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Preliminary assessment of effect of disturbance on natural regeneration in gaps of different sizes

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Abstract: The study focused on natural regeneration of European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) and European larch (*Larix decidua*) within very small and four times bigger size gaps following a disturbance at a mixed temperate forest in the Czech Republic. In spring 2013, experimental gap design starts, when 1 m^2 circular sampling plots along transects were delineated within four selected naturally occurring canopy openings with size below 20 m^2. In December 2013, these initial canopy openings were artificially enlarged by felling to 226 m^2 for small and 904 m^2 for big gaps. Regeneration was monitored in the next two consecutive growing seasons after disturbance. Light conditions were measured before and after disturbance. Results indicated that four times larger gaps increased twice levels of light conditions, and that diffuse light starts to equilibrate to direct light there. Large gaps were favouring larch regeneration. Beech regeneration was predominant, independently on gap size as the study area belongs naturally to Beech Forest Vegetation Zone, however, the decline of spruce regeneration was presumably linked to drought. Gap size explained variation of larch regeneration in gaps. Contrarily, gap size could not be associated with the prolific regeneration of beech and abysmal regeneration performances of spruce in gaps.

Keywords: European beech; European larch; growing season; light conditions; Norway spruce; regeneration

Disturbance is a phenomenal forest activity which paves the way for the creation of canopy openings called canopy gaps. This activity is also termed as gap disturbance because it usually creates gaps. The gap dynamics theory postulates that at any given time within any closed forest stands, disturbances may spontaneously happen to cause the death or injury of one or more canopy trees leading to gaps creation (Gray, Spies 1996; Yamamoto 2000). Gap disturbance is an essential silviculture strategy because it enhances natural regeneration. Due to the positive impact of gap disturbance on the regeneration process within forest ecosystems (Scharenbroch, Bockheim 2007; Lawer et al. 2013), it has been widely described in different forest types, such as tropical moist deciduous forest (Sapkota, Oden 2009; Duah-Gyamfi et al. 2014), tropical dry forest (Kennard et al. 2002), boreal coniferous forests (Kuuluvainen 1994), neotropical forest (Hubbell et al. 1999) and temperate mixed broadleaves forest (Lu et al. 2018a, b). Gap disturbances could be considered as natural or artificial disturbances (Sapkota, Oden 2009; Zhu et al. 2014) depending on the circumstances in which the event occurs, nevertheless, both scenarios can simultaneously happen within the same forest ecosystem. As the concept of close-to-nature forestry (Schütz 1999; Kuuluvainen, Laiho 2004) in silviculture develops, mimicking natural disturbances has become common in modern forest management (Čater, Diaci 2017; Lu et al. 2018b), particularly towards enhancing natural regeneration. In contemporary silviculture, forest management practices are set to imitate natural disturbances for the benefit of complex

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forest stands and this phenomenon, "gap dynamics theory" is closely related to natural regeneration (Yamamoto 2000; Muscolo et al. 2014). So, creating artificial gaps based on stand conditions has emerged as a widespread phenomenon to achieving forest regeneration and succession, including other management objectives (Kollár 2017; Lu et al. 2018a). Disturbances that open gaps provide specific microenvironmental conditions in light, soil moisture, and temperature regimes, which often initiate regeneration processes and development (Yamamoto 2000; Muscolo et al. 2014; Tsvetanov et al. 2018). Seedling establishment, survival, and growth exclusively depend on light (Kyereh et al. 1999; Diaci et al. 2008). Gaps introduce environmental heterogeneity within forest stands (Gendreau-Berthiaume, Kneeshaw 2009; Nagel et al. 2010; Lu et al. 2018b), such as variations in light conditions, regeneration niches (Diaci et al. 2008; Čater et al. 2014; Čater, Kobler 2017), litter depth and nutrient availability (Muscolo et al. 2014). This fine-scale heterogeneity at the forest floor create favourable microsites for seed germination and seedling establishment (Kuuluvainen 1994) and plays an indispensable role in forest dynamics by maintaining species structure and composition following gap disturbance. This serves as a useful predicting tool in assessing the effect of different disturbances intensities in different forest ecosystems (Muscolo et al. 2014; Tsvetanov et al. 2018). Among lists of gap's physical characteristics; percentage gap area, gap shape, and mode of gapmakers, etc. collectively termed as "gap-disturbance regimes", gap size remains the only critical feature that characterises within-stand level forest dynamics following disturbances (Yamamoto 2000; Diaci et al. 2012). Gaps sizes determine the amount of different light conditions that reach the forest floor (Canham et al. 1990) and the type of light condition species exploit in gaps (Nagel et al. 2010). Consequently, gaps are created to stimulate the mechanisms that promote the coexistence of natural regeneration tree species with different shade tolerance levels, preferably favouring shade-intolerant species (Yamamoto 2000; Nagel et al. 2010; Zhu et al. 2014). Depending on the share of direct and indirect (diffuse) radiations in the forest, Diaci (2002); Čater et al. (2014) and Čater and Kobler (2017) defined Direct Site Factor (DSF) and Indirect Site Factor (ISF) as the two important principal light conditions while Guay (2012) described their combination as Total Site Factor (TSF). However, the respective amounts of these light conditions significantly correlate with gap size. Shade-tolerant tree species grow well in small gaps, while shade-intolerant species survive better in large gaps (Nagel et al. 2010). This confirms for example, a study in Slovenia, where small gaps with low direct light levels supported shade-tolerant fir regeneration in mixed Dinaric forests (Čater et al. 2014).

Yet, many authors have limited their works towards the effect of gaps on tree regeneration species with similar life history attributes (Ritter et al. 2005; Čater et al. 2014; Čater, Diaci 2017), given very little attention to natural regeneration of tree species with different light requirements, particularly during their seedling growth stage. To gain a better understanding of the effect of forest disturbance on natural regeneration of tree species with different light requirements in gaps of different sizes is essential. We hypothesised that gap disturbance would improve light conditions in gaps, and this would influence natural regeneration in those gaps. Based on the findings of previous studies that gap creation enhances levels of light conditions (Yamamoto 2000; Ritter et al. 2005; Gendreau-Berthiaume, Kneeshaw 2009) and their influence on tree regeneration and subsequently forest succession (Van Pelt, Franklin 1999; Nagel et al. 2010). Therefore, there is a need to undertake this research. In the light of this, a comparison study between one shade-tolerant, intermediate and light-demanding tree species in mixed forest stands at a mixed temperate forest in central Europe is presented; i.e. regeneration responses of European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) and European larch (*Larix decidua*) species to different light conditions after gap disturbance in small and big size gaps were assessed in 2014 and 2015 growing seasons. Study objectives included: A) investigation of the effect of gap disturbance on microclimatic light conditions in gaps of different sizes, B) evaluation of the dynamics of natural regeneration of beech, spruce and larch tree species in gaps of different sizes at two consecutive growing seasons after gap disturbance.

MATERIAL AND METHODS

Study area. Training Forest Enterprise Masaryk Forest (TFE) Křtiny of Mendel University in Brno, a mixed temperate forest in Central Europe was

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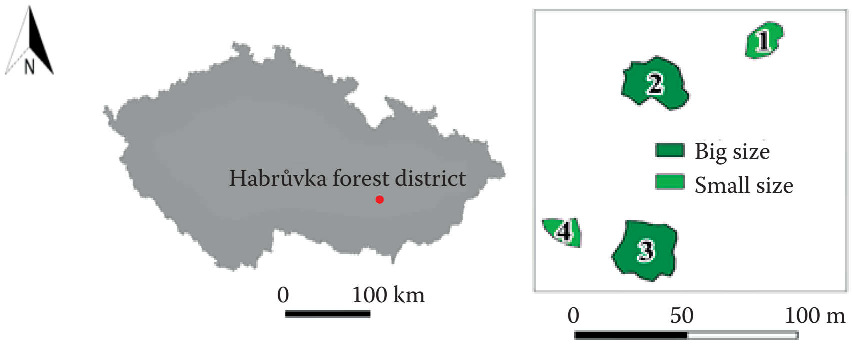

Figure 1. Location of study area highlighted in red dot (in map) and studied gaps (in box) – researchers' own

the study area. TFE is located at North direction from Brno in the Czech Republic, precisely, at longitude 49°15'N and latitude 16°15'E with an altitude range of 210–575 m a.s.l. (Figure 1). The average annual precipitation and air temperature are 610 mm and 7.5 °C, respectively. TFE is occupying a total area of 103 km^2 characterised by a variety of natural geomorphological conditions (Mašínová et al. 2017). Granodiorites, culmian grawacks and limestone are the underlying parent bedrocks (Anonymous 2013). According to the Czech forest typology, TFE sits within Forests Vegetation Zone 4 Beech forests (Beech FVZ 4*)* specifically at sites classified as 4W4 limestone beech – *Fagetum calcarium* and 4A9 stonycolluvial lime-beech – *Tilieto-Fagetum acerosum lapidosum,* respectively (Viewegh et al. 2003). The TFE forests comprise 54 % of broadleaved and 46 % of coniferous tree species (Mašínová et al. 2017). The presented study took place at Stand 156A 10 in the Habrůvka forest district of TFE (Table 1). This forest stand 156A 10 has a forest coverage of about 13.26 hectares thriving on rendzina soil type (Anonymous 2013). The parent stand is about 97 years old. The stand consists of 70% European beech (*Fagus sylvatica*); 14% Norway spruce (*Picea abies*); 6% European larch (*Larix decidua*); 6% European silver fir (*Abies alba)*; 2% Scots pine (*Pinus sylvestris*) 1% sessile oak (*Quercus petraea)*; and 1% Douglas fir (*Pseudotsuga menziesii*) with 337 and 31; 96 and 32; 40 and 34; 40 and 30; 10 and 30; 7 and 36; 3 and 26 as their mean growth stock (volume/ha) and top tree height (m), respectively (Anonymous 2013). Stand 156A 10 was selected for this study because; (*i*) mixed forest stands involve possible regeneration of both sun-loving as well as shade-tolerant tree species, (*ii*) natural canopy disturbance has been occurring in the forest stand and consistently, gap disturbance remains the only preferred silviculture option for stimulating tree regeneration in the forest establishment plan.

Material. Data recording book, short wooden poles, permanent marker, tape measure, calibrated gauge pole, digital compass and WinsCanopy photography instruments with their accessories (Regent Instruments Inc., Canada).

Experimental gaps. In spring 2013, mixed forest stands with four small canopy openings at about ± 45 m away from each other were identified and selected. These initial gaps were naturally originated canopy openings with gap sizes below 20 m^2 that were irregularly shaped (Schliemann, Bockheim 2011). In autumn 2013, experimental gap design was laid out in all considered stands:

Table 1. Description of study gaps at Stand 156A 10

Gap ID	Location (Longitude N, latitude E)	Aspect	Gap area (m^2)	Gap size	Gap shape	Forest type	ORP/RP (years)	Game attack category
1	49º18.95460‘,16°43.60152‘	W	286	small	elliptical	mixed stand	110/40	extremely high
2	49°18.94642',16°43.55067'	W	764	big	circular	mixed stand	110/40	extremely high
3	49°18.89250',16°43.53232'	W	904	big	elliptical	mixed stand	110/40	high
4	49°18.90320',16°43.50110'	SW	226	small	circular	mixed stand	110/40	high

ORP – optimal rotation period, RP – regeneration period, W – west, SW – south-west; data based on guidelines from the forest management plan for Masaryk Forest Křtiny (Anonymous 2013)

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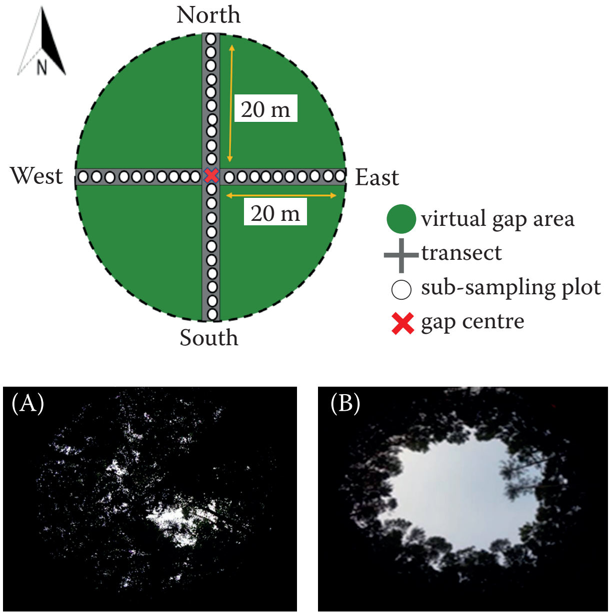

Figure 2. Schematic gap design (top) (Bíšek 2016) and fisheye view of gap transformation (example for Gap ID 2, before gap disturbance (A), after gap disturbance (B))

four semi-permanent transects in the cardinal directions (North-South-East-West) from the gap centre were marked out. Then, ten sub-sampling plots (i.e.; $1 m^2$ circular sampling area with 56 cm radius) at 2 m intervals were delineated with short wooden poles along the individual transect, and one additional sub-sampling plot at gap centre was laid out. Base-line measurement of regeneration was done at that time as well. Further, in December 2013, gap disturbance in the form of group felling was purposefully carried out within the selected stands, leading to the transformation of the small canopy openings into experimental gaps (final gaps formation) with different sizes varying from 226 m^2 to 904 m^2 (see Figure 2). WinsCanopy technology (Regent Instruments Inc., Canada, 2013a) was used to measure gap sizes of both initial and experimental gaps through processing of hemispherical photos. The activity was aimed to mimic natural disturbance in creating viable canopy gaps to facilitate forest restoration through natural regeneration to enhance both forest dynamics and health of the investigated old-growth stands. To reduce adverse effects of felling operation on gaps microsites, moderate soil disturbance was allowed to trigger the natural regeneration process because the soil was in a frozen state as at the time of the operation. For forest management guidelines of natural forest at TFE, usually natural disturbance regime in the form of small-scale disturbance is regular and recommended silviculture practice in the forest region that ensures sustainable forest development.

Data collection. For light conditions data, at every sub-sampling plot along transects and gap centre, one hemispherical photo was captured with WinsCanopy photography instruments comprising tripod of 1.3 m, auto-levelling frame, Sony Nex 10 camera (Sony, Minato, Tokyo, Japan) and calibrated fish-eye lens with an automatic North finder (Nikon, model FC-E8 0.21x, Tokyo, Japan) during before gap disturbance (autumn 2013) and repeatedly in the first growing season after gap disturbance (autumn 2014) respectively within each gap. For natural regeneration data, beech, spruce, and larch seedlings within delineated areas of sub-sampling plots along transects and gap centres were first identified, counted, and afterwards, their respective heights were measured with a calibrated gauge pole (in cm) and then surveyed data were recorded accordingly. This survey was carried out in two consecutive growing seasons (i.e.; 2014 and 2015 autumns) after gap disturbance. For a better appraisal of the effect disturbance on natural regeneration, only seedlings with heights growth ≤ 50 cm were considered as regeneration variables. Nonetheless, regeneration with heights growth > 50 cm, resprouts and advance regeneration including one-year-old seedlings (ephemeral trees which are not a good indicator of light availability) were excluded from the data survey.

Data processing and analysis. WinsCanopy technology (Regent Instruments Inc., Canada, 2013a) was used to process hemispherical photos into three light conditions: Direct Site Factor (DSF), Indirect Site Factor (ISF) and Total Site Factor (TSF) depending on the percentage proportion of direct and diffuse light. TIBCO STATISTICA 13.4.0.14 (SPSS, New York) was used to compute all data analyses. *T*-test was performed to examine the significant differences between the two groups of light conditions in gaps, i.e. before and after gap disturbance at $P \leq 0.05$ alpha level. Analyses of variance (ANOVA) following *post hoc* Tukey HSD were employed to attain significant differences between variables at $P \leq 0.05$ alpha level. A correlation was also performed to know the significant relationship between different light conditions and the three natural regeneration tree species at $P \leq 0.05$ alpha level for determination of correlation coefficient (r).

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Table 2. *T*-test results of the effect of gap disturbance on different light conditions

Light conditions	Proportion of light (%) (± SE)		*t*	df	*P*	Decision
	before gap disturbance	after gap disturbance				
DSF	5.5 (± 0.2)	18.9 (± 3.7)	–3.73	3	0.03	Accept Ho
ISF	6.4 (± 0.1)	22.7 (± 3.4)	–4.81	3	0.02	Accept Ho
TSF	5.6 (± 0.2)	19.4 (± 3.7)	–3.87	3	0.03	Accept Ho

DSF – direct site factor, ISF – indirect site factor, TSF – total site factor, SE – standard error, Ho – null hypothesis

RESULTS AND DISCUSSION

Effect of gap disturbance on different light conditions in gaps

In Table 2, results indicate that mean proportions of DSF, ISF, and TSF light conditions (19–23 %) attained after gap disturbance (2014) were significantly higher from those (5–6 %) obtained before gap disturbance (2013) at $P \leq 0.05$ alpha level. Also, quantified ISF light condition in the two examined groups of gap disturbance was relatively higher than the proportions of DSF and TSF light conditions in the same groups, respectively. Again, Table 3 shows the results of varying proportions of different light conditions measured within small and big size gaps in the first growing season after gap disturbance (2014). In both experimental gap sizes, ISF light condition was observed to be significantly higher than DSF and TSF light conditions, respectively. But then, no significant difference was observed between DSF and TSF light conditions in both gap sizes. Yet still, quantified light conditions in big size gaps (25–28 %) were approximately doubled (2x) comparing to those measured in small size gaps (13–17 %). This illustrates the essential role of "gap size" feature on the quantification of light conditions in gaps.

Gaps increase levels of light conditions (Dube et al. 2001; Ritter et al. 2005). In this study, DSF, ISF, and TSF light conditions were exponentially increased in gaps following gap disturbance in 2014. This demonstrates that gaps or gap creations control microclimatic light condition within forest stands (Yamamoto 2000; Mccarthy 2001; Muscolo et al. 2014). This finding also confirms the assumption that light penetration in gaps is divergent (Gendreau-Berthiaume, Kneeshaw 2009; Nagel et al. 2010; Zhu et al. 2014). In that, heterogeneity of light conditions in gaps is closely related to the gap-disturbance regimes (Mccarthy 2001; Zhu et al. 2014), which skews strongly towards "gap size feature". In general, gap sizes are a major determining factor in the distribution of light conditions in gaps (Canham et al. 1990; Gendreau-Berthiaume, Kneeshaw 2009). The effects of gaps of different sizes providing varying light conditions following gap disturbance have been studied elsewhere (Čater et al. 2014; Čater, Diaci 2017). In the study, ISF light condition became the most pronounced light condition in both small and big size gaps, but then again, its proportion varied completely among studied gap sizes. That, the proportion of ISF light condition within big size gaps was significantly higher than those within small size gaps. But, according to Čater et al. (2014), the proportion of direct and diffuse light conditions within gap microsites of gap sizes between 600 and 750 m^2 is equal. Our finding is because of the natural permanent shading conditions along the South transects and also at forest edges of the North transects in all studied gaps at the study area. Likewise, Muscolo et al. (2014) and Lu et al. (2018b) have also reported that a gradient of an increased level of light condition usually develops from South to North edge in gaps and this is commonly detected along the northern hemisphere during growing seasons.

Table 3. Variations of light conditions between two different sizes of gaps

Gap size	Light conditions	Proportion of light (%)
Small size	DSF	12.8 (± 2.0)^{a}
	ISF	17.1 (± 1.8)^{b}
	TSF	13.3 (± 1.9)^{a}
Big size	DSF	25.1 (± 1.7)^{c}
	ISF	28.2 (± 2.1)^{d}
	TSF	25.5 (± 1.8)^{c}

DSF – direct site factor, ISF – indirect site factor, TSF – total site factor, SE – standard error; different letters represent significant differences while same letters represent not significant differences of means at $P \leq 0.05$ alpha level

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Notwithstanding, sky conditions, solar angle, and height of bordering trees all together define the amount of light received in a gap.

Ecological relationship between enhanced light conditions and natural regeneration in gaps after gap disturbance

The results from correlation analysis between different light conditions and the three natural regeneration tree species in gaps revealed that spruce (r^2_{DSF} = 0.97 at P = 0.014; r^2_{ISF} = 0.96 at P = 0.021 and r^2_{TSF} = 0.97 at P = 0.015) established a significant negative linear relationship with various light conditions while beech and larch had no significant relationship with any of the light conditions at $P \leq 0.05$ alpha level during the first growing season after gap disturbance. Contrarily, in other studies, a positive correlation between light availability and growth of tree regeneration was found (Diaci et al. 2008; Muscolo et al. 2014). This result proves the assertion of Dobrovolný (2016) that light conditions significantly influence spruce regeneration. Our finding indicates that changes in the proportions of microclimatic light conditions within gaps (Čater et al. 2014) following gaps creation have significant influence on tree growth (Dube et al. 2001). In that, gaps creation after gap disturbance resulted in a considerable high light environment in gaps. This condition aggravated microclimatic air temperatures within gaps and in return, discouraged the growth of spruce regeneration in gaps significantly during the first growing season after gap disturbance. Similarly, in secondary spruce stands, a significant negative impact of high air temperatures on growth was observed at Central Bohemia's mixed lowland forests (Vančura et al. 2020). In another observation at mixed beech forests in Kozínek site, spruce became the most vulnerable tree species in growth due to the changing climatic conditions at the study site (Vacek et al. 2019). More so, Kollár (2017) observed a contradictory positive relationship between TSF light condition and height growth of different tree species regeneration in gaps at Sessile-Oak-Hornbeam and Turkey Oak Forests in western Hungary while in this study, we found a strong negative relationship between TSF light condition (correlation coefficient (r) = –0.99) and spruce regeneration in gaps under mixed spruce stands. Recently, Dobrovolný (2016) found 10.7 to 20.8 % of ISF light condition within gaps as the best quantity range for ISF light condition in ensuring sustainable growth of spruce regeneration at two different growing sites in his study. Nonetheless, we observed a higher mean range (17.1–28.2 %) for the estimated ISF light condition in small and big size gaps. This could probably be the reason why densities of spruce regeneration in gaps were comparatively lower in 2014, even though spruce juveniles were growing under spruce dominated mixed stands.

Effect of gap disturbance on natural regeneration dynamics within gaps of two different sizes

In Figure 3, mean regeneration densities of natural regeneration of beech, larch and spruce tree species in two consecutive growing seasons after gap disturbance are presented. During the first growing period after gap disturbance (2014), mean regeneration density of beech (15 257 trees·ha^{-1}) was significantly different (P < 0.05) from these of spruce and larch in small size gaps. In addition, in small size gaps, mean regeneration density of spruce (5 877 trees·ha^{-1}) was significantly higher (P < 0.05) than larch (2 923 trees·ha^{-1}). Therefore, the regeneration was in this proportion among beech-spruce-larch – 5:2:1. In contrast, in big size gaps, mean regeneration density of larch (10 971 trees·ha^{-1}) was not significantly different (P > 0.05) from beech (10 710 trees·ha^{-1}), yet, mean regeneration density of larch was significantly higher (P < 0.05) than mean regeneration density of spruce (879 trees·ha^{-1}) during the first growing season after gap disturbance. Therefore, the regeneration was in this proportion among beech-spruce-larch – 12:1:12. Furthermore, in the second growing period after gap disturbance (2015), we observed significant differences (P < 0.05) in mean regeneration densities between beech (12 485 trees·ha^{-1}), larch (6 145 trees·ha^{-1}) and spruce (1 383 trees·ha^{-1}) in big size gaps respectively. Therefore, the regeneration was in this proportion among beech-spruce-larch – 9:1:4. But, in small size gaps, only beech (13 731 trees·ha^{-1}) species recorded a significantly higher regeneration density (P < 0.05) while mean regeneration densities of larch (1 755 trees·ha^{-1}) and spruce (1 370 trees·ha^{-1}) species were not significantly different (P > 0.05) from each other. Therefore, beech:spruce:larch regenerated in these proportions among each other – 10:1:1. This result confirms the statement of Gendreau-Berthiaume and Kneeshaw (2009) that different light conditions in big gaps statistically allow for difference in the

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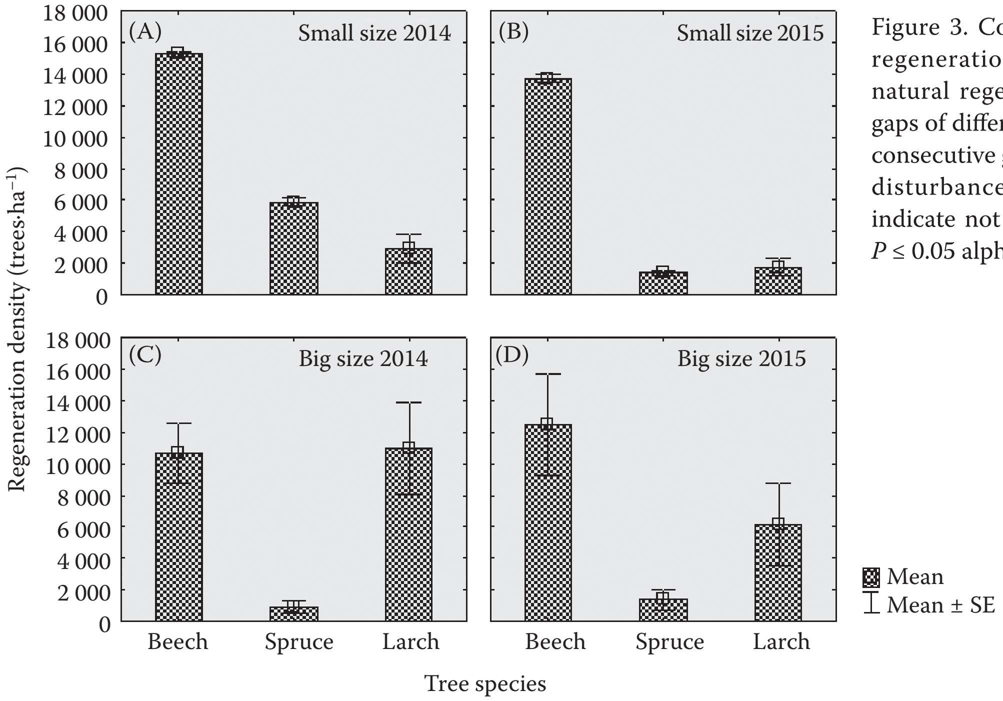

Figure 3. Comparative evaluation of regeneration densities of different natural regeneration tree species in gaps of different sizes recorded in two consecutive growing seasons after gap disturbance (overlapping whiskers indicate not significant differences at $P \leq 0.05$ alpha level)

recruitment and establishment of tree species with different shade tolerance rather than in small gaps which perhaps, might not lead to any significant differences in species regeneration. Aside from small size gaps in 2014 where natural regeneration of spruce encountered a significant rise in mean regeneration density. However, spruce regeneration was comparatively lower in big size gaps in 2014 and similarly, thereafter in both small and big size gaps respectively in 2015. This result describes the ecological regeneration behaviour and growth dynamics of natural regeneration of tree species with different shade tolerance abilities in gaps of different sizes.

Across the two consecutive growing seasons after gap disturbance, small size gaps were observed to have provided optimum growing conditions within their microsites for the rapid establishment of shade-tolerate beech species compared to spruce and larch. By autecology of beech, it thrives better under shelter conditions where diffuse light is high (Ritter et al. 2005; Dobrovolný et al. 2013; Čater, Kobler 2017). Although beech regeneration was expected to have decreased substantially with increasing proportions of light conditions in big size gaps (Dobrovolný, Cháb 2013), comparatively, its regeneration density significantly increased in both assessed different growing seasons after gap disturbance. The abundant shedding of beech seeds from the matured old-growth stand and nearby mother trees (Dobrovolný, Cháb 2013) provided a regular supply of seeds and with time resulted in built of a rich seed reservoir or seed bank at the forest floor. This profuse seed source at gap microsites plus light availability in the first growing season after gap disturbance facilitated the upsurge yield of beech regeneration in gaps. Light is crucial for seed germination (Kyereh et al. 1999), hence, light availability contributes substantially to the success of gap regeneration. This observation is very common in Central European forests where natural regeneration of shade-tolerant species frequently establishes from heaped seed bank at the understory, and this immeasurably boost post-disturbance forest restoration processes in gaps (Čater, Diaci 2017). Likewise, during the second growing season after gap disturbance, the inherent broad light adaptability of beech species (Dobrovolný 2016) empowered beech regeneration to respond rapidly and at the same time, this biological trait assisted beech species to thrive so well in the changing light environment in gaps (Čater et al. 2014; Čater, Kobler 2017) compared to the conifers that gradually responded (Stancioiu, O›hara 2006), noticeably, for spruce. Another explanation for the predominance regeneration status of beech across all gap sizes in the two growing seasons after gap disturbance is connected to the typological designation of the study area as Beech FVZ 4 (Viewegh et al. 2003). Where natural stand conditions favoured beech re-

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generation more than any other tree species though natural regeneration was under spruce dominated mixed stands. Similarly, Dobrovolný (2016) recorded successful colonisation of beech regeneration under the shelter of spruce stands in Fir-Beech Vegetation-Acidic Site in the Czech Republic. In another remark, gaps in old-growth Douglas-fir forests were important sites for the regeneration of shade-tolerant tree seedlings at the Cascade Mountains in America (Gray, Spies 1996). Generally, our observation is consistent with the report of Collet et al. (2001) that beech is able to respond rapidly to canopy gaps. The significant increment of spruce regeneration density in small size gaps during the first growing season after gap disturbance was the consequent of the abundant sources of seeds supply from the dominated parent trees in the investigated stands. According to Hiitola (2018), spruce holds 50 % of the total parent stand composition in the mixed forest type of Stand 156A 10. However, seed germination and seedling establishment were slow due to the improved levels of light conditions in small size gaps. Our finding disagrees with a comment of Tsvetanov et al. (2018) that spruce regeneration might preserve their vitality under forest canopy for several years and then grow vigorously when light conditions improve after forest disturbance. Moving on, natural regeneration of larch species was statistically different from spruce in big size gaps across the studied two consecutive growing seasons after gap disturbance respectively. This validates larch as sun-loving species that regenerates excellently under high light conditions. But then, very poor regeneration records were obtained for larch species in small size gaps. In brief, the above findings suggest that gap size has a strong influence on larch regeneration, especially through its effects on light proportions or intensities. Again, our observation proves the widely held assumption that shade-intolerant tree species germinate, survival and develop best in gaps at both temperate (Mccarthy 2001; Muscolo et al. 2014; Zhu et al. 2014; Lu et al. 2018a; Lu et al. 2018b) and tropical forests (Lawer et al. 2013; Duah-Gyamfi et al. 2014). Our results exclusively confirm a statement from Matras and Pâques (2008) that larch as a light-demanding tree species thrives well after disturbance mainly because of the creation of gaps following the activity which opens up growing space for the reception of increased levels of light penetration. In addition, the fast-growing mode, as well as biologically quick and yielding positive reaction to light environment particularly under gaps conditions (Matras, Pâques 2008), are the attributed factors for the significant rise of natural regeneration of larch species in big size gaps. Moreover, many authors across the globe have attested larch species among the fastest-growing conifer tree species in the world. To name a few, in western and central Europe, *Larix decidua* (Matras, Pâques 2008); in China, *Larix keampferi* and *Larix olgensis* (Lu et al. 2018a; Lu et al. 2018b) and in Japan, *Larix leptolepis* (Qu 2016) because these different larch species demonstrate similar growth traits. Based on the rapid growth of larch at the seedling growth stage, it is, therefore, a good recommendation to be used as a preparatory species when applying different regeneration activities like afforestation or reforestation preferably on either open or disturbed areas (Matras, Pâques 2008). Nevertheless, a decline variation was detected between larch regeneration in the first and second growing seasons in big size gaps after gap disturbance. The explanation is that, with time, for e.g. in the second growing season in 2015 after gap disturbance, the forest region experienced elevated average air temperature of 10.4 °C (CHMI 2018) as against the expected climatic average air temperature of 7.5 °C (Mašínová et al. 2017). This environmental situation increased the rate of soil water loss through higher light intensities within big size gaps. This situation negatively interfered the competition mechanism of larch species for light, nutrients and water hence, triggered poor growth performances of larch regeneration in big size gaps during the second growing season after gap disturbance. In short, the dynamics of different natural regeneration tree species in gaps of different sizes depend greatly on type of vegetation, growth strategies of participatory species, species-specific survival mechanism and gap size factors.

Height growth dynamics of natural regeneration tree species within gaps of two different sizes

Results in Figure 4 presents two juvenile height classes (0–20 cm, 21–50 cm) of natural regeneration of beech, spruce and larch tree species that were enumerated during the second growing period after gap disturbance (2015). For 0–20 cm, beech juveniles (12 954 trees·ha^{-1}) recorded the highest significant (P < 0.05) mean regeneration density in small size gaps. Nevertheless, in big size gaps, mean regeneration density of larch juveniles

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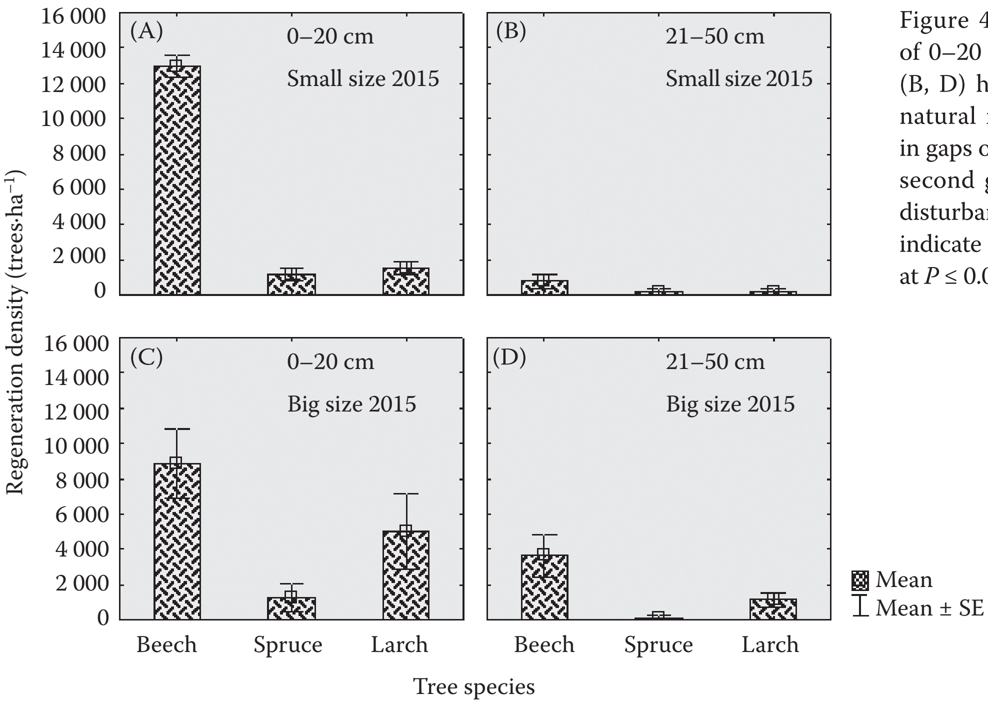

Figure 4. Regeneration densities of 0–20 cm (A, C) and 21–50 cm (B, D) height classes of different natural regeneration tree species in gaps of different sizes during the second growing season after gap disturbance (overlapping whiskers indicate not significant differences at $P \leq 0.05$ alpha level)

(5018 trees·ha^{-1}) was significantly higher ($P < 0.05$) than spruce juveniles (1 264 trees·ha^{-1}) and at the same time, not significantly different ($P > 0.05$) from that of beech juveniles (8847 trees·ha^{-1}). It is, in the same consequence, a proportion of 4:1:7 in regeneration density. For 21–50 cm, all three natural regeneration tree species generally encountered lower alarming regeneration density in both studied gap sizes. Therefore, showing no significant difference ($P > 0.05$) among them in small size gaps was observed. Surprisingly, in big size gaps, mean regeneration density of beech juveniles (3 627 trees·ha^{-1}) was observed to be significantly higher ($P < 0.05$) than larch (1 127 trees·ha^{-1}) and spruce (119 trees·ha^{-1}), respectively (i.e. in a proportion of 30:9:1). At the same time, mean regeneration density of larch juveniles managed to be slightly different (difference of ± 1 008 trees·ha^{-1} at $P < 0.05$) from spruce juveniles significantly in big size gaps. In a general overview, spruce juveniles enumerated the least counts of mean regeneration densities in both small and big size gaps in the study. Therefore, this result indicates the resilient capacity and high ecological tolerability of beech species to withstand a wide range of unfriendly ecological conditions (pro-mortality factors) including increasing levels of light conditions in gaps while natural regeneration of spruce portrayed low resistance potential and ecological intolerance to harsh growing conditions in gaps.

Height growth is a critical morphology parameter that cannot be ignored when assessing tree growth in a light-exposed environment like gaps. Because there is an interesting positive relationship between seedling height and light availability (Caquet et al. 2010), therefore, it is so important to evaluate height growth when considering natural regeneration in gaps (ie., light environment). In this study, by the biological dictate of beech as a shade-tolerant specie (Lödige et al. 2014), natural regeneration of its juveniles under 0–20 cm height class was adequately resourced in small size gaps. Remarkably, this trait influenced the exponential growth of beech species compared to juveniles of the other tree species in that same investigated small size gaps. The regular distribution of low light conditions that formed a continuum of shade environment within small gaps due to their relatively 'small size' area was the reason. However, in big size gaps, the bulk of seeds reservoir at the forest floor, the activity role of browsing animals in seed dispersal at the study area (Hiitola 2018) as well as the physiological and morphological plasticity of shade-tolerant species which allows them to quickly yield to increased light environments (Muscolo et al. 2014) were the reasons why regeneration density of beech juveniles was not significantly different from larch juveniles in natural regeneration under spruce dominated mixed stand. Accordingly, Dobrovolný (2016) stated that in about one-hectare

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area of spruce stand, a few beech trees (only 2–3) could produce nearly 30 % share of beech seeds for beech regeneration in succession. For 21–50 cm height class, widespread abysmal regeneration performances were recognised in both small and big size gaps. This finding could be linked to the extreme activities of browsing animals (Anonymous 2013) and the unfortunate 2015 drought menace at the study area. Previous studies by Hiitola (2018) also attributed the reduction in natural regeneration to the rigorous activity of browsing animals in the study area. This comment substantiates our finding on the effects of animal damage on tree growth (Collet, Chenost 2006; Blackburn et al. 2014). Besides, the recorded average annual precipitation during the second growing season after gap disturbance (2015) was 430 mm (CHMI 2018), and this value was factually lower than the expected climatic average annual precipitation value of 610 mm (Mašínová et al. 2017). This environmental predicament forced natural regeneration to be confronted with intolerable water stress which caused massive mortality in all assessed tree species under 21–50 cm height class. This situation contributed significantly to the lower regeneration densities of natural regeneration of tree species in gaps. Although in big size gaps, microclimate light conditions were conducive (Gendreau-Berthiaume, Kneeshaw 2009) for larch regeneration, however, the existence of other thriving tree species in natural regeneration substantially impeded larch species especially those juveniles under 21–50 cm height class. This statement verifies the pronouncement of Matras and Pâques (2008) that, ensuring excellent natural regeneration of different tree species, including larch species requires thinning in silviculture tending in order to control the inevitable competition among species. Primarily, the success of natural regeneration depends on physical conditions such as weather conditions and activities of browsing animals at the growing site as well as the biological traits of the involving growing tree species (Qu 2016). Furthermore, larch regeneration was significantly higher than spruce, relatively because of the new created ecological settings within gap microsites following gap disturbance (Zhu et al. 2014; Lu et al. 2015). The state of this new microenvironment had a close resemblance to natural growing conditions, which to a fair extent was preferred by larch regeneration (Matras, Pâques 2008; Qu 2016; Lu et al. 2018b). Very importantly, larch is highly susceptible to browsers while spruce is also highly susceptible to climatic drought conditions as mentioned elsewhere by Matras and Pâques (2008) and Vančura et al. (2020) respectively. In brief, both biotic and abiotic factors comprehensively (Mccarthy 2001; Dobrovolný 2016) affect natural regeneration.

CONCLUSION

Gap disturbance improves microclimatic light conditions in gaps through gap creation. Gap size feature is a major distinguishing factor in the quantification of light conditions in gaps. The proportions of Direct Site Factor (DSF), Indirect Site Factor (ISF), and Total Site Factor (TSF) light conditions in big size gaps were comparatively twice higher than those measured within small size gaps, and prevailing diffuse light up to these sizes of gap (around 800 m^2) become equilibrated with the direct light proportion. The geographical characteristics of the study area made ISF significantly more pronounced light condition due to the permanent shading conditions along the South transects and forest edges of the North transects in gaps. The study primarily reveals the importance of the effects of gaps creation on natural regeneration of beech, spruce and larch tree species in the forest. Increasing light conditions after gap disturbance significantly influenced natural regeneration in gaps, as spruce regeneration had a negative correlation with the three examined light conditions in gaps. Furthermore, regeneration densities of larch in big size gaps from the first to second growing seasons after gap disturbance were significantly higher than those enumerated in small size gaps. Meanwhile, beech regeneration in big size gaps was indifferent from small size gaps. Moreover, regeneration density of spruce encountered in small size gaps during the first growing season after gap disturbance was significantly higher than those enumerated in both small and big size gaps during the second growing season after gap disturbance. Therefore, large gaps were important for favouring larch regeneration. Beech regeneration was largely predominant because the study area belongs to Beech Forest Vegetation Zone, however, the decline of spruce regeneration was linked to microclimatic conditions in gaps and presumably drought at the stand level. Gap size explained variation of larch regeneration in gaps. In contrast, gap size could not be

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associated with the prolific regeneration of beech and abysmal regeneration performances of spruce in gaps. In summary, this study proves the importance of gap openness as a preliminary step in the natural regeneration process (Kollár 2017). Also, physical conditions such as weather conditions and activities of browsing animals at the growing site as well as the inherent biological character of regenerating tree species, determine the success of natural regeneration of different tree species in gaps of different sizes.

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