude soils (Reich et al. 2004). Plants receive N from the soil in the form of NH₄⁺, NO₃⁻ or amino acids. An exceptional position in the input of N into the organic is occupied by

the fixation of air N_2 . Only a small group of prokaryotic organisms, including several bacteria, actinomycetes, and cyanobacteria, are able to bind molecular N_2 . These contain nitrogenase, the enzyme that convert N_2 to NH_4^+ , which can be absorbed by plant roots. In the soil, N can be bound in organic compounds derived from dead tissues of organisms as well as from excreta or exudates (Brady and Weil 1996; Vitousek et al. 2002).

Availability of N plays an important role in many ecosystems and its deficiency limits plant growth and early stages of decomposition (Santiago 2007). But if N is not limiting, plants react with significant enhancement of N in foliage (Field 1983; Vogel and Gower 1998; Cunningham et al. 1999; Güsewell and Koerselman 2002; Ackerly 2004). On the contrary, deficiency of N affects important plant physiological functions, including assimilation and sequestration of CO_2 (Brady and Weil 1996).

4.2.2.3. Phosphorus

P is usually present in ecosystems at a substantially lower concentration than N. In some ecosystems, especially on older tropical soils, P is the major nutrient limiting primary production (Reich et al. 2004; Vitousek et al. 2010). In soil, P occur predominantly in the form of $H_2PO_4^-$ or HPO_4^- in the soil solution, adsorbed onto the surfaces of inorganic soil components, it is bound in organic matter and it is also part of amorphous and crystalline minerals. P is the one major element in organic matter which must be supplied almost entirely by the parent material and in contrast with C, N and S, P is cycled mainly in geological time (Walker and Syers 1976; Manzoni et al. 2010). Significant amount of P is cycled by microorganisms through mineralization of organic matter. The total amount of P available to plants is relatively low because soil organisms bind P in organic substances that are not utilizable by plants (Brady and Weil 1996; Manzoni et al. 2010).

In plants, H_3PO_4 phosphate is an important component of many molecules, especially adenosine triphosphate (ATP), which is used for energy transfer and, along with other components serves as the base unit of nucleic acid synthesis. It is found, for example, in nicotinamide adenine dinucleotide phosphate (NADP) or phosphorylated carbohydrates of the Calvin cycle. It is structurally bound in membrane phospholipids. The availability of P influences the processes of photosynthesis, N fixation, fruiting and seed production, and maturation (Walker and Syers 1976; Brady and Weil 1996). P is also a potent regulator of nitrification in soil (Pastor et al. 1984). The deficiency of P reduces the photosynthetic capacity of the plant which is mostly visible as bluish-green color of foliage or reproduction disfunction. The uptake is significantly influenced by the soil reaction. Plants are able to

receive P in the form of the phosphate anion H_2PO_4^- , which is very sparingly soluble in water and is bound to the Al and Fe ions in the soil. Mycorrhiza is also important for P nutrition (Brady and Weil 1996).

Organic phosphorus represents 30-50 % of total P in soil (Zechmeister-Boltenstern et al. 2015). The source of organic P compounds in the soil are mainly dead cells and remnants of microorganisms, plants and soil animals, as well as root exudates and other substances released into the soil by organisms (Zechmeister-Boltenstern et al. 2015). Most of the organically bound P is present in unidentifiable compounds. Accumulation of P in plants and in decomposing litter may affect the depth distribution of P, resulting in a high P content in organic layers near the soil surface. Most P in forest soil is accumulated on or near the soil surface (Knops et al. 2002).

4.2.2.4. Potassium

K is the third most likely nutrient, after N and P, to limit plant productivity whose soil deficiency can greatly reduce plant growth and productivity. Similarly to N and P it is commonly applied to soils as fertilizer and is a component of most mixed fertilizers. The primary sources of K are igneous rocks. The K cycle is similar to the P cycle, but K is present in the soil solution only as a positively charged cation K^+ . Its behavior in the soil is influenced primarily by soil cation exchange properties and mineral weathering. K is incorporated into the structures of organic compounds and acts as an activator for cellular enzymes. K plays an important role in reducing the loss of water from leaf stomata and increasing the ability of root cells to take up water from the soil. K is also essential for photosynthesis, for N fixation and for translocation of sugars (Brady and Weil 1996). K is important in helping plants adapt to environmental stress, such as drought tolerance, improved winter hardiness, better resistance to certain fungal diseases and insect impact (Sardans et al. 2016b). Deficiency of K is mainly manifested by yellowing of the leaves. During ecosystem development, K is lost by leaching from upper soil layers due to higher mobility (Brady and Weil 1996).

4.2.2.5. Calcium and Magnesium

A number of other macrobiogenic and microbiogenic elements are important for the nutrition of plants, animals and other organisms. These elements are taken up by plants only in soluble form, usually in the form of cations or anions present in soil solution or bound to the surface of soil colloids. Among macrobiogenic elements, calcium (Ca) and magnesium (Mg) are

among the most important. The source of the above-mentioned elements is mainly the parent material; they can also be introduced into the soil with aerosol, by leaching and anthropogenic way (fertilization, precipitation from the air) (Brady and Weil 1996; Campo et al. 2000).

Ca is the most abundant cation of the exchange complex in most soils (Raheison and Grouzis 2005). This element in their exchangeable and weatherable form influences all ecosystems through its critical role in counteracting soil and water acidification. This nonacid cation status of soils has a major influence on the species composition and productivity of terrestrial ecosystems. The amount of Ca in plant foliage varies widely from as low as 0.1 % to 5 % of the dry matter. In plants, Ca is a major component of the middle lamella of cell walls and it is involved in membrane permeability and the activation of critical enzymes. Most of Ca is taken up by the youngest fine roots. Deficiency of Ca may cause other metals including Mg, Zn, Mn, Al to become toxic to the plant and the root membranes to loss integrity (Brady and Weil 1996).

Mg is a relatively abundant element (1.94 % Mg in the crust rocks). Similar to Ca, Mg is released by the weathering of minerals and forms a readily soluble acid carbonate ($\text{Mg}(\text{HCO}_3)_2$). Overall however, Mg mobility is about half that of Ca. Plant generally take up Mg in similar amount or smaller amount than Ca. About 1/5 of the Mg in plant tissue is found as the central component of the chlorophyll molecule and so is intimately involved in photosynthesis. Mg plays a critical role in the synthetis of oils and protein and in the activation of enzymes (Brady and Weil 1996; Campo et al. 2000). The Mg^{2+} ion forms create a bridge connecting ATP molecules. Deficiency of Mg is expressed as yellowing of older leaves or needles (chlorosis) (Brady and Weil 1996).

4.2.3. Plant functional traits

Plant functional traits strongly affect C cycling and the energy balance of the ecosystem, which can in turn influence regional and global climates (Cornelissen et al. 1997, 2007; Lavorel and Garnier 2002; Berner and Law 2016; Bjorkman et al. 2018). Plant traits are related to the specific leaf area (SLA), leaf N content and leaf dry matter content and affect primary productivity, litter decomposability, soil C storage, nutrient cycling and soil biota (Cornelissen et al. 2007; Cortez et al. 2007; Klimešová et al. 2008; Moradi et al. 2017). Generally, plant species handle nutrients differently and can influence nutrient return to the forest floor and nutrient cycling through the amount and chemical composition of throughfall and plant litter (Warren and Adams 2001; Reich et al. 2004;

Carnol and Bazgir 2013; **Publication 1**; Zhang et al. 2018). It is already well known that low nutrient input supports conservative plant species which grow slowly and have a very closed nutrient cycle, hold nutrients in biomass, produce plant litter with high C:N ratio and release only little nutrients into soil (Chapin et al. 1986; Aerts and Chapin 1999; Reich et al. 2003). But on the contrary, higher input of nutrients stimulate nutrient cycling, plants produce plant litter with low C:N, increase N availability which supports loss of nutrients from the system, eutrophication, acidification and reduction of biodiversity (Brady and Weil 1996; Elser et al. 1996; Högberg and Read 2006; Vitousek et al. 2010; Sardans et al. 2016b; Xia et al. 2017). Leaf N and P increase from tropics to the cooler and drier mid-latitudes because of temperature-related plant physiological stoichiometry and biogeographical gradients in soil substrate age and then plateau or decrease at high latitudes because of cold temperature effects on biogeochemistry (Reich and Oleksyn 2004). N:P ratio increases with mean temperature (Reich and Oleksyn 2004).

4.3. Leaf traits

Green foliage is fundamental for the functioning of terrestrial ecosystems. Their pigments are the predominant signal seen from space. N uptake and C assimilation by plants and the decomposability of leaves drive biogeochemical cycles (Wright et al. 2004). Leaf size varies by several orders of magnitude between species, and leaf traits are typically normalized by mass or area to study relationships among them (Osnas et al. 2013). Leaf traits underlay grow-survival trade-off that species with shortlived physiologically active leaves have high growth but low survival chance (Poorter and Bongers 2006). Therefore, the theory of leaf traits proposes that plants with fast growth have cheap short-lived thinner leaves with a high SLA which enables them to maximize light capture and forage opportunistically for light. Also plant with lower leaf C:N ratio have faster and more open nutrient cycling, pre-empt resources and outcompete their neighbors (Chapin et al. 1987; Cornelissen et al. 1997; Aerts and Chapin 1999; Poorter and Bongers 2006; Santiago 2007; Campanella and Bertiller 2008; Rahman et al. 2013; **Publication 5**). Poorter and Navas (2003) also found that fast growing, high SLA species allocated a large proportion of their leaf N into Rubisco instead of chlorophyll. On the other hand, plants with formation of long-lived well-protected leaves with low supply of N must acquire as much N as possible to allocate it in a way that maximizes biomass accumulation, high C:N ratio, minimizes the losses of nutrients and long-term competitive superiority for nutrients in low supplied ecosystems (Wedin and Tilman

1990; Reich et al. 2003). Longer-lived, better-protected leaves with lower nutrient concentration lead to reduced biomass loss by herbivory, mechanical disturbance, or leaf turnover and high plant resistance (Poorter and Bongers 2006). During succession in restoration areas, species with high SLA, high leaf N contents, and low C:N ratios, are progressively replaced by species with the opposite characteristics (Cortez et al. 2007; Frouz et al. 2014).

Different tree species have different nutrient release patterns, which are related to leaf litter quantitative traits and seasonal environmental factors (Rahman et al. 2013). Ca, Mg, K and N concentration in foliage and leaf litter are tree-species specific. Therefore, leaf traits belong to the most important factors by which plants influence biogeochemistry of their stand (Carnol and Bazgir 2013; **Publication 5**).

4.3.1. Foliage and litter fall chemical and structure characteristics

Differences in nutrient concentrations (Ca, Mg, K, P and N) between foliage and leaf litter depend both on the element concerned and on tree species (Johansson 2000; Wright and Westoby 2003; Carnol and Bazgir 2013). As shown in several studies (e.g. Swift et al. 1979; Cornelissen et al. 1997; Santiago 2007; Osnas et al. 2013) chemical and structure characteristics of foliage and litter fall are correlated and control decomposition rates. Leaf stoichiometry is strongly influenced by bedrock, climate, soil fertility or availability of light (Warren and Adams 2001; Reich and Oleksyn 2004; Zhang et al. 2018), but also plant species with different ecological lifestyles have different N and P concentrations and N:P ratio, and plants with higher growth rates typically have a higher leaf N and P concentrations (lower C:N and C:P) and lower leaf N:P ratio (Zechmeister-Boltenstern et al. 2015a). Soil substrate age has been shown to influence soil N and P availability and leaf N and P, with lower levels in very young and old soils than in young to intermediate age soils (Reich and Oleksyn 2004). Mean N and P concentrations (%) of green leaves were generally higher at the nutrient-rich site and higher at the drier sites (Wright and Westoby 2003). Evergreens have lower litter P concentrations than deciduous species, while N₂ fixers have higher litter N concentrations than non-N₂ fixers (Killingbeck 1996). Foliage litter contains on average 0.3-2 % of N and in general broad-leaved trees shows high values (Killingbeck 1996; Wright and Westoby 2003). Litter that contains more P is demonstrably decomposed twice as fast as that with a lower concentration of the same species (Vitousek et al. 1993). Carnol and Bazgir (2013) found that fresh foliage and litter fall N concentrations were highest in alder and

willow, while Ca, Mg and K were highest in rowan. Alder and willow also had higher K concentrations in fresh foliage than the other species.

The structure characteristics are given by number of components, mainly SLA, phenols, lignins, chlorophylls, polysaccharides or ratio of nutrients (Swift et al. 1979; Santiago 2007). Plants grown at low nutrient sites develop significantly lower leaf area in spring than plants at high nutrient sites (Gloser 2005). Also plant adaptations to defoliation include a suite of morphological and physiological responses which allow plants to use internal reserves of C and N to re-establish photosynthetically active leaf area rapidly and to supply maintenance demands of the remaining organs. These adaptations are one of the key factors affecting plant survival during the first days of regrowth at spring (Kavanová and Glöser 2005). Water extractable polyphenols or polyphenols:N ratio may be a good chemical index of N release (Domenach et al. 1994). Several studies have shown that polyphenol content is a better predictor for litter decomposition, determinant of C quality, nutrient availability, net N mineralization and N immobilization, and that together with tannins content they are important in shaping plant soil nutrient environments (Field et al. 1983; Rahman et al. 2013). Plants rich in phenolics compounds negatively affect neighboring plants by restricting the N supply and they stimulate microbial activity and subsequently reduce plant-available N (Meier and Bowman 2008; Rahman et al. 2013). A high amount of phenolics in litter fall can reduce soil nutrient availability, either indirectly by stimulating microbial N immobilization or directly by enhancing physical protection within the soil and have an inhibitory effect on mycorrhizal fungi (Rahman et al. 2013). Lignin is the most important. It gives strength to the cell wall and allows water to be transported through plant vessels. Lignin together with N content control CO₂ production and N mineralization in soils (Austin and Ballaré 2010; Rahman et al. 2013). Lignin is preferentially degraded under photodegradative conditions because it absorbs light over a wide range of wavelengths (Austin and Ballaré 2010; Frouz et al. 2011a). Compounds of lignin degradation often inhibit the activity of soil microflora and slow down the turnover of nutrients. Lignin is one of the most slowly decomposing components of dead vegetation and during an initial-controlled phase it accumulates in litter and starts governing the litter decomposition rate (Staaf and Berg 1981). Its degradation is generally assisted by the physical activity of soil fauna. Lignin is typically considered as a recalcitrant material that is resistant to microbial decomposition; only fungi are able to synthesize extracellular enzymes that break the structure into biologically usable forms (Swift et al. 1979). It has been proposed that microorganisms use

some of the ring structures from lignin in the synthesis of stable organic matter (Melillo et al. 1982; Brady and Weil 1996; Flaig 1964). Cellulose is the most abundant polysaccharide on Earth, because the C-O-C chemical bonds linking the sugar molecules of cellulose together are much more difficult to break than those in starch. The initial chain-breaking step in cellulose decomposition requires the activity of specialized organisms that produce the enzyme cellulase. The amounts of bacteria are limited by the amount of N in the soil. If the N content of the soil is low, the cellulose decomposition rate is reduced (Brady and Weil 1996). Cellulose can account for between 30 and 60 % of plant materials and its decomposition is of major importance to the biogeochemical cycling of C and essential plant nutrients. Increasing the growth rate (higher production of polysaccharides) is the common reaction of plants to increased CO₂ concentration in the environment (Rahman et al. 2013).

4.3.2. Senescence and reallocation of nutrients

Nutrient foliar resorption is a primary mechanism of nutrient conservation in plants (Vitousek 1984; Shaver and Chapin 1991; Aerts 1996; Yuan et al. 2005) which allows to organisms repeated use in metabolism within one ecosystem. The reallocation efficiency increases considerably with decreasing nutrient availability (Chapin et al. 1986). The cycle starts with the uptake of nutrients by plant roots and their mycorrhizae, followed by allocation of nutrient to biomass construction and maintenance, then nutrient reabsorption from senescing tissue and consequent return of nutrients to the soil via above- and below-ground litter and then microbially mediated release of inorganic nutrients to the soil solution (mineralization) (Rahman et al. 2013).

Foliar resorption efficiency is dependent mainly on ratios of foliar nutrients, plant growth type, ecosystem type and physiological limitations (Sohrt et al. 2018). This process varies between species because diverse strategies evolved to overcome the nutrient shortage, competition between species, nutrient uptake and consequent biomass productivity (Killingbeck 1996; Han et al. 2013). For example, differences in fresh foliage nutrient concentrations and retranslocation resulted in higher concentrations in the foliar litter of alder (N), willow (N, K), rowan (Ca, Mg, K), and birch (Mg), relative to the other species (Carnol and Bazgir 2013). The highest concentration of Ca, Mg and K in fresh foliage may be explained by plant physiological characteristics leading to better exploitation of soil resources of available nutrients (Attiwill and Adams 1993; Larcher 2003). The level to which nutrient concentrations are reduced in senescent leaves or litter (resorption proficiency) is a different index of nutrient conservation from the proportion of nutrients resorbed (Wright and Westoby

2003). Evidence from the literature suggests that across a broad array of species, nutrient reallocation of nutrients from leaves to other parts of the plant occurs during senescence during which on average around 50% of nutrient contents can be resorbed (Lodhiyal et al. 1995; Aerts 1996; Killingbeck 1996; Heilman and Norby 1998; Aerts and Chapin 1999; Prescott 2010; Sohrt et al. 2018) but some studies suggest that even from less than 5 % to 80 % of the total leaf N may be resorbed (Aerts and Chapin 1999). Once leaves senesce and a proportion of a leaf nutrient is resorbed by the plant, the resulting litter nutrient concentration has a strong influence on decomposition (Swift et al. 1979; Aerts and Chapin 1999; Cornelissen et al. 2007). Foliar nutrient resorption from senescent foliage provides easily available nutrients for re-use in the next spring from nutrient storage pools when nutrient uptake from the soil is limited due to low temperature or because of competition (Han et al. 2013; Sohrt et al. 2018).

Nutrient resorption from foliage in temperate forest trees prevents nutrient losses of the individual trees and supports nutrient conservation in the ecosystem (Sohrt et al. 2018). Plant nutrient resorption efficiency is higher on soils with low nutrient availability (Zechmeister-Boltenstern et al. 2015; Sohrt et al. 2018; **Publication 5**) where the lower nutrient concentration in litter reduces decomposition rates, nutrient release and energy transfer to the other trophic levels. But on the one hand, foliar N and P concentration are resorbed less at N and P rich sites and under optimal climatic conditions (Zechmeister-Boltenstern et al. 2015). The ability of plants to reduce N in senescing leaves is significantly correlated with their ability to reduce P. The remobilization of P from leaves is induced by P availability (Killingbeck 1996) and usually decreases with the aging of the stand (Uri et al. 2002). For example, alder litter is highly rich in N (easily mineralized N) due to very low nutrient retranslocation from senescing leaves (2,5 % to 14 %) (Mikola 1958; Vares et al. 2004) but alder litter is poor on P due to high reallocation (Uliassi and Rues 2002).

The decline of N and P in leaves in autumn is strongly indicated by nutrient resorption. A significant correlation between P resorption efficiency and the foliar N:P ratio was found for deciduous but not for coniferous trees (Sohrt et al. 2018). Killingbeck (1996) found that evergreens were significantly more proficient at resorbing P than deciduous species (0.045 % vs. 0.067 % P in senesced leaves) and plants capable of symbiotic N₂ fixation were significantly less proficient at resorbing N than non-fixers (1.6 % vs. 0.9 % N in senesced leaves). The implication of these findings includes the speculation that evergreens may be able to colonize P deficient sites more effectively than deciduous species (Killingbeck 1996).

4.4. Process of litter decomposition

Litter decomposition plays an important role in C cycle and cycling of nutrients at both local and global scales (Melillo et al. 1982; Rahman et al. 2013) and can be characterized as a process during which fresh litter fall of different initial properties transforms into chemically very uniform soil organic matter (Aerts 1997). Thus, plant litter decomposition is a critical step in the formation of soil organic matter and the mineralization of organic nutrients (Austin and Ballaré 2010). Due to the strong climatic control of litter decomposition, climate change may significantly affect this pathway (Aerts 1997). The main drivers of litter decomposition are generally water availability, litter chemical composition as indicated by its C:N ratio (Melillo et al. 1982; Aerts 1997), soil organisms, and environmental conditions such as temperature (Domenach et al. 1994; Sterner and Elser 2002; Zechmeister-Boltenstern et al. 2015). The soil type more than species composition of vegetation may influence decomposition via the composition of the decomposer community and the resource quality of the plant litter input (Aerts 1997; Reich et al. 1997; Rahman et al. 2013).

Decomposition involves the breakdown of large organic molecules into smaller, simpler components. In the first phase of decomposition, plant litter is broken down by detritivores to smaller pieces which can be chemically reduced. This phase is characterized by the fast weight loss through leaching of soluble components (especially inorganic ions, later soluble polyphenols) and by the decomposition of cellulose during the next wave of microbial activity, following the mechanical disintegration of the material. Rapid loss of cellulose compounds is accompanied by a relative accumulation of N in the remaining material leading to a decrease of C:N ratio, which affects decomposition rate of structural material (Melillo et al. 1982). In the second phase, these small pieces of organic matter are further reduced and mineralized by microorganisms (bacteria and fungi) into basic inorganic molecules, such as ammonium, phosphate, CO₂, and water. These can be taken up by plants or microorganisms, leached out of the system or, in the case of gaseous break-down products, released into the atmosphere. Later in the second phase, the concentration of resistant components, particularly lignin, in decomposed litter begins to decrease (Swift et al. 1979; Staaf and Berg 1981; Melillo et al. 1982; Berg and McLaugherty 1989; Aerts 1997; Berg 2000). Complete decomposition may range from weeks to several years and thus substrate quality has long been recognized as a critical factor determining the rate of litter decomposition. In general, mineralization is fast in deciduous stands (1-3 years) and much slower in coniferous stands (4-10 years) (Reich et al. 1997). This is in particular due to the

chemical properties of needles, which contain a number of impregnating compounds resistant to decomposition, such as lignin, or wax. These properties result in an unfavorably high C:N ratio and thus reduced litter degradability since many studies have shown the direct relationship between the decomposition rate of litter and its N content (e.g. Aber and Driscoll 1997). Optimal conditions for optimal decomposition rate are near-neutral pH, 60 % of soil pore space filled with water providing enough soil moisture and good aeration, temperatures of 25-35 °C and high quality of the added residues as a food source for soil organisms (Swift et al. 1979). Slower rates of litter decomposition and nutrient cycling lead to organic matter accumulation in forest floor (Van Cleve et al. 1971). Slower decomposition rate is also visible in litter exposed to air and photodegradation. This type of litter is decomposed mainly by fungi which resist water stress better than bacteria and can deal with limitation by N (Facelli and Pickett 1991; Frouz et al. 2011a; [Angst et al. 2017](#)). On the contrary, faster decomposition rate is found at nutrient-rich sites because litter with high initial N concentration exhibit relatively faster decomposition (Berg and Matzner 1997; Hobbie et al. 2010).

4.4.1. Plant litter

Plant litter is the basic energy source for detrital food web through which nutrients and energy stored in plant fresh tissue are returned back to the environment. Decomposition research has primarily focused on leaf litter fall, likely because leaf litter is large and visible and can be therefore easily sampled (Xia et al. 2015). But plant litter is divided into (i) aboveground litter - litterfall, dead wood, and (ii) belowground litter - dead fine roots which represent the most important source of organic carbon input to the forest floor (Facelli and Pickett 1991; Ekblad and Nordgren 2002; Prescott 2010; Miletic et al. 2012; Xia et al. 2015; Wu 2016; Lasota et al. 2018; Świątek et al. 2019). Distribution of litter fall throughout the year differs among climatic zones. In tropical zone, it is evenly distributed throughout the year, while in the colder temperate zone it is concentrated with maximum intensity in the very short autumn season, usually with a peak in October or November (Campanella and Bertiller 2008; Prescott 2010; Carnol and Bazgir 2013). The age of trees is important for the size of litter production only at a younger age. The amount of litter increases with the age of the trees until the canopy closes, then the annual amount of litter tends to remain almost constant (Bray and Gorham 1964).

Mainly, fine roots are an important source and sink for nutrients in terrestrial biogeochemistry (Gordon and Jackson 2000; Dornbush et al. 2002). Plants depend on fine

roots (<2 mm in diameter) for water and mineral uptake. Net primary production can be greater belowground than aboveground, nutrient concentrations in fine roots may be higher than those in foliage and the life-span of fine roots are considerably shorter than that of foliage (Meier and Bowman 2008). In temperate forests, average contribution of aboveground litter to roots is approximately 42 % to 48 % (Freschet et al. 2013) but some research assumes that fine roots represent up to 75 % of total nutrient input into the soil (Mcclaugherty et al. 1984). Fine roots are more biochemically resistant to decomposition than leaf litter and they are the dominant source of recalcitrant plant materials returned to soil (Xia et al. 2015). The biomass of fine roots has been found to increase with age at both reclaimed and unreclaimed sites and was significantly higher at unreclaimed sites than at reclaimed ones (Frouz et al. 2014). Dead wood is ecologically important to the forest by slowly releasing C back into the atmosphere and moreover dead wood plays a role in long term C storage (Wu 2016). Also, dead wood of different tree species in various stage of decomposition affects nutrient dynamics. Water penetrates deadwood, dissolving and leaching different substances, and as a result, making deadwood poorer in these substances (Lasota et al. 2018).

4.4.2. Factors controlling process of decomposition

Decomposition rate and organic matter turnover in the soil are determined by three unrelated groups of factors: chemical (litter chemical composition and litter quality, soil chemistry), physical (climate and weather conditions) and biological (microorganisms and soil biota involved in litter decomposition) (Heal et al. 1997). But most studies are focused mainly on temperature, soil aeration and moisture, pH, soil biota and chemical composition of litter that varies between species, or within species depending on the age of litter. Organic matter accumulates more in the soil in a cooler climate and in an oxygen-deficient environment. (Brady and Weil 1996; Aerts 1997).

Laboratory experiments have shown that temperature together with moisture has a great influence on the phase of mineralization of readily available forms of C and N (Stott et al. 1986). The influence of moisture is limiting for decomposition, especially in extreme values, where deterioration processes do not get moisture or oxygen. Decomposition and mineralization increase exponentially with increasing temperature in the temperature range up to 30-35 °C (Lloyd and Taylor 1994).

pH primarily affects biological activity in the soil. pH has a great influence on the solubility of many important soil substances and thus affects the availability of nutrients for

plants. The optimal pH for biochemical transformations in the soil is 6.6–8.0. However, most reactions occur at low pH levels (Brady and Weil 1996). It has been found that increasing pH positively affects N mineralization. The degree of nitrification in soil is limited in acidic soils by low pH and faster rate of fixation of N₂ (Robertson 1982). Low pH in soil causes higher leaching of negatively charged compounds, such as phenols and higher fatty acid (Berg and McLaugherty 1989).

The type and composition of litter is a very important factor affecting decomposition (Swift et al. 1979; Santiago 2007). Plant biomass contains 60-90 % of water and the rest is dry matter containing mainly C (42 %), O (42 %), H (8 %) and other elements (8 %). Furthermore, ash contains organic components such as cellulose (45 %), sugars (5 %), proteins (8 %), lignin (20 %), polyphenolic substances (2 %), hemicellulose (18 %) and fats and waxes (2 %). Organic compounds can be divided into the classification according to the degree of their degradability: sugar, starch, simple protein> unprocessed proteins> hemicellulose> cellulose> fats, waxes> lignin and phenolic compounds (Brady and Weil 1996).

While the content of N, P and other nutrients changes during litter decomposition, the C content remains practically constant (with a change of about 1 %) (Anderson 1973). Rustad (1994) stated that C content decreases as decomposition coincides with the litter incorporation into soil organic matter, its decrease highly correlates with the loss of litter fall weight. In most studies, N has an increasing trend during the first phase of decomposition, while the C:N ratio decreases (Anderson 1973; Staaf and Berg 1981; Berg et al. 1987; Rustad 1994). The importance of N for the decomposition process is discussed in a number of studies and most of them stated that N plays a dominant role in decomposition processes because it significantly affects the richness of soil microorganisms. (Tanner 1981; Aber et al. 1990; Köchy and Wilson 1997). During decomposition, C:N of litter fall decreases rapidly because this decrease in ratio is mostly attributed to immobilization of N from the surrounding soil (Fujii et al. 2016). Some authors report that the rate of the second phase of decomposition is often slower in N-rich litter fall (Berg and McLaugherty 1989). So the obvious important factors regulating litter the decomposition is still considered initial C:N, N:P of plant litter (Rahman et al. 2013) and microbial community ([Angst et al. 2019](#)). Prescott et al. (2000); Fujii et al. (2016) report that the critical CN ratio below which mineralization begins to prevail over immobilization is 25-32. Moreover, Takeda (1998) showed that if C:N ratio is less than 32, the microbial mineralization of N has overcome N accumulation and the release

of N mineral forms has increased exponentially. Mineral N is not assimilated to microbial biomass but is released in excess when the C:N ratio falls below the critical level 32. This may result in increased N-leaching from litter to deeper soil. Another important factor is the concentration of P in a litter. The concentration of extractable P in litter and soil slightly increases during the decomposition and positively influences the rate of decomposition (Pastor et al. 1984; Berg 2000). The amount of P released by litter decomposition is practically equal to the P received by the plants.

Lignin concentrations and lignin:N ratios are key factors determining the turnover rate of forest deciduous trees. The lignin contents of plant litter range from less than 2 % to more than 50 % (Brady and Weil 1996). The dependence of the N content in litter on the lignin:N ratio has an exponential character - with increasing lignin:N ratio, the amount of N decreases in litter (Binkley et al. 1992; Köchy and Wilson 1997; Reich et al. 1997). It is known that lignin degradation can be strongly suppressed by the high mineral N content of the substrate (Berg 2000). Polyphenol compounds found in plant litter may also inhibit decomposition. These phenolics are often water soluble and may be present in concentrations as high as 5 % to 10 % of the dry weight. By forming highly resistant complexes with proteins during residue decomposition, these phenolics can dramatically slow the rates of both N mineralization and C oxidation (Brady and Weil 1996).

4.5. Interaction of litter decomposition with soil and ecosystem development

4.5.1. Influence of plant litter on decomposition and soil development

Plant litter strongly influences soil development by supplying easy-to-use nutrients and organic matter (Brady and Weil 1996; Carnol and Bazgir 2013). Plant litter is the main source of nutrient input into the soil more than about 80 % (Cape et al. 1991; Knops et al. 2002). Amount and quality of plant litter have a major impact not only on decomposition rate but also on soil quality, microclimate, and conditions for germination and plant growth. Organic matter from plant litter improves soil structure and increases the ability of soil retain water (Sydes and Grime 1981). Decomposition of litter is the most important process in determining the flow of nutrients and organic matter in the ecosystem and their entry into the soil. Characteristics of litter and its quantity also serve to determine the phenological development of the stand and its year-on-year changes, sprouting, development of foliage,

flowering, and occurrence of fruits, fallen leaves, needles in relation to the health of the stand and climatic conditions (Mcclaugherty et al. 1984). Individual plant species had developed their own strategies which help them in competition for nutrients, especially in soils with low availability of nutrients. This has been shown in the **Publication 3** where the highly competitive rhizomatous grass *Calamagrostis epigejos* with hardly decomposable litter showed that during decomposition of its litter, N is immobilized from soil which reduces availability of N for other plants particularly at the beginning of growing season in spring.

4.5.2. The role of soil biota in litter decomposition

Plants and soil organisms play a crucial role in soil formation (Frouz et al. 2014). The presence of plant litter alters the development of the microenvironmental conditions of the topsoil and the vegetation type is a principal factor determining microbial biomass and respiration (Frouz et al. 2007a; Frouz et al. 2014). Plant litter intercepts incident light and rain and changes the structure of a surface, which affects the transfer of heat, water, and gases between the soil and the atmosphere (Facelli and Pickett 1991). The development of soil biota plays an important role in litter decomposition and soil organic matter accumulation. Soil biota may affect plant fitness by several interactions with roots (mycorrhiza, N₂ fixation, root herbivory) and by other activities of various beneficial or pathogenous microorganisms in the rhizosphere. Soil biota have many important functions such as litter decomposition, nutrient release, formation of soil structure and mixing the soil profile (Frouz et al. 2014). Soil microorganisms are divided into r-strategists and K-strategist. R-strategists are limited by easily decomposable plant litter in the first initial phase and the decomposition rate is faster. K-strategists can decompose plant litter with less available organic nutrients, population grow slowly, and decomposition rate is more effective (Brady and Weil 1996).

Many groups of soil fauna, such as earthworms, millipedes, diptera larvae or various groups of soil mesofauna, can have a significant effect on soil formation because they are important detritivores in terrestrial ecosystems (Edwards and Bohlen 1996, Frouz et al. 2007b, 2014). Soil fauna participates in the decomposition process mainly by fragmentation of litter and its incorporation into soil (Brady and Weil 1996). But the transformation of soil organic matter is carried out mainly by soil microflora. However, soil fauna may substantially affect the living conditions of microflora and thus indirectly affect microbial activity (Frouz and Nováková 2005). The most important macrofauna decomposers are earthworms (*Lumbricidae*) (Rusek 2000). Earthworms incorporate organic matter into the soil profile by bioturbation, create the various biopores which increase soil porosity, water infiltration and C

accumulation in the mineral topsoil (**Publication 1**; Frouz et al. 2014). Earthworms also transform organic matter through their digestive tract and make forms of P, K and Ca available to plants. Moreover, earthworm biomass is a better predictor of foliar nutrient concentrations than either exchangeable or total nutrient concentrations (Chaoui et al. 2003; Dobson et al. 2017). The study of Mudrak and Frouz (2018) has shown that the effects of earthworm presence on plants decreases during succession but earthworms significantly affect plant growth, especially in young soils. But soil fauna is also positively correlated with an increase in plant cover, litter input and had higher abundance at older ecosystems (Moradi et al. 2017).

When organic residues are added to the soil, bacteria and fungi grow rapidly on this new food source, produce large biomass of bacterial and fungal cells that contain much of the N in the residues (priming effect) (Kuzyakov 2010). After the decomposition process begins, some of the N from organic compounds is released into the soil solution which increases the amount of soluble N available directly for plant uptake. Generally, N rich material decomposes quite rapidly and increases microbial growth and activity without N deficiency. But if C:N ratio is high, N is accumulated and immobilized in litter fall by decomposers because initial litter fall N concentration was below the requirements of decomposers (Staaf and Berg 1981). Similar results were found in the **Publication 3** with biomass of *Calamagrostis epigejos*, where microorganisms (especially fungi) transport N from the surrounding soil into the hardly decomposable litter which support the utilization of more accessible organic C in marcescent litter. It is because the C:N ratio of microorganism bodies is not so variable as plant tissues, but much lower, ordinarily falling between 5:1 and 10:1 (Brady and Weil 1996). Changes in nutrient inputs to soil can influence the composition and the activity of the litter and soil microbial community (Ritchie et al. 1998). Change of litter N:P by addition of N may enhance soil N availability, leading to a shift in decomposer community to a less efficient microflora (Mo et al. 2006). Litter fall which is hardly decomposable have low participation of the soil fauna in decomposition and leads to the formation of a moor type of humus (Frouz et al. 2001, 2008, 2014).

The process of N mineralization involves the entire food web, not just the saprophytic bacteria and fungi. But once easily decomposable components run out, microbial biomass begins to die off, the N is immobilized and it is not available to plants (Brady and Weil 1996). Additions of N may also suppress the growth of fungi, which supply the vegetation with nutrients (Berg and Matzner 1997). The low pH of the litter eliminates bacterial

decomposers but support fungi decomposers (Frouz et al. 2014). Litter with a high C:N (difficult to decomposed) suppresses the activity of soil biota, litter accumulates on the soil surface and especially fungi are involved in decomposition (Ponge 2003). But on the contrary, at sites with easily decomposable litter soil biota mix plant litter into the soil profile (Lavelle et al. 1997; Ponge 2003).

4.6. Nutrient cycling

The most important for the function of individual forest ecosystems is the transfer of elements between plant and soil and their repeated use in plant metabolism within one ecosystem. Dynamics of nutrient cycling in the forest ecosystem can be expressed as nutrient uptake by plants, producing biomass, reallocation of nutrients from senescent plant biomass (foliage, fine roots, branches), litter fall, litter decomposition by decomposers, mineralization, immobilization, nutrient uptake and nutrient leaching (Brady and Weil 1996). Nutrient cycling is not always regular but some periods (accumulation of organic matter) may stagnate and cycles may temporarily or completely stop (Duvigneaud 1974). The main force which influences nutrient cycling is solar energy. The important parts of the whole nutrient cycle are individual cycles of water, C, P, S, K, Ca and Mg. Disrupting of some part of the cycle can lead to a reduction in productivity or to a collapse of the ecosystem functions (Rastetter et al. 1991; Manzoni et al. 2010).

4.6.1. Nutrient input into the soil

Nutrients enter the soil in several ways. The most important long-term source for nutrients is rock weathering and organic matter (Chapter 4.4.1. Plant litter). This is true mainly for nutrients such as Ca, Mg, K, Na, Fe, Al, P, Si. The main source for C, H, N is in the atmosphere and the decomposition of organic matter. The second input of large quantities of nutrients is added from the atmosphere as atmospheric deposition through the precipitation, fog, canopy and stemflow leaching or by biological processes (N₂ fixation by soil biota). C is absorbed by way of photosynthesis. N is produced by lightning and precipitation. S, Cl, Ca and Na is deposited by precipitation (Brady and Weil 1996; Pidwirny 2006).

Atmospheric input may substantially affect biochemical cycling of the ecosystem. With annual N input ranging from 15 to 50 kg ha⁻¹ in central Europe, the amounts added to the soil of nutrient-poor forest can far exceed the annual contribution of the only natural source, which is N₂ fixation (Berg and Matzner 1997; Holub et al. 2012). Most of the studies are

focused on N deposition and its influence on ecosystems (e.g. Berg and Matzner 1997; Köchy and Wilson 1997; Macdonald et al. 2002; Sun and Liu 2007; de Vries et al. 2009; Sardans et al. 2016b; Xia et al. 2017, 2018). It is already known that atmospheric N deposition increases forest C sequestration across broad parts of the Northern Hemisphere (Xia et al. 2017). It is related to slower organic matter decomposition and greater soil C accumulation which could contribute to this increase in C sequestration and alter the activity of microbial community (Aerts 1997; Deforest et al. 2004; Xia et al. 2017, 2018). In the study of Xia et al. (2017), N deposition tends to decrease lignin degradation in litter fall and to slow down fine root mass loss. Also increase in N deposition can increase the immobilization of P in the soils of forested areas through the high uptake of P by the soil food web (Sardans et al. 2016a) and several studies have shown that high and continuous N loadings increase P limitation (Boxman et al. 1994; Gradowski and Thomas 2008; Sardans et al. 2016a). During long-term N deposition, its concentration in leaves and litter rises, and tree growth can also be positively affected by this process (Sardans et al. 2016a).

In forest ecosystems, throughfall and stemflow are an important source of nutrients, but also a source of higher acidity (Carnol and Bazgir 2013). Large part of nutrients is caught by and released from the canopy, foliage, branches and stem bark to the surrounding of the bases of trees (Cape et al. 1991). The proportion of precipitation and input of nutrient is strongly influenced by the tree species, density of the tree crowns, presence or absence of foliage and meteorological factors controlling the evaporation (Cape et al. 1991). Stemflow is important in depositing large amounts of water and solutes because solutes in stemflow waters are usually more concentrated than in throughfall (Ovington 1954; Cape et al. 1991). Higher N deposition is responsible for increasing of N concentrations in litter fall which lead to changes in concentrations of other nutrients as well. For example, concentrations of P and S in soil organic matter usually increase, whereas those of Mn and Ca decrease (Berg and Matzner 1997). Also in **Publication 4** higher input of N mostly by N₂ fixation and by litterfall with low C:N supported higher leaching of other essential nutrients (Ca, Mg, K, P) from the soil system at alder reclamation. For Ca and Mg, dry deposition is more important than canopy leaching but still, most of the input of Ca and Mg comes into the soil with plant litter (Knops et al. 2002).

4.6.2. Nutrient leaching

Nutrient leaching is an important process of nutrient loss and it is known that leaching from the soil is a consequence of increased N input into the ecosystem (Aber et al. 1989; Lehmann

and Schroth 2003). Leaching is initiated by water flowing vertically through the soil which transports nutrients in solution down the soil profile. Many nutrients can be completely lost from the soil profile and get into the groundwater and then be transported into rivers, dumps, and ponds. The leaching process is generally higher in disturbed ecosystems or in ecosystems without efficient nutrient cycling (Brady and Weil 1996; Pidwirny 2006). Mineralization of nutrients subsequently accelerates nitrification and denitrification processes. In the internal cycle N, a breakpoint occurs when the ecosystem is saturated with N and it begins to leach out of the ecosystem (Gundersen et al. 1998). Saturation by N leads to an imbalance in the nutritional system, acidification of the soil and decay of the forest (Brady and Weil 1996; Hogberg et al. 2001; Vitousek et al. 2010; Xia et al. 2017). In a Norwegian study by Dise and Wright (1995), N-deposition thresholds were determined above which N was leached out of the ecosystem in a certain amount. Below $10 \text{ kg ha}^{-1} \text{ year}^{-1}$, there was no increased leaching of N from the ecosystem. Significant nutrient leaching was found at sites with a deposition value of $25 \text{ kg N ha}^{-1} \text{ year}^{-1}$. Also, Tieterna et al. (1998) recorded significant NO_3^- losses in localities with increased N deposition and, on the other hand, the released NO_3^- decreased when deposition decreased. Elevated NO_3^- leaching also showed a relationship with soil pH, with high rates of NO_3^- leaching observed at sites with a $\text{pH} < 4.5$ or N input $> 30 \text{ kg N ha}^{-1} \text{ y}^{-1}$ (McDonald et al. 2002).

4.7. The consequence for soil development

Soil is one of the basic non-renewable natural resources that perform many important functions. It is a dynamic system that is constantly evolving and transforming. The pedogenic process is influenced by many factors, such as parent rock, climate, relief, time, organisms and human activities. The properties of upper soil horizons are mainly influenced by the composition, growth, and development of vegetation at the site (Bradshaw 1997). But in **Publication 1** it has been suggested that the effect of tree species on soil development is substantially mediated by soil fauna activity and especially by earthworm bioturbation. Moreover, bioturbation has effect not only on the biomass and activity of microorganisms but also on the composition of the soil biota and other soil fauna. In course of soil development, plants have an important role in protecting the soil surface from erosion and allowing the accumulation of fine particles. But plants also cause the accumulation of nutrients in an available form and control stocks of organic matter in forest floor (Bradshaw 1997; Frouz et al. 2011b; Frouz et al. 2014; **Publication 1**). Generally, the cover of moss, herb and woody

species layers increased with succession age, but the herb layer temporarily decline at the time when woody vegetation formed a closed canopy (15 to 25 year of succession) (Frouz et al. 2014). Trees are dominant factor ecosystems and affect many ecosystem properties including soil. Changes in soil properties are likely to change future vegetation development on the site (Frouz et al. 2008; **Publication 1**). Trees have both direct and indirect effects on soil. Direct effects result from root growth, which supports the formation of soil pores and soil aggregates (Angers and Caron 1998), and indirect by the production of plant litter and, exudates and throughfall, which greatly affects soil organic matter content, chemistry, and soil structure (Brady and Weil 1996; Prescott et al. 1999; Carnol and Bazgir 2013). But in the study, Reich et al. (1997) argue that the mineralization and decomposition of organic litter input depend more on soil quality than on the species composition of vegetation. Moreover, soil development is enhanced by the input of high-quality litter (litter with a low C:N, easily decomposable) which causes the consequent increase in the activity of soil fauna (Frouz et al. 2006, 2013b) and a dense layer of herbaceous vegetation (Frouz et al. 2008; Mudrak et al. 2010).

4.8. The consequence for restoration practice

During open-cast coal mining, a large amount of spoil material is excavated and deposited in heaps. This material typically contains a low amount of recent organic matter and display low soil biological activity (Frouz et al. 2001). The reclamation of such post-mining sites is dependent on the restoration of their ecological functions. This can be achieved by controlled reclamation by planting grass or forest or by spontaneous succession. The selection of woody species for afforestation plays a key role in the succession of reclaimed forest ecosystems (Bradshaw 1997; Wos et al. 2018). Woody biomass is important from an economic perspective but also from an environmental perspective. Particularly, the forest that produces wood also provides many ecosystem services including C sequestration, which is correlated with tree biomass (Barford et al. 2001; Frouz et al. 2013b, 2015a). The decision on tree species used for afforestation might shorten the period needed for soil restoration and achievement of sustainability of novel ecosystems (Horodecki and Jagodzinski 2017). However, differences between species in nutrient return to the forest floor might evolve during stand development and these differences are most important for soil fertility during its early stages. In early stages of tree growth, trees rely mostly on soil for their nutrient

requirements, so that soil enrichment is particularly important during early stand development for avoiding deficiency of nutrients for its grow (Carnol and Bazgir 2013).

During spontaneous succession, species with highly specific leaf areas, low leaf dry matter contents, high leaf N contents, and low C:N ratios, are progressively replaced by species with the opposite characteristics (Cortez et al. 2007). As consequence, the litter of early succession plant species is decomposed faster than that of late succession species (Cortez et al. 2007). The productivity of forest ecosystems is closely related to the availability and demand for nutrients, especially N and P (Sharma 1993; Vares et al. 2004). Using N₂ fixing plants is often recommended in restoration practice for faster recovery of soil and namely the N pool which is essential for ecosystem functioning (Manzoni et al. 2010; Mudrak et al. 2010; Macdonald et al. 2015; Swiatek et al. 2019). However, N₂ fixing plants have some disadvantages (Frouz et al. 2015; **Publication 4**). Furthermore, addition of N in the ecosystems leads to more open biogeochemical cycling which may cause higher nutrient loss from the system, especially in soil with nutrient poor stock. In alder reclamation, soil N concentration increased with stand age, also increase the soil organic matter, initial high pH decreases but also decreases P concentration (Kuznetsova et al. 2011). This decrease is cause by a loss of P through leaching but also by growth of plants, which bind P in their biomass (Frouz et al. 2014). Also, in **Publication 4** were found higher leaching of basic nutrients (Ca, Mg, K) and P from the ecosystems under alder stands, in comparison to succession sites where most nutrients cycled through the plants. But in the study (Uri et al. 2002b) were found increase P availability in soil under alder reclamation by the activity of its roots and associated microbial communities. So, the right chosen of reclamation practice is dependent on the soil properties. For example, planting rowan (*Sorbus*) as accompanying species may, therefore, represent an interesting management option for improving soil chemistry on nutrient poor sites at reclamation areas through Ca, Mg and K nutrient return via rowan litter fall (Carnol and Bazgir 2013).

4.9. Conclusion

Ecological stoichiometry seeks to understand how the balance between multiple chemical elements in organisms and their environmental controls. Ecosystem processes are strongly influenced by the stoichiometric ratio (C:N:P) which is highly variable in terrestrial ecosystems. Understanding of stoichiometry of plant-soil dynamics allows predicting future development of an ecosystem. Different plant species have a different strategy in nutrient dynamics and allocation of nutrients in plant biomass and plant litter. The quantitative traits

of leaf litter are important predictors of decomposition and decomposition rates which increase with greater nutrient availability in the forest ecosystems. At the ecosystem level, litter quantitative traits are most often related to the physical and chemical characteristics of the litter, for example leaf toughness and leaf mass per unit area, C:N ratio, lignin, and total phenolics. Apart from plant species composition, also other factors such as the soil itself (chemical and physical parameters), soil biota and soil moisture are important for soil development. The decomposition of plant material is an important component in the study of terrestrial ecosystems because of its critical role in nutrient cycling. The analysis of litter quantitative traits and decomposition is highly important for the understanding of nutrient cycling in forest ecosystems. The process of decomposition is influenced by several factors such as the main chemical composition of plant litter (e.g. C:N ratio, content of lignin), water availability and soil biota. Nutrient-poor ecosystems are dominated by plants with a more conservative nutrient strategy. In these ecosystems, plants use nutrients more efficiently and thus produce litter of lower quality which is characterized by higher lignin content and higher C:N ratio. On the other hand, plants growing at nutrient-rich ecosystems produce a litter with higher concentration of N which decomposed faster. Faster mineralization increases the rate of nutrient leaching from the ecosystem and can cause acidification and eutrophication of the ecosystem. By studying the role of litter quantitative traits on decomposition and nutrient cycling in forest ecosystems provide valuable insight into how quantitative traits influence ecosystem nutrient dynamics. This knowledge is important in the decision about future restoration practices in disturbed areas after coal mining.

5. References

- Aber J, Driscoll CT (1997) Effects of land use, climate variation, and N deposition on N cycling and C storage in northern hardwood forests. *Global Biogeochem Cycles* 11:639–648.
- Aber JD, Nadelhoffer KJ, Steudler P, Melillo JM (1989) Nitrogen Saturation in Northern Forest Ecosystems. *Bioscience* 39:378–386.
- Aber JD, Wessman CA, Peterson DL, Melillo JM, Fownes JH (1990) Remote sensing of litter and soil organic matter decomposition in forest ecosystems. In *Remote sensing of biosphere functioning*. Springer 87–103.
- Ackerly D (2004) Functional Strategies of Chaparral Shrubs in Relation to Seasonal Water Deficit and Disturbance. *Ecol Monogr* 74:25–44.
- Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79:439–449.
- Aerts R (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? *J Ecol* 84:597–608.
- Aerts R, Chapin FS (1999) The Mineral Nutrition of Wild Plants Revisited: A Re-evaluation of Processes and Patterns. *Adv Ecol Res* 30:1–67.
- Anderson JM (1973) The Breakdown and Decomposition of Sweet Chestnut (*Castanea sativa* Mill.) and Beech (*Fagus sylvatica* L.) Leaf Litter in Two Deciduous Woodland Soils. I. Breakdown, Leaching and Decomposition. *Oecologia* 12:251–274.
- Angers DA, Caron J (1998) Plant-induced changes in soil structure: Processes and feedbacks. *Biogeochemistry* 42:55–72.
- Angst Š, Cajthaml T, Angst G, et al (2017) Retention of dead standing plant biomass (marcescence) increases subsequent litter decomposition in the soil organic layer. *Plant Soil*.
- Angst Š, Harantová L, Baldrian P, et al (2019) Tree species identity alters decomposition of understory litter and associated microbial communities: a case study. *Biol Fertil Soils*.
- Attiwill BM, Adams MA (1993) Nutrient cycling in forests. *New Phytol* 124:561–582.
- Austin AT, Ballaré CL (2010) Dual role of lignin in plant litter decomposition in terrestrial ecosystems. *Proc Natl Acad Sci U S A* 107:4618–4622.
- Barford CC, Wofsy SC, Goulden ML, et al (2001) Factors Controlling Long- and Short-Term Sequestration of Atmospheric CO₂ in a Mid-latitude Forest. *Science* (80-) 294:1688–1692.
- Begon M, Harper JL, Townsend CR (1996) *Ecology: Individuals, Populations, Communities*. Third Ed. Blackwell Science Ltd., Oxford, United Kingdom, 247pp.
- Berg B (2000) Litter decomposition and organic matter turnover in northern forest soils. *For Ecol Manage* 133:13–22.
- Berg B, Matzner E (1997) Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. *Environ. Rev.* 5:1–25.
- Berg B, McClaugherty C (1989) Nitrogen release from litter in relation to the disappearance of lignin. *Can J Bot* 67:1148–1156.
- Berg B, Staaf H, Wessén B (1987) Decomposition and nutrient release in needle litter from nitrogen-fertilized scots pine (*Pinus sylvestris*) stands. *Scand J For Res* 2:399–415.
- Berner LT, Law BE (2016) Plant traits, productivity, biomass and soil properties from forest sites in the Pacific Northwest, 1999-2014. *Sci Data* 3:1–14.

- Binkley D, Sollins P, Bell R, et al (1992) Biogeochemistry of Adjacent Conifer and Alder-Conifer Stands. *Ecology* 73:2022–2033.
- Bjorkman AD, Myers-Smith IH, Elmendorf SC, et al (2018) Plant functional trait change across a warming tundra biome. *Nature* 562:57–62.
- Boxman AW, VanDijk FG, Roelofs JGM (1994) Soil and vegetation responses to decreased atmospheric nitrogen and sulphur inputs into a Scots pine stand in the Netherlands. *For Ecol Manage* 68:39–45.
- Bradshaw A (1997) Restoration of mined lands—using natural processes. *Ecol Eng* 8:255–269.
- Brady NC, Weil RR (1996) *The nature and Properties of Soils*. Upper Saddle River: Pearson Prentice Hall.
- Bray, J.R. and Gorham, E., 1964. Litter production in forests of the world. In *Advances in ecological research* (Vol. 2, pp. 101-157). Academic Press.
- Campanella M V, Bertiller MB (2008) Plant phenology , leaf traits and leaf litterfall of contrasting life forms in the arid Patagonian Monte , Argentina. *J Veg Sci* 75–85.
- Campo J, Maass JM, Jaramillo VJ, Yrizar AM (2000) Calcium , Potassium , and Magnesium Cycling in a Mexican Tropical Dry Forest Ecosystem. *Biogeochemistry* 49:21–36.
- Cape JN, Brown AHF, Robertson SMC, et al (1991) Interspecies comparisons of throughfall and stemflow at three sites in northern Britain. *For Ecol Manage* 46:165–177.
- Carnol M, Bazgir M (2013) Nutrient return to the forest floor through litter and throughfall under 7 forest species after conversion from Norway spruce. *For Ecol Manage* 309:66–75.
- Chaoui HI, Zibilske LM, Ohno T (2003) Effects of earthworm casts and compost on soil microbial activity and plant nutrient availability. *Soil Biol Biochem* 35:295–302.
- Chapin F, Vitousek P, Cleve K (1986) The Nature of Nutrient Limitation in Plant Communities. *Am Nat* 127:48–58
- Chapin FS, Bloom AJ, Field CB, Waring RH (1987) Plant responses to multiple environmental factors. *Bioscience* 37:49–57.
- Chapin FS, Zavaleta ES, Eviner VT, et al (2000) Consequences of changing biodiversity. *Nature* 405:234–242.
- Cleveland CC, Liptzin D (2007) C:N:P stoichiometry in soil: Is there a “Redfield ratio” for the microbial biomass? *Biogeochemistry* 85:235–252.
- Cornelissen JHC, Lang SI, Soudzilovskaia NA, During HJ (2007) Comparative cryptogam ecology: A review of bryophyte and lichen traits that drive biogeochemistry. *Ann Bot* 99:987–1001.
- Cornelissen JHC, Werger MJA, Castro-Díez P, et al (1997) Foliar Nutrients in Relation to Growth, allocation and Leaf Traits in Seedlings of a Wide Range of Woody Plant Species and Types. *Oecologia* 111:460–469.
- Cortez J, Garnier E, Pérez-Harguindeguy N, et al (2007) Plant traits, litter quality and decomposition in a Mediterranean old-field succession. *Plant Soil* 296:19–34.
- Cunningham SA, Summerhayes B, Westoby M (1999) Evolutionary Divergences in Leaf Structure and Chemistry , Comparing Rainfall and Soil Nutrient Gradients. *Ecol Monogr* 69:569–588.
- Cusack DF, Markesteijn L, Condit R, et al (2018) Soil carbon stocks across tropical forests of Panama regulated by base cation effects on fine roots. *Biogeochemistry* 137:253–266.
- de Vries W, Solberg S, Dobbertin M, et al (2009) The impact of nitrogen deposition on

- carbon sequestration by European forests and heathlands. *For Ecol Manage* 258:1814–1823.
- Deforest JL, Zak DR, Pregitzer KS, Burton AJ (2004) Atmospheric Nitrate Deposition , Microbial Community Composition , and Enzyme Activity in Northern Hardwood Forests. *Soil Sci Soc Am J* 68:132–138.
- Dise NB, Wright RF (1995) Nitrogen leaching from European forests in relation to nitrogen deposition. *For Ecol Manage* 71:153–161.
- Dobson AM, Blossey B, Richardson JB (2017) Invasive earthworms change nutrient availability and uptake by forest understory plants. *Plant Soil* 421:175–190.
- Domenach AM, Moiroud A, Monrozier LJ (1994) Leaf carbon and nitrogen constituents of some actinorhizal tree species. *Soil Biol Biochem* 26:649–653.
- Dornbush ME, Isenhardt TM, Raich JW (2002) Quantifying Fine-Root Decomposition : An Alternative to Buried Litterbags. *Ecology* 83:2985–2990.
- Duvigneaud P (1974) A synthesis of ecology: populations, communities, ecosystems, biosphere and noosphere. Doin. 296pp.
- Edwards CA, Bohlen PJ (1996) Biology and ecology of earthworms (Vol. 3). Springer Science & Business Media.
- Ekblad A, Nordgren A (2002) Is growth of soil microorganisms in boreal forests limited by carbon or nitrogen availability? *Plant Soil* 242:115–122.
- Elser JJ, Bracken MES, Cleland EE, et al (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol Lett* 10:1135–1142.
- Elser JJ, Dobberfuhl DR, MacKay NA, Schampel JH (1996) Organism size, life history, and N:P stoichiometry: Toward a unified view of cellular and ecosystem processes. *Bioscience* 46:674–684.
- Facelli JM, Pickett STA (1991) Plant Litter : Its Dynamics and Effects on Plant Community Structure. *Bot Rev* 57:1–32.
- Fiala K, Tůma I, Holub P, Jandák J (2005) The role of *Calamagrostis* communities in preventing soil acidification and base cation losses in a deforested mountain area affected by acid deposition. *Plant Soil* 268:35–49.
- Field AC, Merino J, Mooney HA (1983) Compromises between Water-Use Efficiency and Nitrogen-Use Efficiency in Five Species of California Evergreens. *Oec* 60:384–389.
- Field C (1983) Allocation Leaf Nitrogen for the Maximization of Carbon Gain: Leaf Age as a Control on the Allocation Program. *Oecologia* 56:341–347.
- Field CB, Chapin III SF, Matson PA, Mooney HA (2016) Responses of Terrestrial Ecosystems to the Changing Atmosphere : A Resource-Based Approach. *Annu Rev Ecol Syst* 23:201–235.
- Flaig W (1964) Effects of micro-organisms in the transformation of lignin to humic substances. *Geochimica et Cosmochimica Acta*, 28(10-11), 1523-1535.
- Freschet GT, Cornwell, W K, Wardle DA, et al (2013) Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. *J Ecol* 101:943–952.
- Frouz et al. (2014): Soil Biota and Ecosystem Development in Post Mining Sites. CRC press. 316pp.
- Frouz J, Cajthaml T, Mudrak O (2011a) The effect of lignin photodegradation on decomposability of *Calamagrostis epigeios* grass litter. *Biodegradation* 22:1247–1254.
- Frouz J, Dvorscık P, Vavrova A, et al (2015) Development of canopy cover and woody

- vegetation biomass on reclaimed and unreclaimed post-mining sites. *Ecol Eng* 84:233–239.
- Frouz J, Elhottová D, Kuráž V, Šourková M (2006) Effects of soil macrofauna on other soil biota and soil formation in reclaimed and unreclaimed post mining sites: Results of a field microcosm experiment. *Appl Soil Ecol* 33:308–320.
- Frouz J, Elhottová D, Pižl V, et al (2007a) The effect of litter quality and soil faunal composition on organic matter dynamics in post-mining soil: A laboratory study. *Appl Soil Ecol* 37:72–80.
- Frouz J, Kalčík J, Velichová V (2011b) Factors causing spatial heterogeneity in soil properties, plant cover, and soil fauna in a non-reclaimed post-mining site. *Ecol Eng* 37:1910–1913.
- Frouz J, Keplin B, Pižl V, et al (2001) Soil biota and upper soil layer development in two contrasting post-mining chronosequences. *Ecol Eng* 17:275–284.
- Frouz J, Pižl V, Tajovský K (2007b) The effect of earthworms and other saprophagous macrofauna on soil microstructure in reclaimed and un-reclaimed post-mining sites in Central Europe. *Eur J Soil Biol* 43:
- Frouz J, Prach K, Pižl V, et al (2008) Interactions between soil development, vegetation and soil fauna during spontaneous succession in post mining sites. *Eur J Soil Biol* 44:109–121.
- Fujii S, Makita N, Mori AS, Takeda H (2016) A stronger coordination of litter decomposability between leaves and fine roots for woody species in a warmer region. *Trees - Struct Funct* 30:395–404.
- Giovannoni SJ, Stingl U (2005) Molecular diversity and ecology of microbial plankton. *Nature* 437:343–348.
- Gloser V (2005) The consequences of lower nitrogen availability in autumn for internal nitrogen reserves and spring growth of *Calamagrostis epigejos*. *Plant Ecol* 179:119–126.
- Gordon WS, Jackson RB (2000) Nutrient Concentrations in Fine Roots. *Ecology* 81:275–280.
- Gradowski T, Thomas SC (2008) Responses of *Acer saccharum* canopy trees and saplings to P, K and lime additions under high N deposition. *Tree Physiol* 28:173–185.
- Graneli E, Wallstrom K, Larsson U, et al (1990) Nutrient Limitation of Primary Production in the Baltic Sea Area. *Ambio* 19:142–151.
- Gundersen P, Callesen I, de Vries W (1998) Nitrate leaching in forest ecosystems is controlled by forest floor C/N ratio. *Environ Pollut* 102:403–407.
- Güsewell S & Koerselman W (2002) Variation in nitrogen and phosphorus concentrations of wetland plants. *Perspect Plant Ecol Evol Syst* 5:37–61.
- Güsewell S (2004) N : P ratios in terrestrial plants : variation significance. *New Phytol* 164:243–266.
- Heal O W (1997) Plant litter quality and decomposition: an historical overview. *Driven by nature, plant litter quality and decomposition*.
- Heilman P, Norby RJ (1998) Nutrient cycling and fertility management in temperate short rotation forest systems. *Biomass and Bioenergy* 14:361–370.
- Hermans C, Hammond JP, White PJ, Verbruggen N (2006) How do plants respond to nutrient shortage by biomass allocation? *Trends Plant Sci* 11:610–617.
- Hessen DO, Ågren GI, Anderson TR, et al (2004) Carbon Sequestration in Ecosystems : The Role of Stoichiometry. 85:1179–1192.
- Hobbie SE, Oleksyn J, Eissenstat DM, Reich PB (2010) Fine root decomposition rates do not

- mirror those of leaf litter among temperate tree species. *Oecologia* 162:505–513.
- Hogberg P, Nordgren A, Buchmann N, et al (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411:789–792.
- Högberg P, Read DJ (2006) Towards a more plant physiological perspective on soil ecology. *Trends Ecol Evol* 21:548–554.
- Holub P, Tůma I, Fiala K (2012) The effect of nitrogen addition on biomass production and competition in three expansive tall grasses. *Environ Pollut* 170:211–216.
- Horodecki P, Jagodziński AM (2017) Tree species effects on litter decomposition in pure stands on afforested post-mining sites. *For Ecol Manage* 406:1–11.
- Ingestad T (1981) Nutrition and growth of birch and grey alder seedlings in low conductivity solutions and at varied relative rates of nutrient addition. *Physiol Plant* 52:454–466
- Johansson T (2000) Biomass equations for determining fractions of common and grey alders growing on abandoned farmland and some practical implications. *Biomass and Bioenergy* 18:147–159.
- Kavanová M, Gloser V (2005) The use of internal nitrogen stores in the rhizomatous grass *Calamagrostis epigejos* during regrowth after defoliation. *Ann Bot* 95:457–463.
- Killingbeck KT (1996) Nutrients in Senesced Leaves: Keys to the Search for Potential Resorption and Resorption Proficiency. *Ecology* 77:1716–1727.
- Klimešová J, Latzel V, de Bello F, van Groenendael JM (2008) Plant functional traits in studies of vegetation changes in response to grazing and mowing: Towards a use of more specific traits. *Preslia* 80:245–253.
- Knops JMH, Bradley KL, Wedin DA (2002) Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecol Lett* 5:454–466.
- Köchy M, Wilson SD (1997) Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass prairie. *Ecology* 78:732–739.
- Kurokawa H, Peltzer DA, Wardle DA (2010) Plant traits, leaf palatability and litter decomposability for co-occurring woody species differing in invasion status and nitrogen fixation ability. *Funct Ecol* 24:513–523.
- Kuznetsova T, Lukjanova A, Mandre M, Lohmus K (2011) Aboveground biomass and nutrient accumulation dynamics in young black alder, silver birch and Scots pine plantations on reclaimed oil shale mining areas in Estonia. *For Ecol Manage* 262:56–64.
- Kuzyakov Y (2010) Priming effects: Interactions between living and dead organic matter. *Soil Biol Biochem* 42:1363–1371.
- Larcher W (2003) *Physiological plant ecology: ecophysiology and stress physiology of functional groups*. Springer Science & Business Media.
- Lasota J, Błońska E, Piaszczyk W, Wiecheć M (2018) How the deadwood of different tree species in various stages of decomposition affected nutrient dynamics? *J Soils Sediments* 18:2759–2769.
- Lavelle P, Bignell D, Lepage M, Wolters V, Roger P, Ineson POWH, et al. (1997) Soil function in a changing world: the role of invertebrate ecosystem engineers. *Eur J of Soil Biol (France)*. 33(4):159–193.
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct Ecol* 16:545–556
- Lehmann J, Schroth G (2003) Nutrient Leaching. *Trees, Crop Soil Fertil* 151–166.
- Lloyd J., Taylor JA (1994) On the Temperature Dependence of Soil Respiration. *Funct Ecol* 8:315–323.

- Lodhiyal LS, Singh RP, Singh SP (1995) Structure and function of an age series of poplar plantations in central Himalaya: Dry matter dynamics. *Ann. Bot.* 76:191–199.
- Macdonald JA, Dise NB, Matzner E, et al (2002) Nitrogen input together with ecosystem nitrogen enrichment predict nitrate leaching from European forests. *Glob Chnage Biol* 8:1028–1033.
- Macdonald SE, Landhäusser SM, Skousen J, et al (2015) Forest restoration following surface mining disturbance: challenges and solutions. *New For* 46:703–732.
- Manzoni S, Trofymow J a, Jackson RB, et al (2010) Stoichiometric controls on carbon, nitrogen, and phosphorus dynamics in decomposing litter. *Ecol Monogr* 80:89–106.
- Martiny AC, Pham CTA, Primeau FW, et al (2013) Strong latitudinal patterns in the elemental ratios of marine plankton and organic matter. *Nat Geosci* 6:279–283.
- McLaugherty ACA, Aber JD, Melillo JM (1984) Decomposition Dynamics of Fine Roots in Forested Ecosystems. *Oikos* 42:378–386.
- McDonald EP, Erickson JE, Kruger EL (2002) Research note: Can decreased transpiration limit plant nitrogen acquisition in elevated CO₂? *Functional Plant Biology*, 29(9), 1115–1120.
- McGroddy ME, Daufresne T, Hedin OL (2004) Scaling of C : N : P Stoichiometry in Forests Worldwide : Implications of Terrestrial Redfield- Type Ratios. *Ecology* 85:2390–2401.
- Meier CL, Bowman WD (2008) Links between plant litter chemistry, species diversity, and below-ground ecosystem function. *Proc Natl Acad Sci* 105:19780–19785.
- Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and Lignin Control of Hardwood Leaf Litter Decomposition Dynamics. *Ecology* 63:621–626.
- Mikola P (1958) Liberation of nitrogen from alder leaf litter. *Acta For Fenn* 67:1–9.
- Miletić Z, Knežević M, Stajić S, et al (2012) Effect of European black alder monocultures on the characteristics of reclaimed mine soil. *Int J Environ Res* 6:703–710.
- Mo J, Brown S, Xue J, Fang Y, Li Z (2006) Response of litter decomposition to simulated N deposition in disturbed, rehabilitated and mature forests in subtropical China. *Plant and soil*, 282(1-2): 135-151.
- Moradi J, Mudrák O, Kukla J, et al (2017) Variations in soil chemical properties, microbial biomass, and faunal populations as related to plant functional traits, patch types, and successional stages at Sokolov post-mining site - A case study. *Eur J Soil Biol* 83:58–64.
- Mudrák O, Frouz J (2018) Earthworms increase plant biomass more in soil with no earthworm legacy than in earthworm-mediated soil, and favour late successional species in competition. *Funct Ecol* 32:626–635.
- Mudrák O, Frouz J, Velichová V (2010) Understorey vegetation in reclaimed and unreclaimed post-mining forest stands. *Ecol Eng* 36:783–790.
- Osnas JLD, Lichstein JW, Reich PB, Pacala SW (2013) Global Leaf Trait Relationships: Mass, Area, and the Leaf Economics Spectrum. *Science* (80-) 340:741–745.
- Ovington AJD (1954) Studies of the Development of Woodland Conditions Under Different Trees. *J Ecol* 42:71–80.
- Paris Q (2006) The von Liebig Hypothesis. *Am J Agric Econ* 74:1019.
- Pastor J, Aber J, McLaugherty C, Mellilo J (1984) Aboveground Production and N and P Cycling Along a Nitrogen Mineralization Gradient on Blackhawk Island, Wisconsin. *Ecology* 65:256–268.
- Pidwirny M (2006) Biogeochemical cycling: inputs and outputs of nutrients to ecosystems.

Fundamentals of Physical Geography. <http://www.physicalgeography.net/fundamentals/9p.html>.

- Ponge JF (2003) Humus forms in terrestrial ecosystems : a framework to biodiversity. *Soil Biol Biochem* 35:935–945.
- Poorter H, Navas ML (2003) Plant growth and competition at elevated Co₂: On winners, losers and functional groups. *New Phytol* 157:175–198.
- Poorter L, Bongers F (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* 87:1733–43
- Prescott CE (2010) Litter decomposition: What controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry* 101:133–149.
- Prescott CE, Chappell HN, Vesterdal L (2000) Nitrogen Turnover in Forest Floors of Coastal Douglas-Fir at Sites Differing in Soil Nitrogen Capital. *Ecology* 81:1878–1886.
- Prescott CE, Kabzems R, Zabek LM (1999) Effects of fertilization on decomposition rate of *Populus tremuloides* foliar litter in a boreal forest. *Can J For Res* 397:393–397.
- Raherison SM, Grouzis M (2005) Plant biomass, nutrient concentration and nutrient storage in a tropical dry forest in the south-west of Madagascar. *Plant Ecol* 180:33–45.
- Rahman MM, Tsukamoto J, Tokumoto Y, Shuvo MAR (2013) The Role of Quantitative Traits of Leaf Litter on Decomposition and Nutrient Cycling of the Forest Ecosystems. *J For Environ Sci* 29:38–48.
- Rastetter EB, Ryan MG, Shaver GR, et al (1991) A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO₂, climate, and N deposition. *Tree Physiol* 9:101–126.
- Redfield AC (1958) The biological control of chemical factors in the environment. *Am Sci* 46:205–221.
- Reekie EG, Bazzaz FA (1987) Reproductive Effort in Plants 1. Carbon Allocation to Reproduction. *Am Nat* 129:876–896.
- Reich PB, Grigal DF, Aber JD, Gower ST (1997) Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* 78:335–347.
- Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc Natl Acad Sci U S A* 101:11001–6.
- Reich PB, Oleksyn J, Tilman GD (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc Natl Acad Sci* 101:11001–11006.
- Reich PB, Wright IJ, Craine JM, et al (2003) The Evolution of Plant Functional Variation : Traits, Spectra, and Strategies Source : The University of. *Int J Plant Sci* 164:143–164.
- Reiners WA (1986) Complementary Models for Ecosystems. *Am Nat* 127:59–73.
- Ritchie ME, Tilman D, Knops JMH (1998) Herbivore Effects on Plant and Nitrogen Dynamics in Oak Savanna. *Ecology* 79:165–177.
- Robertson GP (1982) Regional nitrogen budgets: Approaches and problems. *Plant Soil* 67:73–79.
- Rusek J (2000) Soil invertebrate species diversity in natural and disturbed environments. Invertebrates as webmasters in ecosystems, 233-252.
- Rustad LE (1994) Element Dynamics along a Decay Continuum in a Red Spruce Ecosystem in Maine , USA. *Ecology* 75:867–879.
- Santiago LS (2007) Extending the Leaf Economics Spectrum To Decomposition : Evidence From a Tropical Forest. *Ecology* 88:1126–1131.
- Sardans J, Alonso R, Carnicer J, et al (2016a) Factors influencing the foliar elemental

- composition and stoichiometry in forest trees in Spain. *Perspect Plant Ecol Evol Syst* 18:52–69.
- Sardans J, Alonso R, Janssens IA, et al (2016b) Foliar and soil concentrations and stoichiometry of nitrogen and phosphorous across European *Pinus sylvestris* forests: Relationships with climate, N deposition and tree growth. *Funct Ecol* 30:676–689.
- Sharma E (1993) Nutrient Dynamics in Himalayan Alder Plantations. *Ann. Bot.* 72:329–336
- Shaver GR, Chapin FS (1991) Production : Biomass Relationships and Element Cycling in Contrasting Arctic Vegetation Types. *Ecol Monogr* 61:1–31.
- Sinsabaugh RL, Lauber CL, Weintraub MN, et al (2008) Stoichiometry of soil enzyme activity at global scale. *Ecol Lett* 11:1252–1264.
- Sohrt J, Herschbach C, Weiler M (2018) Foliar P- but not N resorption efficiency depends on the P-concentration and the N:P ratio in trees of temperate forests. *Trees - Struct Funct* 32:1443–1455.
- StAAF H, Berg B (1981) Plant litter input to soil. *Ecol Bull* 33:147–162
- Sturner RW, Elser JJ (2002) *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere.* 439pp.
- Stott DE, Elliott LF, Papendick RI, Cambell GS (1986) Low temperature or low water potential effects on the microbial decomposition of wheat residue. *Soil Biol Biochem* 18:577–582.
- Sun ZG, Liu JS (2007) Nitrogen cycling of atmosphere-plant-soil system in the typical *Calamagrostis angustifolia* wetland in the Sanjiang Plain, Northeast China. *J Environ Sci* 19:986–995.
- Swift MJ, Heal OW, Anderson JM, Anderson JM (1979) *Decomposition in terrestrial ecosystems (Vol. 5).* Univ of California Press.
- Świątek B, Chodak M, Pietrzykowski M, et al (2019) Fine root biomass and the associated C and nutrient pool under the alder (*Alnus* spp.) plantings on reclaimed technosols. *Geoderma* 337:1021–1027.
- Sydes AC, Grime JP (1981) Effects of Tree Leaf Litter on Herbaceous Vegetation in Deciduous Woodland : II . An Experimental Investigation. *J Ecol* 69:249–262.
- Takeda H (1998) Decomposition processes of litter along a latitudinal gradient. In *Environmental forest science.* Springer 197–206.
- Tanner EVJ (1981) The Decomposition of Leaf Litter in Jamaican Montane Rain Forests. *J Ecol* 69:263–275.
- Tieterna A, Boxman AW, Bredemeier M, et al (1998) Nitrogen saturation experiments (NITREX) in coniferous forest ecosystems in Europe : a summary of results. *Environ Pollut* 102:433–437.
- Uliassi DD, Ruess RW (2002) Limitations to Symbiotic Nitrogen Fixation in Primary Succession on the Tanana River Floodplain. *Ecology* 83:88–103.
- Uri V, Tullus H, Lõhmus K (2002) Biomass production and nutrient accumulation in short-rotation grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural land. *For Ecol Manage* 161:169–179.
- Van Cleve K, Viereck LA, Schlentner RL (1971) Accumulation of Nitrogen in Alder (*Alnus*) Ecosystems near Fairbanks, Alaska. *Arct Alp Res* 3:101–114.
- Vares A, Lohmus K, Truu M, et al (2004) Productivity of black alder plantations on reclaimed oil-shale mining areas. *Oil Shale* 21:43–58.
- Vitousek PM (1984) Litterfall , Nutrient Cycling , and Nutrient Limitation in Tropical

- Forests. *Ecology* 65:285–298.
- Vitousek PM, Hättenschwiler S, Olander L, Allison S (2002) Nitrogen and Nature. *AMBIO A J Hum Environ* 31:97–101.
- Vitousek PM, Porder S, Houlton BZ, et al (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen — phosphorus interactions. *Ecol Appl* 20:5–15.
- Vitousek PM, Walker LR, Whiteaker LD, Matson PA (1993) Nutrient Limitations to Plant Growth during Primary Succession in Hawaii Volcanoes National Park. *Biogeochemistry* 23:197–215.
- Vogel JG, Gower ST (1998) Carbon and Nitrogen Dynamics of Boreal Jack Pine Stands With and Without a Green Alder Understory. *Ecosystems* 1:386–400.
- Walker TW, Syers JK (1976) The fate of phosphorus during pedogenesis. *Geoderma* 15:1–19.
- Wang JR, Zhong AL, Comeau P, et al (1995) Aboveground biomass and nutrient accumulation in an age sequence of aspen (*Populus tremuloides*) stands in the Boreal White and Black Spruce Zone, British Columbia. *For Ecol Manage* 78:127–138.
- Warren CR, Adams MA (2001) Distribution of N, Rubisco and photosynthesis in *Pinus pinaster* and acclimation to light. *Plant Cell Environ* 24:597–609.
- Wedin D a, Tilman D (1990) International Association for Ecology Species Effects on Nitrogen Cycling: A Test with Perennial Grasses. *Oecologia* 84:433–441.
- Woś B, Pietrzykowski M, Józefowska A (2018) Reclaimed mine soil substrates and tree stands vs. successional forest floor vegetation: A case study of developing ecosystems on afforested mine sites. *Ecol Eng* 120:504–512.
- Wright IJ, Reich PB, Westoby M, Ackerly DD (2004) Worldwide leaf economic spectrum. *Nature* 8:153–162.
- Wright IJ, Westoby M (2003) Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. *Funct Ecol* 1:1-11–19.
- Wu C (2016) Dead Wood Is Not Dead : The Ecological Functions and Management of Dead Wood
- Xia M, Talhelm AF, Pregitzer KS (2017) Chronic nitrogen deposition influences the chemical dynamics of leaf litter and fine roots during decomposition. *Soil Biol Biochem* 112:24–34.
- Xia M, Talhelm AF, Pregitzer KS (2015) Fine roots are the dominant source of recalcitrant plant litter in sugar maple-dominated northern hardwood forests. *New Phytol* 208:715–726.
- Xia M, Talhelm AF, Pregitzer KS (2018) Long-Term Simulated Atmospheric Nitrogen Deposition Alters Leaf and Fine Root Decomposition. *Ecosystems* 21:1–14.
- Yuan ZY, Li LH, Han XG, et al (2005) Nitrogen resorption from senescing leaves in 28 plant species in a semi-arid region of northern China. *J Arid Environ* 63:191–202.
- Zechmeister-Boltenstern S, Keiblinger KM, Monnshammer M, et al (2015) The application of ecological stoichiometry to plant-microbial-soil organic matter transformations. *Ecol Monogr* 85:133–155.
- Zhang G, Zhang P, Peng S, et al (2017) The coupling of leaf, litter, and soil nutrients in warm temperate forests in northwestern China. *Sci Rep* 7:1–11.
- Zhang J, He N, Liu C, et al (2018) Allocation strategies for nitrogen and phosphorus in forest plants. *Oikos* 127:1506–1514.

6. Major aims and outputs of the thesis

6.1. Major aims

Publication 1: To evaluate the effect of tree species on soil faunal communities and on the contribution of such fauna to changes in soil properties during early pedogenesis.

Publication 2: To describe the life cycle and population dynamics of *Penthetria holosericea* in an alder forest.

Publication 3: To investigate the role of standing dead biomass of *Calamagrostis epigeios* in interactions within the plant community and in nutrient cycling.

Publication 4: To explore the effect of nitrogen availability on cycling of N and other nutrients and compare nutrient stock and nutrient cycling in reclaimed alder plantation (with high N input due to N₂ fixation) and unreclaimed sites covered by successional vegetation (with lower N input) of the same age.

Publication 5: To explore seasonal dynamics of foliage and litter fall quality during the vegetation season in reclaimed and unreclaimed sites of Sokolov area.

6.2 Major outputs

6.2.1. Publication 1

Frouz J, Livečková M, Albrechtová J, Chroňáková A, Cajthaml T, Pižl V, Háněl L, Starý J, Baldrian P, Lhotáková Z, Šimáčková H, Cepáková Š (2013) Is the effect of trees on soil properties mediated by soil fauna? A case study from post-mining sites. *Forest Ecology and Management* 309/1:87–95.

In publication 1, the effect of tree species of different foliage and litter chemistry was studied on the chemical, micro-morphological, and biological properties of soil. The study compared sites on post-mining sites afforested with one of six tree species (spruce, pine, larch, oak, lime, and alder) with sites left to natural succession (with willow as dominant tree species). It was found that a higher N content was greater in the litter produced by deciduous tree species which resulted in lower C:N ratio in deciduous than in evergreen litter. Faster soil development with thick organomineral A horizon was observed in sites with litter fall of lower C:N ratio. A higher accumulation of undecomposed litter fall at Oe horizon was evident in sites with evergreen trees producing litter fall of high C:N ratio. A high abundance of earthworms and bioturbation activity were the strongest predictor of faster soil

development of A horizon and C accumulation in the mineral topsoil. Sites with high accumulation of C in mineral soil had higher microbial biomass and lower microbial respiration which is caused by the higher stock of C. Soil C stock significantly differed among the sites and was highest in lime and alder sites and lowest in successional sites. Results suggest that soil development differed significantly between sites afforested with different tree species and it is strongly influenced by the presence and activity of soil fauna, especially by earthworm bioturbation.

6.2.2. Publication 2

Frouz J, Jedlička P, Šimáčková H, Lhotáková Z (2015) The life cycle, population dynamics, and contribution to litter decomposition of *Penthetria holosericea* (Diptera: Bibionidae) in an alder forest. *European Journal of Soil Biology* 71:21–27.

Publication 2 examined the population dynamics of *Penthetria holosericea* and its influence on litter decomposition of alder (*Alnus glutinosa*) litter. The life cycle, population dynamics as well as the rate of litter consumption were described in the study. Samples were taken in monthly intervals (February to November) in alder forest near Český Krumlov. Results showed that larval abundance peaked in June (1078 ind m⁻²) and larval abundance peaked in August (1.3 g m⁻²), which was before maximum litter fall in September and October. This might be explained by higher litter quality during summer, but this was not confirmed in our study because the lowest litter C:N ratio was found in November. Therefore, the results suggest that the life cycle of *P. holosericea* is not dependent on seasonal changes in the quality and quantity of food. Overall, the annual alder litter consumption by the population of *P. holosericea* was about 40 % of the annual alder litter fall.

6.2.3. Publication 3

Veselá H, Mudrák O, Frouz J (2018) The role of dead standing biomass of *Calamagrostis epigejos* in nutrient turnover during spontaneous succession. *Science of The Total Environment* 644:717–724.

The role of dead standing biomass of rhizomatous expansive grass *Calamagrostis epigejos* in nutrient turnover during spontaneous succession was studied in publication 3. *C. epigejos* is well known for its high productivity of hardly decomposable standing litter which remains undecomposed long time without contact with the soil surface. This strategy gives a strong competitive advantage to *C. epigejos* over other plant species and can block the course of succession. *C. epigejos* also shows a high tolerance to very low soil N levels by reducing its

growth which is also due to its higher N-use efficiency compared to other grasses. We found that *C. epigejos* reabsorbed most nutrients before the senescence of leaves at older sites while reabsorbing much less at the younger sites. Standing dead biomass was turned to lying dead biomass during winter and spring and its decomposition N then immobilized N from soil. Moreover, the greatest release of nutrients was observed from lying dead plant biomass immediately after death of living biomass and then losses of nutrients were slower. This competitive advantage of *C. epigejos* reduced the availability of N for other plant species especially at the beginning of the growing season in spring especially at younger nutrient poor sites, when *C. epigejos* can use N stored during the previous season.

6.2.4. Publication 4

Veselá H, Veselá M, Cejpek J, Frouz J (manuscript) Reclaimed alder plantation in post mining sites have more open nutrient turnover causing loss of nutrients from the soil in comparison unreclaimed woody regrowth.

In publication 4, the nutrient budget and nutrient turnover were compared in post-mining sites with alder reclamation and with spontaneous succession in the Sokolov area. Use of N₂-fixing trees is a favorite practice in restoration of disturbed areas after coal mining which supports faster soil development (due to the enhancing effect of litter with low C:N ratio) with higher availability of nutrients, especially N for plants and soil biota. In the study, measurements of nutrient concentration in biomass compartments, plant litter, throughfall, and in lysimetric leachates were collected during the whole year. The total content of P, Ca, Mg, K in plant biomass was found to be higher in spontaneous succession sites in comparison to the alder reclamation sites while the opposite was true for N. In the reclaimed sites, the higher amount of N released from plant litter caused a higher loss of nutrients (basic cations and P) from the ecosystem which can lead to earlier depletion of nutrients in these sites, soil acidification due to high N input into the soil and consequent eutrophication with decrease in biodiversity of the ecosystem. On the contrary in succession site, there is more suitable nutrient efficiency because more nutrients are stored in the plant biomass, plant litter is decomposed slowly and leaching of nutrients is not high. Our study supports the idea that mixed stands should be used in further reclamation practice rather than alder monocultures.

6.2.5. Publication 5

Veselá H, Lhotáková Z, Albrechtová J, Frouz J (manuscript) Seasonal changes in foliage and litterfall bio-chemistry in reclaimed and unreclaimed sites.

Publication 5 examined relationship between seasonal changes in tree foliage and litter fall quality / composition in reclaimed and unreclaimed post-mining sites. Different tree species differ in their nutrient management which strongly influences nutrient return to the forest floor and nutrient cycling in the ecosystem. Leaves and litter fall chemical characteristics were measured during the vegetation season from April to December. The study showed different foliage composition between individual tree species and between sites, especially in concentration of N, Ca, Mg, K and content of lignin. As expected the highest amount of N was found in alder foliage and litter fall due to symbiosis with N₂ fixing bacteria. However, concentration of other nutrients (Ca, Mg, K) was found to be higher in the foliage and litter fall of tree species at unreclaimed sites. The content of lignin slightly increased during the vegetation season in foliage and litter fall of all studied tree species. Litter fall at unreclaimed sites had the highest content of lignin which can be responsible for the slower decomposition of litter fall.

7. Major conclusions

Ecological stoichiometry provides us the understanding of ecological dynamics and processes. The three most basic elements C, N, P in living organisms and plants play crucial roles in activities and functions of organisms, but stoichiometry relationship (especially other essential nutrients such as Ca, Mg, K) among leaf, plant litter, and soil is still poorly understood in the literature particularly in plant-soil systems at sites after coal mining in restoration areas.

Different plant tree species treat differently with nutrients and can influence nutrient cycling and return of nutrients to the soil. The higher nutrient concentration (except N) was found in biomass at spontaneous regrowth vegetation in nutrient-poor sites, which shows better treating with nutrients without wasting in comparison to sites with high availability of N in alder reclamation sites. Using N₂ fixing plants is a favorite restoration practice used for faster soil development, but as it was shown N₂ fixing plants have some disadvantages such as high leaching of nutrients from the system and low efficiency of nutrients by plants. Presented research supports the idea that for further reclamation practice will be useful plant mixed stands rather than alder monocultures.

Foliar resorption efficiency depends mainly on ratios of foliar nutrients, plant growth type, ecosystem type, and physiological limitations. Nutrient resorption from leaves is the prevention of nutrient losses and supports nutrient conservation in the ecosystem. Plant nutrient resorption efficiency is higher on soils with low nutrient availability where the lower nutrient concentration in litter fall reduce decomposition rates, nutrient release and energy transfer to the other trophic levels.

Herbal species developed their own strategies for nutrient competition. These strategies are important in soils with low availability of nutrients. A good example of studying competition strategy provides rhizomatous grass *Calamagrostis epigejos* which reabsorb most of nutrients just before senescence of leaves in older developed sites but much less in the young sites. This competitive advantage reduced the availability of nutrients for other plant species especially at the beginning of the growing season in spring because *C. epigejos* can use N and other nutrients stored during the previous season. This strategy is most important in undeveloped young soils.

Also, soil development varies between plant species and it is strongly influenced by the presence and activity of soil fauna. Especially bioturbation of earthworms changes physical

and chemical conditions in the soil and influence the composition of the soil microbial community as well. According to the presented study life cycle of *Penthetria holoserica* was not dependent on seasonal changes in the quality and quantity of food (litter fall of alder).

To conclude, this thesis provides insight into the importance of ecological stoichiometry as one of the key factors that influence the plant-soil system and soil fauna development at restoration areas after coal mining.

Publication 1

Frouz J, Livečková M, Albrechtová J, Chroňáková A, Cajthaml T, Pižl V, Háněl L, Starý J, Baldrian P, Lhotáková Z, Šimáčková H, Cepáková Š (2013) Is the effect of trees on soil properties mediated by soil fauna? A case study from post-mining sites. *Forest Ecology and Management* 309/1:87–95.

Publication 2

Frouz J, Jedlička P, Šimáčková H, Lhotáková Z (2015) The life cycle, population dynamics, and contribution to litter decomposition of *Penthetria holosericea* (Diptera: Bibionidae) in an alder forest.

Publication 3

Veselá H, Mudrák O, Frouz J (2018) The role of dead standing biomass of *Calamagrostis epigejos* in nutrient turnover during spontaneous succession.

Publication 4

Veselá H, Veselá M, Cejpek J, Frouz J (manuscript) Reclaimed alder plantation in post mining sites have more open nutrient turnover causing loss of nutrients from the soil in comparison unreclaimed woody regrowth.

Publication 5

Veselá H, Lhotáková Z, Albrechtová J, Frouz J (manuscript) Seasonal changes in foliage and litterfall bio-chemistry in reclaimed and unreclaimed sites.