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Plant-soil interactions in succession on post-mining sites

Ph.D. Thesis

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Annotation

Field observation and manipulative experiments were carried out to describe and test important processes affecting the plant succession on Sokolov post-mining sites. Examined was mainly effect of dominant tree species (which are planted or spontaneously established) on understory plants, litter decomposability and effect of earthworms (*Lumbricidae*) on late successional plant species.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

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Mgr. Ondřej Mudrák

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List of papers and author's contribution

The thesis is based on the following papers (listed chronologically):

I. Roubíčková, A., **Mudrák, O.,** Frouz, J., 2009. Effect of earthworm on growth of late succession plant species in postmining sites under laboratory and field conditions. Biology and Fertility of Soils 45, 769–774 (IF = 2.156).
Ondřej Mudrák participated in substrate collection in field, measurements done on plants, statistical analysis, and revision of the manuscript and was responsible for all works on the second laboratory experiment.

II. **Mudrák, O.,** Frouz, J., Velichová, V., 2010. Understory vegetation in reclaimed and unreclaimed post-mining forest stands. Ecological Engineering, 36, 783–790 (IF = 2.203).
Ondřej Mudrák participated in substrate sample collection and field data collection, preparation of samples for chemical analyses and was responsible for statistical analyses and manuscript writing.

III. Frouz, J., Cajthaml, T., **Mudrak, O.,** 2011. The effect of lignin photodegradation on decomposability of *Calamagrostis epigeios* grass litter. Biodegradation 22, 1247–1254 (IF = 2.012).
Ondřej Mudrák participated in litter collection, substrate collection, preparation of samples for chemical analyses, statistical analyses, manuscript revision and was responsible for the field part of the experiment.

IV. **Mudrák, O.,** Frouz, J., 2012. Allelopathic effect of *Salix caprea* L. litter on late successional plants at different substrates of post-mining sites – pot experiment studies. Botany, accepted (IF = 1.098).
Ondřej Mudrák collected the substrates, prepared leachates from litter and was responsible for all work on experiments, statistical analyses, and manuscript writing.

V. **Mudrák, O.,** Uteseny, K., Frouz, J., Does litter quality alter the effect of earthworms on plants and on Collembola in early successional substrate? Manuscript.
Ondřej Mudrák collected the substrate and litter in field, established the experiment, participated in preparation of samples for chemical analyses and was responsible for all measurements done on plants, data assembly, statistical analysis, and manuscript writing.

Contents

General introduction

Contemporary industrial economy requires extensive mining of mineral resources which results in large areas of land being disturbed or destroyed. These areas often remain without the original ecosystems and are covered just by spoil (Bradshaw, 1983). In the Czech Republic, the most extensive destruction of landscape is caused by surface mining of brown coal such as that in the Sokolov region.

In Sokolov, the brown coal mining has a long tradition (since the 17th century) with open pit mines being used since 1950s (Frouz et al., 2007a). The coal layer in the Sokolov area is approximately 100 m deep and to reach the coal a large amount of spoil material from coal overburden has to be extracted and putted aside into heaps. During the process, original ecosystems are either extracted or overlaid by the heaps of spoil. At the time of termination of the mining activities, the total area affected by mining in the Sokolov region will consist of approximately 9000 ha. In such degraded landscape the ecosystem functions and services are considerably harmed. The raw spoil substrate lacks soil functions and cannot sufficiently support plant growth (Bradshaw, 1997, 1983; Frouz, 2008). The negative impact of open pit mines has been recognized since the very beginning of mining. The reclamation measures are required by law, which basically desire restoration of the prior mining land use. In the first step of the restoration procedure, the surface of the spoil heaps is leveled and only gentle slopes are allowed. In the later phase, the reclamation of spoil heaps most commonly continues with afforestation. Plant seedlings of various tree species (both native and exotic) are planted in a 1-m grid directly into the raw spoil substrate which is not improved (Figure 1).

This method is in contrast with methods used in other large coal mining regions, such as the Most region, where the spoil is covered by topsoil (from A horizon) or by other carbon rich material (Hodačová and Prach, 2003). Pastures have been also established on extensive areas to restore the agricultural land use (Frouz et al., 2007a). Some areas have been also left unreclaimed (Figure 2 and 3) which provides a great opportunity to study various aspects of spontaneous succession and compare the succession with the reclamation measures.

Substrate conditions represent important factors affecting the succession, because if the substrate properties are unsuitable, the plants would be starving or would not grow at all (Bradshaw, 1997). The soil formation depends on climate, vegetation, soil biota, topography, bedrock, and time (Brady and Weil, 1998). An important source of organic matter is provided by the first plant colonizers; organic matter can be incorporated into the soil by roots but also by the activity of soil biota incorporating the above ground parts of the plants shed on the ground (i.e., litter). The quality of the litter is essential for such process, since the litter is a source of nutrients for soil biota and it forms a basis for soil organic matter (Lavelle et al., 1997; Flegel et al., 1998; Frouz et al., 2007b). The litter quality is usually estimated by C:N ratio, but many species bring in structural or chemical obstructions preventing the litter decomposition (Cornelissen,1999; Graca et al., 2005). Especially in the latter case, the negative impact of chemical compounds may extend also to other organisms, not just the decomposers, and suppress them by allelopathy (Rice, 1979). The litter chemistry can affect soil formation in many ways including various interactions with soil biota. The consumption of the litter by soil dwelling animals often leads to stabilization of carbon in soil and formation of soil structures (Jones et al., 1994; Lavelle et al., 1997; Frouz et al., 2008). Such processes need time to produce a recognizable effect, usually at least several decades (Brady and Weil, 1998; Frouz et al., 2001). The topography of the surface, i.e. its elevation or depression, is also important since the depressions have a tendency to be wetter and accumulate more of the material (Frouz and Nováková, 2005; Frouz et al., 2008). Climate and bedrock are often the main factors affecting the soil formation (Brady and Weil, 1998). However, their effects are similar over the heap (Frouz et al., 2009) and therefore other factors can be studied in the Sokolov region more deeply.

Figure 1 Forest reclamation in the Sokolov district – in the foreground a one-year old tree plantation of *Larix decidua*, in the background a 35-year old stand of the same species.

Despite rather unfavorable conditions of the spoil substrate (tertiary alkaline clay), the first plant colonizers appear in the Sokolov district shortly after the substrate deposition. They are mainly ruderal species such as *Daucus carota*, *Poa compressa*, *Tanacetum vulgare* and *Tussilago farfara* but also tree seedlings of goat willow (*Salix caprea*), birch (*Betula pendula*), and aspen (*Populus tremula*) establish and later dominate the plant community. At first *Salix caprea* dominates and reaches the dominance around the 20th year of the succession. At the same time the herb layer decreases in cover. *S. caprea* is later outcompeted by *Betula pendula* and *Populus tremula*. Between the 20th and 30th year of the succession a mull humus layer (A horizon) is formed on the unreclaimed sites by a pedogenic process in the soil profile. The changes in the soil conditions are accompanied by changes in vegetation in which species native to meadow and forest communities increase in dominance. After more than 40 years the succession leads to a development of sparse birch and aspen woodland with a species-rich understory (up to 49 species per 25 m^2) mainly dominated by meadow species such as *Arrhenatherum elatius*, *Festuca rubra*, *Plantago lanceolata*, and *Lotus corniculatus*. In these stages, however, also the competitively strong grass *Calamagrostis epigejos* increases in dominance and often suppresses other species (Frouz et al., 2008).

Therefore, the formation of the humus layer appears as crucial for the plant succession. A detailed study of the soil structures revealed that the humus layer is formed mainly by earthworm casts (Frouz et al., 2008). Earthworms are known as the ecosystem engineers with substantial effect on soil properties (Jones et al., 1994). They colonize the heap around the 20th year of the succession, at the time when organic matter (in litter and fermentation layer) is accumulated on the substrate surface. Earthworms mix the litter and the fermentation layer into the mineral spoil and they form stable soil aggregates by consumption of a large amount of substrate. In this way they stabilise the organic matter in substrate. Once formed, these soil structures remain stable over the years. The soil processed by earthworms is therefore not only an important sink of atmospheric carbon, but it also has better physical properties. It is more aerated, has more hospitable water regime and is more resistant to erosion (Jones et al., 1994; Lavelle et al., 2006, 1997; Marashi and Scullion, 2003; Scullion and Malik, 2000). Moreover, mixing of the litter into the substrate supports litter decomposition and subsequent release of nutrients (Haimi and Huhta, 1990; Postma-Blaauw, 2006; Wurst et al., 2004). Earthworms also affect soil microbial community (Scheu, 1987; Gómez-Brandón, 2010) and populations of other soil animals (Dunger and Voigtländer, 2005; Migge-Kleian, 2006; Straube et al., 2009). In general, these earthworm effects increase plant productivity (Scheu, 2003).

Figure 2 Spontaneously overgrown site on the spoil heap 8 years old (time since the heaping).

Figure 3 Spontaneously overgrown site at the edge of the spoil heap surrounded by levelled surface prepared for afforestation.

Earthworms affect the plants also in several other ways, such as by selective ingestion of the plant seeds. The ingestion depends on the seed size and shape with the preference of small or thin seeds with smooth surface (Asshoff et al., 2011; Clause et al., 2011; Milcu et al., 2006; Shumway and Koide, 1994). The seeds are often not digested and the seed transport over the soil profile represents another important effect of seed ingestion by earthworms. Seeds are transported not only downwards but commonly also upwards (Zaller and Saxler, 2007). Earthworms put a substantial amount of seeds into the soil seed bank and simultaneously transport a lot of seeds from the soil seed bank into the soil surface (Thompson, 1987; Eisenhauer et al., 2009). In chalk grasslands of the Netherlands, Willems and Huijsmans (1994) estimated the upward transport of seeds at soil surface as at least 60-100 seeds/m^2 per year. Moreover, earthworms can break the seed dormancy (Ayanlaja et al., 2001; Scheu, 2003) and earthworms' casts (in which the seeds are transported to soil surface) are nutrient rich and support plant growth (Milcu et al., 2006). Earthworms also ingest plant seedlings with preference for the nitrogen rich legumes. For the seedlings the ingestion is lethal (Eisenhauer et al., 2010). Another way in which earthworms can affect plants is excretion of hormone-like compounds affecting plant growth (Suthar et al., 2010) and suppressing plant diseases (Stephens and Davoren, 1997).

Earthworm species are not equal in their behaviour and effect on environment and three different functional groups (without sharp borders) of earthworms are commonly distinguished (Bouché, 1977). The first subgroup consists of epigeic species which live in organic layers on the soil surface and predominantly feed on organic matter. The second group is formed by endogeic species which build permanent horizontal burrows in the upper mineral soil and ingest organic matter together with large amounts of mineral soil. Endogeic species are considered to be important soil-forming agents. The third group represents anecic species which live in the permanent horizontal burrows. They mostly feed on the litter. Anecic species are mostly responsible for the litter burial into the soil and for the seed transport over the soil profile as described above (Ashoff et al., 2011; Curry and Schmidt, 2007; Edwards and Bohlen, 1996; Eisenhauer et al., 2008; Willems and Huijsmans, 1994). In the Sokolov spoil heaps, the epigeic species are represented mainly by the species *Dendrodrilus rubidus* (Savigny 1826) and *Dendrobaena octaedra* (Savigny 1826). The edogeic species are mainly represented by *Aporrectodea caliginosa* (Savigny 1826) and *Octolasion lacteum* (Örley 1881). Anecic behaviour is represented mainly by the species *Lumbricus rubellus* (Hoffmeister 1843) which is, however, generally considered as an epigeic species (Pižl, 2001).

In Europe, earthworms are very common; they have already colonized all suitable natural habitats and their effect on soil is wide spread (Migge-Kleian, 2006) as they build persisting soil structures which can remain long after earthworm extinction. Possibly for these reasons, ecologists have still rather overlooked the effect of earthworms on ecosystem functioning (Scheu, 2003). However, as it is apparent from the forests of North America where an invasion of European earthworms is in progress, the effect of earthworms on ecosystem functioning is strong (Frelich et al., 2006). By mixing the litter into the soil, earthworms substantially change the forest floor and forest nutrient regime. This together with the plant seed burial leads to considerable changes in species composition and even physiognomy of the North American forest understory (Bohlen et al., 2004a, b). Post-mining sites represent one of the few examples, where we can observe the earthworm colonization of previously earthworm free environment in Europe (Migge-Kleian, 2006).

Despite the fact that many ecosystems' functions and services have potential to be restored by spontaneous succession similar to the one described above, the human assisted technical reclamation of the post mining sites still prevails in the Czech Republic. Similarly to the Sokolov region, the majority of the post mining sites all over the Czech Republic have been afforested or established as the agricultural land. Succession is not even recognized by law as a possible method of post-mining site restoration. Although many steps have been recently done to include succession into the legislation, the unequal position of succession in relation to technical reclamation substantially reduces the natural value of post mining sites. The unreclaimed post mining sites are important refuges of many rare and endangered species which prefer the low vegetation cover and nutrient poor conditions of early successional sites (Frouz et al., 2007a; Hodačová and Prach, 2003; Tropek et al., 2012, 2010). As an example from the Sokolov region we can mention the toad *Bufo calamita* which formed the largest stable population in the Czech Republic in the Sokolov spoil heaps (Frouz et al., 2007a). Study of the succession is therefore important not only because it brings knowledge that can make the restoration of the ecosystem functions and services more effective, but in this way we can also demonstrate the efficiency of the succession to local authorities.

The spoil heaps of the Sokolov provide a good opportunity to study spontaneous processes in the succession. Here, relatively large areas have remained unreclaimed and the substrate development starts in comparable conditions both in reclaimed and unreclaimed sites. That enables to study the effect of various factors on soil formation and through that also on plants, because the site specific development can be attributed to known factors, such as the age of the site, identity of the planted tree species dominant, and others.

The aim of the present study is to describe and test in manipulative experiments important processes affecting the plant succession on Sokolov spoil heaps. In the Paper I, we compare spontaneously established understory of sites reclaimed by various forest plantations and unreclaimed sites overgrown by trees during the succession. In Paper II, we test the assumption based on previous field observation (Frouz et al., 2008) that late successional substrate is more hospitable for plants and that earthworms support plant growth. Since individual plant species dominants produce litter substantially differing in quality, in the Paper III we test whether the litter quality mediates the effect of earthworms on plants. In the Paper IV, we analyse whether the low cower of the understory species of *S. caprea* stands can be caused by allelopatic effect of the litter which was reported for this species (Schütt and Blaschke, 1980). In the Paper V we describe the processes of changing the quality of the litter which was produced by dominant species of spoil heap vegetation – *Calamagrostis epigejos*.

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Paper I

Mudrák, O., Frouz, J., Velichová, V., 2010. Understory vegetation in reclaimed and unreclaimed post-mining forest stands. Ecological Engineering, 36, 783–790.

Abstract

In the Sokolov coal mining district of the Czech Republic, spoil heaps are reclaimed by forest plantations, which are planted directly into the rough substrate (alkaline tertiary clay). We compared the understory that spontaneously developed in seven types of forest stands: one type was unreclaimed stands (spontaneously overgrown by *Betula pendula* and *Salix caprea*) and six were plantations, each dominated by one tree genus (*Alnus, Larix, Picea, Pinus, Quercus*, and *Tilia*). The age of the stands ranged from 22 to 33 years. The cover of understory plant species in each stand was estimated, and 16 other environmental and community variables were quantified. The number of plant species was highest in *Quercus*, *Larix*, and unreclaimed stands, and was negatively correlated with forest canopy cover and with the cover of the understory dominant, the grass *Calamagrostis epigejos*. Understory composition differed considerably among the types of forest stands and was significantly explained by the measured environmental variables. Forward selection in redundancy analysis indicated that the most important variable driving understory composition was thickness of the fermentation layer, which is clearly connected with soil development. Environmental variables, including fermentation layer, were also affected by the type of forest stand. Therefore, all of the explained variability in understory composition could be attributed to the type of forest stand, which apparently affected the understory by its impact on soil formation. However, the most favorable soil conditions were not favorable for understory development, as they supported mainly *C. epigejos*, which suppressed other species. Our study also showed that even in the absence of reclamation measures, mining sites can be successfully restored due to spontaneous succession.

Keywords

Coal, Restoration, Spoil heaps, Succession, Soil formation, Vegetation

Abstrakt

Na Sokolovsku jsou výsypky po těžbě uhlí rekultivovány převážně lesními výsadbami. Stromky se zde sázejí přímo do výsypkové hlušiny, kterou tvoří alkalický třetihorní jíl. Porovnávali jsme podrost, který se spontánně vyvinul v sedmi typech lesních porostů, jež se zde vyskytují: nerekultivované plochy (spontánně zarostlé stromy *Betula pendula* a *Salix caprea*) a šest různých rekultivačních výsadeb lišících se v dominujícím rodu dřeviny (*Alnus, Larix, Picea, Pinus, Quercus* a *Tilia*). Stáří porostů bylo 22 až 33 let. V podrostu jsme odhadli pokryvnost jednotlivých druhů cévnatých rostlin a kvantifikovali 16 různých proměnných charakterizujících abiotické i biotické prostředí. Počet druhů rostlin podrostu byl nejvyšší v porostech rodu *Qercus*, *Larix* a v nerekultivovaných plochách a byl negativně korelován s pokryvností dominanty podrostu, trávou *Calamagrostis epigejos*. Druhové složení podrostu se průkazně lišilo mezi jednotlivými typy porostů a bylo průkazně vysvětleno měřenými proměnnými. Krokový dopřený výběr v redundanční analýze ukázal, že rozdíly v druhovém složení podrostu nejlépe vysvětluje síla fermentační vrstvy v půdním profilu, což ukazuje, že rostlinný podrost je do značné míry ovlivněn půdotvorným procesem. Měřené proměnné prostředí, včetně síly fermentační vrstvy, byly ovlivněné typem lesního porostu, proto veškerá vysvětlená variabilita v druhovém složení podrostu je určena typem lesního porostu, který ovlivnil půdotvorný proces na lokalitě. Nejpříznivější půdní podmínky ale nebyly nejvhodnější pro rozvoj podrostu, protože podporovali především *C. epigejos*, která potlačovala ostatní druhy. Naše studie taktéž ukazuje, že i bez rekultivačních opatření můžou být místa zničená těžbou úspěšně obnovena díky spontánní sukcesi.

Klíčová slova

Uhlí, Obnova, Výsypky, Sukcese, Tvorba půdy, Vegetace

Následující pasáž o rozsahu 20 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.

Publikace vyšla tiskem v časopise Ecological Engineering.

Podíl studenta na publikaci: 70%.

Paper II

Roubíčková, A., **Mudrák, O.,** Frouz, J., 2009. Effect of earthworm on growth of late succession plant species in postmining sites under laboratory and field conditions. Biology and Fertility of Soils 45, 769–774.

Abstract

Earlier studies of postmining heaps near Sokolov, Czech Republic (0–46 years old) showed that massive changes in plant community composition occur around 23 year of succession when the heaps are colonized by the earthworms *Lumbricus rubellus* (Hoffm.) and *Aporrectodea caliginosa* (Savigny). The aim of the current study was to test the hypothesis that the introduction of earthworms into a postmining soil enhances growth of late succession plant species. In a laboratory experiment, earthworms significantly increased biomass of *Festuca rubra* and *Trifolium hybridum* grown in soil from a 17-year-old site. The biomass increase corresponded to a significant decrease in pH and an increase in oxidable C, total N, and exchangeable P, K, and Ca content. A second laboratory experiment showed higher biomass production of late successional plant community (*Arrhenatherum elatius, Agrostis capillaris, Centaurea jacea, Plantago lanceolata, Lotus corniculatus*, and *Trifolium medium*) in soil from late successional stage (46 years old); the introduction of earthworms into soil from an early successional stage (17 years old) increased biomass production. In a field experiment, introduction of *L. rubellus* to enclosures containing a 17-year-old soil not colonized by earthworms significantly increased the biomass of grasses after 1 year. The results support the hypothesis that colonization of postmining areas by earthworms can substantially modify soil properties and plant growth.

Keywords

Earthworms, Plant succession, Plant growth, Postmining soils

Abstrakt

Dřívější studie na výsypkách po těžbě uhlí, ve stáří 0-46 let, v okolí města Sokolov (Česká republika) ukázali, že okolo 23. roku sukcese nastávají v rostlinném společenstvu značné změny a to právě v době, kdy jsou výsypky kolonizovány žížalami *Lumbricus rubellus* (Hoffm.) a *Aporrectodea caliginosa* (Savigny). Cílem studie bylo otestovat hypotézu, že introdukce žížal do post těžební půdy podpoří růst pozdně sukcesních rostlin. V laboratorních pokusech žížaly průkazně zvýšili biomasu rostlin *Festuca rubra* a *Trifolium hybridum* rostoucích v půdě ze 17

let staré lokality. Nárůst biomasy korespondoval se změnami v půdě a to sníženým pH a zvýšením oxidovatelného C, celkového N a dostupného P, K a Ca. Druhý laboratorní pokus ukázal vyšší produkci biomasy pozdně sukcesních druhů (*Arrhenatherum elatius, Agrostis capillaris, Centaurea jacea, Plantago lanceolata, Lotus corniculatus* a *Trifolium medium*) v půdě z pozdně sukcesního stádia (stáří 46 let). Přidání žížal do ranně sukcesní půdy (stáří 17 let) rovněž zvýšilo produkci biomasy rostlin. V terénním pokusu přidání žížal druhu *L. rubellus* do boxů obsahujících 17 let starou žížalami nekolonizovanou půdu po 1 roce průkazně zvýšilo produkci trav. Výsledky podporují hypotézu, že kolonizace post těžebních lokalit žížalami značně mění půdní podmínky a růst rostlin.

Klíčová slova

Žížaly, Rostlinná sukcese, Růst rostlin, Post těžební půdy

Následující pasáž o rozsahu 11 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.

Publikace vyšla tiskem v časopise Biology and Fertility of Soils.

Podíl studenta na publikaci: 30%.

Paper III

Mudrák, O., Uteseny, K., Frouz, J., Does litter quality alter the effect of earthworms on plants and on Collembola in early successional substrate? Manuscript.

Abstract

Previous field observations indicated that earthworms promote late-successional plant species and reduce collembolan numbers at post-mining sites in the Sokolov coal mining district (Czech Republic). Here, we established a laboratory pot experiment to test the effect of earthworms (*Aporrectodea caliginosa* Savigny and *Lumbricus rubellus* Hoffm.) and litter of low, medium, and high quality (the grass *Calamagrostis epigejos*, the willow *Salix caprea*, and the alder *Alnus glutinosa*, respectively) on late successional plants (grasses *Arrhenatherum elatius* and *Agrostis capillaris*, legumes *Lotus corniculatus* and *Trifolium medium*, and non-leguminous dicots *Centaurea jacea* and *Plantago lanceolata*) in spoil substrate originating from Sokolov post-mining sites and naturally inhabited by abundant numbers of Collembola. The earthworms increased plant biomass, especially that of the large-seeded *A. elatius*, but reduced the number of plant individuals, mainly that of the small-seeded *A. capillaris* and both legumes. Litter quality affected plant biomass, which was highest with *S. caprea* litter, but did not change the number of plant individuals. Litter quality did not modify the effect of earthworms on plants; the effect of litter quality and earthworms was only additive. Species composition of Collembola community was altered by litter quality, but earthworms reduced the number of individuals, increased the number of species, and increased species evenness consistently across the litter qualities. Because the results of this experiment were consistent with the field observations, we conclude that earthworms help drive succession of both plant and Collembola communities on post-mining sites.

Key words

Decomposition, Multitrophic interactions, Plant growth, Post-mining soils, Restoration, Soil fauna

Abstrakt

Dřívější pozorování indikovala, že výskyt žížal v post těžebních oblastech v Sokolovské hnědouhelné pánvi podporují pozdně sukcesní druhy rostlin a redukují počty chvostoskoků. Proto jsme založili laboratorní experiment, kterým jsme otestovali vliv žížal (*Aporrectodea caliginosa* Savigny and *Lumbricus rubellus* Hoffm.) a opadu nízké (pocházející z trávy

Calamagrostis epigejos), střední (pocházející z vrby *Salix caprea*) a vysoké kvality (pocházející z olše *Alnus glutinosa*) na pozdně sukcesní druhy rostlin (trávy *Arrhenatherum elatius* a *Agrostis capillaris*, dusík fixující dvouděložné rostliny *Lotus corniculatus* a *Trifolium medium* a dusík nefixující dvouděložné rostliny *Centaurea jacea* a *Plantago lanceolata*) vysetých do hlušiny pocházející ze sokolovských výsypek a spontánně kolonizované početnými populacemi chvostoskoků. Přítomnost žížal zvýšila celkovou biomasu rostlin, zejména u *A. elatius*, který má velké semena, a naopak snížili počet jedinců rostlin, zejména pro *A. capillaris*, který má malá semena, a pro oba dusík fixující druhy. Kvalita opadu ovlivnila biomasu rostlin, která byla nejvyšší v přítomnosti opadu druhu *S. caprea*, ale neovlivnil počet jedinců rostlin. Kvalita opadu nezměnila vliv přítomnosti žížal na rostliny. Vliv žížal a opadu byl čistě aditivní. Druhové složení společenstva chvostoskoků bylo změněno druhem opadu. Žížaly však nezávisle na vlivu opadu snížili počet jedinců chvostoskoků a zvýšili počet a vyrovnanost zastoupení jejich druhů. Protože výsledky experimentu se shodují s terénním pozorováním, můžeme konstatovat, že žížaly napomáhají sukcesnímu vývoji rostlinného společenstva a společenstva chvostoskoků v post těžebních lokalitách.

Klíčová slova

Dekompozice, Multitrofické interakce, Růst rostlin, Post těžební půdy, Obnova, Půdní fauna

Následující pasáž o rozsahu 16 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.

Publikace byla zaslána do tisku.

Podíl studenta na publikaci: 80%.

Paper IV

Mudrák, O., Frouz, J., 2012. Allelopathic effect of *Salix caprea* L. litter on late successional plants at different substrates of post-mining sites – pot experiment studies. Botany, accepted.

Abstract

The willow *Salix caprea* is a common colonizer of post-mining sites including those in the Sokolov coal mining district (Czech Republic) where this study was conducted. In one bioassay and two pot experiments, we investigated the effect of *S. caprea* litter on three plant species (*Arrhenatherum elatius*, *Plantago lanceolata*, and *Lotus corniculatus*) that commonly grow in late successional stages on these sites. In a sandy soil, leachate from fresh *S. caprea* litter reduced the number of germinated individuals (experiment 1) and shoot and root growth (experiment 2). In the clayey substrate originally unaffected by the *S. caprea* (experiment 3) leachate suppressed germination of all three species, but no reduction of biomass (both aboveground and belowground) was observed. Biomass was enhanced, however, in substrate that was naturally enriched with *S. caprea* litter (i.e. substrate collected on the same locality as previously mentioned substrate but beneath the *S. caprea* shrubs). *S. caprea* therefore can suppress the establishment of new plants that arrive as seeds, but this suppression may only occur with seeds that directly contact the litter. When *S. caprea* litter is incorporated into the substrate, it can considerably improve substrate quality and the growth of successional plants.

Keywords

Restoration, Succession, *Salix caprea*, Allelopathy, Litter, Vegetation

Abstrakt

Vrba jíva (*Salix caprea*) běžně kolonizuje post těžební oblasti včetně Sokolovské hnědouhelné pánve, kde byla provedena tato studie. Ve třech experimentech jsme zjišťovali vliv listového opadu jívy na tři druhy rostlin (*Arrhenatherum elatius*, *Plantago lanceolata* a *Lotus corniculatus*), které se běžně vyskytují v pozdně sukcesních vegetaci na sokolovských výsypkách. Výluh z čerstvého opadu jívy snížil v písčité půdě počet klíčících jedinců (pokus 1) a snížil růst prýtu i kořenů rostlin (pokus 2). V jílovitém substrátu původně neovlivněném jívou (pokus 3) potlačil klíčení všech tří sledovaných druhů, ale žádná redukce biomasy (jak v nadzemí tak v podzemí) nebyla pozorována. Biomasa druhů ale byla podpořena v substrátu, který byl přirozeně obohacen o opad jívy (tj. substrát odebrán na stejné lokalitě jako dva dříve zmíněné substráty, ale pod keřem jívy). Jíva tedy může potlačit uchycování nových druhů, kteří se na výsypku dostanou v semenech, ale potlačení může nastat jen při přímém kontaktu

s opadem. Pokud je opad jívy začleněn do substrátu, může zvýšit jeho kvalitu a podpořit růst pozdně sukcesních druhů rostlin.

Klíčová slova

Obnova, Sukcese, *Salix caprea*, Alelopatie, Opad, Vegetace

Následující pasáž o rozsahu 14 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.

Publikace byla přijato do tisku v časopise Botany.

Podíl studenta na publikaci: 90%.

Paper V

Frouz, J., Cajthaml, T., **Mudrák, O.,** 2011. The effect of lignin photodegradation on decomposability of *Calamagrostis epigeios* grass litter. Biodegradation 22, 1247–1254.

Abstract

The common grass *Calamagrostis epigeios* produces a large amount of dead biomass, which remain above the soil surface for many months. In this study, we determined how exposure of dead biomass above the soil affects its subsequent decomposition in soil. Collected dead standing biomass was divided in two parts, the first one (initial litter) was stored in a dark, dry place. The other part was placed in litterbags in the field. The litterbags were located in soil, on the soil surface, or hanging in the air without contact with soil but exposed to the sun and rain. After 1 year of field exposure, litter mass loss and C and N content were measured, and changes in litter chemistry were explored using NMR and thermochemolysis-GC–MS. The potential decomposability of the litter was quantified by burying the litter from the litterbags and the initial litter in soil microcosms and measuring soil respiration. Soil respiration was greater with litter that had been hanging in air than with all other kinds of litter. These finding could not be explained by changes in litter mass or C:N ratio. NMR indicated a decrease in polysaccharides relative to lignin in litter that was buried in soil but not in litter that was placed on soil surface or that was hanging in the air. Thermochemolysis indicated that the syringyl units of the litter lignin were decomposed when the litter was exposed to light. We postulate that photochemical decay of lignin increase decomposability of dead standing biomass.

Keywords

Thermochemolysis-GC–MS, 13C NMR, Decomposition, Plant litter, Post mining sites, Light

Abstrakt

Běžná tráva *Calamagrostis epigeios* produkuje velké množství mrtvé biomasy, která zůstává nad povrchem půdy po mnoho měsíců. V této studii jsme determinovali jak vystavení mrtvé biomasy mimo kontakt s půdou ovlivňuje její následnou rozložitelnost v půdě. Sebraná stojící mrtvá biomasa byla rozdělena do dvou částí. První část (iniciální opad) byla uložena na temné a suché místo. Druhá část byla umístněna v pytlíků z jemné síťoviny do terénu. Pytlíky byly umístněny v půdě, na povrchu půdy a pověšeny nad povrch půdy, kde byly vystaveny jen slunci a dešti. Po jednom roce expozice v terénu jsme změřili ztrátu hmotnosti opadu, obsah C a N a sledovali jsme i změny v chemizmu opadu za pomocí NMR a termochemolýzy-GC–MS. Potenciální rozložitelnost opadu byla kvantifikována zanořením opadu z pytlíků a iniciálního

opadu do půdních mikrokosmů a měřením půdní respirace. Půdní respirace byla vyšší u opadu, který vysel ve vzduchu, než u všech ostatních druhů opadu. Tento nález nemohl být vysvětlen změnami v hmotnosti opadu či C:N poměru. NMR ukázala úbytek polysacharidů spřízněných s ligninem a to v opadu, který byl zanořen v půdě, ale ne v opadu, který byl na povrchu půdy či vysel nad ním. Termochemolýza ukázala, že syringilové jednotky ligninu opadu byly rozloženy, pokud byl opad vystaven světlu. To ukazuje, že fotochemický rozklad ligninu zvyšuje rozložitelnost mrtvé stojící biomasy.

Klíčová slova

Termochemolýza-GC–MS, 13C NMR, Rozložitelnost, Rostlinný opad, Post těžební místa, Světlo

Následující pasáž o rozsahu 13 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.
Publikace vyšla tiskem v časopise Biodegradation.
Podíl studenta na publikaci: 25%.

Summary and general discussion

The plant succession in Sokolov spoil heaps is connected with substrate conditions which are, beside original geological conditions, mainly determined by joint effect of dominant trees and soil biota, namely earthworms. The present studies (Paper II and III) demonstrated a strong positive effect of earthworms on late successional plants. Earthworms are, however, affected by dominant tree species that strongly modify the effect of earthworms on substrate condition. Sites afforested in reclamation measures by trees with easily decomposable litter (*Alnus* spp. and *Tilia cordata*) host large populations of earthworms which consecutively promote fast formation of a humus layer (A horizon). Sites afforested by trees with hardly decomposable litter (*Pinus* spp., *Picea* spp.) are almost devoid of earthworms. Here, litter is not mixed with spoil substrate and it accumulates in a fermentation layer at the substrate surface (Frouz et al., 2009). Modification of substrate conditions is followed by changes in plant community. However, on the sites with the fastest formation of the humus layer the productivity of understory plants is promoted and not their diversity. It is due to the expansion of competitive grass *Calamagrostis epigejos* which suppresses other plant species. Apart from the effect on substrate, trees can affect understory plant species in more direct ways, such as by shading (Paper I).

The joint effect of dominant tree species and earthworms is important also for the plant succession at unreclaimed sites. Early successional vegetation establishes shortly after heaping but the increasing dominance of *Salix caprea* in the middle stages of succession is accompanied by the suppression of this vegetation (Frouz et al., 2008). The potential of *S. caprea* to suppress understory plants by allelopathy (Schütt and Blaschke, 1980) does not seem to come into effect, since the spoil substrate naturally enriched by the *S. caprea* litter supports the plant growth well (Paper IV). Based on our unpublished results (Mudrák, Hermová, and Frouz, unpublished), it seems more likely that *S. caprea* suppress plants by other below ground interactions. The pruning of *S. caprea* and the subsequent increasing of light penetration to understory plants had just low effect on understory plants, but the reduction of below ground competition (by iron frames preventing the root penetration) caused a substantial increase of understory cover and biomass (Mudrák, Hermová, and Frouz, unpublished).

In the later phases of the succession, *S. caprea* is outcompeted by *Betula pendula* and *Populus tremula* and the cover of understory increases again but at this time it is dominated by late successional plants. However, at the same time when *S. caprea* starts to decline, the humus layer is formed in the soil profile (Frouz et al., 2008) due to earthworm colonization of the sites. Such coincidence makes it difficult to separate the effect of *S. caprea* from the effect of earthworm colonization but it seems likely that both effects influence the understory in joint action. At first, *S. caprea* suppresses the early successional vegetation and produces a large amount of litter that enables earthworm colonization and formation of the humus layer. When the *S. caprea* is outcompeted by other tree species, the late successional plants can profit from the improved soil conditions and become abundant. It is also because the late successional plants get competitive advantage over the early successional plants in the presence of earthworms (Mudrák, Hynšt, and Frouz, unpublished).

S. caprea litter appears to have a positive effect on plants growth at clay spoil substrate. As mentioned in Paper IV *S. caprea* litter enhanced plant growth and, as mentioned in Paper III, it supported the plant growth more than low quality litter of *Calamagrostis epigejos* but also more than high quality litter of *Alnus glutinosa*. Despite the fact that in the pot experiment we did not find any evidence that litter quality modify the effect of earthworms on plant, litter quality can still modify the earthworm effect on plants in field. In the pot experiment, earthworm survival was comparable in the litter of different quality, but in field we may expect that the sites with low quality litter will not attract earthworms or will not enable the establishment of permanent earthworm population (Curry and Schmidt, 2007). The decomposability and hence nutrition value of the litter produced by one species (*Calamagrostis epigejos* in our case) is not, however, constant over time. Even when dead plant tissues are not in the contact with the ground and decomposers cannot reach them, the decomposability can be enhanced by UV radiation due to photodegradation of the lignin (Paper V).

The present studies stressed the need for multidisciplinary approaches in the research of the mechanisms of succession. Due to the inclusion of different trophic levels into the studies we obtained valuable information about the functioning of the studied ecosystem. The less studied belowground interactions seemed to have at least the same importance for the plant succession as the more studied above ground interactions. In addition, the presented studies contributed to a better understanding of succession mechanisms by showing strong potential of spontaneous succession to restore the natural values and ecosystem function and services on the spoil heap. Similarly to other studies concerned with the topic (Hodačová and Prach, 2003; Pensa et al., 2004; Tropek et al., 2012, 2010), we found that succession does not restore productivity but rather biodiversity of post mining sites. Therefore, including spontaneously developing sites into new post-mining landscape substantially increases their natural values.

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