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Quarter of a century of forest fertilization and liming research at the Department of Silviculture in Prague, Czech Republic

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Abstract

Fertilization and liming began to be used in forestry at the beginning of the 20th century in order to increase growth, for improvement of health status or higher resistance to biotic and abiotic factors. The review summarizes results of 48 studies of forest fertilization, nutrition and liming published in scientific journals by authors of Department of Silviculture in Prague over the past more than 20 years. They deal mainly with monitoring of the effect of fertilization and liming applied during planting or shortly after planting of 18 tree species. Moreover, the results of fertilization in older stands are presented. Separate chapters deal with enhancing substrates (soil conditioners and phytohormones). All forest vegetation ranges are covered, from lowland forests to the subalpine belt of grass vegetation in 11 Natural Forest Areas. Forest fertilizing and liming proved beneficial according to most of the studies. The use of fertilizers can be detected in soils after decades. On the other hand, only in a minority of cases was fertilization reflected in the chemistry of the assimilation apparatus and other parts of the trees for a longer period. The main positive effect of fertilization and liming was increase of tree growth and foliation and decrease of mortality and yellowing symptoms. Inconsistent results were documented in some cases, especially for brassinosteroids and alginite compared to good results in slow release fertilizer done by spot-application. The type of product, concentration, time and method of application play an important role in the appropriate use of fertilization and liming.

Key words: afforestation; chemical amelioration; nutrition; tree resistance; growth increase

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1. Introduction

Forests respond slowly to management activities and the possibilities to increase the growth in a short-term perspective and meet swift increases in society demand for timber are small (Hedwall et al. 2014). At the same time, increased demands for timber and forest products can be expected as a result of current policies and climate change mitigations (Marland & Obersteiner 2008; Daioglou et al. 2019; Vacek et al. 2021). At present, climate change due to long-term periods of drought, frequent climatic extremes and secondary bark beetle outbreaks causes unprecedented forest decline, increasing the salvage logging and negatively affecting production sustainability (Dobor et al. 2020; Šimůnek et al. 2020; Toth et al. 2020). Moreover, second problem are the enormously high game population and damage (browsing, bark striping, subsequent rot) on forests in the Czech Republic (Čermák et al. 2004; Cukor et al. 2019; Prokůpková et al. 2020; Vacek et al. 2020a). On the other hand, in terms of policy instruments, increased afforestation, biomass production and the associated carbon sequestration play an important role in climate change adaptation strategies (Cukor et al. 2017b; Law et al. 2018; Podrázský et al. 2020; Smith et al. 2020). All this can be positively affected by fertilization and liming of forest stands.

Fertilizers can be one of the ways to speed up plant growth, increase production efficiency and improve health status of forest stands (Saarsalmi & Mälkönen 2001; Remeš et al. 2005; Fox et al. 2007). Over the last years, interest in fertilizing of forests is increasing, however forestry is still a minor user of fertilizers compared to agriculture (Smethurst 2010; Lindkvist et al. 2011). However, there may be both economic and environmental constraints on the large-scale application of fertilizers in forests (Hedwall et al. 2014). Fertilizers may not only increase the tree growth, economic profitable and climate change mitigation in relation to carbon store (Albaugh et al. 2019; Petaja et al. 2018). Enriched soils can also have a significant effect on wood quality (Mäkinen et al 2002; Cukor et al. 2020), ground vegetation (Hejcman et al. 2007; Strengbom & Nordin 2008), seed production

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(Williams et al. 2003), mycorrhiza community (Baum & Makeschin 2000; Klavina et al. 2016) and what is particularly important – on the health status of forest stands (Podrázský et al. 2005; Vacek et al. 2019b).

During the second half of the 20th century, Central Europe was strongly affected by air pollution, especially by high concentrations of SO_2 and acid deposition (Małek et al. 2012; Král et al. 2015; Králíček et al. 2017; Putalová et al. 2019; Vacek et al. 2020c). In addition to the air pollution damage to forest stands, the so-called "New type of forest decline" began to appear in Europe in the 1970s, which manifested itself primarily in the yellowing of the assimilation apparatus, especially in Norway spruce (*Picea abies* [L.] Karst) (Vejre 1999; Van der Perre et al. 2012). As a result, extensive experiments have been established with liming and fertilization of forest ecosystems and their impact on health status (Lomský et al. 2012; Vacek et al. 2019b). In recent years, instead of SO_2 – O_3 and NO_X air pollutions have significantly affected forest stands (Vacek et al. 2017; Giovannelli et al. 2019; Mikulenka et al. 2020).

Through decades, it has been shown that fertilization as well as liming can be beneficial especially at early stages of stand development (overcoming transplant shock) (Berger & Glatzel 2001; Kuneš et al. 2011). Fertilizing, and especially liming should be regarded as immediate help to improve the vitality of forest stands in a short period of time (Podrázský et al. 2005). Long-term cultivation is a question of appropriate silvicultural treatments, tree species composition, spatial and age structure (Remeš et al. 2015b; Švec et al. 2015; Štefančík et al. 2018; Sharma et al. 2019; Vacek et al. 2019a, 2019c). Reaching stability of forests is important under the conditions of ongoing climate change and large-scale forest disturbances (Kolář et al. 2017; Gallo et al. 2020; Vacek et al. 2020b, 2021). Healthy forests are also a reservoir of natural resources in the age of different economic problems of societies (Trumbore et al. 2015; Gallo et al. 2018).

The review article summarizes results of the 48 research articles of fertilization, liming and nutrition in forest ecosystems published by authors at the Department of Silviculture of Faculty of Forestry and Wood Sciences in Prague in scientific journals over the past more than 20 years (Table 1). Forest fertilizing and liming are considered two more or less controversial and intensive interventions into forests (Podrázský 2006a; Ferreira et al. 2020). These activities are costly and therefore their effects need to be studied and evaluated in order to make qualified decision in critical situations (Podrázský 2006b). This review shows most important studies in terms of fertilizing and liming, just as it presents some alternatives of intensive care of emerging forest cultures and mature forest stands. The study area covers all forest vegetation ranges from lowland forests to the subalpine belt of grass vegetation including 11 Natural Forest Areas (Fig. 1). The review consists of 18 tree species, with the greatest emphasis on Norway spruce. The objective of this review was to summarize the main results of the studied research and to make recommendations and limits for forestry practices.

2. Fertilizing in maturing stands and underplantings

The extensive symptoms of Norway spruce yellowing were recorded in the late 1970s in the Šumava National Park (Kovářová & Vacek 2003; Podrázský et al. 2003b), so the effect of slow release fertilizer was investigated in the maturing and mature forest stands (44–107 yrs). The aim of fertilization was to alleviate the symptoms of needle yellowing, which was probably caused by the deficiency of Mg in the naturally acidic and further acidified soils. Fertilizer named Silvamix Mg NPK was manually placed on the soil surface at a dose corresponding to the following hectare amount of pure nutrients: 100 kg N, 96.5 kg Mg, 54 kg K, 57 kg P. After application, fertilization significantly increased the magnesium content (by more than 30%) and base saturation in soils and decreased the amount of exchangeable aluminum and hydrolytic acidity. In the short term (after two years), the effect of fertilizer application on tree defoliation and yellowing symptoms was significantly positive, especially in case of weakened and supressed trees. Fertilization further promoted the growth of trees which persists even in the second decade after application, while positive effects lasted for a shorter time than the effect on foliage (Podrázský et al. 2002, 2003b, 2005; Vacek et al. 2006, 2009). During 15 years after fertilization, defoliation and yellowing decrease by 5% and 10 % and radial growth increase by 15% (Vacek et al. 2019b).

Two experiments in the territory of the School Forest Enterprise in Kostelec nad Černými lesy (localities Aldašín and Krymlov) were based on analogous methods consisting of application of full (complex) fertilization and nitrogen fertilization in Norway spruce stands at the age of 70 yrs, based on the application of a complex fertilizer and nitrogen fertilizer. The applied hectare dose in the variant complex fertilizer (with balanced content of N, P, K, Ca) was as follows: 150–200 kg of pure N, 50–100 kg P, 100 kg K, 100–400 kg Ca. The hectare dose used in the nitrogen fertilizer variant was 180–200 kg N in the form of ammonium nitrate. A positive response of complex fertilization to soil chemistry was registered even after 40 years after application, but unbalanced N–fertilization resulted in increased leaching of ions from the soil (Mg, Ca), thus contributing to acidification of the site. The volume production of the entire stand increased only slightly, more distinct differences can be seen on the individual tree level (Remeš & Podrázský 2006; Podrázský 2006b; Remeš & Podrázský 2009).

In the Babín locality (Žďárské vrchy), Norway spruce and Scots pine (*Pinus sylvestris* L.) dominated stand with individual admixture of white fir was underplanted using giant fir (*Abies grandis* [Douglas ex D. Don] Loudon)

Table 1. Selection of the research articles of fertilization, liming and nutrition in forest ecosystems published by authors at the Department of Silviculture of Faculty of Forestry and Wood Sciences in Prague, study objectives (SP – soil parameters, HS – health status including foliation and mortality, GR – growth rate, FN – foliar nutrients) and effect (positive, negative, both, no effect) on different species (see Notes).

Reference	Locality	Species	Objective	Effect
Baláš et al. 2010	Forest nursery Louňovice	CB	GR	Both
	Forest nursery Čikov			
Nováková et al. 2015	Forest nursery Tišice	NS, SP, EB	HS, GR	Both
	Forest nursery Klášterec n. O.			
Nováková et al. 2014				
Kuneš et al. 2016	Truba Research Station	DF, NS, SP, EO	HS	Both
Gallo et al. 2017		EB	HS, GR	Both
Hanzal et al. 2015				Positive
Lorenc et al. 2016	Forest nursery Obrovice (Doupov)	NS	SP	Negative
Kupka et al. 2015			HS, GR	Both
		EO, RO, NM, SP		Positive
Cukor et al. 2017a	Polabí (Hovorčovice) – "U Lomu"	DF, SP, EO, RO, NM		Both
Tužinský et al. 2015		NM, RO, EO, DF, SP	HS, GR, FN	Positive
Cukor et al. 2017b	Polabí (Hovorčovice) – "U Hnojiště"	SP, EO, RO, NM		Both
Remeš et al. 2015a				
Remeš et al. 2016	Doksy	SP	HS, GR	Positive
Bílek et al. 2016				
Petrovský et al. 2018				
Remeš & Podrázský 2006	ŠLP Kostelec (Aldašín)	NS	HS, GR, SP	Both
Remeš & Podrázský 2009	ŠLP Kostelec (Krymlov)			
Podrázský & Remeš 2007	Babín (Žďárské vrchy)	NS, SP	GR	Positive
Podrázský & Remeš 2008				
Hejcman et al. 2007	Krkonoše	DP	GR	Positive
Semelová et al. 2008				
Podrázský, Balcar 1996		NS	HS, GR, FN	Positive
Balcar et al. 2009		WE	GR	Positive
Balcar et al. 2011		SM, EB	SP, FN	Positive
Jakl et al. 2015		GA	SP	Negative
Koňasová et al. 2012			HS, GR, FN	
Kuneš et al. 2004		NS	HS, FN	Positive
Kuneš et al. 2007a			HS, GR, FN	
Kuneš et al. 2007b		CB	SP, GR, FN	Both
Kuneš et al. 2007c	Jizerské hory Mts.	NS	SP	
Kuneš et al. 2009		GA	GR	Positive
Kuneš et al. 2011		GRA	HS, GR, FN	
Kuneš et al. 2013a		NS	HS, GR, SP	Both
Kuneš et al. 2013b				
Kuneš et al. 2014a		GA	SP	Positive
Kuneš et al. 2014b		CB, R	HS, GR, FN	
Špulák et al. 2011		EB	SP, GR, FN	Positive
Špulák et al. 2014		CB	HS, GR, FN	Both
Podrázský 2003a	Boleboř (Krušné hory Mts.)	BS, EWP, LP, NS	HS, GR	Both
Remeš et al. 2005		NS		
Podrázský 2006a	Velká Deštná (Orlické hory Mts.)	GA, EL	HS, GR	Both
Kovářová & Vacek 2003				
Podrázský et al. 2002				
Podrázský et al. 2003b				
Podrázský et al. 2005	Šumava	NS	HS, GR, FN, SP	Positive
Vacek et al. 2006				
Vacek et al. 2009				
Vacek et al. 2019b				

Species: BS – blue spruce (*Picea pungens* Engelm.), CB – Carpathian birch (*Betula carpatica* W. et K.), DF – Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco), DP – dwarf-pine (*Pinus mugo* Turra), EB – European beech (*Fagus sylvatica* L.), EL – European larch (*Larix decidua* Mill.), EO – English oak (*Quercus robur* L.), EWP – Eastern white pine (*Pinus strobus* L.), GRA – green alder (*Alnus alnobetula* [Ehrh.] C. Koch), GA – grey alder (*Alnus incana* Moench.), LP – lodgepole pine (*Pinus contorta* Dougl.), NM – Norway maple (*Acer platanoides* L.), NS – Norway spruce (*Picea abies* [L.] Karst.), R – rowan (*Sorbus aucuparia* L.), RO – red oak (*Quercus rubra* L.), SM – sycamore maple (*Acer pseudoplatanus* L.), SP – Scots pine (*Pinus sylvestris* L.), WE – wych elm (*Ulmus glabra* Huds.).

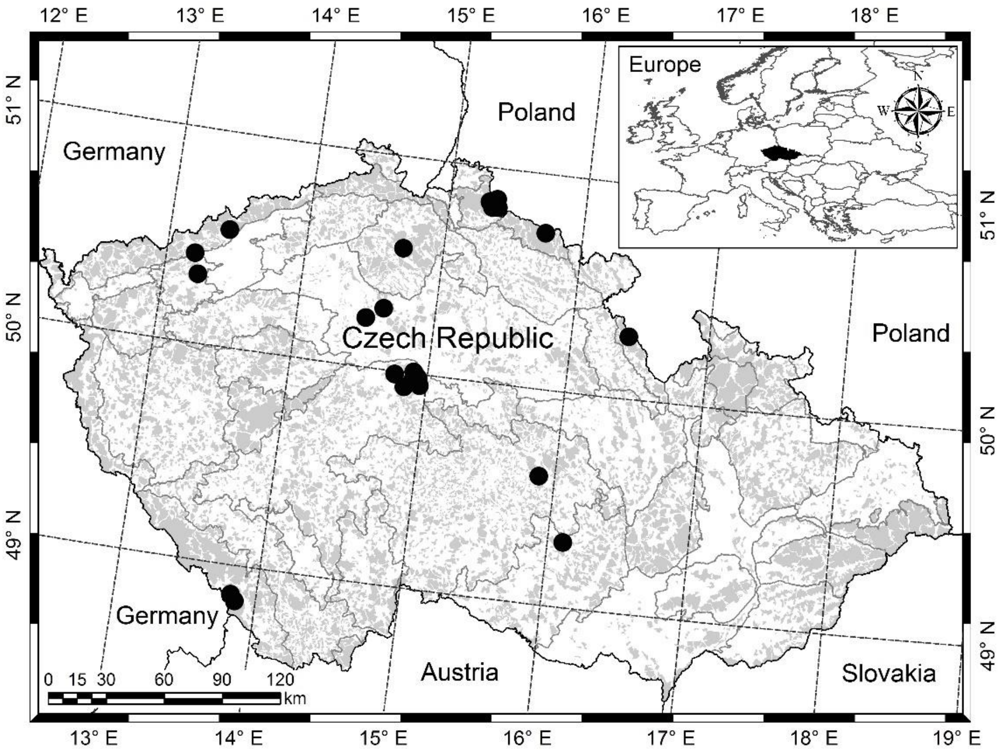

Fig. 1. Location of 24 study areas engaged in fertilization and liming research (black dots); gray lines showing separating Natural Forest Areas and gray dots forest cover in the Czech Republic.

(habitat 5K8, 580 m asl, soil type Dystric Cambisol). The underplantings were gradually released. In order to support the fir transplants, the application of Silvamix Forte fertilizer in the forms of tablets and powder was performed 6 years after outplanting, namely by fertilizers under the trade name Silvamix Forte (4 tablets of 10 g per transplant) and Silvamix MG fertilizers (40 g of powdered fertilizer per transplant). Markedly positive effect of fertilization on the height increment of giant fir transplants was observed already in the first year after application, with highest effect occurring 5 years after application. The effect of the tablet form was slightly higher, probably because of the higher nitrogen content. The application of fertilizer thus demonstrably increased the height increment of the underplanted transplants, which accelerated the growth of the trees under the influence of roe deer. After about 7 years, the effects of fertilization, manifested by increased growth, gradually disappeared, but the difference in the average height of transplants remains more than 1 m in favor of fertilized variants. The experiment confirmed that in the conditions of nutrient poor habitat, the application of slow release fertilizer can effectively support the growth performance of nutrient-demanding tree species (Podrázský & Remeš 2007, 2008).

The effect of different uses of individual parts of tree biomass remaining after harvesting (chipping, burning, piling up vs. export of biomass out of habitat) on the nutrient cycle as well as on the growth of the next generation of Scots pine forest in Doksy were investigated. The most favourable growth performance was registered for transplants on the plots with the harvest residues crushed and dispersed. Treatments with the removal or burning of the residues were comparable (Remeš et al. 2015a, 2016). Growth of pine transplants was positively influenced by additional woody ash, with the greatest effect on poor habitats. The magnetic mapping method revealed that the dispersed ash remains on the surface and does not penetrate to deeper layers (Petrovský et al. 2018).

In order to understand the distribution of mineral nutrients in the individual parts of pines in rotation age, sample trees were analysed. The highest nutrient concentration was in needles, bark and wood branches. The lowest concentration was in trunk, but with a high weight (approx. 5 times) it exceeds the sum of the weight of all the other fractions. Therefore, it is desirable to limit the removal of debris on poor habitats to reduce soil depletion of mineral nutrients (Bílek et al. 2016).

3. Use of fertilizers on afforestations of the clear-cuts caused by air-pollution

The research facility was located in Boleboř (Ore Mts. – Krušné hory) on a large clear-cut caused by air-pollution calamity in the 1980s. Before the reforestation, bulldozer soil preparation was performed. Different treatments of amelioration (2-phase full-area fertilizing) measures were implemented on individual sub-areas in combination with the planting of fallowing tree species: blue spruce (*Picea pungens* Engelm.), European larch (*Larix* *decidua* Mill.), lodgepole pine (*Pinus contorta* Dougl.), Eastern white pine (*Pinus strobus* L.), grey alder (*Alnus incana* Moench.) and European beech (*Fagus sylvatica* L.). The results show that chemical amelioration is registrable in soil chemistry even after 20 years by increased pH, bases content, macroelements and saturation of the soil complex. The tree species composition has even greater influence on soil chemistry than amelioration measures (alder – influence was very positive vs. spruce and larch – negative), (Podrázský et al. 2003a).

Another Norway spruce plantation at the same locality was studied. This site was affected by spreading of windrows created by a previous bulldozer site preparation done before afforestation after the air-pollution forest decline. Three treatments of fertilization were performed: the complex fast-release fertilizer Cererit and the slow-release Silvamix fertilizer in powder and tablet form. The impact of Silvamix fertilization was evident in a very short time. It was manifested by a reduction in mortality (more than 2.3× lower in comparison to control) and a significant increase in plant growth. Silvamix fertilization also almost eliminated mortality and colour changes on leaves. On the contrary, the application of Cererit led to an unbalanced nutrition status (foliage discoloration), and a lower increment. Also particularly increased mortality was noted for the Cererit-fertilized treatment (2.5× in comparison to control). Besides, a significant reduction in the nitrogen foliage content of the Cererit fertilized treatment, no consistent and significant changes of foliar chemistry were recorded (Remeš et al. 2005).

Experimental liming was done in the plantation of Norway spruce on mountain sites devastated by air pollution on the locality Velká Deštná (1,100 m asl, habitat 8Z2, soil type Histic Podzol), situated in the ridge part of Eagle Mts. (Orlické hory) (Podrázský 2006a). The area was established in 1988 in the then 4-year planting of Norway spruce. On partial plots (10 × 10 m) a manual surface application of limestone crumb was performed in 4 variants [0; 1,308; 2,826; 3,924 and 8,478 kg of fine grains (< 1 mm) per ha], combining coarsely and finely ground crumb and dose size 3 and 9 t ha^{-1}. The aim of the experiment was to monitor for a long time the effect of different intensities of liming and coarseness of the crumb on soil chemistry and the growth of spruce cultures in the exposed mountain habitat. Some parameters of soil chemistry were positively adjusted (increase of pH, base content and cation exchange capacity). The greatest effect was observed in the case of surface humus horizons about 10 years after application, in the case of deeper horizons (H, A) about 15 years after application. A positive effect on the growth of spruce plantings was recorded at lower doses of liming. The best growing variant (high dose, coarse crumb) had an average height of 178 cm 10 years after application, compared to the control with a height of 146 cm. However, growth depression was recorded on the strongest calcareous variant (high dose, fine pulp) – the average height was only 127 cm. Liming has adversely affected the acceleration of humus mineralization, which is associated with an increased risk of nutrient loss. During the observed period, there was a significant improvement in most soil characteristics in all variants. This was probably the result of a combination of favourable effects (reduction of emissions and coverage of the soil with grass turf with a more favourable fall), which demonstrates the considerable regenerative capacity of the soil (Podrázský 2006a).

Many of particular experiments focused on afforestation in harsh mountain condition were done around the Jizerka locality (Jizera Mts. – Jizerské hory), (Balcar & Podrázský 1994). Norway spruce plantation (Děčín town environs originated) was treated by dolomitic limestone on the surface and into the holes during planting. A positive effect on soil chemistry, growth and nutrient content in needles has been demonstrated. However, adverse effects on the nitrogen and phosphorus content of the soil were recorded (Podrázský & Balcar 1996).

The analysis of sample trees was done in the same plantation. The limestone fertilizing boosted the growth of both aboveground and belowground biomass, while not limiting the growth of roots from the fertilized planting hole to the surrounding soil. The concentration of nutrient elements in biomass did not differ between the limed and control variant. Total amount of nutrient elements due to higher biomass volume was higher in the limed treatment. The distribution of elements in biomass followed the standard model – most in the needles, then bark and small branches, least in trunk wood (Kuneš et al. 2007a).

Subsequently, in the part of the plantation treated by spot-fertilization of limestone, the soil chemistry was evaluated in the fertilized hole and at a distance of 40 cm and 80 cm from the hole. Apparent evidence of soil chemistry change in the soil of the planting hole was observed, but only a minimal effect at a distance of 80 cm compared to control, taken outside the fertilized planting. Spot-fertilization is considered laborious, but sensitive method of fertilization, where almost no surrounding environment is affected, serving only to fertilize the target tree (Kuneš et al. 2006). In case of the surface liming treatment, the effect on soil chemistry was also studied. It was found to be positive but considering the large dose, it was a slight influence on soil chemistry. The limestone treatment contained less organic matter and nitrogen (Kuneš et al. 2007c).

Neighbouring Norway spruce plantation of the Giant Mts. (Krkonoše) origin was treated with crushed amphibolite and limestone placed in planting holes. After 15 years, the positive effect of fertilization on mortality and growth was found. The effect on foliage nutrient content was negligible. The control option had more nitrogen concentration, probably due to the support of microbial activity in the soil, leading to higher consumption of nitrogen (Koňasová et al. 2012).

Norway spruce plantation of the Beskydy Mts. origin, fertilization of the amphibolite (surface) and Silvamix (tablets into the soil) was done during the outplanting. After 10 years, reduced mortality and higher content of most nutrients in needles was proved for fertilized treatments (Kuneš et al. 2004).

The evaluation of the same plantation 14 years after the planting showed significantly more biomass amount in the fertilized treatments. The absolute amount of nutrients bound to fertilized trees was therefore higher due to higher biomass, but the effect of both fertilization treatments on the nutrient concentration in the above-ground parts of the trees was insignificant. However, lower P and N concentrations were recorded in root biomass in fertilized treatments. The highest nutrients content was detected in the needles and bark, small branches. The lowest content has a trunk wood. Significant individual differences were found in both biomass and nutrient concentration (Kuneš et al. 2013b). In other study from the same planting, the growth was significantly higher for the Silvamix-fertilized treatment. In the amphibolite-fertilized treatment, the positive effect on growth was apparent but not conclusive. Unlike Silvamix, the decrease in mortality was seen in the amphibolite variant. Repeated foliage analyses have shown a gradual decrease in concentration of phosphorus, which is considered a potentially deficient element (Kuneš et al. 2013a).

Using DGT (diffusive gradient in thin film) units, heavy metals content in the soil were analysed for amphibolite treatments. There was a slight increase in the concentrations of some heavy metals in the soil in the fertilized treatment, the increase in the concentration of Al being more pronounced (Jakl et al. 2015).

The planting of grey alder established in 2000 was after 2 years fertilized with a mixture of crushed limestone and basalt with surface application. It was evaluated as 8-year old plantation, with a positive height increment reaction to fertilization. The effect on nutrient content in leaves was insignificant (Kuneš et al. 2009).

Nearby planting of grey alder established in 2003 was fertilized with a mixture of crushed amphibolite and limestone with spot and surface application. There was a significant impact on biomass growth and accumulation in both treatments (minimal differences between the fertilized treatments). The nutrient concentrations in different parts of trees were more or less the same between treatments (except for Mg, in particular). A slight change in the proportion of element content in different parts of trees was registered. In fertilized treatments, the biomass growth within stems was relatively higher than in leaves. Pioneer species often respond better than climax species. It is therefore beneficial to support pioneer species, which then efficiently transform fertilizer into a litterfall (Kuneš et al. 2014a).

In 2-year old plantation of green alder (*Alnus alnobetula* [Ehrh.] C. Koch), a surface application of a mixture of crushed limestone and basalt was performed. From the beginning, fertilization has a significant positive effect on growth. Later, fertilized treatment equalized with the control one. The positive effect of fertilization on mortality and a slight increase in Ca and Mg in leaves was noted. In the case of P and N, the influence was not detected (Kuneš et al. 2011).

For plantings of European beech and sycamore (*Acer pseudoplatanus* L.), when placing the crushed limestone into planting holes, the beneficial effect of liming on soil chemistry was still proven 15 years after planting. The influence on nutrient content in leaves was recorded only in Ca, otherwise without evidence (Balcar et al. 2011). The same beech plantation was treated with crushed limestone during the planting. The evaluation was carried out in a 17-year-old stand. Apparent positive effect of fertilization on nutrient content in soil has been documented. However, the nutrient content of the leaves did not differ. The fertilized trees also showed an improvement of some measured parameters of chlorophyll fluorescence (Špulák et al. 2011).

Fertilization by the crusted limestone and amphibolite positively influenced the growth performance of wych elm (*Ulmus glabra* Huds.) plantation which substantially suffers from the harsh condition of this locality (Balcar et al. 2009).

During outplanting, plantation of the Carpathian birch (*Betula carpatica* W. et K.) was spot-fertilized with crushed limestone and basalt. Approximately 15 years after the planting, in the limestone variant a partial positive influence of soil chemistry (in Mg, Ca) was observed, but at the same time the leaching of N, P, K was registered. In the variant with basalt, the influence was similar but significantly lower. The content of foliage nutrients was not significantly affected by fertilization. Only in the case of Ca there was a higher content in the fertilized treatments (negative correlation with the growth). In terms of growth, the substantial growth retardation persisted in fertilized variants, probably due to the specific physiological properties of Carpathian birch, which requires nutritionally poor and acidic soil (Kuneš et al. 2007b).

The findings from the field study were verified under controlled conditions of the forest nursery. Seedlings of Carpathian birch were treated by combined different intensity of nitrogen fertilization (urea) with liming. Weak liming and fertilization with nitrogen fertilizer had rather positive effect on growth; simultaneously strong urea fertilization had a neutral but not negative effect. A markedly positive growth response was noted in a combination of strong urea fertilization and weak or null liming (Baláš et al. 2010).

In the bottom of Jizerka valley, the plantation of rowan (*Sorbus aucuparia* L.) was established in order to assess whether the large-sized or common-sized planting stock show better ability to overcome the stress from the late and early frost events, commonly occurring in this locality (Gallo et al. 2014). Additionally, the fertilization by the Silvamix tablets was applied. The large-sized planting stock showed better growth performance and lower damage from the frost events and from the snow pressure. However, fertilization did affect neither growth nor the foliage chemistry (Kuneš et al. 2014b).

Plantation of the Carpathian birch in the same location was established in 2008-9, the primary objective of which was to test the capacity of the Carpathian birch to survive and grow in one of the most extreme frost-stressed locations in the Czech Republic. One year after planting it was fertilized with surface fertilizers – control treatment and treatments with an increased content of phosphorus and a treatment with a balanced composition of the elements were included. Already 2 years after application, a significantly higher content of phosphorus in leaves was found, but it exhibited worse chlorophyll fluorescence parameters. The Carpathian birch plantation was compared with 17-year-old planting of Carpathian birch on the side ridge on the former air-polluted clear-cut area (placing crushed limestone into holes during outplanting). In the fertilized treatment, there were still higher concentrations of nutrients in the leaves. However, the fertilized treatment exhibited significantly worse increment (Špulák et al. 2014).

4. Experiments with long-term fertilization of subalpine grasslands

The effect of fertilization was also investigated in the dwarf-pine (*Pinus mugo* Turra) vegetation zone on subalpine grasslands in the Giant Mountains, where Ca (20–2,130 kg ha^{-1}), N (50–500 kg ha^{-1}), P (0–240 kg ha^{-1}) and S (0–300 kg ha^{-1}) fertilizers were applied between 1965 and 1967. Following variants of fertilizers were used: $CaSO_4 + Ca[H_2PO_4]_2$, $NH_4NO_3 + CaCO_3$ and CaO. In 2004, the effect of all fertilizer applications on the stand structure was still evident 37 years after the last fertilizer application. *Avenella flexuosa* and *Anthoxanthum alpinum* were the dominant species on phosphorus-fertilized plots, while *Nardus stricta* was the dominant species on control plots even after Ca and N application. *Anthoxanthum alpinum* biomass production was higher in all fertilized variants than in the control. Total standing biomass as well as dead biomass and sward height were lowest on plots fertilized with P (Hejcman et al. 2007).

The grassland called "Grass Garden" on the subalpine meadow in the Giant Mountains has been fertilized for more than 200 years with ash from Norway spruce and dwarf pine. Mean annual doses of applied nutrients per hectare calculated from the number of kept animals and volume of burned firewood in sub-alpine grassland were 90–140 kg N, 250–350 kg K, 30–50 kg P, 300–450 kg Ca, 80–130 kg Mg. After 62 years, *Deschampsia caespitosa* and *Avenella flexuosa* significantly dominated the fertilized areas, while *Nardus stricta* dominated the unfertilized areas. The Ca concentration in the soil was more than twice as high in the fertilized variants as in the control, which suggests that it was very difficult to deplete the applied Ca even on extreme podzol soils and under climatic conditions of the subalpine vegetation stage. The concentrations of Mg and P and the N : P ratio were significantly affected in the aboveground plant biomass of the fertilized variants (Semelová et al. 2008).

5. Other enhancing substances (non-fertilizers)

Alginite is a rock of fossilized algae and it can serve as soil conditioner to hold water in the soil. Eco-fertilizer alginite used in the studies had following content of macroelements: Ca 15,528 mg kg^{-1}, Mg 1,841 mg kg^{-1}, P 43 mg kg^{-1}, K 196 mg kg^{-1} and N total content was 0.207%. The influence of alginite application on growth of forest trees is very ambiguous. The impact was evaluated on growth parameters (height increment, mortality and foliar nutrient content) of Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco), Scots pine, English oak (*Quercus robur* L.), red oak (*Quercus rubra* L.) and Norway maple (*Acer platanoides* L.) seedlings on former agricultural land near Hovorčovice in the Polabí region under warm and dry climate. Two variants with the application of 0.5 kg and 1.5 kg of alginite per planting point were planted. There was a slight positive effect on pine growth and mortality but only in the first year. In following seasons, however, mortality has increased. Slightly positive results were recorded in maple and red oak (Kupka et al. 2015; Tužinský et al. 2015; Cukor et al. 2017c). In terms of growth, the application of alginite had a slightly positive effect, but rather in the following years after planting (in the first years it was rather negative). The influence of alginite on the nutrient content of the assimilation apparatus was neutral to slightly positive (mostly slightly higher content of N, P, Ca, Mg), (Kupka et al. 2015; Cukor et al. 2017a). The unconvincing results of the alginite application seem to be related to its essential characteristic, the ability to bind water. This is, on one hand, a positive effect (slower drying, more available water for plants), on the other hand, in a longer dry season, the alginite-enriched soil needs more water to increase moisture to a level that is available for roots.

Positive effect of bio-algeen stimulator (liquid or gel of algae extract) on the growth of Norway spruce seedlings in a forest nursery (Hanzal et al. 2015) was registered, but a suppression of the active mycorrhiza emerged (Lorenc et al. 2016).

The phytohormones brassinosteroids should help plants overcome stress conditions like drought. The effect of application by spraying on seedlings in the forest nursery was studied. In Scots pine nursery plantation, there was a decrease in mortality, but also decrease in growth. In nursery Norway spruce plantation, the results were ambiguous and inconsistent (Nováková et al. 2015). In the case of plantation established on abandoned agricultural land in the locality of Truba (Kostelec nad Černými lesy), a positive effect on mortality was observed in the European beech plantation (Gallo et al. 2017). On the contrary, in the same locality, the effect on mortality and growth performance of Scots pine plantation was significantly negative (Nováková et al. 2014). Furthermore, the effect of brassinosteroids in overcoming stress during germination was investigated. The results were again quite inconsistent. A slight positive effect was observed on Norway spruce seeds, while it was negative for Douglas fir (Kuneš et al. 2016). The published results show that the effect of brassinosteroids is mostly apparent but is significantly different for individual species and application methods.

6. Conclusion

Forest fertilization has great potential to increase productivity of forest biomass, decrease risks, and strengthen sustainability production. Fertilizers mostly showed a positive effect on the forest growth and mortality rate. The use of fertilizers was detected by the soil analysis sometimes after decades of application. Only in a minority of cases was fertilization reflected in the biomass of the trees. Well-designed fertilization can be beneficial especially at early stages of stand development (overcoming planting shock). Spot-applied fertilizing with a slow release fertilizer (preferably in the form of tablets) is effective in comparison to brassinosteroids and alginite with inconsistent results. However, artificial fertilization is to be considered as a means of helping to long-term improve the vitality of the forest in a short period of time. In particular, middle-aged spruce stands with marked symptoms of yellowing can be grown to a harvest age after a suitably selected application of fertilization. This may become more important in the light of the air pollution and ongoing climate change in relation to drought, weather extremes and infestation by secondary pathogens (especially bark beetles). However, it is necessary to achieve the optimization of the fertilization process to provide a high rate of economic return in terms of increased biomass production for owners.

In the stands of younger and middle age, the cooperation of the process of fertilization and thinning of forest stands is very important. The long-term quality cultivation is a question of appropriate species composition, genetic properties, spatial and age structure. On the other hand, the possible environmental and economic risks of fertilization should be also taken into account and more research is needed on the effects of fertilizers on the stand level and the landscape level. Moreover, further long-term and complex research on resource use efficiency, wood quality, root development, mycorrhiza systems, ground vegetation, water quality and resistance to abiotic stresses in relation to fertilization is also necessary.

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ORIGINAL PAPER

Gap regeneration and dynamics: the case study of mixed forests at Křtiny in the Czech Republic

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Abstract

Gap regeneration remains the best silviculture technique for sustainable forest regeneration in mixed forests. The study examined tree species composition, diversity and dynamics of natural regeneration in gaps under three contrasting forest stands at Křtiny in the Czech Republic. In spring 2013, experimental gap design begins, when semi-permanent 1 m^2 circular sub-sampling plots along North-South-East-West transects were delineated under 6 selected natural canopy openings ≤ 20 m^2. In winter 2013/14, these naturally originated openings were artificially enlarged to the current gap sizes ranging between 255 and 1149 m^2 through group felling. Natural regeneration in gaps was measured four times: from the growing season before disturbance (BD) in 2013 to the next three consecutive growing seasons after disturbance in 2014 – 2016, respectively. Seven (7) new species with light demanding growth strategy that were previously not present at mother stands were occurring there during the first growing season after disturbance (FGS), yielding the highest taxa (14 species) and diversity (Shannon diversity index, H = 1.7) while BD attained the lowest (8 species; H = 0.9), respectively. Study site being part of *Fagus sylvatica* vegetation community and providing favorable natural conditions for the optimal growth of *Picea abies* significantly explains the regeneration dominance of these species in gap regeneration from BD until the third growing season after disturbance (TGS), respectively. Small scale gap-disturbance contributed to the higher regeneration densities of all studied species during FGS. However, drought, competition from other life forms, and browsing activities substantially caused a progressive decline in natural regeneration during three consecutive years after disturbance.

Key words: composition; diversity; disturbance; growing season; tree species

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1. Introduction

Gap regeneration is a nature-promoting silviculture technique that champions the quest for sustainable natural forest management. Within the last 30 years, this concept has gained much research attention globally (e.g., Runkle 1990; Bullock 2000; Dusan et al. 2007; Wang et al. 2017b; Hammond & Pokorný 2020a) since its inception in the 20th century (Watt 1947; Runkle 1981) due to its unmatched positive ecological importance on sustainability of mixed-species forests. The recent promotion of mixed stands in sustainable forest management is unquestionably owing to the importance of species diversity (Pretzsch 2009; Hammond et al. 2020) in providing numerous forest functions and services (Del Río et al. 2018). In Central Europe, the rising importance of mixed forests reflects the growing complexity of societal demands for forest ecosystems (Bravo-Oviedo et al. 2014; Sedmákov et al. 2019). Mixed forests are known to be resilient to environmental threats and also possess a more diversified portfolio of environmental benefits (Bravo-Oviedo et al. 2014; Del Río et al. 2016). The "insurance hypothesis" postulates that mixed forests response to disturbance is less intense and their recovery is much quicker than monocultures (Pretzsch 2018). The greater demand for knowledge regarding regeneration and dynamics of mixed forests is the reason behind increasing number of studies focusing on the effect of gap regeneration on forest dynamics, growth and yield in mixed-species stands (Griffiths et al. 2007; Vilhar et al. 2015; Khodaverdi et al. 2019; Hammond & Pokorný 2020b). Recently, many researchers have been focusing on the understanding of appropriate silviculture methods of the underlying mechanisms that control the interactions among species, and also between species and their growing environments in order to more adequately predict the outcomes of forest activities (Bravo-Oviedo et al. 2014).

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Forest management approaches that emphasize wholly on a diverse forests' agenda rely heavily on natural disturbances as key drivers that promote and maintain tree species diversity (Sommerfeld et al. 2018; Jaloviar et al. 2020). In many gap-recruitment studies, small scale gap-disturbance has been identified as influencing the structure and development of natural forests essentially through the emergence and survival of natural regeneration in a variety of conditions within gaps (Hammond & Pokorný 2020b; Jaloviar et al. 2020). The regime of small scale disturbances is characterized by low intensity felling of few individual trees for the forest management purpose of gap creation (Rugani et al. 2013; Hammond & Pokorný 2020b). Mostly, disturbances that initiate gap formation are accompanied by environmental heterogeneity that generate favorable microclimatic light conditions in gaps that offer a broad spectrum of growing niches which enable ecological organization, regeneration and coexistence (Busing & White 1997) of tree species with different life history attributes (Dusan et al. 2007; Kollár 2017; Vacek et al. 2017). Often creating comparable occupancy opportunity for natural regeneration of contrasting light demanding and shade-tolerant species simultaneously in gaps (Sapkota & Odén, 2009; Nagel et al. 2010; Hammond & Pokorný 2020b). In view of this, several studies have found gap regeneration as an appropriate forest management technique for the maintenance of mixed-species stands in many forest types (Sapkota & Odén 2009; Kollár 2017; Hammond et al. 2020).

Natural regeneration is an excellent gap-beneficial tree regeneration option that is ecologically pivotal to mixed forest management. For decades, mixed forests at Křtiny in the Czech Republic have set a long-standing silviculture record of sustainable natural regeneration. However, there has been minimal research on the comprehensive effect of gap regeneration and its accompanying dynamics in the forests. Hence, the main objective of this paper is to examine the dynamics of natural regeneration in gaps, comparing from the growing season before disturbance (BD) to the third consecutive growing season after disturbance (TGS) under mixed forest stands at Křtiny. We, therefore, compared species composition and species diversity of natural regeneration tree species in gaps within four consecutive growing seasons (2013 – 2016) and evaluated the ecological dynamics and distribution of future natural regeneration potential under three different forest stands.

2. Materials and methods

2.1. Study site

The study site (49° 13'– 49° 21'N; 16° 34'– 16° 40'E) on the Mendel University's Training Forest School Enterprise (UFE), is located in Křtiny, North of Brno in the Blansko District of the South Moravian Region in the Czech Republic (Fig. 1). UFE established in 1923, is situated between 210 m to 575 m a.s.l. altitude with prevailing continental temperate humid climate according to Köppen climate classification. The mean annual precipitation sum is 610 mm while mean annual tem-

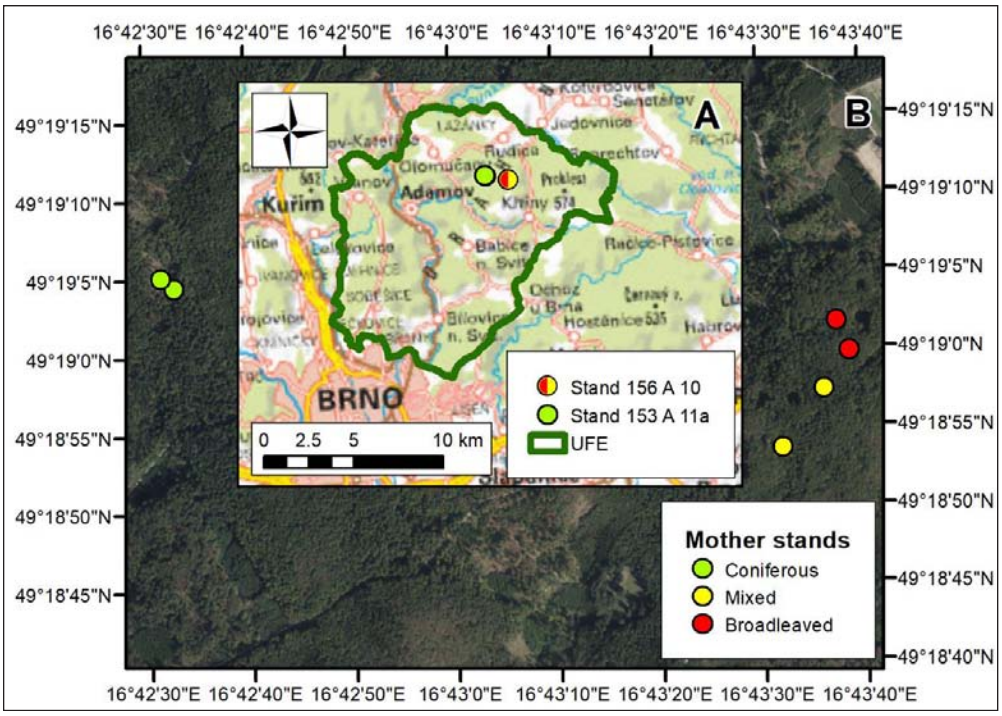

Fig. 1. Geographical positions of six research gaps (B) from three distinct mother stands under two categorized forest management stands (A) within temperate mixed Mendel University's Training Forest School Enterprise (UFE) at Křtiny in the Czech Republic.

perature is 7.5 °C (Hammond et al. 2020). Bedrock varies from granodiorites to culmian grawacks and limestone. The predominant soil types are cambic rendzinas, luvisols, brown earth and mesotrophic cambisols, broadly grouped under the cambisol (kambizem) soil type category based on the Czech taxonomic soil classification system. The UFE region is naturally represented by mixed forests dominated by 54% of broadleaved and 46% coniferous tree species. The whole forest area of UFE covers approximately 10,265 ha under some 116 management units/stands categorized into three forest districts. We selected two mixed forests of management stands 156A 10 and 153A 11a (520 m – 570 m a.s.l.) in the Habrůvka forest district. The forest district where natural regeneration remains the long-lasting preferred tree regeneration method and group selection silviculture system is encouraged to a certain level in forest management.

Six gaps numbered from Gap 1 to Gap 6 under three different mature stands were considered for the study. Gap 1 – 2 under coniferous forest type (100% *Picea abies*) in Forest Management Stand 153A 11a (109 years old) and Gap 3 – 4 under mixed forest type (50% *Picea abies*), and Gaps 5 – 6 under broadleaved forest type (90% *Fagus sylvatica*) in Forest Management Stand 156A 10 (97 years old) situated within two main forest associations, 3S7 medium-nutrient oak-beech – *Querceto-Fagetum mesotrophicum* and 4W1 limestone beech – *Fagetum calcarium* (Anonymous 2013), respectively.

2.2. Gap design and expansion of experimental gaps

In 2013 spring, we purposively selected six(6) naturally occurred gaps with irregular shapes. Gaps were defined as 15 – 20 m^2 forest canopy openings formed through the mortality of one or more canopy trees with diameter at breast height (dbh) above 20 cm due to natural disturbances. Next, four(4) independent transects of 20 m length in the North-South-East-West cardinal directions were demarcated from individual gap center. Then, one(1) semi-permanent 1 m^2 circular sub-sampling plot (i.e., 56 cm in radius) was established first at gap center and then followed by forty(40) additional sub-sampling plots, i.e., ten(10) placed at 2 m intervals along each transect.

In 2013/14 winter, small-scale artificial disturbances (i.e., felling of a few number of trees by man) were carried out within the stands of the three selected forest types. In this regard, a group felling comprising three mature trees ≥ 30 cm dbh minimum were harvested for the gap disturbance procedure. This silviculture procedure resulted in the enlargement of already existing canopy openings. As a result, original gaps were expanded into gaps of different sizes varying from 255 to 1149 m^2 (see Table 1). WinSCANOPY (2012a edition, Regent Instruments Canada Inc.; Quebec Canada) was used to measure both pre-and post-disturbance gap sizes as canopy openings of natural-original and artificial-final gaps using hemispherical photos. The procedure was carried out during winter so as to either minimize or possibly prevent any adverse effects that may accompany disturbances on the gap microsites. For forest management guidelines of mixed forests, Křtiny, usually a natural disturbance regime in the form of small-scale disturbance, is regular and recommended silviculture practice in the forest establishment that warrants sustainable forest development.

2.3. Field measurements

To assess microclimatic light condition, one hemispherical photo was shot at all forty-one (41) sub-sampling circular plots with WinSCANOPY photography accessories; 1.2 m tripod, auto-leveling frame, Sony Nex 10 camera (Sony, Minato, Tokyo, Japan) with an inbuilt automated N90° search engine calibrated fish-eye lens (Nikon, model FC–E8 0.21x, Tokyo, Japan) during the first growing season after disturbance (autumn 2014) within each selected gap. Subsequently, natural regeneration status was surveyed within every delineated circular plot along transects and gap centers in the growing season before disturbance (autumn 2013) and repeatedly in the following three consecutive growing seasons after

Table 1. Basic characteristics of research gaps within the three studied forest types at Mendel University's Training Forest School Enterprise Křtiny.

Gap no.	Gap Area [m^2] Nat – Org/ Art- Exp	Gap size/shape	Aspect[b]	Mother Stand[b]	Forest Management Stand (coverage)[a]	Percentage composition of stand species with their respective dbh, height and tree volume [cm/m/m^3][a]	Growing stock [m^3 ha^{-1}][a]	Living stock [m^3][a]
1	18/255	Small-size/Elliptical	SE	Coniferous	153A 11a (7.4 ha)	61% *Picea abies* (35/31/1.26); 25% *Larix decidua* (43/33/1.99); 6% *Fagus sylvatica* (33/28/1.06); 6% *Pinus sylvestris* (42/31/1.75); 1% *Acer pseudoplatanus* (43/32/2.17) and 1% *Carpinus betulus* (30/26/0.73).	536	4139
2	20/713	Big-size/Circular	SE	Coniferous				
3	20/286	Small-size/Elliptical	W	Mixed	156A 10 (13.3 ha)	70% *Fagus sylvatica* (35/31/1.33); 14% *Picea abies* (39/32/1.58); 6% *Larix decidua* (50/34/2.54); 6% *Abies alba* (37/30/1.53); 2% *Pinus sylvestris* (43/30/1.78); 1% *Quercus petraea* (67/36/4.74) and 1% *Pseudotsuga menziesii* (42/26/1.63).	533	7087
4	20/904	Big-size/Circular	W	Mixed				
5	15/282	Small-size/Elliptical	NW	Broadleaved				
6	20/1149	Big-size/Circular	NW	Broadleaved				

Nat – Org/Art- Exp is Natural – Original/Artificial – Expansion. Data based on guidelines from the forest management plan for Training Forest School Enterprise Křtiny. [a]Anonymous (2013); [b] iitola (2018).

disturbance (i.e. 2014, 2015 and 2016 autumns). Naturally regenerated tree species were firstly identified at the species level (name), assessed morphologically (height growth 0 – 350 cm limit), counted (frequency), and recorded appropriately. Base-line measurement of regeneration was also carried out at the same time. Advance regeneration, new recruits, as well as resprouts with maximum 350 cm height were surveyed. However, one-year-old regeneration (ephemeral tree species that are not a good indicator of light availability) were excluded from the data survey.

2.4. Data processing and analysis

Regent's WinSCANOPY Technology (2012a edition, Regents Instruments Canada Inc; Quebec, Canada) processed hemispherical gap photos into Total Site Factor (TSF) light condition. TSF light condition is the combination of Direct Site Factor (DSF) and Indirect Site Factor (ISF) (Guay 2012). STATISTICA software (13.4.0.14 edition, TIBCO Corporation Inc; Palo Alto, California, USA) was employed for all data analyses. Prior to analyses of variance (ANOVA) and post hoc Fisher's LSD analyses were computed to obtain the significant difference at $p < 0.05$ significance level, data were checked for normality and variances of homogeneity conditions. Simple linear regression was also performed to determine the significant relationship between TSF light condition and natural regeneration of tree species at $p < 0.05$ significance level for the determination coefficient of the linear regression (r^2). Paleontological Statistics Software (3.24 edition) (Hammer et al. 2001) was used for biodiversity estimation. Four (4) diversity indices [equations 1 – 4] relevant to the study objectives were considered.

Firstly, Shannon diversity index (H) was used to ascertain species diversity in gaps (Harper 1999).

$$H = -\sum_i \frac{ni}{n} \text{In} \frac{ni}{n} \qquad [1]$$

where:

ni – number of encountered individuals of i^{th} taxon,
n – the number of all encountered individuals within a particular growing season,
In – logarithm sign.

Secondly, Pielou's Evenness (J) was used to measure species evenness within gaps (Harper 1999).

$$J = \frac{H}{In(S)} \qquad [2]$$

where:

H – Shannon diversity index,
S – number of taxa.

Thirdly, Berger-Parker Index (D) simply measured the numerical importance of the most abundant species in gaps (Berger & Parker 1970).

$$\text{D} = \frac{\text{N}max}{n} \qquad [3]$$

where:

$Nmax$ – number of individuals of the most abundant species.

Finally, Sorensen's Coefficient (SC) index measured species similarity of gap regeneration among the three studied growing seasons (Raup & Crick 1979).

$$SC = 2M / (2M+N) \qquad [4]$$

where:

M – number of shared similar species of the compared pair,
N – total number of species frequencies of growing seasons in a column with presence in just one row of species frequency.

In addition, relative density (%) was used to calculate abundance proportions of all encountered tree species in natural regeneration.

$$\text{Relative density} = \frac{Total\ number\ \ of\ a\ specific\ \ species}{Overall\ \ total\ of\ \ all\ presented\ \ species} \times 100 \qquad [5]$$

3. Results

3.1. Description of species composition and diversity in gaps

A total number of fifteen (15) different species belonging to six (6) families identified within four consecutive growing seasons are presented in Table 2. Pinaceae (5 species) had the greatest number of occurrences, whereas Oleaceae (1 species) family had the least. Eleven (11) species out of the overall species presented were found to be possessing non-dominant status in regeneration, while two species each were observed to have exhibited predominant and dominant statuses in regeneration.

Species with light-demanding and intermediary (6 species each) growth strategies topped species composition, while those with shade growth strategy (3 species) attained the least representation in gap regeneration. The lowest species turnout (8 species) was enumerated in BD, while the highest (14 species) was attained in FGS. During BD and SGS, *F. sylvatica* (69.41%; 31.49%) displayed the highest relative densities. Also, *L. decidua* (25.60%) and *P. abies* (68.90%) displayed the highest relative densities in FGS and TGS, respectively. On the other hand, *A. platanoides* (0.33%), *B. pendula* (0.05%), *F. excelsior* (0.07%) and *P. menziesii* (0.07%), and *C. betulus* (0.06%) had the lowest relative densities in BD, FGS, SGS and TGS, respectively. Besides, *F. excelsior, F. sylvatica, P. abies* and *A. alba* were present throughout the four growing seasons while *L. decidua, P. menziesii, P. sylvestris* and *S. alba* were only absent in BD and likewise for *C. betulus* in FGS and *A. pseudoplatanus* in TGS. Natural regeneration of *B. pendula* and *Q. petraea* species were exclusively present in FGS.

The estimation of diversity indices revealed a general higher species diversity in FGS and SGS compared to TGS and BD in Table 3. It is evident that after two

Table 2. Species composition of gap regeneration within four consecutive growing seasons at mixed forests at Křtiny.

Common name	Scientific name	Taxonomic family designate	Regeneration dominance category	Guild	Relative density [%]			
					BD	FGS	SGS	TGS
European beech	*Fagus sylvatica* L.	Fagaceae	Predominant	Shade	69.41	22.39	31.49	13.73
Norway spruce	*Picea abies* (L.) Karst.	Pinaceae	Predominant	Inter	17.93	25.10	23.95	68.90
European larch	*Larix decidua* Mill.	Pinaceae	Dominant	Light	—	25.60	25.16	3.01
European silver fir	*Abies alba* Mill.	Pinaceae	Dominant	Shade	7.40	16.87	14.78	11.35
Black poplar*	*Populus nigra* L.	Salicaceae	Non-dominant	Light	—	0.20	—	0.06
European ash*	*Fraxinus excelsior* L.	Oleaceae	Non-dominant	Inter	0.99	0.15	0.07	0.09
European birch*	*Betula pendula* Roth.	Betulaceae	Non-dominant	Light	—	0.05	—	—
European hornbeam	*Carpinus betulus* L.	Betulaceae	Non-dominant	Shade	0.66	—	0.14	0.03
Douglas fir	*Pseudotsuga menziesii* (Mirb.) Franco	Pinaceae	Non-dominant	Inter	—	1.05	0.07	0.54
Horse chestnut*	*Aesculus hippocastanum* L.	Sapindaceae	Non-dominant	Inter	0.66	0.10	—	—
Norway maple*	*Acer platanoides* L.	Sapindaceae	Non-dominant	Inter	0.33	0.10	—	0.31
Scots pine	*Pinus sylvestris* L.	Pinaceae	Non-dominant	Light	—	0.35	0.35	0.11
Sessile oak	*Quercus petraea* (Matt.) Liebl.	Fagaceae	Non-dominant	Light	—	0.15	—	—
Sycamore maple	*Acer pseudoplatanus* L.	Sapindaceae	Non-dominant	Inter	2.63	0.65	0.21	—
Willow*	*Salix alba* L.	Salicaceae	Non-dominant	Light	—	7.23	3.77	1.87
Total					100	100	100	100

BD – The growing season before forest disturbance, FSG – First growing season after forest disturbance, SGS – Second growing season after forest disturbance and TGS – Third growing season after forest disturbance. Shade – shade tolerant, Inter – intermediate and Light – light demanding species. Absence of species indicated by (—). Tree species with indicated (*) are not present in mother stands but presumably from the nearest seed trees of those species: *Populus nigra* (9500 m), *Fraxinus excelsior* (400 m), *Betula pendula* (280 m), *Aesculus hippocastanum* (3000 m), *Acer platanoides* (350 m) and *Salix alba* (2000 m) with distance in parentheses.

growing seasons after forest disturbance, all the indices reached the same values as BD. When subjected to an analysis of variance test, the mean values of the indices for the four growing seasons revealed a significant difference ($p < 0.001$) among growing seasons in each case. Mean Shannon diversity index values of H = 1.67, H = 1.51, H = 1.02 and H = 0.98 were recorded for FGS, SGS, TGS, and BD, respectively. However, measured species evenness in SGS (J = 0.66) was significantly higher than indices attained in FGS (J = 0.63), BD (J = 0.47) and TGS (J = 0.43), respectively. Furthermore, BD and TGS showed no significant difference for Berger-Parker index estimation, but FGS and SGS showed significant difference. This clearly showed the significant influence of species dominance in species diversity.

Table 3. Species diversity of gap regeneration within four consecutive growing seasons.

Growing seasons		Shannon diversity index (H)	Pielou's Evenness (J)	Berger-Parker Index
BD	Mean	0.98 a	0.47 b	0.69 c
	Std. dev.	±0.02	±0.01	± 0.01
	Minimum	0.97	0.46	0.69
	Maximum	1.00	0.48	0.70
FGS	Mean	1.67 d	0.63 c	0.26 a
	Std. dev.	± 0.01	± 0.00	±0.00
	Minimum	1.67	0.63	0.25
	Maximum	1.68	0.64	0.26
SGS	Mean	1.51 c	0.66 d	0.31 b
	Std. dev.	± 0.01	± 0.00	± 0.00
	Minimum	1.51	0.65	0.31
	Maximum	1.52	0.66	0.32
TGS	Mean	1.02 b	0.43 a	0.69 c
	Std. dev.	± 0.04	± 0.01	± 0.2
	Minimum	0.99	0.41	0.67
	Maximum	1.06	0.44	0.70
	P value	***	***	***

Means presented with the same letters in a column represent homogenous groups with statistically insignificant difference at p = 0.05 level. Estimated p values at 0.001 significance level indicated as (***). BD – The growing season before forest disturbance, FSG – First growing season after forest disturbance, SGS – Second growing season after forest disturbance and TGS – Third growing season after forest disturbance.

The SC values of 0.86, 0.75 and 0.64 for SGS × TGS, FGS × SGS and BD × FGS combinations, respectively indicate that despite the differences in the species diversity observed among the four growing seasons, there was, however, a contradictory high level of species similarity among growing seasons (see Tables 3 and 4).

Table 4. Sorenson's coefficient index of species composition of natural regeneration in gaps within four consecutive growing seasons.

Comparing seasons	Comparing species		Sorenson's coefficient
	Shared species	Unique species	
BD × FGS	7	8	0.64
FGS × SGS	9	6	0.75
SGS × TGS	9	3	0.86

BD – The growing season before forest disturbance, FSG – First growing season after forest disturbance, SGS – Second growing season after forest disturbance and TGS – Third growing season after forest disturbance.

3.2. Effects of disturbances on dynamics of natural regeneration of tree species with different growth strategies

Three categories of tree species with different growth strategies in gaps depending on their physiological light preferences are presented in Fig. 2. FGS was the best performing growing season (mean regeneration density = 70,662 trees ha^{-1}) as higher regeneration yields were attained for all three studied growth strategies (Shade = 26,695 trees ha^{-1} , Inter 23,523 trees ha^{-1} and Light = 20,444 trees ha^{-1}) of tree species. Followed by SGS (53,910 trees ha^{-1}) and BD (26,436 trees ha^{-1}), while TGS (12,467 trees ha^{-1}) stood as the poor performing growing season for species performances. Apart from BD, when light strategy species were absolutely absent, all the other growing seasons showcased every considered growth strategy of species within gaps. Notwithstanding, both FGS and SGS presented a balanced proportion of Light: Inter: Shade (1:1:1) species in gaps, while TGS showed an imbalanced proportion among species under various categories of growth strategy.

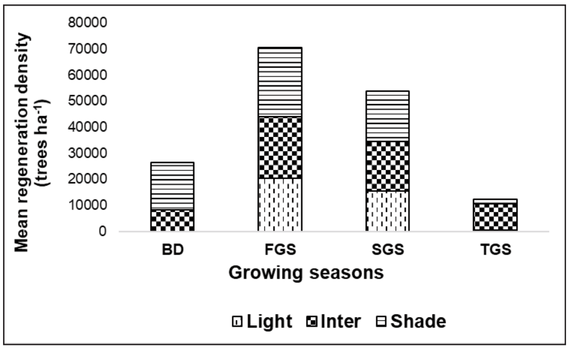

Fig. 2. Dynamics of natural regeneration tree species with light demanding (Light), intermediate (Inter) and shade tolerant (Shade) growth strategies in gaps during four consecutive growing seasons in mixed-species forest. BD – the growing season before forest disturbance, FSG – First growing season after forest disturbance, SGS – Second growing season after forest disturbance and TGS – Third growing season after forest disturbance.

3.3. Effects of parent stand on dynamics of natural regeneration of tree species in gaps

According to Bonham (2013), density is the number of individuals within a defined area, while De Rio et al. (2018) defined density as the abundance of an organism per unit area. From the presented results in Fig. 3, it can be seen that *P. abies* (BD = 18,339 trees ha^{-1}; FGS = 49, 617 trees ha^{-1}) was abundant under coniferous forest stands while *F. sylvatica* (BD = 24,824 trees ha^{-1}; FGS = 14,683 trees ha^{-1}) was highly abundant under broadleaved forest stands in the two assessed growing seasons. Meanwhile, *A. alba* and *L. decidua* grew abundantly in gaps during FGS, however, the abundance of *A. alba* (26,219 trees ha^{-1}) was detected under mixed forest stand while that of *L. decidua* was noticed under coniferous (31,108 trees ha^{-1}) and broadleaved (16,280 trees ha^{-1}) forest stands. On the other hand, *A. alba* and *L. decidua* showed poor regeneration performances in gaps with zero regeneration occurrence under coniferous and broadleaved forest stands during BD and again for only *A. alba* under coniferous forest stand during FGS. Looking at presented mean regeneration densi-

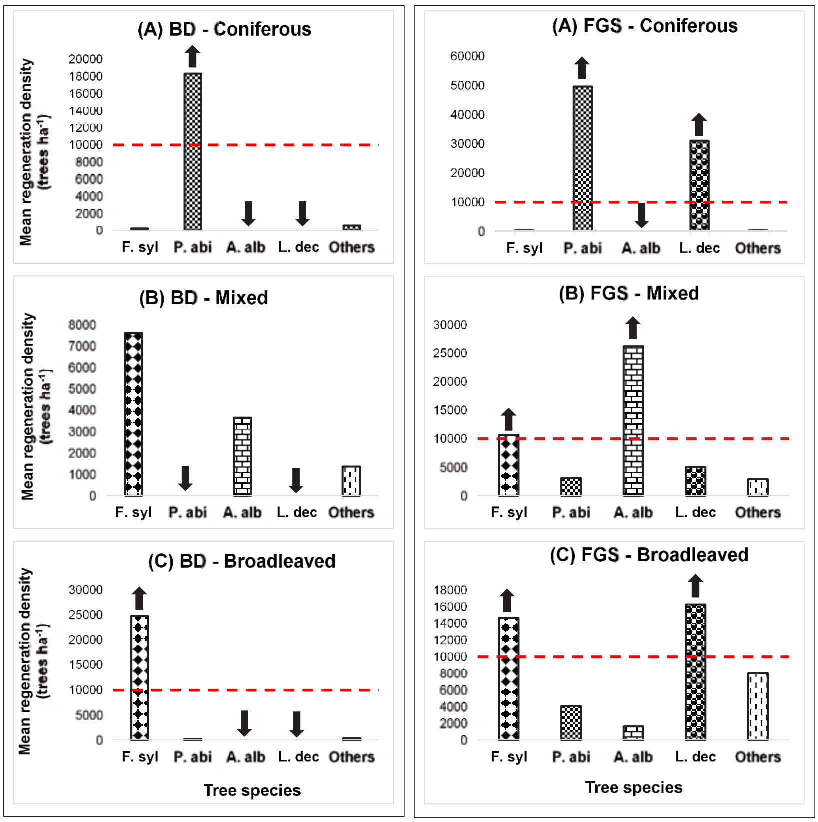

Fig. 3. Comparative assessment of different natural regeneration tree species under three distinct parent stands between the growing season before forest disturbance (BD) (left) and First growing season after forest disturbance (FGS) (right). The dashed lines denote the regeneration threshold (10,000 trees ha^{-1}) for various species to demonstrating high potential for establishment and recruitment prospects presently at stand-level and in the future at forest-level. Upward arrows represent leading species with great natural regeneration prospects while downward arrows represent poor performing species with zero records of natural regeneration. *A. alb* – *Abies alba*, F. syl – *Fagus sylvatica*, L. dec – *Larix decidua, P. abi* – *Picea abies* and Others – the remaining encountered tree species.

ties of species (> 10,000 trees ha^{-1}), it is presumed that at every 1 m^2 area of forest floors under gaps, at least one seedling each would be encountered as *P. abies* species under coniferous forest stand, *F. sylvatica* species under broadleaved forest stand, *A. alba* species under mixed forest stand and *L. decidua* species under coniferous and broadleaved forest stands. Hence, showing great establishment, recruitment and survival potentials of natural regeneration of these tree species under the predicted forgoing associated forest stands, respectively. From results, mirroring overstory tree species composition, *P. abies* would likely be the most prolific understory species under coniferous forest stand and similarly for *F. sylvatica* seedlings underneath broadleaved forest stand. The result in Fig. 2 describes the stimulating effect of forest stand on the distribution, proportions, and dynamics of natural regeneration tree species in gaps.

Furthermore, the simple linear regression results showed that measured TSF light condition significantly influenced natural regeneration of *F. sylvatica* ($r_{TSF} = -0.58$ at $p = 0.012$) and *L. decidua* ($r_{TSF} = 0.62$ at $p = 0.006$) in gaps during FGS in opposite ways (i.e., in a negative way for *F. sylvatica* and positive for *L. decidua*). On the contrary, the natural regeneration of other tree species was not significantly influenced by this light condition factor at the $p < 0.05$ significant level.

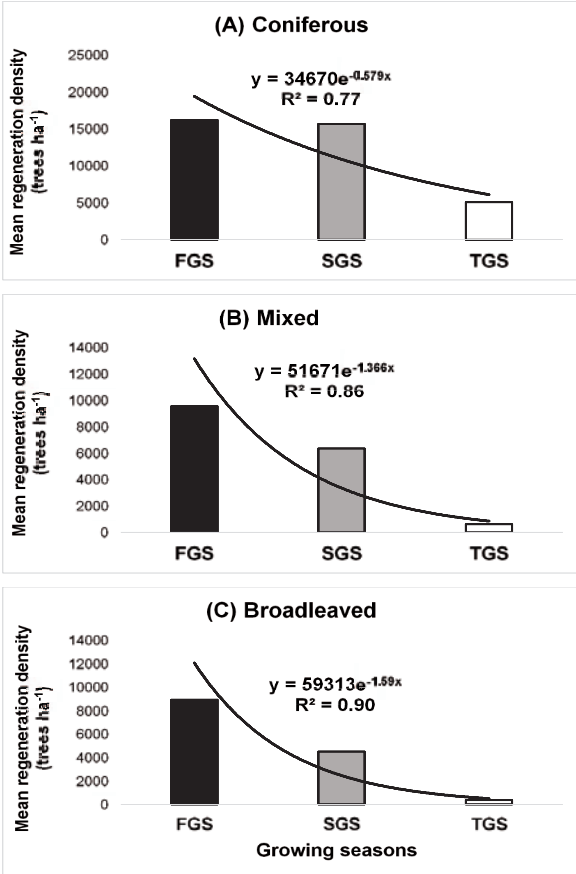

Fig. 4. Dynamics of gap regeneration under three distinct parent stands within three consecutive growing seasons after forest disturbance. FSG – First growing season after forest disturbance, SGS – Second growing season after forest disturbance and TGS – Third growing season after forest disturbance.

3.4. Effects of parent stand on dynamics of overall natural regeneration in gaps

Fig. 4 presents a forest undergoing natural regeneration processes and development in gaps under three distinct parent stands following small scale gap-disturbance. It was observed that during both FGS (16,197 trees ha^{-1}) and SGS (15,660 trees ha^{-1}), coniferous stand recorded the highest mean natural regeneration densities. In contrast, during TGS, the lowest comparable mean natural regeneration densities were found in gaps under mixed (623 trees ha^{-1}) and broadleaved (371 trees ha^{-1}) stands. Overall, natural regeneration in gaps declined from FGS to TGS in coniferous, mixed, and broadleaved stands at rates of 78%, 86% and 90%, respectively (see Fig. 4), demonstrating the ecological dynamics of natural regeneration in gaps after disturbance.

3.5. Effects of parent stand on dynamics of natural regeneration tree species in gaps

Dynamics and distribution of *F. sylvatica* and *P. abies, L. decidua* and *A. alba* including "Others" (any other participatory tree species) natural regeneration in gaps under three distinct parent stands within three consecutive growing seasons after small scale gap-disturbance are presented in Fig. 5. In the coniferous stand, the mean regeneration densities of *P. abies* and *L. decidua* during FGS and SGS were significantly higher ($p < 0.05$) than those recorded in TGS. However, no significant difference ($p > 0.05$) was found for *A. alba* and "Others" regeneration in the various growing seasons. Also, natural regeneration of *F. sylvatica* was totally absent during SGS and TGS while *A. alba* was only missing during FGS in gaps under the coniferous stand. Under the mixed stand, there were no significant observable differences ($p > 0.05$) among FGS, SGS and TGS for *P. abies, L. decidua* and Others regenerations. By contrast, significant differences ($p < 0.05$) were observed among the various growing seasons for *F. sylvatica* and *A. alba* regeneration under mixed stand. Beneath the broadleaved stand, all species except *A. alba* showed significant differences ($p < 0.05$) among the three growing seasons for their respective natural regeneration.

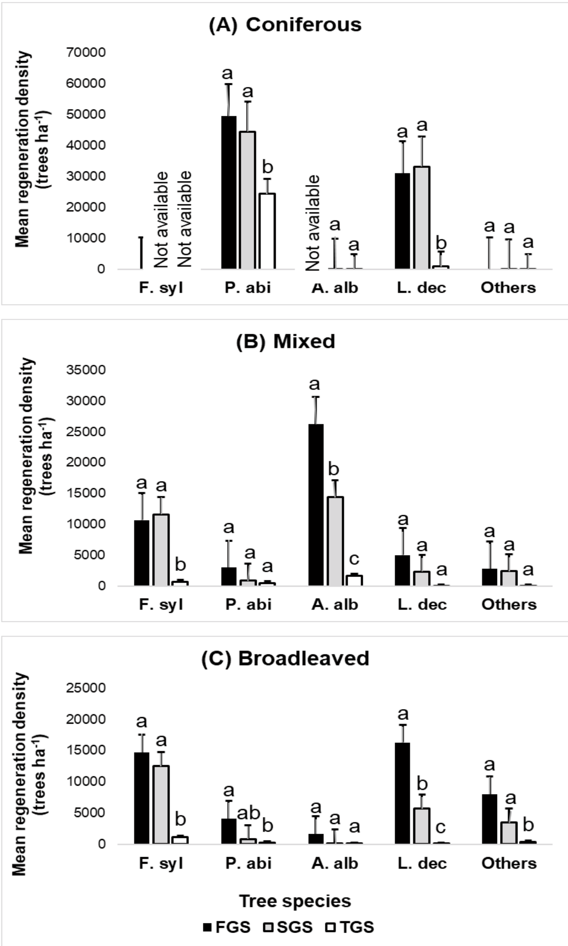

Fig. 5. Dynamics of natural regeneration tree species in gaps during three consecutive growing seasons in mixed-species forest. FSG – First growing season after forest disturbance, SGS – Second growing season after forest disturbance and TGS – Third growing season after forest disturbance. Not available signifies represent zero regeneration records. Bars with the same letters show homogenous group statistically ($p > 0.05$). *A. alb* – *Abies alba*, F. syl – *Fagus sylvatica*, L. dec – *Larix decidua, P. abi* – *Picea abies* and Others – the remaining encountered tree species.

4. Discussion

4.1. Impacts of gaps on species diversity and composition

Species composition is a fundamental structural characteristic in mixed-species stands. By definition, a mixed-species stand is a stand with at least two species (Del Río et al. 2018; Khodaverdi et al. 2019). In this study, we report the relevance of species diversity on forest functioning including: establishment, biodiversity preservation and stability through gap-based regeneration that safeguards sustainable forest development. We considered both species diversity and species composition to give a more detailed description of diversified tree species undergoing natural regeneration in gaps and simultaneously to accurately characterize future species composition and structure at the stand level of mixed forests dominated by small scale gap-disturbance regimes. From our results, we determined that, species diversity increased significantly after the small-scale gap dynamics treatment (see Table 3). Small-scale disturbances have been found to enhance species diversity in forests (Busing & White 1997). Our findings, therefore, support the studies of Dobrowolska (2007) and Khodaverdi et al. (2019) but disagrees with Griffiths et al. (2007). Several researchers have also stressed the role of gap disturbance on species diversity (e.g., Busing & White 1997; Dobrowolska 2007; Khodaverdi et al. 2019) via the subsequent creation of favorable conditions at growing sites especially increasing light condition (Bullock 2000; Dusan et al. 2007; Vilhar 2015) and explaining the mechanisms of species coexistence in gaps (Pacala & Levin1997; Wang et al. 2017b).

Contrary to our findings, Bullock (2000) claimed that gaps always allow increased light intensities, which often raise soil temperature and deplete soil water resources, weakening the vigor of regenerating species, thus accelerating mortality and eventually reducing species diversity in gaps. Other studies emphasize functional diversity more than species diversity (e.g., Hammond & Pokorný 2020a), because they believe that species with similar functional traits tend to occupy the same niche and therefore show similar behavior in growth pattern (de Bello et al. 2007) following openings in the canopies of forests. The regeneration dominance of *F. sylvatica* (69.4%) during BD and *P. abies* (68.9%) during TGS substantially influenced species diversity and this could also be explained for the similar estimated Pielou's Evenness (BD = 0.47 J, TGS = 0.43 J) and Berger-Parker index (BD = 0.69 D, TGS = 0.69 D) values attained for the two growing seasons. Besides, the similar relative densities of natural regeneration of *F. sylvatica* and *P. abies* during BD and TGS suggest that they were the most successful gap fillers under recent forest management (small-scale disturbance regime) during the study period. The same observation has been made elsewhere (Vilhar et al. 2015). In other observations, Rugani et al. (2013) described F. *sylvatica* as autochthonic dominant tree species in Central Europe, which has a typically competitive advantage over other tree species in various mixed-species forests under ecologically-based forest management. Grassi et al. (2004) observed that *P. abies* was one of the best performing tree species in natural regeneration under proper silvicultural practices and favorable conditions for the temporal and spatial continuity of the regeneration process.

Nonetheless, no absolute species dominance was found during FGS and SGS, but rather higher species diversity of the population and a significant balanced proportion between various natural regeneration tree species of different regeneration dominance categories in gaps were observed. Hence, indicating that gap-oriented silviculture procedure in winter 2013/2014 hastened the processes of forest restoration and dynamics through gap regeneration. Even though other studies have stated that gaps do not necessarily provide the ideal environment for regeneration (e.g., Busing & White 1997; Jaloviar et al. 2020). Our study confirmed a higher gradient of species composition observed during FGS in enlarged gaps from enhanced growing conditions to the improved establishment of advance regeneration and greater regeneration through buoyant recruitment mechanism.

Moreover, similar species composition observed across all four growing seasons suggests homogenous tree species composition at the stand level. Our results do support the hypothesis that similar species assemblages result in similar species composition (e.g., Wang et al. 2017b), but contradict a statement from Myers et al. (2013) that forests with similar overall structure vary in recruitment mechanisms, demonstrating divergent forest types through a shift in the emergent patterns relative to the community assembly mechanisms. Also, Bravo-Oviedo et al. (2014) categorically stated that under analogous forest where similar species, objectives and site conditions exist, for example, in the case of mixed forests, adoption of successful management guidelines may not be straightforward as similarity among species mixtures is not easy to be achieved. Our observation was completely different from this statement.

Furthermore, the regime of small scale gap-disturbance to light availability favored light-demanding species (*B. pendula, L. decidua, P. sylvestris, P. nigra, Q. petraea* and *S. alba*) and intermediate species (*P. menziesii,*) to regenerate, establish, grow, and recruit in large gaps (Qu et al. 2004; Hammond et al. 2020), while shade tolerant species (*C. betulus* and *F. sylvatica*) preferred the original small-sized naturally occurring gaps for enhanced natural regeneration processes, optimum growth and survival (Nagel et al. 2010; Feldmann et al. 2020). The ecological relationship between gaps (formation or size) and tree species with different growth behaviors (Hammond & Pokorný 2020a) was confirmed in our study. Also, it should be taken into consideration that SGS was an extremely dry year, thus light demanding species could disappear due to shade tolerant species, but both tree species could be diminished due to drought in TGS. Therefore, presumably, intermediate species could be less susceptible to drought and light changes.

4.2. The ecological contribution of parent stands towards growth potential of natural regeneration of different tree species in gaps

The results showing a higher proliferation (> 10,000 trees ha^{-1}) of predominant *F. sylvatica* and *P. abies* species in gaps under broadleaved and coniferous stands, respectively in both BD and FGS, tells the importance of species identities or species composition (Töigo et al. 2015) on future stand composition and structure through natural regeneration. In contrast to our findings, Vacek et al. (2017) observed that stand canopy had a negative effect on regeneration density of *F. sylvatica* natural regeneration in gaps under broadleaved forests. In another observation, Hammond and Pokorný (2020c) also saw a reduced growth dynamics of *P. abies* in gaps under *P. abies* dominated mixed stand. In this presented study, *F. sylvatica* and *P. abies* demonstrated a considerable advantage over the other species in gap regeneration. The basic characteristics (i.e., the widespread species composition in stand) of forest stand type strongly associated with this finding. This is because both broadleaved and coniferous stands retained the heavy presence of parent trees. The proximity of seed trees facilitated the regular supply of seeds for regeneration processes, seed establishment, and seedlings recruitment. This finding shows the important role of constant seed supply, the quantity of seed supply and reliable seed source for a successful gap regeneration.

The observed favorable regeneration densities of *F. sylvatica* and *A. alba* species in gaps under mixed canopies during FGS is consistent with Čater et al. (2014) hypothesis, which states that the growth behaviors of mentioned species under gap regeneration is mostly influenced by the ability to outcompete their neighbors under favorable light conditions through a fine adjustment of light permeability and improving conditions for their growth and development. However, the higher comparative regeneration density of *A. alba* confirms earlier findings in Slovenia that among variuos tree species in gap recruitment under mixed-species stands, *A. alba* always has a competitive advantage in regeneration (Čater et al. 2014). In order to favor *A. alba* regeneration, gap expansion is an essential silviculture practice (Čater et al. 2014).

Not with standing, the observed higher regeneration densities of *L. decidua* under broadleaved and coniferous stands in FGS could be attributed to the regime of small scale gap-disturbance, which mimicked the natural disturbances that favored the species. Another explanation was the accompanied improved light factor following disturbance and resultant gap expansion state favored the biological light demanding trait of *L. decidua* species causing profuse regeneration under broadleaved and coniferous stands in FGS. This evidently validates other research that found *L. decidua* to be sun-loving species (Qu et al. 2004; Matras & Pâques 2008) that grows best after forest disturbance (Wang et al. 2017a). Many gap-related processes and factors produce the mosaic spatial structure of the gap regeneration and recruitment in mixed forest stands. Our study shows that differentiation in the regeneration niche (Pretzsch 2009) including production of seeds–mast seeding, seed dispersal, germination, and establishment of seedlings (Grubb 1977), presence, location and abundance of parent trees and seed dispersers, advance regeneration (Yan et al. 2015; Wang et al. 2017a) as well as different life strategies of tree species in accessing the gap space (Bullock 2000), consequently create new disturbance regimes (Sommerfeld et al. 2018) that have significant influence on gap regeneration and dynamics.

The significantly higher mean regeneration densities of *F. sylvatica, P. abies*, *A. alba* and *L. decidua* species in stands give a good prediction that their proportions are expected to rise significantly in the future, since they were the most prevalent species in the natural regeneration layer (5 – 350 cm) of mixed forests at Křtiny (Hammond et al. 2020). Also, because their population, in terms of diameter structure and distribution, is substantially younger than populations of other species on sites where all species cohabit. We hypothesize that species with 10,000 trees ha^{-1} or more density records would have better forest restoration strategies after a small scale gap-disturbance regime and would tend to exhibit greater growth abundances in gap-based regeneration than those observed with less regeneration density (< 10,000 trees ha^{-1}) in gaps. Therefore, requiring different gap sizes, *F. sylvatica, P. abies*, *A. alba* and *L. decidua* may have greater prospects in future forest stand structure in mixed forests Křtiny than any other encountered species in gaps. This knowledge can be a helpful reference for designing silvicultural systems that aim to conserve diverse forest structures by mimicking natural disturbance dynamics in managed mixed-species stands growing on similar sites (Jaloviar et al. 2020).

4.3. Dynamics of natural regeneration in gaps under three distinct parent stands

Our result clearly indicates the significant decrease in natural regeneration densities in gaps within a short-term (over three years) after a small scale gap-disturbance regime. The mixed-species Křtiny forests showed declining and unsustainable regeneration and recruitment of tree species in gaps from FGS to TGS after small scale gap-disturbance. Although the primary objective of small scale gap-disturbance was to enlarge gaps for the promotion of natural regeneration and gap-recruitment and improvement of diversified tree species. Contrary to our findings, Jaloviar et al. (2020) stated that small scale gap-disturbance primarily maintains forest structure through the emergence and survival of natural regeneration upon canopy openings in a variety of conditions and that canopy gaps increase regeneration densities. Progressive mortality of natural regeneration tree species in gaps under mother stands was the typical feature. A significantly similar response of overall natural regeneration between different mother stands during FGS, SGS and TGS periods was observed. Quantification of ecological relationship between the various mother stands and related environment along with the trend of natural regeneration prediction over a period of time is not straightforward. Distribution of the site environmental conditions along stand level-gap gradient (Yan et al. 2015) is probably of higher importance than species relationships and gap environmental conditions. The low amount of extracted variability in natural regeneration dynamics in gaps under coniferous, mixed and broadleaved stands found in our study suggests that a regeneration process is more likely influenced by other factors rather than the general "gap characteristics (size, shape, geographical exposition)" factor of gaps under mixed forests. For instance, during FGS, natural regeneration was seriously compromised by competition from other life forms, to name a few; *Asperula* spp., *Cardamine* spp., *Carex* spp., *Dentaria* spp., *Luzula* spp., *Oxalis* spp., *Urtica* spp. etc. which grew more rapidly, intensely and finally, became more resilient in growth immediately after the completion of small scale gap-disturbance activity in winter 2013/14 for the reason of favorable growing sites conditions (Hammond et al. 2020). Likewise, Vacek et al. (2017) observed similar circumstances at the Krkonoše National Park where seedlings from natural regeneration received keen competition from *Calamagrostis villosa* and *Avenella flexuosa* grasses in mountainous European beech forests.

Nevertheless, the unexpected abiotic drought conditions in 2015 (i.e., expected annual mean precipitation (EMP)/real annual mean precipitation (RMP): 610/430 mm) through to 2016 (i.e., EMP/RMP: 610/533 mm) calendar years (CHMI 2020) and the high air temperature events (2015 EMT/RMT: 7.5/10.4 °C; 2016 EMP/RMP: 7.5/9.7 °C) coupled with the climatic history of very low air humidity in the region resulted in extreme evaporative conditions for regenerating species during vegetation period alongside the extreme browsing activities at the study site (Hammond & Pokorný 2020c) significantly influenced the high mortality among various natural regeneration tree species in gaps. Similar to our findings, many authors have cited the significant effects of browsing pressure (Dusan et al. 2007; Vilhar et al. 2015; Kupferschmid et al. 2019) and drought conditions (Anderegg et al. 2013; Sedmáková et al. 2019) as major sources of tree mortality among species undergoing regeneration at temperate forests in East-Central Europe. Overall, our results also support the contention that natural beech forests in Central Europe are characterized by local biotic and abiotic events (Feldmann et al. 2020).

At the individual species level, poor regeneration performances of *F. sylvatica* in gaps under coniferous stand in this study agrees with Dobrovolný and Cháb (2013) but disputes Sterba and Eckmüllner (2008), who stated that the rate of invasion potential for *F. sylvatica* to occupy an area within a pure conifers forest in central European forests is unmatched. However, the comparably good regeneration densities of *F. sylvatica* during FGS and SGS in gaps under mixed and broadleaved stands, respectively, demonstrate the resilience of *F. sylvatica* species to light-exposed environments (Čater et al. 2014) and browsing damage (Vilhar et al. 2015). Further, our study result revealing the excellent regeneration of *P. abies* in gaps from FGS to SGS under a coniferous overstorey is consistent with Dobrovolný & Cháb (2013), who also reported the same observation. On the other hand, the evidenced low yield shift of *P. abies* and *A. alba* species in gaps under broadleaved canopies indicates the significant relationship between cohabiting species at the understory. Although regeneration of *L. decidua* in gaps following disturbance was expected to be profuse across all forest types due to its fast-growing pioneer behavior in gaps (Matras & Pâques 2008). Species competition especially from *F. sylvatica* and lack of silviculture interventions such as thinning, weed control, protection against browsers etc. and other special management activities could explain the relatively limited growth of *L. decidua* in gaps.

The higher regeneration densities of all studied species during FGS illustrate the relevance of the current canopy removal management guidelines at mixed forests, Křtiny, towards the sustainability of natural regeneration. The outcome of gap-disturbance in the preceding growing season (BD) where disturbance regime characterized by small-scale and low-intensity disturbances that were variable in space resulted in favorable light conditions for the successful seedling recruitment in FGS (Rugani et al. 2013). However, under the same intensity of canopy removal management guidelines in Romania, our results of *F. sylvatica*, *P. abies* and *A. alba* natural regeneration in the three mother stands are directly opposite to the results of Stancioiu and O'Hara (2006) studies where gap-disturbance promoted vigorous growth at similar rates for all three species.

Apart from this, our results revealed that TSF light condition established negative and positive significant effects on gap regeneration of *F. sylvatica* ($r^2 = 0.34$) and *L. decidua* ($r^2 = 0.39$), respectively, during FGS. The positive significant linear relationship between abiotic TSF and biotic *L. decidua* in gaps has been mentioned already in a different study conducted at Sessile-Oak-Hornbeam and Turkey Oak Forests in western Hungary (Kollár 2017). Apparently, in another recent research under predominantly *P. abies* mixed stands, *P. abies* was the only natural regeneration tree species that established a significant negative linear relationship with TSF light condition ($r^2_{TSF} = 0.97$ at $p = 0.015$) in gaps (Hammond & Pokorný 2020c). The quantified TSF light condition in Hammond and Pokorný (2020c) ranged between 13.3 – 25.5%, while we estimated comparatively lower minimum and higher maximum values (10.6 – 28.4%) for the same gap-light condition. Generally, our finding projects the integral role of a light factor on the growth of tree regeneration and at the same time, portrays the potent ecological relationship between a particular light condition and specific species with different biological life-history attributes.

5. Conclusions

In contemporary forest management, gap regeneration is an appropriate silviculture technique for sustainable forest management in mixed stands. Our conclusions highlight the potential effect of gaps following disturbance, comparatively smaller in sizes (0.03 – 0.11 ha) but contributing significantly to increasing species composition and species diversity in mixed-species Křtiny forests. Seven (7) new species with light-demanding growth strategy (*Betula pendula, Larix decidua, Pinus sylvestris, Picea abies, Populus nigra, Quercus petraea* and *Salix alba*) that were not present in gaps in the growing season prior to disturbance in 2013 were added to species composition in the first growing season after disturbance (FGS) increased species diversity in the growing seasons after disturbance (2014 – 2016). However, all four studied growing seasons shared similar tree species in gap regeneration. *Fagus sylvatica* and *Picea abies* dominating regeneration, not surprising given the former's roles as climax species on study site and the latter's prominence in the overstorey as a planted species. Besides, stand type could probably be attributed to the prolific regeneration of *Fagus sylvatica* and *Picea abies* under broadleaved and coniferous stands while biological light demanding traits of *L. decidua* could significantly be explained for the excellent performances in gaps during the first two years after small-scale disturbance.

Generally, the micro-growing sites of gaps alone could not be associated to the dynamics and distribution of overall natural regeneration in gaps under various mother stands because the variability that can distinctively be attributed to gap and stand-level related environmental factors seems very high. Progressive decline in regeneration densities of gap regeneration was common from FGS to TGS. To a large extent, extrinsic factor like drought condition in 2015 and intrinsic factors like competition from other life forms and increasing browsing activities (unfortunately not avoided by fencing) were the explanatory factors for the observed natural regeneration dynamics in mother stands. However, at species level, inherent tolerability to light and browsing damage conditions significantly explained variations of *F. sylvatica* regeneration in gaps under coniferous, mixed and broadleaved stands from FGS to SGS, whereas growth of *P. abies* and *A. alba* were greatly hindered by the competitive presence of *F. sylvatica* under broadleaved stand. Nevertheless, lack of silviculture interventions could be explained for the growth variations of *L. decidua* in gaps under the three mother stands. The current management guidelines for small scale gap-disturbance regimes at mixed forests, Křtiny significantly influenced the higher regeneration densities of all studied species during FGS.

It is self-evident that gaps are preferential growing habitats for natural regeneration tree species with different growth strategies under mixed forests, however further management and silviculture protocols like thinning (to enhance light), vegetation control and protection against browsers etc. including climate-change tolerability strategies should be pursued for the sustainable development of natural regeneration of different tree species.

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ORIGINAL PAPER

Spatial resolution of unmanned aerial vehicles acquired imagery as a result of different processing conditions

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Abstract
Increasing availability of Unmanned aerial vehicles (UAV) and different software for processing of UAV imagery data brings new possibilities for on-demand monitoring of environment, making it accessible to broader spectra of professionals with variable expertise in image processing and analysis. This brings also new questions related to imagery quality standards. One of important characteristics of imagery is its spatial resolution as it directly impacts the results of object recognition and further imagery processing. This study aims at identifying relationship between spatial resolution of UAV acquired imagery and variables of imagery acquiring conditions, especially UAV flight height, flight speed and lighting conditions. All of these characteristics has been proved as significantly influencing spatial resolution quality and all subsequent data based on this imagery. Higher flight height as well as flight speed brings lower spatial resolution, whereas better lighting conditions lead to better spatial resolution of imagery. In this article we conducted a study testing various heights, flight speeds and light conditions and tested the impact of these parameters on Ground Resolved Distance (GRD). We proved that from among the variables, height is the most significant factor, second position is speed and finally the light condition. All of these factors could be relevant for instance in implementation of UAV in forestry sector, where imagery data must be often collected in diverse terrain conditions and/or complex stand (especially vertical) structure, as well as different weather conditions.
Key words: spatial resolution; ground resolved distance; light conditions; object identification; forestry sector

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1. Introduction

Unmanned aerial vehicles (UAV) or Unmanned aerial systems (UAS) have recently become increasingly available and thus ceased to be the prerogative of the army, and few scientific institutes. At present, inexpensive, user-friendly UAVs, with sufficient potential for aerial imaging can be easily purchased. Together with recent development in processing of digital imagery this brings new opportunities for on-demand monitoring available even for non-specialized practitioners (Pricope et al. 2019).

Consequently, new questions related to UAV imagery do emerge, such as what is the smallest object that can be identified on the image acquired on certain flight height, or what are the minimum required lighting conditions to perform imagery obtaining mission suitable for measurement of selected forest or tree parameters.

In other words, UAV imagery is facing new challenges in terms of describing requirements necessary to meet expected quality (Lee & Sung, 2016) or quality standardization (Meißner et al. 2018). These challenges would be managed with regard to specific natural conditions. That is very relevant in forestry, a sector which is typical with very complex and variable conditions as for topography and forest stand traits. Spatial resolution is one of the basic characteristics of digital imagery with significant impact on object recognition results, therefore influencing any output derived from original UAV imagery. The smallest detectable object is related to this resolution and for the user interested in mensuration of particular variable or object (crown, individual tree), the information about the spatial resolution is crucial. Spatial resolution is often described by Ground Sampling Distance (GSD) (Orych 2015) which is a measure, that builds on known geometric parameters of camera and distance between camera and target.

Few studies examine further concepts such as Resolution, Resolution power (Lee & Sung 2016), Ground resolved distance (GRD) (Orych 2015) or True Ground

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sample distance (tGSD) (Meißner et al. 2020) which takes into account whole complex of characteristics influencing the result image quality, including such variables as optical error of camera, atmospheric conditions etc. These approaches are based on visual analyses of different calibration targets, such as Bar target, Slanted edge test or Siemens star test to name few (Orych 2015).

Trends of spatial resolution related studies are described by Lee and Sung (Lee & Sung 2016). Siemens star calibration target is one of the methods, which is repeatedly reported to be used, to evaluate GRD (Cramer 2013; Dabrowski & Jenerowicz 2015; Dabrowski et al. 2015; Orych 2015). This test does not need any special equipment in terms of calibration target designing. Evaluation can be done based on visual analyses, without any special software. This target is also flexible in terms of flight direction and allows for defining resolution in a continuous way (Orych 2015).

This article is a first stage of study aimed at exploring the spatial resolution of images obtained by UAV DJI Phantom 3 Professional in different conditions. Following stage will explore how this spatial resolution influences the outcomes of typical Structure From Motion SFM processing pipeline resulting in surface point cloud of mixed forest stand.

Basic hypothesis assuming, that spatial resolution depends inter-alia on the flight altitude, flight speed and lighting conditions is examined in this first stage. The main aim of this work is to analyse which flight parameter, and with what impact is influencing the final GRD.

2. Material and methods

2.1. Explanation of basic terms

First of all, it is necessary to explain basic terms, which relates to the merit of our study. The terms are specifically Ground sampling distance, Ground resolved distance and Siemens star.

Ground sampling distance (GSD) in digital imagery represents the size of surface represented by single pixel of image. It is a theoretical measure that takes into account only geometry of camera (resolution of the sensor and lens focal distance) and distance to imaged surface or object. Other factors, such as system optics, interior noise, etc. are not considered (Orych 2015).

GSD can be calculated based on the real size of a single pixel on the sensor x, focal length of camera f and distance between camera and target h through formula:

$$GSD = x * h / f \qquad [1]$$

Ground resolved distance (GRD) represents the smallest recognizable element on image. It can be determined by visual analysis on the basis of specific calibration targets, such as Siemens star (Orych 2015). Contrary to GSD, GRD is evaluated as a result of all factors influencing spatial resolution of imagery.

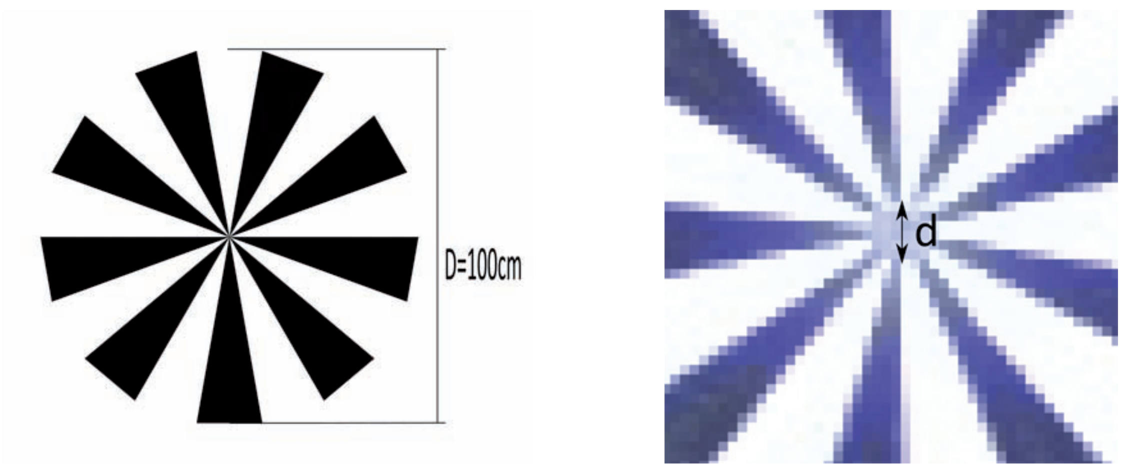
Siemens star represents the calibration target suitable for determination of GRD without any specific equipment other than target. Two types of Siemens star are used. Sinusoidal type for laboratory uses and Binary for outdoor testing. Binary Siemens star is formed by radial sectors alternating black and white color (Fig. 1a).

GRD determination using Siemens star with n sectors and diameter D is based on measuring the diameter d of blurred center up to the point where black and white sectors can be easily recognized (see Fig. 1b).

GRD can be then calculated based on formula:

$$GRD = \pi * d / n \qquad [2]$$

GRD is key factor in subsequent analysis and data extraction from the imagery. And worse GRD definitely leads to lower success in studies dependent on pixel quality. For example, when detecting the tree position in small trees and regeneration of forest stands, or when trying to evaluate spectral reflectance on studies of tree health and physiology status (Klouček et al. 2019).



a) b)

Fig. 1. Siemens star calibration target used in study (a). Blurred center (with diameter d) of Siemens star calibration target (b).

2.2. Calibration target and study site

Binary Siemens star with 18 sectors of 100 cm diameter (Fig. 1a) printed on paper and laminated to prevent damage, served as a calibration target. Such target in theory allows measuring GRD from 0 to 17.453 cm. This should be sufficient, as the maximum planned flight height was 100 m with GSD 4.375 cm.

Target was placed in a paved, level area allowing for undisturbed UAV flying in vicinity of Forest Management Institute in Brandýs nad Labem, Middle Bohemia region (WGS 84: 50.1876N, 14.6702E).

2.3. Images acquisition

DJI Phantom 3 Professional as an example of low-cost, user friendly, widely available UAV was used to acquire images. Parameters of camera DJI FC300X carried by this UAV are specified in Table 1 (DJI 2017).

Table 1. DJI FC300X Camera specification.

Sensor	Sony EXMOR 1/2.3" CMOS Effective pixels: 12.4 M
Lens	20 mm (35 mm format equivalent) f/2.8 focus at ∞
ISO Range	100–1600 (photo)
Electronic Shutter Speed	8–1/8000 s
Image Size	4000×3000

Overall, four flight missions were performed to cover different light conditions, acquiring images in different altitudes roughly in 5-meter steps and different horizontal speed of flight. Camera pitch was set to 90 degrees and according to EXIF data originating from UAV Inertial Measurement Unit (IMU) this value was kept in all images with maximum deviance 0.1 degree, therefore all images are considered as nadir images.

2.4. Images processing

Non nadir exclusion: The distance between Siemens star target and image center is expected to influence GRD (Honkavaara et al. 2006a). As this study is primarily targeted on other influential conditions, images where Siemens star was out of the middle area of image defined according to grey area (see Fig. 2) were discarded, to eliminate influence of this variable.

EXIF metadata of relative altitude, x, y, z axis speed, aperture, exposure time and ISO, were extracted from all images using Exiftool utility (Harvey 2016). Images where z axis speed was higher than 0.1 m/s as well as images with ISO value other than 100 were discarded. Speed was calculated based on x, y, z axis speed vectors. Aperture was set to constant value (maximum aperture was used that equals to 2.0 in case of this camera) in camera settings prior to each flight. Still EXIF metadata were used to confirm (successfully), that all images are of the same aperture value.

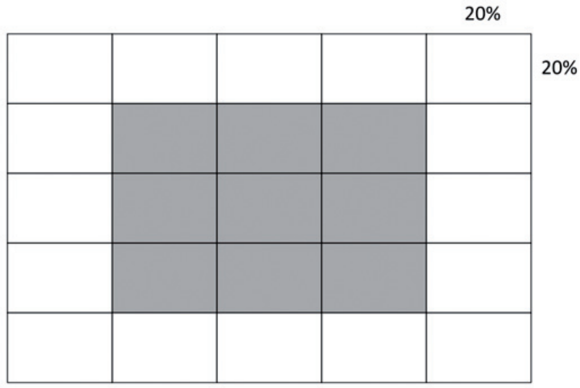


Fig. 2. Middle area (gray rectangles) of picture.

Using only images with same ISO and aperture allows to use exposure time as a descriptor of lighting conditions. Characteristics of resulting images set are summarized in Table 2.

2.5. GRD determination

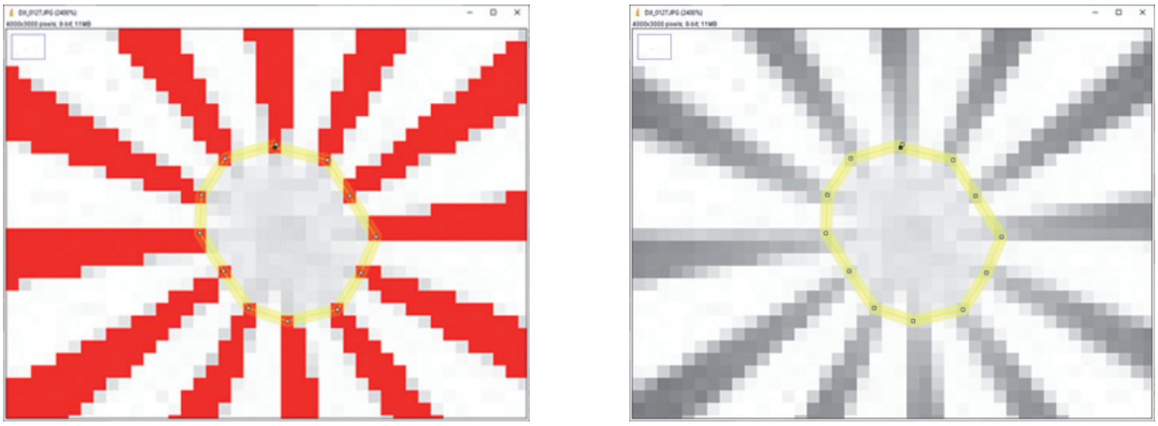
In each image of resulting dataset, perimeter of blurred center area of Siemens star calibration target was measured using ImageJ software (Schneider et al. 2012).

Original RGB image was first transformed to 8-bit grayscale type using the ImageJ function Type/8-bit which uses the formula gray =(red + green + blue)/3. In such image value of each pixel varies from 0 to 255. Using threshold function, area with pixel values from 0 to certain value, well corresponding with blurred center area, was highlighted. In each of nine dark (highlighted) sectors the closest-to-the-center point was identified as a border of blurred center area.

As this area is rarely of regular circular shape, rather than measuring the diameter of this area, segmented line tool was used to connect all sectors and measure the perimeter p of blurred area as in example Fig. 3a. Same area without applied threshold highlighting is in Fig. 3b.

Table 2. Flight missions characteristics.

Date	Weather	Images	Altitude [m AGL]		Speed [m/s]		Exposure [s]	
			min	max	min	max	min	max
2019–07–26	Sunny, very light wind	21	4.9	105.2	0.0	0.1	1/1750	1/811
2020–01–17	Sunny, very light wind	60	30.3	100.8	0.0	14.4	1/514	1/252
2020–10–08	Partly cloudy, light wind	64	6.2	70.3	0.0	12.6	1/736	1/176
2020–10–24	Mostly sunny, light wind	39	10.0	70.0	0.0	9.5	1/561	1/336
Total		184	4.9	105.2	0.0	14.4	1/1750	1/176



a) b)

Fig. 3. Identification of blurred center area with (a) and without threshold highlight (b).

Using this method, formula to determinate GRD can be adjusted accordingly with perimeter *p* and number of segments *n*.

$$GRD = p/n \qquad [3]$$

GSD was derived from altitude and known parameters of camera according to formula 1.

All statistical analyses were carried out in R-Studio version 1.4.1103 (RStudio Team 2019) with R version 4.0.3 (R Core Team 2020) using following libraries: JTools(Long 2020), Readr (Wickham & Hester 2020), GGplot2(Wickham 2016).

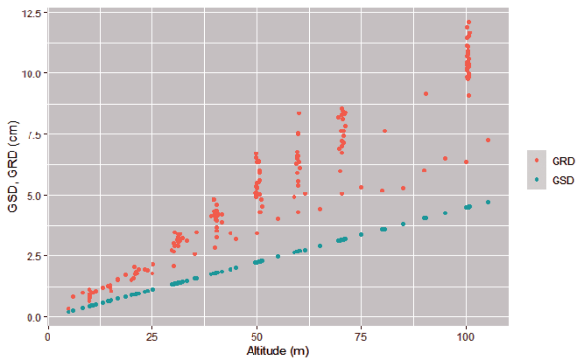


Fig. 4. Plot of GSD and GRD related to altitude.

3. Results

In total 184 images from 4 flight missions were used for GRD evaluation (results overview is in Table 3).

Table 3. Basic statistics of GSD and GRD parameters of each of 184 images.

	GSD	GRD	GRD/GSD
	[cm]		[unitless]
Min	0.221	0.340	1.389
Median	2.250	4.864	2.220
Mean	2.335	5.205	2.189
Max	4.734	12.113	3.087

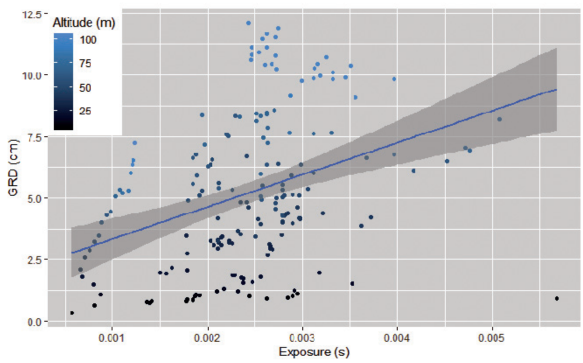


Fig. 5. Scatterplot of relation between GRD and **e**xposure.

Impact of altitude on GRD is clearly visible in Fig. 4 with higher values of GRD in higher altitudes, though it is obvious that in higher altitudes additional factor influences the resulting GRD.

Inspecting the relationship between GRD and exposure time shows certain positive trend (Fig. 5). This can be translated as a better spatial resolution (lower GRD) is reached in better lighting conditions (shorter exposure time).

Also, relation between GRD and flight speed shows expected trend describing that with increasing speed the GRD is increasing (Fig. 6). In other words, spatial resolution gets worse with increasing speed.

To describe GRD dependence on predictor variables (exposure, altitude and speed), linear regression methods were used.

First attempts led to models violating the basic linear model assumptions, namely the assumption of normally distributed residuals.

Therefore, different transformations of GRD variable were applied with the best results of square root transformation. This transformation used in stepwise modelling approach led to final linear model described in Table 4.

Table 4. Results of linear model describing the relationship of square root of GRD as a dependent variable of predictors: Altitude, Speed and Exposure. $F(3,180) = 855.306$, $p = < 0.001$, $R^2 = 0.934$, Adjusted $R^2 = 0.933$. All predictors are mean-centered and scaled by 1 s.d.

Variable	Estimate	Std. Error	t value	p value
(Intercept)	2.167	0.014	159.527	< 0.001
Altitude	0.614	0.015	41.054	< 0.001
Speed	0.115	0.015	7.474	< 0.001
Exposure	0.066	0.014	4.561	< 0.001

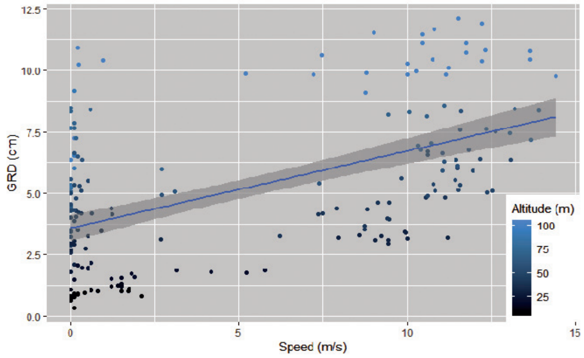


Fig. 6. Scatterplot of relation between GRD and speed.

Using Shapiro-Wilk normality test on residuals of this model resulted in p–value of 0.7285, therefore normal distribution of residuals could not be denied. Linear model is described in Fig. 7, 8 and 9. Histogram of residuals and other results indicate good fit of the model.

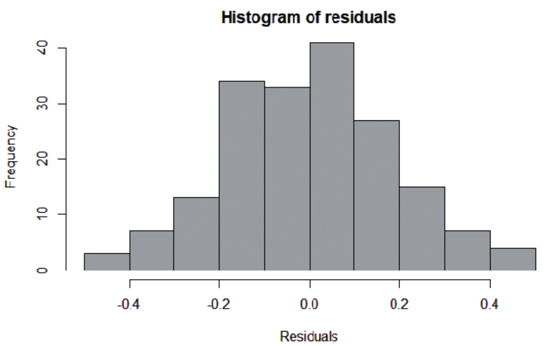


Fig. 7. Linear model – histogram of residuals.

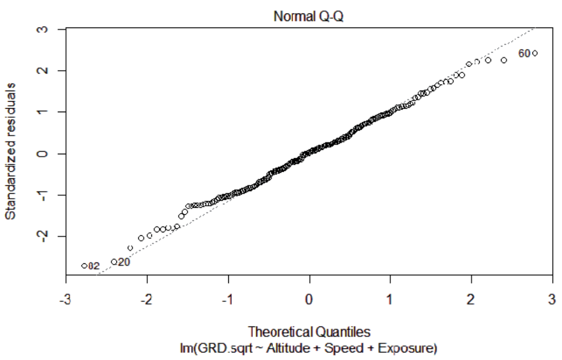


Fig. 8. Linear model – Q–Q plot.

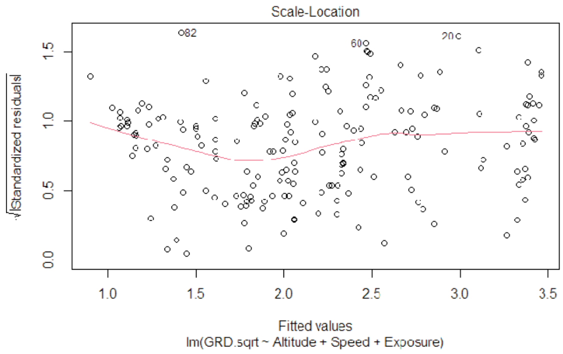


Fig. 9. Linear model – Scale – Location plot.

Further attempts on creating linear model with interactions between predictors led to only slightly better results in Adjusted R^2 with high trade-offs in terms of increased complexity and lower explanatory value of the model.

4. Discussion

Recently mensuration of various variables by means of UAS become more and more available to broad audience, interested in the output. Though they don't need any more to study principles of UAV flying (propellers, flying mechanisms etc.) which are sufficiently handled by computers, they still face challenges how and when acquire the imagery to get the best results. Influence of different conditions (lighting conditions, flight height and flight speed) on resulting spatial resolution was examined in this study.

Existing studies targeted on UAV imagery acquiring mission options deal usually with GSD in terms of spatial resolution. This study goes further and demonstrates easy procedure to estimate more realistic spatial resolution in form of GRD for particular UAV setup, thus increasing the predictability of acquired image quality and also increasing the accuracy and precision of the results. Our main question was to provide readers with information: which of the selectable flight parameters height, speed, light has the highest influence on final quality and which is lowest (potentially could be sacrificed in favor of the most important one).

Evaluation of presented linear model, apart from expected negative influence of altitude on spatial resolution, proved also negative influence of speed and positive influence of better lighting conditions. In other, more general words, results of this study confirm, that best spatial resolution of UAV imagery can be reached by performing flight missions in lower flight height, with lower flight speed and better conditions in terms of available light. These results are in line with expected outcomes, although the influence of lighting conditions seems to be rather minor.

Results show, that GRD was always higher than GSD as GRD/GSD ratio takes on values from 1.4 to 3.1 with mean value 2.2. Similar trend with higher GRD compared to GSD was published by Lee (Lee & Sung 2016) although the difference was much lower with GRD/GSD ratio between 1.2 and 1.4. Cameras used in quoted study (Lee & Sung 2016) were Canon (IXUS 127 HS) and Sony (NEX-5 N), both of them of better specification than camera used in this study.

Similar results were achieved by Dabrowski (Dabrowski et al. 2015). In this case GRD was examined as a linear function of altitude with GRD/GSD ratio approximately 2.6 and 2.5 for Sony (NEX-5) and miniMCA camera respectively.

GRD to GSD ratio of 1.3, 1.8 and 1.3 was reported in (Cramer & Zhang 2020), using images of Siemens star captured by DJI Phantom 4 , DJI Phantom 4 RTK and Phase One iXM100-RS camera in flight altitudes 28,25 and 47 respectively.

Resolving power derived by the means of Siemens star target on imagery obtained by Intergraph DMC digital large-format photogrammetric sensor carried on airplane led to 1.2 to 1.5 times higher results than GSD as concluded Honkavaara (Honkavaara et al. 2006a, b).

Worse spatial resolution was observed on images taken at higher horizontal flight speed. These results can be compared to much higher GRD to GSD ratio (10 to 15 times higher) of images obtained by S.O.D.A camera on SenseFly eBee Plus fixed wing UAV in (Stöcker et al. 2018). Quoted study does not state the values of UAV horizontal flying speed, but considering the fixed wing design of UAV in this case, higher speed might be one of the reasons for worse results of spatial resolution, same way as our study suggests. Results also indicate positive relation of spatial resolution to better lighting conditions. This is in line with Lim (Lim et al. 2018a), who reported different results of GRD based on lighting conditions. Using Sony A5100 camera carried on octocopter UAV, GRD was 1.1 to 2.3 (depending on the flight altitude) times higher than GSD in images taken on sunny conditions, whereas 1.6 to 3.7 times higher than GSD in images obtained at cloudy day.

Similar relationship to lighting conditions were reported in (Lim et al. 2018b). Images of Siemens star, captured by octocopter carried Sony A5100 in altitudes 20 to 80 meters, resulted in GRD 3–12 times higher than GSD in very cloudy day comparing to 1.2 to 3 times higher GRD than GSD in sunny or little cloudy day.

5. Conclusions

Our work focused on description of the first stage of exploring processes for the optimal ways to quantify characteristics of remote sensing data obtained by common commercial UAV (in our case DJI Phantom 3 Professional UAV) in forestry. The main motivation was to provide the reader and potential practitioner of forest mensuration by the means of remote sensed data with information about the impact of different height, speed and possible light condition on the image quality. In general, the image quality is clearly linked to quality and accuracy of information obtained from such image by means of photogrammetry.

Spatial resolution of imagery is considered as one of the most important preconditions influential to any result of remote sensing application. Therefore, special care was given in this first stage to Ground resolved distance as an objective means to describe spatial resolution. Influence of different conditions in form of flight altitude, flight speed and lighting conditions on resulting spatial resolution was examined. Study proved, that spatial resolution is highly dependent on flight altitude with better resolution resulting from lower flight altitudes, less influential, but still highly significant proved flight speed. Comparing to previous two factors, lighting conditions, although still significant, are of the least influence. This can be translated as a positive message for the flexibility of use of UAV in forestry, as the most unpredictable characteristics of flight mission, lighting conditions as a result of the weather conditions, seems to be of rather low impact on resulting spatial resolution. Concluding knowledge both from previous studies and this work, UAVs can be recommended for forestry sector as a reliable device in terms of imagery data acquisition in forest stands and open areas.

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Qualitative and value production of tree species in mixed spruce-fir-beech stands under the conditions of the Western Carpathians

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Abstract

Value production is one of the most important information for comparing different tree species composition and management strategies in forestry. Although the value production of forest stands is affected by various factors thinning can be considered as one of the most important one. This paper aims at the evaluation of qualitative and value production in mixed Norway spruce (*Picea abies* [L.] Karst.), silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) stands, which were managed by crown thinning for a period of 44 to 50 years and/or left to self-development. More than 1,500 individual trees aged from 61 to 132 years from 15 subplots established in western part of the Low Tatras Mts. and the Great Fatra Mts. in Slovakia were assessed. The proportion of stems in the highest quality A (stem quality classes) reached a low percentage, i.e. 12% in beech, 28% in spruce and 13% in fir out of the number of evaluated trees. The percentage of the highest quality log classes (assortments I + II) of beech ranged from 0 to 23% and of coniferous ones from 2 to 12%. Regarding the management method used, this percentage accounted for 0.1 to 23% for plot with self-development, whereas in plots with tending it was from 1 to 23%. Value production of coniferous tree species was always higher compared to beech, regardless of the management method. Regarding individual tree species, we found the highest value production in fir (81.4 € m^{-3}) and the lowest in beech (46.5 € m^{-3}).

Key words: Norway spruce; silver fir; European beech; stem quality; assortment structure; thinning

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1. Introduction

Extensive dieback of spruce monocultures in recent years (Hlásny & Sitková et al. 2010; Hlásny et al. 2017) or the high proportion of salvage cutting was evident due to abiotic (wind, drought) and biotic (bark beetles) harmful factors in Slovakia (Kunca et al. 2019) and also in other countries, for example in Czech Republic (Šimůnek et al. 2020). It result in establishment or formation of mixed stands (Pretzsch et al. 2014, 2015) which are generally considered to be more resistant (Vacek 2017; Vacek et al. 2020). This means especially the so-called Carpathian mixture of Norway spruce, silver fir and European beech. The mixed stand can make better use of the habitat and its available space (Bulušek et al. 2016), especially if the represented tree species have different biological properties and ecological requirements (Korpeľ 1989; Králíček et al. 2017; Vacek et al. 2017; Mikulenka et al. 2020).

The research of mixed stands focused mainly on monitoring the height or diameter growth of individual tree species (Künstle 1962; Monserud & Sterba 1996; Petráš et al. 2014a; Sharma et al. 2019). Attention was also paid to the evaluation of results of volume production and increments (Kennel 1966; Míchal 1969; Prudič 1971; Hink 1972; Pretzsch 1992; Pretzsch & Schütze 2009; Lebourgeois et al. 2014; Petráš et al. 2014b; Röβiger et al. 2019). By investigation the causes of different growth and production of mixed stands, most authors focused on site conditions, climate, tree species composition, social status of trees, method of mixture, historical land use and age of stands (Magin 1954; Kennel 1965, 1966; Hausser & Troeger 1967; Mitscherlich 1967; Hink 1972; Mettin 1985; Kramer et al. 1988; Pretzsch 2009; Pretzsch et al. 2010; Bosela et al. 2015; Slanař et al. 2017). Such results were mostly derived from measurements performed on simultaneous plots in homogeneous or mixed parts of stands. Relatively fewer results come from permanent research plots established and managed in young mixed stands (Štefančík 1977; Paumer 1978; Novák et al. 2017). More attention was paid to thinnings, or the long-term impact of tending on their structure, production and stability (Assmann 1961; Molotkov 1966; Leibundgut et al. 1971; Štefančík 1977; Hladík 1992; Štefančík & Štefančík 2001, 2002, 2003; Adamic et al. 2017; Hilmers et al. 2019).

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Only few authors evaluated by more detailed effect of tending (Štefančík 1977, 2004a, b) or different management (Štefančík et al. 2018) on quality classes. Rais et al. (2020) investigated beech sawn timber and Pretzsch & Rais (2016) compared the wood quality in monocultures with mixed stands. On the value production in mixed stands were focused papers by Petráš et al. (2015, 2016, 2017). Tree species diversity versus wood quality were studied by other authors (Hausser & Troeger (1967; Kramer et al. 1988; Benneter et al. 2018). Therefore, our intention was to fill the existing gaps and connect knowledge in this area to the value production of mixed spruce-fir-beech stands.

The aim of this work was to evaluate (i) quality of stem and stem damage, (ii) assortment structure, (iii) value production in mixed spruce-fir-beech stands, which were systematically managed for about 50 years and their comparison with stands without interventions. We hypothesise that coniferous tree species in mixed stands might produce higher value production in comparison to beech because better quality wood is expected to be produced.

2. Material and methods

2.1. Study area

Empirical material from repeated measurements on four series (Fig. 1) of 15 permanent research plots (PRPs), with different area from 0.10 to 0.56 hectare was an objective of the study. They were established in the 60s and 70s of the 20th century, was used for this purpose. Plots are located in the western part of the Low Tatras Mts. and the Great Fatra Mts (Fig. 1). They are at an altitude of 690–970 m and according to the phytocenosis they are classified into following forest types groups: *Fageto-Aceretum* (FAc), *Abieto-Fagetum* (AF) and *Fageto-Abietum* (FA). Plots are situated in the 5th and 6th forest altitudinal zone with an average annual temperature of 4.2–6.8 °C and an average annual precipitation between 900 and 1200 mm. The age of tree species (stands) at the time of the PRP establishing ranged from 15 to 80 years and/or 61–132 years at the last evaluation (Sharma et al. 2019). Tree species proportion on PRPs is in a wide range (Table 1).

Until the establishment of PRPs, almost no systematic tending interventions were carried out. If yes, then only a slight intervention solely for the purpose of removing dying and dead trees was carried out (Štefančík 1977). Measurements were repeatedly performed on all research plots and/or evaluations at regular 5-year intervals. So far, 10 or 11 measurements have been carried out. The area of the PRP varies between 0.10 and 0.56 ha. All living trees with a diameter of 3.6 cm ($d_{1.3}$) and more are registered by numbering on all plots. On the plots marked as H, Štefančík's free crown thinning is applied (Štefančík 1984) and plot 0 serves as the control (without interventions).

2.2. Data collection

In addition to standard biometric measurements (breast-height diameter and height of trees), the trees were classified according to their sociological status into the tree class 1–5 (according to Kraft 1884) and the quality char-

Fig. 1. Localization of mixed stands on four series of permanent research plots.

Table 1. Tree species composition according to basal area on investigated permanent research plots (PRPs).

PRP	Plot	Age [years]	Tree species [%] Spruce	Fir	Beech	Other	Altitude [m a.s.l.]	Soil type
Stará Píla	I – 0	17 – 21	16.1	33.9	50.0	—	690 – 720	Cambisol
		61 – 65	5.1	18.9	75.4	0.6		
	II – 0	17 – 21	19.6	60.1	19.6	0.7		
		61 – 65	26.9	30.0	31.1	12.0		
	I – H	17 – 21	1.6	54.8	43.6	—		
		61 – 65	6.0	53.7	40.3	—		
	II – H	17 – 21	55.6	24.4	17.8	2.2		
		61 – 65	43.5	11.4	34.3	10.8		
Motyčky	II – 0	41 – 48	15.7	50.9	23.5	9.9	810 – 870	Calcaric Cambisol
		86 – 93	18.8	20.8	47.8	12.6		
	I – H	41 – 48	13.2	51.8	27.3	7.7		
		86 – 93	17.2	30.9	41.0	10.9		
	III – H	41 – 48	13.3	49.2	26.4	11.1		
		86 – 93	18.9	30.5	37.7	12.9		
	IV – H	41 – 48	6.8	36.7	50.8	5.7		
		86 – 93	7.7	30.6	56.8	4.9		
Korytnica	I – 0	50 – 58	24.3	25.3	46.2	4.2	930 – 970	Cambisol
		100 – 108	30.5	17.8	48.0	3.7		
	III – 0	50 – 58	16.3	17.1	55.7	10.9		
		100 – 108	22.6	10.5	54.3	12.6		
	I – H	50 – 58	28.3	30.0	37.0	4.7		
		100 – 108	31.3	9.5	54.5	4.7		
	II – H	50 – 58	5.6	29.1	55.5	9.8		
		100 – 108	9.4	19.0	64.1	7.5		
	III – H	50 – 58	16.7	12.6	61.1	9.6		
		100 – 108	25.7	7.9	61.6	4.8		
Hrable	0	74 – 82	3.0	24.3	59.8	12.9	820 – 840	Dystric Cambisol
		124 – 132	—	17.9	80.5	1.6		
	H	74 – 82	9.9	40.5	35.8	13.8		
		124 – 132	1.6	39.5	58.7	0.2		

Spruce – *Picea abies* [L.] Karst., Fir – *Abies alba* Mill., Beech – *Fagus sylvatica* L., H – plot with crown thinning, 0 – plot with no intervention (control).

acteristics of the lower third of the stem were evaluated according to the following classification:

A – Straight, non-twisted stem, centric, without shape deformations and knots; suitable for sliced veneer production;

B – Stem with minor technical defects with solid and loose knots up to 4 cm (1–2 pieces per meter);

C – Stem with large technical defects, greater curvature, and twisted up to 4%, solid knots without limitation; unsound knots up to 6 cm for conifers and for deciduous species up to 8 cm; suitable especially for lower quality saw logs or cellulose;

D – Stem inferior to the class C, with the extensive rot, and only suitable as fuelwood.

Stem damage quite significantly predetermines the internal defects of the wood, such as rot and, in the case of beech, especially the false-heart. For this reason, not only the mechanical damage of the stems was evaluated, but also of the buttress and surface roots. During its detection, only its presence was recorded, regardless of size, intensity and position on the stem.

2.3. Data processing

From the latest measurements and evaluations of stems, the proportion of quality classes A–D and the proportion of damaged stems were calculated on each PRP. An average proportion was also calculated for each tree species. According to the models of tree assortment tables (Petráš & Nociar 1991; Petráš 1992), the assortment structure was calculated for each tree and tree species. To simplify the analysis and evaluation of results, all partial plots (subplots) with the same regime were merged. The mentioned models indicate the proportion of assortments in % for all tree species, depending on the tree diameter, the quality class of the stem, the occurrence of stem damage and, in the case of beech, on the tree age as well.

Assortments represent quality and diameter classes of logs. The quality classes of logs are characterized by the purpose of their end-use as follows:

Class	End-use
I	sliced veneers, special sporting and technical goods,
II	peeled veneers, matches, sporting goods,
III(A, B)	saw logs (IIIA – better quality, IIIB – worse quality), building timber and sleepers,
V	pulpwood, chemical and mechanical processing for cellulose and agglomerated boards production,
VI	fuelwood.

I–IIIB classes defined in the assortment tables model are also separated into 1–6+ diameter classes (1 – from 16 to 19 cm; 2 – from 20 to 29 cm; 3 – from 30 to 39 cm; 4 – from 40 to 49 cm; 5 – from 50 to 59 cm; 6+ more than 60 cm).

The assortment structure for homogeneous spruce, fir and beech stands was calculated according to the models of assortment growth tables (Petráš & Mecko 1995; Petráš et al. 1996), where the proportion of assortments in % depends on age and site index of stands.

The value of assortments was calculated as the product assortments volume and timber prices by log quality and diameter classes. Timber prices were taken from the state enterprise Forests on the Slovak Republic, Assortment price list published in 2014 (Table 2).

3. Results

3.1. Stem quality and damage

The quality and damage of stems was expressed as the proportion out of the number of trees on the PRP (Fig. 2).

The highest stem quality (A) in deciduous species (beech) was not found only on the PRP Stará Píla .

Within coniferous tree species (spruce, fir), trees with the highest quality were found only in two localities (Motyčky, Hrable). The proportion of stems in the highest quality A reached a low percentage, which did not exceed 12% for beech, 28% for spruce and 13% for fir. The higher percentage of spruce was influenced by the low number of trees (only 10% out of the total number of evaluated trees).

The proportion with the highest stem quality (A) for beech was less than 12%, with regard to two management variants monitored (tending – H, control – 0). The

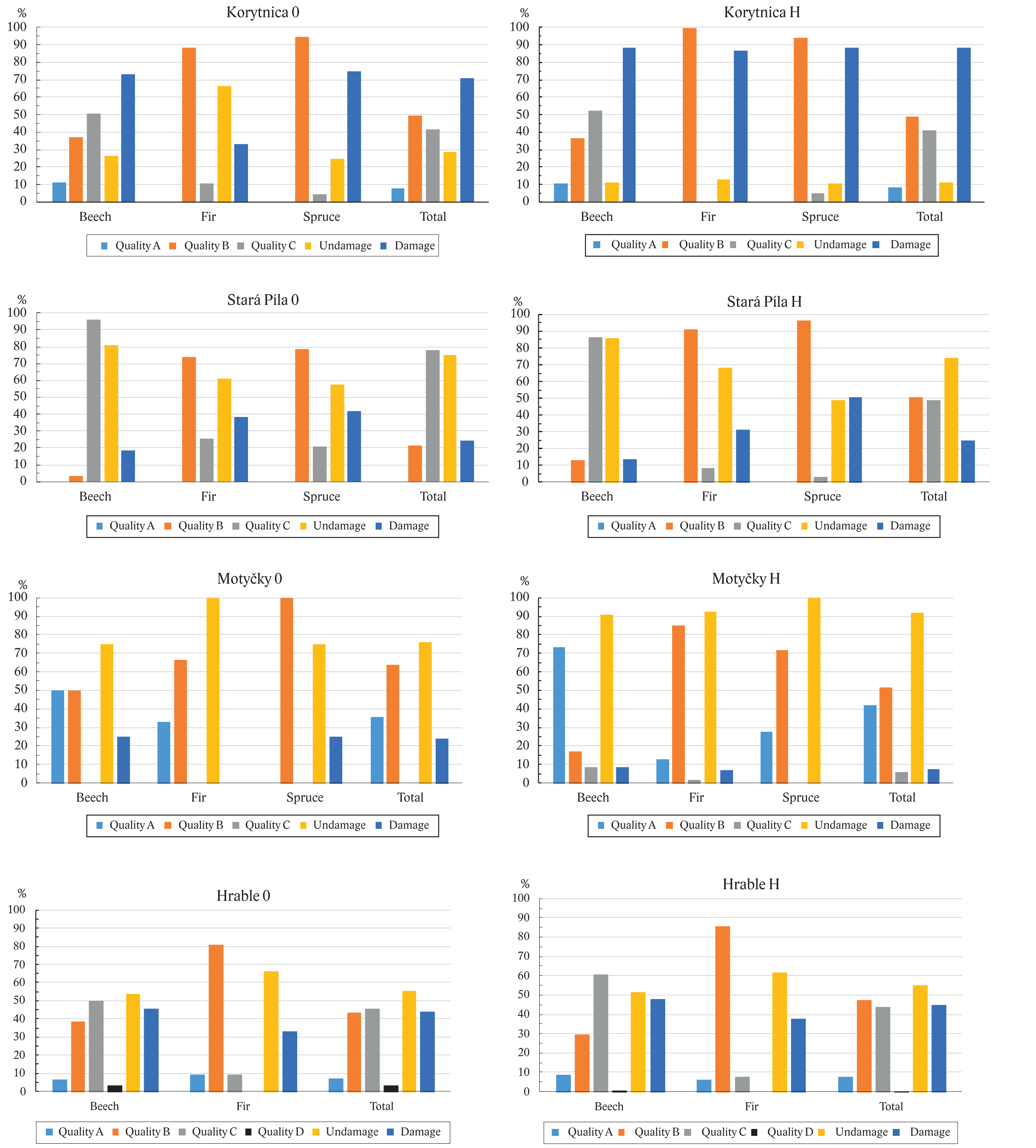

Fig. 2. Proportion of quality classes and damaged stems on given PRPs calculated from the number of trees of each tree species.

Table 2. Assortments prices (€ m^{-3}) by log quality and diameter classes of 1 – 6+ for spruce, fir and beech.

Tree species	I.4	I.5	I.6	II.2	II.3	II.4	II.5	II.6
Fir, Spruce	111	118	122	86	95	99	101	101
Beech	186	206	234	82	104	113	118	124
	IIIA.1	IIIA.2	IIIA.3	IIIA.4	IIIA.5	IIIA.6		
Fir, Spruce	37	80	84	85	85	84		
Beech	49	52	65	67	68	68		
	IIIB.1	IIIB.2	IIIB.3	IIIB.4	IIIB.5	IIIB.6	V	VI
Fir, Spruce	37	73	77	77	77	77	37	26
Beech	48	55	55	26	57	57	42	43

only exception is for the PRP Motyčky, where there was a higher proportion (50 to 74%). For conifers, the proportion of class A was from 6 to 28% in plots with tending and/or in control plots it was from 10 to 33%. In addition, highest quality of spruce did not occur in the control plot Motyčky, in contrast to the plot with tending, and/or it was completely absent in the PRP Hrable (the oldest plot) due to missing spruce proportion.

The proportion of trees with the stem quality B was always higher in coniferous species (67 to 100%) compared to beech (4 to 50%) in all plots (regardless of the management method). In total, with the exception for the control plot Stará Píla (the youngest) and control plot Hrable (the oldest), trees with the stem quality B (average quality) formed the highest percentage, with their proportion in plots with tending from 48 to 52%, and/or in control plots from 22 to 64%.

In total, the proportion of stems of quality C (worst) reached higher values in control plots (42 to 78%) compared to the plots with tending (6 to 49%). From the viewpoint of tree species, it amounted to 0 to 26% in coniferous species, or 0 to 96% in beech.

In total, the evaluation of stem damage showed everywhere always higher proportion of undamaged stems, which ranged from 11 to 92% (with the exception for the PRP Korytnica). Apart from the PRP Motyčky, the proportion of damaged stems found in control plots was always lower in comparison with the plots where thinning were carried out. In total, the proportion of damaged stems ranged from 8 to 45%, except for the PRP Korytnica, where it reached 71% in the control plot and up to 89% (Fig. 3) in the plot with tending. In the control plots, coniferous species were damaged from 25 to 75% and beech from 19 to 73%. In total, in plots with tending, it was 7 to 89% for coniferous species, and/or 9 to 88% for beech. According to species, we practically found the same damage in spruce (0 to 89%), fir (0 to 87% and beech (9 to 88%).

3.2. Assortment structure

The structure of assortments is evaluated by the proportion of quality classes of logs (Fig. 4). The proportion of the highest quality classes of logs (I + II) of beech ranged from 0 to 23% and in coniferous species from 2 to 12%. From the view the management method, the proportion in control plots varied from 0.1 to 23%, while in plots with tending it was from 1 to 23%.

The highest proportion of assortments was found for the class IIIA, where the proportion of saw logs was several times higher for conifers compared to beech. From the viewpoint of management (tending versus control), the proportion of this class was higher both for coniferous and beech.

The pulpwood proportion (Class V) was several times higher in beech compared to conifers. In terms of management, there was always higher proportion of this

Fig. 3. Damage to beech trees on the PRP Korytnica after rock landslide during the construction of a forest road (Photo: Igor Štefančík).

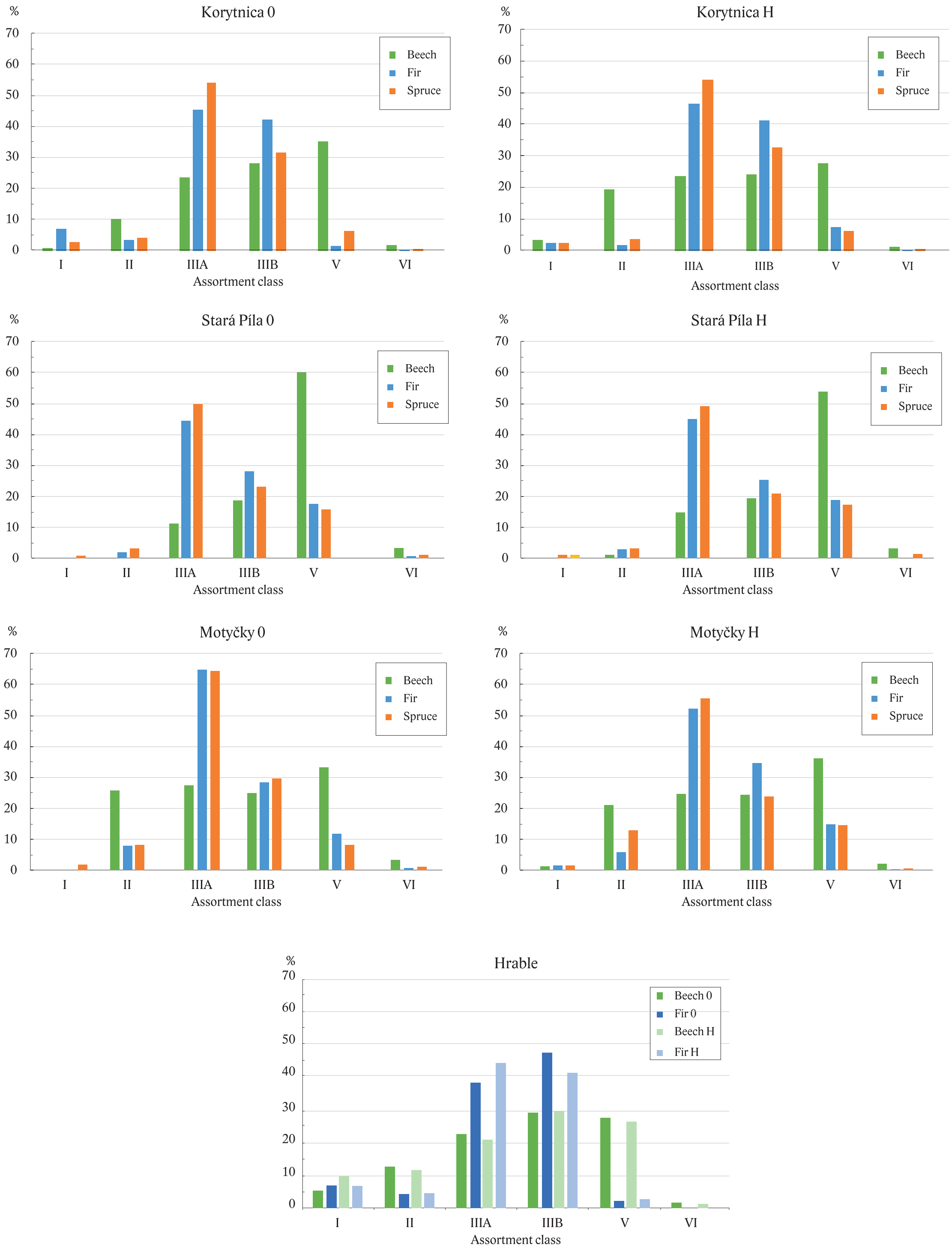

Fig. 4. Proportion of logs in assortment classes by tree species on PRPs.

class in plots with tending in comparison with the control plots, for coniferous tree species. In case of beech, it was found opposite relationship.

3.3. Value production

It is presented in € per 1 m^3 (Fig. 5). For control plot of beech it ranges from 47 to 51 € m^{-3}, and/or 65 to 81 € m^{-3} for coniferous species. In plots with tending, it varied from 47 to 61 € m^{-3} for beech, and for conifers it was from 66 to 80 € m^{-3}. From the mentioned above, it is clear that the value production of conifers was always higher compared to beech, regardless of the method of management. In terms of individual species, fir has the highest value production (81 € m^{-3}) and beech the lowest (47 € m^{-3}). As for beech, the mean value production for control plot was 54 € m^{-3} and 57 € m^{-3} for thinned plots.

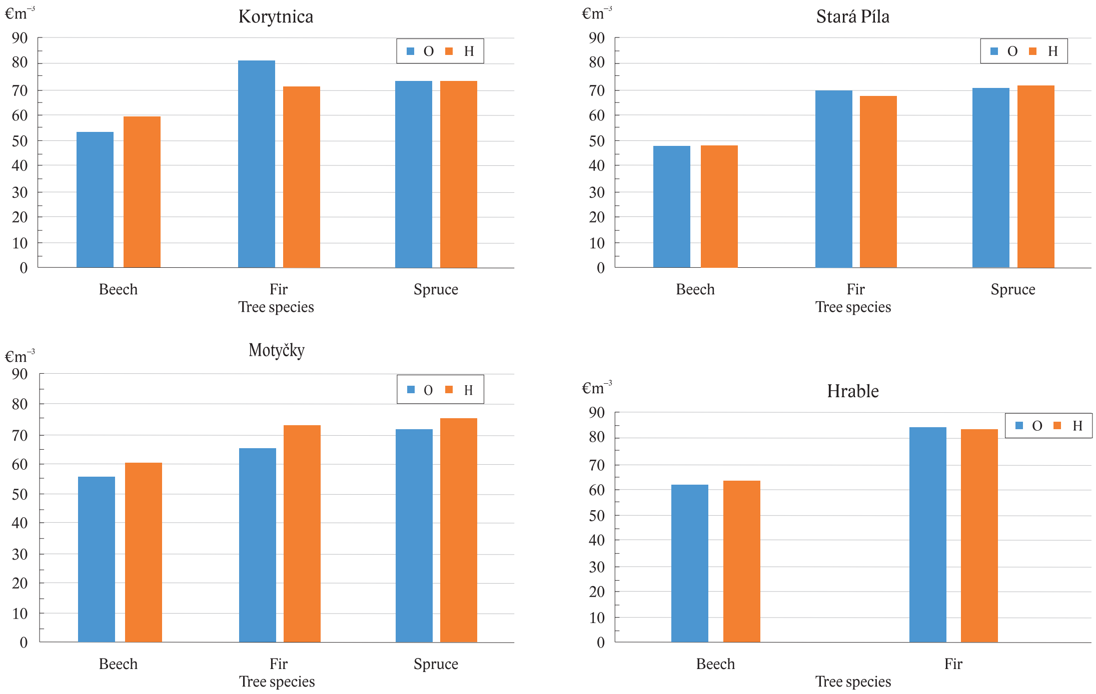

Fig. 5. Average value production on the PRPs by tree species and management.

Consequently, the mean value production for conifers was practically the same (72 and 73 € m^{-3}).

4. Discussion

4.1. Stem quality and damage

The proportion of the highest stems quality (A) reached a low percentage for all species on all plots. Similar results were found by Petráš et al. (2015) for mixed stands of spruce, fir and beech, when the proportion of beech in the highest quality class A was only 6.4%. Much higher values for beech, but in pure beech stands were reported by Štefančík et al. (2017). The proportion of 31 and 39% was found for control plots, and/or on a plot with crown thinning it was up to 57–69%. Similarly, Petráš et al. (2015, 2016) state a significantly higher proportion of up to 30% of the highest quality stems in homogeneous beech stands. In contrast, in mixed stands (beech with spruce and fir), they found 24% less stems of the highest quality (Class A) and 13% fewer stems of average quality (Class B) compared to pure stands. Our results confirmed worse stem quality of beech in mixed stands in comparison with pure ones. Wiedemann (1951) suggested this was due tu vertical and horizontal structure of mixed forests where less dense crown canopy enables longer survival and consequent branch roughening than in pure stands with their more concentrated single-layer canopy.

Stem damage will significantly reduce stem quality (Račko & Čunderlík 2011) and thus its proportion in the quality class A (Petráš et al. 2015). Results showed larger damage in plots with tending, which is related to the performance of felling interventions. As a result, stems are often damaged when they are pulled out of the stand. Spruce and beech in the growing season are particularly sensitive (Vacek et al. 2019, 2019a). Higher proportion of damaged spruce trees in mixed stands compared to pure ones was also found by Petráš et al. (2015). From the PRPs monitored, the proportion of damaged stems in the PRP Korytnica was significantly the highest, regardless of the management variant. The explanation is a little bit paradoxical. This PRP is located on a steep slope below the forest road. During the construction of this road in the past, larger rocks collapsed due to gravity and thus significantly damaged most trees by hitting the stems (Fig. 3). Beech stem quality can also be influenced by extreme slope, stem bending with skew tree should be caused by tree competition and plagiotropic growth of beech crowns (Bulušek et al. 2016). Furthermore, strong heliotropism negatively influences beech lengthwise and crosswise shape and also its spiral grain (Krammer et al. 1988; Pretzsch & Schütze 2009).

4.2. Assortment structure

The finding of the higher proportion of better assortments in plots with tending in comparison with control plots is also confirmed by our results from pure beech stands (Štefančík et al. 2018). For beech, they found 4 to 22% of I+II assortments from the stand volume of plots with tending, and/or 6 to 19% on control plots. For comparison, in mixed stands of spruce, fir and beech in this study, the classes I+II accounted for 1 to 23% for beech in the plots with tending, or 0.1 to 23% in control plots. We found lower values for fir (2 to 12%) and spruce (3 to 13%). Petráš et al. (2015) found similar values in mixed stands, i.e. 5% for beech and for fir and spruce 8% each. The importance of tending with an emphasis on its timeliness for achieving quality beech assortments is also stated by Klädtke (2002), who found a remarkable reduction in value production in the case of delayed thinning realisation.

The dominance of assortments IIIA and IIIB of coniferous species (spruce, fir) with the proportion of 30 to 50% is also stated by Petráš et al. (2015). These values are very similar to our results (22 to 57%). We found the lower proportion of IIIA and IIIB beech assortments (12 to 24% and/or 20 to 30%), which corresponds to the data published by Petráš et al. (2015), i.e. 18 and 27%.

4.3. Value production

The resulting effect of tending is reflected by value production, which depends on the stem quality and its damage, volume, assortment structure and prices, which are higher for valuable assortments and vice versa (Petráš et al. 2015). Results of value production showed higher values for spruce and fir, and lower for beech. This corresponds to the course of value production of trees by assortment tables and wood prices (Kulla et al. 2016). Hausser & Troeger (1967) reported that fir produces 9% greater value than spruce in mixed spruce-fir stands because of their greater diameter. At the same time, this is in accordance with the research results of Petráš et al. (2017), who determined the value production of different tree species, depending on the diameter, stem quality and damage as well. For mean diameters in the stands monitored by us, they state value production in damaged stands for fir in the range of 55 to 80 € m^{-3}, depending on the stem quality (A–C), for spruce 60 to 83 € m^{-3}, and/or 43 to 63 € m^{-3} for beech. A comparison of the value production of beech in pure stands (aged 83 to 105 years in the plot with tending) showed values of 71 to 82 € m^{-3}, which are higher values than in mixed stands (Štefančík et al. 2018). It is also related to the competition (intraspecific or interspecific) of tree species, which plays an important role in the quality of stems (Merganič et al. 2016; Höwler et al. 2019). This is in accordance with the statement about the poorer quality of beech in mixed stands compared to pure ones, and/or about its lower value production (Petráš et al. 2015, 2018). For comparison, Kożuch, Banaś (2020) reported the average price (value production) of 77.5 € m^{-3} for beech roundwood in Austria for the period of 2005–2018.

It can be stated that in terms of quality and value production, the cultivation of mixed (spruce, fir and beech) stands is justified and/or desirable. Firstly, from the aspect of increasing biodiversity (Bauhus et al. 2017), strengthening static stability (Pretzsch & Forrester 2017) and, last but not least, from an ecological point of view (Bauhus et al 2017a), especially in connection with the impacts of climate change on forest stands (Pretzsch et al. 2017; Bravo-Oviedo et al. 2018).

5. Conclusions

A comparison of the quality and value production of mixed spruce-fir-beech stands (aged 61 to 124 years) showed differences that depended on age, tree species composition and stand management. In general, a relatively low proportion of the highest quality assortments for all tree species was achieved, regardless of tending or self-development. In terms of the assortment structure, a slightly higher proportion was achieved in plots with long-term tending (44 to 50 years). Value production of conifers was always higher in comparison with beech, regardless of the management method. From the viewpoint of tree species, the highest value production was found for fir (81 € m^{-3}) and the lowest for beech (47 € m^{-3}). The hypothesis about pure value of beech in comparison to spruce and fir in mixed stands was confirmed, as we found a higher value production of conifers compared to beech in mixtures.

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ORIGINAL PAPER

Effect of game browsing on natural regeneration of European beech (*Fagus sylvatica* L.) forests in the Krušné hory Mts. (Czech Republic and Germany)

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Abstract

Tree damage by game browsing is one of the biggest threats to forest ecosystems at the time of climate change and large-scale forest disturbances. The aim of the paper was to determine the effect of browsing by ungulates on the diversity, abundance and species composition of natural regeneration in forest stands dominated by European beech (*Fagus sylvatica* L.). The research was conducted on 10 permanent research plots in the Krušné hory Mts. in the Czech Republic and Germany. The density of natural regeneration was in the range of 23,300–114,100 recruits ha^{-1}. A higher proportion of silver birch (*Betula pendula* Roth.) and rowan (*Sorbus aucuparia* L.) was found in the regeneration compared to the mature stands. A total of 78% of recruits was damaged by browsing. The most frequently damaged tree species were sycamore (*Acer pseudoplatanus* L.; 98%) and black alder (*Alnus glutinosa* [L.] Gaertn.; 97%), while Norway spruce (*Picea abies* [L.] Karst; 31%) and sessile oak (*Quercus petraea* [Matt.] Liebl.; 50%) were the least affected. Seventy-nine percent of European beech recruits were damaged. The game significantly reduced the height of regeneration by up to 40%, especially by terminal browsing. Browsing also negatively affected the quality and abundance of regeneration. For successful dynamics of species-rich natural forest ecosystems, it is necessary to minimize tree damage by game browsing. These main measures include the reduction of ungulate population levels and the optimization of their age structure and sex ratio, an increase in the number of overwintering enclosures and food fields for game and a change in the political approach to game management with sufficient consideration of forestry interests.

Key words: tree damage; forest structure; biodiversity; forest protection; Central Europe

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1. Introduction

Central European forest stands are characterized in the climax stage by occasional disturbances (Glončák 2009), which can be described by the gap disturbance regime (Korpeľ 1995; Jaworski & Kołodziej 2002). From this point of view, natural disturbances contribute positively to the dynamics of climax stands (Yamamoto 2000; Franklin et al. 2002; Sage et al. 2003; Manning 2007). Disturbance in the form of the death of a small number of trees contributes to the release of production space for new individuals of the tree layer that will occupy these newly opened niches in future (Kneeshaw & Gauthier 2003; Angelstam & Kuuluvainen 2004; Kucbel et al. 2010; Rugani et al. 2013). Natural regeneration, as a basic and essential element of forest dynamics, forms and ensures the continuity of the forest ecosystem (Veblen 1992; Vacek et al. 2010; Wagner et al. 2010). One uses this element and transforms it according to current and local needs (Paluch 2005; Collet & Chénost 2006; Collet et al. 2008). Through its intervention in this system, additional energy is created, without which the current concept of forest establishment could not exist (Korpeľ 1995; Pretzsch 2009; Trotsiuk 2012). In addition to disadvantages such as the specificity of the time of seeding of the mature stand (Ambrož et al. 2015; Vacek et al. 2017a), inequality of seedling density (Kantor 2001; Wagner et al. 2010) and the restoration of only such species composition that is already in the stand (Poleno et al. 2009), natural regeneration has also its advantages. Typical advantages include, for example, ensuring the natural occurrence of genetically native tree species (Korpeľ et al. 1991; Gömöry et al. 2011; Gallo et al. 2020a) that can make use of the local microrelief in an outstanding

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way (Barna 2004; Poleno et al. 2009; Vacek et al. 2015b). With its high adaptability, non-deformed root system (Mauer 2005) and, last but not least, its high number of individuals (Reininger 1992; Hájek et al. 2020), natural regeneration is a prerequisite for seed, shelterwood and selection silvicultural systems (Slanař et al. 2017; Vacek et al. 2019b). The specifics of natural regeneration are based on the precisely timed moment of intersection of individual assumptions that ensure its origin (Jarčuška 2009; Barna 2011; Jarčuška 2011). These assumptions include the occurrence of the seed year of the tree species present, optimum temperature, condition of the seed germination bed, light conditions and also soil moisture (Bellemare et al. 2002; Fischer & Lindner 2002; Bolte & Villanueva 2006). If these assumptions are not synchronized at the appropriate moment, full seeding does not occur, and the effect of natural regeneration loses its significance. This phenomenon is also exacerbated by the occurrence of the herbaceous and moss layer, which significantly reduces or eliminates the survival of seedlings on strongly infested soils (Kühne & Bartsch 2003; Jaloviar 2005; Collt & Chenost 2006; Provendier & Balandier 2008). The microrelief also plays an important role if the successful growth of natural regeneration, affecting water retention and the amount of available nutrients (Vacek et al. 2015b, 2017b).

In the area of interest, the Krušné hory Mts., European beech (*Fagus sylvatica* L.) forms the main part of forest stands on the mid- and lower elevation sites, where it has its production optimum (Plíva & Průša 1969; Neuhäuslová et al. 1998; Burda 2016). This tree species accounts for 5.3% in the Czech part and for 4.2% in the German part of Krušné hory Mts., however natural tree species composition was significantly higher (ÚHÚL 2019; SEKUL 2020). In the Czech Republic, the natural species composition reached 40. %, while the current tree species composition is only 8.8% (Ministry of Agriculture 2020). Both ecologically and economically, it is the most important and widespread deciduous tree in Europe (Bolte et al. 2007; Štefančík et al. 2018; Sharma et al. 2019a; Šimůnek et al. 2021). Due to its ecological plasticity, it is able to grow even in relatively heavily shaded and weed-infested places, and subsequently respond well to the release of canopy (Ellenberg et al. 1992; Bulušek et al. 2016). This predisposition predestines it to be the ideal tree species for regeneration by border felling, shelterwood system, or selection system (Kantor 2001; Poleno et al. 2009; Podrázský et al. 2019). These methods are suitable for optimal beech growth in conditions where there is no risk of damage by drought, sun exposure or late frost (Ningre & Colin 2007; Gallo et al. 2014), to which beech shows high vulnerability (Gallo et al. 2017; Šimůnek et al. 2019). The highest amounts of natural beech regeneration can be found on lush, mineral-rich soils (Musil & Möllerová 2005). Beech can form ideal vegetation mixtures with various deciduous trees (ash, maple, hornbeam, birch, rowan, cherry, linden), or conifers (spruce, larch, fir, Douglas fir, pine) (Dittmar et al. 2003; Wagner et al. 2003, 2010; Podrázský et al. 2014; Králíček et al. 2017; Vacek et al. 2019a). In addition, in mixed stands, beech can achieve higher production potential, stability and resistance to extreme weather fluctuations, drought and climate change (Schäfer et al. 2017; Pretzsch et al. 2021; Vacek et al. 2021). In later stages of growth, tending has a great importance from the silvicultural point of view (Remeš et al. 2015; Štefančík 2017, 2019; Sharma et al. 2019b). In the submontane and mountain areas forest regeneration is often damaged by ungulates – browsing, bark stripping and fraying (Rooney 2001; Vacek et al. 2018; Cukor et al. 2019; Gallo et al. 2020b; Prokůpková et al. 2020; Vacek et al. 2020a). Growth is strongly negatively affected mainly by the browsing of terminal buds (Schulze et al. 2014). This damage limits terminal bud growth, individual height, vitality, and ability to survive in subsequent years (Ammer 1996; Vacek et al. 2014). This preference of ungulates for the tree species mainly results in a change of species composition, especially to the detriment of interspersed and admixed deciduous trees and firs attractive to game (Motta 2003; Konôpka & Pajtík 2015; Vacek et al. 2015a; Slanař et al. 2017). Suppression of species diversity by game or humans leads to unification of the tree layer (Poleno et al. 2009). This reduction in species diversity in turn brings about a change in the stability and vitality of the forest ecosystem. Heterogeneous ecosystems have higher productivity at a later stage of development compared to monocultures (Pretzsch et al. 2010; Dănescu et al. 2016; Zeller & Pretzsch 2019; Gallo et al. 2020c). In addition, mixed and largely structured forests are more resilient to ongoing climate change that is manifested by higher mean annual temperatures, uneven precipitation distribution and more frequent climatic extremes (Pretzsch et al. 2013; Seidl 2017; Ammer 2019; Vacek et al. 2020b).

Successful growth of natural as well as artificial regeneration requires individual or areal protection, most often in the form of deer enclosure fencing (Švestka et al. 1996; Jurásek 1998; Sage et al. 2003; Baumhauer et al. 2005; Olesen & Madsen 2008; Hanophy 2009). Maintaining the regulated numbers of game individuals as biological protection seems to be a difficult task in the long run (Švarc 1981; Poleno et al. 2009). The use of repellents in the form of chemical protection is not very effective (Cislerová 2001). Regular reinstatement of repellents is laborious and the efficiency does not achieve lasting effects (Vosátka 2007).

The aim of this research was to determine the effect of game on the natural regeneration of beech stands in the German and Czech part of the Krušné hory Mts. and the subsequent proposal of appropriate silvicultural measures to reduce damage by game to natural regeneration. The specific objectives were to i) evaluate the quantity, silvicultural quality and structure of natural regeneration in 10 permanent research plots (PRPs), ii) compare species composition and diversity of natural regeneration and tree layer, iii) determine the effect of browsing damage on dynamics and species composition of natural regeneration and iv) to assess interactions between natural regeneration, tree layer, habitat and the influence of wildlife.

2. Material and methods

2.1. Study area

The area of interest, located in the central part of the Krušné hory Mts. at an altitude of 635–804 m a.s.l., was composed of 5 forest stands, and 2 PRPs were established in each stand. Four stands were located in the Czech Republic and 1 stand in Germany (Fig. 1). The average monthly temperature was around 5.9 °C and the total annual precipitation reached 780 mm. The temperature reached a maximum in July (15.2 °C), while the lowest temperature was in January (−3.4 °C). The minimum and maximum precipitation was in February (49 mm) and June (87 mm) (1961–2019 CHMI). The study area was qualified as a humid continental climate zone, characterized by warm to hot, humid summers and cold to severely cold winters (Dfb) as defined by the Köppen climate classification (Köppen 1931). The predominant soil type was modal Cambisol and the bedrock was mainly formed by crystalline shales (schists) and granites. The slope ranged from 5 to 23 degrees.

Data collection was performed in 5 stands with dominant European beech (its share was over 75%) aged over 120 years and stocking less than 0.8 (Table 1). Other tree species occurring in the upper storey included Norway spruce (*Picea abies* [L.] Karst), silver birch (*Betula pendula* Roth.), sycamore maple (*Acer pseudoplatanus* L.) and sessile oak (*Quercus petraea* [Matt.] Liebl.). From a typological point of view, it was a habitat of the *series trophicum*, specifically *categoria mesotrophica* (*Fagetum mesotrophicum*, *Abieto-Fagetum mesotrophicum*, *Piceeto-Fagetum mesotrophicum*) and *categoria subxerothermica* (*Fagetum subxerothermicum*) (Viewegh et al. 2003).

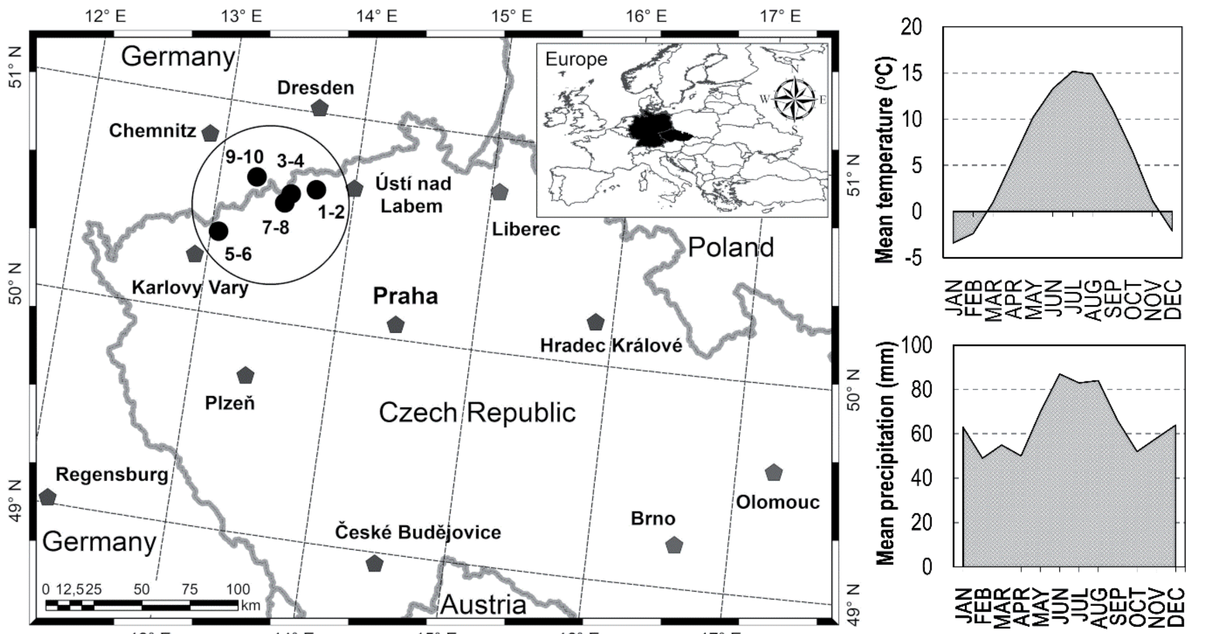

Fig. 1. Localization of European beech stands on permanent research plots in the Krušné hory Mts. and mean monthly climatic values (1960–2020); the map was created in ArcGIS 10 software (Esri).

Table 1. Overview of basic site and stand parameters of permanent research plots 1–10 in the Krušné hory Mts. according to Forest Management Plan.

PRP	GPS coordinates	Country	Altitude [m a.s.l.]	Exposure	Slope [%]	Forest site type	Stand volume [m³ ha⁻¹]	Age [y]	Stocking
1	50°38'37.1"N, 13°39'44.0"E	Czechia	804	E	23	6S	280	171	0.7
2	50°38'34.3"N, 13°39'45.5"E	Czechia	800	E	20	6S	280	166	0.7
3	50°35'50.5"N, 13°30'01.6"E	Czechia	682	SW	12	6S	337	166	0.7
4	50°35'50.2"N, 13°30'02.2"E	Czechia	679	W	10	6S	337	166	0.7
5	50°21'31.7"N, 13°02'55.3"E	Czechia	672	SW	5	4C	64	130	0.3
6	50°21'31.4"N, 13°02'54.4"E	Czechia	668	SW	5	4C	64	168	0.3
7	50°35'19.3"N, 13°30'12.2"E	Czechia	633	NW	8	5S	396	168	0.8
8	50°35'21.2"N, 13°30'16.1"E	Czechia	637	NW	5	5S	396	149	0.8
9	50°39'03.3"N, 13°17'46.6"E	Germany	662	SW	7	4S	247	149	0.7
10	50°39'03.6"N, 13°17'45.0"E	Germany	665	S	6	4S	247	149	0.7

Notes: 4S – nutrient-medium beech site (*Fagetum mesotrophicum*), 4C – water-deficient beech site (*Fagetum subxerothermicum*), 5S – nutrient-medium fir-beech site (*Abieto-Fagetum mesotrophicum*), 6S – nutrient-medium spruce-beech (*Piceeto-Fagetum mesotrophicum*; Viewegh et al. 2003).

2.2. Data collection

A total of 10 PRPs of 3 × 30 m in size were established along the slope using a steel diameter tape. The PRPs were randomly selected by the coordinates using the RNG function. The boundaries of the area were marked at least 10 m from the edge of the stand. All corners of the PRPs were stabilized. Subsequently, the PRPs were delineated and divided into 10 square transects (3 × 3 m). Natural regeneration was recorded in each of the squares, i.e. individual seedlings (recruits) from 10 cm in height up to 4 cm of diameter at breast height (DBH) were measured. In addition, the following data were recorded for each individual: identification numbers of transects (1–10), numbers of recruits, tree species, height, silvicultural quality (evaluated only in individuals over 1 m in height on a scale of 1–4), browsing status (old, new, repeated, no damage) and type of damage (terminal, lateral, both, no damage). The height was measured with a lath to the nearest 1 cm.

The evaluation of the silvicultural quality of recruits was performed according to the following scale:

1. a straight vital individual without forking showing good height growth and representing the future basic element of the stand,
2. a slightly curved individual or individual with slight branching, which, if necessary, can still replace an individual with quality 1, good growth again,
3. a crooked branched individual unsuitable for future growth from the silvicultural point of view, shows irregular or poor growth,
4. a severely deformed or highly forked individual showing minimal to zero growth or dying individual with the typical "bonsai appearance".

2.3. Data analysis

In terms of species diversity, indices of species richness (Margalef 1958; Menhinick 1964), species heterogeneity (Shannon 1948; Simpson 1949) and species evenness (Hill 1973; Pielou 1975) were calculated for individual PRPs (Table 2). The vertical structure was evaluated according to the Gini index (Gini 1921) and the spatial distribution according to the index of cluster size (David & Moore 1954). The equations of diversity indices are given in Vacek et al. (2020c).

Microsoft Excel was used for basic data analysis and creation of graphs, especially species composition and height distribution. Statistica 13 (StatSoft, Tulsa) was used for statistical analyses. The nonparametric Kruskal-Wallis test was used to evaluate the differences between heights in relation to tree species and tree damage by game browsing, because the data did not meet the normality according to the Shapiro-Wilks test. In the graphical outputs, the error bars show the standard error.

Principal component analysis (PCA) was performed in CANOCO 5 (Ter Braak, Šmilauer 2012) to evaluate the relationships between stand structure (stocking, stand volume, height, diameter, age), natural regeneration (density, height), tree damage by game browsing and habitat conditions (slope, altitude). Data were logarithmized and standardized prior to analysis. The results of multidimensional PCA analysis were visualized in the form of an ordination diagram. The overview map was created in ArcGIS 10 (Esri).

3. Results

3.1. Density and tree species of natural regeneration

Sufficient potential of natural regeneration was found on the PRPs, ranging from 23,300 recruits ha^{-1} (on PRP 2) to 114,100 recruits ha^{-1} (on PRP 9; Fig. 2). European beech was dominant on all PRPs, accounting for 75–100%. On most PRPs (1, 2 and 5 to 10) mixed species composition of sycamore, black alder, silver birch, rowan, sessile oak and Norway spruce was recorded, always up to 10%. The exclusive occurrence of natural beech regeneration was recorded on two PRPs (3 and 4). The average number of beech recruits was around 63,900 recruits ha^{-1}. The most numerous admixtures included silver birch (on average 3,600 recruits ha^{-1}) and rowan (1,700 recruits ha^{-1}). The maximum number of recruits was observed in European beech on PRP 8 and 9 (93,200 recruits ha^{-1} and 92,700 recruits ha^{-1}, respectively). The minimum number of beech recruits was recorded on PRP 2 (19,300 recruits ha^{-1}). The highest number of species was found on PRP 8 and 9, where, in addition to European beech (84%), also Norway spruce (10%), sessile oak (1%) and silver birch (5%) were present.

Table 2. Overview of indices describing the stand diversity and their common interpretation.

Criterion	Quantifiers	Label	Reference	Evaluation
Species diversity	Species richness	D_1 (Mai) D_2 (Mei)	Margalef 1958 Menhinick 1964	minimum D = 0, higher D = higher values
	Species heterogeneity	λ (Sii) H´ (Shi)	Simpson 1949 Shannon 1948	range 0–1; minimum λ = 0, maximum λ = 1 minimum H´ = 0, higher H´ = higher values
	Species evenness	E_1 (Pii) E_2 (Hi)	Pielou 1975 Hill 1973	range 0–1; minimum E = 0, maximum E = 1
Vertical diversity	Gini index	G (Gi)	Gini 1921	range 0–1; low G < 0.3, very high differentiation G > 0.7
Horizontal structure	Index of cluster size	CS (D&Mi)	David & Moore 1954	mean value CS = 0, aggregation CS > 0, regularity CS < 0

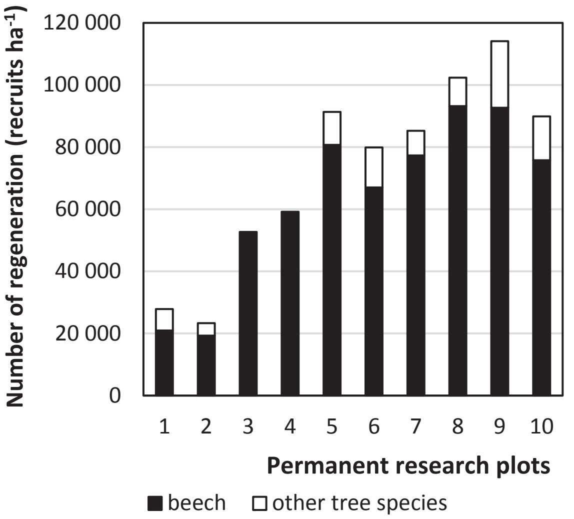

Fig. 2. Density of natural regeneration on permanent research plots 1–10 differentiated according to tree species composition of European beech and other tree species in 2020.

The proportion of European beech in natural regeneration was by 2% lower (88%) in comparison with the tree layer (90%; Fig. 3). In the mature stand, European beech reached 100% representation on six PRPs (3 to 8), while in the regeneration it was only on two PRPs (3 and 4). On PRP 1 and 2, there was an admixture of sycamore in the mature stand (up to 5%). In addition to European beech, PRP 9 also included rowans and Norway spruce (up to 10%). In addition to beech, sessile oak and Norway spruce were present on PRP 10, both up to 5%. The average stand volume of the mature stand was around 300 m^3 ha^{-1} (269 m^3 ha^{-1} for beech).

3.2. Height structure and quality of natural regeneration

The highest mean height of natural regeneration was registered on PRP 9 (144 cm), on the contrary, the lowest mean height was found on PRP 3 (43 cm). The determined heights of natural regeneration were divided into individual height classes using a 20-cm interval (Fig. 4). On all PRPs, beech was most common in the height class of 40 to 60 cm (11,800 recruits ha^{-1}), then in the height class of 60 to 80 cm (11,700 recruits ha^{-1}) and subsequently in the height class of 80 to 100 cm (9,500 recruits ha^{-1}). The height of the beech was significantly greater than that of the other tree species, individuals with a height over 300 cm were recorded. At higher heights, the number of beech recruits gradually decreases. The smallest representation of beech was in the height class up to 20 cm (1,500 recruits ha^{-1}). The height competition consists mainly of silver birch in the height class of 80 to 100 cm (700 recruits ha^{-1}) and also of rowan in the height class of 60 to 80 cm (400 recruits ha^{-1}). The greatest frequency of admixed tree species in natural regeneration was in the height class from 60 to 80 cm (14,900 recruits ha^{-1}). On the contrary, it was the smallest in the height class from 0 to 20 cm (1,700 recruits ha^{-1}).

The significant difference between tree species was found in the mean height of recruits (Kruskal-Wallis test, Chi-square = 166.0, df = 6, $p < 0.001$; Fig. 5). Sessile oak (113 cm), Norway spruce (108 cm) and silver birch (103 cm) had significantly ($p < 0.05$) higher mean height. On the other hand, significantly ($p < 0.05$) lower height was observed in maple (48 cm), alder (49 cm) and rowan (69 cm). European beech reached the mean height of 88 cm across all PRPs.

For silvicultural quality of natural regeneration, quality 2 was the most frequent with 49% (35,600 recruits ha^{-1}). It was followed by quality 1 with 32% (23,200 recruits ha^{-1}) and quality 3 with 18% (13,100 recruits ha^{-1}). The worst quality 4 was represented by 1% (700 recruits ha^{-1}).

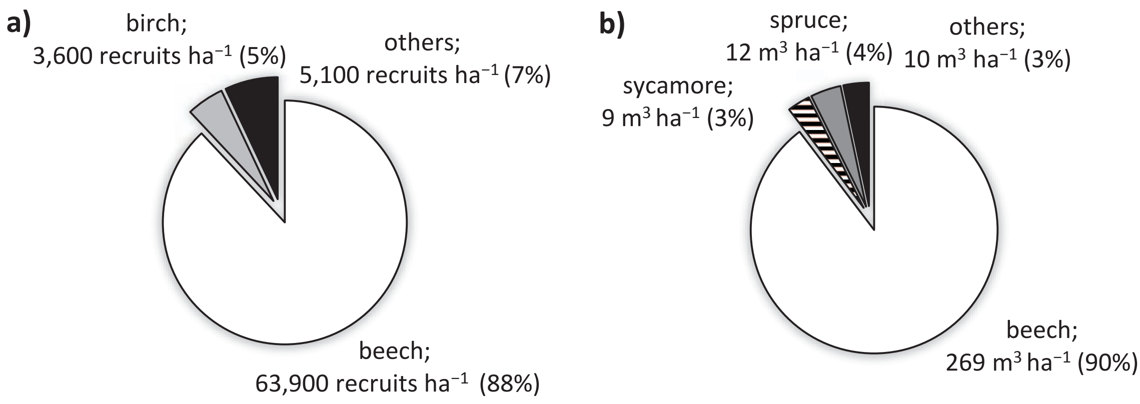

Fig. 3. Tree species composition of a) natural regeneration (according to numbers) and b) mature stand (according to stand volume) for all permanent research plots in 2020.

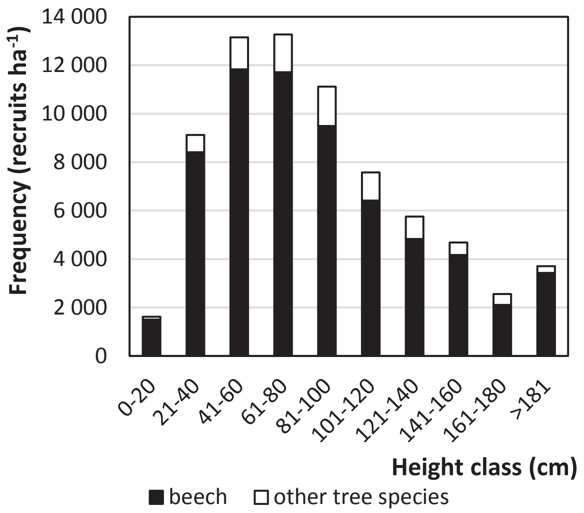

Fig. 4. Height structure of natural regeneration on permanent research plots differentiated according to tree species composition of European beech and other tree species in 2020.

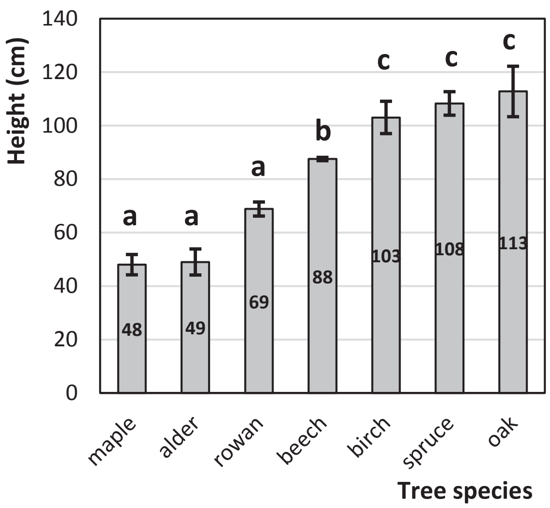

Fig. 5. Mean height of natural regeneration on permanent research plots differentiated according to tree species in 2020; error bars indicate standard error; significantly (Kruskal-Wallis test, $p < 0.05$) different values are designated by different letters.

3.3. Diversity of natural regeneration

In view of species diversity, natural regeneration showed low species richness, similarly like species heterogeneity (Table 3). Only on PRP 1 and 9 the heterogeneity reached higher values (medium diversity). Higher variability between PRPs was in species evenness. According to the E_2 index, the evenness on all PRPs was high, except for PRPs 2 and 3, where there was only natural regeneration of beech. The species evenness was the highest on PRP 1, in the plot with the lowest share of beech (75%) of all monitored PRPs.

As for the structure of natural regeneration, the height diversity reached medium values except for PRPs 9 and 10, where the diversity was high due to the high number of advanced individuals. The horizontal structure was significantly ($p < 0.05$) aggregated on all PRPs, only PRP 2 showed the random distribution of recruits. The highest aggregation of recruits was in stands with the highest stocking (PRPs 7 and 8).

3.4. Effect of browsing on natural regeneration

Out of the total number of recruits, on average 78% of individuals were damaged by browsing. Thus, 22% of recorded individuals were without damage. The type of browsing showed that out of the total number of recruits on all PRPs, most individuals were damaged by both terminal and lateral browsing (33,400 recruits ha^{-1}, 51%), fewer individuals suffered from lateral browsing only (12,900 recruits ha^{-1}, 17%), and similarly from terminal browsing only (5,900 recruits ha^{-1}, 10%). The degree of damage indicated that natural regeneration was most frequently damaged by repeated browsing (41,800 recruits ha^{-1}, 58%), followed by old browsing (7,900 recruits ha^{-1}, 11%) and new browsing (6,900 recruits ha^{-1}, 9%).

The species preference of ungulates with respect to damage to natural regeneration is depicted in Fig. 6. The most frequently damaged individuals were sycamore maple (98%), black alder (97%) and rowan (94%). The least damage was recorded for sessile oak (50%) and Norway spruce (31%). Seventy-nine percent of Euro-

Table 3. Diversity of natural regeneration on permanent research plots 1–10 in 2020; the highest values are in bold and the lowest in italics.

PRP	D_1 (Mai)	D_2 (Mei)	λ (Sii)	H′ (Shi)	E_1 (Pii)	E_2 (Hi)	G (Gi)	CS (D&Mi)
1	0.195	0.018	**0.402**	**0.727**	**0.662**	0.628	0.466	0.817*
2	0.199	**0.020**	0.289	0.235	0.493	0.564	0.427	*0.639*
3	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	0.399	1.720*
4	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	*0.397*	1.477*
5	0.088	0.007	0.205	0.156	0.517	0.597	0.405	2.414*
6	0.089	0.007	0.271	0.192	0.637	**0.668**	0.415	2.474*
7	0.088	0.007	0.168	0.134	0.445	0.559	0.460	**3.310***
8	0.087	0.006	0.164	0.131	0.437	0.555	0.451	2.698*
9	0.258	0.012	0.328	0.295	0.490	0.501	0.506	1.690*
10	**0.263**	0.013	0.277	0.244	0.405	0.509	**0.570**	0.855*

Notes: D_1 and D_2 – indexes of species richness, λ and H′ – indexes of species heterogeneity, E_1 and E_2 – indexes of species evenness; G – Gini index of vertical structure, CS – index of cluster size; *statistically significant (0.95 confidence interval) aggregated horizontal structure (CS indexes).

pean beech recruits were damaged, similarly like in silver birch (78%).

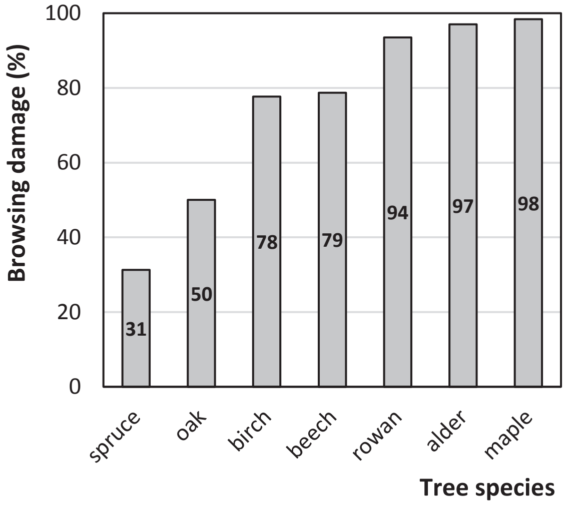

Fig. 6. Proportion of tree damage caused by game browsing (terminal, lateral, both) of natural regeneration on permanent research plots differentiated according to tree species in 2020.

The game also had a significant (Kruskal-Wallis test, Chi-square = 576.0 df = 3, $p < 0.001$) effect on the height of natural regeneration in relation to the browsing status (Fig. 7). The significantly ($p < 0.05$) highest mean height was observed in natural regeneration without browsing damage (119 cm). In contrast, the significantly ($p < 0.05$) lowest recruits were those damaged by new (63 cm) and repeated browsing (79 cm). Individuals of natural regeneration damaged by old browsing reached a height of 95 cm. The mean height of natural regeneration significantly (Kruskal-Wallis test, Chi-square = 710.8, df = 3, $p < 0.001$) corresponded to the type of browsing. Terminal and combined browsing significantly ($p < 0.05$) limited the height of natural regeneration (71 cm and 73 cm, respectively). In contrast, individuals with lateral browsing and those without browsing damage reached the significantly ($p < 0.05$) highest mean heights (104 cm and 119 cm).

3.5. Interactions between natural regeneration, stand parameters, sites and tree damage

The results of the PCA expressing the interactions between natural regeneration, tree damage by game browsing, tree layer and habitat on 10 PRPs in the Krušné hory Mts. are presented in the form of an ordination diagram in Fig. 8. The first ordination axis explains 40.3% of data variability, the first two axes explain 72.8% and the four axes together explain 94.8% of data variability. The x–axis represents the height of natural regeneration and its species evenness. The y–axis represents the altitude and horizontal structure of natural regeneration. The quality of natural regeneration was negatively correlated with damage by game. The density of natural regeneration was negatively correlated with stand stocking, which was positively correlated with mean DBH, age and stand volume. The frequency of regeneration was also influenced by the slope and elevation. With increasing elevation, the number of recruits decreased and the horizontal structure tended more towards a regular spatial pattern (aggregated distribution decreased). The lowest explanatory parameter in the ordination diagram was the vertical structure. In terms of typology and forest types, habitats in a lower forest vegetation zone had a higher number and quality of recruits, while stands in higher vegetation zones were characterized by higher tree damage by game browsing. The lowest variability within the stands

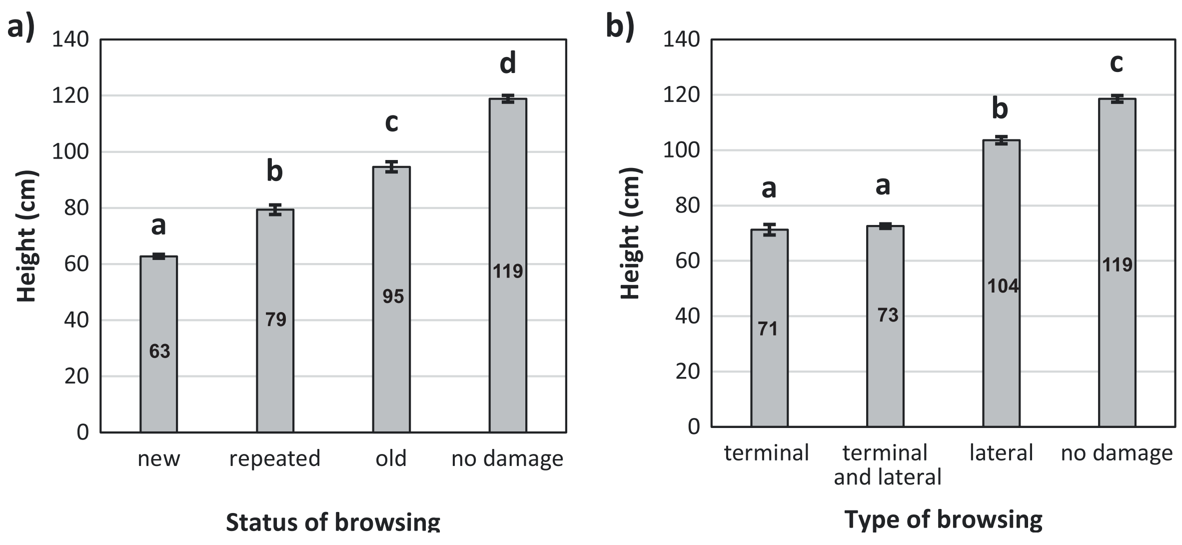

Fig. 7. The status a) and type b) of game browsing in relation to the height of natural regeneration on all permanent research plots in 2020; error bars indicate standard error; significantly (Kruskal-Wallis test, $p < 0.05$) different values are designated by different letters.

was found in the stand where only European beech was present in species composition (PRPs 3 and 4).

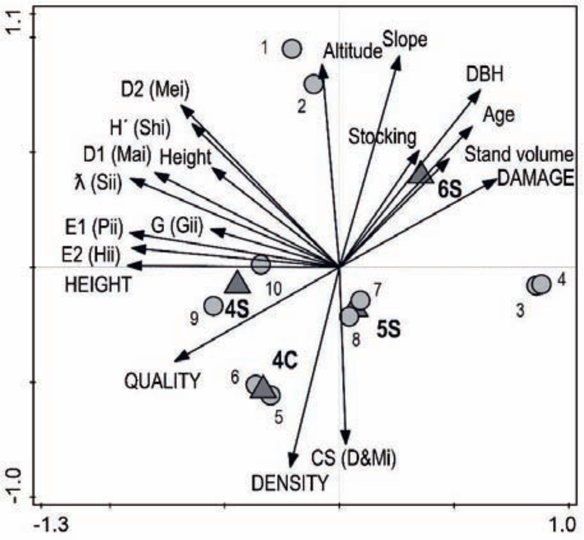

Fig. 8. Ordination diagram showing the results of PCA of the relationships between mature stand (stocking, stand volume, height, diameter, age), natural regeneration (DENSITY, HEIGHT), tree damage by game browsing (DAMAGE), diversity of natural regeneration (see Table 2) and habitat characteristics (slope, altitude); ● symbols indicate the permanent research plots (1–10), ▲ the group of forest site types (see Table 1).

4. Discussion

4.1. Density and tree species of natural regeneration

The representation of different tree species was mainly based on the present mature stand, altitude, soil composition and precipitation total (Pretzsch et al. 2014; Vacek et al. 2017b). Because individual PRPs were located in beech stands, the share of European beech was dominant, ranging from 75% (PRP 1) to 100% (PRPs 3 and 4). Admixed individuals of sycamore, black alder, silver birch, rowan, sessile oak and Norway spruce always accounted for up to 10%. The average number of recruits in the central part of the Krušné hory Mts. reached 72,600 recruits ha^{-1}, i.e. it ranged from 23,300 to 114,100 recruits ha^{-1}. A high abundance of natural regeneration was documented in the beech-dominated stands also in other localities in the Czech Republic and in other countries, e.g. in the Orlické hory Mts. the natural regeneration reached 37,200 recruits ha^{-1} (Vacek et al. 2014), 41,700 recruits ha^{-1} in the Jizerské hory Mts. (Slanař et al. 2017), 76,700 recruits ha^{-1} in the Krkonoše Mts. (Vacek et al. 2017b), 100,200 recruits ha^{-1} in the Broumov region (Hájek et al. 2020) or 27,300 recruits ha^{-1} in Tworylczyk in Poland (Jaworski et al. 2002). Substantially lower numbers (3,200 recruits ha^{-1}) of recruits were reported by Oheimb et al. (2005) from close-to-nature beech forests in north-eastern Germany. The admixture of silver birch and rowan recruits (3,600 and 1,700 recruits ha^{-1}, respectively) corresponds to their usual number in similar stand and habitat conditions (Van Hees et al. 1996; Żywiec & Ledwoń 2008). The number of recruits was in negative correlation with altitude, stand stocking and tree damage by game browsing. Canopy of the mature stand significantly affects the density of natural regeneration in beech stands (Vacek et al. 2017b). Ambrož et al. (2015) and Turczański et al. (2021) reported the high intensity of game pressure as a limiting factor for the occurrence and frequency of natural regeneration.

The representation of European beech in natural regeneration (88%) corresponds to its proportion in the parent stand (90%). Admixture of other tree species is based on dispersal of the seed material by wind from the surrounding stands (Suchockas 2002) and also on the introduction by game and birds (Karlsson 2001; Dobrovolný & Tesař 2010). In our case, these are tree species with scattered occurrence, such as silver birch (PRPs 5, 6) and rowan (PRPs 7, 8), which do not occur in the mature stand on PRPs. The increased share of these two pioneer tree species in natural regeneration was also documented for example by Slanař et al. (2017) from the Jizerské hory Mts. The average stand volume of the mature stand was around 300 m^3 ha^{-1} (269 m^3 ha^{-1} for beech), which corresponds to stands with reduced stocking (Condés 2013).

4.2. Height structure and quality of natural regeneration

The height of recruits ranged from 43 cm (PRP 3) to 144 cm (PRP 9), similarly like in the Krkonoše Mts. (Prokůpková et al. 2020). As for height structure, most beech recruits were in the height class from 40 to 60 cm (11,700 recruits ha^{-1}), on the contrary, the smallest number of recruits was in the height class up to 20 cm (1,700 recruits ha^{-1}). The dominance of European beech is partly competed by silver birch with 700 recruits ha^{-1} in the height class of 80 to 100 cm or rowan in the height class of 60 to 80 cm (400 recruits ha^{-1}). In beech forests in the Broumovské stěny National Nature Reserve, the average height of regeneration, depending on the microhabitat, ranged from 74 cm on the ridges to 121 cm in the depressions (Vacek et al. 2015). According to species, the largest mean height of recruits was found in sessile oak (113 cm), while the lowest mean height was recorded for sycamore (49 cm) in our study. Beech reached the mean height of 88 cm. Qualitatively, silvicultural quality 2 (49%) and quality 1 (32%) predominate on all PRPs. Quality 4 is represented by 1% only. Browsing of any type has a strong impact on quality, as documented by Olesen & Madsen (2008) and Madsen & Hahn (2008). The silvicultural quality of natural regeneration can also be significantly influenced by management methods and by the edge effect of the stand (Bílek et al. 2018).

4.3. Diversity of natural regeneration

Considering the species diversity, natural regeneration showed low species richness and species heterogeneity. Similarly, low values of diversity were documented by Vacek et al. (2015b) in beech stands in the Broumovsko Protected Landscape Area, while significantly higher species diversity was found in mixed beech stands (Slanař et al. 2017; Hájek et al. 2021). On the contrary, the species evenness was mostly high on all PRPs, where there were more tree species. The species evenness was the highest on PRP 1, in the area with the lowest share of beech (75%) of all monitored PRPs. The largest number of species was found on PRPs 8 and 9, where, in addition to European beech (84%), there was also Norway spruce (10%), silver birch (5%) and sessile oak (1%). The spatial distribution of regeneration was strongly aggregated in most cases. The clustered horizontal structure of regeneration was also reported by other researchers from dominant beech stands from other parts of the Czech Republic (Vacek et al. 2014; Ambrož et al. 2015; Slanař et al. 2017), and also from Slovenia (Nagel et al. 2006) and Poland (Paluch 2007). The aggregation of recruits increased with the increasing number of individuals. This positive correlation was also found in the mature stand in beech forests (Vacek et al. 2015c; Bulušek et al. 2016).

4.4. Effect of browsing on natural regeneration

Out of the total natural regeneration, 78% of recruits were damaged by browsing. Similarly, the negative influence of browsing on species composition and the future dynamics of forest in the Czech Republic was documented by Vacek (2017) from the Orlické hory Mts., Slanař et al. (2017) from the Jizerské hory Mts., Vacek et al. (2019) from Broumovsko and Prokůpková et al. (2020) from the Krkonoše Mts. The extremely high game damage is caused by its disproportionately large population in relation to forest stands or agricultural land, which is constantly rapidly increasing in the Czech Republic. Deer game has increased by 146% and wild boar even by 8,526% in the last 53 years (Hunting records of ÚHÚL).

In the area of interest, sycamore (98%) and black alder (97%) were the tree species most affected by game browsing. On the other hand, the least frequent damage was recorded in Norway spruce (31%). Seventy-nine percent of European beech recruits were damage. In contrast to the study of Baran (2015), the species preference is different in the Orlické hory Mts.; the browsing of rowan prevails amounting to 44%, spruce 37% and only then beech 20% with a similar representation of beech in the species composition. Similarly, Vacek (2017) described the preference of some tree species in the Orlické hory Mts., where the highest level of damage occurred on fir (100%), rowan (94%), beech (56%) and the lowest damage was observed on spruce (18%). The preference of some tree species, especially less represented broadleaves or firs, was also mentioned by foreign researchers from Germany (Ammer 1996), Italy (Motta 1996; D'Aprile et al. 2021), Slovakia (Konôpka & Pajtík 2015) and France (Bernard et al. 2017).

Damage by game not only affected the abundance, growing quality and species composition, but also the mean height and growth of natural regeneration. The mean height significantly corresponds to browsing (Ammer 1996; Vacek et al. 2014). Natural regeneration without damage had a significantly higher mean height (119 cm). On the contrary, individuals damaged by new browsing reached half the mean height (63 cm), due to severe damage of young and low-height regeneration. This was followed by repeated browsing with the recruit height of 79 cm. Recruits suffering from old browsing reached an average value of 95 cm and showed then vitality of natural regeneration and its subsequent growth, similarly like it was reported by Rozas (2003). Repeated browsing was registered as the most common damage to natural regeneration (58%). Taking into account the type of browsing, lateral browsing did not distinctly affect the height of recruits (height reduction by 12%, 104 cm). Terminal and combined browsing reduced the mean height (71 and 73 cm) of natural regeneration by 40% compared to regeneration without damage. Natural regeneration was most often damaged by the combined browsing of terminal and lateral buds (52%). The destruction of terminal buds causes a significant reduction in height increment (Dittmar 2003). This fact is also confirmed by repeated browsing, which not only reduces the increment, but also the vitality of individuals (Reimoser & Gossow 1996).

5. Conclusion

In the area of interest of the Krušné hory Mts., natural regeneration in European beech stands shows a high potential (72,600 recruits ha^{-1}). The species composition of natural regeneration, like other parameters, is linked to the character of the tree layer. On all permanent research plots, in the mature stands there was a dominant proportion of beech (90%) with a minimum admixture of other tree species. The natural regeneration of beech accounted for 88% with an admixture of other species, especially silver birch and rowan. This expansion of pioneer trees, which do not occur in the mature stand, is mainly due to seeding from the surrounding stands. Among the most damaged tree species by browsing were scattered broadleaves such as sycamore (98%), black alder (97%) and rowan (94%). Norway spruce (31%) and sessile oak (50%) were the least frequently damaged tree species. In total, 79% of beech recruits were damaged. In addition to the change in species composition, game had a significant negative effect on the silvicultural quality and extent of regeneration. The largest damage was caused by terminal browsing (height reduction by 40%). Due to the high number of damaged individuals, it is necessary to protect the young stands with fences and reduce the high numbers of ungulates to an ecologically acceptable level. In view of hunting management, in addition to regulating the ungulate population levels, it is important to optimize the sex ratio and age structure of the population. As an alternative, it is possible to include individual mechanical fencing of valuable admixed tree species and support the natural predators of ungulates. The ever-increasing numbers of wolves (*Canis lupus*) could also contribute to limiting the number of ungulates in future. Another possible way to reduce the ungulate damage to stands is to increase the number of overwintering game enclosures and food fields for game. Overall, however, there is a need to harmonize hunting management and forest management with emphasis on silvicultural practices to support admixed trees and the creation of diversified forests. These mixed forests are characterized by high stability and sustainable productivity in the time of ongoing climate change.

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ORIGINAL PAPER

Optimization of maturity age for coppice oak forests within Left-Bank Forest-Steppe in Ukraine

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Abstract

Oak (*Quercus robur* L.) forest stands are among the most common forest formations in the forest-steppe zone of Ukraine. Investigations of the patterns of distribution of trees by diameter and the dynamics of the commodity structure of mature oak stands of coppice origin were carried out based on the forest survey data from 28 temporary sample plots, on the sites designated for the final felling in the Left-Bank Forest Steppe of Ukraine (Sumy, Kharkiv, and Poltava Regions). We distributed trees by diameter classes and technical suitability categories. To establish the commodity structure of the stand, we selected model trees that corresponded to the average size of trees in terms of diameter classes and their qualitative characteristics. Then, we constructed a model tree stem profile using Institute of Forest Ecosystems Research (IFER)'s method of "6 points". Based on stands' structure and quality condition as well as on the growth tables, the commodity structure dynamics table for the changes in the commodity structure for the coppice oak stands in the Left-Bank Forest Steppe of Ukraine has been developed. The results of the analysis of wood stock dynamics showed that the maximum average increment of class A and B wood is 90–100 years. Therefore, the age of technical maturity and the associated age for the final felling in commercial oak forests of second site class and above should be assigned to 91–100 years.

Key words: oak; industrial timber; coppice stand; commodity structure; marketability dynamics

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1. Introduction

Pedunculate or English oak (*Quercus robur* L.) is widespread in Europe (Eaton et al. 2016), and its stands provide important environmental and economic services. Oak-dominated forests occupy about 28% of the total forest area and 24% of gross living stock in Ukraine (Forestry of Ukraine 2017). Other oak species: Pubescent oak (*Quercus pubescens* Willd.), Sessile oak (*Quercus petraea* (Matt.) Liebl.), Northern red oak (*Quercus rubra* L.) occupy a relatively small area. In the Forest-Steppe zone of Ukraine, oak forest stands are among the most common forest formations in the forest-typological area of fresh temperate climate (Ostapenko & Tkach 2002) (Fig. 1). The forests of the Left-Bank Forest-Steppe are represented mainly by the stands of common oak, which occupy 46.4%. The area of natural oak stands is more than 280 thousand hectares (46% of oak forests total area of the study region), the share of natural seed origin stands is only 7.0%, the rest – stands of coppice origin. The largest share of oak stands of the Left Bank Forest Steppe is concentrated in fresh fertile (74%), fresh relatively fertile (12%) and dry fertile (6%) forest site conditions. English oak is a valuable deciduous species that is rather vulnerable to climate change (Shvidenko et al. 2018; Árvai, M. et al. 2018). The most valuable oak wood has narrow rings and is produced in high mixed forests on fertile sites with a long rotation period (about 130 years) (Praciak et al. 2013).

Specification of the optimal rotation period of forest growth is essential in the system of adaptive forestry activities under changing conditions for forest species growth (Climate change guidelines for forest managers 2013; Forest Europe 2020). The maturity age and the associated age of final felling is the most important elements of sustainable forest management systems (Duncker et al. 2012).

The maturity of a forest is a condition in which it is best suited to the purpose of the economy, that is, it most fully meets the needs for specific wood assortments or exhibits its useful properties. The "forest maturity" term

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Fig. 1. Forest map of Ukraine (left) and distribution of oak forest in the region of study (right, dark gray color).

should be specified for a certain object, that is, for the stands of specific forest tree species within a natural zone or for a specific enterprise and forest area. The age of maturity of forest stands is determined based on the main purpose of the forests, the functions they perform, productivity, biological features of tree species, forest types, natural zones, as well as methods of forest regeneration.

All types of maturity can be divided into two groups, namely biological and economic. There are two phases of biological maturity in the life of the forest: restorative and natural. These types of maturity, which are limited by the biological characteristics of tree species, have been studied for the forest conditions of Ukraine (Girs 2011).

Economic maturity can also be divided into two subgroups. The first subgroup combines the types of maturity associated with the use of timber obtained during forest growing (quantitative, technical, and economic maturity); the second one includes types related to a variety of beneficial properties of the forest (water conservation and protective).

Quantitative maturity, indicating the moment at which the forest stand has the highest productivity in the growing stock, can only satisfy the one-sided requirement for the most favourable production of volumes of timber, regardless of its quality. In modern conditions, quantitative maturity can determine the age of felling only in limited areas of commercial forests where low quality and fine timber is harvested. It should be considered that there is a minimum age of stands at which the physical properties of the timber acquire the necessary parameters and the timber becomes the most suitable for wood processing (Girs 2011). Therefore, technical maturity has recently become decisive for commercial forests.

At the age of technical maturity, the maximum average increment of the leading assortment or group of major assortments is recorded. Technical maturity reflects the targeting of forest management in certain economic and natural conditions. Determining the age of technical maturity is based on the data on the stand marketability dynamics (Petráš et al. 1996), the relevance of which is also due to the introduction in Ukraine since 2019 new standards for round timber, harmonized with European ones (Hardwood round timber – Qualitative classification 2018).

The main disadvantage of the current maturity ages standards is that they are insufficiently differentiated by productivity, origin, types of forests, and almost do not consider the age structure of the forests of Ukraine. In particular, for seed-origin oak forests of site index I and above, within the commercial forests for Forest zone and Forest steppe, the maturity age by current standards is the same as for coppice oak stands of site index II (101–110 years), although the biological and growth characteristics of the latter are substantially different (Davidov 1987; Kashpor & Strochynskyi 2013).

For coppice oak stands, the current age of maturity is too high. First, it concerns the recreational and conservation forests included in the calculation of the annual allowable cutting rate (131–140 years). In the Forest-Steppe of Ukraine, at this age, the marketability of such stands and their health are deteriorating; as a result, forest stands perform important ecological and protective functions less effectively. The same maturity age for oak stands of different origins is not justified (Tkach et al. 2002). Silvicultural Guidelines for European Coppice Forest (Nicolescu et al. 2017) propose a short rotation period of 35–40 years for oak stands.

The aim of the study is to estimate commodity structure dynamics and substantiate the optimal maturity age for oak coppice forests of Left-Bank Forest-Steppe of Ukraine.

2. Material and methods

To analyse indicators of the forest fund and to develop marketability tables, we used the "Forest Fund of Ukraine" database as at 2014 and data of 28 temporary sample plots (measurements were performed on 2011–2018 years) in Sumy (State Enterprises "Lebedyn Forestry" and "Konotop Forestry"), Kharkiv (State Enterprise "Gutianske Forestry") and Poltava (State Enterprise "Gadiatske Forestry") Regions in the Left-Bank Forest-Steppe (Table 1). On the sample plots we investigated the patterns of distribution of trees by diameter and the dynamics of the commodity structure of mature oak stands of coppice origin.

Table 1. Distribution of sample plots by forest site condition and site indexes.

Site index	Forest site condition						Total
	B_2	B_3	C_2	C_3	D_2	D_3	
I	—	—	—	—	1	—	1
II	—	—	9	2	12	1	24
III	1	1	1	—	—	—	3
Total	1	1	10	2	13	1	28

In the Ukrainian forest type classification scheme, there are four classes of forest site condition distinguished by soil fertility, which is considered as soil richness in nutrients. These classes are the following: poor (A), relatively poor (B), relatively fertile (C) and fertile (D). The second variable for forest site condition type differentiation is soil moisture. Six classes are distinguished by this parameter. These classes are the following: 0 – very dry, 1 – dry, 2 – moist, 3 – damp, 4 – wet, 5 – swampy (arranged according to raise of water availability). A combination of soil fertility and soil moisture classes forms a forest site condition class, which is indicated by two characters e.g. A_1 or D_2. Thus, a forest site condition type class is considered as a set of conditions, which can support certain type of forest vegetation that is characterized by particular productivity, composition and structure (Bondar et al. 2020).

By types of forest site conditions, the largest share is occupied by D_2 (46.4%) and C_2 (35.7%), and by productivity – site index II (85.7%). The sample plots cover forest stands between 76 and 139 years old, with an average diameter of 28.2–55.8 cm and an average height of 19.1–29.2 m.

On the sample plots, we distributed trees by diameter classes and technical suitability categories. To establish the commodity structure of the stand, we selected model trees that corresponded to the average size of trees in terms of diameter classes and their qualitative characteristics. Then, we constructed model tree stem profile using IFER's method of "6 points". For this purpose, heights of stems and diameters at the stumps, heights of 1.3 and 2 m, half of the height of the crown and at the base of the crown, and the heights of trees were measured, then model trees were cross-cut into logs considering the size and quality of stems, as well as the requirements of standards (Černý & Pařez 2005). Model tree measurement data were used to parameterize the stem profile equations by which the volumes of model trees and their distribution by assortment were calculated. In total, 234 model trees were measured, and 66 models were cut down and divided into assortments. Inside 12 trees, internal rot was found.

According to new standards for round timber, logs are sorted into four quality classes, namely A, B, C, and D. By the average diameter of logs without bark, industrial timber is divided into ten classes (D0 <10 cm, D1a 10–14 cm, D1b 15–19 cm, ..., D10 ≥60 cm) (Hardwood round timber – Qualitative classification 2018).

Class A includes timber of the highest quality, mostly from the bottom of the trunk, without defects or with minor defects. Class B includes middle-class timber with less quality requirements for timber that has restricted knots. Assortments below the middle quality class that allow defects that do not significantly reduce the natural properties of wood are classified as class C. Quality class D includes timber that does not satisfy any of the higher classes, but from which industrial timber can be obtained.

When evaluating economic types of stand maturity, in particular quantitative and technical the research was based on the growth tables (Kashpor & Strochynskyi 2013). The age of technical maturity is primarily influenced by the average diameter of the most valuable assortments and wood quality. For determining the age of technical maturity of coppice oak stands, it is also necessary to take into account a decrease in the industrial timber yield due to damage by rot as well as weakening of stands beyond the age of 120.

The calculations of the marketability dynamics were performed based on the growth tables of modal coppice oak stands and stem distribution models. Following on the above parameters, we calculated the trees distribution by diameter using the STRUK program (β–distribution) (Girs et al. 2017).

3. Results

According to the analysis of forest stands designated for final felling, the proportion of commercial stems decreases by an average of 25% and the diameter of rot in the butt-log part increases as the age of stands rises from 110 to 140.

The change in the proportion of marketable stems (Pmark) with the stand age (A) was determined from the growth tables of coppice oak stands of the respective site index and data on the distribution of stems by category on temporary sample plots (Fig. 2). Considering the quality deterioration of coppice oak timber aged over 90 years, the percentage of marketable stems in the 80–140 age range was determined by the formula, obtained on the base of data on Fig. 2:

$$P_{mark} = -114.9 + 3.208 \cdot A - 0.0147 \cdot A^2 \ (R^2 = 0.59)$$

According to the calculations, the proportion of marketable stems is the maximum at 110 years, which corresponds to the average diameter of 36 cm for the forest stands of the II site index class.

The table of commodity structure dynamics for modal oak stands (II site index) according to our data is given below (Table 2).

4. Discussion

The quantitative and qualitative wood structure of the studied coppice stands is worse than that of seed stands. Such significant differences are explained by the fact that the oak trees of coppice origin in the study area at an earlier age (110 years) and more frequently affected by rot (Girs et al. 2018). Peculiarities of the structure of the coppice oak stands are factors as well, which should be taken into account in forest management. Tkach (1999) also found a significant reduction in the increment of large industrial timber in coppice oak stands after 90 years of age. We compared the growing stock of large industrial timber graphically (Fig. 3).

The largest values of the yield of large industrial timber were given by Girs (2011) for seed-origin oak stands (Fig. 3). According to our study, stocks of large industrial timber are significantly smaller; this is due to smaller stocks of industrial timber in general and a smaller proportion of large timber in the forests of the study area. Thus, with an average diameter of 24 cm, the proportion of large industrial timber is 13% according to our data and 26% according to Girs (2011). Such differences can be explained by the peculiarities of the structure of oak stands in the Left-Bank Forest-Steppe, as well as the fact that Girs' data were obtained for fully stocked high-class seed-origin oak stands.

The age at which the maximum average increment for industrial timber is equal to the current increment is considered to be the age of technical maturity of the stand. The age of technical maturity for A and B classes of industrial timber is 101–110 years for B and C classes of industrial timber is 81–90 years and for industrial timber in total is 91–100 years (Table 3).

In similar conditions of the Russian Federation (forest-steppe of Belgorod and Voronezh Regions), in protective forests, the following ages of final felling were established: 101–120 years for coppice oak stands II and above site indexes, 141–160 years for oak stands of seed origin III and above site indexes (The order of Rosleskhoz 2015).

In Belarus, the lower age limit for final felling for oak stands is set at 101 years (Baginskiy et al. 2019).

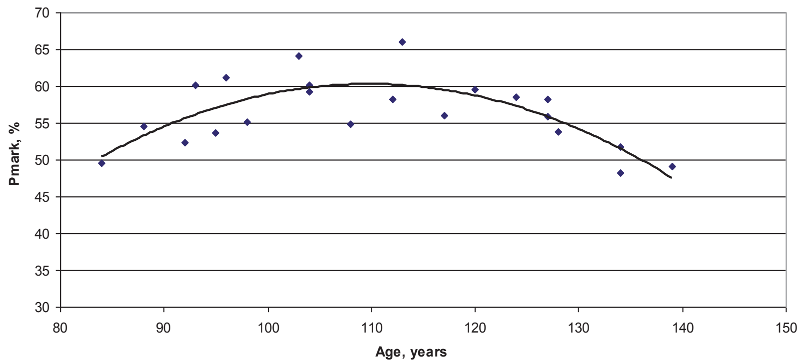

Fig. 2. Proportion of marketable stems in coppice oak stands depending on age.

Table 2. Commodity structure dynamics of modal coppice oak stands.

Age [years]	H [m]	D [cm]	Growing stock [m³·ha⁻¹]	Distribution of growing stock by size and quality categories [m³·ha⁻¹]					
				industrial timber					fuelwood
				A	B	C	D	total	
70	22.6	26.9	324	0	30	62	53	145	152
80	23.9	29.6	353	10	37	70	57	174	149
90	24.9	31.9	376	19	43	75	61	198	144
100	25.6	33.9	394	25	49	79	65	218	140
110	26.2	35.5	407	29	52	81	68	230	138
120	26.6	36.9	418	32	55	83	70	240	138
130	26.9	38.1	425	33	57	84	72	246	142
140	27.1	39.2	427	32	58	83	73	246	147

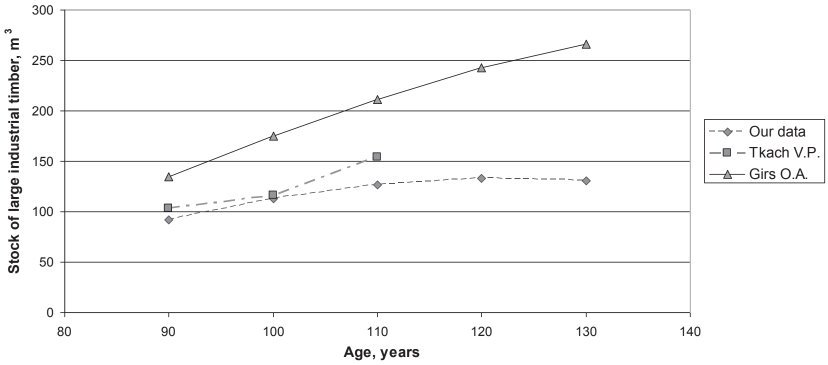

Fig. 3. The growing stock of large industrial timber in oak stands according to different authors (O.A Girs for seed-origin oak stands, V.P. Tkach for floodplain forests).

Table 3. Data for calculation of technical maturity indicators for coppice oak stands of II site index.

Age [years]	Growing stock [m³ ha⁻¹]	Average change in stock [m³ ha⁻¹]	Average change in stock of industrial timbe [m³ ha⁻¹]		
			classes A and B	classes B and C	total
70	324	4.63	0.43	1.31	2.07
80	353	4.41	0.59	1.34	2.18
90	376	4.18	0.69	1.31	2.20
100	394	3.94	0.74	1.28	2.18
110	407	3.70	0.74	1.21	2.09
120	418	3.48	0.73	1.15	2.00
130	425	3.27	0.69	1.08	1.89

Girs et al. (2018), taking into account average increment of industrial timber, proposed to set the age of maturity of 91–100 years for coppice oak stands of II site index for saw logs. Thus, the maturity ages in our study, are close to the data for all coppice oak forests in Ukraine.

Researches from Ukrainian Research Institute of Forestry and Forest Melioration (Torosov et al. 2019) proved the feasibility of applying the projected maturity ages for oak stands by forest categories in the Left-Bank Forest-Steppe (Kharkiv and Chernihiv Regions). Reducing maturity ages (by 1–3 age classes) in coppice oak stands results in an increase of the area of final felling. Further, after 2040, due to the creation of seed oak stands by planting or promoting natural regeneration on-site of former coppice stands the proportion of high-yield oak stands with improved commodity structure will increase (Torosov et al. 2019).

5. Conclusion

The commodity structure of oak stands in the Left-Bank Forest-Steppe part of Ukraine has its specificities, which are manifested in smaller stocks of commercial timber as compared to oak stands of Right-Bank Forest-Steppe zone of Ukraine. That is due to the predominance of coppice stands here and inappropriate ages of maturity established earlier. Our investigations show that the maturity age and associated age of final felling for commercial oak forests of coppice origin (II and higher site index) within the Left-Bank Forest-Steppe should be set at 91–100 years (X age class).

Setting the optimum maturity ages for oak stands improves the commodity structure of timber produced from logging in rotation period.

We suggest using the proposed tables to evaluate the commodity structure of mature oak coppice stands. Transformation of coppice oak stands into seed stands will improve their productivity and marketability.

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