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Effects of gap size on natural regeneration and micro-environmental soil conditions in European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst) dominated mixed forest

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Abstract: The study focused on the effects of gap size on natural regeneration of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* L.) and micro-environmental soil conditions in gaps of different sizes under temperate mixed forest in the Czech Republic. Six gaps comprising two for small (≥ 200 m^2), medium (≥ 500 m^2) and big (≥ 900 m^2) each were selected. Ten circular 1 m^2 subsampling plots were established at 2 m intervals along individual North-South-East-West transects, including one at the gap centre. Regeneration was monitored in 2014 and repeatedly in 2019. Soil conditions were only measured in 2019. Gap size was found to be a significant parameter for European beech natural regeneration in 2014. Besides, the quick occupation of European beech in gaps at natural beech zone provoked its prolific regeneration compared to Norway spruce in 2014. However, in 2019 the recent threat of weather variabilities was responsible for the general abysmal growth performance of natural regeneration. Division of gap microsites into different within-gap positions based on prevailing light or shade conditions was helpful in assessing the significant variations of soil conditions within-gap positions and among gap sizes. Soil temperature and moisture significantly influenced the regeneration of European beech and Norway spruce, respectively.

Keywords: competition; forest dynamic; microclimate; regeneration density; electrical conductivity

Gap creation by small-scale disturbance is a major characteristic disturbance event that has become a prominent theme in forest dynamics research, particularly in the natural regeneration of many temperate forests today (Feldmann et al. 2020, Hammond and Pokorný 2020). This is because natural disturbances that lead to gap creations are usually small-scaled (Čater and Diaci 2017). In Europe, simulating natural disturbances through silviculture operations of combined single-tree selection and group selection systems, viz., small-scale disturbances in closed matured forests, are relevant to conservation management. Patterns of both long-term survivals of forest-dwelling species and tree regeneration are key driving forces in forest management (Kenderes et al. 2009). Small-scale disturbances that create gaps play integral roles in forest development by maintaining the structure of old-growth forest mainly through the emergence and survival of natural regeneration (Jaloviar et al. 2020) and also, through the regulation of heterogeneity of micro-environmental conditions (light, temperature, moisture, and nutrient) (Bílek et al. 2014) that are crucial for seedling establishment and growth (Muscolo et al. 2011, Vilhar et al. 2015).

For natural regeneration in gaps, "gap size" is the most singular essential feature (Hammond and Pokorný 2020) that is key to regeneration patterns of different tree species with divergent life-long attributes (Jaloviar et al. 2020). Hence, over the years, the effects of gap size on natural regeneration (Čater

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et al. 2014) and variability of micro-environmental soil conditions (Latif and Blackburn 2010, Kučera et al. 2020) have been studied widely. Therefore, gaining an in-depth understanding on the effects of gap size and micro-environmental soil conditions on natural regeneration is a prerequisite for developing techniques of nature-based forestry (Gálhidy et al. 2006). This is because gaps are tools used in close-to-nature forestry to optimise structural diversity by mimicking natural processes in forests of different tree species composition. Besides, gap ecology depends enormously on site conditions, silvicultural management systems and goals, especially in changing environmental conditions.

However, in temperate mixed forest Křtiny in the Czech Republic, very little research has been carried out on the effects of gap size on natural regeneration and micro-environmental soil conditions in gaps of different sizes. Thus, this study aimed at (1) assessing the variability of regeneration performance of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst) within the small, medium, and big gap-size environments during two separate growing seasons; (2) assessing the ecological patterns of micro-environmental soil moisture, temperature and electrical conductivity conditions within the three gap sizes, and (3) assessing the effects of mentioned abiotic micro-environmental soil conditions on biotic natural regeneration of tree species in those gap sizes.

MATERIAL AND METHODS

Study area

Temperate European beech-Norway spruce-dominated mixed forests under investigation are located in the south of the Czech Republic (49°13'–49°21'N, 16°34'–16°40'E, elevation 210–575 m a.s.l.) precisely in Křtiny, Blansko District of the South Moravian region. This forest is an active, practical and research site for the Mendel University in Brno, that was established in 1923. The area's climate is humid continental with annual mean precipitation of 610 mm alongside 7.5 °C mean annual air temperature. Limestone is the predominant underlying bedrock with cambic rendzinas, luvisols, brown earth and mesotrophic cambisols as the most prevailing soil units, broadly classified under the cambisol (kambizem) soil type category according to the Czech taxonomic soil classification system.

The study was conducted in the forest management stand 156 A 10 (13.26 ha; 97 years old) of the Habrůvka Forest District. This section forms part of the *Fagetum calcarium* vegetation community. Species composition of the stand comprises 70% European beech (*Fagus sylvatica* L.), 14% Norway spruce (*Picea abies* (L.) Karst), 6% European larch (*Larix decidua* Mill.), 6% European silver fir (*Abies alba* Mill.) and 2% Scots pine (*Pinus sylvestris* L.) while Sessile oak (*Quercus petraea* (Matt.) Liebl) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) comprise 1% each of the total stand composition. The growing stock of stand 156 A 10 under the Forest Management Plan is 533 m^3/ha. Natural regeneration remains the most preferred silviculture practice (Anonymous 2013).

Study gaps

Six study gaps (Table 1) were formed in winter 2013/2014 following small scale disturbances:

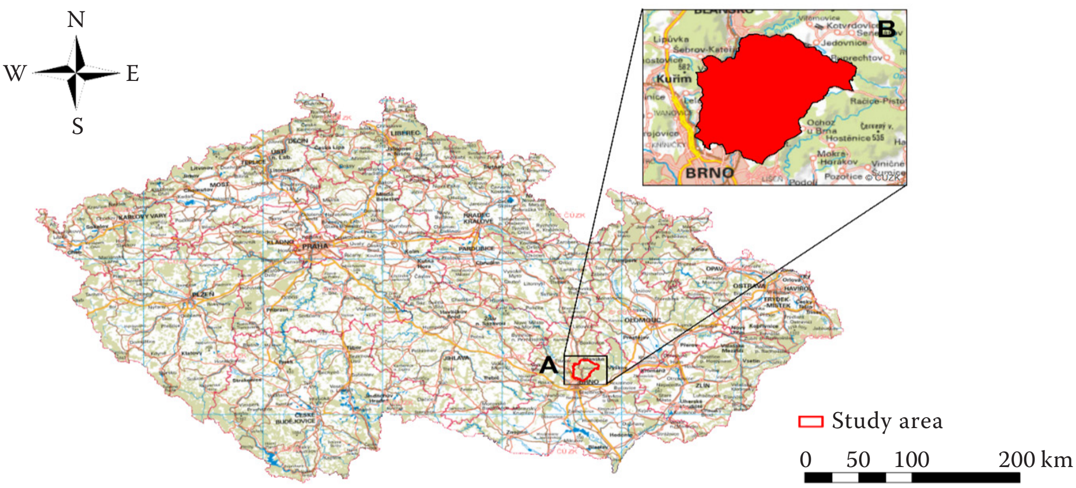

Figure 1. Study area

https://doi.org/10.17221/397/2020-PSE

Table 1. Basic characteristics of research gaps

Gap No.	GPS location	Gap size/forest type (m^2)
1	49°19.06768'N, 16°43.66460'E	medium/broadleaved European beech dominated (528)
2	49°19.02657'N, 16°43.62308'E	small/broadleaved European beech dominated (282)
3	49°18.99488'N, 16°43.64303'E	big/broadleaved European beech dominated (1 149)
4	49°18.95460'N, 16°43.60152'E	small/mixed Norway spruce – European beech dominated (286)
5	49°18.94642'N, 16°43.55067'E	medium/mixed Norway spruce – European beech dominated (764)
6	49°18.89250'N, 16°43.53232'E	big/mixed Norway spruce – European beech dominated (904)

European beech – *Fagus sylvatica* L.; Norway spruce – *Picea abies* (L.) Karst

2 × small gaps (a single tree cut; diameter of ca. 30 m); 2 × medium gaps (a double tree cut; diameter of ca. 30 m), and 2 × big gaps (a thrice tree cut; diameter of ca. 30 m). Three gaps each were selected from broadleaved European beech dominated (90% European beech) and mixed Norway spruce-European beech dominated (50% Norway spruce, 30% European beech) forest types (Table 1).

Sampling design

Within each gap, a total number of 41 circular (1 m^2 area of 56 cm radius) semi-permanent subsampling positions were set up at 2 m intervals. Thus, ten plots each along 20 m long individual North-South-East-West transects, including one additional plot at the gap centre (Figure 2).

Furthermore, three within-gap positions based on prevailing light or shade conditions were delineated at each given gap site; (1) centre or gap centre representing the most light-exposed within-gap position; (2) HL representing high light-low shade within-gap position (1–5 subsampling positions/plots along individual transects), and (3) LH representing low light-high shade within-gap position (6–10 subsampling positions/plots along individual transects).

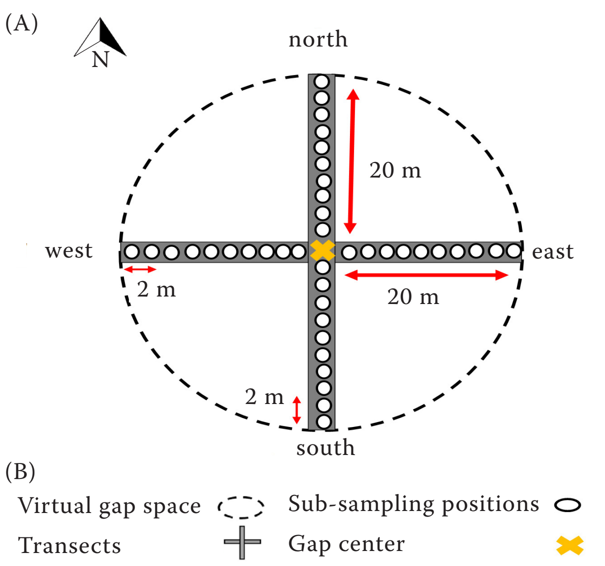

Figure 2. Gap design for (A) sampling and (B) legend

Monitoring of natural regeneration performances. During autumns 2014 (one year after gap creation) and 2019 (five years after gap creation), all European beech and Norway spruce regeneration, including resprouts and advance regeneration (DBH < 10 cm and height 0–350 cm) within subsampling plots were first identified at the species level, counted and recorded accordingly. Nevertheless, all one-year-old ephemeral seedlings were excluded from the data survey.

Micro-environmental soil conditions measurements. In autumn 2019, precisely on the 4th November 2019, where rainfall had not occurred seven days before the field survey, measurements of micro-environmental soil moisture (%), temperature (°C) and electrical conductivity (EC) (dS/m) were carried out across all 41 subsampling positions delineated within gaps with the aid of a time-domain reflectometry (Trime TDR) equipment (IMKO's technologies, Ettlingen, Germany). The Trime TDR consists of a pair of 160 mm long probes of 6 mm diameter at 40 mm apart (Trime-Pico64 model), including a portable Trime HD2 device with an inbuilt screen that displays values of respective soil conditions at ± 0.2%, ± 0.5 °C, and ± 0.05 dS/m accuracy. At every subsampling position, the Trime TDR probes were carefully lowered at the prescribed soil depth (16 cm) within the topsoil horizon and instantly, the Trime HD2 device displayed measured values of micro-environmental soil moisture, temperature and electrical conductivity conditions digitally. Immediately, these values were respectively recorded. The topsoil material of all studied gaps is loess loam (Kučera et al.

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2020). To prevent measurement errors, probes were thoroughly cleaned after every insertion because the Trime TDR equipment is highly material-sensitive.

Statistical analyses

Analyses of variance (ANOVA) and post hoc *LSD* (least significant difference) analysis were performed to determine differences after testing data to meet conditions of normality and homogeneity of variances. Probability values of $P < 0.05$ were considered significant. Data analysis and the regression between measured variables were analysed with the Statistica data analysis software system (13.4.0.14 version, ©1984–2018 TIBCO Inc), obtaining the significance of the regression coefficient (p) and the determination coefficient of the linear regression (r^2).

RESULTS AND DISCUSSION

Effects of gap size on natural regeneration performances

Densities of European beech and Norway spruce natural regeneration in gaps of different sizes during the 2014 and 2019 growing seasons are presented in Figure 3. Apart from medium gaps, regeneration densities of European beech within small and big gaps were significantly higher ($P < 0.05$) than Norway spruce in 2014. However, during 2019, no significant difference ($P > 0.05$) was measured between regeneration densities of European beech and Norway spruce across all the studied gap sizes. Meanwhile, highly significant differences ($P < 0.05$) were found between measured regeneration densities in 2014 and 2019 for European beech in all three studied gap sizes.

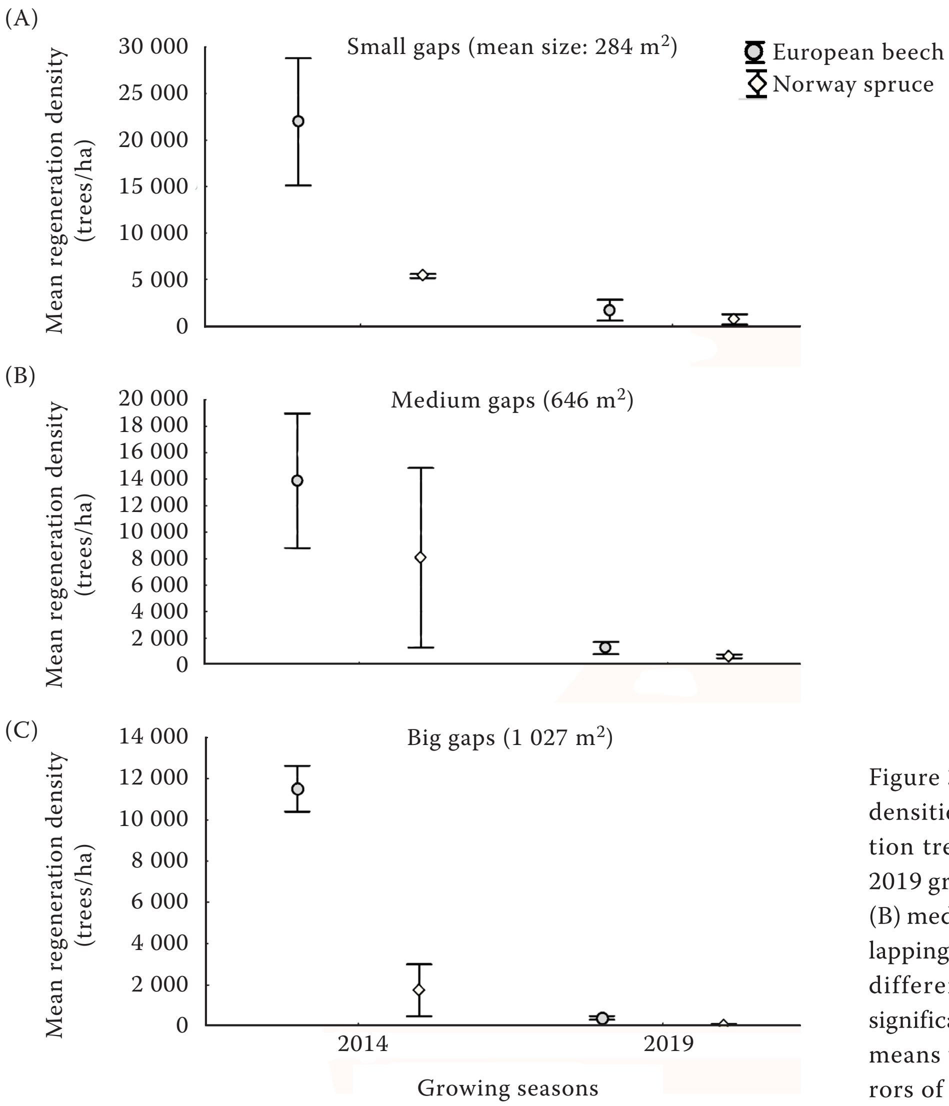

Figure 3. Comparing regeneration densities of two natural regeneration tree species during 2014 and 2019 growing seasons in (A) small; (B) medium and (C) big gaps. Overlapping bars indicate not significant differences of means at $P < 0.05$ significance level. Whiskers indicate means while bars are standard errors of means

https://doi.org/10.17221/397/2020-PSE

Likewise, similar results were obtained for Norway spruce in small gaps only. Generally, measured regeneration densities in 2014 were significantly higher ($P < 0.05$) than those evaluated in 2019.

European beech demonstrating significantly superior growth performance over Norway spruce during 2014 within small and big gaps may not be ascribed to the gap size effect, but to the quick occupation of European beech species in gaps due to the biological traits of this shade-tolerant species. Most importantly, by (1) the quick light adaptability trait (Dobrovolný and Cháb 2013) and (2) the inherent behavior of morphological plasticity in new light environments (Collet et al. 2002). Wherefore, it is no surprise that the natural regeneration of European beech species in gaps was advantageously competitive than slow light adaptable Norway spruce. A similar observation has been mentioned in a study conducted in another temperate European forest (Stancioiu and O'Hara 2006). This typical growth behavior of conifers in gaps always gives European beech species a more growing opportunity to flourish when growing together in the same light-exposed environment. Our results corroborate the reports of Peters (1997) and Bílek et al. (2014) that European beech is a strong competitor species that is commonly present in a variety of mixed-species forests and pure stands. Furthermore, in 2014, gap size was found to be a significant parameter for European beech natural regeneration in gaps. Our findings that European beech achieved its best regeneration performance in small gaps is consistent with previous studies of Čater et al. (2014) and Feldmann et al. (2020) that European beech obtains optimal growth under small canopy openings. Besides, it could be likely that the heavy shade-tolerant character of European beech, including favourable light conditions following gap creation from small-scale disturbance, influenced its successful seedling recruitment, seed establishment (Feldmann et al. 2020) and the maintenance of its excellent growing performances within small gaps during 2014 growing season. Similarly, in old-growth mixed-species Dinaric forests in Slovenia, a report on gap regeneration of European beech by Čater et al. (2014) was indifferent. More so, the optimal significant natural regeneration performance of European beech in big gaps during 2014 could be linked to the studied site forming part of the natural beech vegetation zone (Anonymous 2013) and abundant seeds production from proximate mother trees in stands. This finding is in agreement with a statement from Král et al. (2010) that beech species dominate natural forests in the Czech Republic, and at the same time, it is consistent with Dobrovolný and Cháb (2013) view that the reproduction potential of mother trees of European beech is highly productive. Seemingly, this could be another reason for the prolific regeneration performance of European beech compared to Norway spruce in big gaps during 2014. Evidence demonstrating increasing deciduous European beech dominance at the expense of coniferous Norway spruce has already been documented elsewhere (Parobeková et al. 2018).

Notwithstanding, the observation of better comparative regeneration densities of Norway spruce in 2014 due to increased light levels in gaps following disturbance is consistent with the studies of Dobrovolný and Cháb (2013), Bílek et al. (2014) and Čater and Diaci (2017) who remarked that Norway spruce density increases with increasing light intensity. However, the result of Hammond and Pokorný (2020) who found a negative linear relationship between Norway spruce regeneration and improved light conditions in gaps following disturbance disputes it. Also, adequate water supply during the 2014 growing season was another reason for the relatively higher regeneration densities of Norway spruce regeneration in gaps. In that, the recorded annual mean precipitation in the study area for 2014 (622 mm) (CHMI 2020) was slightly higher than the historical records of 610 mm (Figure 4).

Contrarily, the general failure of European beech and Norway spruce regeneration performance in 2019 may be attributed to the environmental gradient rather than the "gap size" or "gap environment" gradient. The lower amount of precipitation in 2019 (587 mm)

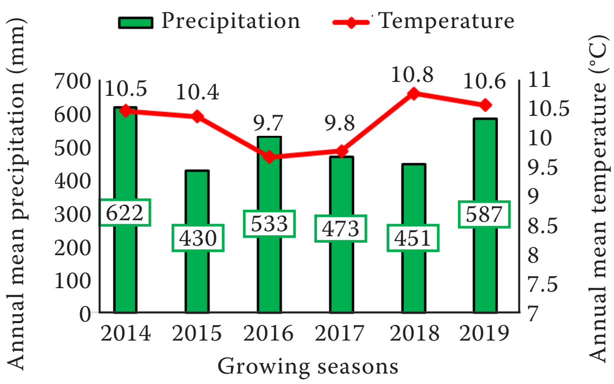

Figure 4. The trend of annual mean precipitation and annual mean air temperature from 2014 to 2019 based on the Czech hydrometeorological standards (ISO 9001, 2015) for the South Moravian region

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(CHMI 2020) coupled with the high air temperature (10.6 °C) (Figure 4) and low air humidity situation caused extremely high evaporative demands among natural regeneration tree species. Consequently, this resulted in lethal water stress incidents leading to massive seedling mortalities and abysmal regeneration performance among assessed species during the 2019 growing season. The evidence of drought-induced tree mortality is well documented (Choat et al. 2018). According to Sedmáková et al. (2019), the recent threat of weather variabilities is accountable for the overall poor regeneration performance of drought-sensitive European beech and Norway spruce in East-Central Europe. In brief, our investigation reveals that the responses of European beech and Norway spruce to growth under present-day climate change phenomenon could cause decline shifts in their competitive ability, sustainability and productivity in temperate European forests in the future.

Effects of gap size on variabilities of micro-environmental soil conditions

Upon all evaluated micro-environmental soil conditions presented in Table 2, only soil temperature showed significant differences (P < 0.05) among gap sizes. The average highest significant temperature value was attained in medium gaps (11 °C) followed by small (10 °C) and big (8 °C) gaps, respectively. This observation opposes the results of Sluiter and Smit (2001) that soil temperature is hardly influenced by the gap size factor but supports conclusions of Ritter et al. (2005). Hence, our results describe the important effect of the gap size feature on the variability of soil temperature in gaps. Although several papers have reported that gap size strongly influences micro-environmental conditions (e.g., Latif and Blackburn 2010, Kučera et al. 2020), contrariwise, soil moisture and EC results in this study disproved it. Generally, our results are in opposition to the opinion that micro-environmental soil conditions increase significantly with gap size (Latif and Blackburn 2010).

Table 2. Statistical results of effects of gap sizes on micro-environmental soil moisture, temperature, and electrical conductivity (EC) in gaps

Gap size	Micro-environmental soil conditions		
	moisture (%)	temperature (°C)	EC (dS/m)
Small	42.4 ± 1.1	9.7 ± 0.2^{a}	1.5 ± 0.1
Medium	41.6 ± 1.1	11.2 ± 0.2^{b}	1.4 ± 0.0
Big	42.3 ± 1.1	8.3 ± 0.2^{c}	1.5 ± 0.0
df	2	2	2
F-ratio	0.141	57.136	0.109
P-value	ns	***	ns

Means bearing different letters are significantly different while means without letters are not significantly different from each other at P < 0.05 significance level ± standard errors. ***P < 0.001; ns – not significant

Effects of gap size and within-gap positions on variabilities of micro-environmental soil conditions. Division of gap microsites into different within-gap positions (centre or gap centre, HL and LH) based on prevailing light or shade conditions was helpful in assessing the significant variations of micro-environmental soil conditions in multiple comparison ways among within-gap positions and between-gap sizes (Figure 5). Firstly, under within-gap position variation, results showed that for moisture, only the gap centre significantly (P < 0.05) explained the difference between gap sizes, whereas HL and LH within-gap positions proved no significant differences (P > 0.05) among gap sizes as shown in Figure 5. Also, for temperature, all categorised within-gap positions revealed significant differences (P < 0.05) among gap sizes. However, for EC, only HL within-gap position demonstrated a significant difference (P < 0.05) among gap sizes while the other within-gap positions did not. Secondly, between individual gap sizes and within-gap positions variation, significant differences (P < 0.05) were observed between within-gap positions under moisture and EC conditions, only moisture condition, and moisture, temperature and EC conditions for small, medium and big gaps, respectively, as presented in Figure 5.

Our results support earlier comments on the importance of both gap size and within-gap positions effects on the variations of micro-environmental conditions in gaps of different sizes (Gálhidy et al. 2006, Latif and Blackburn 2010, Čater et al. 2014, Vilhar et al. 2015). Higher penetration levels of solar radiation in big gaps were responsible for the lowest soil moisture content measured at the gap centre. Gap centre being the most exposed within-gap position to light (solar radiation), the anticipation of fast evaporation conditions leading to lower moisture content was expected. Similarly, Ritter et al. (2005) and Gálhidy et al. (2006) encountered the same findings, too. Nevertheless, the comparable higher soil moisture contents measured at gap centres of small and medium gaps could be attributed to the lower proportion of

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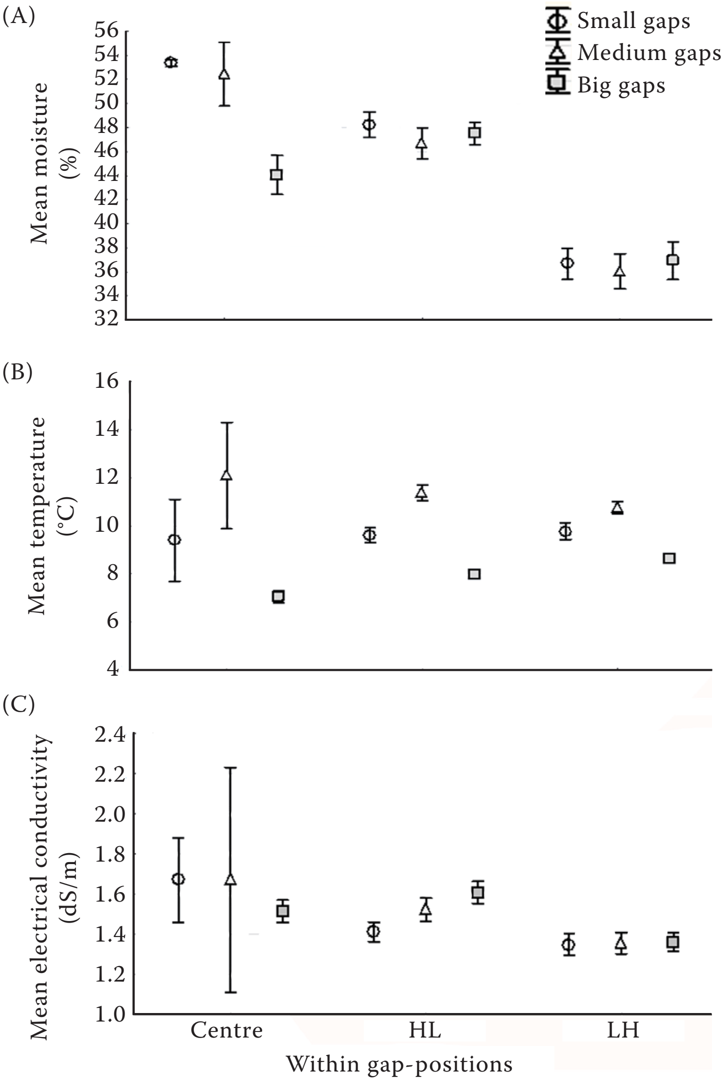

Figure 5. Variabilities of micro-environmental (A) soil moisture; (B) temperature and (C) electrical conductivity conditions at centre (gap centre). High light-low shade (HL; 1–5 subsampling positions), and low light-high shade (LH; 6–10 subsampling positions) within-gap positions between small, medium and big gaps. Overlapping bars indicate not significant differences of means at $P < 0.05$ significance level. Whiskers indicate means while bars are standard errors of means

direct radiation that reached their respective gap centres mainly due to the area of their gap sizes. In contrast to this study, Vilhar et al. (2015) observed a contradictory situation in another temperate mixed-species forest where measured topsoil water content was significantly influenced by within-gap position gradients rather than the gap size effect. Moreover, big gaps registering the highest significant EC value while small gaps recording the lowest significant EC value at HL within-gap position could probably be attributed to the variations of diurnal soil temperature variations in those mentioned gap sizes. In another study carried out in the Finnish Lapland, measured soil EC exhibited temperature dependency as it exponentially increased with rising soil temperature across all five studied mechanical site preparation (MSP) sites within 255–305 m a.s.l. (Sutinen et al. 2010).

Interestingly, the variability of soil temperature in gaps was explainable by both within-gap position*s* and gap size factors. This result confirms our hypothesis that in gaps of different sizes, micro-environmental soil temperature across different within-gap positions differs. The coverage of relatively dense herbaceous layer at forest floor within big gaps blocked soil surfaces from the direct heating-up effect of the incoming solar radiation. This, therefore, led to the observation of low soil temperature readings across all three within-gap positions in big gaps. Contrarily, the presence of low coverage of herbaceous layer in medium gaps enabled heating-up of the soil surfaces by penetrative solar radiation, resulting in high soil temperature readings across studied within-gap positions. Further, the heavy shading conditions within small gaps caused comparable soil temperature readings across all studied within-gap positions. In brief, our results suggest that variations of soil temperature under different within-gap positions within gaps of different sizes are closely connected to the complex interaction of shading, evaporative cooling and insulating effects of understory vegetation. Nonetheless, this suggestion is subjective to further testing. Similar findings have been mentioned elsewhere in the Caribbean (Sluiter and Smit 2001) and Europe (Ritter et al. 2005).

Interaction among abiotic micro-environmental soil conditions and repeatedly between biotic tree species in gaps

Results from regression analysis revealed that moisture (P = 0.0001) and temperature (P = 0.0458) explained variations of EC readings in medium gaps (r^2 = 0.52). However, EC increased significantly with increasing moisture but decreased significantly with increasing soil temperature at $P < 0.05$ significant level. An earlier study by Brevik et al. (2003) in the United States of America confirmed how much of the variation in soil EC values could be explained by variations in soil moisture and soil temperature using TDR probes (Campbell Scientific Inc., Logan, USA) technique. Meanwhile, some researchers have hypothesised that variations in temperature would have a negligible impact on EC readings taken in a single day (e.g. Brevik et al. 2004). Our results, therefore, suggest that such assumptions may not be outrightly true under forest gap conditions, especially when carrying out experiments in gaps of areas ranging between 500–800 m^2. Moreover, in big gaps only moisture (r^2 = 0.64; P = 0.0001) significantly related to the variations in EC readings. The estimated 64% regression coefficient marked the potential influence of moisture on EC status in soils within big gaps. This substantiates the widely held notion that moisture is a crucial soil property that influences micro-environmental soil EC (Brevik et al. 2003, Badewa et al. 2018). On the other hand, there were no significant interactions between dependent soil EC and independent soil moisture-temperature variables in small gaps at $P < 0.05$ significant level. Our result perhaps shows that EC variations cannot be explained sufficiently by soil moisture and temperature in gaps with less than 300 m^2 area.

Besides, the effects of the investigated micro-environmental soil conditions on natural regeneration of European beech and Norway spruce tree species in small, medium, and big gaps were observed during the 2019 growing season only. It was recorded that temperature had a significant ($P < 0.05$) effect on European beech regeneration in small (r^2 = 0.86, P = 0.0032) and medium (r^2 = 0.53, P = 0.0482) gaps but not in big gaps. This result validates a remark from Sedmáková et al. (2019) that European beech growth is temperature-driven but then contradicts a comment from Farahat and Linderholm (2018) that European beech is less sensitive to temperature. For Norway spruce, moisture was observed to have influenced its natural regeneration significantly in medium (r^2 = 0.68, P = 0.0414) and big (r^2 = 0.86, P = 0.0467) gaps but not in small gaps. The estimated 86% regression coefficient in big gaps for the effect of moisture on Norway spruce natural regeneration was comparatively higher than the estimated 68% value in medium gaps. This demonstrated that soil moisture had a much stronger ecological impact on Norway spruce regeneration in big gaps (≥ 1 000 m^2 than in medium gaps (≤ 700 m^2). Our results support the fact that gaps with expansive areas (> 500 m^2) normally permit entry of a higher amount of light into gap environments. Subsequently, this intensifies micro-environmental air temperature conditions within such gaps (Hammond and Pokorný 2020) and as a result, it causes soil moisture content to reduce drastically *via* evaporation or evapotranspiration mechanism. Hence, it is undoubtful that Norway spruce regeneration suffered massive water stress conditions in big gaps. Likewise, other studies have shown that Norway spruce is a water stress-intolerant tree species (e.g., Parobeková et al. 2018, Sedmáková et al. 2019). However, in small gaps, this study showed no significant ($P > 0.05$) ecological relationship between Norway spruce regeneration and the studied soil properties. Finally, our result showing that soil EC has no significant ($P > 0.05$) influence on natural regeneration was in opposition to a study conducted in Iran where soil EC had a significant effect on the natural regeneration of *Haloxylon aphyllum* (Minkw.) Iljin species (Zehtabian et al. 2010).

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