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ORIGINAL PAPER

Variation in irradiance, soil features and regeneration patterns in experimental forest canopy gaps

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Abstract
• ***Key message*** **Natural regeneration of beech, maple and fir was investigated in relation to irradiance, ground vegetation and soil features. Seedling establishment may be favoured by creating small and irregular gaps and by successive extension of gaps along the sun-exposed gap edge.**
• ***Context*** To successfully manage natural regeneration, it is important to understand the interactions of forest gap micro-climates and soil features.
• ***Aim*** The aim of this study was to identify conditions for successful natural regeneration of European beech, sycamore maple and silver fir in mixed forests.
• ***Methods*** Seedling growth and survival were recorded within and around two artificial gaps, and the relationships to irradiance, ground vegetation and soil features were examined. A simple conceptual model was applied to identify optimal micro-sites for regeneration.
• ***Results*** Ground vegetation hindered the establishment of natural regeneration in the centre of the gaps. Small seedlings of maple and beech were more abundant within the small gap and along gap edges; beech had the highest density on sun-exposed edges and maple on shaded gap edges. Tall beech and maple seedlings were more abundant along sun-exposed gap edges. Greater variability of irradiance in the larger gap contributed to greater micro-site heterogeneity relative to the small gap.
• ***Conclusions*** Seedling establishment may be favoured by creating small and irregular gaps and by successive extension of gaps along the sun-exposed gap edge. Circular gaps with diameters greater than stand height contribute to increased ground vegetation coverage and hinder tree regeneration, including semi-shade tolerant maple and spruce.

Keywords Gap partitioning · Natural regeneration · *Abies alba* · *Fagus sylvatica* · *Acer pseudoplatanus* · Solar radiation · Micro-site variability · Ground vegetation · Dinaric Alps

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Dr. Primož Simončič: contribution to data analysis, supervision of PhD thesis, research project management and preparation of the manuscript.
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1 Introduction

Successful natural regeneration of mixed forests requires knowledge of the effects of the partitioning of micro-sites in canopy gaps on the coexistence of tree species (Gray and Spies 1996; Carlson and Groot 1997). An understanding of the interactions of the forest gap micro-climate and the soil features that define the partitioning of the gap micro-site is important for successfully managing natural tree regeneration.

The gap size, shape, orientation and spatial dynamics (hereafter referred to as gap spatiotemporal geometry) have important effects on many ecological factors and processes in gaps. Both canopy release and gap creation induce sudden changes in solar radiation and other micro-climate variables, such as air and soil temperature, rainfall, air humidity and wind (Morecroft et al. 1998; Aussenac 2000; Proe et al. 2001). The micro-climate affects nutrient release through decomposition and mineralisation processes (Muscolo et al. 2010) and, together with water fluxes (Vilhar et al. 2010), results in the loss of nutrients from the forest ecosystem (Madsen 1994; Katzensteiner 2003; Walters et al. 2006). Micro-climatic changes (Ritter et al. 2005; Renaud and Rebetez 2009) and the undesirable loss of nutrients (Ritter and Vesterdal 2006) are less pronounced in small canopy gaps than in large areas of open space. Furthermore, the growth of regeneration and edge trees in small and irregular canopy gaps, which result in increased interception, shading (Čater et al. 2013) and water extraction by roots (Cudlin et al. 2007), may modify the gap effect as early as the second year after gap creation in semi-natural beech-dominated forests (Ritter et al. 2005).

Ecological differences among positions within gaps may be partly due to the variability of factors that do not depend on irradiation, such as micro-relief, soil substrates and woody debris (sensu Brandani et al. 1988), and could partially be affected by the north–south solar radiation asymmetry within the gaps (Takenaka 1988; Poulson and Platt 1989). In addition to the gap spatiotemporal geometry, any micro-scale heterogeneity within gaps significantly affects regeneration success (Gray and Spies 1996).

The natural regeneration of managed mixed silver fir (*Abies alba* Mill.; hereafter fir) and European beech (*Fagus sylvatica* L.; hereafter beech) forests has been investigated in many studies (e.g. Schmidt-Vogt 1972; Matić 1983; Mosandl 1991; Stancioiu and O'Hara 2006; Klopcic and Boncina 2012). The results indicated that fir exhibits superior establishment potential at a low irradiance, followed by beech and Norway spruce (*Picea abies* (L.) Karst; hereafter spruce). In addition, sycamore maple (*Acer pseudoplatanus* L.; hereafter maple) is rated as moderately shade tolerant. Because of the prevalence of shade-tolerant species in this type of forest, natural regeneration is often induced by the creation of small, diffuse canopy openings, by their gradual formation and extension and by the favouring of advance regeneration (irregular shelterwood systems sensu Matthews 1999). Generally, this system emulates natural disturbance dynamics, which are driven by endogenous factors (Leibundgut 1982). In addition, recent studies of disturbance regimes (e.g. Nagel et al. 2013) have revealed that intermediate disturbances such as windstorms also play an important role. However, regarding managed silver fir forests, there is little information regarding the regeneration processes in medium-sized gaps, i.e. those with diameters larger than the height of the surrounding stand. Such gaps are often considered important for promoting moderately shade tolerant, commercially valuable tree species, such as maple (Kobal et al. 2013).

Knowledge of the optimal micro-site conditions for the regeneration of tree species within gaps is useful to silviculturists when developing optimal models of gap spatiotemporal geometry during regeneration (Diaci 2002; de Chantal et al. 2003). Consequently, simple conceptual models of the distribution of ecological factors within gaps may help silviculturists improve regeneration success. However, these mechanisms should be studied over long time intervals in experimental gaps with a well-documented stand history (Čater and Levanič 2013) because an inadequate time series of measurements, abundant advance regeneration and gradual gap extension may significantly affect the results.

The aim of this study was to evaluate the optimal micro-site conditions regarding the irradiance, ground vegetation and soil features on the natural regeneration patterns in two experimental canopy gaps of different sizes in a mixed forest of fir and European beech. The specific objectives were (1) to assess the variability of regeneration performance between gap positions while hypothesising larger survival and growth of the moderately shade-tolerant species in the high-light conditions, (2) to assess the ecological factors aside from irradiance that control the regeneration (e.g. ground vegetation coverage and soil water content) and (3) to apply a simple conceptual model for distinguishing four distinct micro-sites within and around gaps based on the distribution of irradiance.

2 Methods

2.1 Site and stand description

The fir-beech forests under investigation are located in south-eastern Slovenia (45° 20′ N, 14° 30′ E, elevation 860–890 m a.s.l.) in the northern Dinaric Alps in the western Balkan Peninsula. The bedrock consists of Cretaceous limestone, and the soil depth varies from 10 to 40 cm depending on the highly variable karstic micro-relief. The prevailing soil units were *Eutric Cambisols* and *Rendzic Leptosols* (Urbančič et al. 2005). The climate of the region is montane with an annual precipitation of up to 1,600 mm. The long-term (1961–1990) mean annual air temperature recorded at the nearest meteorological station (Kočevje, 45° 39′ N, 14° 51′ E, 467 m a.s.l.) was 8.3 °C (Supplementary data 1). Based on this value and on an environmental lapse rate of 6 °C per kilometre of elevation, the long-term mean annual temperature at the study site was 5.9 °C (Vilhar et al. 2006).

The vegetation type of the stand in which the study was conducted was classified as *Omphalodo-Fagetum* (Puncer

1980). The species composition, based on the stand volume in forest compartment 14 (39.32 ha) of the Črmošnjice forest management unit where the gaps were created, was 55 % fir, 25 % beech, 15 % spruce and 5 % maple (2007). Elm (*Ulmus glabra* Huds.) and lime (*Tillia cordata* Mill.) comprised less than 1 % of the total volume. The total volume in the forest compartment was 255 m^3 ha^{-1}, and the total basal area was 52 m^2 ha^{-1}. The forest had previously been managed using the irregular shelterwood system (sensu Matthews 1999).

2.1.1 Study forest and gaps

In the 2000/2001 winter, two circular experimental gaps were created by way of a single cut: a medium gap (diameter of ca. 55 m) and a small gap (diameter of ca. 30 m). The distance between the two gap centres was 75 m. In the small gap, the prevailing slope aspect was to the east, whereas the medium gap had a predominantly south-eastern aspect. The slope gradients in both gaps were similar, with mean gradients of 18.4° in the small gap and 20.2° in the medium gap. The stand was mature, with closed canopies and no advance regeneration taller than 20 cm; the few larger seedlings present were all removed. For our study, all of the trees within the areas of the planned canopy gaps were harvested and carefully removed by horse skidding. In the spring of 2001, 113 sampling plots in the medium gap and 43 sampling plots in the small gap were set up in a grid with an internal spacing interval of 5×5 m in the compass directions. The grid extended into the adjacent forest at the gap edges. Each sampling plot was 1.5×1.5 m.

2.2 Woody regeneration performance

All tree seedlings at the sampling plots were recorded based on their species and height (small seedlings with heights of up to 20 cm and tall seedlings with heights of more than 20 cm) (sensu Ott et al. 1991), and their density was calculated as the number of individuals per meter squared. The results for the spruce seedlings were recorded only as total numbers due to their low density. For the five tallest beech seedlings in the plot, the average heights, the height increments of the terminal shoots in the final year, and the diameters above the root collars were measured.

In the summer of 2001 and 2006, browsing damage to all seedlings in the sampling plots was estimated. The visible browsing damage to the main stem and side shoots was assigned to two classes as follows: (a) undamaged seedlings, i.e. those seedlings with no or limited damage with up to 10 % damaged shoots and no damage to the terminal shoot, and (b) damaged seedlings, i.e. those with more than 10 % damaged shoots and/or terminal shoot damage.

2.3 Variability of ecological factors

2.3.1 Irradiance

In the summer of 2003, the irradiance parameters in each sampling plot were assessed using digital hemispherical photos that were taken at an elevation of 0.8 m above the ground during completely overcast sky conditions near dawn or dusk to avoid direct radiation (Roženbergar et al. 2011). A Nikon Coolpix 995 digital camera equipped with a calibrated fisheye lens from Regent WinScanopy was used. Pixel classification was performed automatically using the blue colour channel in the SideLook 1.1 software (Nobis and Hunziker 2005). Next, the irradiance parameters were processed using the WinScanopy 2003 pro-b software (Regent 2003). For further analysis, the indirect site factor (ISF), which is defined as the relative proportion of the diffuse components of the radiation fluxes at the measuring point to the diffuse components in the open area conditions, and the direct site factor (DSF), which is defined as the relative proportion of the direct component of the radiation fluxes at the measuring point to the direct component in the open area conditions, were selected (Fig. 1).

2.3.2 Ground vegetation coverage

Stands were relatively dense before the creation of gaps; therefore, only some advance regeneration was removed. After the gap creation in the summer of 2001 and again in the summer of 2006, we recorded the coverage (%) of all vascular plants in each sampling plot (VEGE). In each sampling plot, the site indices of irradiance, soil moisture, pH and soil nitrogen content were assessed using the phyto-indicator methods that were developed by Ellenberg et al. (1992).

2.3.3 Soil properties and soil water content

The thicknesses of the Of and Oh horizons (O), A horizon (A), B and E horizons (B + E), the total thicknesses of the mineral part of the soil (M, which is the sum of A, B and E) and the percentage of gravel (>2 mm) were assessed in each sampling plot in 2004. The water content of the topsoil was measured monthly in all of the plots during the 2003 and 2004 growing seasons using time domain reflectometry (TDR; Prenart equipment ApS) with probes that were extended to a depth of 10 cm (Vilhar 2006). For further analysis, the minimum (SM MIN), maximum (SM MAX) and average (SM AVG) topsoil moisture contents during the measuring period were used. In addition, topographical variables, including the slope aspect, slope gradient, coverage of rocks (ROCK) and

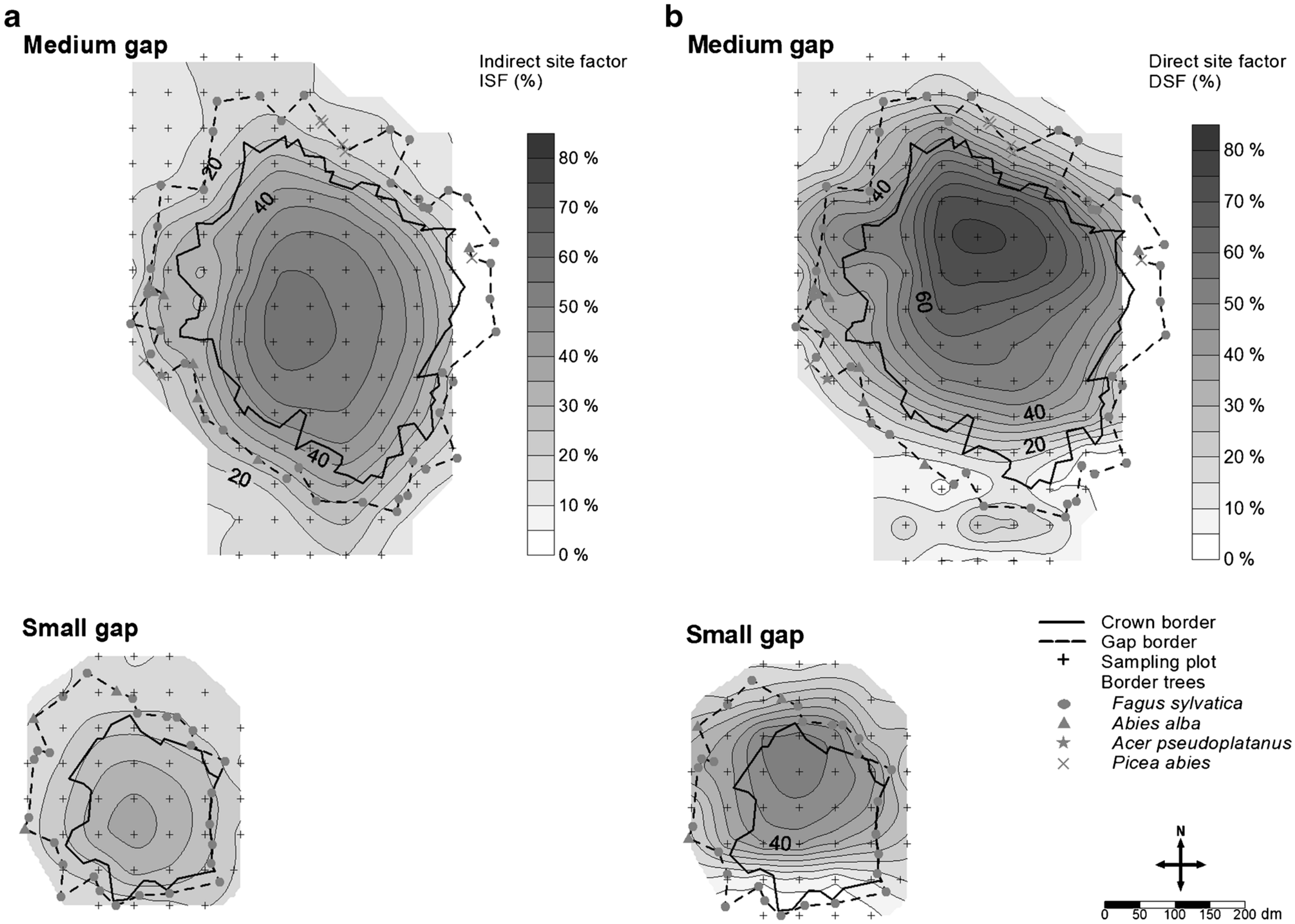

Fig. 1 **a** Indirect site factor (ISF %) and **b** direct (DSF %) site factor values for the sampling plots in the medium gap (n=113) and in the small gap (n=43)

proportion of gravel (GRAVEL) in the soil stratum, were estimated in each sampling plot (to the nearest 10 %).

2.4 A conceptual model for distinguishing micro-sites

To distinguish optimal micro-site conditions for woody regeneration within and around gaps, all of the sampling plots in the gaps were assigned to four classes of gap positions (A, B, C and D) based on their direct and indirect site factors (DSF and ISF). This method was developed by Diaci (2002) based on the variable eco-physiological responses of tree seedlings in four gap positions (Čater et al. 2014) and has been found to successfully facilitate the transfer of results to silvicultural practice (*ibid.*). Due to the non-normal distribution, the following median values of the DSF and ISF were used as thresholds: for M_{DSF} was 31.2 %, for M_{ISF1} was 17.5 % and for M_{ISF2} was 33.7 % (Fig. 2). Consequently, 39 plots located along the gap edges with high ISFs and low DSFs were assigned to a gap edge with less sun exposure (gap position A). In addition, 38 plots in the gap centres with the highest irradiance, which corresponded to the highest ISFs and DSFs, were assigned to the gap centre (gap position B). Furthermore, 40 plots under the forest canopy with the lowest ISFs and DSFs were assigned to gap position C. Finally, 38 plots along the edges of the gaps, which corresponded to low ISFs and high DSFs, were assigned to the sun-exposed gap edge (gap position D) (Fig. 3).

2.5 Statistical analyses

The response of woody regeneration (density of seedlings, average height, height increment of the terminal shoot in the final year and diameter above the root collar of the five tallest beech seedlings) to selected ecological factors (Table 1) was assessed using the Kruskal–Wallis test. All of the plots (113 plots in the medium gap and 43 plots in the small gap) were grouped based on their gap positions (A, B, C and D). A post hoc comparison of the forest gaps and the plots grouped in terms of their gap positions was assessed using Nemenyi and Dunn *post hoc* tests (Zar 1999). Statistical data analysis was performed using the program Statistica for Windows 10.0 (2011).

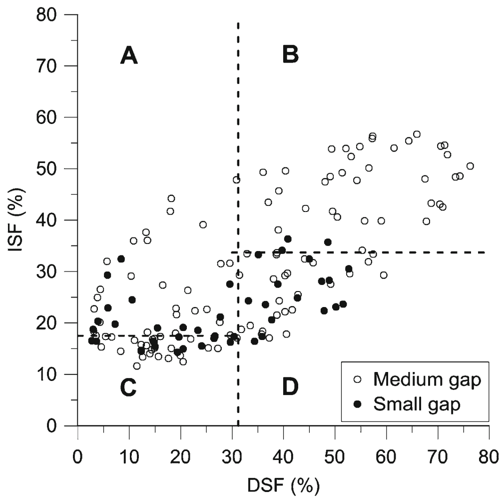

Fig. 2 Distribution of sampling plots (n=156) in the medium gap and the small gap based on the indirect (ISF %) and direct (DSF %) site factor values. The *dashed lines* denote the median values of DSF and ISF that were used as thresholds for the assignment of the plots to four gap positions (*A*, *B*, *C* and *D*): M_{DSF}=31.2 %, $M_{ISF\ 1}$=17.5 %, $M_{ISF\ 2}$=33.7 %

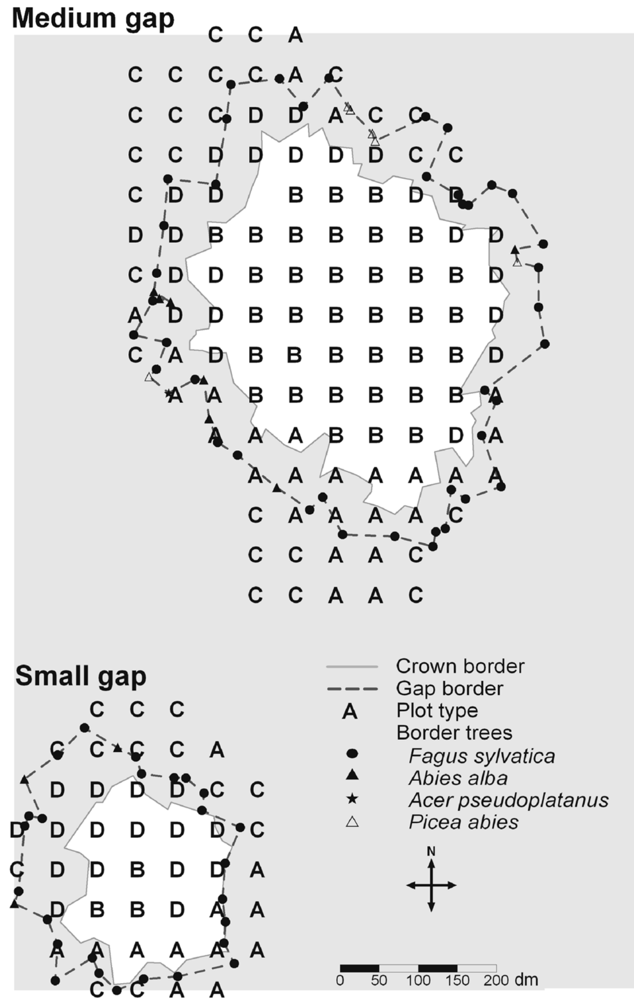

Fig. 3 Assignment of research plots to four gap positions based on direct (DSF %) and indirect (ISF %) site factors in the medium gap and the small gap: gap position *A*—plots located along the gap edges with less sun exposure; gap position *B*—plots in the gap centres with the highest irradiance; gap position *C*—plots under the forest canopy, which correspond to the lowest ISFs and DSFs; gap position *D*—plots along the sun-exposed edges of the gaps. The median values of DSF and ISF were used as thresholds: M_{DSF}=31.2 %, $M_{ISF\ 1}$=17.5 %, $M_{ISF\ 2}$=33.7 %

3 Results

3.1 Woody regeneration performance

One year after the creation of the gaps in 2001, the average density of all seedlings in the gaps amounted to 2.2 individuals per meter squared. The woody regeneration measured in the spring of 2001 reflects similar pre-harvesting histories of the gaps that were created in the former closed canopy stand and could not reflect the effect of the gap creation itself. The majority of the seedlings emerged after 2004, and by 2006, the average density had increased to 5.4 individuals per meter squared. In 2001, the maple displayed the highest density of all seedlings, at 3.8 individuals per meter squared (78 %), followed by beech at 0.7 individuals per meter squared (15 %) and fir at 0.4 individuals per meter squared (7 %). There were only 16 individuals of beech and one maple among the tall seedlings (0.2 m<h<0.5 m), whereas none of the regenerated seedlings was taller than 0.5 m. During the next five growing seasons, the densities of all maple, beech and fir increased to 6.0, 3.5 and 2.8 individuals per meter squared, respectively, which correspond to 49, 29 and 23 % of all seedlings, respectively. Spruce regeneration was first observed in the spring of 2004 (0.1 individuals per m^2). The most successful species in terms of recruitment from small to tall seedlings was beech, which comprised an 80 % share of the tall seedlings and an increasing density over time (2004 versus 2006). In contrast, the share of maple among the tall seedlings in 2006 amounted to only 20 %. In 2006, we observed only one tall fir seedling in the experimental gaps.

The densities of maple and beech were higher in the small gap than in the medium gap in all observation years (Fig. 4, Supplementary data 2). In the small gap, we observed larger increases from 2001 to 2006 in the small beech seedling density (i.e. 0.7 to 5.1 individuals per m^2; $H=25.7$, $p<0.001$) and the small maple seedling density (i.e. 8.0 to 12.9 individuals per m^2; $H=31.7$, $p<0.001$). The fir density was low in both gaps during all years of the study; therefore, there were no significant differences recorded between the fir densities in the medium and small gaps. For the small fir seedling densities, significant differences were only shown in 2001 between the four gap positions ($H=8.6$, $p=0.035$) (Fig. 5, Supplementary data 3). Small fir seedling densities were the highest along the sun-exposed gap edges (0.6 individuals per m^2, gap position D) and the lowest along the gap edges with less sun exposure (0.1 individuals per m^2, gap position A). Small beech seedling densities were highest under the forest canopy (1.3 individuals per m^2, gap position

Table 1 Variables and their abbreviations used in the analysis

Variable	Description	Unit
DSF	Direct site factor	%
ISF	Indirect site factor	%
ROCK	Surface covered by rocks	%
GRAVEL	Gravel content	%
O	Thickness of Of and Oh horizons	cm
A	Depth of A horizon	cm
B + E	Depth of B and E horizons	cm
M	Depth of mineral part of soil (sum of A and B + E horizons)	cm
VEGE	Ground vegetation cover	%
SM MAX	Maximal soil water content in years 2003 and 2004	vol%
SM MIN	Minimal soil water content in years 2003 and 2004	vol%
SM AVG	Average soil water content in years 2003 and 2004	vol%

C) and lowest in the central parts of the gaps (0.2 individuals per m^2, gap position B). In 2001, the tall beech seedling densities were highest along the gap edges with less sun exposure (0.2 individuals per m^2, gap position A) and lowest under the forest canopy (0.1 individuals per m^2, gap position C). The small maple seedling densities were highest along the gap edges with less sun exposure (6.1 individuals per m^2, gap position A) and lowest in the central portions of the gaps (1.6 individuals per m^2, gap position B).

In 2006, the small fir seedling density was the highest along the sun-exposed gap edges (3.2 individuals per m^2, gap position D) and was the lowest in the central parts of the gaps (1.6 individuals per m^2, gap position B; $H=9.4$, $p=0.024$). The small beech seedling densities remained the highest under the forest canopy (5.0 individuals per m^2, gap position C) and the lowest in the central parts of the gaps (0.3 individuals per m^2, gap position B; $H=36.5$, $p<0.001$). The tall beech seedling densities in 2006 were the highest along the sun-exposed gap edges (1.2 individuals per m^2, gap position D) and remained the lowest under the forest canopy (0.2 individuals per m^2, gap position C; $H=20.9$, $p<0.001$). In addition, the small maple seedling density in 2006 remained the highest along the gap edges with less sun exposure (10.4 individuals per m^2, gap position A) and lowest in the central parts of the gaps (1.7 individuals per m^2, gap position B; $H=17.4$, $p=0.001$), similar to 2001. The increases in the densities of the beech, maple and fir tall seedlings from 2001 to 2006 were lowest in the central parts of the gaps (0.2 individuals per m^2, gap position B).

In 2004 and 2006, the diameters, heights and height increments of the five dominant beech seedlings in each plot were lowest under the forest canopy (gap position C) and significantly greater in the central parts of the gaps (gap position B) with the largest irradiance (Fig. 1) and soil water availability (Supplementary data 4) ($p\leq0.003$). From 2001 to 2006, the greatest increases in the diameters and height increments of the five dominant beech seedlings were observed along the sun-exposed gap edges (gap position D) ($p<0.001$).

There were no significant differences between the degrees of browsing damage among the gaps or gap positions. The total proportion of browsed regeneration decreased substantially during the 5-year period, from 64 to 18 % damaged seedlings per plot. The decrease in damage was most noticeable among the beech seedlings, which declined from 81 % in 2001 to 6 % in 2006. During the same period, the proportion of damaged fir and maple seedlings decreased from 17 to 4 % and from 65 to 27 % per plot, respectively.

3.2 Variability of ecological factors

3.2.1 Irradiance

The irradiance differed significantly between the gaps (for ISF $p=0.005$). Lower values of the direct (DSF) and diffuse site factors (ISF) were observed in the small gap (Fig. 6, Supplementary data 2) and under the forest canopy (gap positions A and C) (Fig. 7, Supplementary data 3). The variability in the irradiance was significantly higher in the medium gap (interquartile range of 36 % DSF/25 % ISF) than in the small gap (25 % DSF/11 % ISF); thus, there was a higher potential for micro-site partitioning in the medium gap (Figs. 2 and 3).

3.2.2 Ground vegetation coverage

In 2001, specifically during the first growing season after the gap formation, there was no significant difference between the ground vegetation coverage in the two gaps, which was 6.2 % in the small gap and 5.5 % in the medium gap. In addition, there was no significant difference in the ground vegetation coverage between the gap positions in 2001. This trend anticipates similar pre-harvesting histories of both gaps that were created in the formerly closed canopy stand.

In the autumn of 2004 and 2006, the ground vegetation coverage markedly increased in both gaps, but the differences among the gaps were not statistically significant ($p>0.05$). The increase in the ground vegetation coverage was greater in the small gap (from 35.9 % in 2004 to 44.9 % in 2006) than in the medium gap (from 51.8 % in 2004 to 55.7 % in 2006). The ground vegetation coverage was significantly greater in the central parts of the gaps (87.4 % in 2004 and 82.5 % in 2006, gap position B) and lowest under the forest canopy (21.9 % in 2004 and 22.5 % in 2006, gap position C) ($p<0.001$).

In 2001, the three plant species that displayed the highest mean rates of coverage were *Dryopteris filix-mas* (2.0 %), *Lamium orvala* (1.8 %) and *Polystichum aculeatum* (1.5 %) in the medium gap and *Salvia glutinosa* (1.7 %), *L. orvala*

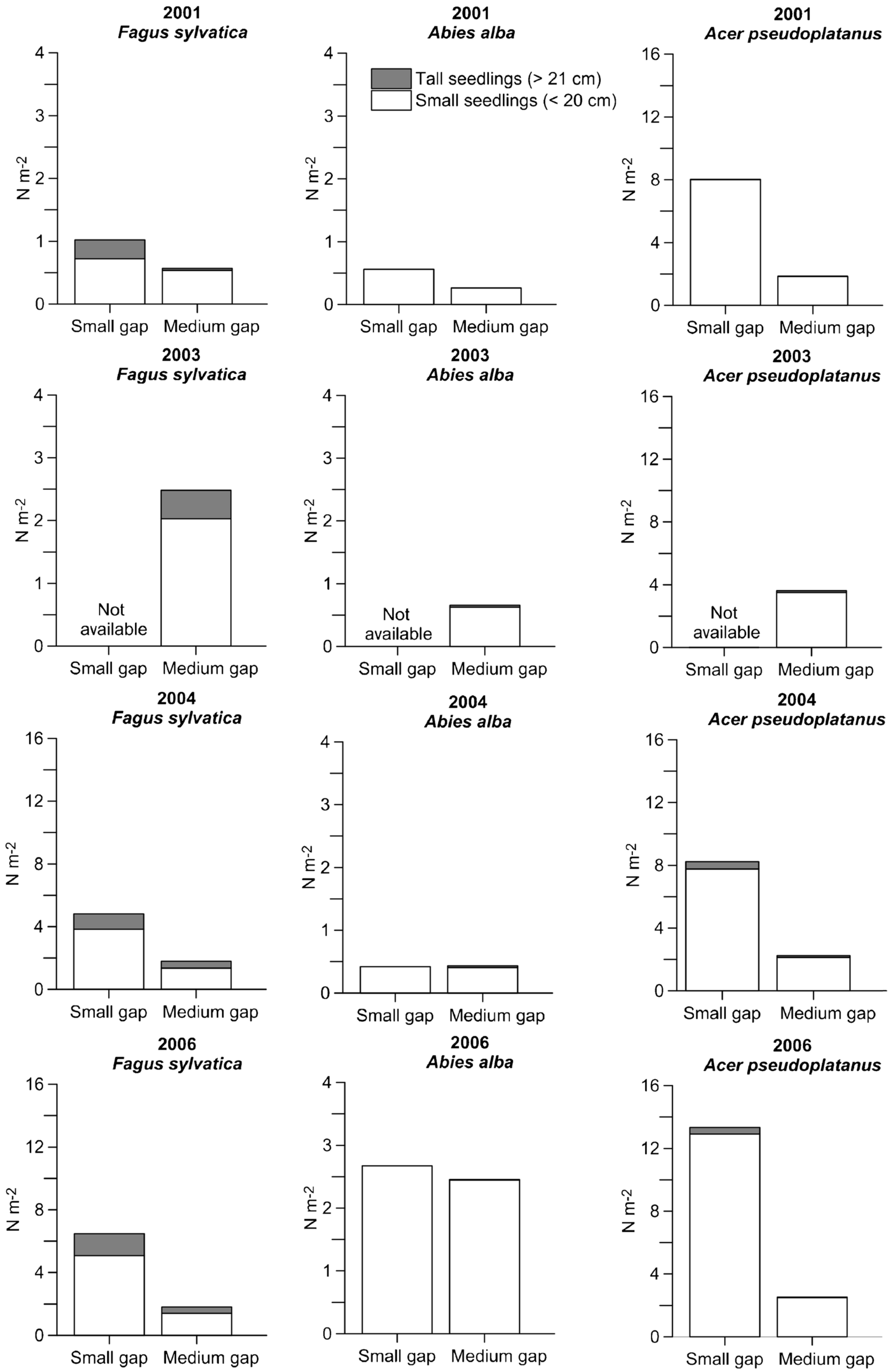

Fig. 4 Density of seedlings up to 20 cm tall and taller than 20 cm in the medium gap and small gap during the years 2001, 2003, 2004 and 2006. Please note the different scales for the different species. *Not available* refers to missing data

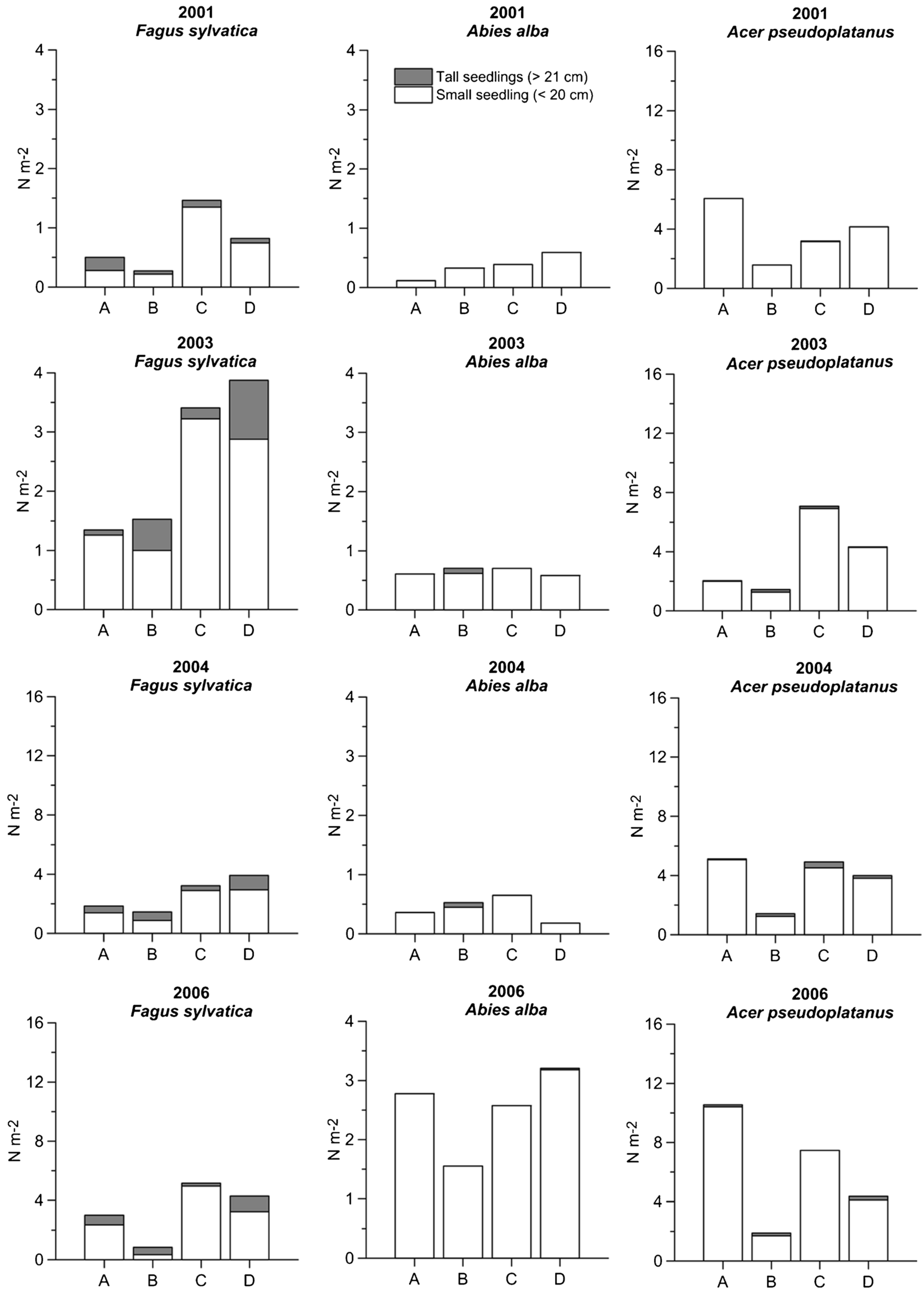

Fig. 5 Density of small seedlings (heights up to 20 cm) and tall seedlings (taller than 20 cm) in the medium gap and small gap based on four within-gap positions (*A*, *B*, *C* and *D*) during the years 2001, 2003, 2004 and 2006: gap position *A* - plots located along the gap edges with less sun exposure; gap position *B* - plots in the gap centres with the highest irradiance; gap position *C* - plots under the forest canopy, which correspond to the lowest ISFs and DSFs; gap position *D* - plots along the sun-exposed edges of the gaps. Please note the different scales for the different species

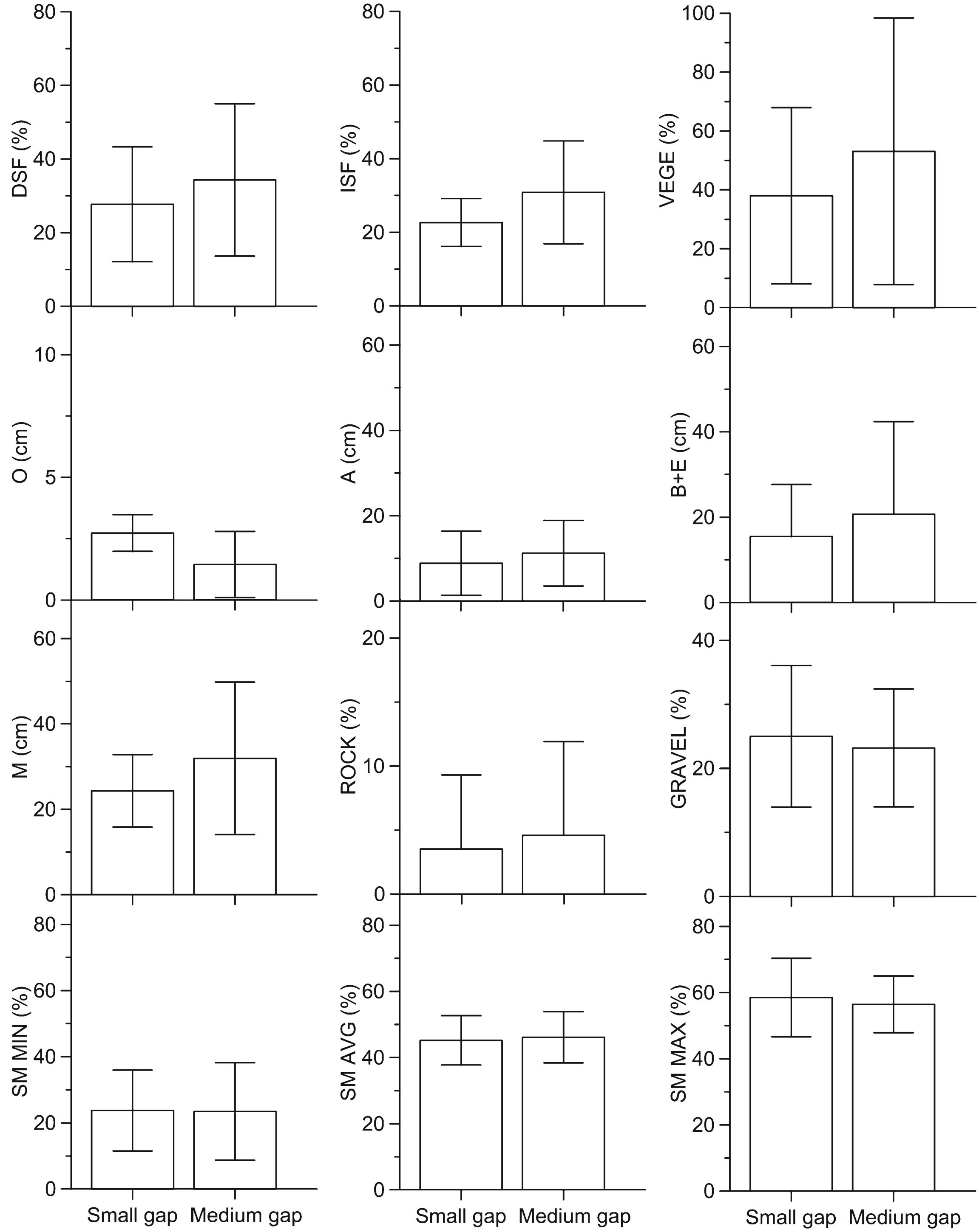

Fig. 6 Mean values and standard deviations of variables in the medium gap and the small gap for the year 2004: *DSF* direct site factor (%), *ISF* indirect site factor (%), *ROCK* surface covered by rocks (%), *GRAVEL* gravel content (%), *O* thickness of Of and Oh horizons (cm), *A* depth of A horizon (cm), *B + E* depth of B and E horizons (cm), *M* depth of mineral part of soil (sum of A and B + E horizons) (cm), *VEGE* ground vegetation cover (%), *SM MAX* maximum soil water content in 2003 and 2004 (%), *SM MIN* minimum soil water content in 2003 and 2004 (vol%), *SM AVG* average soil water content in 2003 and 2004 (vol%)

(1.2 %) and *Senecio fuchsii* (1.2 %) in the small gap. The species compositions of the plants with the highest mean coverage changed markedly during the 5-year period. The most common plant species in 2006 were *Carex pendula* (29.0 %), *Fragaria vesca* (22.7 %) and *Carex sylvatica* (19.7 %) in the medium gap and *Atropa belladonna* (29.0 %), *Brachypodium sylvaticum* (15.2 %) and *Fragaria vesca* (27.8 %) in the small gap. Although the most abundant

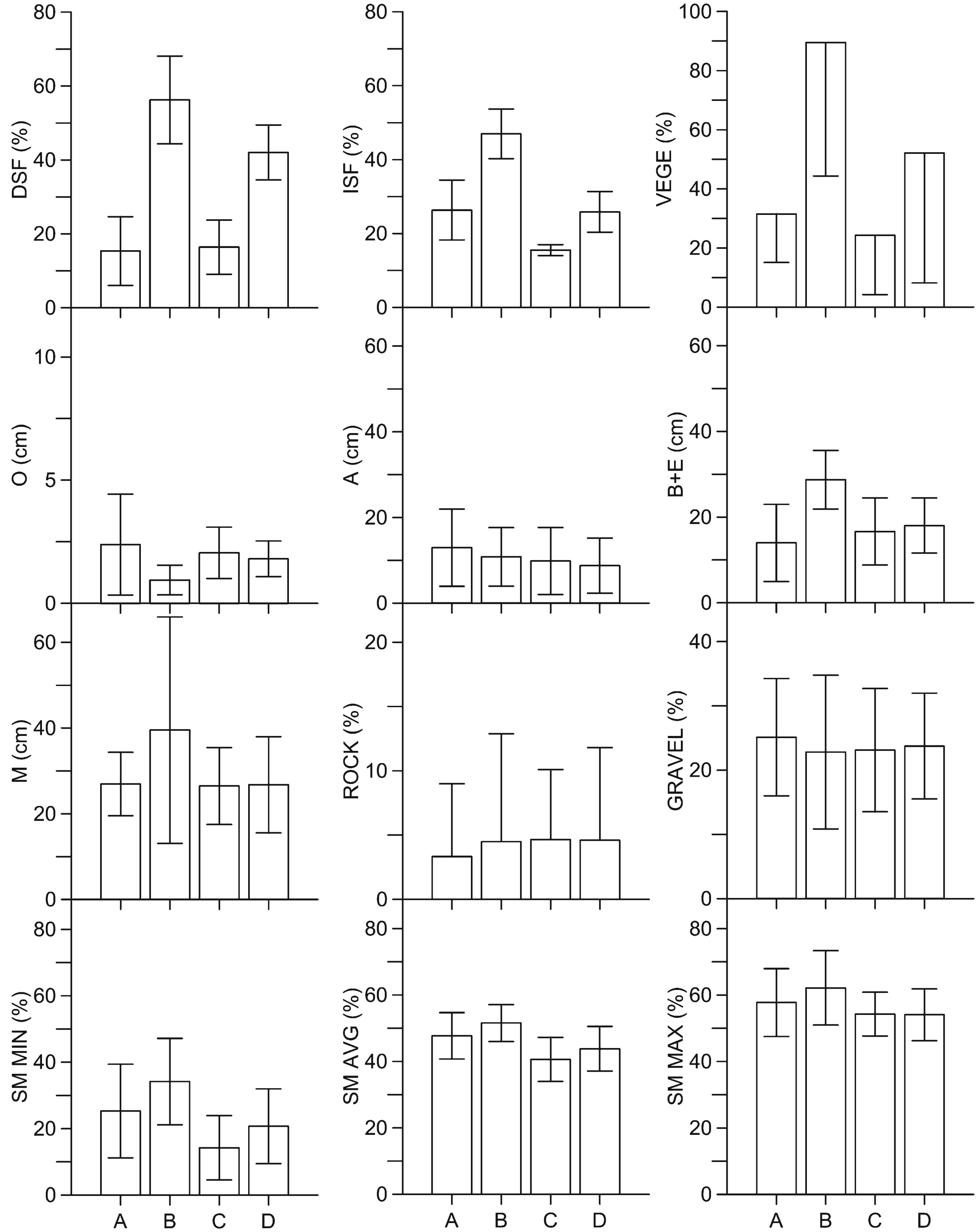

Fig. 7 Mean values and standard deviation of variables per gap position (*A*, *B*, *C* and *D*) for the year 2004: gap position *A* - plots located along the gap edges with less sun exposure; gap position *B* - plots in the gap centres with the highest irradiance; gap position *C* - plots under the forest canopy, which correspond to the lowest ISFs and DSFs; gap position *D* - plots along the sun-exposed edges of the gaps. Variable descriptions: *DSF* direct site factor (%), *ISF* indirect site factor (%), *ROCK* surface covered by rocks (%), *GRAVEL* gravel content (%), *O* thickness of Of and Oh horizons (cm), *A* depth of A horizon (cm), *B + E* depth of B and E horizons (cm), *M* depth of mineral component of soil (sum of A and B + E horizons) (cm), *VEGE* ground vegetation cover (%), *SM MAX* maximum soil water content in 2003 and 2004 (%), *SM MIN* minimum soil water content in 2003 and 2004 (vol%), *SM AVG* average soil water content in 2003 and 2004 (vol%)

plant species in the two gaps differed between 2001 and 2006, no significant differences were observed in terms of the site indices of irradiance and soil moisture, pH and soil nitrogen content based on the phyto-indicator methods (Ellenberg et al.

1992). However, we recorded an increase in irradiance (from 4.0 to 4.3) and a decrease in the soil nitrogen content in the soil indication (from 7 to 5) from 2001 to 2006. The plant species with the highest coverage (the three species dominating each gap position) in 2006 were as follows: *B. sylvaticum*, *Athyrium filix-femina* and *Fragaria vesca* along the gap edges with less sun exposure (gap position A); *C. pendula*, *C. sylvatica* and *Athyrium filix-femina* in the central parts of the gaps (gap position B); *B. sylvaticum*, *Galium odoratum* and *Salvia glutinosa* under the forest canopy (gap position C); and *B. sylvaticum*, *C. pendula* and *C. sylvatica* along the sun-exposed gap edges (gap position D). The phyto-indicators recorded in the four gap positions revealed differences in of the irradiance, soil moisture and soil nitrogen contents. In general, the differences in the recorded phyto-indicators were consistent with our measurements, but not in every detail. For example, based on the phyto-indication classification, the gap edges with less sun exposure (gap position A) were the least humid micro-sites. However, these areas were ranked as the second most humid areas based on the soil water content measurements.

3.2.3 Soil properties and soil water contents

The thicknesses of the Ol and Of horizons (O) were significantly greater in the small gap, along the gap edges with less sun exposure (gap position A) and under the forest canopy (gap position C) ($p<0.001$) (Supplementary data 2, 3 and 5). The thicknesses of the A horizons ($p=0.023$) and the mineral soil layers (M) ($p=0.015$) were significantly greater in the medium gap. The topsoil water content was more strongly influenced by the position within the gaps (Supplementary data 3) than by the size of the gaps. The size of the gaps did not correspond to significant differences in the minimum (SM MIN) and maximum (SM MAX) soil water contents (Supplementary data 4). The lowest soil water contents were measured under the closed canopy (gap position C), followed by the gap edges (gap positions D and A), whereas the highest soil water contents were measured in the central parts of the gaps (gap position B) ($p<0.001$). There were no significant differences among the gaps or gap positions in terms of the coverage of rocks (ROCK) or the share of gravel (GRAVEL) in the soil stratum (Supplementary data 6).

4 Discussion

The results of this study suggest that natural regeneration patterns in selected gaps may be induced by variations in irradiance, ground vegetation and soil features within and among gaps. Although this study involved only one small gap and one medium gap and is therefore limited by the lack of gap replication, the differentiation within and around gaps by the use of several plots does allow for an assessment of the interactions among micro-climate and soil features and the success of natural regeneration.

4.1 Woody regeneration performance

The central parts of the gaps were expected to be the most favourable for the regeneration of moderately shade-tolerant tree species (e.g. maple and spruce) due to a number of factors, such as high irradiance, increased soil depth, the highest topsoil water content (considering the extreme drought event of the summer of 2003), the higher anticipated N availability (Ritter et al. 2005) and the reduced nutrient uptake by the tree roots (Bormann and Likens 1986). Nevertheless, the competition of ground vegetation hindered the establishment of tree species in the gap centres. Similar results were reported in other studies (e.g. Diaci 2002; Modry et al. 2004; Mountford et al. 2006; Van Couwenberghe et al. 2010). The exception was the growth of already established, dominant beech seedlings. Furthermore, we recorded higher densities of maple and beech small seedling in the low-light conditions within the first year after gap creation, as previously confirmed by Diaci (2002), Mountford et al. (2006) and Roženbergar et al. (2007). The densities of the small fir seedlings and tall beech seedlings were highest along the sun-exposed gap edges (gap position D), whereas there was more small maple seedlings along the gap edges with less sun exposure (gap position A). Furthermore, these less sun-exposed gap edges had less ground vegetation coverage, less direct and total irradiance, higher topsoil moisture and a thicker organic layer than the sun-exposed edges (gap position D). Both of these transition positions (gap positions A and D) received more irradiance than the nearly closed canopy (position C) and are likely important for the survival of tall seedlings and saplings. These observations are consistent with previously reported recruitment patterns of canopy gaps in beech forests in England (Mountford et al. 2006) and canopy gaps in mixed broadleaved stands in northern France (Van Couwenberghe et al. 2010). In this study, small maple seedlings were not favoured in the central parts of the gaps, even a few years after the gap creation. This result may be attributed to the maple's shade tolerance during its early developmental stages (seedling bank) and more favourable growing conditions along the gap edges. Because we did not perform any assessment before creating the gaps, it may be assumed that the different seedling banks before the creation of the gaps and the larger survival of the newly established seedlings contributed to this early difference among the gap positions. The latter assumption was supported by larger survival of the maple seedlings under the low-light conditions in subsequent years. In addition, the average distance to seed trees was used as an indicator for differences in seedling banks. The results show that the average distance to maple seed trees was greater for the plots in the gap centres, compared to those along the gap edges. Nevertheless, the differences in the distances were small (4 m). After the creation of the canopy gaps, the proportion of small maple seedlings (based on density) decreased from 78 % in 2001 to 49 % in 2006. Spruce seedlings were not present in the gaps at the start of the experiment. However, they began to emerge after the creation of the gaps, which indicated that spruce is the least shade tolerant during the early establishment phase.

In addition to vegetation competition, heavy browsing by roe and red deer hindered the recruitment of tree seedlings to higher classes. In particular, fir demonstrated a high establishment potential and an increase in the proportion of small seedlings (from 7 % in 2001 to 23 % in 2006), but the proportion of tall fir seedlings remained low (1–2 %). In fir-beech forests and other mixed mountain forests, fir is one of the most susceptible species to browsing (Klopčič et al. 2010). Strong impacts of ungulate browsing on regeneration, with negative consequences for the recruitment of fir into the upper stand canopy (Senn and Suter 2003; Heuze et al. 2005), have been reported in the region during the last two centuries (Roženbergar et al. 2007; Klopčič et al. 2010). In our case, the recruitment was most successful for beech and spruce. Roe deer is usually attracted to sunny patches or areas with dense understories (Heuze et al. 2005) around and within newly created canopy gaps. Despite the improved food supply due to the development of the ground vegetation layer in the gaps and general decrease in the browsing damage for beech, the fir and maple were highly preferred as ungulate food in our study.

4.2 Variability of ecological factors

The results of this study demonstrate that the varying distributions of diffuse and direct irradiance (light asymmetry sensu Poulson and Platt 1989) contributed to the variable climate within the gaps (Takenaka 1988). Moreover, our study indicates that the micro-climate differences within and around gaps may affect certain soil features and processes, such as soil moisture, temperature and accelerated decomposition (Muscolo et al. 2010), while other features, such as the relief and depth of mineral horizons, remain stable. The lower soil water contents observed under the closed canopy versus in the central parts of the gaps potentially resulted from the increased soil water extraction by the plant roots and the higher interception of the canopy trees under the closed canopy (Vilhar and Simončič 2012). In addition, the significantly lower soil water content along the sun-exposed gap edges (gap position D) appeared to be affected by the asymmetrical irradiance within the gaps and the south to south-eastern aspect, which contributed to the higher soil evaporation rates along these gap edges. The greater variations in the factors characterising the micro-climates in the medium gap contributed to greater heterogeneity of the micro-sites in that gap. Still, the topsoil water content, ground vegetation coverage and plant composition did not differ between the small and medium gaps, whereas substantial differences occurred between these factors within and around the gaps. This pattern indicates that the partitioning of micro-sites within and around the gaps may be more important than gap size differentiation. Nevertheless, future studies involving additional gaps of various sizes are warranted to provide further support for the conclusions from our study.

4.3 Application of the conceptual model for distinguishing micro-sites

In our study, the assignment of gap areas to four gap positions based on direct and diffuse site factors was helpful for assessing the variations in irradiance, ground vegetation and woody regeneration dynamics within and around the gaps. Additionally, other soil features, such as the depth of the organic horizon and the availability of soil moisture, were dependent on their gap positions. The results of this study clearly demonstrate that in the medium gap (i.e. central parts of the gaps, gap position B: 31 % of the sample plots), there were a greater number of plots with smaller survival of woody regeneration. The other gap positions (A, C and D) showed larger seedling survival and were evenly represented (21–24 % of the sample plots). In the small gap, only 7 % of the sample plots were assigned to the central parts of the gaps (gap position B), whereas 35 % were assigned to the sun-exposed gap edges (gap position D), and 28 % were assigned to the gap edges with less sun exposure (gap position A). These results indicate that in the small gap, the micro-sites were more suitable for the regeneration of tree species.

Silviculturists should consider the spatial distribution of seed trees, mast years, browsing and forest operations, when developing forest management guidelines. The applied conceptual model using four positions based on diffuse and direct irradiance is easy to comprehend and to apply. For example, ground vegetation competition hindered the establishment of tree species in the gap centres. The overall regeneration success was greater along the gap edges, which suggests that irregular gap shapes of small sizes should be created to provide as many of optimal micro-sites as possible or that the gaps should be expanded accordingly while accounting for the specific micro-relief (e.g. avoiding larger canopy gaps on steep south-facing slopes).

5 Conclusions

This study presented a few of the mechanisms that affect regeneration in a mixed forest of silver fir and European beech (e.g. the importance of advance regeneration of beech, maple and fir and the overall low survival of woody regeneration in gap centres). Taking into account similar site and stand conditions in selected gaps, the higher densities of maple compared to more shade-tolerant beech and fir were expected within the medium gap and within the sun-exposed microsites (D and B). However, in contrast to our expectations, this study indicated that creating almost circular gaps greater in diameter than the stand height may lead to increased ground vegetation coverage that hinders the regeneration of semi-shade tolerant species such as maple and spruce.

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