

Dear readers,

Our journal has entered into 63rd year of its publication. Its content and formal layout has changed during its development. In spite of several societal changes in our region over the past six decades it always tried to focus on purely professional issues excluding the signs of political impacts or tendentiousness. Let us mention here that the original title of the journal was *Lesnícky časopis* (in English: Forestry Journal). In 1993 the name changed to a bilingual title *Lesnícky časopis - Forestry Journal*. **In 2016 the editorial board of the journal suggested to change the title to Central European Forestry Journal. This change has taken place since the first issue of the current year.** As the title indicates, the journal has an ambition to present not only the works of the authors from the former Czechoslovakia, but also from other European countries, mainly from the region of Central Europe. Although the political, geographical, or cultural definition of the Central European region is inconsistent, the editorial board of the journal expressed an idea that the magazine should serve as a publishing platform (apart for the Czech Republic and Slovakia) especially for Austria, Germany, Hungary, Poland, Romania and Ukraine. This should not be taken as a strict definition of contributors, as the journal remains open also to other European countries.

In our country the age of 63 years represents the retirement age in human life, and hence the end of the productive employment period. However, we firmly believe that our journal has not reached this stage yet. We hope that it does not limp nor look for a place where it could sit down and recall past successes or failures. We want to move on, move forward, and improve. The step forward should be another change in the journal, namely the exclusion of short forms of contributions, i.e. book reviews, reports, and chronicles. Although this type of contributions has also an informative significance, modern scientific journals focus exclusively on articles that bring research results and findings. Therefore, starting from the volume 63 we will publish exclusively original scientific papers and review papers.

Over the last years of journal publication we came to a conclusion that one of the ways how to attract the attention of contributors and readers is to periodically compile a special thematic issue. The first special issue was published four years ago (2013/3) and was focused on the results of the production and ecological studies at the research object of Vrchslatina. One year later another special issue (2014/1) dealing with drought impact on tree species as an inherent phenomenon of climate change was published. One issue in the year 2015 (2015/3) was devoted to disturbance and post-disturbance processes in forest ecosystems. And in the last year (2016/4) we focused on forest entomology.

For these reasons, we prepared this double-issue, which focused on these two main topics:

- (i) Properties of forest soils and soil-related processes,**
- (ii) Carbon sequestration in forest biomass.**

The double-issue contains 10 original scientific papers and 1 review paper. The papers were written by the authors from the former Czechoslovakia, as well as from Germany and the Great Britain.

The first thematic part consists of 6 contributions. The paper of *Lukac* in the form of summarisation and analysis of knowledge from the European region explains the interactions between soil biodiversity and environmental changes (primarily climate change). The author pointed out at the fact that the knowledge on soil biodiversity is far more incomplete than the information about the above-ground parts of forest ecosystems. Due to this it is necessary to deal with this issue, particularly in the context of ensuring forest ecosystem services. *Holík et al.* monitored the ammonification of arginine (one of the proteinogenic amino acids) in the soil under the spruce stand. They revealed a substantial impact of microclimate on the decomposition of this amino acid in the soil, which can be influenced by the thinning regimes in the stands. The works of *Homolák et al.* and *Bebej et al.* present results describing physical characteristics of soil, the role of the humus in the infiltration of water into the soil, and the transport of elements through the soil profile. Since all these soil characteristics affect ecological stability and productivity of forest stands, such research in the field of forest ecology cannot be omitted. Next *Hanajík et al.* investigated biochemical processes (dehydrogenase activity) in the soil at the

post-disturbance area of the High Tatras. They revealed the impact of post-disturbance forest management on soil processes. *Cukor et al.* focused on carbon sequestration in the soil after afforestation of former agricultural soils. This issue is very serious from the point of mitigation measures against climate change.

At the beginning of the second part, the article of *Wellbrock et al.* who quantified carbon in tree biomass and soil in German forests is presented. They used two cycles of national forest inventory. These data allowed them to determine not only the static state, but also the changes in carbon stocks over the last ten years. Similarly, *Merganič et al.* quantified carbon stock in forest biomass at a national Czech level and at individual regional levels. The authors quantified the share of individual tree species and individual tree components. *Pečanec et al.* used possibilities of remote sensing (Landsat) for the estimation of above-ground biomass (or amount of sequestered carbon) in the Czech Republic. The work of *Šebeň et al.* focused on the quantification of carbon stock in living and dead trees of young beech and spruce stands. They confirmed the assumption that in the young dense stands with high tree mortality (due to competition) a large part of carbon is transferred from biomass to necromass and then by its subsequent decomposition to the atmosphere. The last paper of *Konôpka et al.* presents carbon amount in the above-ground vegetation biomass in the High Tatras 12 years after a large-scale wind-throw. The authors revealed that while the major part of carbon was sequestered in tree biomass, the substantial part of rotating carbon originated from the fall of ground vegetation.

The papers in this double-issue confirmed that soil is an important part of a forest ecosystem, either as a medium for biodiversity or as a carbon reservoir. Monitoring of physical, chemical and ecological relationships in the soil on one hand, and between the soil and vegetation on the other hand creates a knowledge base for optimal management that supports all forest functions. Apart from forest soil, forest biomass, particularly its dendromass is an important reservoir of carbon. In comparison with soil, forest managers can affect tree biomass more effectively whether with regard to carbon balance or biodiversity. Obviously, both components of forest ecosystems are mutually connected and every treatment in a forest stand (affecting the tree part) affects soil conditions.

At the end of our Editorial we would like to remind of the upcoming anniversary. In the year 2018 we will celebrate 120th anniversary of the forestry research in Slovakia. We assume that our journal will react to this anniversary by publishing another special issue. At the same time, let us take this opportunity to thank all contributors and readers for their interest in the journal. We wish you and our Central European Forestry Journal many successful years!

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Soil biodiversity and environmental change in European forests

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Abstract

Biodiversity not only responds to environmental change, but has been shown to be one of the key drivers of ecosystem function and service delivery. Forest soil biodiversity is also governed by these principles, the structure of soil biological communities is clearly determined by spatial, temporal and hierarchical factors. Global environmental change, together with land-use change and forest ecosystem management, impacts the aboveground structure and composition of European forests. Due to the close link between the above- and belowground parts of forest ecosystems, we know that soil biodiversity is also impacted. However, very little is known about the nature of these impacts; effects they have on the overall level of biodiversity, the functions it fulfills, and on the future stability of forests and forest soils. Even though much remains to be learned about the relationships between soil biodiversity and forest ecosystem functionality, it is clear that better effort needs to be made to preserve existing soil biodiversity and forest conservation strategies taking soils into account must be considered.

Key words: forest soils; community structure; ecosystem function; conservation

Editor: Erika Gömöryová

1. Introduction

Aboveground, sustained research effort has shown that biodiversity – whether that of species, guilds, functional traits or even genes – has a strong and positive relationship with ecosystem productivity (Worm & Duffy 2003) and that this relationship is valid across a range of ecosystems, including forests. At the same time, recent and accelerating loss of biodiversity may be linked to a reduction of ecosystem productivity as well as other functions, but also ecosystem stability, resilience and productivity (Cardinale et al. 2012). Past decades have witnessed an explosion of experimental and theoretical research effort aimed at understanding the role of biodiversity in the myriad of ecosystems on Earth. Due to the obvious advantage of being able to see it, the vast majority of studies and conceptual developments in terrestrial systems have focused on the aboveground part. Repeated and replicated manipulation experiments have shown that ecosystem function and biodiversity are intrinsically linked – at least aboveground (Grime 1997; Oliver et al. 2015; Schulze & Mooney 1994). However, low accessibility of forest ecosystems and their long life cycles, coupled with laboriousness of soil research have hindered experimentation and thus our understanding of the

contribution of the diversity of forest soil biota to ecosystem function. Our knowledge of the contribution of belowground biodiversity to overall ecosystem function is some way behind that for the visible part, despite the implied functional connection between the two. This lack of knowledge limits our ability to harness belowground biodiversity to deliver functions in the here-and-now and to predict its capacity to continue delivering in the future (Bardgett & Van Der Putten 2014).

2. Soil biodiversity and its organisation

Soil is the largest reservoir of biodiversity on Earth, one gram of soil has been shown to contain over 1 billion individual bacterial cells representing a large community of tens of thousands of species (Decaëns 2010), the identity, biology and function of many of these are completely unknown at present and may never be fully understood. Soil biodiversity however encompasses many other organism types besides bacteria; there are fungi, nematodes, earthworms, arthropods and even mammals who complete at least part of their life cycle in the soil and thus contribute to the overall soil biodiversity. One thing all of these life forms have in common is the fact that they

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all depend on aboveground primary production as their ultimate source of energy (Wardle et al. 2004). In forest ecosystems, organic matter rich in carbohydrates is either deposited on the soil surface or released into the soil profile from live and dead tree roots. A long chain of soil-dwelling organisms then utilizes energy contained in organic matter to power their metabolism, growth and reproduction. Soil food web is also the main driving engine of nutrient acquisition and recycling in forest ecosystems, many of which would be unable to exist without the functional contribution of soil biota (Fischer et al. 2006). The dependence on aboveground primary productivity, together with the seasonal nature of organic matter input, leads to spatial, temporal and hierarchical arrangement of soil biodiversity. Correct understanding of the contribution of soil biodiversity to soil function thus implies knowledge of the input of each species, its variation in space and in time and the interactions between species and communities of organisms.

Recent developments and decreasing cost of molecular methods have led to the creation of a growing collection of evidence documenting the level of species diversity present in many soils on Earth, together with the identification and description of species performing key functions. Long-standing assumptions guiding our approach to spatial distribution of soil biodiversity at global or biome scales – that any soil organism has the capacity to inhabit all soils – may not have been correct; it is now clear that soil organisms are spatially distributed and do not have the capacity to inhabit any soil (Callaway & Maron 2006). Global distribution of soil-dwelling species is restricted, probably by a combination of climatic, soil and plant composition factors (Öpik et al. 2006; Tedersoo et al. 2012), an observation especially relevant for forest ecosystems given the long life cycle of the dominant form of vegetation which tends to dictate many ecosystem characteristics. Since the life span of nearly all soil organisms is an order of magnitude shorter than that of trees, it is likely that soil biodiversity ‘acclimates’ to tree species identity and diversity. Spatial distribution of soil biodiversity is clearly linked to soil organism size, which ranges from single micrometres for bacteria, to tens of centimetres for earthworms, to several hectares for some soil fungi – a specimen of *Armillaria solidipes* covering an area of about 10 km² in the Malheur National Forest in Oregon (USA) is thought to be the largest organism on Earth (Richardson Dodge 2000). At the smallest scale, the distribution of soil biota is governed by soil structure which determines resource availability (Elliott 1986; Rasche et al. 2011). Biotic interactions such as competition and predation, root exudation by trees, turning-over of soil by larger organisms also play a part, mainly by affecting chemical composition of soil solution and thus speeding up or slowing down growth of microbial populations (Langenheder & Prosser 2008; Stark & Firestone 1995). At centimetre to metre scale, diversity of soil biota is affected by local variation of soil

conditions such as texture, organic matter content and water holding capacity (Wardle et al. 2004), which tends to be rather high in forest soils due to the often rugged nature of the terrain where most European forest are. Finally, at ecosystem level, spatial patterns of soil biodiversity are governed by topography and related climatic factors, disturbance regime and landscape connectivity (Fierer & Jackson 2006; Reinhart & Callaway 2006). As a result, spatial distribution of forest soil biodiversity is fragmented, as is our understanding of its function which is largely dependent on the body size of the organism as larger species tend to be better studied.

Analogous to the factors affecting spatial distribution, temporal changes in the diversity of soil organisms are very much dependent on the size of the organism in question. Population size of species with the smallest body size is usually governed by minute availability of resources such as water, nutrients and oxygen. An increase of water content in dry soil or a nutrient availability pulse can cause a rapid response of microbial populations (Austin et al. 2004), fast multiplication of single cell organisms drives an increase in population size. Nutrient pulses may be both biotic or abiotic in nature, exudation by tree roots has been shown to trigger growth of specific groups of microorganisms at the expense of others (Bais et al. 2006; El Zahar Haichar et al. 2008) – a clear example of an interaction between above- and belowground diversity. Temporal changes in microbial community composition at the smallest scale can take minutes to hours and are usually accompanied by a rapid change of the dominant function performed by microbes at their location. Longer-term fluctuation of resource availability over seasons or years, however, affects soil biodiversity at all levels (Lauber et al. 2013). The main reason for this effect is the fact that all are dependent on aboveground productivity as their energy source – aboveground seasonality must find its reflection belowground. At present, we have only a very fragmented picture of this relationship, there is some evidence that microbial communities undergo a complete turnover from winter to summer (Hamel et al. 2006), are differentially affected by seasonal resource availability and that changes in plant community exert strong influence over the composition of soil biota. The latter factor might be of critical importance in forest ecosystems, especially in the case of conversion of natural forests to plantations or restocking of stands with the view of increasing their climate change resilience. At the largest temporal scale – and the one currently least supported by evidence – there is an indication that specific communities inhabit soils at different stages of natural succession or post-disturbance recovery (Neutel et al. 2002).

Vast numbers on individuals, large variation in body size and often rather constricted specialisation in the food source or life strategy of soil biota, gives rise to a range of complex hierarchical arrangements of communities within forest soils. The simplest soil food-webs may con-

sist of heterotrophic, nitrogen-fixing and autotrophic photosynthesising bacteria, with little reliance on plant productivity (Mikola & Setälä 1998). However, with any increase of aboveground productivity comes an influx of different soil-inhabiting life forms which self-organise into communities performing a variety of functions such as organic matter fragmentation, element cycling or water uptake. Over time, and in an absence of disturbance, such communities become more and more complex by increasing food-chain length, accumulating larger levels of biodiversity and attaining higher level of stability (Neutel et al. 2007; Rooney et al. 2006). The mechanics of the relationship between complexity and stability of function of forest soil biological communities is not clear. However, it is becoming evident that soil biodiversity might have direct implications for forest ecosystem stability, for example under environmental change (Isbell et al. 2015). Much is known about individual functions performed by specific groups of organisms, but our knowledge of how widely functions are distributed among species within those groups is far from complete. Thus, assigning an estimate of redundancy to any given species within a community is fraught with difficulty – changes in species composition may or may not translate to changes in function (Strickland et al. 2009).

3. Forest soil biodiversity and ecosystem function

Forest soil biodiversity is considered to be the driving engine of soil based ecosystem services such as aboveground primary production, nutrient cycling, carbon sequestration and water purification (Turbé et al. 2010). As already mentioned, our understanding of the relationship between biodiversity, ecosystem functions and services in forest ecosystems is rapidly improving, although most of current research on biodiversity–ecosystem functioning in the forests still focuses on aboveground part of forest ecosystems. European forests are expected to play a large role in future provision of ecosystem services that underpin continuous existence of human society and contribute to climate change mitigation (e.g. (García-Nieto et al. 2013; Schröter et al. 2005) and it is clear that the soil ecosystem is an integral and essential component of this process. With particular reference to ecosystem functions supported by soil biota, the marked difference in framing socio-economic perspectives on biodiversity between agriculture and forestry must be pointed out (Mori et al. 2017). Many currently promoted agricultural practices focus specifically on soils and the maintenance of their productive functions, with increasing realization that it is the biological component that guarantees soil productivity (Foley et al. 2011). There is no equivalent of this approach for forestry, current forest management or conservation practice considers soil an in situ resource which somehow delivers functions but can be

treated as a ‘black box’. This means that we are unable to assess the trade-offs among different soil biodiversity levels and multiple ecosystem services they deliver. However, a number of studies linking biodiversity (e.g. genetic, functional) to ecosystem function (e.g. nitrogen fixation, phosphorus mining, organic matter decomposition, soil structure formation) have revealed that biodiversity promotes functionality and thus supports a range of ecosystem services (e.g. tree growth, forest fruit production, climate regulation, water filtration; Cardinale 2012). This is especially true for forests, which are characterized by higher structural complexity, longer life cycles of the dominant taxa and larger-scale spatiotemporal dynamics (Scherer-Lorenzen 2014). Humanity’s need to preserve ecosystem productivity and resilience thus brings us to the issue of preserving soil biodiversity. Land-use changes affected by humans, being it complete deforestation or just a change of tree species in a forest stand, invariably introduce some level of physical and chemical soil disturbance, which usually interferes with soil biota and the processes it supports (Altieri 1999). One of the most striking effects of human land-use is simplification of soil biological communities and thus a decrease in soil biodiversity (Giller et al. 1997). Ecosystem functions delivered by soil biota will inevitably be impaired as soil biodiversity underpinning each and every function is reduced. Reduction of diversity will negatively impact the resilience of soil biological communities in terms of supporting soil functions under changing environmental conditions (Folke et al. 2004). Less diverse communities will contain fewer redundant species which may have the capacity to sustain soil functions under a new set of conditions. Even when starting from a position where a single 3-dimensional soil profile may contain more biodiversity than the entire aboveground ecosystem (Myers et al. 2000), gradual and continuing reduction of soil biodiversity may lead to eventual loss of function.

4. Forest ecosystem stability and environmental change

Human activity is the driving factor behind global environmental change we are experiencing at present. Although the exact onset of Anthropocene has not been determined yet (Smith & Zeder 2013), it is apparent that world’s ecosystems are facing a period of rapid change. It is also clear, that high levels of biodiversity in all of its forms are essential for maintaining and safeguarding ecosystem function at this time. Biodiversity has been linked to fundamental ecosystem functionality and is known to contribute to the maintenance of resilience in ecosystems (Elmqvist et al. 2003). Forest ecosystem stability, or resilience, can be defined as the capacity of a system to absorb changes and to maintain fundamental controls on its function and structure (Curran 2011). Forest ecosystem structure is most often perceived in terms

of the 3-dimensional aboveground structure generated by trees and ground vegetation, however this accepted view completely ignores the spatial and temporal structure of subterranean hierarchies of soil organisms. Biodiversity of the latter might be just as important determinant of ecosystem resilience as the aboveground part. When facing uncertainty, unpredictability, nonlinearity and changeability of conditions, surely the overall diversity and structure of a forest ecosystem must be taken into account. It is also painfully clear, however, that currently we do not have a fit-for-purpose concept of forest resilience thinking that includes soil biodiversity, nor do we know how to apply this type of thinking to forest management.

The overriding issue of forest ecosystem resilience is how to secure the fundamental functionality of the whole and its constituent parts. The insurance hypothesis (Yachi & Loreau 1999) predicts that ecosystem function is maintained and stabilized in communities where higher redundancy of species is guaranteed by higher species diversity. Many species fulfill the same function and thus reduce suboptimal delivery of that function across space and time. For example, in a soil with several species of saprophytic fungi all competing for the same food resource, should one taxon disappear due to its sensitivity to environmental change, others will continue to fulfill its function and contribute to overall ecosystem stability. Conversely, if diversity is reduced, a fundamental control on ecosystem function in the face of environmental change may be lost from soil communities (Elmqvist et al. 2003).

To date, little is known about the contribution of forest soil biodiversity to overall ecosystem stability. A growing chorus of alarms calls for the investigation of anthropogenic impacts on forest biodiversity (Newbold et al. 2014; Wilcove et al. 2013); land-use change associated with deforestation, forest degradation or tree species replacement in plantations have threatened forest-dependent taxa across many regions. The knowledge of impacts of land-use change of soil dwelling organisms dependent on specific tree communities is however still in its infancy. Some inference can be drawn from studies carried out in grassland or agricultural ecosystems, there is some evidence to suggest that the commonly observed relationship between diversity and stability are applicable to forests, but the underlying mechanisms are not necessarily the same (Mori et al. 2017). We thus face a situation where we need to manage the survival and functionality of forest ecosystems (i) without having full understanding of the relationship between biodiversity and resilience and (ii) without having a working description of forest soil biodiversity and all its functions. Some modeling studies explore the implications of rapid environmental change for forest ecosystem service delivery; Duveneck & Scheller (2015) advocate a climate-suitable planting regime in which tree species from outside their current distribution are planted to anticipate a northward shift. Needless to say, the study does not take any account of

soil biodiversity which will need to support the new tree species and maintain ecosystem function under new conditions. We have learnt that global patterns of soil biodiversity are determined by several factors and that forest soil communities acclimate to local conditions which include tree species (Callaway & Maron 2006). Clearly, with specific regard to soil communities and their diversity, there is a need to broaden the scope of assisted migration and perhaps to explore the possibility and limitation of assisted evolution of forest communities.

5. Forest conservation and soil biodiversity

Biodiversity conservation has traditionally focused on the preservation of a small subset of species present in an ecosystem, most often on species perceived as iconic of key-stone in that ecosystem (Mace et al. 2012). This approach has been proved as suboptimal, improved knowledge of biodiversity and its role in ecosystem function has shown that it is the ecosystem functions and services (often epitomized as habitats) that should be the focus of conservation effort as their preservation aids the survival of individual species. Reflecting soil biodiversity distribution, both spatial and temporal aspects of forest conservation must be considered. Effects of soil biodiversity on the functionality and stability of forest ecosystem function are spatially constrained and are especially significant at local scale (Pasari et al. 2013). In a human-modified landscape such as that of Europe, the connectivity and heterogeneity of forest habitat patches containing levels of soil biodiversity correspondent to those of natural forests are the key determinant of ecosystem resilience at landscape scale (Standish et al. 2014). A diverse patchwork of structurally complex forest stands connected by corridors can maintain and safeguard higher levels of biodiversity that may increase forest ecosystem resilience to disturbance (Fischer et al. 2006). Higher above- and belowground biodiversity is likely to foster faster post-disturbance recovery from remnant patches of surviving trees or to contain an assembly of species suitable to build an alternative stable state. The capacity of soil biota to travel across landscape and to colonise new habitats obviously varies with organism type and size, however it is unlikely to match tree species movement during assisted migration, only highlighting the need for close scrutiny of suitability between 'resident' soil biota and tree species.

Having considered the spatial aspect of conservation of soil biodiversity, the question of temporal continuity of forest cover deserves equal importance. Forest soil biota is fully dependent on forest primary productivity for all of its energy needs, any discontinuation of forest cover will thus affect availability of carbohydrates and impact soil biodiversity at various levels. Of course, forest soils have evolved in the presence of disturbance which repeatedly discontinues food supply to soil webs and thus have an inherent level of resilience. It is recognized that anthropocene, with its multiple pressures on soil

biological functioning (climate change, pollution, lowering of tree species diversity or complete replacement, shorter rotations), may lead to critical changes in soil biodiversity which will eventually impact soil function (Folke et al. 2004). Thus, reduced-impact logging and retention forestry is becoming popular across a range of managed forest ecosystems (Lindenmayer et al. 2012). Both approaches aim to preserve key structural elements of a forest stand during harvesting to preserve the continuity of forest cover which is beneficial to biodiversity (Fedrowitz et al. 2014). One benefit of this approach is the continuity of several factors affecting soil condition and thus the survival of forest soil biological community. Maintaining (soil) ecosystem function over time will positively affect the delivery of ecosystem services by European forests. However, despite the recent rise in the popularity of multifunctional forestry, rigorous ecological and socio-economic evaluation of the costs and the benefits associated with reduced-impact logging and retention forestry for biodiversity conservation are still scarce (Messier et al. 2015).

6. Conclusion

A growing body of scientific evidence indicates that biodiversity not only responds to environmental changes, but that it is a key determinant of a multitude of ecosystem functions and services that are of crucial importance to the survival of human society. This paper has argued that forest soil biodiversity represents a key asset in the human 'environmental portfolio', albeit one about which little is known. It is clear that soil biology drives and regulates key ecosystem functions in forests and that ongoing environmental change will impact soil biodiversity. It is also clear that some of our knowledge exploring the functionality and relationships of aboveground biota are applicable belowground, however the specific nature of spatial, temporal and organizational structure of soil biodiversity merits a separate line of investigation. Forest ecosystems are notorious for the high levels of difficulties in manipulating environmental factors and for large variation of soil factors. Nevertheless, a combination of experimental and observational (forest monitoring plots) research methods may be able to provide insights into the role of soil biodiversity in ecosystem function and resilience as affected by environmental change.

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Seasonal dynamics of arginine ammonification in forest soils of Norway spruce pure stands under different silvicultural practices

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Abstract

Effects of seasonal dynamics and silvicultural practice on ammonification of arginine, one of the proteinogenic amino acids, were assessed in surface organic H-horizon of three Norway spruce pure stands in medium altitudes (600 – 660 m a.s.l.). Contents of ammonium ions NH_4^+ measured monthly in the field and contents of NH_4^+ after laboratory incubation of these samples with arginine were taken as dependent variables in ANOVA and in linear regression model using generalised linear model. The aim of the analyses was to determine the significance of decomposition of this amino acid in H-horizon of forest soils and to determine categorical and continuous predictors which influence intensity of the ammonification. Laboratory experiments confirmed its close link to seasonal dynamics, as well as to forest management; however the last mentioned was firstly found as less significant when compared within whole season. As regards to seasonal dynamics in forest soils, the highest amount of ammonium ion was released in May and the lowest in July. As regards to the silvicultural practice applied, more ammonium ion was released under mature spruce monoculture, especially in August and May; in the young stands, the method of thinning had no effect on the ammonium ion release. However, the arginine ammonification was found to be influenced by ammonium nitrogen content (slight, less significant negative correlation) and by soil water content (stronger positive significance), especially in the stand with thinning from below. This was concluded to be caused by changes in stand microclimate in function of the silvicultural practice.

Key words: ammonium availability; arginine deaminase; forest management; Norway spruce

Editor: Erika Gömöryová

1. Introduction

Nitrogen is an essential element for plant growth (Wang et al. 2007). Mineralization and nitrification of soil nitrogen directly affects his income by plants and losses at the interface plant and soil environment (Yang et al. 2008). Soil microorganisms and enzymes are responsible for maintaining soil fertility through degradation and mineralization of organic matter. Changes in conditions for plant growth, such as silvicultural measures necessary aging stands, can cause changes in microbial communities and their biochemical activity and affect the availability of nutrients for plants (Singh & Singh 2005; Novák et al. 2015). Ammonification of arginine has a significant relationship with the soil microbial biomass and affects their biochemical activity (Davis et al. 1978; Alef & Kleiner 1986; Singh & Singh 2005).

Arginine is one of the more than 300 naturally occurring amino acids and only 20/21 of them occur in

proteins solely in the form of L- α -amino acids (except glycine which has no chiral carbon) (Moe 2013). The combination of these proteinogenic amino acids form all known proteins. After appearance of dead organic matter in soil, proteinogenic amino acids begin to decompose. Ammonification is an important initial stage of organic matter mineralization when proteins and other organic compounds containing amino groups are decomposed by proteolytic enzymes to amino acids which are further deaminated to ammonium ion NH_4^+ (Abdelal 1979; Bonde et al. 2001; Lin & Brookes 1999).

The presented study deals with seasonal dynamics of ammonification of arginine, one of the proteinogenic amino acids, in Norway spruce (*Picea abies* [L.] Karst., *Pinaceae*) monocultures and the applied silvicultural practice in medium altitudes. The study was focused on the surface organic H-horizon.

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2. Material and methods

2.1. Site description and soil sampling

The research was carried out at the Rájec-Němčice Ecosystem Station, the Dražanská vrchovina uplands (the Czech Republic), located at 49° 29' N and 16° 43' E at an altitude of 600 – 660 m a.s.l. Geological subsoil is acid granodiorite, soil type Dystric Cambisol (IUSS Working Group WRB 2006), humus form Humic Mormoder (Klinka et al. 1997). Mean annual air temperature is 6.5 °C and the mean annual sum of precipitation is 717 mm. From the viewpoint of forestry, the ecosystem station belongs to the 4th forest vegetation zone (fir – beech vegetation zone); forest type *Fageta quercina abietina*.

The middle-aged stand was divided into several experimental plots (25 × 25 m) where different silvicultural practices were carried out. Primarily, seedlings were planted with the spacing 2.5 × 2 m on the clearing after felling of the previous mature spruce stand. The spruce stand, aged 33 years, was tended by strong thinning from above and from below with the intensity of 30%. The initial planting density was 4200 trees per ha, tending felling was performed in 1986, 2002 and 2010, reducing the density to 2381 trees per ha.

Three study plots were chosen among silvicultural management practices (SilvPra): i) MSS – mature spruce stand, 105 years, monoculture; ii) STFA – stand thinned from above (middle-aged stand thinned from above), 33 years, monoculture; iii) STFB – stand thinned from below (middle-aged stand thinned from below), 33 years, monoculture. The data collection was performed with the aim to focus on the arginine ammonification process inside the soil system in relation to stand and soil microclimate including MONTH (with categories Apr – April, May, Jun – June, Jul – July, Aug – August, Sept – September) and SilvPra (with categories STFA, STFB and MSS) as qualitative predicting variables and selected soil properties (see below) as quantitative predicting variables. As well, the soil was sampled from organic H horizons (IUSS Working Group WRB 2006) from each SilvPra treatment (one sampling plot per treatment) each MONTH through the year 2014 as mixed sample in five repetitions per sampling plot using surface preparation method. The sampling depth was from 2.5 to 4 cm depending on stratigraphy of surface organic horizons. In the laboratory, the naturally-moist samples were sieved through a 5 mm sieve, mixed and stored at 5 °C.

2.2. Soil analysis

Determination of arginine ammonification rate (Alef & Kleiner 1986) was based on soil samples incubated with arginine producing the ammonium which is extracted with potassium chloride solution and determined colorimetrically after addition of chromogenic reagents. Deter-

mination of ammonium nitrogen in soil extract was performed by Kučera et al. (2013). Determination of mass water content (w) was performed according to Zbiral et al. (2010).

2.3. Statistical processing

The key to clarify the relationship between arginine ammonification detected by means of arginine deaminase, the H-horizon of three studied spruce forests throughout the vegetation season was ANOVA, correlation analysis and regression analysis (GLM). Individual dependent variables were the contents of ammonification products (NH₄⁺) as measured each month and the laboratory-determined values of arginine ammonification in the same soil samples. The arginine ammonification analysis was carried out using two grouping variables: i) months, for the seasonal dynamics, and ii) spruce stands differing in age and the applied silvicultural practice (SilvPra) and finally two continuous variables: i) soil water content and ii) ammonium nitrogen content, which were considered as well predicting factors.

ANOVA was performed as one-way (with the factor being either the month or the silvicultural practice applied) or two-way (the month and the silvicultural practice are tested simultaneously) without and with interactions. The null hypothesis was tested via the p-value and the Tukey's HSD test was used as the multiple comparison post-hoc procedure, with the significance level alpha = 0.05 (conf. level = 0.95). When the direct dependences were studied, the test determined the differences between the individual datasets as statistically significant in all performed analyses of variance.

Relations between observed variables were analysed using Spearman's correlation coefficient r_s , compared with critical value with significant level alpha = 0.05 with two-tailed probabilities.

Dependence of arginine ammonification was analysed with use of generalised linear model (GLM) with Gamma distribution and inverse link function. To select optimal model for the dependence explanation, we used AIC: Akaike's an information criterion (Sakamoto et al. 1986) and vif: variance inflation factors (Fox & Monette 1992). The statistics were carried out in Statistica Cz, version 12 and R software environment, version 3.2.3 (2015-12-10), The R Foundation for Statistical Computing, using car package version 2.1-1 (Fox & Weisberg 2015; Lin 2015), ggplot2 package version 2.0.0 (Wickham & Chang 2016).

3. Results

In general, the highest ammonium ion content was found in MSS in August and in May. In other months the content was similar. In STFA and STFB the differences were not as significant except for July and May (Fig. 1). One-

way ANOVA found both variables significant: MONTH as well SilvPra with p -values < 0.002 and < 0.0002 , respectively (Fig. 2).

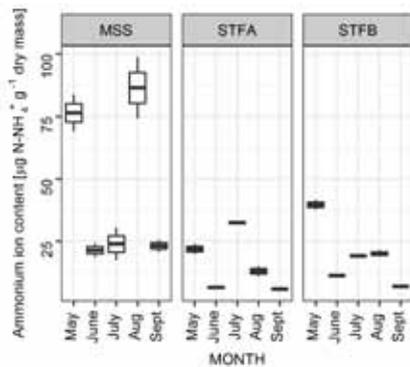


Fig. 1. Ammonium ion content in the H-horizon, seasonal dynamics in three treatments of spruce stand. MSS – mature spruce stand, STFA – stand thinned from above, STFB – stand thinned from below.

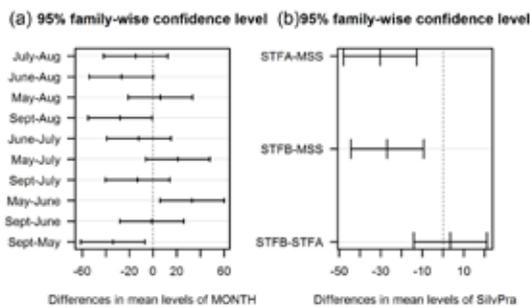


Fig. 2. Post-hoc analysis of ammonium ion concentration following one-way ANOVA with grouping variable (a) MONTH; (b) SilvPra. MSS – mature spruce stand, STFA – stand thinned from above, STFB – stand thinned from below.

Statistically significant differences were found in three comparisons: i) May – September; ii) May – June; iii) August – September. The differences between variables were even more significant using two-way ANOVA (either without or with interactions when p -values for both variables were $< 1.02e^{-5}$ and $< 2e^{-15}$, respectively). Therefore, from the viewpoint of seasonal dynamics (i.e. in case of individual months), ANOVA rejected the null hypothesis of the correlation of the statistical data sets and, simultaneously influence of seasonal dynamics of ammonium concentration depends on silvicultural practice.

For silvicultural practice and soil ammonium ion statistically insignificant differences in the content of NH_4^+ in both young stands, with a slightly higher value observed in the stand thinned from below. In the comparison of the young stands with the mature stand, the differences were statistically significant with the higher content of NH_4^+ always found in the mature stand.

The one-way ANOVA for the ammonium ion content revealed differences between MONTH, as well SilvPra (Fig. 2). Significantly the highest content of NH_4^+ was found in the samples collected in May and in August (without mutual significant difference) compared to the June and September.

The ammonium production after addition of arginine was markedly higher in September (Fig. 3). Results of seasonal dynamics of arginine ammonification in laboratory conditions (Fig. 4) are characterized by marked differences within the season. The highest values of the ammonification were detected in September followed by May. These two months were far more active in ammonification, especially the September.

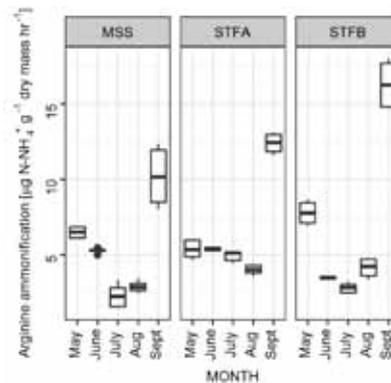


Fig. 3. Production of ammonium ion after addition of arginine, seasonal dynamics of arginine ammonification in H-horizon in spruce stands. MSS – mature spruce stand, STFA – stand thinned from above, STFB – stand thinned from below.

One-way ANOVA of arginine ammonification found the SilvPra as none-significant variable. However, two-way ANOVA revealed significant differences both between the individual MONTH and SilvPra (p -values were $< 2e^{-16}$ and 0.00115, respectively). The differences were insignificant only in three cases (in descending order August vs. July, August vs. June; June vs. July). In descending order, in September, the intensity was markedly higher compared to July, August, June and May. The lowest activity was found in July followed by August and June.

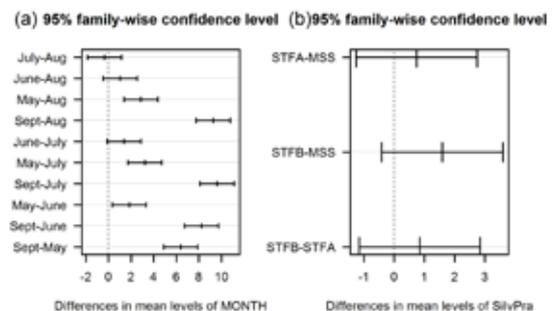


Fig. 4. Post-hoc analysis of arginine ammonification following one-way ANOVA with grouping variable (a) MONTH; (b) SilvPra. MSS – mature spruce stand, STFA – stand thinned from above, STFB – stand thinned from below.

For ANOVA of SilvPra without and with interactions, p-values were 0.00115 and 3.05e⁻⁹, respectively. Regarding silvicultural practices applied at the studied plots, the two-way ANOVA revealed more significant differences between both middle-aged and mature stand and rather equal values of the arginine ammonification when compared the middle-aged treatments (STFA vs. STFB).

As regards seasonal dynamics, the arginine ammonification was significantly different in two-way ANOVA both without and with interactions ($p < 2e^{-16}$).

Regarding the minimum values, the data from field and from laboratory were consistent in the summer months when the low amount of ammonium ion in soil corresponded to the low decomposition of arginine in the laboratory.

More ammonium ion was released in soil under the mature spruce monoculture compared to the young stands. Relation between arginine ammonification and its expected higher intensity in the mature stand was not confirmed. In the laboratory experiment, higher arginine ammonification was also found in the soil from the mature stand.

Ammonium nitrogen can be considered a product of arginine ammonification and thus it is expectable that its increased concentration is a result of increased ammonification. Conversely, it can be regarded as a predictor

of arginine ammonification which gets stronger with decreasing concentration of N-NH₄⁺ in soil. Another significant predictor of arginine ammonification is water, or, more precisely, water content. Intensity of arginine ammonification under significant influence of water content, both within the whole monitored season and within the individual months (Table 1), with the exception of May when this relationship showed statistically non-significant negative correlation. Very strong correlation of water content and arginine ammonification is evident also from the aspect of SilvPra, being the least distinctive in STFA (thinning from above) and the strongest in MSS (mature stand). Intensity of arginine ammonification in relation to the content of N-NH₄⁺ is characterized by a reverse trend, accompanied by a higher number of negative correlation coefficients in the individual months and overall inversely proportional trend in SilvPra, where the only statistically significant correlation coefficient was found in STFA.

Relationships between arginine ammonification and predicting factors (soil moisture, ammonium nitrogen content, MONTH, SilvPra) are described through a generalized linear model (Table 2). The two considered models, of which the first one (m1) covers the influence of water content and content of N-NH₄⁺ and the second one (m2) only water content as continuous variables, show

Table 1. Mean values and standard deviation of water content (w), ammonium nitrogen content (N-NH₄⁺) and arginine ammonification (Arg.: N-NH₄⁺) and Spearman's correlation coefficient (r_s) for each group of variables (MONTH and SilvPra). Statistically significant values p are highlighted in *Italic font*. MSS – mature spruce stand, STFA – stand thinned from above, STFB – stand thinned from below.

Month	w		N-NH ₄ ⁺		Arg.: N-NH ₄ ⁺		r _s		n
	mean	sd	mean	sd	mean	sd	Arg. * w	Arg. * N-NH ₄ ⁺	
May	53.38	7.63	45.99	24.40	7.11	1.12	-0.017	0.471	9
June	35.07	4.54	13.05	6.77	4.66	0.91	0.800	-0.233	9
July	45.86	9.90	25.10	6.68	3.58	0.85	0.600	0.750	9
August	48.31	6.77	39.86	35.65	3.31	0.57	0.450	-0.783	9
September	64.03	2.46	11.96	8.48	12.65	4.09	0.150	-0.417	9
Seasonal	49.33	11.55	27.19	23.73	6.26	3.99	0.656	-0.207	45
SilvPra									
STFA	52.49	10.30	15.92	10.45	6.31	2.96	0.395	-0.459	15
STFB	46.93	14.06	19.39	11.70	7.26	5.79	0.719	-0.171	15
MSS	48.57	9.91	46.27	30.54	5.21	2.31	0.674	-0.300	15

Table 2. The resulting model describing the relationship between the study variables (arginine ammonification depending on water content and N-NH₄⁺) in the months of May to September (MONTH) and various types of management (SilvPra); two final models, including two continuous variables w: soil water and N-NH₄⁺ (m1) and one continuous variable w: soil water (m2) are given below. The test criteria are described using vif (variance inflation factor), AIC (Akaike's information Criterion) and R² (coefficient of determination). Statistically significant p-value are highlighted in *italic font*. MSS – mature spruce stand, STFA – stand thinned from above, STFB – stand thinned from below.

Coefficients	p-value ^{m1}	p-value ^{m2}	variable	vif ^{m1}	vif ^{m2}	AIC ^{m1}	AIC ^{m2}	R ^{2m1}	R ^{2m2}
Intercept (including May and MSS)	3.48E-06	1.26E-06	—	—	—	135.682	135.045	0,915	0,912
w: soil water [%]	0.021365	0.023663	w:soil water [%]	5.506	5.467				
N-NH ₄ ⁺	0.287766	—	N-NH ₄ ⁺	5.842	—				
MONTH – Jun	0.500667	0.136274	MONTH	18.993	5.475				
MONTH – Jul	4.44E-06	2.78E-07							
MONTH – Aug	2.38E-08	9.82E-09							
MONTH – Sept	0.007777	0.004177							
SilvPra – STFA	0.028702	0.029675	SilvPra	2.693	1.040				
SilvPra – STFB	0.000732	0.000118							

m1: y ~ w + N-NH₄⁺ + MONTH + SilvPra

m2: y ~ w + MONTH + SilvPra

Equation^{m2} (arginine ammonification)

$$y = 1/[0.27325 - 0.00201 \times w + 0.03467(\text{Jun}) + 0.12294(\text{Jul}) + 0.14967(\text{Aug}) - 0.03887(\text{Sept}) - 0.02366(\text{STFA}) - 0.04205(\text{STFB})]$$

the effects of MONTS and SilvPra on arginine ammonification. In m1, the effect of $N-NH_4^+$ concentration was classified as insignificant ($p = 0.287766$) – despite to high coefficient of determination R^2 . After elimination of ammonium content from the model (m2), the p -value for w (water content) slightly increased, while the importance of the individual months as predictors of arginine ammonification decreased. Variance inflation factor (vif) indicated multicollinearity of regressors MONTH in the case of m1, which was removed together with the factor $N-NH_4^+$ (vif < 10 and close to 5). In the m2 model, the markedly lowest value is the AIC indicating an insignificant difference in the explanatory power of the models.

After close inspection of the relationships (Fig. 5, Fig. 6) between the individual parameters by regression

analysis, the content of ammonium nitrogen also shows negative correlation, nevertheless, for the final model it seems to be an insignificant predictor. According to Table 1, the link between arginine ammonification and content of ammonium nitrogen was the closest in August while in the other months it was more or less indifferent. In August, the dependency is markedly negative at a very low content of $N-NH_4^+$ and with its increasing concentration, the link between the intensity of arginine ammonification and concentration of ammonium nitrogen assumes an opposite trend: although the overall intensity of arginine ammonification increases, it becomes negatively dependent on $N-NH_4^+$ concentration while in the same period, the role of water content increases. From the aspect of SilvPra, there is closer dependency (negative again) of

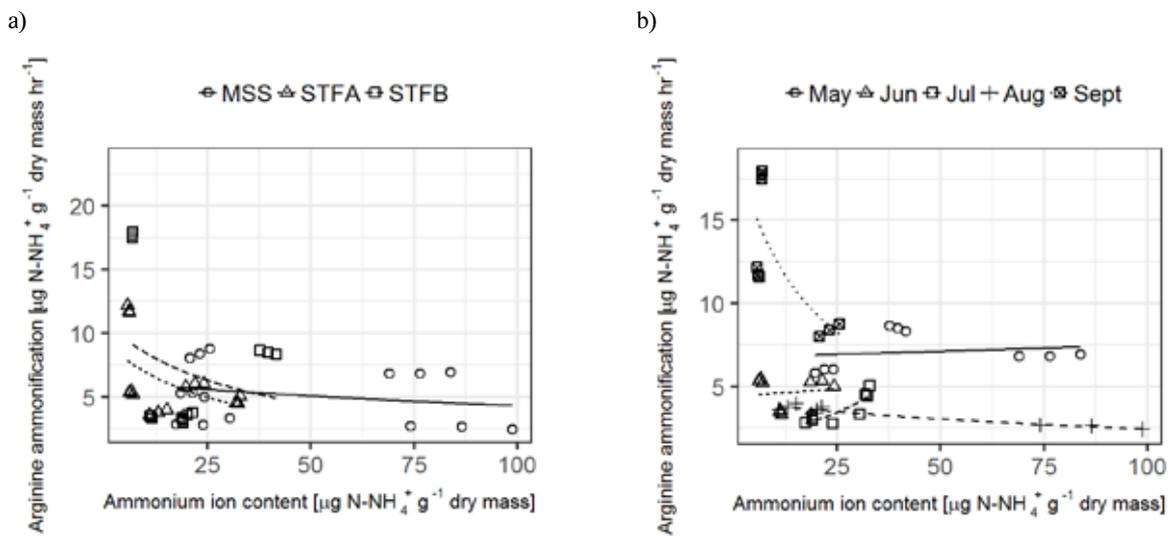


Fig. 5. Arginine ammonification [$\mu\text{g N-NH}_4^+ \text{g}^{-1} \text{dry mass hr}^{-1}$] in relation with ammonium content [$\mu\text{g N-NH}_4^+ \text{g}^{-1} \text{dry mass}$] and MONTH (a) and SilvPra (b). MSS – mature spruce stand, STFA – stand thinned from above, STFB – stand thinned from below.

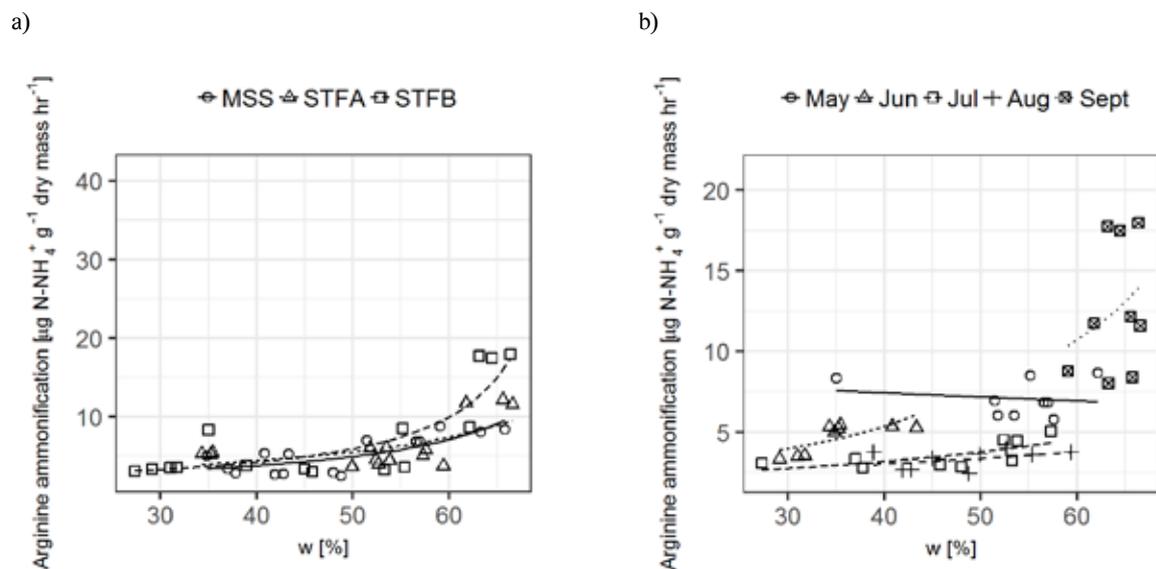


Fig. 6. Arginine ammonification [$\mu\text{g N-NH}_4^+ \text{g}^{-1} \text{dry mass hr}^{-1}$] in relation with soil water content [%] and MONTH (a) and SilvPra (b). MSS – mature spruce stand, STFA – stand thinned from above, STFB – stand thinned from below.

arginine ammonification on the content of ammonium N in the thinned (younger) stands. Firstly, they are predetermined by their generally low maximum content of N-NH_4^+ in soil (max. $42 \mu\text{g g}^{-1}$ dry mass) compared to MSS, secondly, the negative correlations prevailing here (stronger in the younger thinned stands) correspond to the fact that the maximum ammonification of arginine in MSS does not exceed $8.8 \mu\text{g N-NH}_4^+ \text{g}^{-1} \text{hr}^{-1}$, while in STFA and STFB it reaches more than 12 or even $18 \mu\text{g N-NH}_4^+ \text{g}^{-1} \text{hr}^{-1}$, respectively, precisely at the end of the vegetation season in September. From the above said it can be concluded that the tendency to ammonify arginine decreases with stand age as well as with increasing overall content of ammonium nitrogen.

The relation between water content and arginine ammonification is markedly positive as with increasing water content, intensity of ammonification increases, with the trend culminating in September (Fig. 6b). A slight decrease of ammonification (negative relation to water content) was observed in May; at the beginning of the vegetation season, still indifferent reaction of soil biota to changes in water content is to be expected, while at the end of summer, it culminates. Of the stand types (Fig. 6a), the closest relation appeared in STFB; in case of STFA and MSS, the trend is less significant and markedly steady.

4. Discussion

Stand thinning leads to higher penetration of light through the canopy, which provokes higher activity and increased population density of soil biota (Tang et al. 2005; Vranová et al. 2010). Thus the overall potential of soil for arginine ammonification increases as well. In this context, it is possible to identify two, or eventually three factors considerably determining the ammonification of arginine in forest soils under spruce stands: (1) content of N-NH_4^+ , when with its increased content, the “motivation” of soil biota to obtain ammonium nitrogen from an amino-acid by such energy-intensive way decreases – from the aspect of statistical significance it cannot be seen as implicitly significant; (2) type of forest management, or more precisely, its consequences in the form of stand and soil microclimate alteration – thinning operations that ensure better opening-up of the canopy and subsequent reaction of soil biota in the form of increased activity and population growth (Vesterdal et al. 1995; Gömöryová et al. 2014); and (3) water content (Bonde et al. 2011). Hence, the arginine ammonification culminates at optimum conditions, i.e. at increased water content, generally lower content of ammonium nitrogen and in soil environment with higher population density following a thinning operation.

There is a knowledge gap in the present literature about the direct impact of arginine ammonification on forest soil and availability of nitrogen. Arginine is an important proteinogenic amino acid; and its hydrolysis may play a significant role in nitrogen cycling in forest soils (Moe 2013). From the obtained results it is evident that the controlled laboratory experiments confirmed its seasonal dynamics, as well as its close link to forest management, but also to contextual soil properties, such as soil water content and ammonium nitrogen content.

Measurements carried out in the framework of this study confirm the findings of studies by other authors. For example, Edwards et al. (2006) or Weintraub & Schimel (2005) describe an increase in microbial activity and thus microbial nitrogen in the fall, in early spring its rapid decline and then its increase again during the late spring (May). Pandey & Singh (2006) also indicate a close correlation between arginine deaminase activity and respiratory activity of the soil and the amount of carbon in the soil.

5. Conclusions

The presented study generally confirmed the ammonification of arginine as significantly depending on seasonal dynamics, forest management and soil properties such as soil water content and ammonium nitrogen content. As the arginine is considered as a significant source of nitrogen after the decomposition of proteins, our findings can be regarded as important for nitrogen cycling control, as well as for its availability for soil biota and plants in consequence. In the case of the spruce forest type, arginine seems to copy the trend of intensifying decomposition with the late spring increase of temperatures (after the winter) and with the increasing amount of dead organic matter at the end of the vegetation season. Beside to the seasonal weather variation, the arginine ammonification significantly depends on stand microclimate being influenced by forest management (technique of thinning), which surprisingly can partially even hide the effect of the season (month). The results of observed seasonal dynamics of arginine ammonification in soil H-horizon in spruce monocultures of different ages and silvicultural practices in medium altitudes support the longstanding perception of ammonification of proteinogenic amino acids as an important part of dead organic matter decomposition.

Acknowledgement

This research was supported by Internal Grant Agency of FFWT, MENDELU, Czech Republic No. 55/2013–2015, and with project NAZV No. QJ1320040 (Revitalization of ecosystem units with the use of ecological principles on the sites with strong anthropic influence in the past and extreme sites).

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Effect of surface humus on water infiltration and redistribution in beech forest stands with different density

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Abstract

The aim of the paper is to demonstrate how the beech surface humus form and forest density affect the infiltration and redistribution of rainwater into the soil matrix. Beech as the most-abundant tree species in Slovakia has a tendency to form a compact humus layer with specific structure, leading to a reduction in the soil surface infiltration area and a significant influence on the preferential flow generation. The research was carried out in beech forests with different forest stand density in the Vtáčnik Mountain (Central Slovakia). The maximal infiltration surface area $35.11 \pm 6.58\%$ of sand surface infiltration area was reached at the plot A (0.8). The minimal infiltration surface area was reached at the plot B (0.8) and was $19.45 \pm 2.52\%$. Statistical tests confirmed a significant effect of the forest stand density on the surface infiltration area ($p = 0.05$) and number of infiltration inputs ($p = 0.05$). The results show a statistically significant influence of surface humus form and stand density on infiltration and redistribution of rainwater into the soil matrix. The influence results in water flow changes from matrix flow to preferential flow and fingering. As a consequence deeper infiltration of water and solutions, e. g. dissolved organic carbon, to deeper soil layers is observed.

Key words: surface humus; beech forests; infiltration; water regime

Editor: Zuzana Sitková

1. Introduction

Surface humus plays a key role in mediating interactions between the atmosphere and soil. Its quantity, composition and origin of the individual components, internal structure and spatial distribution affect mainly water, heat, air retention and accumulation regime. Along with filtration, buffering, transformation and anti-erosion function it defines the entire portfolio of ecological and environmental functions of soil.

Research on a surface humus in forest ecosystems has been mainly focused on the quantitative characteristics (e.g. Ottmar & Andreu 2007), to a lesser extent on its quality properties, especially regarding the origin of the individual components, and the causes and impact of its various forms on bulk density and porosity (e.g. Ogée & Brunet 2002; Matthews 2005). Later the research focused on the internal and spatial surface humus structure, the heterogeneous distribution in space and the resulting effect on important processes in forest ecosystems, such as the infiltration of water into the soil (Campbell et al. 2004). Many studies are also oriented on spatial and temporal variability of interception of surface humus (e.g. Gerrits et al. 2010) and percolation of

rainfall through humus layer (e.g. Dunkerley 2015) but without direct measurement of soil surface area affected by percolated water. Surface humus form and thickness ultimately affect the entire range of environmental functions of soil not only in terms of soil water redistribution, but also e.g. the release of dissolved soil organic carbon and its accumulation in deeper soil layers, which is directly relevant to the process of infiltration (Qualls et al. 2002). Infiltration into forest soil is affected by soil cracks, soil texture and structure, root system and especially by surface humus which reduces destructive effects of raindrops on soil surface, reducing the water level formation on a soil surface, which allows the outflow of air from pore space and the increase of infiltration intensity. In contrast, the layer of undecomposed leaves, especially when they are compressed by snow or rain, can reduce penetration of rainwater into the soil and support the surface runoff (Valtýni 1985). However, according to Kantor & Šach (2007) surface runoff in beech forests during growing season in 2005 and 2006 on approximately 30% slope reached only 0.5% of annual rainfall. Very low surface runoff was found also by Jankov & Gubka (2013). In beech forest on 65% slope they found average surface runoff 1.2% of annual rainfall. Forest soils are character-

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ised by very low compaction with relatively high porosity and water conductivity and contribute to the reduction of surface runoff and minimise the peak of storm flows (e.g. Hegg et al. 2004; Hümann et al. 2011; Robinson et al. 2003)

Walsh & Voigt (1977), Ponge (1999, 2002), Ampe & Langohr (2003) highlighted the impact of litter on geomorphological and hydrological processes in forest soils. Walsh & Voigt (1977) investigated the potential water retention capacity of beech litter compared with pine litter. The quotient of mean retention capacity is 0.87 at beech litter and 0.54 at pine needle. That means 1 g of beech litter can absorb 0.87 g of water. In addition, in the thick layer of litter, especially in beech forests, it was observed tendency of water flow in a temporal concentrated paths which supported generation of funnel flow into the soil matrix. Following this process significant part of surface humus is excluded from the retention process, and therefore water retention is less than expected (Walsh & Voigt 1977). According to Krečmer (1975) surface humus in pine forests can retain up to 32% of precipitation.

Surface humus thickness is influenced by internal processes within the forest ecosystem itself such as downslope transport (Stear et al. 2006; Abe et al. 2009) on the one hand, and external influences, mainly due to the changes in the forest density (e.g. natural disturbances or management activities), on the other hand. Reduction of forest stand density leads to faster decomposition and mineralisation of surface humus, which results in changes of surface humus form and its thickness. The aim of this work was to find out how the surface humus in beech forest with different stand density contribute to the percolation of water into the soil and how surface humus properties contribute to the reduction of soil surface infiltration area.

2. Material and methods

The series of plots were established in the Vtáčnik Mountain (48° 37'32"N, 18° 38'49"E) (Central Slovakia) in the European beech (*Fagus sylvatica* L.) forests. It falls into a cool mountainous and humid region (Lapin et al. 2002) with average annual temperature 3.0 °C, and the annual precipitation amount 950 mm. The soils are classified as Fulvic Andosols (WRB 2007) developed from andesite slope deposits. The texture of the soil represents silty loam.

2.1. Description of the experimental plots

Samples of surface humus for laboratory tracer experiment were taken from four research plots with similar ecological conditions. All four plots have the same SEE exposure, inclination 10°, altitude 1,130 – 1,160 m a. s. l. Beech represents 100% in the stand composition.

Three plots are located in the beech forest with full forest stand density, and one is located in the beech forest with reduced stand density (Fig. 1):

- Plot A (0.8): located in the beech forest with dense regeneration in the understorey (the height of regeneration is appr. 70 cm), stand density 0.8, stand age 130 years, humus form moder;
- Plot B (0.8): located in the beech forest without regeneration, stand density 0.8, stand age 110 years, humus form moder;
- Plot C (1.0): located in the young beech forest, stand density 1.0, stand age 45 years, humus form moder;
- Plot D (0.4): located in the beech forest with reduced stand density, stand density 0.4, stand age 90 years, humus form mull.



Fig. 1. Localization of experimental plots in central part of Vtáčnik Mts. (<http://gis.nlcsk.org/lgis/>, 2017).

2.2. Infiltration experiment

Infiltration experiment was performed on a series of surface humus samples with dimension 50 × 35 cm in triplicate from each experimental plot (in duplicate in case of forest with reduced stand density). The thickness of the surface humus samples range between 5 – 6 cm. In total, 11 surface humus samples were taken for the laboratory analyses. Samples of surface humus from plots with full stand density were taken in autumn 2005 (experimental plots A (0.8), B (0.8) and C (1.0)), samples from plot with reduced stand density in autumn 2007 (experimental plot D (0.4)). In the laboratory, samples of the surface humus were placed on a wire sieve above the white sand. To each sample, a solution of Brilliant Blue FCF dye tracer was applied with concentration 10 g L⁻¹ and in an amount of 2,550 ml, which is the equivalent of 15 mm rainfall. Application of the dye tracer solution consisted of 19 intervals, each lasting 10 minutes, during which the solution of about 135 ml (approx. 0.8 mm of rainfall) was applied to the surface humus. The dye tracer solution percolated through the surface humus layer and infiltrated into the white sand column. After every solute

application the surface humus samples were removed for a short time and the sand surface was photographed.

The sand surface pictures were analysed using the Dyeeye software package (developed by Department of Agronomy, Iowa State University, Ames, IA), acting at the optimization of visual colour differences (Ewing & Horton 1999), which allowed to select areas affected or not affected by dye solution. After that, the colour distribution histogram in each pixel was obtained using Image J software package. For the blue colour, colour range 160 – 180 at 256 colour spectrum was used. The infiltration surface area represents the number of blue pixels in each application interval. In addition to the percentage of infiltration area the number of infiltration inputs in each pictures was detected. The number of infiltration inputs was obtained by counting of blue spots on sand surface at each picture. During the infiltration tracer experiment, a total of 209 pictures (after 19 pictures per area) were obtained that display the infiltration surface area and number of infiltration inputs related to particular simulating cumulative precipitation. Surface humus samples were cut at 5 cm intervals at the end of infiltration test and picture of each cut was taken. These images were used for assessing the degree of the influence of the internal structure of humus for the regulation of water infiltration into the soil (Fig. 2).

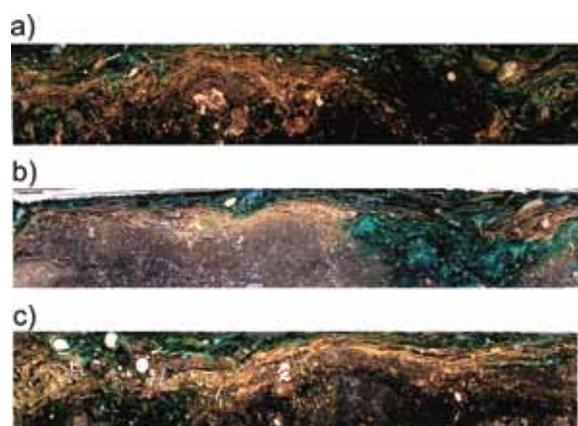


Fig. 2. Surface humus after application dye tracer (Brilliant Blue FCF) solution at the plot A (0.8) (a), plot B (0.8) (b) and plot C (1.0) (c).

2.3. Statistical analyses

The effect of different forest stand density on the cumulative infiltration on surface area and number of infiltration inputs were tested by Analyses of Covariance (Sokal & Rohlf 1995). Subsequently, differences between separate forest stands were tested using Tukey's HSD post-hoc test (Tukey 1949). All statistical analyses were performed using STATISTICA 12 (StatSoft, Inc., Tulsa, USA) software package.

3. Results

Increase in the infiltration surface area is affected by the thickness of sand column placed under the each surface humus sample. It is expected that after reaching the bottom of the sand column the additional infiltrating water is distributed more laterally which causes the increase of infiltration surface area and the decrease of a number of infiltration inputs. Based on this we assumed that the maximal infiltration surface area affected by surface humus properties is reached when the number of infiltration inputs reaches local maximum and starts to decrease. The distribution of number of infiltration inputs and infiltration surface area are shown in the Fig. 3 and 4, respectively.

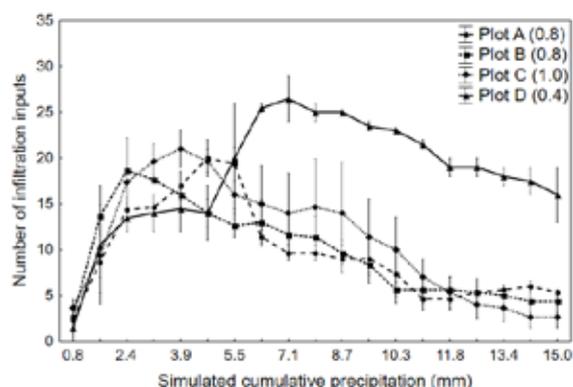


Fig. 3. The distribution of infiltration inputs with increasing cumulative precipitation at plots with different stand density.

Number of infiltration inputs at the plot A (0.8) increases to the value of 2.4 mm cumulative precipitation, at a level of 3.2 mm new infiltration inputs are activated and the maximum number of inputs is achieved at a level of 4.7 mm simulating cumulative precipitation. Plot B (0.8) shows the steepest increase in number of infiltration inputs, with a maximum value achieved even in 2.4 mm simulating cumulative precipitation. Interesting fact is that at this low value of simulated cumulative precipitation the infiltration surface area reaches the highest value of all plots. Number of infiltration inputs at the plot C (1.0) reaches its maximum value at 3.9 mm simulated cumulative precipitation. This value is also the highest value of number of infiltration inputs of all plots with full stand density. The maximal number of infiltration inputs of all beech plots was reached at the plot D (0.4). The number of infiltration inputs is increasing to the value 2.4 mm of simulated precipitation and remained relatively constant. At the value 4.7 mm of simulated precipitation new infiltration inputs were activated and the maximum was reached at the value 7.1 mm of simulated cumulative precipitation.

Based on above mentioned assumption the maximal infiltration surface area at the plot A (0.8) was reached at 4.7 mm of the simulated precipitation what corresponds with $35.11 \pm 6.58\%$ of sand surface infiltration area. This value of infiltration surface area was the high-

est value of all beech forest plots. The minimal infiltration surface area was reached at the plot B (0.8) and was $19.45 \pm 2.52\%$. This value was also reached at the lowest simulated precipitation (2.4 mm) of all studied plots. At the plot C (0.8) the infiltration surface area was $31.92 \pm 1.81\%$ and was reached at 3.9 mm of simulated precipitation. At the plot D (0.4) the infiltration surface area was reached at the highest value of simulated precipitation (7.1 mm) and was $28.48 \pm 1.67\%$.

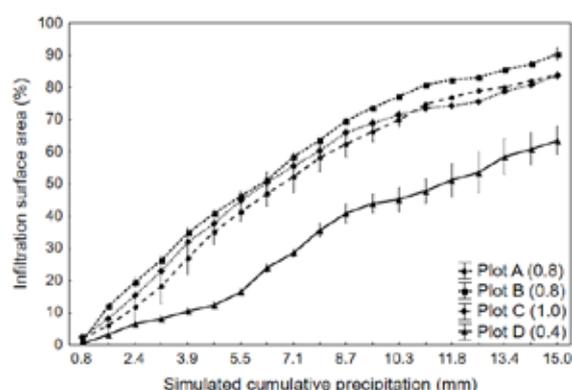


Fig. 4. The growth of infiltration surface area with increasing cumulative precipitation at plots with different stand density.

Statistical tests confirmed a significant effect of the forest stand density on the surface infiltration area (Table 1 and 2). The significant difference between plots with full forest stand density (plots A (0.8), B (0.8), C (1.0)) on one hand and plot D (0.4) with reduced forest stand density on the other hand was found. In the forest with full stand density, the surface infiltration area at the plot B (0.8) differed significantly ($p = 0.05$) from the plots A (0.8) and C (1.0). Similarly, statistical tests have confirmed a significant effect of the forest stand density on the number of infiltration inputs (Table 3). The Tukey's post-hoc test confirmed the statistical difference in infiltration inputs at the plot D (0.4) (forest with reduced stand density) from other plots (beech forests with full stand density) (Table 4). Among the plots with full forest stand density, the statistical significant differences in infiltration inputs were not confirmed.

Table 1. Analyses of covariance of infiltration surface area (significance of *F*-tests).

	SS	Degr. of	MS	F	p
Intercept	582,1	1	582,1	8,174	0,005
Simulated cumulative precipitation	128414,7	1	128414,7	1803,092	0,000
Forest stand density	13084,6	3	4361,5	61,241	0,000
Error	14528,7	204	71,2		

Table 2. Tukey HSD post-hoc test of the differences in the infiltration surface area between plots.

Forest nature	Plot A (0.8)	Plot B (0.8)	Plot C (1.0)	Plot D (0.4)
Plot A (0.8)		0,001439	0,780152	0,000008
Plot B (0.8)	0,001439		0,033339	0,000008
Plot C (1.0)	0,780152	0,033339		0,000008
Plot D (0.4)	0,000008	0,000008	0,000008	

Table 3. Analyses of covariance of infiltration inputs (significance of *F*-tests).

	SS	Degr. of	MS	F	p
Intercept	12503,24	1	12503,24	359,5763	0,000
Simulated cumulative infiltration	978,54	1	978,54	28,1416	0,000
Forest stand density	2117,13	3	705,71	20,2953	0,000
Error	7093,52	204	34,77		

Table 4. Tukey HSD post-hoc test of the differences in the number of infiltration inputs between plots.

Forest nature	Plot A (0.8)	Plot B (0.8)	Plot C (1.0)	Plot D (0.4)
Plot A (0.8)		0,999908	0,571533	0,000008
Plot B (0.8)	0,999908		0,612186	0,000008
Plot C (1.0)	0,571533	0,612186		0,000008
Plot D (0.4)	0,000008	0,000008	0,000008	

4. Discussion

There exist very few studies dealing with infiltration processes throughout the surface humus and therefore information about soil surface affected by infiltration under forest surface humus is very rare. Campbell et al. (2004) studied infiltration processes by simulated rainfall on slope in the oak forest before and after the removal of surface humus. Significant difference was found only in the topsoil to the depth of 30 cm, in subsoil significant differences were not found.

In our study, we found a clear effect of dense beech regeneration on the increase of infiltration at the plot A (0.8). The stems of young beech trees form direct infiltration paths, which allow easier infiltration of water from precipitation and stemflows. This finding is in line with Schume et al. (2004). They stated the rainfall water in beech forests preferentially infiltrate near stems. This phenomenon is related mainly to the initial increase in number of infiltration inputs. Subsequent increase in number of infiltration inputs can be caused by saturating of inhomogeneity in surface humus, which does not correspond directly with the position of beech regeneration stems and their activation for infiltration requires higher precipitation. The number of infiltration inputs at the plot B (0.8) is influenced by the internal structure of surface humus, which is mainly composed of beech compact litter. This compact litter layer supported a priority water movement only in the lateral direction and the vertical movement of water is possible only at the places where the interruptions in the compact humus layer exist (therefore fewer inputs infiltration and higher reduction effect of surface humus on infiltration process). Based on the smallest infiltration area we can conclude that each infiltration paths in surface humus allows to infiltrate the same amount of water in fewer infiltration inputs (they are more abundant). At the plot C (1.0) the number of infiltration inputs is probably affected by the higher number of discontinuities destroy homogeneity of surface humus (e.g. twigs, wild boar activity). The increase in number of infiltration inputs at the plot D (0.4) is affected by the different surface humus form, where water is infiltrating more downward. The different surface humus form is a

product of reduction of forest stand density which results in rapid humus decomposition and disruption of compact Oof-humus subhorizon.

No significant differences in infiltration surface area between the plot A (0.8) and C (1.0) can be attributed to humus form changes during the forest stage changes. Ponge (2002) also found that more favourable humus forms are in disintegration and ingrowth stage of forest stands which partially corresponds with our plots (plot A (0.8) is at the beginning of disintegration stage, plot C (1.0) represents the ingrowth stage). In managed forest (plot D) the surface humus structure has a significant effect on infiltration processes. Pichler (2007) studied how surface humus properties affect retention, accumulation and transformation processes of water and solute in managed forest with different stand density. He found in managed forest under shelterwood cut activation of soil macropore due to surface humus properties (lateral movement of throughfall on short distance). Through these macropores water flows directly into the deeper soil layers, while soil volume affected by infiltrating solute in the upper layers was lower compared to the plot with full stand density. The author also showed that infiltration paths after the dye tracer infiltration tests are typical for macroporous flows. The water flow through macropores in soils under beech forests have been also found by Hümann et al. (2011) and Schume et al. (2003). This macropore preferential flow pathways were formed after coarse roots decay or by mezo- and macro- fauna activities. The macropores in beech forest soils are also very effective drainage system. Through these infiltration processes with synergy of microtopography of soil surface can surface humus support reduction the risk of overland flow (Jost et al. 2012). No overland flow in beech forest was observed also by Hümann et al. (2011) due to higher infiltration capacity and no hydrophobicity of humus layer (surface humus layers were moistened). Infiltration processes of rainfall into the soil affect not only water regime of these soils but also e.g. accumulation and retention of dissolved substances present in the soil solution (Pichler 2007).

Statistically significant effect of reduced forest stand density on the number of infiltration inputs confirms the fact that a complete change of surface humus form is needed to the change of infiltration process. This is confirmed by the fact that on beech plots with full stand density and similar surface humus form the statistically significant differences were not found.

5. Conclusions

Our results showed that surface humus form associated with a beech forest stand density has a distinct impact on distribution of rainfall water and infiltration processes in beech forest. Its properties significantly reduce the potential for surface runoff and contribute to the more selective and downward infiltration of water into deeper soil

layers. The highest impact was observed in beech stand without a regeneration, where the reduction of infiltration surface area was more than 80%. Plot with very dense beech regeneration and plot in young beech stand showed lower level of reduction in the infiltration surface area. Indicator experiment also showed that the biggest differences among the beech forest stands showed the forest stand with reduced stand density. The higher number of infiltration inputs in forest with reduced stand density do not lead to higher infiltration surface area. The reduction of infiltration surface area was over 70% despite the differences in surface humus form, surface humus thickness and higher number of infiltration inputs. From this it can be inferred that the regeneration methods based on small-scale shelterwood cut are in stands composed mainly by European beech an appropriate method of regeneration, taking into account the relevant spatial and temporal variability. As prevention to the unproductive surface humus mineralization, it is necessary to take into account the state of the second-growth stand and subsequent final cutting of parent stand performed after eliminating this possibility.

Acknowledgement

This contribution is the result of the project implementation VEGA 1/0783/15, VEGA 1/0710/17 and APVV-15-0176 supported by the scientific grants awarded by Research and Development Agency.

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Interaction of Brilliant Blue dye solution with soil and its effect on mobility of compounds around the zones of preferential flows at spruce stand

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Abstract

We performed field experiment with 10 g l⁻¹ concentration of Brilliant Blue solutes in 100 l of water sprinkling on 1 × 1 m surface of the Dystric Cambisol. Consequently, four vertical profiles were exposed at experimental plot after 2 hours (CUT 2), 24 hours (CUT 24), 27 hours (CUT 27) and after 504 hours (CUT 504) in order to analyse spatio-temporal interactions among the BB solution (Na-salts), soil exchangeable complex and fine earth soil (%) samples extracted from both the high and low coloured zones located around the optically visualised macropore preferred flow (PF) zones. The concentration changes were quantifying via soil profiles not affected by BB (termed as REF) located in the close vicinity of experimental plot. Observed changes in pH (H₂O), chemical composition of fineearth soil, as well as in concentration of Na⁺ in soil exchangeable complex to suggest, the BB dye solution didn't represent an inert tracer, but compounds strongly involved in reaction with surrounding soils. Recorded chemical trends seems to be the result both the competitive processes between the Na⁺ of BB dye solution and composition of surrounding soil exchangeable complex, as well and the spatial-temporal controlled mechanism of dye solution transfer in soil.

Key words: preferential flow; compounds migration; spatial-temporal evolution; dye solution- soil interaction; Brilliant Blue dye

Editor: Pavel Pavlenda

1. Introduction

Bundt et al. (2001a, b) were probably the first to investigated whether preferential flow path (PF) have higher microbial biomass and different microbial community structures than the rest of soil at a forested site. Bogner et al. (2012) showed the different pH values, concentrations of C, N, Fe, Ca and Mg in zones of preferential flow in comparison with rest of soils. The cited authors used Brilliant Blue (BB) dye solution to visualisation of macropore preferential flow path and its research was based on assumption the stained areas of preferential flow paths remain stable down to subsoil (Ritsema & Dekker, 2000) and the BB represents an inert compound not involved into the dye solution-surrounding soil interaction.

On the other hand, Flury & Flühler (1994) noted the BB dye represents Na-salts much more susceptible to sorption processes in soil when compared to anionic forms of the dye and in consequence, its complex reactions with surrounding, soil can alter soil sorption characteristics leading to risk of fatal misinterpretations

by studying chemical processes in soil while using dye solution (Flury & Wai 2003). The properties of BB as Na salts in field condition have not been explored till now, and only the results of laboratory batch sorption studies are available to show, the adsorption of BB on soil particles can be described by the Freundlich isotherm if the dye concentration is low 0.1 – 15 mg l⁻¹ (Flury & Flühler 1995; Perillo et al. 1998), or by the Langmuire isotherm by concentrations 100 – 5000 mg l⁻¹ (Ketelsen Meyer-Windel 1999). Some breakthroughs of these experiments to show relationships among the dye sorption, the pH, the clay content as well as the composition of secondary minerals in soils (Germán-Heins & Flury 2000).

The role on sodium as component of Brilliant Blue FCF (BB) (5.8% of the BB molecule weight) may have essential effect not only on movement and redistribution of chemical elements around the PF paths (Sparks 2003), but also on modification of soil structure and resulting water transport processes on the boundaries between the gravitational pores and the soil matrix themselves (Brady & Weil 2001).

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The information about spatial-temporal controlled process of dye solution movement around the zones of macroscopically visible PF pathways in soils are missing till now, due to the disadvantage of staining experiments during the soil sampling: excavation of pedon is destructive and experimental results cannot be repeated at the same location (Flury et al. 1994), hence the sampling is limited usually per sole vertical dye pattern of soil profile exposed on experimental plot usually 12 or 24 hours after the dye application (Flurry & Flühler 1994; Flurry et al. 1994; Hagedorn & Bundt 2002; Bogner et al. 2012; Bundt et al. 2001; Garrido et al. 2014). On the other hand, the movement of water in soil around the zones of PFs can be extremely dynamic process, different types of PFs: macropore flow, finger flow (Ritsema & Dekker 1995) and funnelled (or heterogeneous) flow (e.g. Kung 1990; Roth 1995) may occur individually, in tandem (Jury & Horton 2004), or over time they can convert to s matrix flow (Jarvis & Dubus 2006).

In order to evaluate the concept of spatial-temporal controlled movement of dye solution in soils, as well as to screening the role of sodium during the BB dye solution movement in soils around the zones of PF, we designed the field experiment based on next working hypothesis:

- the object of study on experimental plot – a soil pedon – represents spatially homogenous body, with identical stratification of soil horizons, identical soil textures, the same chemical and mineralogical composition of fine earth soil and volumetric content of soil skeleton,
- macropore PF pathways visualised by BB dye solution in particular soil profiles (CUTs), exposed on experimental plot in different time will represents 2D cross sections of different PF pathways, but with common history of dye solution movement,
- the observed chemical changes in dye pattern profiles exposed in different time are to be the consequences of dye solution movement and its interaction with surrounding soils,
- the soil profiles labelled as reference (REFs) non affected by dye solution irrigation experiment and excavated in close vicinity of experimental plot, with identical stratification of soil horizons, soil textures, chemical, mineralogical composition and volumetric content of soil skeleton as recorded on the experimental plot, will enable to quantify the effects of chemical changes observed.

The objective of proposed article is:

- (I.) to analyse and to quantify the chemical changes in composition of fine earth soils sampled of soil profiles exposed in different time induced by Na salt BB dye solution movement in soil pedon after irrigation experiment within the spatial-temporal framework,

- (II.) To analyse and to quantify the spatial-temporal chemical changes in concentration of Na⁺ in soil exchangeable complex and corresponding changes at pH (H₂O) induced by application of Na salt BB dye solution,

- (III.) To evaluate the consequences of finding obtained regarding the concept of spatial-temporal controlled movement of dye solution in soils proposed.

2. Material and methods

2.1. Description of the experimental site

The research was performed at Panský diel (N 48°48'25,76", E 19°09'20,47") in Slovakia at altitude of 910 m above sea level, covered by a 90-year old mixed forest of Norway spruce (*Picea abies* [L.] Karst.), as a dominant species, silver fir (*Abies alba* Mill.), and European beech (*Fagus sylvatica* L.), Weymouth pine (*Pinus strobus* L.) and European larch (*Larix decidua* Mill), where the climate vary from moderately warm, humid to moderately cold with mean annual temperature of 4.1 °C, and where the mean annual precipitation is 1,023 mm.

The experimental site was located on a flat area with negligible inclination, and its geology contained complexes of sediments formed from schist, acidic granites, arkoses, greenish and reddish mica-slates and quartzite (Andrusov et al. 1985). These rocks were also the forming substrate of the local soil. The soil in the experimental site is *Dystric Cambisol* (IUSS Working Group WRB, 2015), with three mineral horizons (Au, 0 – 5.0 cm, Bv horizon 5 – 110 cm with gradual transition to C horizon).

2.2. Field and laboratory work

2.2.1 Dye tracer application

In April 30, 2012, BB solution with 10 g l⁻¹ concentration was applied by a sprinkler with 100 mm h⁻¹ intensity over a 1 × 1 m plot. Prior to the BB application, the litter horizon was removed because of its high interception capacity. After the dye application a series of four vertical profile cuts were excavated at different times after 2 (CUT 2), 24 (CUT 24), 27 (CUT 27), and 504 hours (CUT 504) after the application of the BB solution. The air temperature, precipitation, and potential evapotranspiration at the experimental site monitored by automatic station of the EMS Brno Company, are presented in Fig. 1. As can be seen from the Fig. 1, no rainfall was fell during the period between the BB application and the excavation of the CUT 2, CUT 24, and CUT 27 profiles, but some rains fell between the CUT 27 and CUT 504 exposition times (Fig. 1).

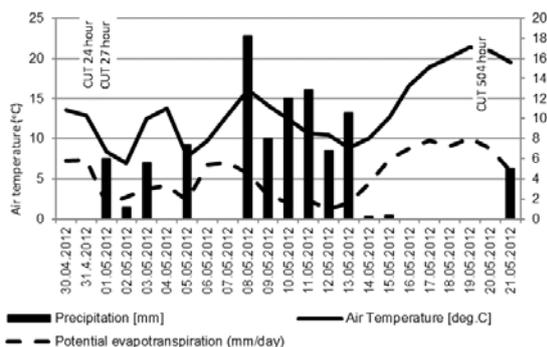


Fig. 1. Temperature, potential evapotranspiration and precipitation at the experimental site.

2.2.2 Dye coverage determination

After exposition of particular CUTs, the 1×1 m grey frame was installed around each soil profile and digital photographs were obtained. After taking digital photographs several procedures were performed to evaluate the spatial concentration of the BB dye (i) Geometric correction; (ii) white-balance and exposure correction; (iii) calibration and (iv) evaluation of the dye concentration. To evaluate dye coverage (D_c) the processing framework in GNU R (R Development Core Team) and C with help of ImageMagick image processing library and with a resolution of $500 \times 1,000$ pixels (i.e., one pixel represents a 1×2 mm), were used.

Dye coverage (D_c) calculation is described in Eq. [1] (Flury et al. 1994):

$$D_c = \left(\frac{D_a}{D_a + ND_a} \right) \times 100 \quad [1]$$

where, D_a is the surface area in the cut that stained by dye, and ND_a is the surface area in the cut that is not stained.

2.2.3 Sampling procedure

Three samples from each 10 cm layer of each CUTs by Kopecky-cylinder with volume of 100 cm^3 were taken with consideration of colouring intensity: samples labelled as NC (from sites not affected by BB dye), MC (taken from zones with middle colouring) and IC (samples intensively coloured by BB dye solution). Totalling, 120 soil samples were taken for physical and chemical analysis during 20 days from CUT 2 to CUT 504 soil profiles, but only NC and IC samples (80 samples in total) were taken into the account regarding proposed article. Finishing the sampling at experimental site, the soil samples were taken from the both the right and the left sides of CUTs located approx. 35 cm apart from 1×1 m experimental plot, where no BB tracer had been applied on soil surface (referred as REFs). Two samples were taken from each 10 cm layer, i.e. 20 samples in total from REF zone.

2.2.4 Soil texture and skeleton content determination

In order to specify soil skeleton volume in soil samples from both the CUTs and the REF profiles, separation of the skeleton from the fine earth was achieved by dry and wet sieving, additional washing of the rock fragments gave clast with clean surfaces following the procedure proposed by Corti et al. (1998) and Certini et al. (2004). The soil skeleton volume was obtained by water displacement after the clast were completely water saturated (Corti et al. 1998). Soil texture, or size distribution of mineral particles was determined by standardized sedimentation pipette method in water column in sense of Fiala et al. (1999).

2.2.5 Determination of Na^+ in soil exchangeable complex

The concentration of Na^+ in soil exchangeable complex was determined by its replacing with $0.15 \text{ M NH}_4\text{Cl}$ and by AAS analysis of leachate via Avanta AAS, with nitroacetylene burner with automatic rotation.

2.2.6 Determination of pH (H_2O)

The pH (H_2O) as an indication of the acidity or alkalinity of soil was measured according to Fiala et al. (1999), by pH meter Hamma HI 221 of soils suspended in a distilled water (from which CO_2 was abstracted via 30 min. boiling), under 1 : 2.5 soil : water ratio and mechanical stirring. Laboratory balance Mettler PL 1200 were used for weighing of fine earth (20.00 g).

2.2.7 Determination of total content of Al, Si and Fe

Total chemical analyses of soil (called as silicate analysis) of REF soil profiles were determined by inductively coupled plasma atomic emission spectrometry (ICP-AES) by EL spol. s r. o. accredited laboratory. However, before the ICP-AES analyses, the soil samples were crushed and pulverized in agate mill. After that, the specific dissolution was made.

The dissolution of Na_2O , K_2O , LiO_2 , P_2O_5

The HF and HClO_4 were added into the samples in the Teflon dishes and the samples were evaporated. After cooling, HF and a the saturated H_3BO_3 solution were added. After drying, the samples were dissolved in nitric acid (1 : 1) and transferred into the graduated flasks. After evaporation to dryness and next cooling, the samples were dissolved in HNO_3 1 : 1 and, after cooling, the samples were transferred into the polypropylene graduated flasks.

The dissolution of SiO_2 , Al_2O_3 , Fe_2O_3 , TiO_2 , MnO , CaO , MgO

Na_2O_2 and samples were weighed into the Pt crucibles, where they were thoroughly mixed with plastic rod. The crucibles with the lids were put into the muffle furnace. After removing the crucibles from the furnace, the samples were cooled, transferred into beakers and sprinkled with hot distilled water. After 20 minutes, concentrated HCl was added into the samples and the samples were leached in the baths. Subsequently, the crucibles, as well as the lids, were rinsed with distilled water and the resulting aliquots were poured into the graduated flasks, to which the internal standard solution, as well as the distilled water were added to the marks, and after that, the samples were mixed.

S – Total

The samples were weighed into the beakers, where a 1 : 3 mixtures of HCl and HNO_3 were added. The beakers were covered with a glass slides where they cooled to next day. After that, the solutions were heated for 1 hour in sand bath. Subsequently, the glass slides were rinsed with distilled water and the solutions were evaporated to dryness. Concentrated HCl was added, causing the dissolution of samples under a clock glasses in a sand bath for 30 minutes. After that, the glass slides were rinsed with distilled water, the solutions were cooled, and transferred with distilled water into the graduated flasks. The graduated flask was filled with distilled water to the marks and thoroughly mixed.

S – SO_3

The samples were weighed into the breakers. HCl 1 : 1 was added, the beakers were covered with a glass slide and, upon completion of the reaction, they boiled on a cooker. After cooling, the slides were rinsed and the samples were poured into graduated flasks filled with distilled water and thoroughly mixed.

S sulphidic: S total – SO_3

The XRF spectrometry for analysis of Al, Si, Fe concentration in fine earth soil samples was applied, as validation characteristics of this analytical method provided by Vojteková et al. (2010) to show its compatibility with the methods used in reference laboratories. We used Thermo Scientific Niton XL3t Series XRF analyzer with GOLDD technology, with low detection limits of light elements (e.g., Mg, Al, Si, P). The sensitivity, or limits of detection (LOD) in ppm (mg kg^{-1}) of the Niton XL3t GOLDD technology analyzer, for SiO_2 matrix, SiO_2 matrix with 10% iron, and a typical Standard Reference Material (SRM) can be find on thermofisher.com website. During the measurement, the Mining Calibration Mode was used and the MAIN, HIGH, LOW, LIGHT filters with time measurement of 30.0 s. per filter were applied.

The fine earth soil samples were before XRF analyses pulverized and homogenized using the RETSCH Mixer

Mills (MM 301). After that, by SPECAC hydraulic press with a maximum pressure limit of 15.000 kg, the pellets with diameter (32 mm) were prepared. In total, 80 pellet samples from IC and NC zones of CUT2 – CUT 504 were measured, 20 pellet samples from REF profile, and each sample were measured twice, to ensure representativeness of acquired chemical analyses.

2.2.8 The stocks of elements

Because we knew the bulk density and volume of the soil (as the soil samples were taken by Kopecky cylinder of 100 cm^3), i.e., fine earth + soil pores, without coarse fragments with diameter $>2 \text{ mm}$, the concentration of chemical elements, or Na^+ concentration in soil exchangeable complex (CC) stock (CCS) was computed by assuming the CCS in all ten 0.1 m layers of all four soil profiles (CUTs) derived from both the IC and the NC zones surrounding the PF pathways as well as separately for the REF CUTs not affected by BB dye, at each sampling point according to:

$$CCS = BD \times CC \times d \times (1 - cf) \quad [2]$$

where CCS , BD , CC , d and cf are, element stock (kg m^{-2}), bulk density (kg m^{-3}), element stock (kg kg^{-1}), soil layer thickness (0.1 m) and volumetric fraction of soil skeleton ($\text{m}^3 \text{ m}^{-3}$), respectively.

3. Results

3.1. Verification of working hypothesis

The study of soil texture differences among the particular CUTs and the REF zone according to USDA soil taxonomy detected minimal differences regarding soil texture (Fig. 2) and volumetric skeleton contents (Fig. 3). The homogeneity of soil pedon under investigation was confirmed by both the electric resistivity and the GPR measurements (Bebej et al. 2013) to suggest, the minimal spatial variances in soil pedon exist. From mineralogical point of view, the soil skeleton is monotonous and consist of clasts of extremely acid quartzite, sandstones and mica slates.

The mica slates are represented by grey-green one's, and red coloured varieties, but its chemical composition, as compared with the fine earth soil samples (Table 1), is relatively similar. Generally, the silicate analyses of fine earth soil samples to show no differences in chemical and mineralogical composition of soil in upside of REF profile (0 – 60 cm), therefore regarding the skeleton composition, its volumetric content and soil textures in the CUTs soil profiles we can propose the chemical composition is similar that determined in REF profile, and working hypothesis proposed about spatial homogeneity of soil pedon is true.

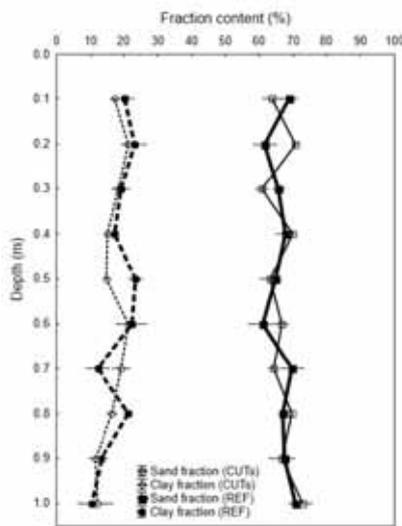


Fig. 2. Particle size distribution of sand and clay fractions within the CUTs and REF zone profiles.

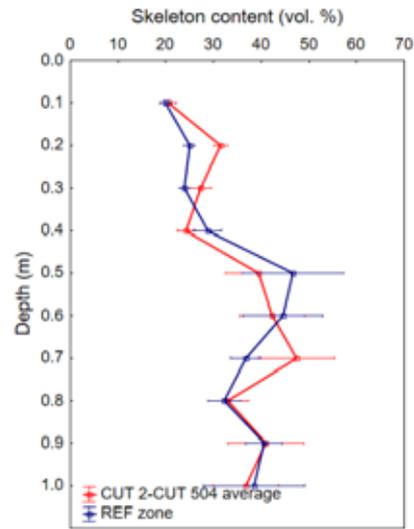


Fig. 3. Volumetric skeleton contents in soil samples with withdrawal from both the experimental plots (CUT 2 – CUT 504) and the REF zone.

3.2. Characterisation of dye pattern profiles

Typical infiltration patterns observed in particular CUTs, as well as their dye coverages (D_c) are documented in Fig. 3. In all soil profiles macropore dye pathway structures are well visible, but some differences among them also manifested. Within the CUT 2, macropore pathways are narrow and the top of CUT 2 profile is only slightly covered by BB dye. On the contrary, within the CUT 24 the top layer of soil profile is heavily covered by BB dye and in both the CUT 24 and CUT 27 profiles the macropore pathways are broad what indicate the growth in macropore-soil matrix interaction. The macropore pathways in CUT 504 is different the rest CUTs and finger-like structures are evident.

3.3. pH (H_2O) values

The distribution of pH (H_2O) values in both the experimental plot (CUT 2–CUT 504) and the REF soil profile are presented in Fig. 4. It can be seen from Fig. 4, that irrigation with BB dye solution (pH = 7) abruptly increased the pH (H_2O) values recorded in soil profiles of experimental plot, and that these changes are visible in all soil samples from both the IC and the NC zones. The second important feature is zonal character of pH (H_2O) curves regarding the REF zone, while this trend abruptly changes about 60 cm depth (Fig. 4): in the top part of the soil profiles the drop in pH (H_2O) is observed from CUT 2 and CUT 24 to CUT 505 profiles, while below 60 cm this trend is opposite.

Surprisingly, the pH (H_2O) changes observed in both the IC and the NC zones manifest, in general, in similar intensity, hence colouring intensity of soil samples is not the indication of pH changes.

Table 1. The silicate analyses of fine earth soil samples from soil profile of REF zone as compared with chemical composition of grey-green slates (GGS), and red-coloured slates (RS) of soil skeleton.

	REF 10 cm	REF 20 cm	REF 30 cm	REF 40 cm	REF 50 cm	REF 60 cm	REF40 cm (GGS)	REF40 cm (RS)
SiO ₂	68.96	68.05	68.76	68.94	70.04	68.81	74.81	70.04
Al ₂ O ₃	14.75	14.91	14.68	14.83	14.13	14.86	14.02	14.13
Fe ₂ O ₃	4.28	4.41	4.33	4.41	4.21	4.36	1.93	4.21
FeO	0.6	0.74	0.4	0.3	0.41	0.14	0.2	0.41
TiO ₂	0.612	0.636	0.613	0.631	0.613	0.629	0.188	0.613
MnO	0.033	0.027	0.042	0.026	0.025	0.024	0.039	0.025
CaO	0.03	0.04	0.12	0.06	0.05	0.06	<0.01	0.05
MgO	1.38	1.4	1.4	1.4	1.36	1.48	1.27	1.36
Na ₂ O	0.49	0.46	0.48	0.46	0.46	0.44	0.69	0.46
K ₂ O	4.07	4.04	4.13	4.08	3.85	4.17	4.23	3.85
Li ₂ O	0.009	0.01	0.009	0.01	0.009	0.009	0.005	0.009
P ₂ O ₅	0.08	0.12	0.08	0.08	0.08	0.09	0.07	0.08
S ²⁻ total	0.01	0.01	0.02	0.02	0.01	0.01	<0.01	0.01
S sulfidic	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01
Loss of ignition	4.94	5.01	4.78	4.56	4.66	4.46	2.83	4.66
Loss of drying	0.66	0.68	0.62	0.64	0.55	0.84	0.27	0.55
Total	100.9	100.5	100.5	100.4	100.5	100.4	100.6	100.5

3.4. Na⁺ concentration in soil exchangeable complex

The sodium represents 5,8% of BB FCF dye molecule weight component; therefore, the sodium represents important part of dye solution to be applied into the soil during irrigation experiment.

The analyses of Na⁺ in dye pattern profiles compared to REF revealed, that in CUT 2 there are biggest differences in Na⁺ concentration between IC zones and REF (Fig. 5), and that in the top part of the soil profile (0 – 60 cm) the gradual drop in Na⁺ concentration i from CUT 2 to CUT 505 profiles s observed in such a way as in case of pH (H₂O) (Fig. 4).

In case of soil samples extracting from NC zones of macropore PF pathflows the differences in Na⁺ concentration between particular CUTs and REF are marginal, especially in bottom part of soil profiles (Fig. 4 b). The discrepancies between pH (H₂O) values and Na⁺ concentration in both the IC and NC soil samples can be accounted by increasing of exchangeable sodium in soil exchangeable complex as compared of different soil-water ratio existing in IC and NC zones of macropore pathflow (Abrol et al. 1988). In sodic soil, the different Na⁺ concentration in soil exchangeable complex existing at different soil : water ratios in IC and NC zones can produce identical pH (H₂O) values.

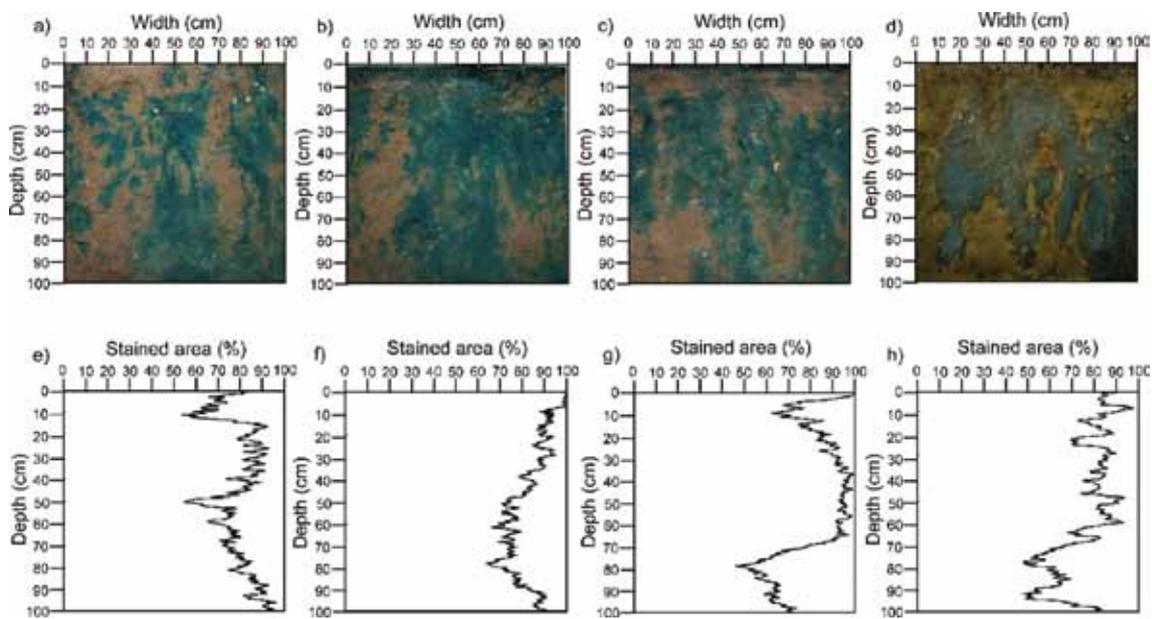


Fig. 4. Infiltration patterns and dye pattern coverages (bottom) within the CUT 2 (a), CUT 24 (b), CUT 27 (c) and CUT 504 (d).

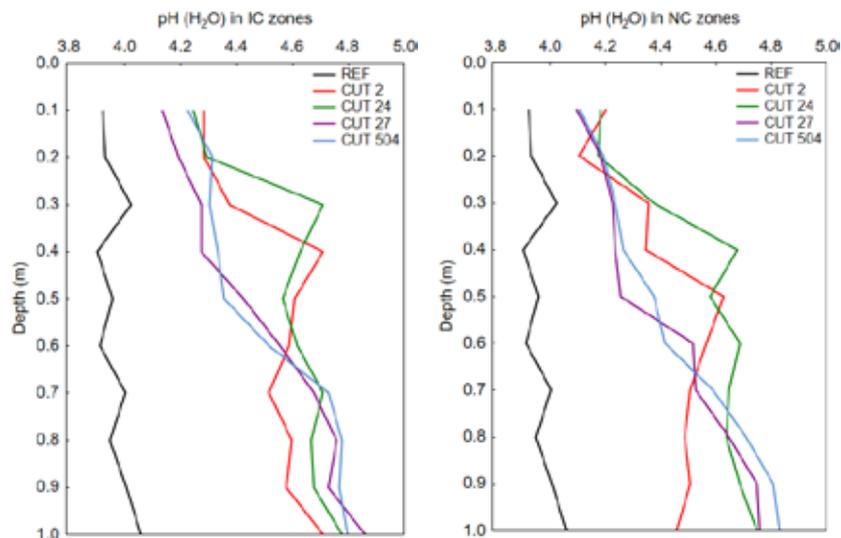


Fig. 5. The pH (H₂O) changes in IC and NC zones of macropore PF pathflows of CUT 2 to CUT 504 soil profiles regarding the pH (H₂O) in soil profile of REF zone.

According to Abrol et al. (1988) difference about 1 pH unit indicates that the soil contains more than 15 percent exchangeable sodium. The principal cause of alkaline reaction of sodic soils is the hydrolysis of the exchangeable sodium by H₂O which results in an increase in the OH⁻ ion concentration and increased soil pH. Ions such as Na⁺ are unable to compete as strongly as the more tightly held ions such as Ca²⁺ and Mg²⁺, so exchangeable Na⁺ is hydrolysed to a much greater extent and produce a higher pH than do exchangeable Ca²⁺ or Mg²⁺ (Abrol et al. 1988).

3.5. Al, Si and Fe concentration in fine earth soil samples

The XRF analyses of Al, Si and Fe of fine earth soil samples extracted from IC zones of macropore PF path flows of CUT 2 – CUT 405 soil profiles (Fig. 7) in general to show great concentration changes regarding REF soil profiles and this changes reaches its maximum within the CUT 2 profile. In this case for all analysed elements marked depletion in concentration – regarding to REF – is observed. On the other hand, in the case of CUT 27 and CUT504 soil profiles, the concentration of Al, Si and Fe is close to concentration measured in REF soil profile.

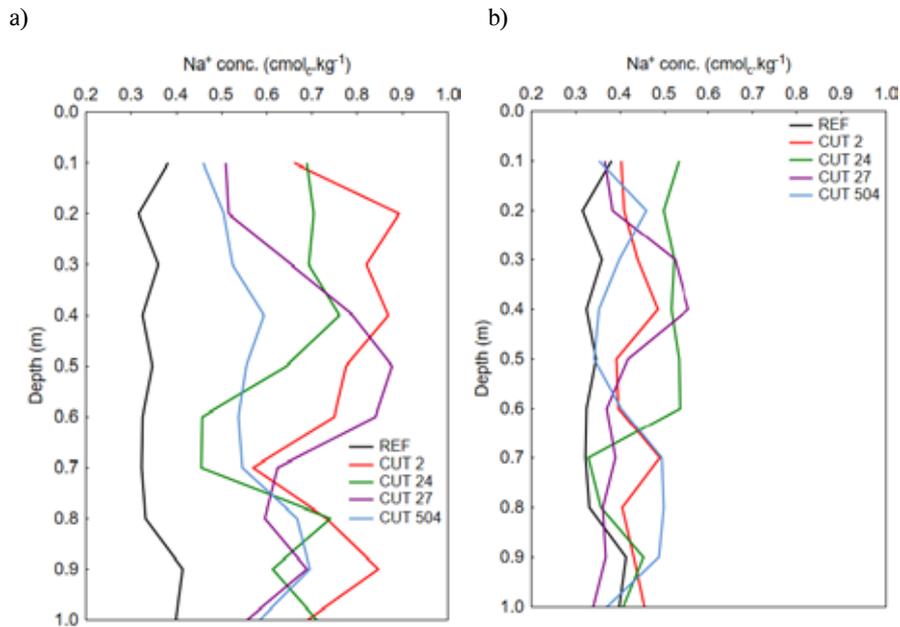


Fig. 6. The concentration changes of Na⁺ (cmol_c kg⁻¹) in soil exchangeable complex extracting from IC (a) and NC (b) zones of macropore PF pathflows of CUT 2 – CUT 504 dye pattern profiles regarding the REF soil profile.

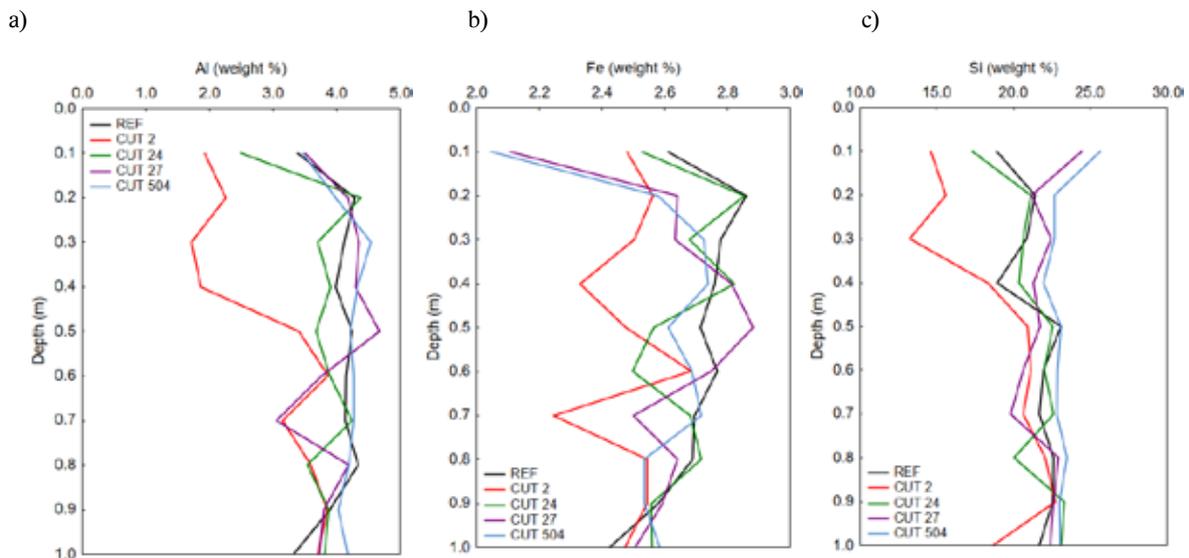


Fig. 7. The concentration changes (weight %) of Al (a), Fe (b) and Si (c) in fine earth soil samples extracted from IC zones of macropore PF path flows of CUT 2 – CUT 405 soil profiles determined by XRF analyses regarding the REF zone soil profile.

4. Discussion

The mobility and transport of Al, Fe, Si and organic matter in soils at present is especially related with the podzolization process issue. According to Bloomfield (1954) dissolved organic matter play an important role in the translocation of Al and Fe in podzols. By fulvate theory (e.g. Petersen 1976) the fulvate acids dissolves primary and secondary minerals as well as the amorphous materials in the E horizon to form dissolved organic Al/Fe complexes. By “anorganic” podzolization theory (Anderson et al. 1982; Farmer & Lumsdon 2001) inorganic Al, Si and Fe are translocated via (proto)imogolite sols from the eluvial to the illuvial horizons, where its precipitation in the form of imogolite, causes the development of Bh and Bs horizons. Gustafsson et al. (2001) propose immobilization of Al in B horizons in the form of inorganic precipitates at the higher pH values (> 4.2), however, they suggest that precipitation is induced by the equilibrium of dissolved Al with $\text{Al}(\text{OH})_3(\text{s})$. Lundström et al. (2000), in contrast with the classical fulvate theory propose that complexation of Al and Fe to low-molecular weight (LMW) organic acids plays a main role in the mobilization of Al, Fe and organic matter from podzol E horizons and microbial degradation of the LMW organic in the soil causes precipitation of inorganic Al and Fe complexes. Mossin et al. (2002), Van Breemen & Burman (2002) supposed that different mechanisms of podzolization taken place in different locations, regarding the composition of parent materials and climate conditions.

Total aluminum is measured in soils because it provides useful information on the characterization of soils with respect to the origin of parent materials and weathering (Mulder et al. 1989), however, much higher attention is addressed to exchangeable and extractable aluminium study, due to formulation of lime requirements for acid soils (Kamprath 1970, 1980; Juo & Kamprath 1979; Oates & Kamprath 1983) and because of its importance as a predominant cation in acid soils, where the exchangeable aluminum is a critical variable in establishing effective cation exchange capacity (ECEC) values. (Mulder et al. 1987; Rasmussen et al. 1991).

Once soil pH is lowered much below 5.5, aluminosilicate clays and aluminum hydroxide minerals begin to dissolve, releasing aluminum-hydroxy cations and $\text{Al}(\text{H}_2\text{O})_6^{3+}$ that then exchange with other cations of soil colloids. The fraction of exchange sites occupied by $\text{Al}(\text{H}_2\text{O})_6^{3+}$ and its hydrolysis products can become large once the soil pH falls below 5.0. Furthermore, as the pH is lowered, the concentration of soluble aluminum, which is toxic, increases.

Generally, the mobilization of aluminium may be due to: dissolution of Al-compounds via acidification process, ion-exchange of Al-ions with cations as H^+ , Ca^{2+} , Mg^{2+} , NH_4^+ , and finally, by complexation with organic substances, like humic and fulvic acids (Kotowski et al. 1994). Kotowski et al. (1994) studied the mobilization of aluminium in laboratory experiments using podzol

soils and mineral acids (H_2SO_4 , HNO_3) and fertilizer salts i.e. $(\text{NH}_4)_2\text{SO}_4$ and HN_4NO_3 . They found, that mobilization of aluminium by HNO_3 was in most cases higher than by H_2SO_4 for the same concentrations, while for fertilizer salt solutions the mobilization of aluminium was between that observed for H_2SO_4 and HNO_3 . These results demonstrate the sodium as essential constituent of BB dye (sodium salt) may mobilize the aluminium from soil exchangeable soil complex of acidic soils, via soil-exchangeable processes.

In acid soils, Al^{3+} and the associated hydrolysis products AlOH^{2+} , and $\text{Al}(\text{OH})_2^+$ dominate exchange phase charge followed by Ca , Mg^{2+} , Na^+ and K^+ (Essington 2015). However, high concentration of one cation will displace an adsorbed cation from the exchanger even if adsorbed cation is higher on the lyotropic series by Mass Action Law. High concentration of sodium in the initial BB solution may indicate situation the mass action law can come in force and Na^+ will displace an adsorbed cation from the exchanger even if the adsorbed cation is higher on the lyotropic series – e.g., Al^{3+} (Plaster 2014).

The irrigation experiment with BB dye solution on experimental plot caused dramatic changes in pH (H_2O) characteristics of soil samples from CUT 2 – to CUT 504 (Fig. 1). The abrupt increase of pH observed in CUT 2 and CUT 24 profiles to show, the dissolved Na^+ ions of dye solution caused increase of exchangeable sodium in acid soil exchangeable complex and Al^{3+} and its hydrolysis products were partly displaced and mobilised. The Fig. 4a and Fig. 5b to illustrate the antagonistic behaviour of Na^+ as constituent of soil exchangeable complex and the aluminium in fine earth soil samples of IC zones within the CUT 2 profile what indicate the ion-exchange reaction can partially explain the chemical changes observable in Al concentration in CUT 2 profile. However, the overall Al, Si and Fe chemical changes recorded within the CUT 2 profile regarding the REF soil profile to suggest the another processes governs the observable mass depletion of fine earth soil samples within this profile and that is way the observed Al (%) vs. Na^+ ($\text{cmol}_c \text{kg}^{-1}$) negative correlation is statistically non-significant ($p = 0.082$) for IC zones.

Existing breaking point in concentration of Al, Si and Fe observed between the CUT 2 and the rest CUTs was changed by slow gradation changes in the case of rest CUTs, and generally, the mass depletion of Al, Si and Fe in top part of CUT 2 soil profile suddenly turned into the enrichment at the same part of the CUT 27 – CUT 505 profiles (Fig. 6). All this means the time factor play key role and that the reasons of dye solution transport inversion should be understood and explained.

The basic characteristics of two factorial ANOVA for concentration of Al, Fe and Si in fine earth soil, as well as for concentration of Na^+ in soil exchangeable complex in soil samples from CUT 2 to CUT 504 soil profiles are presented in Table 2. As can be seen, depth, time as well as their concurrence is statistically very significant for Al, Fe and Si, besides the Na^+ , where statistical dependence

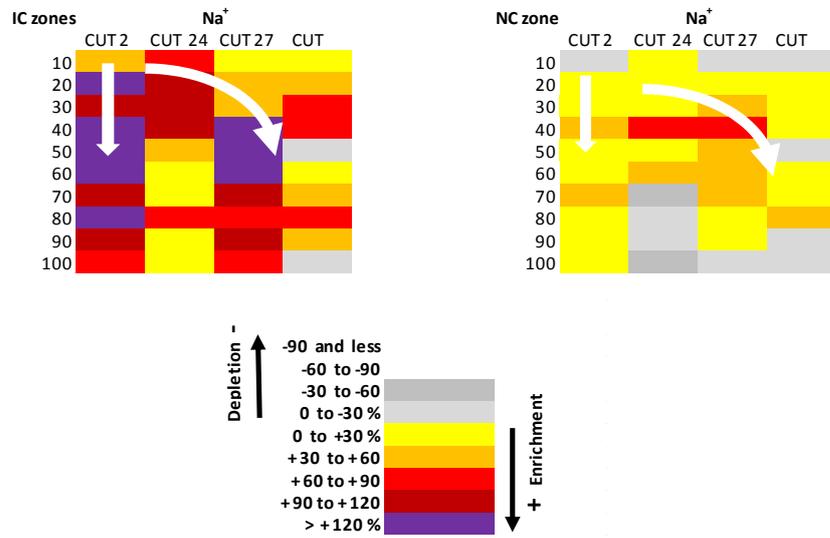
was supported only by one factorial ANOVA. It follows from these data, that the Na⁺ concentration is very significantly influenced by colouring intensity ($p = 0.000$) and time ($p = 0.001$), while for Al, Fe and Si the colouring intensity (IC and NC zones) is non-significant factor from statistical point of view.

Different behaviour of Na⁺ on one hand, and Al, Fe and Si regarding to IC and NC zones on other hand, is key in order to understand the specific behaviour of sodium:

- 1). sodium is essential part of BB dye solution and regarding to other elements present in soils, his concentration is non-stoichiometric, and is controlled by

- 2). sodium as part of dye solution is transported in soil according the processes of adsorption isotherm, where the partitioning of a solute between the aqueous solution and the sorbed phase take place (Kasteel et al. 2002).
- 3). on the interfaces between the dye solution and surrounding soil also the ion exchange processes take place, principally different of sorption processes which take place on free surface sites, while the ion exchange is controlled by the ionic composition of

Na⁺ concentration changes in soil exchangeable complex



Corresponded Al, Si and Fe concentration changes detected by XRF analyses in IC and NC zones

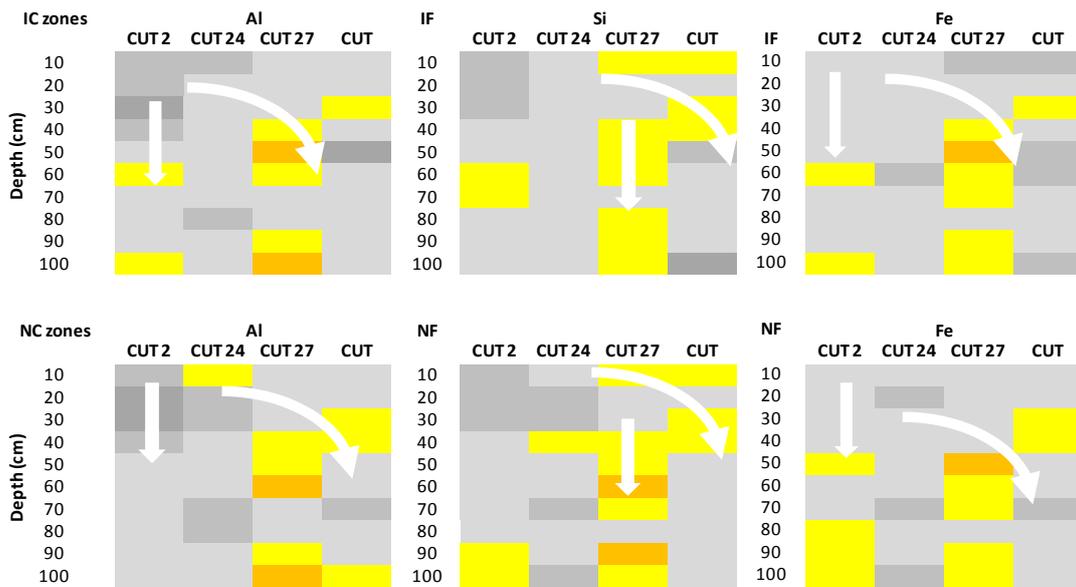


Fig. 8. The concentration changes (%) of Na⁺ in soil exchangeable complex (a), and corresponded Al, Si and Fe concentration changes in coexisted fine earth soil samples extracted from both the IC and NC zones of macropore PF pathflows of CUT 2 – CUT 405 soil profiles (b).

the liquid phase (Nagy & Kónya 2009). In the case of common action of sorption and ion exchange processes, the spatial separation of sodium and the cations displaced of soil exchangeable complex to be the consequence, and coloured, sodium rich IC zones will not spatially coincide with zones, where the displaced cations to be accumulated,

- 4). the chemical changes observed in the CUT dye pattern profiles to show the younger processes to be superimposed to older ones', or depletion in concentration of chemical elements suddenly change to enrichment. The effect of such a processes, in consequences, destroy former NC and IC zones, and the statistical dependencies between the sodium (coloured IC zones) and other chemical components activated by dye solution: soil interaction will reduce.

Table 2. Two factorial analyses of variance of Al, S, Fe and Na concentration according to depth and time and its interactions.

Parameter	Tested factor					
	Depth [cm]		Time [h]		Depth [cm] * Time [h]	
	F-ratio	p	F-ratio	p	F-ratio	p
Al conc.	19.58	0.000	220.26	0.000	12.62	0.000
Fe conc.	13.10	0.000	12.90	0.000	7.05	0.000
Si conc.	17.20	0.000	86.68	0.000	7.40	0.000
Na ⁺ conc.	0.63	0.771	2.58	0.059	0.71	0.845

The interesting fact to imply from documented analytical data regarding the statement of Allaire et al. (2009) suggested, the standardization of tracer application methods is needed in order the results between different studies to be comparable. For an example, the time of vertical soil profile exposition usually vary from 12 hours (Kasteel et al. 2002) to 1 day (24-hour) after finishing the infiltration experiment (Flurry & Flühler 1994; Flurry et al. 1994; Hagedorn & Bundt 2002; Bogner et al. 2012; Bundt et al. 2001; Garrido et al. 2014), or the samples from several vertical profiles exposed on one experimental plot are interpreted without consideration of time factor role (Bundt et al. 2001; Alaoui & Goetz 2008). The same statement concerns the concentration of applied BB dye tracers, from 3 g l⁻¹ (Bundt et al. 2001), 4 g l⁻¹ (Flurry et al. 1994; Alanoui & Goetz 2008) to 10 g l⁻¹ (Kasteel et al. (2002)). Different concentration of BB dye tracers means that different concentration of Na⁺ in dye solution, and different interaction effects of dye solution with surrounding soil will lead to different chemical footprints observed in exposed soil profiles.

The cause of the time-controlled breaking point in observed chemical changes seems to be the spatial-temporal controlled mechanism of dye solution transfer in soil. While classical theory supposes the PF zone to be temporal and spatially stable within the soil (Ritsema & Dekker 2000; Hagedorn & Bundt 2002; Bogner et al. 2012), we suppose dye solution movement via PF to be limited to brief period (CUT 2 profile), as long as are fulfilled the physical preconditions of non-equilibrium flow (Jarvis & Dubus 2006). After that, at moment when

all pores at the soil surface are filled with water, and lateral movement of dye solution from macropore to surrounding soil matrix prevailed, the macropore flow will terminate (Jarvis & Dubus 2006) and homogenous flows of dye solution became dominant (CUT 24 – CUT 504 profiles).

5. Conclusion

The results of small-scale irrigation field experiments to show heavy chemical changes be caused in soil via interaction of BB dye solution with surrounding soils. Observed spatial-temporal changes in pH (H₂O), chemical composition of fine earth soil, as well as in concentration of Na⁺ in soil exchangeable complex suggested, the BB dye solution didn't represent an inert tracer, but its compounds are involved in mass reaction with surrounding soils. Recorded chemical trends seems to be also the result of competitive processes between the Na⁺ of BB dye solution (representing Na-salt) and composition of surrounding soil exchangeable complex, and observed distribution of chemical components around the zones of preferred flows stained by BB dye may cause the risk of fatal misinterpretations in line with the statement of both the Flurry & Flühler (1994) and Flurry & Wai (2003).

The observed breaking point in concentration of Al, Si and Fe we preliminary links with breaking point of dye solution movement, when macropore preferred flow changed to equilibrium one. In order to support proposed scenario, detail analyse of dye pattern profiles and its morphometric parameters is needed.

Acknowledgments

This work was supported both by the Slovak Research and Development Agency under the contract No. APVV-15-0425 and by Scientific Grants Agency of the Ministry of Education and the Slovak Academy of Sciences under the contract No. VEGA 1/0783/15.

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Dehydrogenase activity in topsoil at windthrow plots in Tatra National Park

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Abstract

The aim of the study was to compare the effect of windthrow treatments established after the windstorm in 2004 on the activity of enzyme dehydrogenase (DHA) in forest topsoils. We also focused on the effect of the recent windthrow (May 2014) on the DHA in topsoil. Soil samples were collected in July 2014 from four sites in the Tatra National Park: EXT – tree trunks and wood debris extracted after the windstorm in 2004, NEX – area left for self-regeneration after the windstorm in 2004, REX – tree trunks and wood debris extracted after the windstorm (May 2014), REN – Norway spruce stand set as a control plot. We measured pH, dry weight %, soil organic matter (SOM), carbon content in microbial biomass (C_{bio}) and DHA. Dehydrogenase activity at studied plots was the lowest at the EXT plot and the highest values were measured at the REN plot. DHA at NEX was similar to REN suggesting comparable ecological conditions at these plots comparing to EXT. Carbon content in microbial biomass at plots reflected intensity of dehydrogenase activity in sequence $\text{EXT} < \text{REX} < \text{NEX} < \text{REN}$.

Key words: topsoil; dehydrogenase activity; soil organic matter; windthrow; Tatra National Park

Editor: Erika Gömöryová

1. Introduction

Soil is very heterogeneous ecosystem, where thousands of living species provide number of functions. A vast density and diversity of microorganisms can be detached even in a small soil compartment (Dilly 2010). Physiological functioning and corresponding biochemical reactions of living organisms are mainly controlled by enzymatic reactions catalyzed by specific enzyme or a group of enzymes. Soil enzymes are necessary for maintaining soil ecology, physical and chemical properties or soil health (Paul 2007). Enzymatic activities are closely linked with microbial activity or biomass, thus they can generally serve as indicators of shifts in soil properties (Das & Varma 2011). At ecosystem level, linkage among enzyme activity and the transformation of carbon and nitrogen can indicate a different management approaches (Salazar et al. 2011). DHA is commonly used as an indicator of biological activity in soils. Dehydrogenase is intercellular enzyme that does not accumulate in soil but is an integral part of intact vital cell participating in the respiration metabolic pathways. Main function of dehydrogenase is to transfer protons and electrons from substrates to acceptors, the processes involved in the oxidation of SOM. Many factors, such as soil moisture, redox potential, organic mat-

ter content, pH, temperature, seasonal variations etc. can influence soil characteristics and thus enzymatic activities (Wolinska & Stepniewska 2012). Seasonal changes of dehydrogenase activity were reported in forest soil during wet and dry periods of the year.

Windstorms create gaps in forest canopy effecting soil nutrient availability and enzyme activity. Size of the gap is an important parameter influencing soil characteristics. The large size gaps cause decrease of soil organic matter, nitrogen and phosphorus, enzyme activity and increase the nutrients loss (Xu et al. 2016; Yang et al. 2017). Salvage logging at windthrow sites can result in reduction and more uniform distribution of post-windthrow structural attributes that can cause significant differences between natural disturbances and managed forests (Waldron et al. 2013). Removal of logging residues can have significant effect also on soil processes and enzyme activities. Increase of enzymatic activity on the sites with no removal of logging residues indicates importance of these materials in sustainable productivity of forest ecosystems (Adamczyk et al. 2015). Soil biological activity and decomposition/mineralization of soil organic matter are essential in forest functioning as they make nutrients more available to the vegetation. Relatively to stem-only harvest, microbial activity, enzymatic activities

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and N mineralization fluxes are reduced in intensive harvests. Enzymatic activities involved in N mineralization, C decomposition or phosphate hydrolyze are decreased as well (Achat et al. 2015). Studies also showed that forest thinning and soil disturbance can decrease protease and arylsulfatase activity but may not have affect glucosaminase, glucosidase and acid phosphatase activities. Cellulase, phenoloxidase, arylsulfatase and protease correlate after thinning with active C and peroxidase activity is negatively correlated to active C. Peroxidase, phenol oxidase, arylsulfatase and protease activities correlate with soil microbial nitrogen (Geng et al. 2012).

Among all soil microorganisms, bacteria and microscopic fungi are the most important groups involved in soil biochemically mediated processes. They play irreplaceable roles in nutrient cycling or organic matter dynamics (Pett-Ridge & Firestone 2005). Microorganisms significantly contribute to chemical alteration of organic residues via the enzymes production thus affect organic carbon cycling as well (Bardgett 2005). Dehydrogenase is strongly linked to C-cycling in different forest ecosystems and thus its activity can be correlated with organic carbon content (Salazar et al. 2011) and microbial biomass (Fontaine et al. 2003).

This study focused on the comparison of DHA in topsoils at the plots with different windthrow treatment. Longtime effect of shifted ecological conditions and secondary succession have impact on soil parameters reflecting also in microbial community structure and thus in enzymatic activities as well. Our hypothesis in this study was that DHA at REN and NEX would differ from EXT and REX site.

Ecological conditions at NEX and REN plots have similar effect on topsoil characteristics in contrast to EXT plot where the effect of ecological factors on soil resemble condition of recently damaged plot REX. Shifts in microbial community structure reflect intensity of ecological factors in soils. We can assume that the similar microbial structure identified at studied plots showed also similarity in ecological factors. Microbial community structure on the NEX plot is more similar to reference plot over time while EXT showed significant differences (Hanajík 2015; Hanajík & Fritze 2009). DHA was assumed to be the highest at plot EXT due to herbaceous vegetation cover and its thicker root system which would enhance microbial processes thus also DHA activity. We also expected DHA at plots to be linked with the measured carbon content in microbial biomass.

2. Material and methods

The study plots were located at windthrow area in TANAP in northern Slovakia. Predamaged forest was mostly (72.4%) a 79-year-old Norway spruce (*Picea abies* L.) stand (Koreň 2005). Mineral topsoil 0–10 cm was sampled in July 2014 from four different treatments represented by plots 30 × 30 m. Plot EXT (N 49°07'12.0" E 020°09'47.5") repre-

sented area with removal of fallen tree trunks and wood debris (over 8000 ha) after the windstorm in November 2004 covered mainly by herbaceous vegetation; Plot NEX (N 49°09'60.5" E 020°15'14.8") was set in the area left for self-regeneration (over 690 ha) with domination of *Rubus idaeus* and plot REN (N 49°07'19.5" E 020°06'21.4") was situated in the Norway spruce stand as a control, plot was rich in mosses. Plot REX (N 49°07'17.5" E 020°06'16.4") represented former reference (REF) area of spruce stand damaged by another windstorm in 2014 with following tree trunks and wood debris removal at this site, plot was covered mainly by herbaceous vegetation. For more detail description of vegetation cover on studied plots see Hanajík et al. (2016). The soil type at study plots was Cambic podzol. From each plot 45 individual core samples of topsoil were combined into 3 composite samples. One composite sample included 15 individual core samples. After the plant material was removed, the 12 composite samples were then sieved through a 2.0 mm mesh and stored at 4 °C until analyzed.

To determine dry weight percentage (DW %) of soil, samples were dried at 105 °C overnight. SOM content was measured as a loss on ignition from the dried samples at 550 °C for 4 h. Soil pH was measured by a glass electrode in soil suspension with deionized water pH/H₂O and KCL 0.1 M pH/KCl.

Carbon content in microbial biomass (C_{bio}) was determined by chloroform fumigation extraction (CFE) method according to Vance et al. (1987) using membrane air pump N810.3FT.18 with automatic vacuum controller. For the CFE method, four subsamples of composite samples were fumigated with ethanol-free chloroform in a sealed desiccator in the dark for 24 h at 180 mbar pressure and then extracted using 0.5 M K₂SO₄. Non fumigated controls was extracted under the same conditions at the time fumigation commenced. Organic C_{bio} was then determined in extracts by dichromate digestion.

Quantification of dehydrogenase activity was based on the recommended standard assay. Method was originally described by Benfield & Howard (1977), and adapted from Trevors (1984a, 1984b) and Von Mersi & Schinner (1991). The principle of the method relies on the ability of iodinitrotetrazolium chloride (INT) to act as an artificial electron acceptor in the place of oxygen. Heterocyclic ring structure of INT readily accepts hydrogen atoms and electrons thus becomes reduced. During incubation INT is biologically reduced and forms purple water-insoluble iodinitrotetrazolium formazan (INTF) which can be extracted using organic solvent and amount is determined colorimetrically.

Data were compiled and transformed in Microsoft Excel. Statistics were generated using R software ver. 3.3.2. If the test statistic probability was less than the significance level ($\alpha = 0.05$), the null hypothesis for all tests was rejected. We tested collected data for normality by Shapiro-Wilk test followed by ANOVA and Tukey post hoc test for data from a normal distribution or Kruskal-

Wallis and Kruskal-Wallis multiple comparison test for non-normally distributed data.

3. Results and discussion

Since, chemical reactions catalyzed by dehydrogenase, are associated with protons and electrons transfer pH of soil solution can influence its activity by changing either the ionic form of the active site of enzyme, affinity of substrate to enzyme or its three-dimensional shape (Wolinska & Stepniewska 2012). This can be reflected in solubility and ionization of both organic and inorganic molecules present in soil solution. Interpretation of the pH effect on microbial processes can be difficult. Processes can be affected due to the cation sorption at negatively charged surfaces of soil colloids 10 – 100 times higher than the sorption in soil solution. Hence, pH values of the colloid surface are generally lower comparing to the values measured in the soil solution. For example, the urease activity in soil, with optimum pH range between 8.5 and 9.0, is 1 – 2 pH units higher than pH measured in the soil solution (Hazlett et al. 2007). In general, the optimal pH range for the activity of the enzymes related to the redox reactions is 7.4 – 8.5, in comparison to soil solution, with its pH values 7 – 7.5. However, a very poor activity was determined below pH 6.6 or above 9.5 (Januszek et al. 2015; Shaw & Burns 2006). Dehydrogenase activity strong suppression can be observed at pH(KCl) 4.1 and pH(H₂O) 4.9 (Fernández-Calviño et al. 2010; Trevors 1984a). Different types of assays used in evaluation of the DHA in forest soils proved tight correlation between pH and dehydrogenase activity in Gleyic Podzols and Calcaric Cambisols (Januszek et al. 2015). Higher values of dehydrogenase were measured in sandy soils with neutral or slightly alkaline pH. Positive correlation of dehydrogenase activity was also identified according to clay content and tree species composition (Blońska 2010; Fernández-Calviño et al. 2010). The use of buffer system when analyzing acidic or alcalic soils is recommended to obtain readable results. Comparing to acetate buffer, borate buffer, citrate buffer, and phosphate buffer which generally reduce DHA, TRIS buffer (1 M; pH 7.0) proved to be suitable for reproducibility and for measuring potential DHA (Von Mersi & Schinner 1991). Soil reaction pH (H₂O) at studied plots ranged from 3.8 (NEX) to 4.5 (EXT) and pH (KCl) was 3.2 at EXT, REX and REN and 3.3 at NEX (Table 1).

Table 1. Soil reaction pH (H₂O) and pH (KCl) at studied plots (n = 1).

	pH (H ₂ O)	pH (KCl)
EXT	4.5	3.2
NEX	3.8	3.3
REX	4.4	3.2
REN	4.0	3.2

Soil reaction pH (H₂O) and pH (KCl) at studied plots were strongly acidic and very strongly acidic, respecti-

vely. Differences among pH values can be caused by differences in soil structure affecting bounding of H⁺ cations in soil matrix (Hazlett et al. 2007). This difference in soil structure could be the result of evolution of the vegetation cover and rizosphere at studied plots especially at the EXT and REX where herbaceous vegetation dominated (Hanajik et al. 2016). Root systems and exudates of the vegetation at these plots affected very likely the soil nutrition properties (Chen et al. 2016) and thus were reflected in higher pH (H₂O) values comparing to REN and NEX plots with lower abundance of herbaceous species. However, to our knowledge no research was so far focused on soil structure differences among windthrow plots in the High Tatras proving or disproving significant effect of soil structure or vegetation cover on the soil reaction.

Dry weight percentage can reflect relative content of water in samples thus samples with high DW % represented plots with low moisture content and low dry weight indicated high moisture content at the plots. Water content in soil is very important factor affecting microbial communities and their biomass thus have strong effect on DHA as well (Wolinska & Stepniewska 2012). Dry weight values were the lowest at the NEX plot and the highest values were measured at the EXT plot. The lowest dry weight was detected at NEX plot and the highest at EXT (Fig. 1a). Kruskal-Wallis multiple comparison test then revealed statistical significant difference of plot EXT from all other plots ($p < 0.001$). We recorded the lowest content of water in soil at EXT comparing to NEX, REX and REN where moisture conditions were similar. Since, dehydrogenase activity is strongly dependent also on soil aeration, thus its low values can be measured in soil with high water potential and anoxic conditions (Quilchano & Marañón 2002; Song et al. 2008). Nevertheless we measured low DHA at the EXT site despite the low water content in soil. This could be explained by the complex influence of other ecological factors. Low DHA at REX plot could be caused by recent disturbance of soil system that affected biodiversity of microbiocenosis at this plot and thus werereflected in the lower DHA in spite of of similar C_{bio} content comparing to NEX and REN. Lower water content at EXT plot is probably the result ofthick herbaceous layer at this site that wasformed after removal of damaged tree trunks. Herbaceous community demands higher water supply and causes higher levels of evapotranspiration as well draining water content from soils (Özkan & Gökbülak 2017).

Content of SOM in dried samples was the lowest at the REX plot an the highest values were detected at the REN plot (Fig. 1b). Also data of SOM were not from the normally distributed population due to the Shapiro-Wilk test and thus were tested by Kruskal-Wallis test, showing statistical significancy. Kruskal-Wallis multiple comparison test revealed statistical significant difference of plot REN from all other plots ($p < 0.001$). SOM content provides organic compounds in soils important for metabolic activities of microorganisms which enhance decom

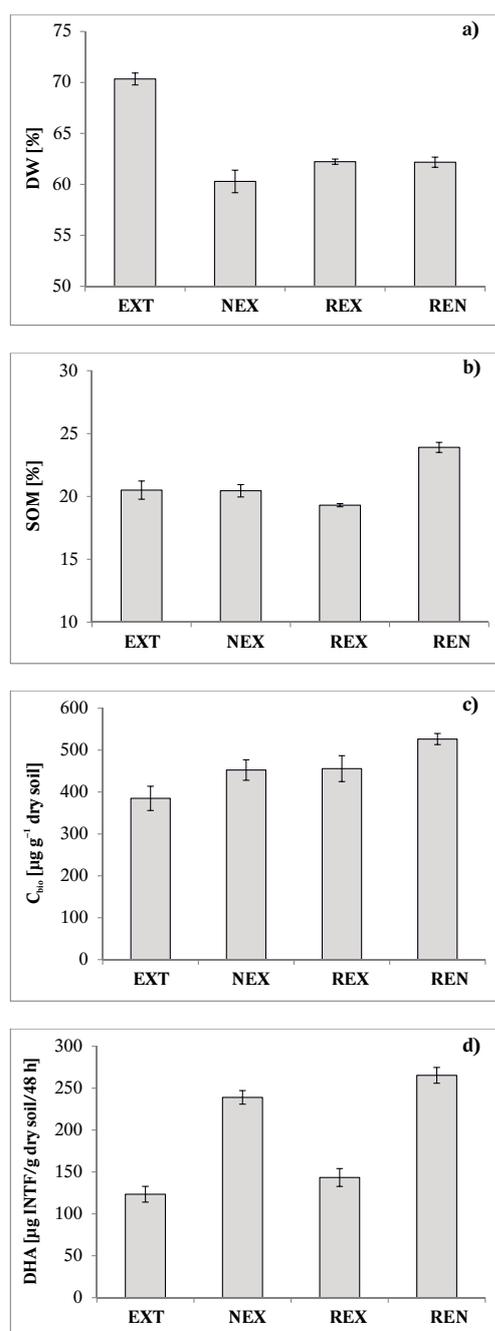


Fig. 1. DW% a), SOM% b), C_{bio} c), DHA d), at studied plots. Values expressed as means with standard error ($n = 12$ for each site).

position processes and nutrient cycles (Adamczyk et al. 2016). Organic matter content at our studied plots was the highest at REN plot where the highest DHA was detected. This could be considered as a confirmation of SOM importance as a factor effecting DHA; however, similar content of SOM at EXT, NEX and REX contrasted with high variation of DHA values at these plots thus contradicted possible main effect of SOM on DHA under field conditions at the studied plots.

Carbon content in microbial biomass C_{bio} was the lowest at the EXT plot and the highest values were

measured at the REN plot. Data were from the normally distributed population due to the Shapiro-Wilk test and thus were tested by ANOVA, showing statistical significance ($p = 0.0052$). Tukey test revealed statistical significance between EXT and REN plot ($p = 0.0023$). Carbon content in microbial biomass tended to increase with increasing DHA at studied plots in sequence: $EXT < REX < NEX < REN$. This findings proved the main influence of microbial biomass in soil on DHA at studied plots. This is however well known fact that microbial biomass generally increases DHA in soils.

Dehydrogenase activity was the lowest at the EXT plot and the highest values were detected at the REN plot (Fig. 1d). Data of DHA were from the normally distributed population due to the Shapiro-Wilk thus tested by ANOVA, showing statistical significance ($p < 0.0001$). Tukey test revealed statistical significance among EXT and REN, REX and REN, EXT and NEX, NEX and REX (Table 2).

Table 2. Statistical evaluation of studied parameter.

Plots	Parameters			
	DW*	SOM*	C_{bio} **	DHA**
EXT vs. REN	<0.001	<0.001	0.0023	<0.001
REX vs. REN	0.6781	<0.001	0.1723	<0.001
EXT vs. NEX	<0.001	0.9864	0.2028	<0.001
NEX vs. REX	0.0856	0.145	0.2715	<0.001
NEX vs. REN	0.1868	<0.001	0.3128	0.2215
EXT vs. REX	<0.001	0.1586	0.9997	0.2502

* – ANOVA (Tukey's test); ** – Kruskal-Wallis (multiple comparison test).

DHA values positively correlated with C_{bio} (correlation coefficient 0.61; $p = 0.035$) (Fig. 2). Statistical evaluation of studied parameters is shown in Table 2. DW and SOM were not correlating significantly with DHA however we identified negative trend between DHA and DW ($c = -0.57$, $p = 0.055$) and positive trend between DHA and SOM ($c = 0.51$, $p = 0.093$).

5. Conclusion

DHA at the plots NEX and REN showed similar values comparing to EXT and REX. We assume that after 10 years of the vegetation succession at self-regeneration plot soil condition at this plot resemble more reference spruce stand comparing to the extracted plot where herbaceous layer dominated. The lowest DHA was recorded at EXT although we expected DHA to be enhanced by root exudates of herbal vegetation at this plot. We assume that this was caused by soil moisture deficiency as well as low C_{bio} content at this plot. Low intensity of DHA at REX plot was probably due to the recent disturbance at this plot destabilizing structure of microbiocenosis resulting in low DHA. Carbon content in microbial biomass at studied plots reflected intensity of dehydrogenase activity in sequence $EXT < REX < NEX < REN$ showing direct linkage between microbial biomass and DHA amounts.

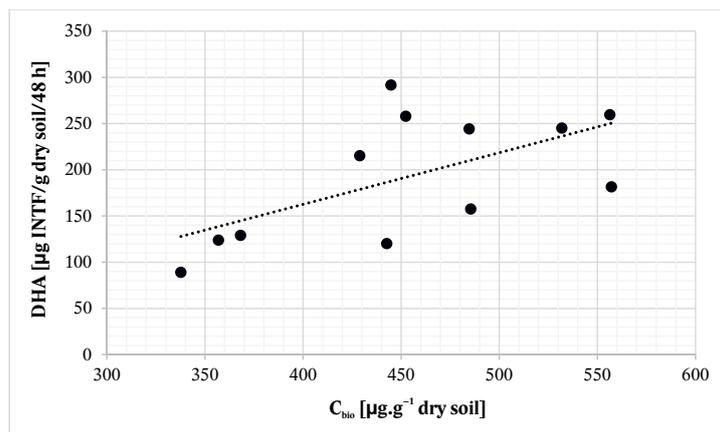


Fig. 2. Correlation between DHA and C_{bio} ($r = 0,61$; $p = 0,035$).

Acknowledgement

The study was supported by the Ministry of Education, Science, Research and Sport of the Slovak Republic – project VEGA 1/0614/17 and by the Slovak Research and Development Agency – project APVV-0866-12.

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Carbon sequestration in soil following afforestation of former agricultural land in the Czech Republic

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Abstract

Soil organic carbon (SOC) is a great component of the global carbon cycle and plays significant role in terms of climatic changes and agricultural land-use. An important management concern is the extent of SOC stocks sequestration when farmland is converted to forest stands. We have reviewed the literature about changes in SOC stock in relation to altitude and stand age and sought differences between former agricultural land and origin forest stands. Accumulation of SOC was monitored in 17 examples (41 samples) in 9 locations across the all Czech Republic with focus on the main tree species Norway spruce (*Picea abies* [L.] Karst.). Results showed a significant increase of SOC stock in an afforested farmland with increasing stand age. Another factor was the altitude. With increasing altitude, the carbon stock in our model gradually decreased. From the data analyzed comparing forest stand and former agricultural land, similar carbon sequestration was documented for both variants with higher SOC for forest stands. However, other conditions affecting SOC stock should be taken into consideration, especially silvicultural management, topography, disturbances, soil properties and cultivation. The general tendencies of SOC changes at the investigated sites are comparable to those in other studies across the Europe.

Key words: carbon storage; soil organic matter; abandoned farmland; land-use change; temperate forest soil

Editor: Bohdan Konôpka

1. Introduction

Forestry is characterized by long-term production cycles (Cienciala et al. 2008) and multifunctionality of forest ecosystems. Forest provides people with a wide range of resources and ecosystem services (Kindler 2016). These benefits are often subdivided into three groups – ecological forest functions, socio-cultural benefits and forest products, especially wood products (Stenger et al. 2009). Ecological forest function comprise prevention of soil erosion, local climate regulation (de Groot et al. 2002; Vacek et al. 2003), and – gaining in importance nowadays – carbon sequestration (Vanguelova et al. 2013; Grüneberg et al. 2014; Pukkala 2014; Ahmed et al. 2016). Forest ecosystems' potential to accumulate SOC and, therefore, mitigate climate change attracts an increasing number of researchers in the environmental field (Cienciala et al. 2008). Forest soils hold an important position in evaluation of forest ecosystems dynamics in anthropogenically influenced areas (Furst et al. 2007). Carbon sequestration is also a political issue with global significance, embodied in international agreements, such as the Climate Convention (UNFCCC – United Nations'

Convention on Climate Change) and the Kyoto Protocol (Cienciala et al. 2008; Lugato & Berti 2008; Grüneberg et al. 2014). The role of forests in the global carbon cycle is thus carbon sequestration from the atmosphere through photosynthesis. During this process, carbon is released into the atmosphere again, or its part is bound to the tree biomass and soil organic matter (SOM) (Post & Kwon 2000).

Overall, forests represent a very important carbon repository (Vacek et al. 2013; Holubík et al. 2014; Fujisaki et al. 2015), with its greater part bound in the forest soil (Guo & Gifford 2002). It is estimated that approximately 30 to 50% of total carbon content in forests is located in soils (Dixon et al. 1994; Paul et al. 2002; Pan et al. 2011; Wiesmeier et al. 2013; Grüneberg et al. 2014). The amount of accumulated carbon and its distribution in the soil profile is influenced by individual tree species (Augusto et al. 2015; Andivia et al. 2016). Carbon accumulation is also significantly affected by the type of economic land use (Blanco-Canqui et al. 2014; Wiesmeier et al. 2015; Fujisaki et al. 2015); in some cases, cultivation of forest soils can even reduce SOC (Murty et al. 2002). Afforestation of agricultural land can – together with

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other benefits such as higher timber mass production or higher biodiversity (Podrázský et al. 2011; Wozniwoda et al. 2014; Vacek et al. 2016; Cukor et al. 2017a; Vacek et al. 2017) – significantly increase the carbon content bound in the ecosystem (Kacálek et al. 2011), which in turn contributes to reducing carbon concentrations in the atmosphere (Novara et al. 2014; Wozniwoda et al. 2014).

The potential of abandoned agricultural land and the total of land suitable for afforestation is quite considerable, from a global perspective. Over the world, there are approximately 385 – 472 million hectares of abandoned farmland suitable to be afforested with fast-growing tree species (Campbell et al. 2008). Similarly in Europe, where agricultural land is assumed to be partially turned into forest land as well (Rounsevell et al. 2006; Stoate et al. 2009; Ruskule et al. 2016). An increase in forest land area and a decrease in farmland area has been observed in Europe since the early 19th century (Wulf 2004; Prishchepov 2012); currently, an area of approximately 12 – 16 million hectares (FAO 2008; Campbell et al. 2008) is considered to be afforested on this continent. The area of agricultural and non-forest land suitable for afforestation can be illustrated on the example of the Czech Republic. The exact size of land suitable for afforestation depends on the criteria of evaluation; in most cases, the estimates range from 50,000 to 500,000 hectares (Podrázský & Štěpáník 2002; Vopravil et al. 2015).

Areas of the land suitable for afforestation are vast, therefore it is important to pay attention not only to production capabilities of various tree species growing on non-forest land, but also to other factors, including accumulation of carbon. In the present study carbon sequestration is studied in the soil organic matter in stands of most common tree species growing in the Czech Republic (Norway spruce /*Picea abies* [L.] Karst./, European beech /*Fagus sylvatica* L./, English oak /*Quercus robur* L./) and tree species with generally high wood production (European larch /*Larix decidua* Mill./, Douglas fir /*Pseudotsuga menziesii* Engelm./). The objective of our study is to investigate how carbon content in the surface humus changes within the altitudinal gradient, species composition (coniferous x deciduous) and the age of the stand on the permanent forest land in comparison to afforested farmland. The development of carbon content in upper humus layer in relation to above-mentioned variables is based on studies already published.

2. Methods

Determination of carbon content in the surface humus of various tree species was based on all previously published data available for the Czech Republic. In the past, studies dealing with raw humus accumulation on agricultural land and on permanent forest land were elaborated at the Department of Silviculture of the Faculty of Forestry

and Wood Sciences of the Czech University of Life Sciences in Prague, at the Forestry and Game Management Research Institute, and at the Forest Ecology Institute of the Faculty of Forestry and Wood Technology of Mendel University in Brno. Distribution of particular locations within the Czech Republic is shown in Fig. 1.

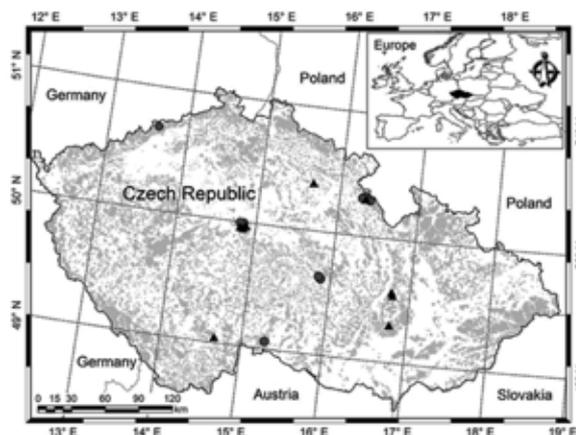


Fig. 1. Location of research plots on former agricultural land (gray circles) and in forest stands (black triangles).

The methodology of holorganic humus collection is always described in the particular work, cited in our paper. Calculation of carbon in tonnes per hectare was based on total humus in accordance with the following equation which calculates the carbon content from the total humus in per cents. The resulting carbon accumulation was based on the sum for particular layers of the humus in L, F and H horizons (Šály 1978).

$$\sum_{(L,F,H)} \frac{h_{(t/ha)}}{100} * \frac{h_{(\%)}}{1.724}$$

$h_{(t/ha)}$ – total upper-layer humus in tonnes per hectare
 $h_{(\%)}$ – total humus in %
 1.724 – coefficient of C content converted to total humus (Šály 1978).

Conversion to the total carbon accumulation and description of particular localities are presented in Table 1 (afforested agricultural land) and in Table 2 (permanent forest land).

3. Statistical evaluation

The location, stand type (broadleaved vs. coniferous), age, altitude (m AMSL), land use (former agricultural land/forest) and relevant soil carbon content data were available for statistical analyses. Tree species were separated into two groups (coniferous and broadleaved) for obtaining more records in each of this group. For modelling of soil carbon content ($t\ ha^{-1}$), generalized linear mixed effect model (GLMM) was selected as the first approach. All computations were performed in R software (R Core Team 2016).

Table 1. Carbon accumulation on former agricultural land.

Locality	Tree species	Age [years]	Altitude [meters]	Forest site type	Carbon accumulation [t ha ⁻¹]	Authors
Kostelec nad Černými lesy	Pine	39	430	4Q1	11.11	Podrázský et al. 2010
	Spruce	39			12.03	
	Dg fir	39			10.3	
Deštné v Orlických horách	Spruce	57	860	6K	3.43	Hatlapatková & Podrázský 2011
	Beech	40	800		1.3	
Fláje	Spruce	18	800	8K1	9.43	Podrázský 2008
	Larch	12	800		2.83	
Bystré v Orlických horách	Spruce	12	517	4K	5.54	Kacálek et al. 2010
	Beech	12	517	4K	5.83	
Krahulec v Orlických horách	Birch	12	590	4K	2.37	Kacálek et al. 2010
	Spruce	50	600	4K	17.67	
Český Rudolec	Red oak	28–37	600–630	5K1	3.43	Podrázský & Ulbrichová 2004
	Birch				4.19	
	Spruce				10.93	
	Larch				14.7	
Krucemburk	Spruce	48	610–640	6P1	11.78	Podrázský et al. 2011
	Spruce	53		6O1	15.38	
	Larch	52		6O1	18.23	
Krahulec v Orlických horách	Spruce	100	600	4K	47.82	Bartoš et al. 2014

Note: Forest site type is classified by the Czech forest ecosystem classification (Viewegh et al. 2003). Explanatory see Table 2.

Table 2. Data for carbon accumulation on forest soil.

Locality	Tree species	Age	Altitude	Forest site type	Carbon accumulation [t ha ⁻¹]	Authors
Kostelec nad Černými lesy	Spruce	120	400–420	4O1	33.86	Podrázský & Remeš 2010
	Fir	140			8.1	
	Beech	36			12.84	
	Oak	36			5.11	
Deštné v Orlických horách	Spruce	136	920	6K	2.85	Hatlapatková & Podrázský 2011
Hořice	Beech	100	850	3K	4.17	Podrázský & Remeš 2005
	Spruce	35	300		7.97	
Kostelec nad Černými lesy	Spruce	61	420–440	4K	20.51	Kupka et al. 2013
	DG fir	45			12.54	
	Oak	61			6.6	
	Spruce	120			34.74	
	Spruce	40			13.7	
Křtiny	Beech	40	520	4P1	8.45	Podrázský & Remeš 2009
	Dg fir	40			7.95	
	Spruce	60			22	
	Dg fir	60			6	
Hůrky	Spruce	65	430	4H	6	Menšík et al. 2009b
	DG fir	65			34	
Němčice	Spruce	30	600–660	3K	23.9	Menšík et al. 2009a
	Beech	40			12.9	
	Spruce	110			600–660	
	Spruce	110	600–660	5S1	26.6	Fabiánek et al. 2009

Note: Forest site type: 6P – *Piceeto-Abietum variohumidum acidophilum*, 6O – *Piceeto-Abietum variohumidum mesotrophicum*, 4Q – *Querceto-Abietum variohumidum oligotrophicum*, 6K – *Piceeto-Fagetum acidophilum*, 8K – *Piceetum acidophilum*, 5K – *Abieto-Fagetum acidophilum*, 4O – *Querceto-Abietum variohumidum mesotrophicum*, 4P – *Querceto-Abietum variohumidum acidophilum*, 4H – *Fagetum illimerosum trophicum*, 3K – *Querceto-Fagetum acidophilum*, 5S – *Abieto-Fagetum mesotrophicum* (Viewegh et al. 2003).

The soil carbon content data were fitted with gamma distribution via R package MASS (Venables & Ripley 2002), while goodness of fit were subsequently tested by Kolmogorov-Smirnov test.

The full model (GLMM) was constructed as follows (notation from R software):

Carbon ~ Land Use + Altitude + Age + Stand type + (1|Location)

The carbon content data were identified as random selection from gamma distribution with parameters $\alpha = 1.83$ and $\beta = 0.14$. The goodness of fit was tested by Kolmogorov-Smirnov test ($p = 0.99$).

The sampling location was identified as random effects, while all other effect were considered fixed. Computations of GLMM were performed via R package lme4 (Bates et al. 2015).

At first, effect of land use was tested via likelihood-ratio test (model with land use parameter vs. model without land use parameter). Secondly, the effect of location

was evaluated. Thirdly, further models (simplified, with non-significant or unreliable factors due to data insufficiency omitted in comparison to full model) were constructed – separate models (generalized linear model – GLM) for these predictors were computed.

The dependence of soil carbon content on the most significant factors was graphically represented. All hypotheses were tested at $\alpha = 0.05$.

Unconstrained principal component analysis (PCA) in the Canoco 5 program (Microcomputer Power) was used to analyze relationships among SOC, stand age, altitude, climatic factors (mean temperature and precipitation), site humidity and nutrients (transformed from Czech forest ecosystem classification), ecological groups, tree species and land use (forest stand, afforested farmland) in order to reveal similarity of 41 records. Data were log-transformed, centered and standardized during the analysis. The results of the PCA analysis were visualized in the form of an ordination diagram.

4. Results

Testing for significance of land use showed non-significant results ($p = 0.97$) and this parameter was therefore omitted. The random effect of location showed relatively low variance ($8.1E-4$) and due to relatively low number of records for some locations was not considered in further analyses.

The testing for significance of effect of tree type was evaluated by likelihood-ratio test ($p = 0.0015$), while coniferous forests showed significantly higher amount of soil organic carbon. In general, there was ca. 1.66 times higher carbon accumulation in coniferous stands compared to stands of broadleaved tree species. For further details about average carbon content depending on stand type see Fig. 2.

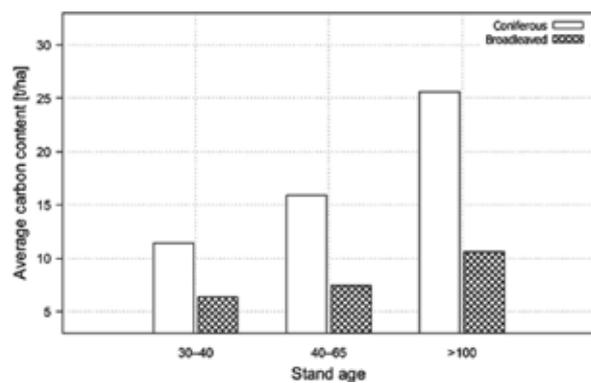


Fig. 2. Average carbon content in coniferous and broadleaved stands depending on its age (years). Coniferous forests showed significantly higher amount of soil organic carbon content ($p = 0.0015$).

The likelihood-ratio tests showed significant results for both predictors ($p = 0.02$ for altitude and $p = 0.001$ for stand age). Representation of model – see Fig. 3.

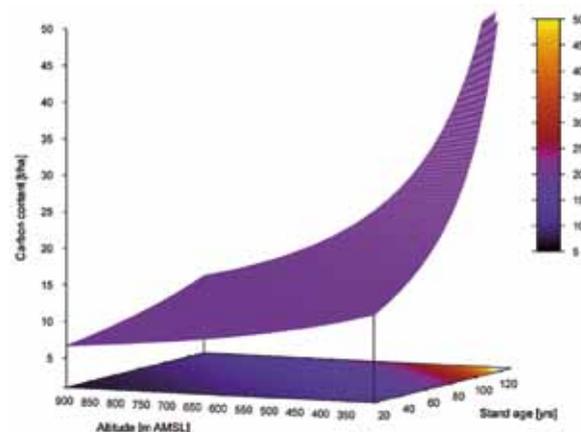


Fig. 3. Model for response of carbon content to altitude and the age of the stand. The “heatmap” at the base of the plot shows projection of estimated function.

The accuracy of the model is depicted by Fig. 4 – histogram of differences of recorded data from suggested

model. The accuracy was evaluated for all selected tree species and separately for Norway spruce.

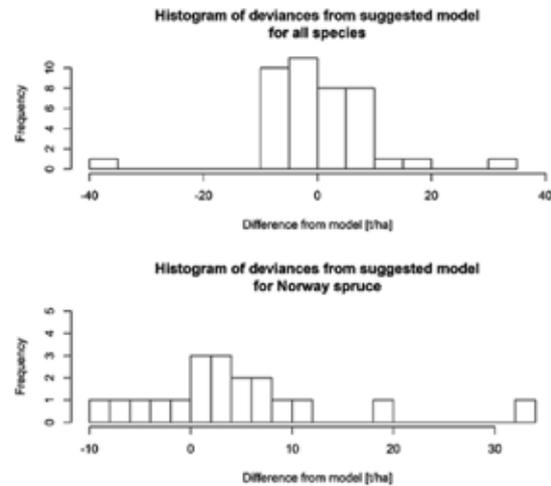


Fig. 4. Histogram of differences of data from suggested model. The accuracy was evaluated for all available records and separately for Norway spruce.

The relationships between SOC, site parameters, climate and tree species are presented in Fig. 5 by the PCA analysis. The first ordination axis explained 45.9% of variability in the data, the first two axes together 70.5% and the first four axes together explained 94.1%. The first x-axis represented the SOC stock and mean temperature with altitude and sum of precipitation. The second y-axis represented site parameters (humidity and content of nutrients). SOC was positively correlated with stand age and temperature, while these parameters were negatively correlated with altitude and precipitation. Site humidity and richness had low impact on content of carbon. Remarkable differences were observed among ecological groups (especially for *Acidophilum* series in terms of carbon), as marks of each record are relatively distant from one another whereas marks for forest stand and afforested agricultural land were fairly close together in the diagram. Tree species were significantly different from one another, but higher SOC stock were typical for coniferous (left part of diagram).

5. Discussion

The most significant factor that distinguishes agricultural land from permanent forest habitats is the null occurrence of upper-layer humus (Torreano 2004). After afforestation of the agricultural soil, a considerable part of the accumulated carbon is concentrated in the upper layers, gradually formed by forest litter; its formation and accumulation is noticeable already in young stands (Kacálek et al. 2011). In the phase immediately following the afforestation of agricultural land, there is a slight decrease in soil organic carbon. In the years to come,

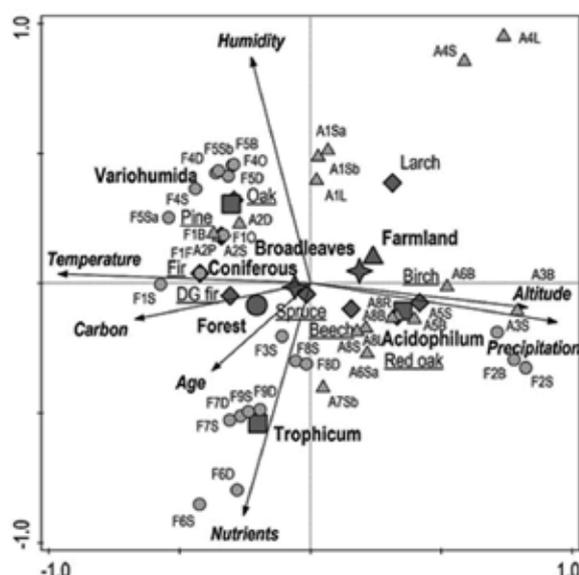


Fig. 5. Ordination diagram showing results of the PCA analysis of relationships among SOC (*Carbon*), stand age, altitude, climatic factors (mean *temperature* and sum of *precipitation*), site *humidity* and *nutrients*/richness (transformed from Czech forest ecosystem classification), ecological groups (*Trophicum* nutrient-rich – mesotrophic, *Acidophilum* acidic-oligotrophic, *Variohumida* gleyed – strongly fluctuating water tables) tree species (*Coniferous*, *Broadleaves*; *Spruce*, *Beech*, *Birch*, *Larch*, *Fir*, *DG fir*, *Red oak*, *Oak*, *Pine*) and land use (*Forest* forest stand, *Farmland* afforested agricultural land); Codes indicate: • forest stand, ▲ afforested farmland; ◆ tree species, ■ ecological groups.

its content is only increasing, and, subsequently, the growth of SOC on afforested agricultural land is gradually documented with increasing age of forest stand and thus with increasing accumulation of upper-layer humus (Laganière et al. 2009; Segura et al. 2016).

This trend of an increasing content of accumulated carbon with increasing age has also been confirmed by our model, which describes rising carbon content in stands up to the approximate age of 120 years. As no statistically significant differences for forest and afforested agricultural land were found, the processed data showed comparable carbon sequestration for both land uses. However PCA analysis suggests, that there is a higher SOC content on the forest soils; this results can be caused by lower age of examined stands on farmland.

Another factor that significantly affected the content of carbon in the upper-layer humus was the altitude. In accordance with our model, the carbon content declined gradually with the rising altitude. Different results were found in Germany, where a higher carbon stock deposited in upper-layer humus at higher elevations and alpine sites where thick organic layers are common (Wiesmeier et al. 2013; Grüneberg et al. 2014). Nevertheless, these results are from alpine areas, where generally higher hummus accumulation occurs because of extreme cli-

matic and site conditions. This results were not included in this study, examined gradient was between 300 to 920 meters above sea level.

However, from the statistical analysis, there is evident, that coniferous tree species accumulate more upper-layer humus (Schulp et al. 2008; Wiesmeier et al. 2013; Grüneberg et al. 2014) and that is why they often have a substantial content of accumulated carbon (Menšík et al. 2009a; Podrázský & Remeš 2010; Kupka et al. 2013). On the other hand, this well documented difference between coniferous and deciduous tree species has in our study a lower importance compared to significant influence of site conditions (Augusto et al. 2003; Holubík et al. 2014).

Other conditions that may affect the accumulated carbon content in the upper-layer humus are: different forest management, previous land use, stand characteristics, pre-planting disturbance, soil clay content, thinning, fertilization, liming, forest fires and, to some extent, the climatic zone (Lal 2005; Schulp et al. 2008; Laganière et al. 2009; Vacet et al. 2009, 2010; Matějka et al. 2010; Blanco-Canqui et al. 2014; Grüneberg et al. 2014; Segura et al. 2016). These circumstances, however, were not taken into account in our generalized model, which is based on data already published, as we lack sufficient data for the Czech Republic. Nonetheless it was shown that afforestation of agricultural land brings, among other benefits at local scale, an increase in the carbon content in units to tens of tonnes per hectare, which can result in an important effect on the global C budget if sufficient agricultural land is converted (Paul et al. 2002). That is why afforestation of agricultural land not only on sites suitable for forest trees but also in less favourable localities will gain on importance as a measure improving soil conditions. Here, planting can be supported by various types of fertilization and other measures aimed at better growth and the survival rate of seedlings (Podrázský et al. 2003; Kuneš et al. 2009; Tužinský et al. 2015; Cukor et al. 2017b).

6. Conclusions

The paper confirms the hypothesis about the influence of altitude and stand age on the SOC stock in the studied localities in the Czech Republic. However, relatively limited and variable number of samples on the compared variants must be considered when interpreting the present results. Stand age has significant positive effect on SOC content, while carbon stock decreased with increasing altitude. Difference between forest stands and afforested farmland, such as conifers and broadleaves was lower in the studied case (minor importance of tree species) compared to site. Considering the current knowledge about this important topic and still the lack of studies about carbon sequestration in soil following afforestation of former agricultural land, it is necessary to continue in

research to answer all questions and ambiguities. The studies should be focused on other factors significantly influencing the carbon content in the soil, especially impact of forest management, soil cultivation, previous land use and actual climatic changes.

Acknowledgments

This study was supported by the Internal Grant Agency (project no. B03/17), Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Prague.

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Carbon stocks in tree biomass and soils of German forests

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Abstract

Close to one third of Germany is forested. Forests are able to store significant quantities of carbon (C) in the biomass and in the soil. Coordinated by the Thünen Institute, the German National Forest Inventory (NFI) and the National Forest Soil Inventory (NFSI) have generated data to estimate the carbon storage capacity of forests. The second NFI started in 2002 and had been repeated in 2012. The reporting time for the NFSI was 1990 to 2006. Living forest biomass, deadwood, litter and soils up to a depth of 90 cm have stored 2500 t of carbon within the reporting time. Over all 224 t C ha⁻¹ in aboveground and belowground biomass, deadwood and soil are stored in forests. Specifically, 46% stored in above-ground and below-ground biomass, 1% in dead wood and 53% in the organic layer together with soil up to 90 cm. Carbon stocks in mineral soils up to 30 cm mineral soil increase about 0.4 t C ha⁻¹ yr⁻¹ stocks between the inventories while the carbon pool in the organic layers declined slightly. In the living biomass carbon stocks increased about 1.0 t C ha⁻¹ yr⁻¹. In Germany, approximately 58 mill. tonnes of CO₂ were sequestered in 2012 (NIR 2017).

Key words: forests ecosystems; soil; carbon stocks; Germany; National Forests Inventory; National Forests Soil Inventory

Editor: Bohdan Konôpka

1. Introduction

Forests influence the global climate in many ways (Bonan 2008). One important point of interest is the service of forests as carbon (C) sink. Forest ecosystems store more than 80% of all terrestrial aboveground C and more than 70% of all soil organic carbon (Batjes 1996; Jobbagy & Jackson 2000; Six et al. 2002). Forests are set apart by the fact that carbon is stored long-term in wood. Moreover, biomass enters forest soils as dead leaves, exudates, roots, wood or animal wastes. A portion of this biomass is converted into various carbon compounds through the metabolic activity of microorganisms. The amount of carbon stored in soil is determined by the net balance of the input from organic matters in the soils and its breakdown by microbes. The rates of tree growth and timber harvesting or natural drain determine the carbon storage capacity in living biomass and deadwood.

Many countries used National Forest Inventories to calculate carbon stocks and sequestration in biomass and dead wood (Vidal et al. 2016; Tomppo et al. 2010). However, estimates of national-wide carbon pools and fluxes from repeated soil inventories or monitoring are still the exception (Bellamy et al. 2005).

The importance of forest soils for the carbon cycle is expected to be more increasing in the future (Liski et

al. 2002). Many studies confirm that management practices (Kowalski et al. 2004), age structure (Kowalski et al. 2004; Loustau et al. 2004; Magnani et al. 2007), nitrogen (N) deposition (Magnani et al. 2007) and changes in CO₂ and climate influence the accumulation of carbon in biomass (Spieker et al. 1996) as well as in soils (Hagedorn et al. 2003). Therefore, the German government decided to report on Greenhouse gas emissions as Kyoto Protocol Article 3.4 required optionally. The national inventories are an important basis for the annual greenhouse gas reporting under the Kyoto Protocol and under the United Nations Framework Convention on Climate Change (UNFCCC, sector LULUCF). When litter and mineral soil as carbon pools are involved in the key categories (see Good Practice Guidance, IPCC 2003), reporting has to be made with increased accuracy and effort in the context of the Kyoto Protocol. As a Party of the UNFCCC, since 1994 Germany has been obliged to prepare and regularly update national emission inventories of greenhouse gases.

The current status and development of carbon pools in living biomass, deadwood, soils and litter (the organic layer) are all components of the inventories and have been reported for the period from 1990 to 2012. There are three National Forest Inventories (NFI) and a special Carbon Inventory Study at a NFI subsample surveying living bio-

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mass and deadwood and two NFSI surveying forest soils. The projected rates of change in carbon stocks, based on data from the NFI and the NFSI, are shared with the Federal Environment Agency and summarised in yearly National Inventory Reports (FEA 2017).

The presented results show the considerable contribution of forests to carbon sequestration. Furthermore the article focuses on how much carbon is stored in the different components of the forest ecosystem such as living biomass or soil and how fast the various carbon pools change.

2. Material and methods

2.1. National Forest Soil Inventory

The National Forest Soil Inventory (NFSI) follows a systematic sampling protocol based on an 8 km × 8 km grid. Inventories were conducted across Germany in the years between 1987 and 1993 (NFSI I) and again between 2006 and 2008 (NFSI II). Here, we used data from 1865 NFSI I plots and 1813 NFSI II plots (Fig. 1). The resampling at the same plots indicates a paired sampling schema. In reference to the NFSI II, 624 plots were not resampled at the original NFSI I plots. On the new federal state-specific inventory grid, 577 new plots were established for sampling.

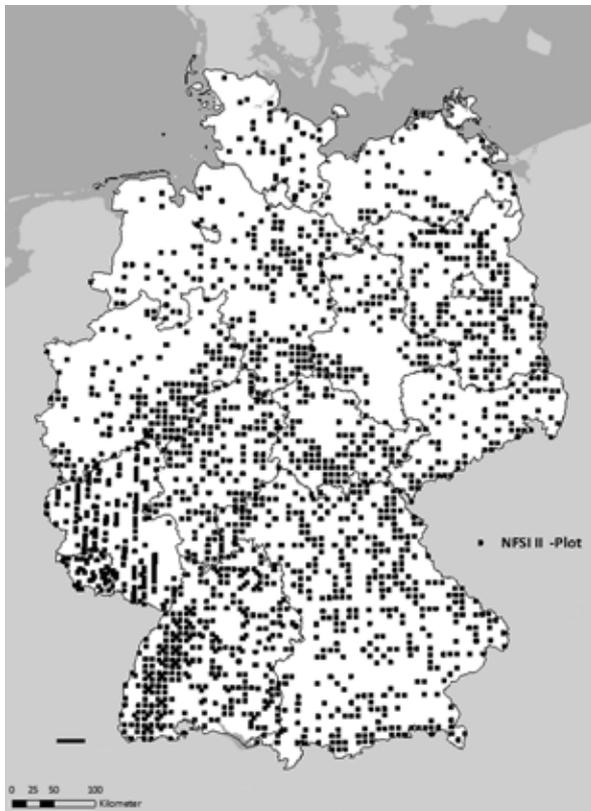


Fig. 1. Spatial distribution of National Soil Inventory plots in Germany.

Soil sampling

The NFSI II was carried out according to a new manual (Wellbrock et al. 2006) based on the German manuals of soil mapping and on the manual from the BMELV (1990) to ensure the comparability of soil sampling. The standard methods for sampling soils at the NFSI-plots involve 8 satellite samples, with a soil profile from the centre of a plot. All 8 samples were mixed to one sample with had been analysed to reduce soil heterogeneity. The sampling of the organic layer was carried out by mixed samples at 8 satellites with metal frames of different sizes. By the first inventory branches and cones were not sampled, however, all fractions were sampled with the NFSI II. The subsequent partition of the coarse fraction of the organic layer was set at a diameter of >20 mm. Sampling of mineral soil was conducted at the profile in the depth 0–5 cm, 5–10 cm, 10–30 cm, 30–60 cm and 60–90 cm.

Estimation of soil carbon stocks

Carbon stocks for the organic layer and the mineral soil down to a depth of 30 cm were estimated according to methods presented by Grüneberg et al. (2014). Carbon stocks down to 90 cm of the mineral soil were obtained by summing up the individual depths increments. If the lowest depth level was only partially included within 0–90 cm carbon stocks were proportionately calculated. Organic soils or strongly anthropogenic transformed soils were not included in the analysis since the sample number was too small.

Initially, the content of the fine-earth fraction was calculated as a function of dry bulk density and the content of the coarse-soil fraction [Eq. 1, 2]. The values were determined by the Federal Forest Research Stations according to the methods of the expert committee on Forest Analysis (GAFA 2006). The Federal State Forest Research Stations delivered either dry density of the fine-earth fraction (g cm^{-3}) or the dry bulk density (g cm^{-3}) as well as the coarse-soil fraction (Vol. %) or the coarse-soil stocks (t ha^{-1}) to the national database. Those variables have to be continuous for at least 90 cm.

$$CFF_i = BD_{FE_i} * D_i * \left(1 - \frac{VCF_i}{100}\right) * 100 \quad [1]$$

CFF – weight of the fine-earth fraction; BD_{FE} – dry bulk density of the fine-earth fraction, D – Depth; VCF – volume of the coarse-soil fraction
or

$$CCF_i = BD_g * D_i * 100 - CCF_i \quad [2]$$

CCF – weight of the coarse-soil fraction; BD_i – dry bulk density of the gross soil.

The organic carbon concentration was determined by the methods of GAFA (2006) measuring the total amount of carbon in consideration of inorganic C. For soils without carbonates it was assumed that organic and inorganic carbon is equal.

Site-related carbon stocks down to a depth of 90 cm of the mineral soil were estimated by applying weighting factors due to different raster densities of the federal states plot grid inventory sites. Weighting factors were derived by calculating the proportion of the federal state forest area in relation to Germany's forest area that were divided by the number of appropriate inventory plots in each federal state [Eq. 3].

$$wl = \frac{Al}{\sum_{l=1}^{16} Al} * \frac{1}{nl} \quad [3]$$

with

wl – weighting factor of the inventory plots of the federal state l , Al – forest area of the federal state l , nl – number of plots within a federal state l .

CORINE land cover data from 1990 and 2006 was used to estimate the proportion of the federal state forest area in relation to Germany's forest area (EEA 2010a; b).

2.2. National Forest Inventory

2.2.1 Sampling methods

The German National Forest Inventory (NFI) was carried out in the years

- 1986 to 1987 (NFI 1987) only in the old federal states and West-Berlin,
- 2001 to 2002 (NFI 2002) in the whole country and
- 2011 to 2012 (NFI 2012) in the whole country,

comprising close to 60,000 forest sampling plots and 420,000 trees (Fig. 2). In the so called Inventory Study in the year 2008 on a $8 \text{ km} \times 8 \text{ km}$ subsample of the NFI grid all relevant parameters were measured within one year to derive the carbon stock stored in forests in the beginning of the 1st commitment period of the Kyoto-protocol. The NFI is a terrestrial sample with permanent sampling points. The samples are distributed in a systematic $4 \text{ km} \times 4 \text{ km}$ basic grid. But in 54% of the area there is a double or fourfold sampling density. Each sampling unit is a cluster of four plots (or less in the near of country or sampling strata borders) located at the corners of a $150 \text{ m} \times 150 \text{ m}$ square.

For the selection of sample trees with a diameter larger than 7 cm at breast height (DBH), angle-count sampling is used. For smaller trees there are installed two sample circles with radius of 1 m and 2 m. Deadwood with a minimum diameter of 10 cm is assessed in sample circles with 5 m radius. Overview information about the sampling methods of the German NFI can be found for example in Polley et al. 2010. A field manual (BMELV 2011a) gives detailed instruction for the data collection.

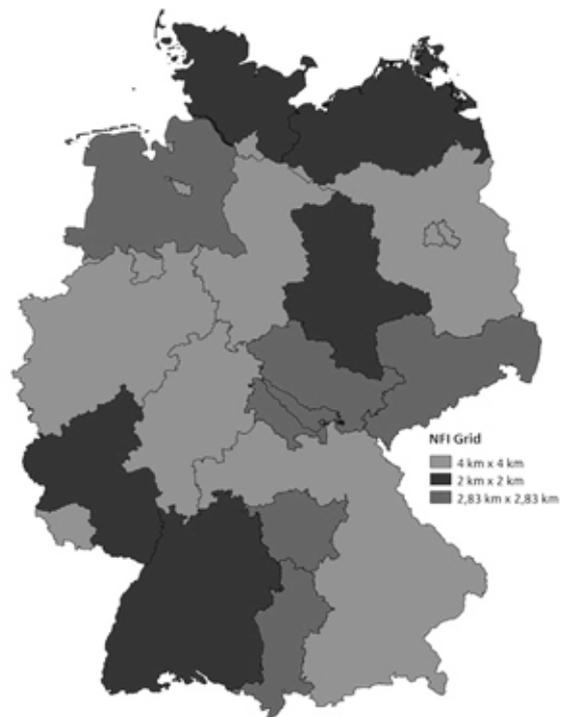


Fig. 2. Sampling grid density of the German National Forest Inventory 2012.

2.3. Estimation of carbon stocks

2.3.1 Above- and below-ground living tree biomass

First the above- and below-ground living tree biomass is estimated by means of biomass functions derived from the data of the National Forest Inventory, described in Röhling et al. (2016). Within the integrated model for estimating the above-ground biomass on single tree level the predictors DBH, height and the diameter in one third of the tree height are used. This integrated model consists of four allometric (after Marklund) functions for different size classes of trees with continuous transition between these size classes. To estimate the below-ground biomass on single tree level only the DBH acts as a predictor. The coefficients of these functions are specific for five tree species groups: spruce, pine, beech, oak and broadleaved tree species with short life span. Further background and comparisons to other estimation methods about the above and below ground biomass functions can be found in Riedel & Kändler (2017) and in Neubauer et al. 2015 as well as in Chapter 6.4.2.2.4 of the NIR 2017 (FEA 2017). Then a value of 0.5 has been applied for conversion of biomass into carbon stocks.

2.3.2 Biomass of deadwood

Since the NFI 2002 the carbon stock in dead wood greater than 20 cm is recorded. In addition dead wood between 10 and 20 cm is measured for purposes of GHG reporting pursuant to the IPCC Guidelines 2006 since the Inventory Study 2008. The relationship between both subpopulations a) pieces between 10 cm and 20 cm and b) pieces greater than 20 cm was extrapolated to the inventory period 2002–2008 to estimate the carbon stock for small dead wood according to the IPCC Guidelines. Within the NFI the sampled dead wood pieces, stumps or dead standing trees were distinguished into three main tree-species groups: conifers, deciduous trees (other than oaks) and oaks. In addition, dead wood was classified into a total of four decomposition-level categories (BMELV 2010; BMVEL 2001). The biomass of the dead wood stocks for the various relevant decomposition classes, was determined with the wood density figures pursuant to Fraver et al. (2002) for conifers, and with the wood density figures pursuant to Müller-Using & Bartsch (2009) for both deciduous tree species (other than oak) and oak tree species. An overview of the biomass-expansion factors is presented in Table 1. To convert the so derived biomass in carbon, the conversion factor of 0.5 is used once again.

Table 1. Biomass expansion factors (BEF) for the various tree-species classes and degrees of decomposition separately for conifers and deciduous trees.

Type of dead wood	Degree of decomposition	BEF	Source
Conifers	1 Just died	0.37	Fraver et al. 2002
Conifers	2 Onset of decomposition	0.31	
Conifers	3 Advanced decomposition	0.14	
Conifers	4 Heavily rotted	0.12	
Deciduous trees	1 Just died	0.58	Müller-Using &
Deciduous trees	2 Onset of decomposition	0.37	Bartsch 2009
Deciduous trees	3 Advanced decomposition	0.21	
Deciduous trees	4 Heavily rotted	0.26	

2.3.3 Estimation of changes in carbon stocks

For calculations of changes between two time points (the periods 1987–2002, 2002–2008 and 2008–2012), under the continuous forest inventory schema the IPCC stock difference method was used. Therefore estimators for one-phase, stratified sampling were applied according to the NFI sampling design. The total amount of carbon stock changes within a period is divided by the amount of years to derive annual estimates. The annual carbon stock change estimates in dead wood were extrapolated from the inventory period 2002–2008 down to the reference year 1990.

3. Results and discussion

3.1. Distribution and changes of carbon stocks in the forests in Germany

Currently, round about 2500 mill. t of carbon are stored in German forests (Fig. 3). In above-ground and below-ground biomass 46% of total carbon stocks are stored, 1% in dead wood and 53% in the organic layer together with soil up to 90 cm. Carbon stocks calculated using the data from the NFI 2012 reflect the total forested areas in the country and yield values of approximately 993 mill. t of carbon in the aboveground biomass, 156 mill. t for below-ground biomass and 20 mill. t for deadwood (Fig. 3).

A study of Grüneberg et al. (2014) analyzed data of the NFSI and provided an estimate of carbon stocks in the organic layer of $18.8 \pm 0.3 \text{ t ha}^{-1}$ (192 mill. t C) and in the upper 30 cm of the mineral soil $61.8 \pm 3.7 \text{ t ha}^{-1}$ (630 mill. t C). The results indicate that the relatively labile carbon pool has remained constant over the period between the inventories since the organic layer comprised $19.0 \pm 0.3 \text{ t C ha}^{-1}$ (203 mill. t C) at the NFSI I,

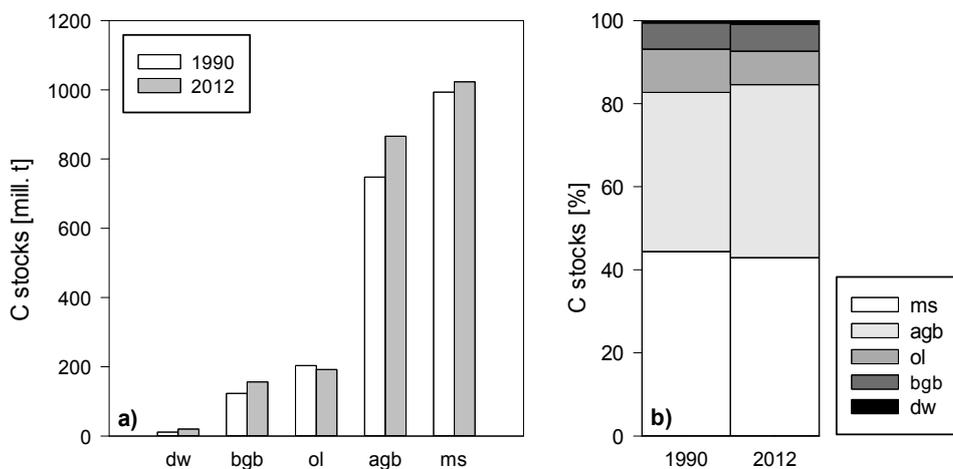


Fig. 3. Distribution of absolute carbon pools in forest ecosystems (a) and relative contribution of the components to total carbon pools (b) in Germany's forests in 1990 and 2012.

Abbreviations of forest ecosystem carbon pools: dw – dead wood, bgb – below-ground biomass, ol – organic layer*, agb – above-ground biomass, ms – mineral soil*.

*Data was obtained in 2006 by the second National Forest Soil Inventory.

while the mineral soil down to a depth of 30 cm stored $55.6 \pm 3.4 \text{ t C ha}^{-1}$ (595 mill. t C) at the NFSI I. Carbon stocks down to 90 cm of the mineral soil showed a different development. Estimates of carbon stocks down to a depth of 90 cm resulted in $84.2 \pm 2.0 \text{ t ha}^{-1}$ (866 mill. t C) and $99.1 \pm 1.8 \text{ t ha}^{-1}$ (1,023 mill. t C) at the first and second NFSI, respectively. The carbon storage is much higher in the upper 30 cm of the mineral soil than in the soil below. In 60 – 90 cm forests soils carbon decrease within the inventories (Grüneberg et al. 2017).

There might be various reasons due to changing impact factors as decreasing atmospheric deposition of acidifying compounds, liming, or large scale forest conversion (Wellbrock et al. 2016). A quarter of the plots have been limed since NFSI I (Grüneberg et al. 2016a). Compared with NFI 2002 the NFI 2012 showed that in German forests growth more broadleaved trees (<https://bwi.info>). It has been shown that broadleaved forests and limed plots store more carbon (Grüneberg et al. 2016b). A lower C/N ratio of broadleaves led to a better humus layer status. Liming or higher pH values might result in leaching carbon from humus layer to upper mineral soil. On a national scale results showed a heterogeneous pattern too (Grüneberg et al. 2014). Changes were particularly significant in northern Germany, whereas the changes in most parts of southern Germany were negligible (Grüneberg et al. 2014). Actually, within the Kyoto-obligation of reporting soil will be reported up to 30 cm. Results of the NFSI showed that approximately $0.90 \text{ mill. t C ha}^{-1}$ are stored in forests soils. Soil carbon stocks within this depth increase about $0.4 \text{ t ha}^{-1} \text{ yr}^{-1}$, and in the biomass the increment is about $1.0 \text{ t C ha}^{-1} \text{ yr}^{-1}$. Closer inspection revealed a slight increase in carbon stocks in deadwood since the 2002 inventory. The increase in carbon stocks in biomass is substantially greater. Since 2008, an annual increase of close to 12 mill. t C has been documented. For German forest an inventory in 2008 showed that $1.43 \text{ mill. t C ha}^{-1}$ were fixed in forests stand. This is 4.7 t C ha^{-1} more than in 2002 (Dunger et al. 2009). However, the net-sink rate of forests stands could decrease in the next years (Krug & Köhl 2010) because wood products became more attractive.

3.2. Impact on carbon sequestration

The impact of forest management and indirect anthropogenic activities on the carbon dynamic in forest ecosystems is high. Various studies have shown a significant influence of tree species selection and accompanied forest stand composition on carbon stocks (Ladegaard-Pedersen et al. 2005; Prietzel & Bachmann 2012). Forest management practices such as drainage, thinning, timber harvesting and liming can also affect soil carbon dynamics (Johnson et al. 2002; Nave et al. 2010). Admittedly, investigations of liming induced effects on carbon stock changes have revealed contradictory results. On

the one hand, it has been shown that after the application of lime the decomposition of the organic layer increased accompanied by an accumulation of carbon in the mineral soil (Andersson & Nilsson 2001; Evers et al. 2008). On the other hand, various studies have demonstrated that a long-lasting decrease ranging from weeks up to one year followed by the initial increase in soil respiration after liming (Illmer & Schinner 1991; Melvin et al. 2013). Other studies suggest an impact of nitrogen (N) deposition on carbon sequestration in forest but the results are highly uncertain and vary by two orders of magnitude (de Vries et al. 2009; Janssens et al. 2005). The increase in nitrogen deposition on forests over a longer time period may reduce the decomposition of organic matter. Increased organic matter input in soil through enhanced aboveground biomass productivity or increased recalcitrance of nitrogen-enriched litter may lead to reduced long-term decomposition rates of organic matter (de Vries et al. 2009) but on the other hand high nitrogen deposition lead to increasing biomass in nitrogen limited forest ecosystems.

Tree growth may reduce the greenhouse effect due to tree assimilation of CO_2 . Living biomass of beech stands store $3.3 \text{ t ha}^{-1} \text{ yr}^{-1}$ and spruce stands $3.2 \text{ t ha}^{-1} \text{ yr}^{-1}$ carbon. The increment of spruce is higher than those of beech, but beech has a higher wood density (Kollmann 1982). If one considers increment and drain (net change) respectively beech stored $0.98 \text{ t ha}^{-1} \text{ yr}^{-1}$ while spruce carbon storage is $-0.39 \text{ t ha}^{-1} \text{ yr}^{-1}$. The negative development in spruce stands can be explained by intensive harvesting activities. Currently in beech stands 127 t ha^{-1} carbon are stored in the aboveground biomass and 101 t ha^{-1} in spruce stands. A sustainable forest management with more beech stands improves to carbon budget of forests. The release of CO_2 can be avoided or reduced as a consequence of carbon storage in forests.

3.3. Forests and wood products are carbon sinks

As proved in the National Inventory Report forests in Germany act as a carbon sink each year since 1990. Thus more carbon was sequestered than released, for example in timber harvest. The estimate of annual carbon sequestration including CO_2 -release due usage of timber (net change) is currently 58 mill. t (FEA 2017). To date, the annual greenhouse gas reporting has included only carbon sequestration – material use of wood and its contribution to annual CO_2 balance is considered. However, this approach is misleading the material use of wood involves the transfer of a quantity of carbon from trees to the wood products – like forests, these products thus serve as carbon sink. Production of energy from the renewable resource also replaces fossil fuel sources (the substitution effect). Between 2005 and 2009 in average close to 15 mill. t of carbon was sequestered in wood products and approximately another 8 mill. t was saved through

energy substitution annually (Rüter 2011). The potential of forests as carbon sinks is therefore even greater than previously indicated in the reports.

4. Conclusions

The representative samples of the NFI as well as the NFSI and their repetitions cover entire Germany and are high quality data to estimate carbon stocks and carbon stock changes in biomass, dead wood, litter and soils up to a depth of 90 cm according to the Kyoto reporting obligations and further relationship- impact studies. Since there are only few comparable qualitative and quantitative data, especially for soils, the analysis of these data sets will provide results that will help to understand carbon storage of forests. Furthermore, the reporting obligations create additional opportunities for quality assessment of the inventory data and set new standards on sampling methods as well as evaluation approaches. Our results show that the carbon pools biomass, dead wood and mineral soils in the German forests act as a carbon sink with an increasing carbon storage within the reporting time. The forest management and atmospheric deposition of sulphur, nitrogen and CO₂ has changed in the second half of the 20th century. The percentage of broadleaves increased in the same time. Furthermore many forests had been limed. This development protects the supply of organic carbon. This way, management may lead temporarily to a higher root penetration into the soil and thus lead to higher carbon entries. Another cause of the high immobilization rates could be that carbon poor soils are not saturated with carbon and which results in an upward trend until a steady state situation is reached. All immobilization rates are quite high. Both inventories are more or less 5 to 15 years old. In 2017 a carbon inventory is carried out on a 8 km by 8 km sub-grid of the NFI to assess the current carbon stock in living biomass and dead wood. The next NFI will be conducted in 2021/2022. The next soil inventory is planned to conduct in 2023–2025. Then, we can see how processes in forests will go on. In addition process-oriented research would be necessary to detect causes of changes.

Acknowledgement

All fieldwork had been done and financed by the federal states in Germany. The Federal Ministry of Food, Agriculture and Consumer Protection financed the Federal Coordination and Federal Evaluation.

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Country and regional carbon stock in forest cover – estimates based on the first cycle of the Czech National Forest Inventory data (2001–2004)

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Abstract

Since forests can play an efficient role in the mitigation of greenhouse gas emissions, objective information about the actual carbon stock is very important. Therefore, the presented paper analysed the carbon stock in the living merchantable trees (with diameter at breast height above 7 cm) of the Czech forests with regard to groups of tree species and tree compartments (wood under bark with diameter above 7 cm, wood under bark with diameter below 7 cm, bark, green twigs, foliage, stump and roots). We examined its regional distribution and relationship to the number of inhabitants and the gross domestic product. The data used for the analysis originated from 13,929 forest plots of the first Czech National Forest Inventory performed between 2001 and 2004. The total tree carbon stock was obtained as a sum of the carbon stock in the individual tree compartments estimated from the biomass amount in the compartments multiplied by the relative carbon content. Wood biomass amount was calculated by multiplying a particular part of tree volume with species-specific green wood density. The total amount of carbon stored in forest trees in the Czech Republic was over 327 mill. t, which is about 113 t of carbon per ha of forests. The highest carbon amount (160 mill. t, i.e. 49.0% of the total amount) was fixed in spruce. The minimum carbon amount fixed in the forest cover (14.35 mill. t) was calculated for Ústecký kraj (region), while the maximum carbon amount (51.51 mill. t) was found in Jihočeský kraj.

Key words: carbon; forest biomass; tree compartments; tree species composition; allometric equation

Editor: Rastislav Raši

1. Introduction

Although the Czech Republic belongs to countries with an average forest cover in Europe, its wood stock per hectare exceeds the European average (Forest Europe 2015). At the same time, the forest area as well as the hectare wood stock of the country and the total standing wood stock have been increasing over the last decades. For instance, while in the year 1950 the total estimated wood stock (expressed as wood with diameter > 7 cm without bark) from the Summarised Forest Management Plans was 322 mill. m³, in 1980 it increased to 536 mill. m³ and in 2010 to as much as 681 mill. m³ (MACR 2016). However, the total growing stock derived from the first National Forest Inventory (NFI) data (2001–2004) was significantly higher (900 mill. m³, Štěrba & Jankovská 2007; Kučera et al. 2014) in comparison to 658 mill. m³, which

was the estimated growing stock in 2004 derived from the Forest Management Plans used in official statistics. The growing stock derived from the second NFI (2011–2014) is 935.8 mill. m³ and is higher than in the first NFI and confirms the trend of the increasing growing stock in the Czech Republic. These estimates indicate that thanks to the gradually increasing forest biomass the country takes an active part in the whole European trend to increase forest stocks and carbon reserves sequestered in it (Lindner & Karjalainen 2007).

Intensive utilisation of land by humans modifies carbon sequestration and emissions in/from forests or other ecosystems as well as the soil. Thus, it is necessary to monitor, and analyse these impacts at specific levels (regional, national, continental and global), and to control them on the base of the actual situation. The United Nations initiated the Framework Convention about Cli-

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mate Change covering also Land Use, Land-Use Change and Forestry (LULUCF, IPCC 2003). The LULUCF activities related to the expansion of forest area and the increase of forest stocks focus on carbon absorption from the atmosphere (see e.g. MacDicken 2015). To optimise human impacts on forests for carbon sequestration, we should have the knowledge about the landscape state, specifically the structure of different types of ecosystems (forests, grasslands, agricultural lands, wetlands, etc.) including their spatial arrangement.

From the point of land utilisation and management, three main strategies to increase the amount of carbon in ecosystems are considered: 1) maintaining carbon sequestration in forests, 2) changes on agricultural lands aimed at reduction of arable fields (prevaillingly in the form of afforestation), 3) conservation of the currently existing carbon storage pools, especially vegetation on wetlands and in old-growth forests (Janssens et al. 2005). Forests, and especially afforestation measures and measures leading to the increase of hectare wood stock, are considered to be the most efficient carbon sequestration systems (see also MacDicken 2015). In general, large differences in forest cover as well as in hectare stock exist not only between individual countries but also at intra-country level, i.e. between individual regions within one country (Andronache et al. 2017). The variability in forest cover among countries and administrative regions results from different political settings, socioeconomic conditions, ownership structure and management practices in the past and present (Cvitanovic et al. 2016, Andronache et al. 2017). At a global level, Keenan et al. (2015) revealed that forest cover increases with the increasing income of the region or the country, while Crespo Cuaresma et al. (2017) revealed a U-shaped relationship between the income per capita and the forest cover of countries. The information about the conditions in specific regions, e.g. administrative units, is necessary for strategic decision-making at a national level. A “dissection” on current situation in forest biomass quantity (amount of fixed carbon) is important particularly for the Czech Republic seeing that the government has declared to support afforestation as an essential part of its national rural developmental program (Forest Europe 2015).

For the estimation of biomass in forest cover, i.e. also carbon accumulated in trees, a variety of terrestrial and aerial methods can be applied. Most developed countries conduct regular national inventories of their forests, which provide valuable data for the estimation of carbon stock at least at a national level, and possibly also at certain regional scales, if they are based on statistically sound design and permanent inventory plots (e.g. Brown 2002). In such cases, individual tree characteristics measured at inventory plots are used in functions for tree biomass estimation. Three methods are frequently used to calculate biomass at a tree level (Brown 1997; West 2010): (1) allometric equations, in which tree height or/and stem diameter are most commonly used independent

variables, (2) expansion factors used for multiplying stem volume as an independent variable, and (3) combination of the first two methods.

As the first NFI in the Czech Republic was performed just at the beginning of the 21st century, the data for the estimation of the actual biomass in forest cover have become available. In 2014 and 2016, the Forest Management Institute estimated the amount of aboveground biomass of trees with tree height ≥ 10 cm from NFI1 and NFI2 data using the allometric equations of four main tree species – spruce, pine, oak and beech (Kučera et al. 2014, 2016). The presented paper uses the combined approach of biomass estimation, since the biomass of wood and bark was derived from wood volume, and the allometric equations were used only for the calculation of foliage and root biomass.

The main ambition of this paper was to quantify and analyse carbon stock in merchantable forest biomass (i.e. in living trees with diameter at breast height ≥ 7 cm) on the base of the first NFI data using a combined method of calculating carbon stock. We focused on the merchantable part of forest ecosystems because it sequesters most of the carbon and is most significantly influenced by human activities. The specific goals of the work were as follows:

1. To present and describe a combined method of biomass estimation based on the calculation of tree and bark volume using species-specific volume equations and models of stem shape, and the calculation of foliage and root biomass using species-specific allometric equations.
2. To quantify carbon stock of the Czech Republic using this method at a national level with regard to individual tree species and individual tree compartments (i.e. foliage, branches, stem under bark, stem bark, and roots) because both tree species and/or compartments differ in their life expectancy and hence, in their carbon sequestration capacity (Loehle 1987; Steele et al. 1997; Helmisaari et al. 2002). In addition, they are also influenced by different management and harvesting practices that reflect the species composition of the stands. Due to this, their current share in the carbon stock may indicate future development of carbon stock.
3. To analyse the regional distribution of carbon stock considering the current administrative units and to examine the relationship of the carbon stock to the number of inhabitants and the regional gross domestic product (GDP) because forest cover is known to be dependent on population density (Li et al. 2013; Van Noordwijk & Villamor 2014; Thorn et al. 2016) and income (Keenan et al. 2015; Crespo Cuaresma et al. 2017).

We believe that the outcome of such analyses may create the information basis for decision-making at both regional and national levels, because it is an inductive method based on “bottom-up” principles.

2. Material and Methods

2.1. Empirical data

The data used for the analysis originate from the NFI1 in the Czech Republic. The NFI in the Czech Republic is set by Act No. 289/1995 coll., on Forests and Amendments to some Acts (The Forestry Act) and the Governmental Regulation No. 193/2000 coll. They declared the implementation of the forest inventory for the period from 2001 to 2004. The NFI in the Czech Republic has been conducted by the Forest Management Institute (FMI) in Brandys nad Labem which is also responsible for NFI data management and data processing.

The applied sampling design of NFI was based on the systematic group sampling in a grid size of 2×2 km (Fig. 1). Two permanent circular plots were established in each grid cell. The position of the first inventory plot was randomly generated within a circle with a radius of 300 m around the centre of the inventory grid cell. The plot was established if the plot centre was located within the category of forest. The distance between the inventory plots of the same cell was set to constant 300 m, while the direction from the first to the second plot was random (Štěrbá & Jankovská 2007). Between the years 2001 and 2004, 39,460 plots were established in total, out of which 25,531 were non-forest plots, and 13,929 were forest plots located in 8,705 grid cells of 2×2 km.

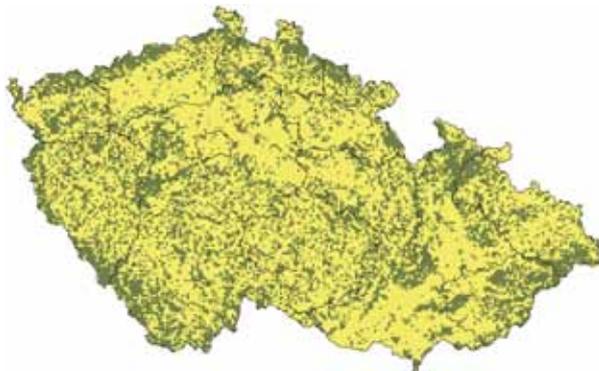


Fig. 1. The map indicates the positions of the NFI plots (first cycle performed during the years of 2001–2004) on the territory of the Czech Republic and their categorisation as forest or non-forest.

Legend:  – forest,  – non-forest, – border of the region.

Each plot was stratified into segments with regard to the specific classes of the land cover. The segment should have a minimum size of 10% of the area of the inventory plot. The plot was a fixed circle of 500 m² for the trees with diameter at breast height (*DBH*) greater or equal to 12 cm. For the trees with *DBH* between 7 and 11.9 cm and for the regeneration with height ≥ 10 cm additional two concentric circles were established in the centre of gravity (location of maximum distance to seg-

ment boundaries) of each polygonal segment of the plot. For the first group a circle with a radius of 3 m and for the second group a circle with a radius of 2 m was established. The number of investigated primary (field) variables per plot was approximately 150 (Štěrbá & Jankovská 2007).

For this work we used tree data of standing living trees with *DBH* over 6.9 cm over bark was measured on every tree over the registration threshold (7 cm) with precision in mm over bark. Tree height was measured on a sample of trees with the following criteria: maximum 50 trees per species on one plot, standing living trees without fresh stem breakage, stem bending or forking below the height of 7 m. If no height was measured for a particular species on a subplot, a model height was used. The model was developed using the data from other inventory plots.

2.2. Biomass and carbon estimate

Mean tree volume was calculated using two-parameter regressions derived for volume tables of Czechoslovakia by Petráš & Pajčík (1991). The authors compiled over 30-year long work in this field in former Czechoslovakia, enhanced some equations and presented the calculation of the following volumes:

- Stem volume under bark (*SVUB*)
- Stem volume over bark (*SVOB*)
- Tree volume over bark (*TVOB*)
- Volume of wood with diameter above 7 cm under bark (*VWUB*)
- Volume of wood with diameter above 7 cm over bark (*VWOB*).

From these volumes we also derived tree volume under bark (*TVUB*) using the procedure described at the end of this section. All volumes are calculated for the particular parts of the tree excluding the stump part (Petráš 1984).

The two parameters in all the functions are tree diameter at breast height (*DBH*) and tree height (*h*). Hence, the general form of the relationship is

$$v = f(DBH, h) \quad [1]$$

The formula and the coefficients used in the equations are presented in Petráš & Pajčík (1991) in the form of a computer program for 11 tree species: 7 broadleaved (beech, oak, hornbeam, birch, ash, poplar, poplar clone, alder) and 4 coniferous tree species (spruce, fir, pine, larch). The equations were derived from felled sample trees measured in 2 m sections including stem and crown woody parts. The collection of empirical data accounted for the regional variability of species composition in the former Czechoslovakia. Hence, the proportion of sample trees from the Czech Republic varied between individual tree species as shown in Table 1 also shows the original authors of the equations.

Table 1. Number of sample trees by tree species used for the creation of volume equations and volume tables derived for the former Czechoslovakia and the authors of the volume equations (information taken from Petráš & Pajčík 1991; Šmelko 2000).

Tree species	Number of sample trees	% from the Czech Republic	Original authors *Authors of amendments
Norway spruce	2,111	71	Korsuň (1961) – *Hubač & Pánek (1979)
Silver fir	1,477	27	Hubač & Šebík (1963) – *Hubač & Pánek (1979)
Scots pine	1,659	76	Korsuň (1962) – *Hubač & Pánek (1979)
Deciduous larch	1,293	74	Čermák et al. (1984)
Oaks	1,893	40	Čermák (1976)
European beech	1,886	21	Hubač (1977)
Common hornbeam	1,535	55	Čermák (1980)
Birches	1,355	60	Košut et al. (1985)
Common ash	1,166	40	Hubač et al. (1987)
Poplars	1,480	64	Korsuň (1967) – *Halaj & Petráš (1981)
Alders	2,232	94	Korsuň (1966) – *Řehák (1981), Petráš & Pajčík (1991)
Sum	20,357	58	All above-listed authors

For other species, for which no volume equations were available, the formulas and the coefficients of the most similar tree species (based on genus and family similarities) were used.

In addition, we also calculated stem volume under bark using the integral equation (*ISVUB*), which was based on the models of stem shape derived by Petráš (1986, 1989, 1990). The general formula is

$$v = \frac{\pi}{40\,000} \times \int_0^h d(h_i, h, DBH, \vec{a}, sp)^2 dh \quad [2]$$

where:

- $v = ISVUB$ – stem volume under bark in m^3 ,
- h – tree height in m,
- DBH – tree diameter at 1.3 m height in cm,
- d – tree diameter at the i^{th} tree height (h_i) in cm,
- a – vector of tree-species specific parameters in the model of stem shape,
- sp – tree species.

The integral equation presented above was used only for the calculation of the integral stump volume (*IVS*). The stump height was equal to a modelled height calculated using the equation of Petráš (1986, 1989, 1990):

$$h_{stump} = a + b \times h^c \quad [3]$$

where:

- a, b, c – regression coefficients,
- h – tree height in m.

By dividing the integral stump volume *IVS* with *ISVUB* we obtained the relative proportion of the stump volume from the stem volume under bark (*%VS*).

$$\%VS = IVS / ISVUB \times 100 \quad [4]$$

The stump volume (*VS*) was calculated by multiplying *%VS* with *SVUB* derived according to Petráš & Pajčík (1991).

$$VS = \%VS \times SVUB / 100 \quad [5]$$

From the calculated volumes we also derived wood volume with diameter below 7 cm, volume and the proportion of bark as follows:

Wood volume with diameter below 7 cm over bark (*VWOBT*)

$$VWOBT = TVOB - VWOB \quad [6]$$

Proportion of bark for wood with diameter below 7 cm

$$(\%bark) = \max \left(\left(\frac{VWOB - VWUB}{VWOB} \right); \left(\frac{SVOB - SVUB}{SVOB} \right) \right) \quad [7]$$

Proportion of bark on stump =

$$\min \left(\left(\frac{VWOB - VWUB}{VWOB} \right); \left(\frac{SVOB - SVUB}{SVOB} \right) \right) \quad [8]$$

Wood volume with diameter below 7 cm under bark (*VWUBT*):

$$VWUBT = VWOBT \times (1 - \%bark) \quad [9]$$

Volume of bark:

$$(Vbark) = TVOB - (VWUB + VWUBT) \quad [10]$$

The maximum and minimum functions in equations [7] and [8], respectively, were applied to consider the negative relationship between the proportion of bark and diameter of wood (Šmelko 2000).

Tree volume under bark (*TVUB*) was calculated as a sum of wood volume with diameter above and below 7 cm under bark:

$$TVUB = VWUB + VWUBT \quad [11]$$

The methodology of biomass estimation was based on the regional studies from the former Czechoslovakia (Petráš et al. 1985; Chmelař 1992; Požgaj et al. 1993; Cienciala et al. 2008). Where regional studies were not available, we used studies published elsewhere (Drexhage & Colin 2001; Miles & Smith 2009) or we approximated the values with similar species. As we only had data about trees with diameter at breast height equal to or above 7 cm, we calculated biomass only for this group of trees. The total biomass of a mean tree consisted of the biomass of merchantable wood under bark with diameter equal to or above 7 cm (B_{WUB}), biomass of wood under bark with diameter below 7 cm (B_{WUBT}), biomass of bark (B_{Bark}), biomass of green twigs (B_{gtwigs}), biomass of foliage ($B_{foliage}$), and biomass of stump and roots ($B_{stump+roots}$).

$$B = B_{WUB} + B_{WUBT} + B_{Bark} + B_{gtwigs} + B_{foliage} + B_{stump+roots} \quad [12]$$

The biomass of wood under bark was defined as oven-dry biomass of wood under bark with diameter equal to

or above 7 cm. It is calculated by multiplying the volume of wood under bark with diameter equal to or above 7 cm ($VWUB$) with green wood density (D_{gw}) of particular species given in Table 2 taken from Klement et al. (2010), Miles & Smith (2009), Meier (2013), Tümen & Hafizoglu (2002).

$$B_{VWUB} = VWUB \times D_{gw} \quad [13]$$

Green wood density was defined as the ratio between the oven-dry wood mass (kg) and green (fresh) wood volume (m^3).

The biomass of wood under bark with diameter below 7 cm was calculated by multiplying the volume of wood under bark with diameter below 7 cm with green wood density of particular species and correction index I_{WUBT} . The values of the correction index were derived from the values published by Požgaj et al. (1993) and Chmelař (1992).

$$B_{WUBT} = VWUBT \times D_{gw} \times I_{WUBT} \quad [14]$$

The biomass in bark was calculated by multiplying the volume of bark with green wood density of particular species and correction index I_{bark} representing the ratio

between bark and wood density. The values of the correction index for individual tree species were derived from the study of Miles & Smith (2009).

$$B_{Bark} = V_{bark} \times D_{gw} \times I_{bark} \quad [15]$$

The biomass in green twigs (B_{gtwigs}), biomass in foliage ($B_{foliage}$), and biomass in stump and roots ($B_{stump+roots}$) were calculated using the two-parameter functions with tree diameter at breast height (DBH in cm) and tree height (h in m) as independent variables entering the models published by different authors. The biomass in green twigs (B_{gtwigs}) and biomass in foliage ($B_{foliage}$) were calculated following the method published by Petráš et al. (1985). The authors published equations for three species: spruce, pine and beech. The biomass in stump and roots was calculated using the work of Drexhage & Colin (2001). The authors derived the coefficients for several species, out of which we used the formulas for Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), common beech (*Fagus sylvatica*), and pedunculate oak (*Quercus petraea*). The original functions were mathematically modified by introducing additional coefficients equal to 0 or 1 to obtain the same mathematical form for all cal-

Table 2. Green wood density (D_{gw}) of individual species and their correction coefficients (I) used for the calculation of oven-dry biomass in individual tree compartments. The values are taken or derived from Klement et al. (2010), Miles & Smith (2009), Požgaj et al. (1993), Chmelař (1992), Meier (2013), Tümen & Hafizoglu (2002). Correction index I_{bark} represents the ratio between bark and wood density, correction index I_{WUBT} represents the ratio between the wood densities of wood below and above 7 cm.

Tree species	D_{gw} [kg m ⁻³]	I_{bark}	I_{WUBT}	Tree species	D_{gw} [kg m ⁻³]	I_{bark}	I_{WUBT}
<i>Picea abies</i>	380	1.25	1.2	<i>Acer campestre</i>	500	1.13	1.1
<i>Picea pungens</i>	380	1.25	1.2	<i>Acer negundo</i>	420	1.19	1.1
<i>Picea mariana</i>	380	1.11	1.2	<i>Acer sp.</i>	500	1.13	1.1
<i>Picea glauca</i>	370	1.05	1.2	<i>Fraxinus excelsior</i>	570	0.91	1.1
<i>Picea omorica</i>	380	1.25	1.2	<i>Fraxinus americana</i>	550	0.91	1.1
<i>Picea engelmanni</i>	380	1.25	1.2	<i>Fraxinus angustifolia</i>	550	0.91	1.1
<i>Picea sp.</i>	380	1.25	1.2	<i>Ulmus minor</i>	540	0.79	1.1
<i>Abies alba</i>	370	1.37	1.2	<i>Ulmus glabra</i>	540	0.79	1.1
<i>Abies grandis</i>	350	1.63	1.2	<i>Ulmus laevis</i>	540	0.79	1.1
<i>Abies concolor</i>	370	1.51	1.2	<i>Robinia pseudoacacia</i>	660	0.44	1.1
<i>Abies nordmanniana</i>	370	1.32	1.2	<i>Betula pendula</i>	520	1.13	1.1
<i>Abies procera</i>	370	1.37	1.2	<i>Betula pubescens</i>	520	1.13	1.1
<i>Abies sp.</i>	370	1.37	1.2	<i>Sorbus aucuparia</i>	531	1.00	1.1
<i>Pseudotsuga menziesii</i>	450	0.98	1.2	<i>Sorbus torminalis</i>	564	1.00	1.1
<i>Pinus sylvestris</i>	430	0.95	1.1	<i>Sorbus aria</i>	530	1.00	1.1
<i>Pinus nigra</i>	430	0.95	1.1	<i>Juglans regia</i>	510	1.00	1.1
<i>Pinus banksiana</i>	400	1.03	1.1	<i>Juglans nigra</i>	510	0.65	1.1
<i>Pinus strobus</i>	340	1.38	1.1	<i>Platanus acerifolia</i>	460	1.30	1.1
<i>Pinus cembra</i>	400	0.95	1.1	<i>Prunus avium</i>	470	1.34	1.1
<i>Pinus contorta</i>	430	0.95	1.1	<i>Prunus serotina</i>	470	1.34	1.1
<i>Pinus sp.</i>	430	0.95	1.1	<i>Pyrus communis</i>	564	1.00	1.1
<i>Pinus mugo</i>	430	0.95	1.1	<i>Malus sylvestris</i>	610	0.82	1.1
<i>Pinus rotundata</i>	430	0.95	1.1	<i>Tilia cordata</i>	440	1.50	1.1
<i>Larix decidua</i>	450	0.65	1.1	<i>Tilia platyphyllos</i>	440	1.50	1.1
<i>Larix sp.</i>	450	0.65	1.1	<i>Tilia tomentosa</i>	440	1.50	1.1
<i>Taxus baccata</i>	600	1.00	1.2	<i>Alnus glutinosa</i>	417	1.51	1.1
<i>Juniperus communis</i>	430	0.82	1.1	<i>Alnus incana</i>	355	1.51	1.1
<i>Quercus robur</i>	550	1.00	1.1	<i>Alnus viridis</i>	355	1.51	1.1
<i>Quercus robur slavonica</i>	550	1.00	1.1	<i>Populus tremula</i>	360	1.33	1.0
<i>Quercus petraea</i>	550	1.00	1.1	<i>Populus alba</i>	360	1.33	1.0
<i>Quercus rubra</i>	560	1.21	1.1	<i>Populus nigra</i>	360	1.33	1.0
<i>Quercus pubescens</i>	550	1.00	1.1	<i>Populus sp.</i>	360	1.33	1.0
<i>Quercus palustris</i>	580	1.03	1.1	<i>Populus × hybr.</i>	360	1.33	1.0
<i>Quercus sp.</i>	550	1.00	1.1	<i>Salix caprea</i>	354	1.39	1.0
<i>Quercus cerris</i>	550	1.00	1.1	<i>Salix alba, fragilis</i>	356	1.39	1.0
<i>Fagus sylvatica</i>	570	1.20	1.1	<i>Aesculus hippocastanum</i>	330	1.52	1.1
<i>Carpinus betulus</i>	650	0.95	1.1	<i>Castanea sativa</i>	400	1.25	1.1
<i>Acer platanoides</i>	500	1.13	1.1	<i>Ailanthus altissima</i>	460	0.98	1.1
<i>Acer pseudoplatanus</i>	500	1.13	1.1				

culated compartments in order to simplify the programming work. The function that we used for the calculation of biomass (*B*) in the three compartments (green twigs, foliage, and stump+roots) has the following form:

$$B = b_1 \times (DBH + b_2)^{b_3} \times h^{b_4} \times b_5 \quad [16]$$

where:

$b_1 - b_5$ are species specific regression coefficients.

Carbon stock (*CS*) in tree compartments was estimated from the biomass amount (*B*) in individual compartments multiplied by relative carbon content in biomass (*CC*)

$$CS_i = B_i \times CC \quad [17]$$

where:

B_i – biomass amount in i^{th} tree compartment,

i – tree compartment as defined above: wood under bark with diameter equal to or above 7 cm (WUB), bark, wood under bark with diameter below 7 cm (WUBT), wood over bark with diameter equal to or above 7 cm (WOB), wood over bark with diameter below 7 cm (WOBT), green twigs (gtwigs), foliage (foliage), stump and roots (stump+roots).

CC – relative carbon content in biomass.

Following “Good Practice Guidance for Land Use, Land-Use Change and Forestry” of Intergovernmental Panel on Climate Change (IPCC, 2003), we used a constant relative carbon content in biomass equal to 0.5 for all tree species.

Tree values are upscaled to a plot level by multiplying mean tree values per species with the respective number of trees per species and summing the species plot values together:

$$X_{plot} = \sum X_{species} \times N_{species} \quad [18]$$

where:

X – is any estimate for a mean tree (e.g. volume, biomass, carbon),

N – is number of trees of a particular species on a plot.

These plot values were further processed to obtain summary information about carbon stock at national and regional levels. The Czech Republic is divided into 14 administrative units called regions (kraj in Czech lan-

guage). Table 3 presents their area together with their forest area and forest cover. The data from this table were used for the calculation of carbon density at national and regional levels.

The summary information on carbon stock at national and regional levels was calculated using the so called “Ratio of Means” method (Cochran 1977). It means that from the sampled data we first derived the values per hectare (X_{ha}), which were afterwards multiplied with the total forest area (A_{tot}) of the country or a region:

$$X_{ha} = \frac{\sum_{i=1}^n X_i}{\sum_{i=1}^n A_i} \quad [19]$$

$$X_{tot} = X_{ha} \times A_{tot} \quad [20]$$

The standard error of the mean was calculated using the model for cluster sampling (Cochran 1977). For the presentation of the results we created 6 groups of tree species named after the most common genera in the tree species composition of Czech forests (Štěrba & Jankovská 2007): Spruce, Pine, Beech, Larch, Oaks, and Others. The spruce group consists of all spruce species occurring in the forests of the Czech Republic: *Picea abies*, *Picea pungens*, *Picea mariana*, *Picea glauca*, *Picea omorica*, *Picea engelmanni*, *Picea* sp. Similarly, the pine group contains all pine species: *Pinus sylvestris*, *Pinus nigra*, *Pinus banksiana*, *Pinus strobus*, *Pinus cembra*, *Pinus contorta*, *Pinus* sp., *Pinus mugo*, *Pinus rotundata*, *Larix decidua* and *Larix* sp. form Larch group. In the group of Oaks there are *Quercus robur*, *Quercus robur slavonica*, *Quercus petraea*, *Quercus rubra*, *Quercus pubescens*, *Quercus palustris*, *Quercus* sp., *Quercus cerris*. The beech group contains only *Fagus sylvatica*. The group of Others comprises *Abies alba*, *Abies grandis*, *Abies concolor*, *Abies nordmanniana*, *Abies procera*, *Abies* sp., *Pseudotsuga menziesii*, *Taxus baccata*, *Juniperus communis*, other conifers, *Carpinus betulus*, *Acer platanoides*, *Acer pseudoplatanus*, *Acer campestre*, *Acer negundo*, *Acer* sp., *Fraxinus excelsior*, *Fraxinus americana*, *Fraxinus angustifolia*, *Ulmus minor*, *Ulmus glabra*, *Ulmus laevis*, *Robinia pseudoacacia*, *Betula pendula*, *Betula pubescens*, *Sorbus aucuparia*, *Sorbus torminalis*, *Sorbus aria*, *Juglans regia*,

Table 3. The basic information about the size and forest area of regions of the Czech Republic.

Code of region	Name of region	Total area ¹ [ha]	Share in the area of CR [%]	Forest area ² [ha]	Share on total forest cover of CR	Relative forest cover ³ [%]
PHA	Hlavní město Praha	49,608	0.63	5,021	0.17	10.12
STČ	Středočeský kraj	1,101,464	13.97	338,251	11.70	30.71
JHČ	Jihočeský kraj	1,005,731	12.75	412,434	14.27	41.01
PLK	Plzeňský kraj	756,107	9.59	324,932	11.24	42.97
KVK	Karlovarský kraj	331,453	4.20	159,425	5.51	48.10
ULK	Ústecký kraj	533,489	6.76	178,294	6.17	33.42
LBK	Liberecký kraj	316,300	4.01	152,300	5.27	48.15
HKK	Královéhradecký kraj	475,824	6.03	166,868	5.77	35.07
PAK	Pardubický kraj	451,860	5.73	146,284	5.06	32.37
VYS	Kraj Vysočina	692,555	8.78	219,003	7.58	31.62
JHM	Jihomoravský kraj	706,674	8.96	206,442	7.14	29.21
OLK	Olomoucký kraj	515,892	6.54	186,566	6.45	36.16
ZLK	Zlínský kraj	396,376	5.03	180,062	6.23	45.43
MSK	Moravskoslezský kraj	553,505	7.02	214,924	7.43	38.83
CR	Czech Republic in total	7,886,838	100.00	2,890,805	100.00	36.65

¹ČÚZK (2005); ²calculated from the relative forest cover; ³calculated from NFI, <http://nil.uhul.cz/>.

Juglans nigra, *Platanus acerifolia*, *Prunus avium*, *Prunus serotina*, *Pyrus communis*, *Malus sylvestris*, *Tilia cordata*, *Tilia platyphyllos*, *Tilia tomentosa*, *Alnus glutinosa*, *Alnus incana*, *Alnus viridis*, *Populus tremula*, *Populus alba*, *Populus nigra*, *Populus* sp., *Populus* × *hybr.*, *Salix caprea*, *Salix alba*, *Salix fragilis*, *Aesculus hippocastanum*, *Castanea sativa*, *Ailanthus altissima*, and other broad-leaved species.

3. Results

3.1. Forest carbon at regional levels

Since the regions, i.e. administrative units, in the Czech Republic are rather heterogeneous territories in both size (area) and forest cover (Table 3), we examined their carbon stock in the merchantable tree forest cover (Fig. 2), carbon density, i.e. carbon amount per unit area (expressed per ha of forests or per ha of the total territory; Fig. 3 and 4, respectively), the relative carbon amount fixed in merchantable forest trees in a specific region calculated as a proportion of the whole country

carbon stock (Fig. 5). Besides, we analysed the carbon stock also with regard to the number of inhabitants and gross domestic product by calculating forest tree carbon per capita (Fig. 6) and per gross domestic product of the regions (Fig. 7). All presented figures clearly show the differences in all carbon stock parameters between the regions. However, the correlation analyses between the regional carbon stocks and population density or gross domestic product did not reveal any significant trends in the carbon stock in relation to the demographic and economic indicators.

3.2. Forest carbon stock at a country level

The total amount of carbon stored in merchantable forest trees of the Czech Republic was over 327 mill. t (Table 4). It is about 113 t of carbon per ha of forests and almost 32 t of carbon per capita. If we consider tree species, the greatest amount of carbon (160 mill. t, i.e. 49% of the total amount) was fixed in Spruce group, followed by Pine group (50 mill. t; 15.4%), Others (45 mill. t; 13.9%), Beech (30 mill. t; 9.3%), Oaks



Fig. 2. Total carbon amount (mill. t) fixed in the forest cover of the Czech Republic represented by living trees with diameter equal or above 7 cm growing in the forests by the regions. Values represent mean ± standard error.

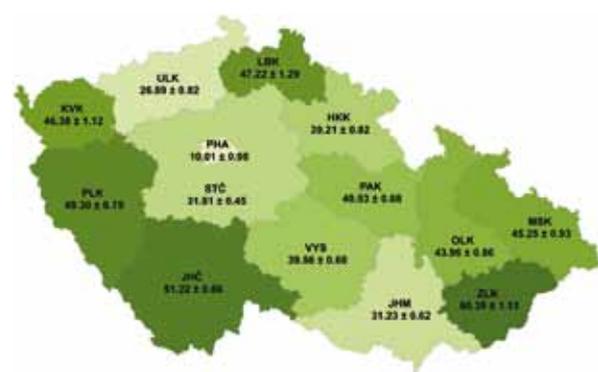


Fig. 4. Carbon amount fixed in the living trees with diameter equal or above 7 cm growing in the forests of the Czech Republic (t) per ha of the region. Values represent mean ± standard error.



Fig. 3. Carbon amount fixed in the living trees with diameter equal or above 7 cm growing in the forests of the Czech Republic per ha of the region forest area (tC ha⁻¹) by the regions. Values represent mean ± standard error.



Fig. 5. Relative contribution (%) of the regions to the total carbon amount fixed in the forest cover of the Czech Republic represented by the living trees with diameter equal or above 7 cm growing in the forests of the Czech Republic. Values represent mean ± standard error.

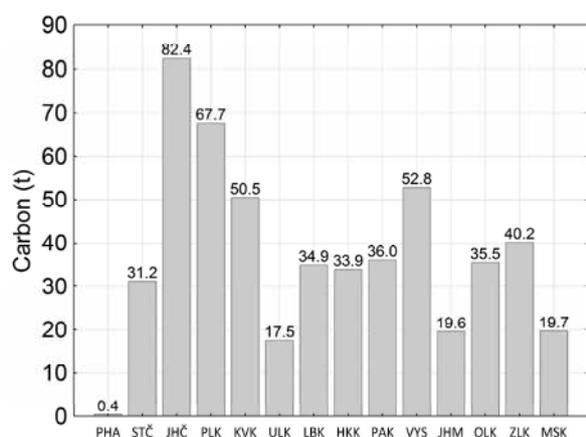


Fig. 6. Carbon amount (t) fixed in the forest cover of the regions expressed per capita.

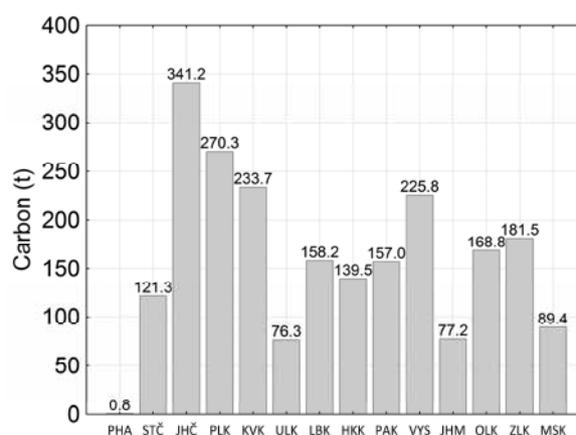


Fig. 7. Carbon amount (t) fixed in the forest cover expressed per gross domestic product of the region (in millions of Czech Crowns).

(25 mill. t; 7.7%) and Larch (15 mill. t; 4.7%). Coniferous species fixed about 230 mill. t of carbon (70.4%) in their biomass, and broadleaved species 97 t (29.6%) of carbon. Considering tree compartments irrespective of tree species (Table 5), wood ≥ 7 cm contributed to the total carbon amount most (58.1%), followed by stump and roots (19.0%), stem bark (8.8%), wood < 7 cm (6.2%), green twigs (4.8%) and finally foliage (3.2%).

The combination of contribution of specific tree compartments of main tree species may provide information about the quantity of carbon fixed in tree biomass for a short or a long period. While carbon in woody parts (branches, stem, coarse roots) is fixed for a long period, carbon in foliage rotates fast: annually in the case of deciduous species, and once per approx. 2.5 years in the case of pine or once per 5 years in the case of spruce. This different foliage rotation is reflected in contrasting contribution of tree species in carbon amount in foliage and

annual foliage fall, which was estimated from the NFI data using the above mentioned assumptions of foliage rotation (Fig. 8). At a country level, as much as 10 million t of carbon was fixed in the foliage at the time of the first national forest inventory (Table 4). Spruce, as a dominant tree species, contributed to as much as 73.2% of the total carbon in the foliage of all tree species (Table 5). On the contrary, the contribution of the main deciduous tree species (beech, oak and larch together) to the total foliage carbon stock was only 8.6% (Table 5).

We estimated that out of the total 10 mill. t of carbon in foliage, approximately 3.6 mill. t is annually “lost” from the living tree biomass due to the leaf fall. The contribution of spruce to the annual carbon loss by leaf fall was only 41.8%, while the contribution of the main deciduous tree species (beech, oak and larch together) to leaf fall was as much as 24.4% (Fig. 8).

Table 4. Total carbon amount (mill. t of carbon) in the forest cover of the Czech Republic distributed among the tree species groups and tree compartments.

Compartment	Carbon amount [mill. t] by tree species group (mean \pm standard error)						
	Spruce	Pine	Beech	Larch	Oaks	Others	Together
Green twigs	11.05 \pm 0.11	1.78 \pm 0.04	0.51 \pm 0.01	0.44 \pm 0.01	0.53 \pm 0.01	1.33 \pm 0.02	15.64 \pm 0.10
Foliage	7.56 \pm 0.08	1.09 \pm 0.02	0.30 \pm 0.01	0.27 \pm 0.01	0.31 \pm 0.01	0.78 \pm 0.01	10.32 \pm 0.07
Wood < 7 cm	7.55 \pm 0.08	2.92 \pm 0.06	2.72 \pm 0.08	0.55 \pm 0.02	1.96 \pm 0.06	4.48 \pm 0.09	20.20 \pm 0.11
Wood ≥ 7 cm	97.88 \pm 1.09	27.19 \pm 0.56	19.13 \pm 0.60	7.93 \pm 0.24	13.62 \pm 0.41	24.41 \pm 0.51	190.16 \pm 1.12
Stem bark	12.68 \pm 0.13	3.12 \pm 0.06	2.31 \pm 0.07	1.59 \pm 0.05	4.26 \pm 0.12	4.67 \pm 0.09	28.64 \pm 0.16
Stump and roots	23.73 \pm 0.24	14.19 \pm 0.28	5.52 \pm 0.17	4.42 \pm 0.13	4.66 \pm 0.13	9.60 \pm 0.20	62.11 \pm 0.34
Whole tree	160.45 \pm 1.72	50.30 \pm 1.01	30.49 \pm 0.93	15.22 \pm 0.45	25.34 \pm 0.74	45.28 \pm 0.90	327.07 \pm 1.74

Table 5. Relative carbon content (%) in tree compartments of individual tree species groups in the Czech Republic.

Compartment	Relative carbon content in the Czech Republic [%] by tree species group (mean \pm standard error)						
	Spruce	Pine	Beech	Larch	Oaks	Others	Together
Green twigs	6.88 \pm 0.27	3.55 \pm 0.20	1.66 \pm 0.14	2.91 \pm 0.18	2.11 \pm 0.15	2.94 \pm 0.18	4.78 \pm 0.23
Foliage	4.71 \pm 0.23	2.17 \pm 0.16	0.97 \pm 0.11	1.81 \pm 0.14	1.23 \pm 0.12	1.73 \pm 0.14	3.16 \pm 0.19
Wood < 7 cm	4.71 \pm 0.23	5.81 \pm 0.25	8.93 \pm 0.31	3.63 \pm 0.20	7.74 \pm 0.29	9.89 \pm 0.32	6.17 \pm 0.26
Wood ≥ 7 cm	61.00 \pm 0.52	54.06 \pm 0.53	62.76 \pm 0.52	52.12 \pm 0.54	53.74 \pm 0.53	53.90 \pm 0.53	58.14 \pm 0.53
Stem bark	7.90 \pm 0.29	6.21 \pm 0.26	7.58 \pm 0.28	10.48 \pm 0.33	16.80 \pm 0.40	10.32 \pm 0.33	8.76 \pm 0.30
Stump and roots	14.79 \pm 0.38	28.21 \pm 0.48	18.10 \pm 0.41	29.05 \pm 0.49	18.37 \pm 0.42	21.21 \pm 0.44	18.99 \pm 0.42
Whole tree	100	100	100	100	100	100	100

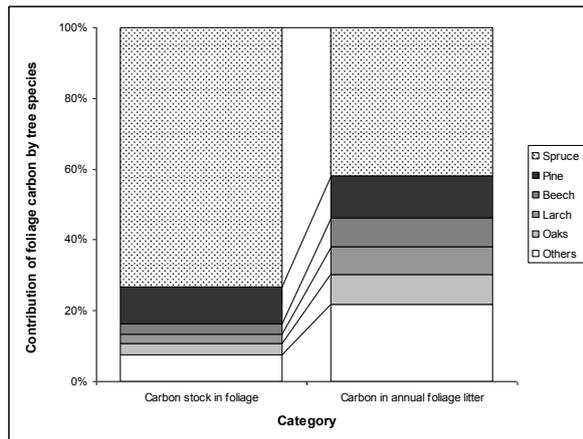


Fig. 8. Contribution of foliage carbon by tree species to total carbon stock in foliage and total carbon in annual leaf fall in the Czech Republic.

4. Discussion

The knowledge on biomass (carbon) allocation in trees is important for understanding and quantification of processes related to carbon sequestration and cycling in forest ecosystems (Dickson 1989). Quantifications of carbon fixed in forest tree biomass with regard to the contribution of individual tree compartments and species at a variety of scales (regional, national, and continental levels) are necessary to assess the importance of forests for the mitigation of climate change. For the thorough monitoring of forest carbon stocks the estimation of carbon amount fixed in all tree compartments is required, as forest management and harvesting activities affect not only the economically interesting biomass compartments, but the whole carbon cycle. However, many studies report only the information about economically interesting biomass compartments, i.e. usually stem or merchantable timber (Wutzler et al. 2008), which contributes to more than a half of the whole tree biomass, e.g. in our case 58% of biomass carbon was sequestered in the timber with diameter equal to or greater than 7 cm. Similarly Wutzler et al. (2011) estimated that stem biomass contributed to 60% of the total tree carbon stock of a German forest.

The presented study attempted to overcome this shortage by covering all living tree compartments including branches, leaves and belowground root biomass. Our results showed that altogether approximately 327 mill. t of carbon is fixed in the tree biomass of the Czech forests, which is about 113 t of carbon per hectare of forests, or 42 t of carbon per hectare of the whole-country area. The total carbon stock corresponds to 322 mill. t, which is the official statistics for the year 2000 published in Forest Europe (2015). The results are slightly higher than the estimates of biomass in Czech forests using allometric relationships, which indicated 586 mill. t of tree biomass (i.e. 293 mill. t of carbon) allocated in the forests of the

Czech Republic or 213 t of biomass (i.e. 106 t of carbon) per hectare (Kučera et al. 2014). The differences between the estimates result from the different subset of trees, different approaches of calculating the biomass and different grouping of tree species. We based our calculations of stem wood biomass on the volume equations compiled by Petráš & Pajčík (1991), because they were derived for 11 different tree species using data from several thousands of sample trees per species (Table 1). On the other hand, Kučera et al. (2014) used allometric relations for four different tree species, which were based on a smaller number of sample trees. For instance Wirth et al. (2004) used the information about 688 sample trees, but Cienčila et al. (2006, 2008) and Vejpustková et al. (2013) used data from less than one hundred sample trees. The problem with small samples has already been discussed by e.g. Brown et al. (1999). The impact of the applied equations on the biomass estimates has been pointed out by several studies, e.g. Neumann et al. (2016). Thus, we assume that the accuracy of the results can be higher if the above-mentioned volume equations derived from large samples collected at the investigated territory together with the available data from NFI (e.g. information about tree species) are applied. In addition, volume equations are frequently used and well understood methods in forestry because of the long-term research in this field. In the compilation of the method we tried to account for all the important factors in biomass estimation, and this gave us a picture of the currently available information. Wood density may be the weak point of the suggested method, as it is known to change with site conditions, tree position within a stand, and position on a tree. Nevertheless, the values of wood density given in Table 2 were taken from national or Central European publications if possible, and hence, they should represent the Czech forests better than e.g. constant values given in IPCC Guidelines.

A similar average hectare value of carbon stock in forests (110 t per ha of forests) was found by Brunner & Godbold (2007) for temperate central European forests. Likewise, in Germany and Slovakia forest carbon stock density in tree biomass was 104 t (Dieter & Elsasser 2002) and 110 t of carbon per hectare, (MA SR, 2016) respectively. However, the countries had contrasting carbon amounts when expressed per capita, since the value for Slovakia was 30% higher than for the Czech Republic. If we consider the European Union (EU) level, the Czech Republic contributes to about 3% of carbon fixed in forest tree biomass, although its share in the EU territory is only 1.8% (Forest Europe 2015; MA CR 2016).

Even though the average Czech carbon stock density in forest tree biomass per spatial unit exceeded the European average, we revealed high regional differences within the country. Those are related to both forest area and forest hectare stock. Our analyses on forest tree carbon stock per hectare of forests and per hectare of region suggested that nearly 1/6 of all carbon was present in Jihočeský kraj. The region is typical with large forest

complexes and high share of spruce growing mainly in the southern part of the region (Šumava and Novohradské hory). Ústecký kraj contributed to forest biomass carbon least, whether it was expressed as total carbon amount per region or as carbon amount per hectare of forests or per hectare of the region. These results are in accordance with Kučera et al. (2014), who also found the highest and the lowest amount of tree biomass in Jihočeský and Ústecký kraj, respectively. The performed correlation analyses between the regional carbon stocks and demographic and economic parameters revealed positive trends with both population density and gross domestic product, but the relationships were not significant (not shown). This can be explained by the regional differences in carbon stock resulting from their long-term historical development and different natural conditions, which have been limiting factors for settlements or agricultural activities (hilliness, wetlands, etc.), and later also to premeditated exertion of human being (Palmer et al. 2008). Since recently the Czech Republic proclaimed national rural development programmes (co-financed by EU) including afforestation (Forest Europe 2015) as a key measure for the implementation of policy on forest carbon, continuously increasing forest area might be anticipated in most regions. The values representing individual regions together with the information about site and terrain conditions and past development of forests can be used to estimate the carbon sequestration capacity of individual regions of the country.

Spruce is the main tree species in the Czech Republic. It covers about 50% of the total forest area of the Czech Republic (MA CR 2016). Congruously to this figure, our calculations demonstrated that this tree species contributed to 49% of the total forest tree biomass of the country. Moreover, the results showed that the ratio of spruce foliage to its total biomass was higher than for other species (4.7% for spruce against 2.2%, 1.0%, 1.8% and 1.2% for pine, beech, larch and oaks, respectively) due to its longer time span of foliage. The opposite situation was observed in the case of shed foliage (annual leaf fall), its proportion to the total tree biomass was in the case of spruce as well as pine only 0.9%, while in the case of beech, larch and oaks it was 1.0%, 1.8% and 1.2%, respectively. These values indicate that spruce trees “lose” lower fraction of carbon fixed in total tree biomass via leaf fall than the deciduous species. This spruce characteristic may together with its high wood productivity (Šebík & Polák 1990) be an advantage of this species in carbon sequestration in comparison with other tree species. On the other hand, spruce is very sensitive to climate change, especially if it is located at lower elevations, i.e. in its ecological suboptimum conditions. Due to this, there is an increased risk of physiological stress caused by drought, more frequent damages caused by abiotic and biotic damages (Lindner et al. 2010), and consequently the loss of the accumulated carbon from the living biomass.

The summary of our results shows that although the Czech Republic covers a small territory in Europe, its carbon stock in forest biomass per hectare exceeded the EU average. Since the country has committed to support afforestation as a part of its national rural developmental program, it can be expected that the importance of forests in carbon sequestration processes will increase.

Carbon sequestration capacity of the Czech forests can be strengthened by promoting forest protection (prevention to wind damage, forest fires, bark beetle outbreaks) as well conservation of forests grown on wetlands. State policy should concentrate on the sustainable development of stable, diverse and productive forests (see for instance Jandl et al. 2007; Nabuurs et al. 2008; Ashton et al. 2012). A forest management map of European forests developed by Hengeveld et al. (2012) defining the most suitable forest management alternative at a 1 km resolution on the base of 8 biotic, abiotic, socio-economic, and political factors suggested that there is a great potential of Czech forestry to apply close-to-nature forest management as defined by Duncker et al. (2012). Although this type of forest management is frequently considered as the best approach with regard to future climate change, it might not always result in the increase of carbon stock because the adaptive mechanisms of this management identified by Brang et al. (2014) include keeping low average volume stocks, and hence also low carbon stocks of forests. Since the increase of carbon sequestration is one of the primary climate change mitigation measures (Sheikh et al. 2014), a consensus between the adaptation to climate change and its mitigation must be solved.

Bellassen & Luysaert (2014) suggested that from the point of carbon sequestration forest management aimed at the increase of forest stocks and timber harvest should always be prioritised. Unlike some adaptation measures, the effect of which is only assumed because it could not have been proven yet, the increase in volume will always increase carbon stock. The picture becomes more complex if we account for the post-growth processes. Harvesting reduces forest cover and thus the amount of carbon stored in forests, but using the harvested wood for construction purposes and long-term wooden products prolongs the time of carbon fixation (Raši et al. 2015). In addition, different wood extraction technologies and post-harvest treatments, e.g. slash burning, also affect carbon stock of the stand and the whole carbon cycle within the ecosystem. Hence, the information about the carbon stock in individual compartments together with the information about the applied management and extraction technologies can provide us with the estimates of future carbon stock. Apart from that, forest management and harvesting methods also affect soil properties including soil carbon, which is very sensitive to above-ground changes. Thus, the whole picture of the carbon cycle including the life cycle of wood products needs to be accounted for. By applying the so called ‘win–win’

or ‘no-regret’ strategies we can save some time until we widen and/or justify our knowledge about forest behaviour in changing climate (Bellassen & Luysaert 2014), because some projections of forest development under climate change indicate increased mortality followed by larger carbon emissions that can exceed its sequestration (Somogyi 2016).

5. Conclusions

The knowledge on biomass (carbon) allocation in trees is important for understanding and quantification of processes related to carbon sequestration and cycling in forest ecosystems. The presented study attempted to cover all living tree compartments including branches, leaves and belowground biomass. Our results showed that altogether approximately 327 mill. t of carbon is fixed in the tree biomass of the Czech forests, which is about 113 t of carbon per hectare of forests. Hence, the Czech Republic contributes to about 3% of carbon fixed in forest tree biomass of the EU, although its share in the EU territory is only 1.8%. Spruce is the main tree species group in the Czech Republic. Our calculations demonstrated that this tree species group contributed to 49% of the total forest tree biomass of the country. Moreover, the results showed that the ratio of spruce foliage to its total biomass was higher than for other species due to its longer time span of foliage. Nearly 1/6 of all carbon sequestered in forests was present in Jihočeský kraj. To strengthen carbon sequestration capacity of the Czech forests, forestry should apply win-win forest management strategies. In addition, forest protection against disturbance factors as well as conservation of forests grown on wetlands (e.g. the Šumava region in Jihočeský kraj) would be promoted.

Acknowledgments

This work was supported by the 7. RP project FORest Management Options for enhancing the MITigation potential of European forests (FORMIT) and in part by the Slovak Research and Development Agency under contracts APVV-0268-10, APVV-14-0086, and APVV-15-0265.

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Carbon stock in forest aboveground biomass – comparison based on Landsat data

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Abstract

The objective of this study was to verify a possibility of the assessment of carbon stock above all in forest aboveground biomass in the area of Czech Republic based on Landsat data and terrestrial mapping of land cover. Landsat 7 ETM+ data and method based on vegetation index ND45 were used. Simultaneously the aboveground carbon stock was assessed by expert based estimations of carbon in aboveground biomass in the various classes of landscape cover, derived from Corine Land Cover 2012 data. By comparison of results obtaining by both methods for the whole investigated area in the Czech Republic the differences reached only 4.68% and for forest stands 7.19%. The results of aboveground carbon stock based on the Landsat 7 ETM+ data did not differ distinctly from the assessment of carbon stock for individual classes of land cover for both vegetation cover of the Czech Republic and forest stands.

Key words: aboveground biomass; carbon stock; remote sensing data; vegetation indices; Czech Republic

Editor: Bohdan Konôpka

1. Introduction

Carbon naturally occurs in many forms. In connection with the climate change carbon dioxide (CO₂) is the most important form of carbon and its fixation in chemical compounds has got an important role. CO₂ in the line with methane, dinitrogen dioxide, sulphate fluoride, water vapour and some other gases are generally marked as greenhouse gases which actively participate on the global climate change. On the first sight the change is mainly linked with increasing of temperature. In the last 100 years the average temperature has increased by 0.74 °C (Marek et al. 2011). According to prediction value of carbon dioxide will reach the limit of 400 ppm very soon (Stocker et al. 2013). It is obvious that this phenomenon has been influenced by human activity, mainly due to combustion of fossil fuels and deforestation of tropical forests (Cudlín et al. 2013).

The Czech Republic extends on the area of 78 866 km². Forest ecosystems cover 29 076 km², i.e. 36.9 % of the whole area of the Czech Republic. Approximately coniferous forests cover 60% of the whole area and deciduous forests 40%. Total timber reserve is about 934 mil. m³ (Vašíček 2015). Up to 45% of the whole terrestrial carbon is fixed in forests (Oulehle et al. 2011). These days scientists have focused on the carbon quantification in ter-

restrial ecosystems and biomass in a different time span. Many studies have been engaged in a question how to assess carbon content by the most simple and exact way.

Assessment of carbon stock in aboveground biomass has been worked out by methods based on both direct measurement and remote sensing (RS) approaches. Methods based on contact measurements always provide the most accurate results but they are highly finance and time consuming (Brown 2002; Coomes et al. 2002; Gibbs et al. 2007; Machar et al. 2016). Satellite or radar data have got great potential for determination of vegetation carbon content. Moreover in inaccessible areas they are the only possibility how to find out the carbon content in vegetation cover. This is the reason why many research studies have been focused on improved carbon assessment using remote sensing methods (Goodenough et al. 2005; Vicharnakorn et al. 2014; Mandal & van Laake 2005).

Basic methods of contact approach are forest inventory, method of production tables and eddy covariance method. Forestry inventory is greatly widespread way of assessment of biomass and carbon stock on the base of parameters realized during ground survey (Brown & Schroeder 1999; Jenkins et al. 2004; Zhang et al. 2012). Ponce-Hernandez (2004) described in detail the principal

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of tree allometry in connection with carbon measurement in biomass. Main-Knorn et al. (2011) compared carbon stock assessed by forest inventory with figures derived on the base of satellite data analysis. Method of production tables, used in the frame of IPCC programme, is based on a link of individual classified categories and prepared values on carbon stock or production, derived from previous contact measurements and literary knowledge. This simple method is implemented by several models e.g. InVEST or NLLUF-KP10 (Cruikshank et al. 2000; Kareiva et al. 2011; Kuldeep 2011; Sanga-Ngoie et al. 2012). Eddy covariance method is based on the direct measurement of CO₂ flows in the frame of ecosystem stations. The method is very precise, but it measures only direct CO₂ flow on small areas (Hunt et al. 2002; Zhang et al. 2012).

Remote sensing can be used for the assessment of carbon stocks by two available means. First one is an assessment of aboveground biomass from that selected eco-physiological parameters (e.g. gross primary production, net primary production, photosynthetically active radiation) are derived and carbon quantity is calculated (Field et al. 1995; Patenaude et al. 2005; Awange & Kyalo Kiema 2013; Pechanec et al. 2014). The second one is a land cover mapping and derivation of basic characteristics (type, spatial distribution and pattern) of its categories and to combine these data with ground forest inventory (Pachavo & Murwira 2014; Iizuka & Tateishi 2015; Zheng et al. 2008).

The aim of this study was to propose some method based on RS data for the assessment of carbon stock of forest aboveground biomass on the territory of the Czech Republic.

2. Material and methods

2.1. Expert data of carbon stock

In accordance with the basic IPCC methodology of carbon stock assessment (Kuldeep 2011; Sanga-Ngoie et al. 2012) expert estimation of carbon stock values has been performed for vector data layer of the most detailed level 3 of individual land cover classes of Corine Land Cover (Corine LC). Particular land cover categories were divided according the presence/absence of natural and near to nature habitats (Chytrý et al. 2010) according to

the Habitat mapping layer provided by the Nature Conservation Agency of the Czech Republic (NCA CR 2014). Proportional representation of non-natural habitats in the territory not covered by the layer of Habitat mapping was estimated using analyses of land use and carbon content on 450 × 450 m plots in the grid 7 × 7 km, made by IFER ltd. in the frame of CzechTerra project (Šimová et al. 2009). The values of carbon stock of aboveground biomass of individual 193 natural, near to nature and non-natural habitats (Seják et al. 1993) were derived from literature (Stará et al. 2011). The carbon values for each Corine LC class were ultimately determined by means of the carbon values of natural and non-natural habitats weighted by their average distribution in the Corine LC classes in the whole territory of the Czech Republic.

2.2. Satellite Landsat 7 ETM+ images

Data were acquired by means of the Earth Explorer tool (<http://earthexplorer.usgs.gov/>). For the territory of the Czech Republic there were selected 9 images of Landsat 7 ETM+ from 20. 5. 2012 to 11. 7. 2015. Date and cloudiness coverage percentage were the key factors for the selection of images. The basic condition was vegetation period, i.e. period from May to October. Mostly there were selected images from the years 2013–2015 because of small cloudiness and other meteorological conditions. Only one image had to be selected from the year of 2012. The list of all images used for an assessment of carbon stock is displayed in the Table 1.

2.3. Satellite data procedure

Cloudiness masking

Because of not all images were obtained without cloudiness and there were not other better images, there was necessary to mask cloudiness on three images with ID LE71910252013168ASN00, LE71920262014162ASN00 and LE71900262015183NSG00.

We use CALCULATE CLOUD MASK USING FMASK tool, which is available in ENVI software. Total area under cloudiness mask covered the area of 32 760 hectares. The results of masking are seen on Fig. 1.

Table 1. Applied satellite Landsat 7 images of sensor ETM+ covering the whole territory of the Czech Republic for aboveground carbon stock assessm.

	ID	Date	WRS path	WRS row	Cloudiness [%]	Format
1	LE71930252015156NSG00	5. 6. 2015	193	25	0	
2	LE71920252012141ASN00	20. 5. 2012	192	25	0	
3*	LE71910252013168ASN00	17. 6. 2013	191	25	18	
4	LE71900252015183NSG00	2. 7. 2015	190	25	8	
5	LE71890252013202ASN00	21. 7. 2013	189	25	0	GEO TIFF
6*	LE71920262014162ASN00	11. 6. 2014	192	24	1	
7	LE71910262013168ASN00	17. 6. 2013	191	24	0	
8*	LE71900262015183NSG00	2. 7. 2015	190	24	3	
9	LE71890262015192NSG00	11. 7. 2015	189	24	0	

Symbol * indicates images with mask by reason of cloudiness.

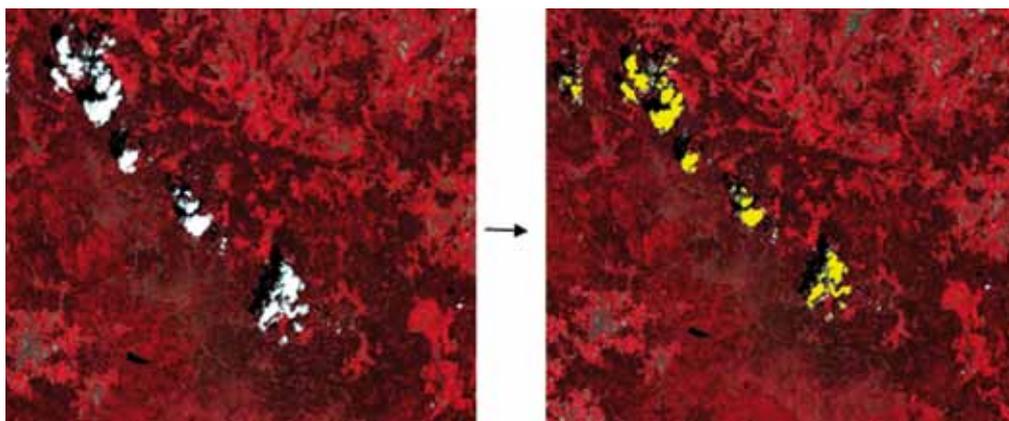


Fig. 1. Final cloudiness mask on the image No. 6 with ID LE71920262014162ASN00 (source: own/personal processing).

Mosaic framing and mosaic trimming for the territory of the Czech Republic

For unified processing of all 9 images their mosaic using the ENVI software (SEAMLESS MOSAIC tool) was carried out. The outputs of this process are pictured on Figs. 2 and 3.

Radiometric and atmospheric corrections of Landsat 7 images

Images from satellites Landsat 7 and 8 dispose of automatic radiometric, geometric and altitudinal corrections at the Level 1T. For next level of atmospheric and radiometric corrections there is necessary to utilize infor-



Fig. 2. Outputs of the mosaic process (source: own/personal processing).



Fig. 3. Trimmed edges of 9 satellite images of the Czech Republic (source: own/personal processing).

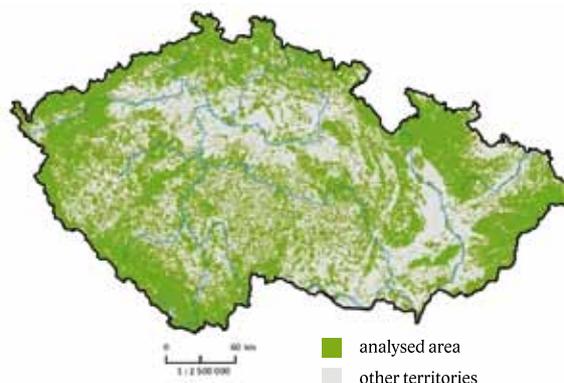


Fig. 4. Final area map delimited for the assessment of carbon stock of an area of the Czech Republic.

Table 2. Calculation by method based on the ND45 index.

Application	Formula	
Generally	$ND45 = 128 \times [(TM4 - TM5) / (TM4 + TM5)] + 128$	1
Band Math	$ND45 = (128 \times ((float(b1) - b2) / (float(b1) + b2))) + 128$	2
Calculation of carbon stock	$Biomass [kg ha^{-1}] = -478.58 + 4.5041 \times ND45$	3
Calculation of carbon stock	$Carbon [kg ha^{-1}] = biomass \times volume \text{ wood density } (400 \text{ kg m}^{-3}) \times 0.5$	4

mation on a specific image from the text metadata file. Since a pixel value is represented after data download by so called *digital number* (DN) which is not suitable for quantitative picture analyses, it is necessary to transpose it to calibrated value of the real image reflectance. This operation is generally called radiometric calibration or correction. This process was performed using ENVI programme by means of the Radiometric Calibration with the output TOA – *Top of Atmosphere Reflectance*. Then atmospheric calibration was carried out using ENVI software by Dark Subtraction, *Quick Atmospheric correction* (QUAC) (Shippert 2013).

Banding elimination of Landsat 7 images

Regarding to the decrease of image quality of Landsat 7 by systematic error in consequence of SLC disturbance in the year of 2003, an image radiometric defect had to be removed. This process was performed with the help of ENVI software using Fourier transformation.

Calculation of the aboveground carbon stock by means of the ND45 index

Calculation of aboveground carbon stock was done by means of the ND45 index (Goodenough et al. 2005) using the Band Math tool (ENVI software). The method consists in an assessment of aboveground biomass on the base of spectral vegetation index ND45. Assessed biomass is then recounted to carbon stock (kg C per hectare). Mathematical notation is described in the Table 2.

Calculation of carbon stock was applied for the selected areas of the Czech Republic (43 841 km²) after subtraction of a) areas of masked cloudiness and b) categories with low vegetation cover (e.g. built-up area) (see Table 3). The plots were spatially defined on the base of land cover class level 3 of the Corine LC 2012 (see Fig. 4).

Calculation of aboveground carbon stock with use of expert assessment

For the assessment of carbon stock of aboveground biomass by means of expert estimations, the same Corine LC 2012 data layer was used. This layer was then segmented according to the presence of natural and non-natural habitats. These segments were attributed by average expert carbon stock values (t ha⁻¹) of aboveground biomass in individual Corine LC classes, containing and non containing natural habitats. Real carbon stock was then calculated.

To obtain carbon stock of aboveground biomass in forest stands the area of broadleaved, coniferous and mixed forests (TAG 311, 312, 313) according to Corine LC 2012 was determined. The Corine LC forest classes

were then assigned expert based carbon values per ha. The carbon stock values determined by method of ground observation and derived from remote sensing data were compared.

Table 3. Land cover classes in the Czech Republic according Corine LC 2012. Symbol * is for categories of higher percentage of vegetation cover.

TAG – level3	Landuse category	Area [km ²]
111	Continuous build-up area	15.7
112	Discontinuous build-up area	3 828
121	Industrial and commercial zones	631.3
122	Public road and railway system	72
123	Ports	0.8
124	Airports	48.7
131	Mining areas	170
132	Dumps	79.4
133	Building sites	10.9
141*	Urban green areas	67
142	Sports and recreational areas	173.3
211	Non-irrigated arable land	28 998
221*	Vineyards	164
222*	Orchards, hop-fields and garden plantations	294
231*	Meadows and pastures	7 946
242*	Mixture of meadows, fields and steady fields	473
243*	Agricultural areas with natural vegetation	7 116
311*	Broadleaved forests	2 839
312*	Coniferous forests	17 129
313*	Mixed forests	6 339
321*	Natural meadows	257
322*	Steppes and bushes	19
324*	Underbrush in forests	1 527
332	Rocks	1.7
333*	Areas with low density vegetation	1.5
411	Marshes and swamps	60.6
412	Peatbogs	46
511	Water flows	46.3
512	Water sheets/areas	530.4

3. Results

The results of carbon stock calculation on the investigated territory of the Czech Republic (43,841 km²), using the method based on the ND45 index, were comparable with expert assessment. Calculated carbon stocks of aboveground biomass in the Czech Republic using ND45 method was 277,842,483 tons, according to expert production table 265,418,848 tons. Values of the carbon stock for the investigated area differed only by 4.68%.

For the assessment of carbon stock of aboveground biomass in forest stands the areas of occurrence of Corine LC 2012 classes (conifer, broadleaved and mixed forests) on the territory of the Czech Republic were summarized and the carbon stock of aboveground biomass was computed according to the expert assessment of carbon values for individual classes. The area used to find out the carbon stock from remote sensing data had to be reduced by area covered by cloudiness and therefore it differed from the total forest area (Table 4).

Table 4. Carbon stock of aboveground biomass in the forest area of the Czech Republic (source: own/personal processing).

Category	Carbon stock [t]	
	ND45 method	Expert assessment
Broadleaved forests	21,727,584	24,667,514
Coniferous forests	135,936,161	164,123,993
Mixed forests	48,534,471	55,968,486
Forests – total	206,198,216*	244,759,992**

* for the total area of 24 517 km²; ** for the total area of 27 009 km².

In the case of entire forest stands there was stated the difference of 7.19%. Difference for broadleaved forests was 2.97%, coniferous forests 8.75% and mixed forests 4.47% in comparison with results obtained by expert assessment. On the base of results we can presume that the method based on ND45 index is suitable for the assessment of above ground carbon stock on the territory of the Czech Republic.

4. Discussion

The assessment of carbon stock of aboveground biomass from RS data seems to be applicable but we should critically discuss not only data processing but also the comparative expert based values. The calculation of aboveground carbon stock was based on biomass estimation by means of the ND45 index. This method belongs to the most frequent if multispectral data are used (Cruickshank et al. 2000); in the case of hyperspectral data, approaches based on LAI index (Liang et al. 2012) or fAPAR index (Hunt et al. 2002) are prevailing. The crucial problem of used approach is the selection of vegetation index; the most frequently used NDVI index has serious problems with the saturation effect at higher biomass values (Sanga-Ngoie et al. 2012). Another frequently used approach based on biomass empirical models works unfortunately only with one picture from main vegetation phase which causes a lot of inaccuracies. The seasonal NDVI index derived from time series could be one of a suitable solution (Zhu & Liu 2014). According to their results NDVI index has stronger relationship with aboveground biomass in the autumn compared to main growing season.

Another aspect influencing the selection of suitable vegetation index is a structure and amount of analyzed vegetation; forests in different vegetation zones differ strongly in their vegetation structure. Therefore we analyzed a couple of indices (Goodenough et al. 2005; Zheng et al. 2008) and selected ND45 index, derived on two localities in Canada with tree species composition, dominant spruce and pine species (Goodenough et al. 2005), relatively similar to our dominant tree species.

The method based on ND45 indicator has been selected as optimal for the assessment of carbon stock of aboveground vegetation by means of RS tools after previous testing on a smaller area of 450 km². The very important role is played by an input value – volume wood

density. For the assessment of carbon stock in the Czech Republic there was set value of 400 kg m⁻³ considering extent and land cover categories of studied area. Using value differentiation according to landscape cover categories could lead to further refinement of the results.

Expert based values of aboveground carbon stock were constructed as a medium value for a given habitat type under conditions of the Czech Republic. It means that this coefficient does not reflect an actual state of an individual habitat, given by above all its health status and age structure. Due to this fact the values obtained by means of the method based on mean ND45 index could provide sufficient information about actual mean state of aboveground biomass.

Only few publications have presented a comparison between carbon computation from remote sensing data and expert estimation. The results of one of them, reporting 4% difference using NDVI index (Sanga-Ngoie et al. 2012), are very similar to our results.

In this paper it was mentioned that the real values of reflectance must be available for the quantitative image analysis. Input units of TOA reflectance were used for the assessment of carbon crop, it means radiometrically calibrated DN values according specific factors (e.g. sun elevation) for each image. Unfortunately, atmospheric influences have not been removed from these data. There were undertaken some tests to remove atmospheric influences using method of Dark Subtraction but obtained results of reflectance were evaluated as unsuitable. Improper removing of atmospheric influences could slightly affect obtained stock values. In a new version of the ENVI software more advanced tools for removing of atmospheric influences – QUAC and FLAASH modules have been implemented but they were not accessible to authors at that time.

5. Conclusion

The aim of this study was to propose some method based on RS data for the assessment of carbon stock of forest aboveground biomass on the territory of the Czech Republic. Comparison of results of aboveground carbon stock computation by RS method based on ND45 index with results obtained by the expert assessment showed that less time consuming RS method is applicable for bigger areas. Values of the carbon stock for the entire valuated area differed only by 4.6%, for forest area the differences ranged from 2.97% to 8.76% according to the forest category. The results of RS method proved to be comparable with methods of ground observation that are often expensive and time consuming. Moreover ground observation methods are not applicable in inaccessible areas. In addition, information about aboveground biomass carbon stock in the Czech Republic in 2012 can be compared in future with up-to-date values to monitor changes in carbon storage.

Acknowledgement

This work was supported by grant from Iceland, Liechtenstein and Norway [grant number EHP-CZ02-OV-1-014-2014 y], by the Grant Agency of Czech Republic [grant number 16-21053S] and by the Ministry of Education, Youth and Sports of CR within the National Sustainability Program I (NPU I), grant number LO1415. Authors thank to Dr. Chobot from the Nature and Landscape Conservation Agency of the Czech Republic for providing habitat mapping data.

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Quantifying carbon in dead and living trees; a case study in young beech and spruce stand over 9 years

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Abstract

In Slovakia, the contribution of young stands to the total forest area has been increasing in the last decade. However, scientific attention to these stands was previously very sparse and they were usually not included in local and country carbon stock estimates. Therefore, we focused on the calculation of tree biomass and necromass in young beech and spruce stands as well as on their development during the period of nine years (aged from 4 to 12 years). For the calculation, we implemented allometric equations using tree diameter and height as independent variables. The results showed very dynamic changes in biomass (carbon) stock. Specifically, tree biomass increased in the period of 9 years from about 2,000 g to 15,000 g (i.e. cca 1,000 to 7,500 g of carbon) per m² in beech, and from 4,500 to 12,000 g (cca 2,300 to 6,000 g of carbon) per m² in the spruce stand. At the same time, the amount of biomass (fixed carbon) was only slightly larger than the accumulated quantity of necromass (carbon loss from living trees). It means that a large portion of carbon was allocated to necromass. We found that not only the foliage fall but also the mass of dead trees, a result of intensive competition, was an important path of carbon flux to necromass. The results proved that although young forests fix much less carbon in their biomass than old stands, they can represent large carbon flux via annual increment of necromass. This indicates that young stands should not be omitted in forest carbon balance estimates of the country.

Key words: young trees; *Fagus sylvatica*; *Norway spruce*; stand development; carbon stock, tree components

Editor: Jan Kašpar

1. Introduction

European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) are the most important species not only in Slovakia but also in the essential part of other European countries. Their importance is linked to their high contribution to species composition of forests, their high commercial value, but certainly also to their large accumulation of carbon.

As for the Slovak Republic, the Green Report (Ministry of Land Management and Rural Development of SR, 2016) shows that in the recent tree species composition of the country, beech made 31% and spruce 26%. Both species are typical with their good regeneration and high capacity in inter-species competition on the territory of Slovakia. Thus, in young stages (categorised as first age class, i.e. 0 – 10 year-old) beech contributed to species composition with as much as 35% and spruce with 25% prevailingly as a result of natural regeneration (Konôpka J. et al. 2016). It means that these species will form a

considerable part of the Slovak forests also in the next many decades. At the same time, a current phenomenon of the Slovak forestry is an over-standard proportion of young forests stands in comparison to the normal forest age class distribution. Specifically, forest stands with age up to 10 years cover 200 thousand ha, which is the largest area from all age classes (Ministry of Land Management and Rural Development of SR, 2016). This is mainly caused by an extraordinary high occurrence of disturbances since the year 2004 (Kunca et al. 2015; Nikolov et al. 2014).

In fact, most previous research activities in Slovakia but also in many other developed countries, including a variety of aspects, were focused on old forest stands rather than on young growth stages. That could be probably linked to a more economical than an ecological vision in a part of scientific community, or specifically in the field of production ecology, perhaps also to an underestimation of the significance of young forests for carbon sequestration and cycling. Thus, for instance biomass

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models were often constructed for large trees but small trees were traditionally omitted (e.g. Wirth et al. 2004).

As for tree biomass, eventually carbon pool in trees, it is undisputable that much larger amounts are in old forests than in young growths (e.g. Helmisaari et al. 2002). On the other hand, young forests are much more dynamic (especially in terms of inter-annual changes in biomass stock) and they have different biomass allocation in comparison with old forest stands (Konôpka et al. 2017). Moreover, young forests have much higher mortality rates than old forests that are related especially to high competition for light in the initial stages of growth (Larson et al. 2015). Although most of the perished trees (obviously suppressed) in young stands are smaller than those in the main canopy layer, they can make a large portion of carbon loss (flux). This carbon flux is considerable especially in naturally regenerated stands with typically high tree density.

Since beech is a deciduous and spruce an evergreen tree species, certain differences can be expected in their biomass allocation and also in their carbon regimes. Previously we showed much higher contribution of foliage to total biomass in spruce young stands than in beech young stands (Pajčík et al. 2013). On the other hand, the contributions of their foliage to net primary productivity were very similar. At the same time, we found much higher mortality rate in spruce than in beech young stands that was explained not only by different light conditions under the canopy but also by contrasting ecological properties of these species. Although our previous study (Konôpka et al. 2011; Pajčík et al. 2013) showed the results on biomass allocation and net primary productivity in developing young beech and spruce stands, we did not estimate either the amount of carbon sequestered in tree biomass or the carbon flux realised via aboveground litter fall from living trees and body of died trees.

In fact, our literature review indicated that this kind of carbon quantification in young stands is totally missing in any other studies conducted all over the world. Thus, this paper focused on the estimation of biomass (living trees) and necromass (all components of dead trees and foliage litter fall from living trees) in young stands of beech and spruce with special attention to their carbon amount. Moreover, we aimed at quantification of carbon fixed and “lost” (transferred) from trees in the form of foliage fall and dead trees in these two stands over the nine-year period. Although the stands were of the same age, they grew under the different site conditions, due to which their contrasting properties (carbon pool and flux) were intended to be interpreted with a certain level of caution.

2. Material and methods

2.1. Research plots

We used a part of data originating from the empirical dataset of 12 research sites situated in forests of the Central and Northern Slovakia. The original dataset was rep-

resented by 6 pure spruce and 6 pure beech stands. The research plots were established for long-term monitoring of development young forests including the assessment of tree growth, competition and mortality. At the beginning of our research, the stands had a different mean age; the youngest stand was 4 years old while the oldest one was 14 years old. Each year, from 2008 to 2016 we measured height and diameter of trees in the young forest stands. Since the main intention of this paper was to record the development of a very initial growth phase, we selected two youngest stands from the dataset: one was the youngest beech stand and the other one was the youngest spruce stand. The chosen beech stand is situated in a locality named the Pustý Hrad Hill (Fig. 1) and the spruce stand was in the locality named Zákopčie.

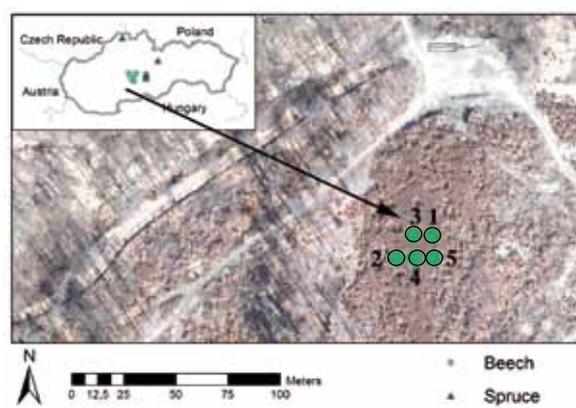


Fig. 1. Location of sites for long-term monitoring of development of young beech and spruce forest stands in Slovakia; a detailed view shows the locality of Pustý Hrad Hill with 5 subplots established in the homogenous beech stand.

The main criterion for the stand selection was that the stand was composed of single tree species, i.e. it was either pure beech or pure spruce stand without admixture of other tree species, originating exclusively from natural regeneration. Five circular subplots were established in every stand. A radius of subplots was variable, specifically between 0.5–2 m that depended on stand density aiming at a minimum number of trees over 30 individuals. The distance between the borders of individual subplots was at least 3 m to ensure their independence. In the locality of Pustý hrad, four subplots with a radius of 0.5 m and one subplot with a radius 0.6 m were established, while in the Zákopčie locality, five subplots with a radius of 0.8 m were set up.

The Pustý Hrad Hill is located near the town of Zvolen, in the volcanic mountain range of Javorie. The forests are managed by the Zvolen Town Forest Enterprise (urban forests). The coordinates of the site are 48.5521° North latitude and 19.1253° East longitude. The elevation is between 460–470 m, the exposure is east. The site represents the oak-beech forest vegetation zone, the primary vegetation is represented by *Querceto-Fagetum* forest type group (oak-beech forests). The bedrock is

made of andesite, the soils are skeletal-mesotrophic cambisols. The forests belong to commercial-purpose forests. In the monitored stands, no thinning cuts have been performed so far.

The locality Zákopčie is located near the town of Čadca, Northern Slovakia, in the Kysuce Beskids Mountains. The territory is owned and managed by the State Forest Enterprise (state forests). The coordinates of the site are 49.4193° North latitude and 18.7328° East longitude. The elevation is between 520–530 m, the exposure is north. The site represents spruce-beech-fir mountain forests; the primary vegetation is represented by *Fageto-Abietum* (nutrient rich beech-fir stands). The territory belongs to the flysch, the bedrock is made of sand-stone, and the soils are skeletal mesotrophic cambisols. The forest belongs to commercial-purpose forests, and in the monitored spruce stands no thinning cut has been performed so far.

2.2. Field measurements

The radius of each subplot was chosen to capture at least 30 trees within the plot area. All individuals were marked with a metal label with a code in 2008 to ensure clear identification of all trees in repetitive measurements. Every year, the life status (living or dead) of each individual was evaluated after the end of the growing period. On living trees, the stem base diameter (SBD) was measured in two perpendicular directions with a digital caliper with an accuracy of 0.1 mm. Moreover, tree heights were measured using the height-patch with an accuracy to the nearest centimeter (up to height 3.0 m) or to the nearest 10 cm (over 3.0 m). In the case when the individual tree height exceeded 1.3 m, diameter at breast height (DBH) was measured to the nearest 0.1 millimeter in two perpendicular diameters. Between 2008 and 2016 nine repeated measurements were performed.

At the beginning of the measurements the average (mean) age rounded to one year was assigned to each stand. The age was assessed by combining the information from the Forest Management Plans and ring analyses of discs (10 pieces) sampled from the stem bases of the trees selected close to the research subplots.

The sites “Pustý Hrad” (beech) and “Zákopčie” (spruce) were selected as youngest and thus with the highest tree density. In the beech stands the smallest number of the measured living trees on the subplots was 29, and the highest number was 68 (average of 43 trees), while in the spruce stands we recorded minimum and maximum of 43 and 75 living trees, respectively (average 58 trees). In both cases, the estimated mean age at the beginning of the measurements in 2009 was 4 years. At the beginning of the measurements we recorded in total 215 trees or 290 trees on all subplots in the beech and spruce stands, respectively. Out of them, 57 beech trees and 48 spruce trees survived 9 years until the last measurement.

2.3. Statistical calculations

The measured values from 9 annual repeated measurements (mortality, height, SBD, and DBH) were edited and the database was debugged. The data were processed in Ms Excel and Ms Access software (Microsoft Office). After the basic data processing, an algorithm for the calculation of average values, standard deviation and the variability of variables (diameter, height, and number of individuals) at the subplot and whole site levels was prepared. The mortality rates were calculated by two methods: based on the tree number and on the basal area (derived from SBD). While the method involving the tree number was calculated for each year as a proportion of the number of dead trees to the initial number of trees (i.e. the same basis), the method linked to the basal area was based on a different principle. Specifically, this method was calculated as a proportion of the basal area of the trees that died in the current year to the basal area of the surviving individuals (i.e. moving value which changes over time as a result of both stem growth and tree mortality).

2.4. Biomass calculation

To calculate the biomass of the whole trees as well as the biomass of individual tree components no samples were taken from the plots, but our previously constructed allometric equations were applied (according to papers of Pajtik et al. 2008; Konôpka et al. 2011; Pajtik et al. 2011; see also Appendix 1 and 2). In the case of dead trees and foliage fall, we used the same calculation method as for the living trees to derive the necromass. We distinguished the foliage fall from the living trees and the dead foliage from the trees that died in a particular year. Foliage fall for beech was derived as an amount of annual living foliage, while the foliage fall for spruce was derived as one fifth of the foliage living in a particular year. The SBD diameter and tree height were used as independent variables in the equations. Thus, the biomass (necromass) for the following tree components: stem (inside bark), branches, leaves (needles) and roots was calculated. Subsequently we calculated the biomass and the newly created necromass (i.e. annual input to necromass) for each year and each subplot, converted the values to area unit, and averaged for the whole site. Note that the results on tree necromass presented in the paper did not represent its total amount starting from the beginning of the stand existence. Actually, our outputs are related to the annual foliage fall and the annual necromass increment in each year of the observations. Besides that, we calculated the cumulated values (during the period of 9 years) for these two variables.

Afterwards, carbon quantity can be estimated as 50% of tree biomass or necromass (see for instance Thomas & Martin 2012). The presented results of the stands used mean values and sampling errors calculated at 68% confidence interval.

3. Results

The comparison of the relationship between SBD and tree height at the beginning and the end of the observation period showed an increase of the variance over time. The ranges of beech and spruce tree heights were comparable at both sites even after 9 years. However, at the same tree height the diameter range of spruce trees is larger than the range of beech trees at either of the two surveys (i.e., in 4 years and in 12 years; Fig. 2).

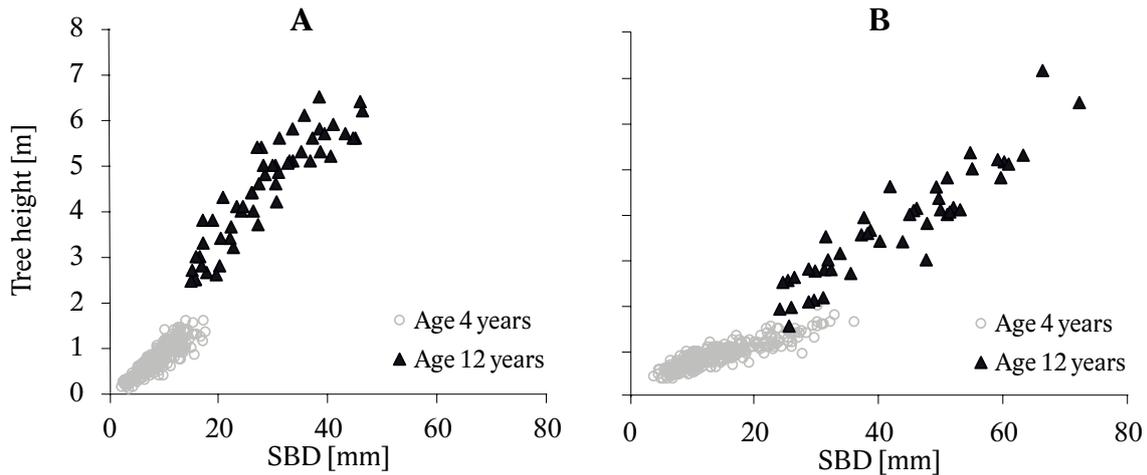


Fig. 2. Confrontation of changes in relationships between SBD and tree height after 9 years in young beech stand (A) and spruce stand (B).

During the 9 years, a severe tree number reduction caused by competition occurred in both young stands (no thinning was performed there). At the age of about 12 years, cumulative stand mortality in the beech stand reached approximately 70% of the number of individuals in the 4-year-old stand, while the cumulative mortality in the spruce stand (Fig. 3) was higher, up to 80% of the initial number of trees.

The mortality rate calculated from stem base basal area has a different temporal development, because the basal area changed in time due to the growth and mortal-

ity. We experienced a gradual increase of mortality until the age of about 9 years. After that, there was a slight decrease in the mortality rate in both beech and spruce stands. From the stand age of about 10 years, the mortality rate based on the basal area started to grow again. However, the differences in the mortality rate between the beech and spruce stands were not large.

The biomass of each tree component as well as the total tree aboveground biomass of beech was gradually increasing between 4th and 12th year of the stand (Fig.

4). In contrast to beech, in the spruce stand we observed the slowdown of biomass increment (or even its slight decrease) at the age of 11 years (Fig. 5), which was linked to the increased mortality.

While the young beech forest at the age of 12 years reached an average total biomass (aboveground and underground) of about 15 kg per m², the spruce biomass reached a lower value of around 12 kg per m². If we consider carbon content in biomass of 50%, these biomass amounts represented the carbon stock of about 7.5 kg and 6 kg per m² in the beech and spruce stand, respectively.

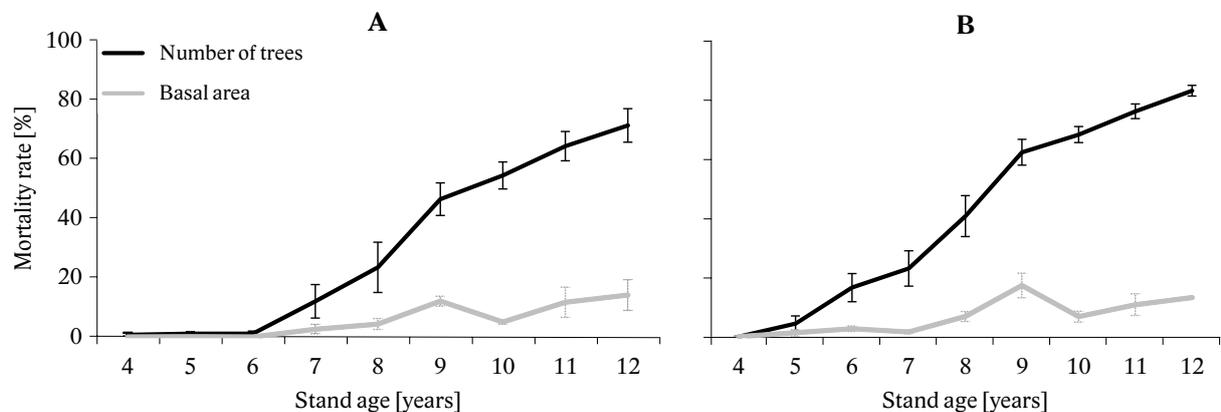


Fig. 3. Development of beech mortality rate (A) and spruce stand mortality rate (B).

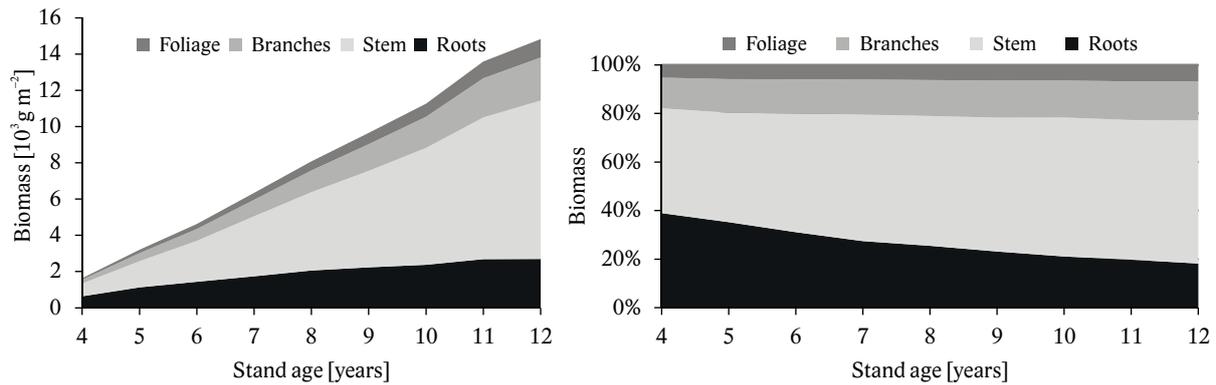


Fig. 4. Biomass development during the period of 9 years in the young beech stand (absolute and relative comparison).

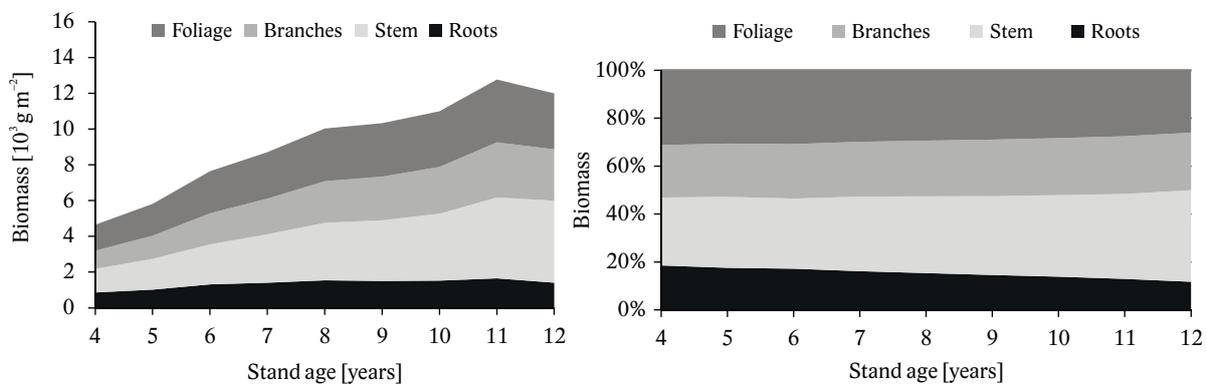


Fig. 5. Biomass development during the period of 9 years in the young spruce stand (absolute and relative comparison).

As for the proportions of the biomass in individual tree components, we identified the differences between the species as well as with the stand development. While beech during 9 years changed the proportion of roots from about 35% to 20%, in the spruce stand the root proportion declined from about 20% to almost 10%. The largest contribution to the total biomass of beech was made by the stem. Its share rose from about 40% to 50%. In the case of spruce, the proportion of the stem biomass from the total biomass was significantly lower, but showed a similar 10% increase (its share was 30% and 40% in the age of 4 and 12 years, respectively). Needles contributed to the total spruce biomass by 30% (in the 4-year-old stand), while its proportion only slightly decreased to about 25% over the 9-year period (12-year-old). The beech leaves accounted for about 5% of the whole-tree biomass at the age of 4 years, which continuously increased to about 7% at the age of 12 years.

The annual input into necromass (i.e. annual foliage fall and annual tree mortality) in the stands is presented in Figure 6 (beech stand) and in Figure 7 (spruce stand). In the first three years of the observations, we recorded only a single component of the necromass in the beech stand aged under 6 years, namely fallen leaves from the

living trees. In the following years, we also observed mortality of individual trees particularly due to the competition processes. From the age of 9 years, the contribution of tree mortality to the annual input into necromass became greater (of around 40%). However, the foliage fall dominated in the annual input to necromass, since it formed more than 50% of the total new necromass. The situation was significantly different in the spruce stand. Although in the spruce stand the needle fall from the surviving individuals also dominated in the annual input into necromass, its proportion was significantly lower than in the beech stand. Moreover, its dominance lasted only until the age of 8 years, after which the woody parts of the perished individuals started to prevail in the newly created necromass.

The development of the living and dead tree parts of the beech and spruce forests are given in Table 1, 2, 3, and 4. The mean stand heights of both tree species in the young stands were similar, but during the monitoring period beech height grew a little faster than spruce height (mainly from the age of 7 years). On the contrary, spruce reached a significantly higher mean diameter (SBD) than beech. Tree mortality in the spruce stand was much higher than in the beech stand.

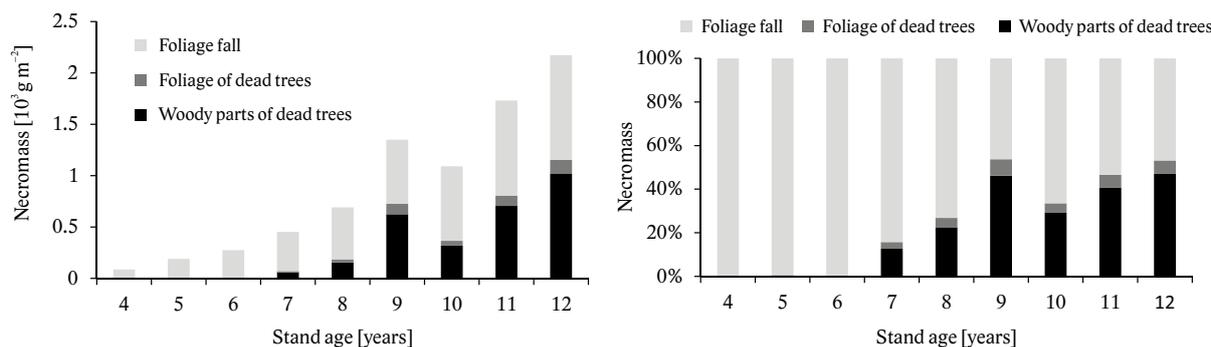


Fig. 6. Development of annual input to necromass during 9-year-development in young beech stand (absolute values in the left graph, relative values in the right graph).

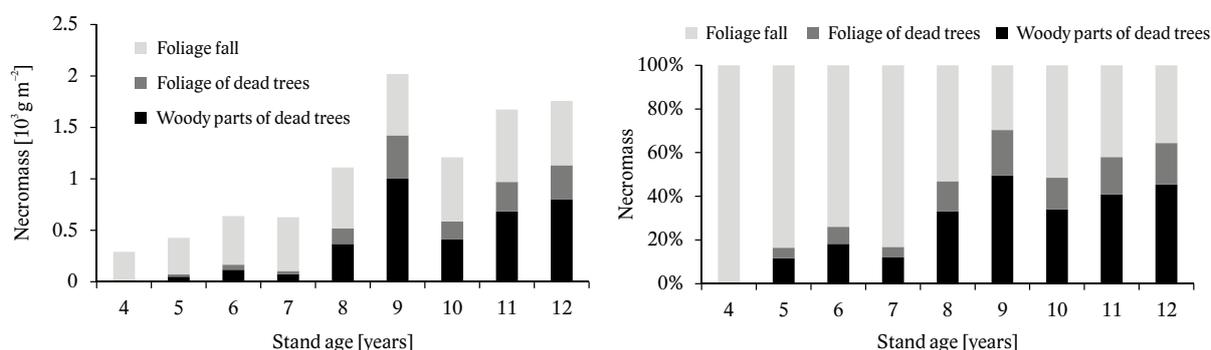


Fig. 7. Development of annual input to necromass during 9-year development in young spruce stand (absolute values in the left graph, relative values in the right graph).

Table 1. Development of stand characteristics of living trees in the young beech stand (mean value ± 68% standard error).

Stand characteristics	Stand age [years]									
	4	5	6	7	8	9	10	11	12	
Height [m]	0.9±0.1	1.2±0.1	1.5±0.1	2.0±0.1	2.4±0.2	3.0±0.2	3.5±0.3	4.1±0.2	4.8±0.2	
SBD [mm]	10.1±0.8	12.8±1.1	14.1±1.3	16.0±1.2	18.3±1.1	21.9±1.2	24.2±1.5	28.2±1.9	31.6±2.0	
Stand density [N per m ²]	52±11	52±11	52±11	44±7	36±4	26±3	22±3	17±3	14±3	
Basal area* [cm ² m ⁻²]	37±2	59±4	72±5	83±7	93±8	95±10	98±10	103±13	101±17	

Note: *Basal area at stem base (calculated from stem base diameter SBD).

Table 2. Development of stand characteristics of trees that died in the particular year in the young beech stand (mean value ± 68% standard error).

Stand characteristics	Stand age [years]									
	4	5	6	7	8	9	10	11	12	
Height [m]	0	0.3±	0	0.5±0.0	0.8±0.1	1.4±0.2	1.8±0.2	2.3±0.2	2.7±0.2	
SBD [mm]	0	5.1±	0	7.1±1.0	8.5±0.5	11.9±1.3	13.3±1.0	15.7±0.9	21.2±2.3	
Stand density [N per m ²]	0±1	0±1	±1	8±6	7±9	11±5	4±5	5±5	4±6	
Basal area* [cm ² m ⁻²]	±0	0±0	±0	2±2	4±2	11±2	5±1	10±5	11±5	

Note: *Basal area at stem base.

Table 3. Development of stand characteristics of living trees in the young spruce stand (mean value ± 68% standard error).

Stand characteristics	Stand age (years)									
	4	5	6	7	8	9	10	11	12	
Height [m]	1.0±0.1	1.2±0.1	1.4±0.1	1.6±0.2	2.0±0.2	2.4±0.2	2.7±0.2	3.4±0.2	4.2±0.1	
SBD [mm]	15.7±0.7	17.5±0.9	21.0±1.4	22.8±1.7	27.2±1.9	33.4±2.0	36.1±1.5	43.0±1.6	47.2±0.7	
Stand density [N per m ²]	29±3	28±3	24±3	23±4	18±4	11±2	9±1	7±1	5±0	
Basal area* [cm ² m ⁻²]	55±3	64±3	80±3	87±3	94±4	90±3	91±5	97±8	84±8	

Note: *Basal area at stem base.

In fact, comparison between live and dead tree mass, eventually proportions of carbon allocation into biomass and necromass, in the developing young stands might be done in a variety of ways. In our case, theoretical comparison between biomass stock of live trees recorded in

the last year of measurements against necromass accumulated over 9 years (i.e. total carbon transferred from biomass to necromass) was used. At the same time, we did not consider processes of necromass decomposition (annual decreases) in the stands.

Table 4. Development of stand characteristics of trees that died in the particular year in the young spruce stand (mean value \pm 68% standard error).

Stand characteristics	Stand age [years]								
	4	5	6	7	8	9	10	11	12
Height [m]	0	0.6 \pm 0.1	0.6 \pm 0.1	0.8 \pm 0.0	1.0 \pm 0.1	1.3 \pm 0.2	1.6 \pm 0.2	1.7 \pm 0.1	2.0 \pm 0.2
SBD [mm]	0	7.9 \pm 1.0	8.6 \pm 0.8	9.9 \pm 0.9	12.6 \pm 1.8	17.9 \pm 1.9	23.1 \pm 3.1	23.5 \pm 1.9	28.6 \pm 3.2
Stand density [N per m ²]	0	1 \pm 3	3 \pm 5	2 \pm 6	5 \pm 7	7 \pm 4	2 \pm 3	2 \pm 2	2 \pm 2
Basal area* [cm ² m ⁻²]	0	1 \pm 1	2 \pm 1	1 \pm 1	6 \pm 2	15 \pm 4	6 \pm 2	10 \pm 4	11 \pm 1

Note: *Basal area at stem base.

The final balance of biomass and necromass quantities in both stands showed a relatively high proportion of the built necromass after 9 years in comparison with the biomass stock of living trees in the last year (Table 5). The total quantity of necromass (foliage fall plus whole body of dead trees) produced over the nine years of observations was about 8,000 g and 9,750 g per m² in the beech and spruce stand, respectively. It represented 57% and 87% of the biomass of living trees in the last year of observations for beech and spruce, respectively (14,160 g per m² in beech and 11,260 g per m² in spruce stand). In the beech stand, as much as 59% of the total necromass production originated from the foliage fall. However, in the spruce stand the contribution of foliage fall to the total aboveground necromass production was significantly lower (49%). If we switch our interpretation from the dry tree matter to carbon amount, we can report that the 14-year-old stand fixed about 7,000 g and 5,600 g of carbon per m² in the tree biomass of beech and spruce, respectively. Moreover, during the nine years of observations, the carbon transfer from the tree biomass to necromass (including both tree mortality and foliage fall) was approximately 4,000 g and 4,900 g per m² in the beech and spruce stand, respectively.

4. Discussion and conclusion

At the beginning of this section we would like to point out again that the beech and spruce stands were of the same ages but grew under the different site conditions. Specifically, the beech stand was on a warmer and drier location, southern part of Central Slovakia and eastern exposition - on a more nutrient rich soil, while the spruce stand was situated in northern Slovakia, at north-oriented exposition on acidic soil. Thus, although the contrasting situations in their developments are commented here, the inter-specific differences might indicate certain general patterns but should not be taken as generally applicable.

Actually, the results showed very dynamic changes in the biomass (carbon) stock. Specifically, in the period of 9 years the biomass of beech increased from about 2,000 g to 14,000 g (i.e. cca 1,000 to 7,000 g of carbon) per m², and from 4,600 to 12,000 g (cca 2,300 to 6,000 g of carbon) per m² in the spruce young stand. Hence, the biomass (carbon) increased more in the beech than in the spruce stand that might be related not only to the inter-specific contrasts in the growth rates but also to the differences in their stand and site properties. In fact, also our previous study (Pajčík et al. 2013) conducted in young beech and spruce stands grown at the identical sites indicated larger net primary productivity of beech than spruce. The difference occurred mainly due to the higher amount of assimilates allocated into beech stems. Similarly, in our present work, stem biomass production of beech was nearly double the production in spruce. We can assume a stem to be a tree component with the longest turnover that would be a positive phenomenon in terms of carbon sequestration. On the other hand, the disadvantage of beech in carbon sequestration is its annual foliage rotation in comparison with spruce (i.e. deciduous versus evergreen species). Thus, while the standing stock of foliage in the spruce stand was approx. triple of that in the beech stand, the amount of foliage fall was very similar in both stands.

The results from our young stands showed, that not only foliage fall but also mass of dead trees (woody parts and foliage) are important paths of carbon flux. We could see that the contribution of the foliage fall to necromass was similar in both stands, but they had a different proportion of dead trees (more in spruce than in beech). Another question is further carbon “fate”, i.e. decomposition rate and subsequently carbon emission from dead woody parts (expecting specific behavior for those in the soil, i.e. roots and on the ground, i.e. stem and branches) and shed foliage. For instance, Konôpka (2017) showed that that aboveground litter in young beech stand (necromass mainly composed of leaves)

Table 5. Tree biomass – status in the last year of observation, and necromass – expressed as cumulative amount during 9-year-observation in the young stands of beech and spruce.

Stand	Expression of quantity [unit]	Live trees – biomass		Live trees – necromass	Dead trees – necromass		Biomass and necromass
		woody parts	foliage	foliage fall – cumulative	woody parts – cumulative	foliage – cumulative	all tree components for 9-year-observation
Beech	absolute [g m ⁻²]	13,142	1,016	4,725	2,882	427	22,192
	relative [%]	59.2	4.6	21.3	13.0	1.9	100.0
Spruce	absolute [g m ⁻²]	8,135	3,125	4,776	3,499	1,471	21,007
	relative [%]	38.7	14.9	22.7	16.7	7.0	100.0

decomposed faster than in spruce stand (needles). This statement is in accordance with the prevailing hypothesis that litter decomposition is faster in broadleaved stands than in coniferous ones (e.g. Berger & Berger, 2014). The differences are often associated with dissimilar lignin and nutrient contents of leaves and needles (Berger & Berger 2014) and possibly with higher diversity of microbial decomposers in broadleaved than coniferous forests (He et al., 2007). As for woody debris, Shorohova & Kapitsa (2016) commented that the decomposition rate in European forests depends on site moisture and on tree species. As for inter-specific differences, Hermann et al. (2015) found significantly higher decomposition rates of beech woody parts than those of spruce.

Concluding our results covering 9 years of observations in the young stands, the amount of biomass (fixed carbon) was only slightly larger than the overall cumulative necromass production (i.e. carbon transferred from biomass to necromass). Hence, a really large portion of carbon is allocated to necromass, from which it is subsequently emitted to the atmosphere. High tree mortality rate is a well-known phenomenon in dense young stands, and it is mostly related to the intensive competition for resources, mostly for light (e.g. Wright et al. 2000). Anyway, the total input to the necromass pool (annually 900 g per m² and 1,100 g per m² in the beech and spruce stand, respectively) can be relatively even larger than in old beech or spruce stand. Healthy old stand (especially if they were regularly thinned) is typical with very low tree mortality rate and the essential part of necromass input is usually represented by foliage fall. For instance, Pavlenda (2011) showed the annual foliage fall equaling about 320 g per m² in a middle-age beech and slightly over 100 g per m² in a middle-age spruce stand. Merganič et al. (2017) estimated about 250 g of foliage annually shed per m² in the forests (prevalingly spruce) of the Czech Republic. Our previous studies (Barna et al. – unpublished data) in an old beech stand showed the annual foliage fall between 300 and 400 g per m². The actual results in this paper indicate as much as 530 g per m² of foliage fall per year estimated in both young beech and spruce stands.

It is generally known that young forests fix in their biomass much less carbon than old stands (see for instance Konôpka B. et al. 2016). However, they can represent (especially those from natural regeneration - usually very dense ones) considerable carbon flux to necromass. In the case of litter fall, the flux it may make up even larger amount than in old forests (compare our results with Merganič et al. 2017). Analogously, young stands should not be omitted in forest carbon balance estimates at regional, country or any other levels.

Acknowledgement

The study was supported by APVV-0273-11, APVV-0584-12, and APVV-14-0086 projects financed by the Slovak Research and Development Agency. It was partly supported by the project QJ 1220316 from the Ministry of Agriculture of the Czech Republic.

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Appendix 1. Parameters of allometric equations for individual tree components of beech stands (after Konôpka et al. 2011).

Tree component	Equation	b_0	b_1	b_2	λ
Foliage	$B = e^{(b_0 + b_1 + DAB + b_2 + h) \cdot \lambda}$	-5.943	2.783	0.332	1.045
Branches	$B = e^{(b_0 + b_1 + DAB + b_2 + h) \cdot \lambda}$	-4.768	2.630	0.423	1.130
Stem	$B = e^{(b_0 + b_1 + DAB + b_2 + h) \cdot \lambda}$	-1.530	1.848	1.015	1.026
Roots	$B = e^{(b_0 + b_1 + DAB + b_2 + h) \cdot \lambda}$	-2.898	2.336	0.025	1.098
Whole tree	$B = e^{(b_0 + b_1 + DAB + b_2 + h) \cdot \lambda}$	-1.236	2.124	0.521	1.038

Appendix 2. Parameters of allometric equations for individual tree components of spruce stands (after Pajtík et al. 2008).

Tree component	Equation	b_0	b_1	b_2	λ
Foliage	$B = e^{(b_0 + b_1 + DAB + b_2 + h) \cdot \lambda}$	-2.487	2.282	0.036	1.082
Branches	$B = e^{(b_0 + b_1 + DAB + b_2 + h) \cdot \lambda}$	-2.553	2.171	0.313	1.089
Stem	$B = e^{(b_0 + b_1 + DAB + b_2 + h) \cdot \lambda}$	-0.469	1.555	0.913	1.020
Roots	$B = e^{(b_0 + b_1 + DAB + b_2 + h) \cdot \lambda}$	-2.869	2.254	-0.142	1.045
Whole tree	$B = e^{(b_0 + b_1 + DAB + b_2 + h) \cdot \lambda}$	-0.579	2.039	0.297	1.030

Carbon stock in aboveground biomass of vegetation at the High Tatra Mts. twelve years after disturbance

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Abstract

The paper focused on the estimation of aboveground biomass and its carbon stock in the vegetation cover on the territory of the High Tatras twelve years after a large-scale wind disturbance. Besides biomass quantification of main plant groups (i.e. trees and ground vegetation) we considered plant components with special regard to carbon rotation rate. The measurements were performed on two transects each containing 25 plots sized 4 × 4 m. Height and stem diameter of all trees on the plots were measured and used for biomass estimation. To quantify the biomass of ground vegetation, six subplots sized 20 × 20 cm were systematically placed on each plot and the aboveground biomass was harvested. The plant material was subjected to chemical analyses to quantify its carbon concentration. The study showed that while the wind disturbance caused dramatic decrease of carbon stock, young post-disturbance stands with abundant ground vegetation, represented large carbon flux via litter fall. Twelve years after the wind disturbance, the trees contributed to carbon stock more than the ground vegetation. However, the opposite situation was recorded for the carbon flux to litter that was related to the dominance of annual plants in the above-ground biomass of ground vegetation. The carbon stock in the biomass of young trees and ground vegetation represented about 8,000 kg per ha. The young stands manifested a dynamic growth, specifically the aboveground biomass increased annually by one third. The results confirmed different carbon regimes in the former old (pre-disturbance) and sparse young (post-disturbance) stands.

Key words: wind disturbance; carbon in biomass; evergreen and deciduous trees; ground vegetation; foliage fall

Editor: Peter Surový

Introduction

Climate change is not only an environmental issue, but recently it has become a serious “civilisation problem”. It can have huge negative consequences on human being welfare or even on human existence all over the world (Moran et al. 2010). Climate change is to main extent caused by the increasing of CO₂ in the atmosphere which is prevalently induced by combustion of fossil fuels. A significant contribution to this process is made by the changes in the landscape use, especially in the form of deforestation, a problem typical for developing countries (MacDicken et al. 2015). Luckily, the oceans as well as terrestrial vegetation cover are able to absorb more CO₂ than they usually emit. Forest ecosystems are the second largest pool of carbon after the oceans. For instance, Dixon et al. (1994) estimated that as much as 80% of aboveground and 40% of belowground (soil, litter, roots) terrestrial carbon is fixed in forests.

It is evident that sustainable development of forests and increasing wood stocks are becoming more ecological than an economical task. Carbon sequestration is currently the most important component of forest ecosystem services (Thorsen et al. 2014). At the same time, carbon sequestration in the tree biomass and in the soil can be partly controlled via forest management. The management should focus on forest protection against harmful agents, stimulation of wood increment and preservation of forest soils.

Increasing forest disturbances in temperate forests triggered by climate change (Seidl et al. 2011) emphasised the need for new knowledge about possible preventive measures that would support the decision making process of forest management. Forest destruction caused by windstorm or other harmful agents brings besides other problems the negative effect on the carbon balance in the landscape (e.g. Dale et al. 2001). Destruction of for-

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est stands means the loss of some parts of carbon stocks in tree biomass (Lindroth et al. 2009). Furthermore, it stimulates carbon emission from the forest soils, and this problem is most relevant in the case of uprooted trees and disturbed soil medium (Liechy et al. 1997). Restitution to the former state (before the disaster episode) takes a couple of decades. Duration of this reversible process is related to time periods of forest regeneration and soil reclamation, while both are regulated by post-disturbance forest management (Fischer et al. 2002). Forest ground vegetation changes rapidly after forest disturbance and in early-successional stages it is formed by non-woody vegetation (Swanson et al. 2010). Consequently, carbon fluxes are also highly dynamic. Although ground vegetation sequesters some carbon and ecosystem productivity recovers very fast (Williams et al. 2013), from the long-term perspective it is not as efficient as tree cover and often delays or slows down forest regeneration (Hansen 2014).

In general, forest growing stocks (i.e. carbon pool) have been gradually increasing in Slovakia. Specifically, the stock of Slovak forests increased by 7.7% in the last decade (Ministry of Agriculture and Rural Development 2016). However, the last few decades in Europe have been characterised not only by increasing volume but also by increasing frequency of disturbance processes. In Slovakia, the incidental felling during the last decade made as much as 42 million m³ of calamity wood, which was about 53% of the total annual cut (Kunca et al. 2016). An extraordinarily large windstorm disturbance was recorded in 2004. The windstorm heavily damaged especially spruce stands. These were subsequently infested by bark beetles resulting in mortality of large forest complexes. Another large scale wind disturbance occurred in 2014 and again, the most serious damages were found in spruce forests. The most intensive wind and bark beetle damage to forests was in the High Tatra Mountains (Nikolov et al. 2014; Økland et al. 2016). There, a considerable part of old forest stands was destroyed and colonised particularly by non-woody ground vegetation (Šoltés et al. 2010; Máliš et al. 2015). Later, the post-disturbance areas were covered by sparse young forest stands with ground vegetation in treeless gaps. In spite of the fact that many large post-disturbance areas currently exist in Slovakia, there is very little information on biomass of their ground vegetation. There are no works focused on carbon stock in post-disturbance vegetation that includes all kinds of plants, i.e. trees and ground vegetation species.

This paper aims at estimating the aboveground biomass and carbon stock in vegetation cover on the territory of the High Tatra Mountains twelve years after the salvage logging that occurred after the wind disturbance in 2004. Besides the quantification of the main vegetation groups (i.e. trees and ground vegetation) we attempted to estimate the biomass of plant components grouped with respect to their carbon rotation rate.

2. Material and methods

2.1. Site and stand description

Our research activities focused on a post-disturbance area arisen after an intensive windstorm that occurred on 19th November 2004 in the High Tatra Mountains. The storm damaged mostly forests at altitudes between 700 and 1,400 m a.s.l. The disturbance of the forests concentrated prevalently in a continual belt oriented in a west-east direction and the affected area was approximately 35 km long and 5 km wide (Šebeň 2011). The wind-disturbed area was managed in three different ways with regard to the degrees of nature protection: from fully-processed calamity wood, through partly-processed calamity wood, up to absolutely untreated parts left exclusively to natural succession. The substantial part of the calamity wood was processed in the years 2005 and 2006. Alike calamity wood processing, forest regeneration was also implemented with regard to the degrees of nature protection in the form of planting, natural regeneration and combination of both approaches. Soil preparation for planting of seedlings was performed manually (hole digging by a hoe).

In 2016 (i.e. in the tenth or eleventh growing season after the salvage logging), the area was prevalently covered by young forests that originated from both natural regeneration and planting. Open areas among the young forest stands were covered by species adapted to forest clearings, particularly by grasses, herbs and shrubs. The forest soils on the post-disturbance area are mainly cambisols and podzols. The bedrock is predominantly formed by fluvio-glacial sediments of granodiorites. The climate is characterised by low mean annual temperatures (around 4.0 °C), high precipitation amounts (about 1,000 mm) and over 120 days of snow cover (Vološčuk et al. 1994).

To study the carbon stock in trees and ground vegetation, two research transects – one near the site called “Danielov dom” (hereinafter as DD transect) and another one close to the Horný Smokovec village (hereinafter as HS transect) were established. The forests at the localities are managed by the State Forests of the Tatra National Park. Both sites belong to the territory with the lowest degree of nature protection. Thus, the post-disturbance management at these sites was represented by full-area processing of calamity wood and combined (both planting and natural regeneration) reforestation.

The transects are located in the central part of the disturbed belt. The orientation of both transects is from Northwest to Southeast. The altitude of the DD transect varies between 970 – 1000 m.a.s.l and that of the HS transect between 920 and 950 m.a.s.l. The transects were 4 m-wide, on which 4 m-long plots for tree measurements were placed and were isolated by 8 m-long gaps without any measurements to ensure that the plots were independent entities. The total length of the DD transect as well as the HS transect was 300 m, i.e. each transect

comprised 25 plots. The corners of each plot were fixed with wooden pegs hammered in the soil. All young trees occurring on the plots higher than 10 cm were labelled with a code written on a metallic tag.

2.2. Measurements and calculations

The field measurements of trees were performed in the first half of the growing season 2016 (after the entire new leaves were out). We recorded species, tree height and diameter at stem base (d_0 hereinafter) for all labelled trees on the plots. Altogether, about 380 and 320 individuals were measured at the DD transect and HD transect, respectively.

The standing stocks of the tree aboveground biomass as well as its components (stem, branches and foliage) were estimated from tree measurements (height and diameter d_0 , i.e. independent variables) using species-specific allometric relations; see also Konôpka et al. (2015). The stock was calculated separately for each transect, first at a plot level (as a sum of all trees on the plot), then as a mean value from the 25 plots. At the same time, two groups of tree components were considered: (1) foliage with fast turnover (shortly fixed carbon) and (2) stem plus branches with slow turnover (carbon fixed for a long period). In addition to biomass standing stock of trees, we attempted to estimate the amount of biomass (carbon) annually “lost” from the living trees in form of the annual foliage fall. In the case of deciduous species (broadleaved and larch), the annual foliage fall equals the foliage stock. As for spruce trees, the annual foliage fall was calculated as 1/5 of their autumn standing stock (see e.g. Schmidt-Vogt 1977; Sander & Eckstein 1994) and for pine as 1/3 of the needle stock in autumn (Konôpka et al. 2003). To estimate the carbon amount in tree foliage, the concentrations of this element were taken from our previous work dealing with the same sites (Konôpka et al. 2016).

The measurements of ground vegetation were performed in August 2016 – the month with the seasonal biomass stock peak. In order to estimate the average standing biomass of ground vegetation, six subplots sized 20x20 cm were placed at each plot using the randomised selection of spots. Altogether, there were 150 sampling subplots per transect. Prior to biomass sampling, all plant species were identified and recorded at the plot level, and their frequency and cover were estimated at the transect level. The frequency was calculated from the species occurrence on 25 plots (for instance, if the species grew on 10 plots, its frequency at the transect was 40%), and the cover was estimated as an average from non-zero numbers of the plots (for example, if the species was not present on 4 plots, the average was calculated from the values on 21 plots, where it occurred).

From each subplot, all present vascular plants except trees were collected. The sampled aboveground biomass

was categorised according to the plant life span to: annual (living for a year), biennial (living for two years), and perennial (living for more than two years). Then, the foliage of biennial and perennial plants with the life span of one year (e.g. foliage of *Vaccinium myrtillus*) was separated and added to the group of annual (i.e. one-year) biomass. Thus, plant biomass was divided into three groups with regard to the period of carbon fixation in biomass of living plants, i.e. one year, two years and over two years. Then, the six samples (coming from the six subplots) originating from the same plot were merged into one mixed sample. Thus, each plot was characterised by three samples representing three different periods of carbon fixation in biomass of living plants. The plant biomass was oven-dried to obtain its constant dry matter (48 hours under 85 °C) and weight with precision ± 0.001 g. The dry matter was subjected to chemical analyses (dry combustion method performed by Flash EA 1112 elemental analyser) to quantify carbon concentration. Since the differences in carbon concentrations between the transects were insignificant, single (i.e. the average of 50 plots) values were used to represent carbon concentration in plants with one year, two years and over two years period of carbon fixation in living biomass.

The standing stock of the plants was calculated separately for each transect as an average value from 25 plots (merged biomass from 6 subplots) considering the groups with one year, two years and over two years period of carbon fixation in living biomass. The biomass was scaled up to a hectare and the carbon amount was estimated with regard to its concentration in a specific group of plants (one year, two years and over two years period of carbon fixation in living biomass).

Data archiving and manipulation was performed in Excel, calculations and analyses were done in Statistica 10.0.

3. Results

The basic stand characteristics (expressed as average values for all plots together) were very similar on both transects (Table 1). While the number of trees and basal area were larger at the DD transect, the mean stem diameter and especially tree height were larger at the HS transect. This contrasting situation was caused mainly by the clearing cut which was performed at the HS transect by the forestry practice in the year 2015. The cut reduced the number of trees, especially of broadleaved species such as *Salix caprea* and *Sorbus aucuparia*. Since the cut aimed more at smaller trees, mean diameter and height increased because they were calculated from larger trees unaffected by cut. The transects differed from each other in their tree species composition (Fig. 1 and 2). The DD transect was characterised by the dominance of evergreen species (61.2%), while the HS transect had more deciduous species (60.0%). The species composi-

Table 1. Basic stand characteristics (average value and standard deviation) for the Danielov dom (DD) transect and Horný Smokovec (HS) transect in 2016. Basal area was calculated using stem base diameter.

Transect	Number of trees [10 ³ per ha]	Diameter d ₀ [mm]	Loresys height [cm]	Basal area [cm ² m ⁻²]
Danielov dom	9.35 ±13.38	50 ±27	320 ±151	12.1 ±10.0
Horný Smokovec	7.94 ±12.58	52 ±45	381 ±174	9.6 ±9.0

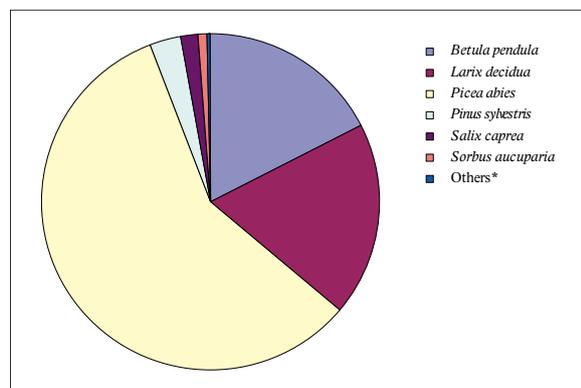


Fig. 1. Average tree species composition (calculated from 25 plots) expressed from basal area at the Danielov dom transect. * *Acer pseudoplatanus*, *Populus tremula*, and a variety of *Alnus* and *Salix* genus

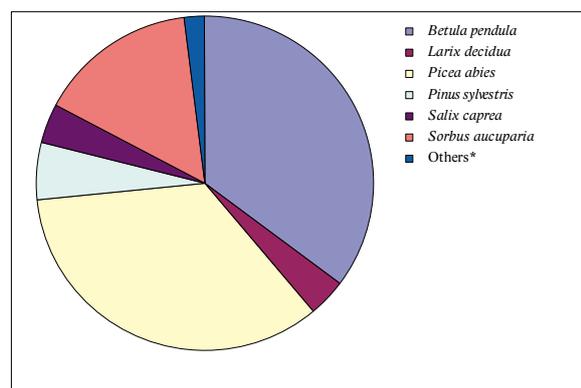


Fig. 2. Average tree species stand composition expressed from basal area (calculated from 25 plots) at the Horný Smokovec transect. **Acer pseudoplatanus*, *Populus tremula*, and a variety of *Alnus* and *Salix*

tion of ground vegetation also slightly differed between the transects, but in both cases they represented later successional stages of post-disturbance forest vegetation (i.e. nearly no presence of ruderal species). The most abundant species which contributed to the total biomass most are shown in Table 2.

The chemical analyses showed that the carbon concentration in foliage varied among tree species from 46.4% (*Salix caprea*) to 51.1% (*Picea abies*; Table 3). As for ground vegetation, its carbon concentration (excluding root systems) varied from 47.6% in annual plants to 51.8% in perennial plants.

Table 2. Frequency and average non-zero cover of ground vegetation species estimated on 25 plots per each transect (each plot was characterised by one mixed sample, generated from six harvested areas – subplots). Only species with frequency above 20% are listed (the total cover of those with frequency lower than 20% did not reach 5%). The species are divided into three groups depending on the life span of their biomass and ordered by the sum of cover values at both transects.

Species grouped by lifespan	Danielov dom transect		Horný Smokovec transect	
	frequency	cover	frequency	cover
[%]				
One-year biomass				
<i>Calamagrostis villosa</i>	28	18.6	100	69.5
<i>Calamagrostis arundinacea</i>	96	35.4	52	3.5
<i>Avenella flexuosa</i>	96	16.5	84	7.5
<i>Luzula luzuloides</i>	88	3.2	72	2.3
<i>Agrostis capillaris</i>	20	3.8	8	1.3
<i>Maianthemum bifolium</i>	88	2.2	88	2.9
<i>Carex pallescens</i>	24	0.7	4	4.0
<i>Epilobium angustifolium</i>	84	2.6	80	1.2
<i>Juncus effusus</i>	8	1.0	24	2.1
<i>Athyrium filix-femina</i>	24	1.9	28	1.0
<i>Veronica officinalis</i>	44	2.0	16	0.4
<i>Galeopsis bifida</i>	52	1.5	28	0.8
<i>Melampyrum pratense</i>	68	1.7	24	0.6
<i>Fragaria vesca</i>	20	1.3	4	1.0
<i>Luzula pilosa</i>	24	1.6	12	0.7
<i>Hypericum maculatum</i>	48	1.2	36	0.9
<i>Oxalis acetosella</i>	56	1.3	12	0.7
<i>Carex pilulifera</i>	28	1.4	8	0.6
<i>Solidago virgaurea</i>	44	0.6	44	0.7
<i>Dryopteris dilatata</i>	36	0.5	28	0.3
<i>Senecio ovatus</i>	4	0.5	28	0.2
Two-year biomass*				
<i>Rubus idaeus</i>	34	25	25	10
More-year biomass*				
<i>Vaccinium myrtillus</i>	92	10.9	80	11.7
<i>Calluna vulgaris</i>	32	1.4	72	1.6
<i>Vaccinium vitis-idaea</i>	20	1.3	8	0.8
<i>Sambucus racemosa</i>	4	0.1	28	0.6

Explanatory note: * The parts of biennial and perennial plants living for only one year (e.g. foliage of *Rubus idaeus*, *Vaccinium myrtillus* etc.) were separated and added to the group of one-year biomass.

Table 3. Carbon turnover of plant biomass and carbon concentration by tree species and grouped plants of ground vegetation.

Tree species (foliage only) or group of ground vegetation	Carbon turnover [proportion per year]	Carbon concentration [%]
<i>Betula pendula</i>	1.0	51.0
<i>Larix decidua</i>	1.0	48.4
<i>Picea abies</i>	0.2	51.1
<i>Pinus sylvestris</i>	0.3	50.9
<i>Salix caprea</i>	1.0	46.4
<i>Sorbus aucuparia</i>	1.0	49.4
Ground vegetation – 1-year	1.0	47.6
Ground vegetation – 2-years	0.5	49.9
Ground vegetation – over 2-years	less than 0.5	51.8

Note: carbon concentrations for tree species were taken from Konôpka et al. (2016), and for ground vegetation were obtained from the chemical analyses performed in this study.

We found huge differences (up to tenfold) in biomass, and thus also in carbon stock, between the plots at both the DD transect (Fig. 3) and the HS transect (Fig. 4). At most plots, the aboveground biomass of trees prevailed over the biomass of ground vegetation. At some plots, the contribution of ground vegetation to total biomass was very low (e.g. 3% at plot 23 on the HS transect). On the other hand, four plots (e.g. plot 4 at the DD transect) were treeless, i.e. ground vegetation made 100% of plot biomass. We found only weak negative relationship

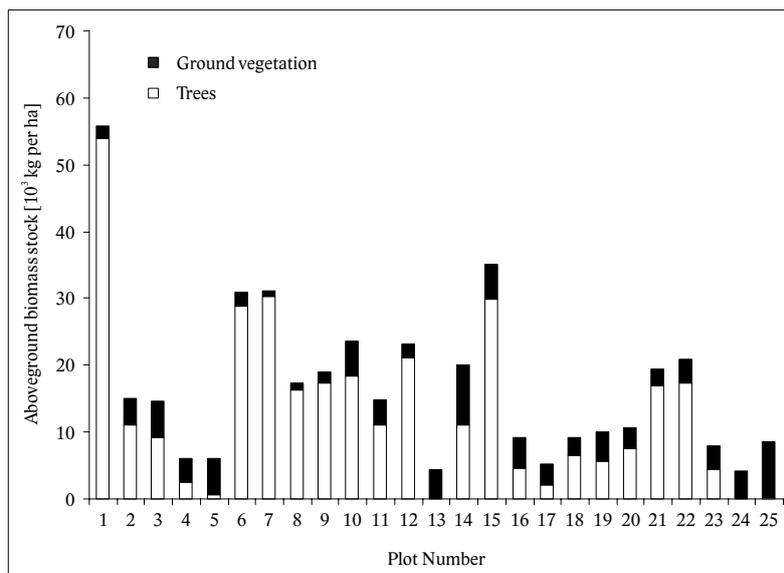


Fig. 3. Aboveground biomass in trees and ground vegetation at the Danielov dom transect.

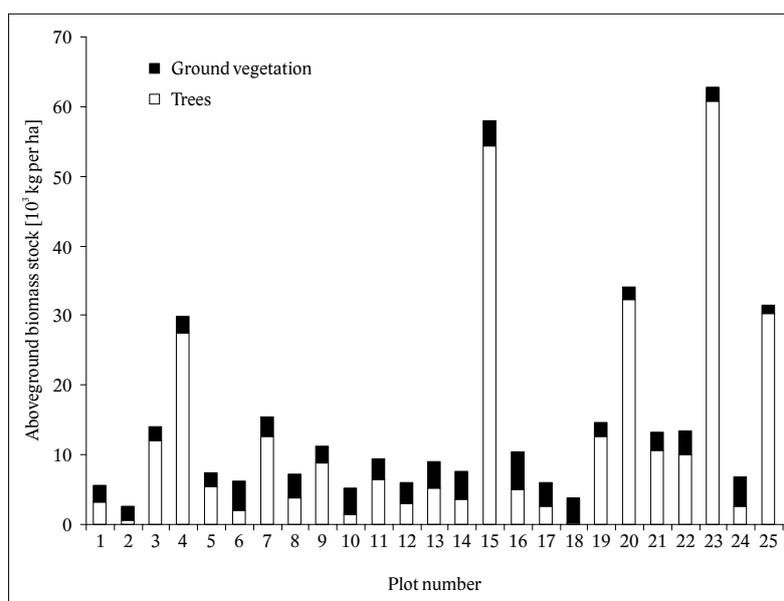


Fig. 4. Aboveground biomass in trees and ground vegetation at the Horný Smokovec transect.

($R^2 = 0.18$; results not shown in this paper) between the biomass of trees and ground vegetation what may suggest only mild influence of tree cover on ground vegetation community.

The total carbon amount fixed in the aboveground tree biomass was 6,566 kg per ha and 6,241 kg per ha at the DD transect and the HS transect, respectively (Table 4 and Table 5). While the contribution of foliage to the total aboveground biomass of trees was 25% at the DD transect, its share at the HS transect was only 17%. The differences are most probably related to contrasting tree species composition at the transects. As for the ground vegetation, slightly larger carbon amount was at the DD transect (1,851 kg per ha; Table 4) than at the HS transect

(1,448 kg per ha; Table 5). The results showed that the carbon amount in the tree aboveground biomass was 3.5 times (DD transect) or 4.3 times (HS transect) higher than in the ground vegetation. The reverse situation was in the carbon flux of the annual foliage fall (Table 6). The carbon in the annual foliage fall from the trees represented only 43% (transect DD) and 44% (transect HS) of the carbon in the annual ground vegetation fall. At the DD transect, the amount of carbon in the annual tree foliage fall was 614 kg per ha, while the carbon amount in the annual ground vegetation fall was 1,442 kg per ha. Similar amounts of carbon, specifically 547 kg C per ha in the annual tree foliage fall and 1,257 kg in the annual ground vegetation fall were found at the HS transect.

Table 4. Carbon amount in the aboveground woody parts (i.e. stem and branches) and foliage of trees and in ground vegetation at the Danielov dom transect.

Tree species or ground vegetation	Carbon stock [kg ha ⁻¹]		
	in woody parts	in foliage	together
<i>Betula pendula</i>	1,449	153	1,602
<i>Larix decidua</i>	1,140	180	1,320
<i>Picea abies</i>	2,173	1261	3,434
<i>Pinus sylvestris</i>	108	35	143
<i>Salix caprea</i>	30	11	41
<i>Sorbus aucuparia</i>	14	4	18
Other broadleaved	6	2	8
Trees together	4,920	1,646	6,566
Ground vegetation – 1-year	—	—	1,262
Ground vegetation – 2-year	—	—	359
Ground vegetation – over 2-year	—	—	230
Ground vegetation together	—	—	1,851

Table 5. Carbon amount in aboveground woody parts (i.e. stem and branches) and foliage of trees and in ground vegetation at the Horný Smokovec transect.

Tree species or ground vegetation	Carbon stock [kg ha ⁻¹]		
	in woody parts	in foliage	together
<i>Betula pendula</i>	2,874	265	3,139
<i>Larix decidua</i>	206	28	234
<i>Picea abies</i>	1,078	519	1,597
<i>Pinus sylvestris</i>	163	58	221
<i>Salix caprea</i>	90	21	111
<i>Sorbus aucuparia</i>	768	98	866
Other broadleaved	61	12	73
Trees together	5,240	1,001	6,241
Ground vegetation – 1-year	—	—	1,225
Ground vegetation – 2-year	—	—	64
Ground vegetation – over 2-year	—	—	159
Ground vegetation together	—	—	1,448

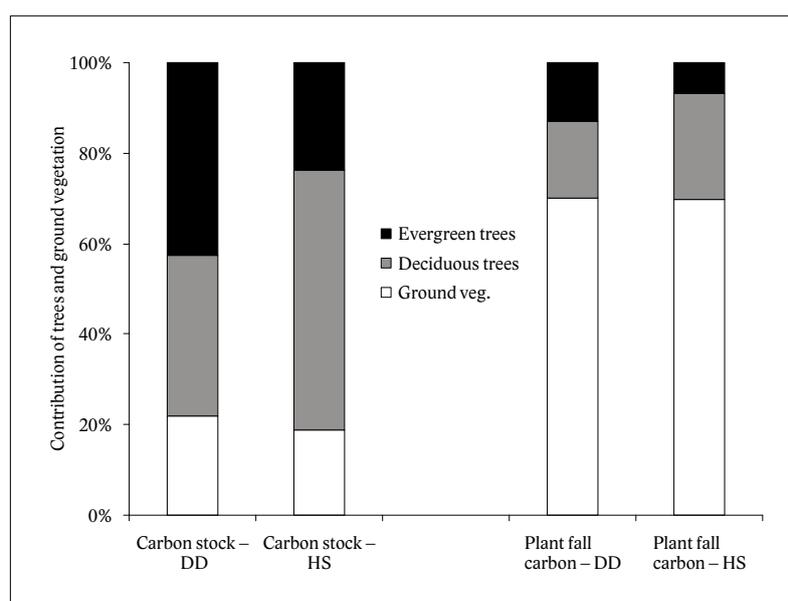
The results proved contrasting contributions of evergreen and deciduous tree species vegetation to carbon stock versus the annually transferred carbon from biomass to necromass (i.e. foliage fall; Fig. 5). Interestingly, the contributions of all tree species to the total

carbon stock in the aboveground plant biomass were similar at both transects (78% and 81%). The differences between the transects were found in the contribution of evergreen and deciduous tree species to the carbon stock, since at the DD transect the evergreen tree species prevailed over the deciduous species, while at the HS transect the situation was reverse. At the same time, the contribution of tree species to the carbon amount in the annual plant fall was very similar at both transects (about 30%).

Table 6. Carbon flux from plant biomass in the form of annual aboveground fall at the transects of Danielov dom and Horný Smokovec.

Tree species or ground vegetation	Annual carbon flux [kg ha ⁻¹] on the transect	
	Danielov dom	Horný Smokovec
<i>Betula pendula</i>	153	265
<i>Larix decidua</i>	180	28
<i>Picea abies</i>	252	104
<i>Pinus sylvestris</i>	12	19
<i>Salix caprea</i>	11	21
<i>Sorbus aucuparia</i>	4	98
Other broadleaved	2	12
Trees together	614	547
Ground vegetation – 1-year	1,262	1,225
Ground vegetation – 2-year	180	32
Ground vegetation – over 2-year	unknown	unknown
Ground vegetation together	1,442	1,257

The differences between the tree species were found also in the share of carbon in the foliage fall to the total carbon amount in the aboveground biomass (Fig. 6). The largest value (13%) was found for *Larix decidua* and the lowest value for *Picea abies* (7%). Moreover, we expressed the annual carbon fall per unit of basal area for each species. Again, the largest value was estimated for *Larix decidua* (82 kg per m²) and the lowest value (34 kg

**Fig. 5.** Contribution of trees (grouped as evergreen and deciduous) and ground vegetation to total carbon stock and to carbon annually transferred via plant fall at the Danielov dom (DD) and Horný Smokovec (HS) transect.

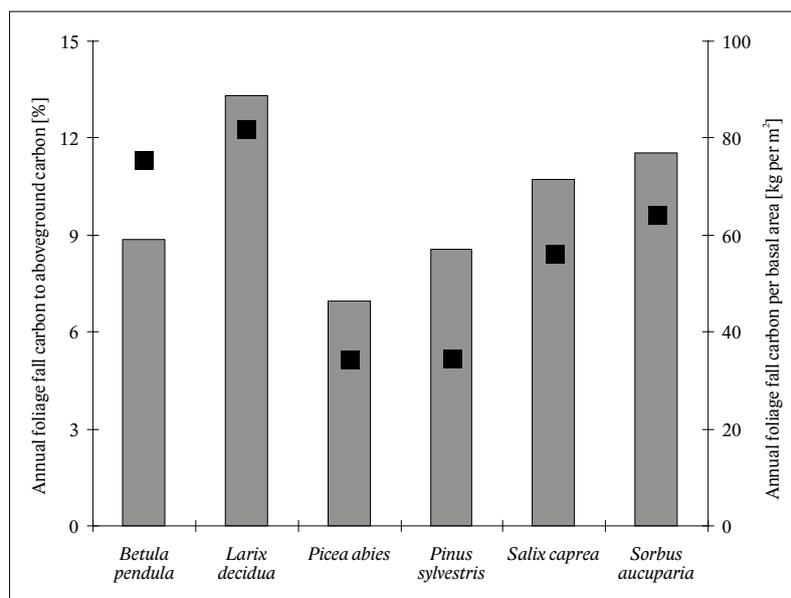


Fig. 6. Carbon in annual foliage fall (i) as a ratio to total aboveground biomass carbon (left y-axis and grey bars) and (ii) per unit of basal area (right y-axis and black squares) in each tree species for both transects together.

per m²) for *Picea abies*. These indicators reflect an efficiency for carbon storage in biomass, i.e. which part of carbon in tree biomass is lost via foliage fall.

Our previous results brought figures on the carbon stock (Table 7) fixed in the aboveground tree biomass of spruce-dominant forest complexes in the central part of the High Tatra region (state to 1997; see Konôpka et al.

Table 7. Contribution of components to total aboveground tree carbon in pre-disturbance forest stands in the High Tatra region – state to 1997 (Konôpka et al. 2016, modified).

Tree component	Carbon amount [kg ha ⁻¹]	Carbon contribution [%]
Foliage	4,557	6.1
Branches	3,891	5.2
Stem	66,605	88.7
Aboveground parts	75,053	100.0

2016 for more details). Since the results contained not only the information about the total aboveground parts but also about the specific tree components, we could use those for a detailed comparison with post-disturbance young stands (comments are in the Discussion and conclusion section).

4. Discussion and conclusion

In general, large scale disturbances in forests, especially windstorms, may temporally interrupt continuity of carbon sequestration in biomass of forest cover (e.g. Seidl et al. 2014). The length of subsequent restoration of carbon stock fixed in tree biomass depends on the rate of forest regeneration and productivity of newly-arisen stands. Our results showed that one decade after the wind disaster, the total carbon amount fixed in the aboveground

biomass of trees was about 6,600 kg and 6,200 kg per ha. The previous estimates in this region (Konôpka et al. 2016) showed that the pre-disturbance forests, prevalently mature spruce stands, contained about 75,000 kg of carbon per ha fixed in the aboveground tree biomass. It means 11–12 times more carbon in the aboveground tree biomass in old (pre-disturbance) stands than in young (post-disturbance) stands. Moreover, since our previous paper (Konôpka et al. 2016) showed the tree carbon stock at the same transects in spring 2015, we can comment on the inter-annual changes. As for the DD transect, the carbon stock in the aboveground tree parts increased by 38% that is a really huge change. The increase at the HS transect was only by 19% because of the reduction of the number of trees by the thinning treatment in the autumn 2015 (the felling decreased the basal area by approx. 20%). Anyway, the inter-annual comparison at the DD transect suggested a very dynamic accumulation of carbon in young stands on the post-disturbance area. That is surely a great difference compared to old stands which can increase their carbon stock in biomass only by a very few percent. This statement conforms with the conclusions of Gower et al. (1996) that the aboveground net primary production declines with age, which is related mainly to changing respiration intensity and carbon gains of trees over their lifespan (Steppe et al. 2011).

Our results for ground vegetation showed the amount of carbon in their aboveground parts of about 1,900 kg and 1,400 kg per ha. This represents the biomass of late successional stages of post-disturbance vegetation (nearly no occurrence of ruderal plant species). The comparison to other studies from the same study area (Křižová et al. 2010; Fleischer & Homolová 2012) showed that this amount is similar to quantities found in the succes-

sional stages developed approximately 5 – 6 years after disturbance. This suggests that the maximum biomass of ground vegetation is accumulated few years after a disturbance, which was also reported by Palviainen et al. (2005). If the observed ground vegetation biomass at our transects is compared to the values of mature spruce-dominant stands in the High Tatra region (Križová et al. 2010; Fleischer & Homolová 2012) or in the Low Tatras (Pavlenka et al. 2011), we find that the ground vegetation biomass in mature stands is approx. 6 – 14 lower than at the transects.

The measurements at the transects showed that while the tree biomass fixed much more carbon than the ground vegetation biomass, the reverse situation was observed in the carbon flux to litter. Previously (Konôpka et al. 2016) we showed that foliage in old (pre-disturbance, spruce dominating) stands made only 6% of aboveground tree biomass. This equals approximately 900 kg of carbon per ha annually lost from trees by annual foliage fall. Our estimates for young post-disturbance stands showed the values of carbon by one third lower. However, if we consider litter originating from ground vegetation, larger amount of carbon rotating via annual fall can be assumed in post-disturbance than in pre-disturbance areas. Our finding concerning much higher portion of annual foliage fall to total aboveground tree biomass in young stands than in old stands conforms to the results of Zhou et al. (2006). Their general model showed that the proportion of NPP allocated to foliage decreases and to stem increases with stand age until approximately 40 – 50 years, and then the proportions of biomass allocated to individual tree components become stabilised.

We would like to point out that our study focused exclusively on the aboveground part of biomass (i.e. living parts of plants) omitting not only belowground parts (roots) of trees and ground vegetation but also necromass (dead parts of plants). As for roots, their higher contribution to total plant biomass might be expected in ground vegetation in comparison to young trees. For instance, under the conditions of Central Slovakia, Máliš et al. (2013) showed that in *Calamagrostis epigejos* dominated grass-bush community belowground parts contributed to total biomass by 40 – 50%. In parallel, Konôpka et al. (2013) estimated the contribution of roots in a young spruce stand at the same site to the total tree biomass only between 22 – 24%. Even much higher proportion of belowground biomass of around 65% was reported by Palviainen et al. (2005) and Pyšek (1991) from post-disturbance communities of ground vegetation developed at sites of spruce-dominated stands. These results indicate that the contribution of ground vegetation to total biomass (i.e. above- and belowground parts of ground and tree vegetation together) at our transects would be larger than to aboveground biomass. The quantification of carbon fixed in plant necromass is rather complicated. The necromass includes mainly debris of roots, stumps, possibly branches of old (pre-disturbance) trees, foliage

litter accumulated on ground as well as young trees perished mostly due to competition in dense tree clusters. However, we were neither able to measure these data ourselves nor we were able to find any results from other papers focused on the post-disturbance territory of the High Tatras.

Moreover, for a complete view on carbon cycling in vegetation cover, respiratory activity via foliage and soil medium should be included. Here, we can suppose certain differences between old and young stands as for foliage respiration, eventually its ratio to net primary productivity. In principal, the ratio of carbon emitted by foliage respiration to carbon invested to building tree biomass decreases with stand age (Mäkelä & Valentine 2001). On the other hand, we can expect higher soil respiration intensity in young (post-disturbance) than old (pre-disturbance) stands. This assumption is based on the fact that young stands were sparse, and contained many gaps with a high level of solar energy input. That would stimulate especially heterotrophic part of soil respiration (see also Karhu et al. 2014).

Concluding our results, we can state different carbon regimes in the compact old (pre-disturbance) and sparse young (post-disturbance) stands in the High Tatra region. The differences were not only in the total amount of carbon fixed in tree biomass, but also in the proportion of carbon from the total tree biomass carbon annually dropped in the form of foliage fall. While the wind disturbance caused the dramatic decrease of carbon stock in the tree biomass, young post-disturbance stands with abundant ground vegetation represented large carbon flux via annual plant fall. In fact, twelve years after the wind disturbance, trees contributed to carbon stock more than ground vegetation. On the other hand, the opposite situation was recorded for carbon flux via annual plant litter that was dominated by annual biomass species (fast carbon turnover, i.e. approx. once a year) in the community of ground vegetation.

Acknowledgements

The research was supported by the projects APVV-0584-12, APVV-14-0086 and APVV-15-0270 from the Slovak Research and Development Agency. Further it was partly supported by the project QJ1220316 from the Ministry of Agriculture of the Czech Republic.

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