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Gap recruitment and partitioning in an old-growth beech forest of the Dinaric Mountains: Influences of light regime, herb competition and browsing

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A B S T R A C T

Canopy gap recruitment in beech (*Fagus sylvatica* L.) old-growth forests is influenced by the interplay of the canopy gap disturbance regime, site factors, and stand history. Persistent seedling and sapling banks of beech and other shade tolerant species often play a major role in canopy gap closure. To gain more insight into interactions between medium-sized gaps and pre-gap ground vegetation patterns, we studied beech regeneration over a 10-year period on a site rich in wild garlic (*Allium ursinum* L.) in a Dinaric beech old-growth forest. In 1999 we selected the five largest newly created gaps (~200 m^2) and systematically established 13 permanent plots (1 × 2 m) in each gap. In 1999, 2004, and 2009, we sampled tree species regeneration (density, cover, and growth), ground vegetation (composition and cover), and light climate. Beech regeneration slowly increased in density and cover despite an overall decrease in light (11.0–5.7%). The same was not true for maple. While beech was present in all regeneration classes, dominant maple seedlings rarely reached 50 cm. Beech also had a significantly greater height increment. Regeneration of both species was negatively affected by *Allium* cover, low light levels, and ungulate browsing. Gap partitioning was observed among shade tolerant Allium, which preferred microsites under closed canopy and low light levels, beech regeneration, which preferred gap periphery, and other less shade tolerant herbs, which favoured gap centres. The slow development of the regeneration indicated the importance of several gap releases. The high maple seedling density and less abundant beech advance regeneration in this study site compared to other beech sites suggests that *Allium* dominated managed forests might present an opportunity for growing less shade-tolerant species, if managed with a gap-oriented silvicultural system (e.g. irregular shelterwood).

1. Introduction

Natural regeneration in beech (*Fagus sylvatica* L.) is a result of the complex interactions of many biotic and abiotic factors (Wagner et al., 2010). Studies have shown that limited seed dispersal, seed predation, the formation of a seedling bank, shade tolerance, susceptibility to competition from herbs, susceptibility to drought, vulnerability to frost, and browsing are among the most important characteristics of beech regeneration ecology (e.g. Watt, 1923; Mosandl and el Kateb, 1988; Schmidt, 1997; Collet et al., 2001; Pages et al., 2003; Diaci, 1997; Mountford et al., 2006; Mihok et al., 2007; Hahn and Emborg, 2007; Petritan et al., 2007). A challenge for studying beech regeneration ecology, however, is that because beech often forms a seedling bank due to its high shade tolerance and overall resource use efficiency during the regeneration phase, making it difficult to accurately assess the effects of various ecological factors and their interplay (Madsen and Hahn, 2008). Thus, in old-growth forests, where stands were not influenced by silviculture, beech seedlings are subjected to extremely low light levels and therefore provide ideal test beds for studying the various ecological factors that influence beech regeneration (Emborg, 1998).

Although old-growth forests are rare in Europe, beech regeneration ecology has been intensively studied in old growth (Leibundgut, 1982; Korpel, 1995; Emborg, 1998; Zeibig et al., 2005; Commarmot et al., 2005; Nagel et al., 2006; Drössler and von Lüpke, 2007; Mihok et al., 2007). Such studies reveal important processes that could be used to improve silviculture in beech forests. Nevertheless, and despite beech's growing importance for its role in mitigating climate change and for its role in close-to-nature silviculture, repetitive measurements of beech regeneration in old-growth forests are rare (sensu Runkle and Yetter, 1987; Hahn and Emborg, 2007). Because one-time observations can be strongly influenced by yearly climatic changes, they may yield only limited insight into the long-term regeneration process. Moreover, since research on stand regeneration patterns is specialised, gap dynamics research rarely includes measurements of ecological factors (sensu Drössler and von Lüpke, 2005). Likewise, specialised research on regeneration ecology rarely

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takes into account the whole regeneration cycle, which includes small trees and potential gapfillers.

Research on disturbance dynamics in European old-growth beech forests has revealed relatively small average gap sizes (Tabaku and Meyer, 1999; Zeibig et al., 2005; Drössler and von Lüpke, 2005), suggesting that these forests are predominantly driven by endogenous events with occasional intermediate disturbances, especially windthrows. Because of the prevalence of small gaps and the fast lateral crown growth of beech canopy trees, it seems likely that the dominant pathway to canopy recruitment involves a combination of beech advance regeneration and several gap releases. However, beech regeneration strategies may be well adapted to different site conditions, especially in its optimum growing range, where it can be found on a variety of substrates and geomorphologic types in an altitudinal gradient from the lowlands to the upper timberline. Research on gap dynamics has often neglected the fine scale site differences and ground vegetation patterns that may significantly influence the establishment and early growth of seedlings.

Many eutrophic and mesotrophic beech forests in Europe are characterised by an early spring herb layer consisting of geophytes. This herb layer is occasionally extremely dense, especially where wild garlic (*Allium ursinum* L.; hereafter *Allium*) dominates. *Allium* can have a strong allelopathic effect on other herbaceous plants and presents a very challenging environment for the growth of woody regeneration (Ernst, 1979; Ellenberg, 1988; Djurdjevic et al., 2004). Geophytes such as *Allium* are characterised by fast growth made possible by the nutrients stored in perennial bulbs and a short aboveground life-cycle that usually lasts less than 3 months. This life history strategy takes advantage of the bounty of early spring resources, such as the light transmitted through bare crowns and the humid, nutrient-rich soils that result from melting snow and little competition from other summer-green plants (Ernst, 1979; Jandl et al., 1997). Competition from *Allium* may influence beech regeneration, especially the formation of seedling banks, although tree regeneration profits from a longer growing season and variability of ground vegetation throughout many years. To better understand the link between these special forests sites and the canopy gap disturbance regime, we studied beech regeneration over a 10-year period in an old-growth beech forest rich in *Allium*. The main objectives of this study were (1) to document changes in light climate and ground vegetation patterns over the observed period, (2) to analyse competition and gap partitioning patterns among *Allium* and woody regeneration, (3) to compare the recruitment success of beech and maple (*Acer pseudoplatanus* L.), and (4) to describe possible scenarios of gap recruitment in medium gaps in *Allium*-rich beech forests.

2. Materials and methods

2.1. Stand and site characteristics

Our study was carried out in the Krokar old-growth forest reserve (74.5 ha) in the Dinaric Mountains of southern Slovenia (45°32′25″N, 14°45′57″E). The parent material is composed of limestone and dolomite. Karstic phenomena such as sinkholes and rocky outcrops are common. The soil type is calcocambisol of variable depth. The elevation of the reserve ranges from 840 to 1170 m a.s.l. Mean annual precipitation often exceeds 2000 mm, and mean annual temperature is about 6° C. In 2004 the growing stock was 636 m^3/ha and was composed of 93% beech, 6% silver fir (*Abies alba* Mill.; hereafter fir), and 1% other broadleaves (Diaci et al., 2011). The average volume of coarse woody debris was 154 m^3/ha, 43% of which was snags and 57% of which was logs. Several site types exist within the reserve (Accetto, 2002). This study focused on a pure beech site on a flat dolomite Karstic plateau (*Isopyro-Fagetum*; hereafter IF). In contrast to the limestone surroundings, there was very little aboveground rockiness and stoniness. The mean inclination of the research plots was 2°. The upper canopy height of gap edge trees was 42 m. In 2000 a total of 49 canopy gaps were inventoried on the IF site. These gaps covered 5.6% of the sampled area and varied from 6 to 833 m^2 (Zeibig et al., 2005). Stand structure was relatively homogeneous on the IF site and gaps were beginning to form in the closed canopy. This structure may be related to stand development following past natural (e.g. windthrow) or anthropogenic disturbances (e.g. logging for charcoal burning). However, based on the historical archival evidence, the stand was not disturbed by humans; the entire forest reserve has been protected for more than 100 years and the upper most area, which includes the IF site, has been protected since 1885 (Hocevar et al., 1985). We did not find any signs of logging or any other human intervention in the research area. However, past changes in the forest structure of the adjacent *Omphalodo-Fagetum* forest site, the decline of silver fir in particular, indicated the indirect influences of air pollution and overbrowsing (Diaci et al., 2011). During the sampling period (1999–2009), a few new gaps were created, but not in the near vicinity of the gaps under research.

2.2. Recordings

In 1999 we selected the five largest gaps on the IF site (average size was about 200 m^2). The relatively recent formation (5–10 years old) of the gaps allowed subsequent comparison of regeneration development. Within each gap we systematically established 13 rectangular permanent plots 1×2 m in size with the shorter side facing north. The first plot was located in the gap centre, and an additional three plots were located in each direction of the compass (Fig. 1). Plots were located 2 m apart, except when obstacles (i.e. CWD, root plates, large trees) were present, in which case plots were moved by 1 metre in the direction of the transect. Using this sampling design, approximately five plots were located in the gap centre, four at the gap edge, and four below closed canopy. All plots were permanently marked with iron stakes for location with a metal detector at the next inventory. In 1999, 2003, and 2009, we recorded the species composition and percent cover of vascular plants on the plots. Plant cover was estimated visually from above and was recorded to the nearest 10% from 10 to 100%, and to the nearest 1% from 1% to 10%, excluding mosses. In 1999 plant cover was recorded in late July, when *Allium* had already begun to wither. Subsequent recordings in 2003 and 2009 were therefore carried out in early July. Most analyses were based on the most recent recording; however, the coverage of geophytes could still be slightly underestimated. Regeneration density was recorded per species in four height classes: small seedlings ($h \leqslant 20$ cm; excluding 1-year-old seedlings), seedlings (20 cm < $h \leqslant 130$ cm), saplings (130 cm < $h \leqslant 250$ cm), and small trees ($h > 250$ cm and dbh < 5 cm). In 1999 and 2009, all beech and maple plants were scored for browsing damage. They were classified as unbrowsed or lightly browsed if less than or equal to 10% of the lateral shoots were damaged. If more than 10% and less than or equal to 50% of lateral shoots were browsed, including the terminal shoot, seedlings were classified as moderately browsed, while plants with even more damage were categorised as heavily browsed.

In 1999 and 2003 we measured the length and last height increment of the two dominant beech or maple plants in each plot. In 2009 the three dominant beech plants in each plot were analysed in the same way. Plants were considered dominant only if they were not overtopped by nearby regeneration or herbs and only if the terminal shoot had not been browsed in the previous 2 years, thus the tallest plants were usually, but not always, dominant. Dominant individuals were not permanently marked, such that dif-

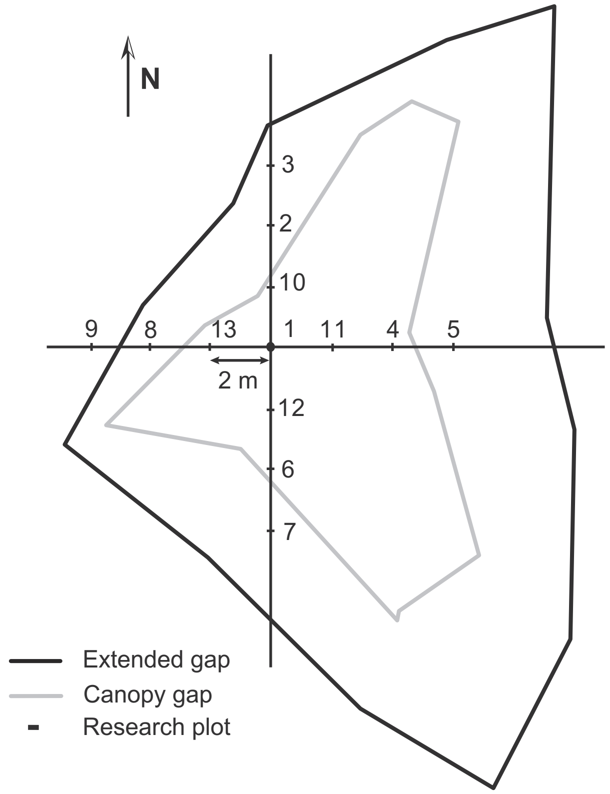

Fig. 1. Projection of canopy gap 3 including the extended gap (sensu Runkle 1982), sampling transects, and research plots in 2009. At the time of recording, the transect intersection was no longer in the gap centre due to the asymmetric lateral growth of beech crowns.

ferent plants may have been measured in different years and consequently measurements were not treated as dependent samples.

In each plot the relative percent diffuse (diff.) and direct (dir.) solar radiation was estimated from hemispherical photographs taken at a height of 1.3 m in completely overcast sky conditions. In 1999 film fish-eye photography was applied as described in Diaci and Thormann (2002), while in 2003 and 2009 the digital fish-eye method (WinScanopy) was used. We opted for the second method after a series of comparative measurements of both methods with LAI 2000, which produced comparable results (Rozenbergar et al., 2011). In 2009 we made a detailed map of the gaps and extended gaps (sensu Runkle, 1982) with measurements of the crown projections of all border trees. We also mapped the location of gapmakers and scored their decay stage into eight classes. The decay classes and estimated age of each class (from 1 to more than 45 years) were adopted from Bartemucci et al. (2002) and Goedhart et al. (2004). In 2009 in each extended gap area, all saplings and small trees higher than 1.3 m and lower than 20.0 m were counted by species, their height was measured, and a definitive gapfiller was determined (sensu Lertzman, 1992). The abundance of taller saplings and small trees were low compared to silver fir-beech old-growth forests and they were located predominantly at gap edges. To compare gap regeneration processes with the average conditions for the whole IF site, in 2010 we overlaid the IF site with a 12.5 × 12.5 m N–S aligned grid. Plots of the same size as those in the gaps were established on the grid intersections and the same recording protocol was applied.

2.3. Analyses

Data were analysed in Microsoft Excel Version 2003 and R Version 2.13.0 (R Development Core Team, 2011). Differences in cumulative and individual plant cover, woody regeneration cover and density, and diffuse light between the plots in gaps and those on the grid were analysed with the nonparametric Mann–Whitney U Test. Principle coordinate analysis (PCoA) and the Bray–Curtis distance measure were used to ordinate plots based on the 2009 vegetation survey. The analysis included only species that occurred in more than one plot and plots with more than one species. Based on inspection of the scree plot of the eigenvalues, we selected only the first two components (axes). Ecological variables (direct and diffuse light), Ellenberg indicator values (EIVs), and beech and maple regeneration density were fitted onto an ordination using the envfit function, and *Allium* cover was plotted as the fitted contours using the ordisurf function in the "vegan" package (Oksanen et al., 2011). A permutation test was used for assessing the significance of fitted vectors. The first ordination axis was associated with the measured ecological factors (e.g. *Allium* cover, diffuse light), while the second axis appeared to be strongly correlated with the Ellenberg indicator value (EIVs) for soil nitrogen (Ellenberg, 1988). Therefore, factor scores for the second axis were coded as a dichotomous variable, which was applied in subsequent analyses as the indicator of soil nitrogen. The effects of ecological factors on regeneration and vegetation cover, density, and growth were analysed with linear mixed-effects models (LMMs). These models allow nested error structures since the research plots were nested within gaps and the measurements were repeated three times. The models were built with the "nlme" package (Pinheiro and Bates, 2000). Gap and year of measurement were considered random factors. However, models with year of measurement nested within gap as random factors failed to converge or had extremely large confidence intervals for parameters; therefore we proceeded with gap as the only random factor, while year was included as a fixed factor. The protocol closely followed the "top-down" strategy described in West et al. (2007). Firstly, different models with all combinations of ecologically meaningful fixed effects were built and compared based on the maximum likelihood method (ML). The best model was further developed by the addition of random effects. For this step, model comparisons based on the restricted maximum likelihood (REML) were applied. Finally, the best model was adjusted for unequal variances (varIdent) if needed. For model diagnostics, we carefully examined confidence intervals of parameters and analysed sets of graphical summaries proposed by Robinson and Hamann (2011). All variables were transformed using the common logarithm function to meet the assumptions of normality and linearity. For the regeneration cover and density model, *Allium* cover was coded as a three level factor to reduce noise in the data. Throughout the paper, numbers in brackets denote the standard error of the mean (SE).

3. Results

The average gap area decreased from about 200 m^2 in 1999 to 122 m^2 in 2009. Gap history was estimated from the decay class of the gapmakers. Gap one was mainly a result of a single disturbance event (gapmakers of the 3rd decay class), gaps two, three, and four were the result of at least two events, and gap five was the result of several events. Most gapmakers were classified into the 3rd decay class, suggesting that most of the gap formation process took place around 15–20 years ago. Many fresh gapmakers in recently formed gaps on the IF site showed signs of wood-decay fungi, suggesting that a combination of fungal attack and windthrow had been the main cause of mortality on the IF site. No gap extension was observed during the research period.

During the research period, 45 vascular plants, including woody plants, were recorded in the gaps and on the grid. Individual plant cover and their relative frequency per plot in gaps remained

Table 1
Relative frequency (%) and average cover (%) of ground vegetation for the eight most abundant species in the gaps ($N = 65$) in 2009 and their Ellenberg indicator values. Values for the same species on the grid ($N = 52$) in 2010 are also shown.

	Gap 2009		Grid 2010		Ellenberg indicator values		
Species	Cover (%)	Frequency (%)	Cover (%)	Frequency (%)	*L*	*H*	*N*
Allium ursinum L.	43.5	89.2	35.1	66.0	2	6	8
Senecio ovatus Willd.	7.9	72.3	3.1	37.7	7	5	8
Galium odoratum L.	5.4	76.9	3.7	79.2	2	5	5
Mercurialis perennis L.	3.7	24.6	5.0	52.8	2	*x*	7
Oxalis acetosella L.	1.6	36.9	0.6	39.6	1	5	6
Cardamine trifolia L.	1.4	47.7	2.3	77.4	3	6	7
Athyrium filix-femina L.	0.9	9.2	0.1	3.8	3	7	6
Anemone nemorosa L.	0.7	13.8	2.4	41.5	*x*	5	*x*

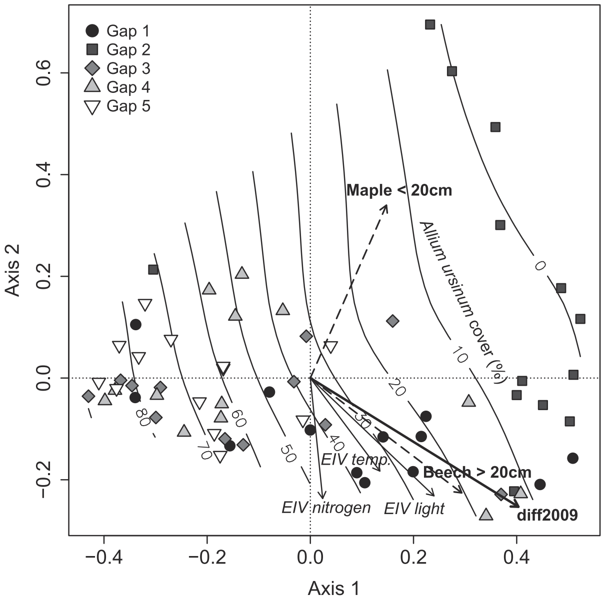

Fig. 2. Ordination-biplot of a Principle coordinate analysis (PCoA) for vascular plant cover in the herb layer (Bray-Curtis distance measure). Thick arrows represent measured diffuse light, broken arrows represent maple and beech regeneration density, and thin arrows represent Ellenberg indicator values. The arrows show the direction of the (increasing) gradient, and the length of the arrows is proportional to the correlation between the variable and the ordination. Only factors with p-value <0.05 were plotted. Smaller angles between the arrow and axis represent a higher correlation between the two values. Fitted contours connect points in ordination space with the same *Allium* cover.

relatively stable over the period. The most frequent plants with the highest cover were similar in gaps and on the grid (Table 1). In 2009 the highest overall ground vegetation cover in the gaps was exhibited by *Allium* (43.5%), followed by beech (18.8%), *Senecio ovatus* (7.9%), *Galium odoratum* (5.4%) *Mercurialis perennis* (3.7%), *Oxalis acetosella* (1.6%), and maple (1.5%). It was indicated that some shade tolerant plants, such as *M. perennis* and *Cardamine trifolia,* had higher cover on the grid, while light demanding *S. ovatus* had higher cover in the gaps. Ellenberg values indicated humid and very productive soils.

We were also interested in the main compositional gradients of the ground vegetation (Fig. 2). The first and second ordination axes explained 40.0% and 14.1% of the variance in species data, respectively. Individual plots in gaps are shown along the first and second ordination axes (Fig. 2). Measured variables having statistical significance greater than 95% are shown as arrows pointing in the direction of their greatest change. The axes position was adjusted so as to attain the maximum correlation. The first ordination axis was positively correlated with *Gentiana asclepiadea* L. and *Calamintha grandiflora* (L.) Moench cover and negatively correlated with *Allium* and *Veratrum album* L. cover. The second ordination axis was positively correlated with *Anemone nemorosa* and *Mycelis muralis* (L.) Dumort. cover and negatively correlated with *Hacquetia epipactis* (Scop.) DC. and *Omphalodes verna* Moench cover. Ellenberg indicator values (EIVs) for soil nitrogen increased inversely but almost parallel to the second axis, while diffuse light, EIV for light and EIV for temperature increased towards the lower right corner of the plot. In contrast to diffuse light, *Allium* cover increased towards the lower left side of the plot. Beech small seedling density linear regression on both axes was not significant since it increased towards all three corners of the imaginary triangle depicting plots on the ordination-biplot. While beech seedling density increased with diffuse light, small maple seedling density increased in plots with low EIV for nitrogen and low *Allium* cover. The first axis appeared to be closely linked with diffuse light and beech cover and negatively associated with *Allium* cover.

The average diffuse light levels in gaps significantly decreased from 11.0% to 5.7% during the 10-year period (LMM, coeff. = −0.02 (0.002), d.f. = 189, $t = -12.65$, $p < 0.0001$; Table 2). The average decrease in light levels in the gaps was about 0.5% year^{-1}. In 2009 diffuse light in the gaps (5.7%) was still slightly higher than the average on the grid (4.3%). Total ground vegetation cover in the gaps did not significantly differ between 2003 and 2009. We did not include 1999 in the statistical test due to the late date of the *Allium* cover assessment. However, ground vegetation not including *Allium* slightly decreased from 34.4% in 1999 to 27.9% in 2009 (LMM, coeff. = −0.02 (0.005), d.f. = 189, $t = -3.44$, $p < 0.0001$). Overall beech and maple regeneration cover and density were relatively low (Table 2). Yet beech cover and seedling density increased significantly over the years, while maple cover did not show any significant change (Table 3). Densities of small seedlings for both species significantly decreased during the period 2003–2009, thus the rate of emergence of new seedlings of both species was lower than the rate of recruitment to larger classes. The recruitment tendency was much more pronounced for beech than for maple, since beech was represented in all regeneration classes, including saplings and small trees, while dominant maples rarely reached 50 cm in height (Table 2, Fig. 5). Maple's share in density among small seedlings, seedlings, and saplings was 30%, 12% and 0%, respectively, and remained stable during the decade. The share of maple on the grid within the same regeneration classes was similar: 20%, 32%, and 0%, respectively. When we compared woody regeneration cover and density between the gaps and the grid, we found significantly higher beech seedling cover and density within the gaps, while differences for maple were not significant (Table 2). No beech or maple saplings were found on the grid.

LMM models revealed that beech cover was significantly negatively related to high *Allium* cover (Table 3, Fig. 3), negatively related to low EIV for soil nitrogen, positively related to maple cover, and showed a negative parabolic relationship with diffuse light. The results for beech seedling density were similar, with the exception that the negative relationship with *Allium* cover was not significant and was replaced by the negative relationship with cumulative ground vegetation cover. The negative quadratic coefficients for the effects of diffuse light for beech cover and seedling density indicated an increase with increasing diffuse light and a decrease at higher relative light levels (Fig. 3). Maple cover also significantly decreased with increasing *Allium* cover and increased with increasing diffuse light (Table 3, Fig. 3). Additionally, small maple seedling density was positively related to low EIV for soil nitrogen. Ground vegetation cover not including *Allium* or woody regeneration (LMM: coefficient = −0.02 (0.01), d.f. = 1, 189,

Table 2
Comparison of light (diff.), ground vegetation cover (veg.), woody regeneration cover (beech, maple), small beech seedling density (beech20), beech seedling density (beech21), beech sapling density (beech130), small beech tree density (beech5 cm), small maple seedling density (maple20), and maple seedling density (maple21) between years and between gap and grid inventories. Least-squares means and SE are presented as well as the significance of the Mann–Whitney U Test between measurements in gaps in 2009 and on grid in 2010. for a description of regeneration height classes, please refer to the recordings subsection.

	Year				p
	1999	2003 Gap	2009	2010 Grid	
N	65	65	65	52	
Diff. (%)	11.0 (0.46)	7.1 (0.31)	5.7 (0.21)	4.3 (0.29)[c]	0.0000
Veg. (%)	64.0 (3.65)	73.0 (5.01)	71.4 (3.68)	78.2 (4.39)	0.0865
Beech (%)	8.2 (1.60)	10.9 (1.96)	18.8 (2.93)	7.1 (2.63)	0.0000
Beech20 (N m^{-2})	1.22 (0.24)	1.91 (0.31)	0.77 (0.22)	1.63 (0.36)	0.0130
Beech21 (N m^{-2})	0.84 (0.15)	1.08 (0.21)	1.38 (0.25)	0.43 (0.25)	0.0000
Beech130 (N m^{-2})	0.05 (0.02)	0.05 (0.02)	0.11 (0.03)	/	/
Beech5 cm (N m^{-2})	na[a]	na	0.01[b]	na	na
Maple (%)	1.46 (0.21)	0.83 (0.16)	1.35 (0.27)	1.46 (0.53)	0.3708
Maple20 (N m^{-2})	0.63 (0.11)	0.63 (0.16)	0.35 (0.10)	0.42 (0.09)	0.1353
Maple21 (N m^{-2})	0.10 (0.03)	0.16 (0.05)	0.18 (0.04)	0.20 (0.07)	0.2797

[a] na – data not available.
[b] Measured in the extended gap.
[c] Area measured on a subsample of 34 plots.

Table 3
Results of the LMM analysis for beech and maple regeneration cover (beech, maple), small seedling (beech20, maple20), and seedling density (beech21, beech21) predicted by year, *Allium* cover, cumulative vegetation cover (vcover), soil nitrogen (Ellenberg indicator value), and diffuse light (diff.) for 195 plots. Gaps were considered as a random effect. Numbers in brackets denote the standard error (SE).

	Dependent variable					
	Beech	Beech20	Beech21	Maple	Maple20	*Allium*
Random effect						
SD (intercept/residual)	0.11/0.33	0.23/0.38	0.13/0.34	0.11/0.23	0.16/0.17	0.60/0.91
Test for Fixed Effects Estimate (SE)						
Intercept	−93.93 (19.85)***	25.83 (8.83)**	−36.67 (14.07)**	0.01 (0.12)	14.1 (4.90)**	2.04 (0.44)*
Year	0.04 (0.01)*	−0.01 (0.01)***	0.02 (0.01)***	ns	−0.01 (0.002)**	ns
Allium3med	−0.10 (0.08)	ns	ns	0.02 (0.04)	ns	–
Allium3high	−0.23 (0.07)*	ns	ns	−0.08 (0.04)***	ns	/
Vcover	ns	ns	−0.18 (0.08)***	ns	ns	/
n.2 low	−0.59 (0.07)*	ns	−0.15 (0.04)**	ns	0.07 (0.02)***	ns
Diff.	12.86 (2.12)*	ns	4.36 (1.32)**	0.26 (0.11)***	ns	−0.84 (0.37)***
Diff.^{2}	−6.58 (1.09)*	ns	−2.13 (0.69)**	ns	ns	ns
Iacer	0.25 (0.12)***	/	/	ns	/	ns
Model Information Criteria						
Variance	Varident (∼1|gap)	Varident (∼1|gap)	Varident (∼1|gap)	/	/	/
AIC	260.6	135.9	134.6	13.3	−63.59	496.4
BIC	305.6	162.0	173.5	32.6	−34.41	522.4

AIC – Akaike information criterion; BIC – Bayesian information criterion.
[***] Significance code: $p < 0.05$.
[**] Significance code: $p < 0.01$.
[*] Significance code: $p < 0.001$.

$t = 3.14$, $p = 0.002$) showed a positive linear relation to diffuse light, while *Allium* cover showed a negative relation to diffuse light (Table 3, Fig. 3).

Inspection of interaction plots for beech cover indicated possible interaction of explanatory variables. A separate LMM analysis confirmed interaction effects of year and EIV for soil nitrogen and year (LMM: coefficient (n.2 low) = −0.04 (0.01), d.f. = 181, $t = 3.02$, $p = 0.0029$) and *Allium* cover and year (LMM: coefficient (*Allium* low) = 0.06 (0.02), d.f. = 181, $t = 3.47$, $p = 0.0007$) on beech cover. Over the observed period, beech cover greatly increased in plots with high EIV for soil nitrogen, while in plots with low EIV for soil nitrogen, beech cover remained low (Fig. 4a). The lowest level of *Allium* cover (ca. 0–20% *Allium* cover) was associated with a large increase in beech cover, while the medium and highest levels of *Allium* cover (ca. 60–100%) were associated with the slower development of beech (Fig. 4b) or even a decrease in beech cover. In summary, the results for beech suggest that *Allium* was a serious competitor to beech in low diffuse light levels, while other herbs competed in high light levels (Fig. 3).

The average height of dominant beech and maple seedlings significantly increased from 436 mm and 150 mm in 1999 to 968 mm and 338 mm in 2009, respectively (Table 4). LMM models for height showed a significantly lower height of maple when compared to beech and adjusted for other predictors of the model (Table 4). The height of both species was negatively related to low EIV for soil nitrogen, and there was also a significant negative quadratic coefficient for the effects of *Allium* cover. The latter suggested that the tallest plants of both species were recorded with intermediate *Allium* cover values. Also, the height increment was lower for maple than for beech after adjusting for other predictors (Table 4, Fig. 5). The increment did not significantly change over the years when adjusted for other predictors. The most important

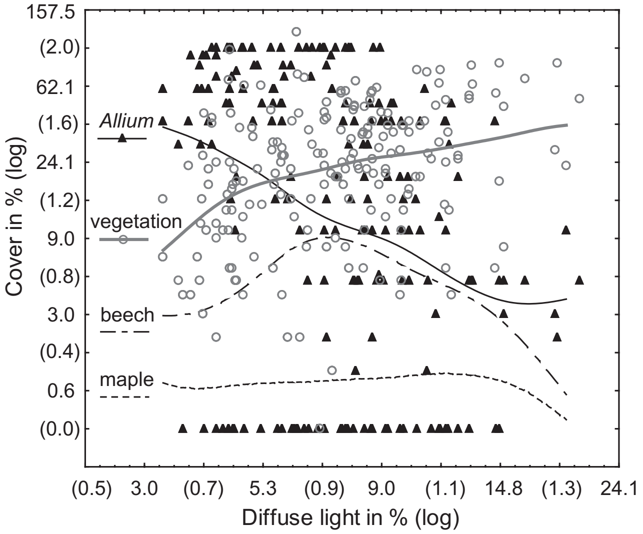

Fig. 3. Relations among covers of *Allium*, ground vegetation not including *Allium* or woody regeneration (vegetation), beech, maple, and diffuse light. All variables are given in percent and were log transformed. Back-transformed values are shown without brackets. The curves result from the distance-weighted least squares smoothing procedure.

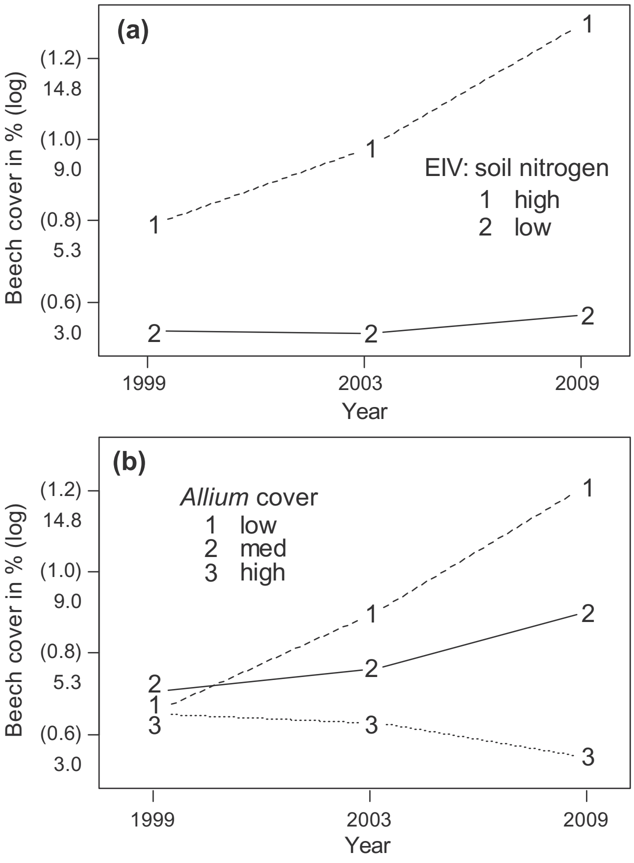

Fig. 4. (a) Effect display for the interaction between year of measurement and Ellenberg indicator values for soil nitrogen. (b) Effect display for the interaction between year of measurement and coded *Allium* cover. Response variable beech cover was log transformed. Values without brackets were back-transformed. Means were calculated from LMM fitted values.

predictor for height increment was height, with a negative quadratic coefficient. *Allium* cover was negatively related to the height increment of both species.

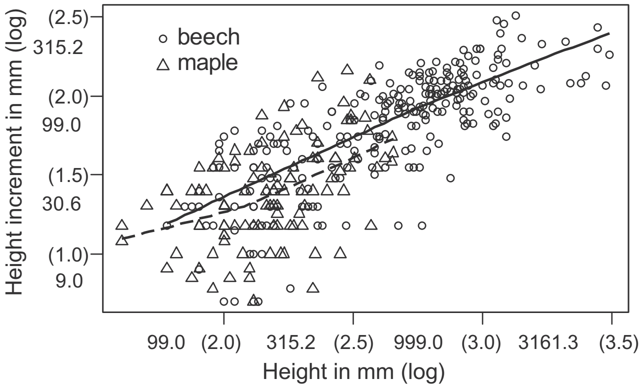

Fig. 5. Scatter plot of height increment of dominant plants by height, coded by tree species. Height and height increment were log transformed. Back transformed values are shown without brackets. Curves result from local polynomial regression fitting (loess).

Seedlings, saplings, and small trees presented in Table 2 and Fig. 5 may not be the trees that will fill the gaps. Four extended gaps had several trees (approx. 30 ha^{-1}) with dbh between 5 and 10 cm at the border of the gaps, while most definitive gapfillers were even larger in diameter and taller. The definitive gapfillers included a fir 15 m in height in gap 1, two beech poles 5 m in height in gap 2, three beech poles 5 m in height and a maple 13 m in height in gap 3, two firs 14 m and 18 m in height, respectively, in gap 4, and a fir 16 m in height in gap 5. The species mixture of gapfillers in density (50% beech, 40% fir and 10% maple) stood in contrast to the composition of the regeneration layer and canopy layer, both of which were almost exclusively composed of beech. While the maple gapfiller might have been a result of a past larger gap or overlapping gaps, we observed scattered suppressed firs between 5 and 30 cm dbh across the entire IF site, which is consistent with the results from the gapfiller analysis.

Besides *Allium* competition and low light levels, ungulate browsing was a serious obstacle for the recruitment of woody plants. The percent of regeneration per browsing score did not change significantly between 1999 and 2009; therefore, averages from both years per species are presented. About 43% of beech seedlings and saplings experienced no browsing or light browsing (<10% of lateral shoots), 42% experienced moderate browsing of more than 10% of lateral shoots and the terminal shoot, while 15% experienced heavy browsing of more than 50% of shoots. Fewer maple individuals were classified into the first and second browsing scores (32% and 28%, respectively) and more into the third score with heavy browsing (40%). Maximum browsing impact occurred in the 21–50 cm size class for both species.

4. Discussion

4.1. Gap characteristics and light climate

The features of the gaps were comparable to those reported by Zeibig et al. (2005) from the total gap inventory of the same site, and by Drössler and von Lüpke (2005), who reported that 85% of the canopy gaps in two beech old-growth forests were smaller than 250 m^2. In a study of Albanian old-growth forests, Tabaku and Meyer (1999) found a slightly smaller average gap size of 60–74 m^2. Thus, the gaps in this study might well be representative of recruitment in medium gaps with several gapmakers.

Light levels in the gaps were comparable to the results of Emborg (1998), who measured 2–10% relative light intensity (RLI) in different developmental phases of beech lowland old-growth forest. Light levels on the grid in this study were similar

Table 4
Results of the LMM for dominant seedling height (h) and height increment (ih) predicted by species (sp_acer), year, Allium cover, and EIV for soil nitrogen (n.2). Gaps were considered as a random effect. Numbers in brackets denote the standard error (SE).

	Dependent variables	
	Height (h)	Height increment (ih)
Random effect		
SD (intercept/residual)	0.12/0.31	0.04/0.27
Test for Fixed Effects Estimate (SE) Significance		
Intercept	−83.77 (8.00)***	−1.21 (0.42)**
sp_acer	−0.30 (0.04)***	−0.12 (0.03)^{c}
Year	0.04 (0.004)***	ns
h		1.68 (0.33)*
h^2		−0.19 (0.06)**
Allium	0.25 (0.07)*	−0.04 (0.02)***
Allium^2	−0.11 (0.03)**	ns
n.2 low	−0.18 (0.03)*	ns
Model information criteria		
N	353	353
Variance	Varident (∼1|year)	Varident (∼1|year)
AIC	105.4	−26.0
BIC	147.7	8.7

AIC – Akaike information criterion.
BIC – Bayesian information criterion.
*** Significance code: $p < 0.05$.
** Significance code: $p < 0.01$.
* Significance code: $p < 0.001$.

to those reported by Messier et al. (2009), who reviewed light levels in temperate old-growth forests and gave an estimate of 4.5% RLI above ground vegetation. Drössler and von Lüpke (2007) also measured an average RLI of 2.5% and 9.4% in the Havesova and Kyjov old-growth beech forests in Slovakia, respectively. Average RLI in gaps and on the grid was above the critical value of 1–3% for beech regeneration as suggested by Watt (1923) and Emborg (1998). However, RLI in gaps was lower compared to light levels reported for the largest gaps in selected fir-beech old-growth forests (Rozenbergar et al., 2007), the main reason being that the gaps were larger in fir-beech forest, probably due to fir dieback and slower gap closure in mixed forests with conifers.

4.2. Effects of Allium on regeneration and gap partitioning

The cumulative density of small seedlings was comparable to data from beech and fir-beech old growth forest in Slovenia and Eastern Europe (Korpel, 1995; Commarmot et al., 2005; Rozenbergar et al., 2007; Drössler and von Lüpke, 2007; Diaci et al., 2011); however, taller seedlings and saplings were significantly less abundant in our study. Vegetation cover, in contrast, was higher in comparison to other sites. This was mostly a result of the dense *Allium* cover. We found evidence that this shade tolerant species hindered the development of beech and maple seedlings and saplings. Moreover, the growth of dominant seedlings – often taller than *Allium* – was also negatively influenced by its presence. Both species attained a maximum height at an intermediate *Allium* cover. Beech and maple are shade tolerant as young plants and may form persistent seedling banks (Madsen and Hahn, 2008; Drössler and von Lüpke, 2007; Caquet et al., 2010). However, this life strategy was not so evident on this site type due to *Allium* competition. As suggested in literature (e.g. Ernst, 1979; Ellenberg, 1988; Jandl et al. 1997) *Allium* may exhibit mechanical, physiological and allelo-chemical effects on competing plants. However, experimental evidence is still deficient with the exception of allelopathic effects via phytotoxins accumulated in the surface soil layer and via volatile compounds which inhibit seed germination and plant growth (Djurdjevic et al., 2004). Contrary to the results of Schmidt (1997), who found a significant decrease in previously dominant *Allium* seven years after the creation of gaps in managed beech forests, *Allium* cover remained stable in this study. This may be attributed to the fact that the gaps in our study were smaller and had relatively low light levels, and thus provided more suitable conditions for shade-tolerant *Allium*. Ernst (1979) also pointed out the relative stability of *Allium* stands in the Göttingen Forest over a period of 25 years. Furthermore, he stressed the importance of *Allium* in improving the nutrient budget of forests due to the capture of nutrients released in early spring that would otherwise be lost in run-off.

There was evidence of gap partitioning among *Allium*, tree seedlings, and other herbs (Fig. 3). While *Allium* significantly decreased with increasing light levels, the highest beech cover was found in intermediate light levels, and maple seedling cover and dominant ground vegetation cover increased with increasing light. In old-growth forest in Rajhenavski Rog, the density of small beech seedlings was negatively related to diffuse light, and they were concentrated below closed canopy or at gap edges (Rozenbergar et al., 2007). The latter can be explained by competition from herbaceous plants, which may result in the higher survivorship of tree seedlings below adult trees (indirect facilitation, see Pages et al., 2003; Wagner et al., 2011). This was not the case in this study due to the shade tolerance of *Allium*. Moreover, gap centres did not prove optimal for beech seedlings due to competition from tall, light-demanding herbs such as *S. ovatus*. Thus, the negative quadratic response of beech cover along the light gradient seems biologically reasonable, and intermediate light levels (5–10%) may provide a window of opportunity for the development of beech on the *Isopyro-Fagetum* (IF) site. There is a significant body of research showing that gap centres and high light levels are generally not optimal for beech regeneration (e.g. Watt, 1923; Mosandl and el Kateb, 1988; Mountford et al., 2006; Wagner et al., 2011).

The results were partially similar for maple with the exception of the positive linear relationship with diffuse light. This may indicate that the window of opportunity for maple is shifted to higher light levels relative to that for beech (see Fig. 3). The absence of maple recruitment to higher developmental classes in the observed light conditions and its lower average height and height increments compared to beech also confirm maple's higher demand for diffuse light and thus more pronounced partitioning between gaps and closed canopy. In our survey of dominant maple plants, only a few specimens taller than 50 cm were found in plots in the gaps or on the grid, suggesting that there is a particular height range in which maple becomes more light demanding. The preference of maple to develop in gaps has been confirmed by many other studies (Diaci, 2002; Petritan et al., 2007). Maple has a unique life history strategy that allows it to compete with tall herbs. Its early-stage shade tolerance enables it to establish below the thick layer of herbs, and its subsequent fast growth as it approaches the height of the herb top enables it to escape. We found some evidence of a positive response of beech cover and seedling density to soil nitrogen, while small maple seedlings ($h < 20$ cm) showed a negative response. This was unexpected since maple is generally regarded as more nutrient demanding than beech (Pages et al., 2003). Maple height positively responded to EIV for soil nitrogen, indicating that there may be a shift in maple's nutrient demand from small seedlings to seedlings. Another possibility could be inaccuracy in the indication of soil nitrogen caused by its indirect estimation through EIV. Dense and competitive ground vegetation that influences tree regeneration may also be found in other forest systems (Wardle, 1959; Butler-Manning, 2008; Wagner et al., 2010). However, canopy species with a seedling bank strategy find spatial or temporal regeneration niches for their establishment. If this is not the case, then semi shade tolerant or even pioneer tree species may be promoted after gaps are created (Abe et al., 2002).

The proportion of browsed regeneration was high but in line with the results of similar research in the Dinaric region (Rozenbergar et al., 2007; Klopcic et al., 2010). Repeat studies in Rajhenavski Rog (*Omphalodo-Fagetum* site) indicated that a similar percentage of browsed seedlings did not prevent beech from recruiting to the thicket stage (Rozenbergar, 2012). However, the higher palatability of maple compared to beech very likely negatively influenced its abundance and height growth. The estimated densities of roe (*Capreolus capreolus* L.) and red deer (*Cervus elaphus* L.) in the area were about 1.4 and 5.6 individuals per square kilometer, respectively (Adamic and Jerina, 2010). Ellenberg (1988) reports that sites on humid, productive soils, including *Allium*-rich beech forests, strongly attract wild ungulates and are thus often overbrowsed. This may also increase the probability of seed dispersal of many geophytes, including *Allium*.

4.3. Scenarios of gap recruitment

Analyses of regeneration cover, density, and growth indicated slow development. This was caused by at least three factors, namely low light levels, *Allium* competition, and ungulate browsing. It therefore seems that several successive canopy openings are needed for gaps to be filled with a new wave of regeneration. Based on the regeneration growth data presented here and in comparable beech regeneration studies (e.g. Nagel et al., 2006; Nagel et al., 2007), we estimated that beech recruitment in general needed 100 years or more to reach 20 m in height and fill the gap. In this study the remaining diameter of gaps was 5–15 m. This means that they will close in the next 15–40 years if we assume the estimated annual decline in light in this study or an average lateral crown growth rate of 18 cm year^{-1} (Runkle and Yetter, 1987) with no gap extension. It seems that medium gaps with an average size of about 200–300 m^2 require 30–60 years to close. This is not enough time for the regeneration to close the gap from below. The presence of advance regeneration and small trees in the middle layer also supports this observation. Bearing in mind the small sample size of advance regeneration and gapfillers in this study, it is still worth mentioning the suppressed firs in the middle layer observed throughout the whole IF site. They stood in strong contrast to the almost exclusive beech dominance in the regeneration and canopy layers. These suppressed firs are likely more than 100 years old and may result from a period when wild ungulates were extinct and the overall presence of fir in the growing stock of the surrounding managed Dinaric silver fir beech forest was significantly higher than that of today (Klopcic et al., 2010).

The evidence of this and past studies (Zeibig et al., 2005) suggests that different gap recruitment patterns are possible on the IF site: gaps with a single gapmaker or several gapmakers created in one or several events with or without advanced regeneration. The probability of the latter scenario seems higher compared to other beech sites due to competition from *Allium*, which hinders regeneration development. Thus, different recruitment patterns appear to be a function of forest site factors (e.g. soil type, ground vegetation, seed years, climatic patterns) and disturbance severity. In the two decades leading up to the research, the IF site experienced a light endogenous disturbance regime; however, in the long-term development cycle of forest patches, intermediate disturbances cannot be excluded.

5. Conclusion

Forest sites dominated by *Allium* are not frequent; however they can be found scattered across all Europe and parts of Asia. *Allium* can form pure stands on eutrophic and mesotrophic forests sites in shady conditions and is thus well represented in ancient woodlands. With restoration of beech forests the share of *Allium* dominated sites is likely to increase. Through 10 years of observation we recorded low recruitment rates of beech and a recruitment failure for maple in medium sized gaps of a beech old-growth forest dominated by *Allium*. A dense layer of shade tolerant *Allium* dominated the forest floor under closed canopies, beech regeneration was well developed at medium light levels, while less shade tolerant herbs favoured gap centres. In addition to competition from *Allium*, ungulate browsing negatively influenced beech and especially maple regeneration. When comparing the regeneration layer of *Allium* dominated beech forests with silver fir-beech forests, fast lateral growth of beech crowns should be taken into account. Moreover, in Slovenian silver fir-beech old-growth forests, canopies were “thinned” by a fir decline from the 1970s to the mid 1990s. For this reason, scattered clumps of declining beech advance regeneration under recently closed gaps were often observed on the *Allium* site, but were rare on fir-beech forest sites in Slovenia. Thus, in medium sized gaps of old-growth forests on similar sites several gap releases may be needed to fill the gaps from below. The results of this study also suggest that it is important that future research in old-growth forests integrates the site ecology and the disturbance regime.

Because this was a case study, general conclusions for managed beech forest on comparable sites are not possible, yet the results indicate some interesting aspects of their regeneration which should gain more attention in the future. The slow recruitment rate of beech and its selection of gap peripheral microsites, due to gap partitioning with *Allium* under canopies and less shade tolerant herbs in gap centres, suggest that diffuse opening of the canopy might not be the optimal solution for natural regeneration. Therefore, single tree selection management or regular shelterwood should not be the primary silvicultural tools in *Allium* dominated beech forests. A better approach seems to be creation and successive extension of small gaps *sensu* the irregular shelterwood system (germ. Femelschlag). In this way more light can reach the forest floor and supress the development of *Allium*. The irregular shelterwood can also create more gap peripheral areas suitable for beech regeneration and gap centre areas that favour more light demanding species. This system, since small-scale and irregular, may also mimic aspects of the natural disturbance regime. The maple seedling density recorded in this study and less developed beech advance regeneration compared to other sites indicated that beech forests dominated by *Allium* might present an opportunity for growing noble broadleaves and other less shade-tolerant species, if managed with an appropriate silvicultural system.

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