Ecophysiological Disturbances of Mycorrhiza Caused by the Application of Forest Operations in Forest Ecosystems – Review

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Abstract:
Forest ecosystems are home to a variety of diverse organisms. These organisms require specific living conditions for their growth. One of the goals of forest management is to ensure the most favorable biological and ecological conditions for forest trees. However, forests have recently undergone extensive and numerous disturbances of biological and ecological balance (pests, changes in the natural composition of communities, weather disasters, pollution, etc). They all have a negative effect on the forest condition.
One of the unfavourable effects on forests is generated by the use of forest operations. Direct and indirect adverse impacts of forest operations on forest trees and forest soil have been described in a number of papers. These impacts include tree damage and reduced tree growth, as well as compaction and degradation of forest soils. Moreover, forest operations have a negative effect on the ecological and physiological processes that are important for the development of forest trees. One of the most important ecological and physiological interactions between forest trees is symbiosis. It is predominantly developed throughout the upper layers of forest soils, at the root of most forest trees, and is therefore extremely vulnerable to forest operations. The most common form of symbiosis on forest trees is mycorrhiza, which has been established on over 2000 plant symbionts. The majority of commercial tree species in Croatia form ectomycorrhiza. There has been very little research into ecophysiological disturbances of mycorrhiza as the consequence of forest operations.
The paper presents research into mycorrhiza development under unfavorable environmental conditions, with an emphasis on disturbances caused by the use of forest mechanization. Ecological, ecophysiological, economic and organizational aspects of the use of mechanization in forest ecosystems are discussed, and suggestions are given for future research. Special focus is placed on the estimate of damage and degradation of forest soils and disturbances in the development of forest trees and mycorrhizae due to forest operations in forests. Opportunities for the development and implementation of long-term sustainable management plans for forests with minimal adverse impacts on forest ecosystems are presented.

Keywords: forest ecosystems, forest operations, mycorrhiza, ecophysiological disturbances, forest ecosystem management

1 Introduction

Certain organisms have a crucial role for the functioning and development of forest ecosystems. In the aboveground part of forest ecosystems it is forest trees, and in the underground part it is microorganisms in the soil (Kimmins 2004). The growth of forest trees largely depends on the action of ecological and biological factors, which influence tree physiological processes. One of the most important physiological processes in the tree is nutrient uptake. It is carried out by means of forest tree roots, but an important role is also played by microorganisms. Roots of forest trees and microorganisms in the soil are most intensively developed in the top parts of the soil. According to Souch et al. (2004) forest tree roots develop most intensively up to 0.3 m in depth, whereas about 45% of fine roots of forest trees develop at soil depth up to 0.1 m.

In the past several decades, forest ecosystems have been subjected to various adverse impacts that have affected the development of forest trees and other organisms. The most important natural unfavourable factors are weather conditions (drought, frost, floods, storms, hail), insects, plant diseases and wildlife. However, a major role is also played by anthropogenic impacts which alter the natural condition of forest communities, lead to changed site conditions and cause damage and degradation of forest soils.

Forest soil is the most important part of forest habitats, although other ecological factors, such as climate, relief and water may also have an important role in the development of certain organism species. Forest soil supports the growth of plant roots and numerous microflora. It is formed through different physical-chemical and biological processes which constantly take place in the soil (Marshall 2000). Biogeochemical processes in the soil that are important for the functioning of forest ecosystems include carbon mineralisation, nitrogen fixation, nitrification and production of trace elements. All these processes depend on the natural properties of forest soils. Forest soils are characterized by diverse physical, chemical and biological properties. Physical features comprise texture, structure, porosity, stability, density, temperature and water in the soil, whereas chemical features comprise ion exchange capacity, soil reaction, and nutrient availability and leaching (Kimmins 2004). Anthropogenic impacts in the course of forest management generally have an adverse effect on these features.

The quality and productivity of forest soils depends on the physical soil properties and presence of microorganisms. One of the most important functions of forest soil is the transfer of water and water dissolved substances. However, equally important is the provision of an optimal quantity of air in the soil needed for the development of forest tree roots and other organisms that participate in the decomposition of organic matter. The process of organic matter decomposition involves microscopic bacteria, fungi and vertebra colonies (Coleman and Crosley 1996). The activity of adverse factors leads to increased degradation of forest soils, which influences processes in the soil and soil functions. The consequences are unfavourably reflected on the condition of trees and stability of forest ecosystems.

The development of forest soils crucially depends on the development of organisms in the soil. Microorganisms are the most numerous and the most diverse group of soil organisms, while symbiotic microorganisms, and especially fungi, constitute the dominant group. They participate in the growth of forest trees (Mukerji et al. 2006). Soil microflora and microfauna mutually interact in the breaking down of leaf litter, mineralisation of basic nutrients and their storage in the soil. According to Marshall (2000), microorganism communities in the soil comprise viruses, bacteria, fungi and blue-green algae, as well as animals (from one-celled protozoa to small vertebrates).

Forest soil is home to tens of thousands of fungi species. One gram of the surface part of forest soil may contain over one million propagules (spores, fragments of hyphae and mycelia in the dormant stage), and may branch out for several metres. Fungi biomass in the forest soil may exceed 1.000 g/m^2. Fungi are the most important decomposers of organic matter in forest soils. However, the most important group of fungi in forests are those that form symbiosis at the roots of forest trees. The most widely represented form of symbiosis on forest trees is mycorrhiza, which was identified in 80 to 90% of land plant species, or in over 8.000 plant symbionts (Smith and Read 1997).

Mycorrhizal communities are formed by numerous plants. They ensure a variety of benefits for the plants, including longer root life, increased possibility of nutrient capture, increased soil volume for nutrient capture, nutrient transfer, the formation of favourable conditions for bacteria development, increased resistance to drought, detoxification of harmful substances, impacts on pathogens in the soil and impact on soil aggregation. Mycorrhizal fungi protect the root from an onslaught of harmful fungi by forming a physical barrier in the form of hyphal cloak, producing substances that are harmful for pathogenic fungi or by accumulating nutrients produced by the plants, so that little free nutrients are left for pathogens.

There are seven main groups of mycorrhizal communities. The most important ones for forest ecosystems are ecto-, endo-, and ectendomycorrhizal communities. There are also arbutoid, monotropoid, ericoid and orchid mycorrhizal communities. According to some estimates, over 10 000 fungi species form ectomycorrhiza. The majority of these species are epigeic fungi, whose fruiting bodies are developed aboveground, whereas one fourth of the fungi are of hypogeic type, which develop underground fruiting bodies. The best known hypogeic fungus is the genus *Tuber*, or truffles. Truffles are a widely distributed fungi species that occur from lowland to mountain areas and from Europe, Africa, Asia, and Australia to America. The majority of commercial tree species in Croatia form ectomycorrhiza, which develops predominantly in the upper layers of forest soil at the roots of forest trees. For this reason, it is particularly vulnerable to disturbances in forest soils (Smith and Read 1997).

Mycorrhiza is a symbiotic relationship between fungi and higher plants, which is established on fine plant roots, while fungi hyphae develop in the surrounding soil. The relationship is mutualistic, which means that it is mutually beneficial for both symbionts. Fungi absorb water and mineral substances from the soil (nitrogen, phosphorus, potassium, magnesium and others) and transport them to the plants, while their widely spread hyphal network increases the effective roots of the plants. The plants provide the fungi with carbohydrates needed for their growth and reproduction. Nitrogen sequestration by means of mycorrhizal symbiosis is 3 to 5 times higher than by means of mycorrhiza-free roots. Mycorrhiza is a particularly useful relationship at the root of forest trees, because it ensures tree survival and growth in unfavourable site conditions (Smith and Read 1997). However, recent disturbances in forest sites have considerably changed the conditions for mycorrhizal development, which results in disturbed stability and functioning of forest ecosystems.

Bacteria are also a large group of microorganisms in the soil. There are thousands of species, while in the zone around the root there may be millions of cells per soil gram. Cyanobacteria or blue-green algae are particularly important because they can sequester nitrogen from the air asymbiotically. Of other microorganisms in the soil, metazoa and protozoa are the most numerous. There may be several million of these in the forest soil with up to one thousand species per square metre. The total fauna biomass in the soil may reach 8 g/m^2 of dry matter (Petersen and Luxton 1982).

The development and functioning of forest ecosystems also depends on management methods. The primary goal of forest management is the production of high quantities of valuable wood matter. Silvicultural procedures are a constituent part of forest management. Forest mechanisation used for their application favourably affects the dynamics, rate, cost and intensity of management treatments, but it has an adverse effect on the condition of forest trees, microorganisms in the soil and soil sites, i.e. forest soil, leaf litter and water courses. Since the majority of the biota in the forest soil develops in the surface parts of the soil, mechanisation significantly impacts their development.

The most important unfavourable impact of forest operations involves forest soil compaction. This is one of the priority topics in the study of forest soil protection in Europe, especially in areas where heavy machinery is used for harvesting operations. This has come to particular notice in recent times due to an increasing demand for wood as a renewable source of energy, ever more frequent natural disasters such as windthrow and snowbreak, and use of forest mechanisation throughout the year regardless of the conditions in forest sites (Sutherland 2003). Soil compaction and wheel tracks directly influence the root system of forest trees and indirectly affect soil organisms and properties of forest soil because of limited movement of water and gasses in the soil.

Adverse effects of heavy forest mechanisation on the physical properties in forest ecosystems have been studied for years (Ballard 2000, McNabb et al. 2001, Shestak and Busse 2005, Schack-Kirchner et al. 2007). Wilpert and Schäffer (2006) confirmed an unfavourable effect of soil compaction on the development of seedling roots of European beech and common spruce coming as a consequence of decreased oxygen content in the soil. They found a significant decrease in forest soil porosity during the utilisation of heavy mechanisation in forest management.

There are numerous unfavourable factors and disturbances in forest ecosystems which affect their stability and functioning. This paper analyzes the effect of forest operations on soil microorganisms and mycorrhiza, or in other words, the stability of forest ecosystems and sustainable management.

2 Results

2.1 Ecological disturbances in forest ecosystems caused by the application of forest operations

The functioning of forest ecosystems and the development of forest trees significantly depend on the action of ecological factors. Unfavourable factors that affect the stability of forest ecosystems are becoming increasingly more frequent. One of such unfavourable factors is forest mechanisation which directly affects forest trees, forest soil and soil organisms. It causes disturbances in the physical, chemical and biological properties of forest soils.

The most important direct effect of forest operations on a forest site is the compaction of forest soil. Compaction reduces the porosity of forest soil, which in turn decreases gas exchange and causes lack of oxygen. This is harmful for soil organisms and, indirectly, for forest trees. Soil porosity is important for the life of microorganisms, fauna and plant roots in the soil, as well as for the processes that constantly take place in the soil, such as infiltration, evaporation, decomposition, nutrient transfer into the deeper soil layers, etc. Soil compaction has an effect on reduced water and nutrient uptake, and directly on the growth and development of forest trees.

Fray et al. (2009) found that soil conductivity for water and air was reduced by 10% on severely compacted wheel tracks, whereas no significant reduction in conductivity in relation to normal soil was found in lightly compacted soil. Soil compaction most severely affects soil macropores (pores > 50 µm), which are crucial for water and soil movement in the soil. Frey et al. (2009) found that the presence of macropores was lower by 53% in moderately compacted soil and by 60% in severely compacted soil. According to the same authors, forest soil compaction becomes harmful for microorganism development if soil density increases by more than 15%. In relation to other microorganisms, forest soil compaction most severely affects fungi development, because fungi are the dominant microorganisms in the soils of land ecosystems (about 70 to 80% of the total microorganism mass consists of fungi). Souch et al. (2004) found that the effect of soil compaction with heavy forest machinery is limited to the zone of 0.4 m under the wheel track. In this zone, root development was very slight, although there was so-called root growth compensation in the soil zone not affected by compaction. The shear effect, together with soil compaction, is also detrimental for forest trees and especially for fine roots, where root hairs and mycorrhiza on the root are damaged (Horn et al. 2007).

2.2 Physiological disturbances in forest trees caused by the application of forest operations

The impact of forest soil compaction on forest vegetation is very complex. Reduced increment is considered the most important consequence, although it is difficult to assess the extent of the impacts of different adverse factors on tree growth and development. Lower increment is the consequence of the lack of nutrients in forest soils. The lack of nutrients is the result of reduced porosity, reduced water cycling and insufficient air for microorganisms which participate in nutrient decomposition and transmission. Organisms which influence the nutrient cycle in the soil include bacteria, viruses, non-mycorrhizal and mycorrhizal fungi, as well as soil fauna. Unlike agricultural soils in which the dominant role in the decomposition of organic matter is played by bacteria, in forest soils the dominant role is played by fungi. They form a conglomeration of hyphae that develop in soil pores, where they decompose organic matter and transmit nutrients to the plant by means of hyphal networks. Ascomycete, fungi imperfecti, phycomycete and numerous basidiomycete are the most numerous in forest soils.

The volume of the rhyzosphere impacted by machine-induced soil compaction can be determined on the basis of the relationship between surface area and depth of wheel tracks. According to Souch et al (2004) it was found that root growth was reduced by 42% in severely compacted soil and by 21% in moderately compacted soil in the *Salix viminalis* plantation on gleyic and sandy loam in Ireland. It was also found that after the root system reaches higher depths (up to 2 m), only 10% of the root system is affected by adverse impacts of severe soil compaction. In severely compacted soil, biomass production on sandy loam was lower by 21% only in the first year, but in the second year a decrease in biomass production was not statistically significant. The results of this research coincide with earlier research in the UK, in which normal harvesting procedures did not have a significant effect on the increment of willow plantations.

2.3 Disturbances in mycorrhiza development caused by the application of forest operations

According to Hagerberg and Wallander (2002) the total number and biomass of ectomycorrhizal root tips decreases in the organic horizon in the areas in which forest residue is utilized, whereas the composition of ectomycorrhizal communities is only slightly affected. Management harvesting procedures significantly decrease the depth of the humus layer, as well as the number of ectomycorrhizal root tips per root length and per humus volume, especially when forest residue is utilized multiply. Soil compaction and removal of leaf litter may deplete the presence of ectomycorrhizal fungi and their diversity by 60% (Wiensczyk et al. 2002). In a study dealing with the effect of harvesting procedures on the diversity of ectomycorrhizal communities (Mahmood et al. 1999) a total of 19 different mycorrhyza types were identified in two different sampling periods (autumn and spring). Of these, 11 mycorrhizal types were identified in both samplings, and five setypes of mycorrhizal fungi were present in 63% of mycorrhizal tips (*Cortinarius* sp., *Telephora terestris*, *Lactarius theiogalus*, *Tylospora fibrillosa* and *Tö-96-12*). According to the similarity index, no differences were found in the structure of mycorrhizal communities between the areas of harvesting procedures and control areas.

There are three factors that affect mycorrhiza in disturbed sites: the relationship between mortality and renewed appearance of propagiles, the presence of symbiotic plants and the diversity of fungi species. It was found that propagiles may retain their metabolism up to 2 years after a disturbance, e.g. tree felling, has taken place. Research into the impact of tree felling on the development of fruiting bodies of symbiotic fungi in Canada (Anonymous 1997) found that the number of species significantly decreases with an increase in forest gaps. Of 80 species of mycorrhizal fungi which fructified in the forest before felling, the number dropped to only several species, which fructified in the gaps larger than 600 m^2 (20 x 30 m). It was also found that mycorrhizal communities in forest gaps were better represented than the very fruiting bodies of certain fungi species. The reason for this is the warmer and drier site that occurs in forest gaps which is not favourable for the development of fruiting bodies.

Disturbances in forests resulting from silvicultural operations in forests, site preparation for regeneration, harvesting procedures, selection of tree species and the use of pesticides have an adverse effect on mycorrhiza, or on the occurrence, productivity and reproduction of mycorrhizal fungi (DeYoe and Cromack 1983). In young regenerated stands, a higher diversity of fruiting bodies of mycorrhizal fungi occurs around the age of 10, whereas the highest diversity of fruiting bodies occurs only at stand age of 30 to 40.

2.4 The effect of forest ecosystem management on mycorrhizal development

Short-term impacts of clearcutting on forest soil biota may be unfavourable, neutral and positive. The biggest unfavourable impact of clearcutting is exerted on mycorrhizal fungi and mites in the soil, whereas the impact is positive on molluscs (earthworms) and collembola in the soil. Mohmood et al. (1999) found that the removal of organic matter from the forest and a thinner humus layer have a negative effect on the number of mycorrhizal roots, but do not have any significant impact on the number of mycorrhizal species. The removal of residue from forests may influence the development, structure and dynamics of the communities and the functioning of ectomycorrhiza.

The most important disturbances in the soil as a consequence of forest management include soil erosion, nutrient removal, soil compaction, and changed (depleted) organic matter content and water content in the soil. Worrell and Hampson (1997) analyzed the effects of forest procedures on sustainable management of forest soils. From a long-term aspect, adequate management procedures do not have an unfavourable effect on natural soil development. Soil erosion is not higher than the degree of new soil development; in other words, nutrient removal is not higher than the input of new nutrients into the soil. The impact of intensive forest management procedures on soil compaction, nutrient removal and the degree of soil erosion is of similar intensity as the regenerative capacity of soil. In sensitive sites subjected to intensive silvicultural treatments, there is a certain degree of long-term degradation of forest soil. Such silvicultural treatments are considered unacceptable, although their intensity is gradually decreasing. In less sensitive sites subjected to less intense silvicultural treatments, the effects on forest soil are low and management procedures are considered acceptable.

The biggest disturbances in forest ecosystems caused by operations include soil compaction by heavy mechanisation and tree-digging machinery, nutrient depletion as a consequence of utilization of whole trees with short rotations in infertile sites, and soil erosion as a consequence of cultivation and utilization in erodible soils.

3 Discussion

3.1 Ecological and physiological aspects of the application of forest operations

The removal of organic matter from forests through harvesting procedures or leaf litter erosion may reduce long-term site productivity due to diminished availability of organic components and disturbed nutrient cycling. This in turn may influence nutrient uptake and tree growth. According to Mahmood et al. (1999), increased and intensive utilisation of forest residue as biofuel may influence the availability of base cations, phosphorus and nitrogen. According to some research in Sweden (Nykvist and Rosen 1985, Bengtsson et al. 1998), clearcutting and slash removal results in depleted base cations and soil acidification as well as long-term impacts on soil arthropods. A thinner humus layer is more vulnerable to changes in air temperature and drought than a thicker humus layer. Fine roots are sensitive to changes in soil temperature and soil moisture (Persson et al. 1995). Many mycorrhizal fungi are also sensitive to such site changes (Soulas et al. 1997, Nilsen et al. 1998). Baar and De-Vries (1995) studied the influence of humus layer removal and humus layer increase in Scots pine forests exposed to nitrogen and sulphur contamination. They found a negative relationship between the thickness of humus layer and number of ectomycorrhizal species developed on tree roots. This was explained with a high degree of nitrogen contamination and competition of herbaceous plants such as *Deschampsia flexuosa*.

According to Lindner (1998), numerous studies confirmed that the predicted climatic changes will significantly affect forest growth and forest composition. This will also have an effect on forest management. In ecologically sensitive site conditions, such as the absence of snow on the soil, high winter temperatures, high soil moisture in the spring and poor soil capacity, management procedures should be adjusted to the existing site conditions so that adverse effects on forest trees and the entire ecosystem are reduced.

An unfavourable effect on mycorrhiza reflects unfavourably on plant condition. This effect is reciprocal to the degree of soil damage, but also relates to the lessened possibility of mycorrhiza development. The factors that contribute to the above include oxygen reduction in the soil resulting from soil compaction by heavy machinery, changes in the degree of soil moisture resulting from soil amelioration, retention of water on compacted soil, chemical changes in the soil due to soil pollution and the growth of plants that excrete inhibitory substances into the soil through the roots, thus preventing the development of mycorrhiza.

Due to the continuous removal of organic matter from the forests, ectomycorrhizal roots may be of crucial importance for tree growth, especially when base cations are missing. In addition, the possibility of spatial distribution of mycorrhiza in the mineral soil layers and not only in the organic soil layer should also be taken into account.

3.2 Economic and organisational aspects of the application of forest operations

Silvicultural procedures that damage forest soil, such as hauling and transport, have a negative effect on tree growth in the stands and mycorrhiza development. It can be assumed that the effect of mechanisation on mycorrhiza development is several times lower than the effect of tree felling, since tree felling significantly decreases the volume of available roots for the development of symbiosis. Long-term consequences of mycorrhiza disturbance in forest ecosystems are hard to assess, but can be identified through stand productivity, their stability and resistance.

The new approach to forest ecosystem management is concerned with the establishment of biological and ecological balance in forest ecosystems aimed at producing large amounts of high quality wood mass and obtaining other benefits that forest ecosystems can offer. Eco-efficiency of forest mechanisation during the application of silvicultural treatments relates to the reduction of unfavourable effects on the sites and trees, but also on the entire forest ecosystem.

Despite carefully planned silvicultural treatments, in cases when weather conditions are unfavourable for the application of the treatments, and in cases of moist and low-capacity soils such as those in lowland forest ecosystems of pedunculate oak and narrow-leaved ash, there may be significant disturbances in forest soils, including soil compaction, wheel tracks and the formation of muddy soils. To address the consequences of soil compaction by mechanisation, changes in the soil's physical features and reduced intensity of the development of forest tree roots, German forestry passed rules for the protection of forest soils. According to these rules, movement of mechanisation in forests is limited, and the system of extraction and transport from forests is regulated. Extraction paths are limited to a distance of 20 to 40 m. Between these more or less parallel lines, heavy mechanisation is not allowed. These recommendations are based on the insights into the long-term duration of forest soil damage caused by mechanisation-induced soil compaction (Pretzsch et al. 2008).

3.3 Damage and degradation of forest soil caused by forest operations

Degradation of forest soils involves changes in natural soil properties, i.e. physical, chemical and biological properties, as well as diminished soil functions. A depleted humus layer and the presence of ectomycorrhizal tips may be the consequence of changes in the physical and chemical soil properties. A lower presence of fine roots needed for mycorrhiza development is the result of lower plant vitality (Neruda 2008). The application of forest operations not only directly damage forest soils but also cause other direct and indirect damage, such as site water logging and soil and leaf litter erosion (Nugent et al. 2003).

According to some research forest soil compacted by machinery recovers after 25 years, and according to Wilpert and Schäffer (2006), recovery takes place after several decades (30 and more years). Some authors, however, maintain that disturbed soil only recovers after 100 years. This process is dependent on changes in the aggregate state of soil water (water freezing and melting), and on the biological activity of roots and organisms in the soil (Ampoorter et al. 2010).

3.4 Disturbed tree and mycorrhiza development as a consequence of forest operations

Apart from damage to forest soil, mechanisation in forests also physically damages aboveground and underground parts of forest trees and other forest vegetation, diminishes the value and volume of wood mass of forest trees and increases their vulnerability to pests and diseases. Disturbances in forests affect the condition of forests. The current condition of forests has been significantly disturbed in certain areas. This is best indicated by decreased increment, yield and growing stock, intensive tree dieback and diminished tree vitality, the occurrence of endangered tree species, and the impossibility of natural forest regeneration. All this has a negative effect on mycorrhiza.

In cases of intensive damage of forest soil, when a large part of the soil is damaged by wheel tracks, logs hauled along the ground or soil compaction, the effect of mechanisation on the development of mycorrhiza can be considerable. It can be evaluated on the basis of the share of damaged or disturbed soil in the total volume of forest soil where mycorrhiza development is the most intensive (up to 60 cm in depth). In order to assess the intensity of mycorrhiza disturbance in forest soils, both directly damaged root volume or forest soil and indirect consequences of mechanisation on the diminished intensity of root development in undisturbed forest soil should be taken into account. The relationship between forest soil damage or tree root damage and mycorrhiza disturbances is not proportional: the degree of mycorrhiza damage is always higher.

3.5 Operative plans and forest ecosystem management

Eco-efficient and sustainable management with forest ecosystems presupposes the reduction of adverse effects of silvicultural operations on the biological diversity of forest soils, soil compaction, leaf litter and soil erosion, soil organic matter, plant diversity and forest microclimate. Guidelines for the protection of forest soils should be established for logging procedures. In addition, silvicultural treatments should be adjusted to different site conditions. Management plans of some USA states set down that 80% of the commercial forest area should have an acceptable soil condition and should not be subject to site disturbances (Grigal 2000).

Eco-efficiency of forest mechanisation in forest management should be viewed in relation to forest soil (damage, compaction), forest site (disturbance, change, excess phenomena – erosion), forest biocoenoses (forest trees, other vegetation, wildlife, microorganisms – mycorrhiza) and other benefits provided by a forest ecosystem (non-market forest functions). Efficient application of silvicultural treatments should take into account the relationship between forest mechanisation towards all the components of a forest ecosystem, which should be ecologically and economically sustainable. The cost of silvicultural operations and damage incurred by these operations in forest ecosystems should not exceed the benefits of harvesting.

Forest ecosystems currently offer multiple functions. This has led to the establishment of multi-functional forestry, which comprises all commercial forest products, but also numerous other forest services. This is the basis of the concept of forest ecosystem management. Management is based on the holistic (integral) approach to making decisions on forest ecosystem management, which connects biological, ecological, silvicultural and socio-economic patterns and principles with the goal of ensuring sustainable production of forest products and forest benefits. This means that the production of wood mass is not the only goal of forest management, but that there are other management goals as well, such as the provision of high quantities of so-called non-wood values, and other forest products.

The relationships among organisms in forest ecosystems are very complex. In order to manage forests in a sustainable manner, it is important to know the relationships among different organism species that are important for the development of forest trees. Ignorance of these relationships does not mean that they do not exist and that they do not have a certain role in the functioning and stability of forest ecosystems. The majority of the studies dealing with impacts of forest operations on forest ecosystems relates to the degree of changes in forest soils, while fewer studies deal with reduced intensity of forest tree growth and development. This issue requires further research in the future.

4 Conclusions

Forest mechanisation has an unfavourable effect on the condition of forest trees and forest soil. It indirectly influences the condition of the sites and other organisms in forest ecosystems. The most important ecological disturbance caused by the application of forest operations is the compaction of forest soil, whereas the most important physiological disturbance affects nutrient cycling. In ecologically sensitive site conditions, management procedures and the application of mechanisation should be adjusted to site conditions. The purpose is to prevent the degradation of forest soils and inhibit unfavourable effects on forest trees and the entire ecosystem. Regeneration of degraded forest soil is a long-lasting process. For this reason, management plans should prescribe protective measures for forest soil that entail the use of mechanisation. The adverse impacts of forest operations can be managed, unlike numerous other unfavourable factors that cannot be managed.

Mycorrhiza is a natural symbiotic relationship at the roots of the majority of woody forest tree species. It has an important role in the development, survival and all life functions of forest trees. Mycorrhiza predominantly develops in the upper layers of forest soils, where the largest part of fine roots of forest tree is developed; consequently, it is exceptionally sensitive to the use of mechanisation. For this reason, silvicultural procedures should be applied in such a way as to preserve a minimum of 80% of forest soil in natural condition so that the stability of forest ecosystems is sustained.

Optimal management with forest ecosystems requires that all adverse impacts on forest ecosystems are minimized, including the unfavourable effect of forest operations. Eco-efficiency of forest mechanisation should be viewed in relation to forest biocoenoses, forest sites and other benefits offered by forest ecosystems.

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