Gap-phase regeneration of a Central-European sessile oak-hornbeam forest

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Background and purpose:
Gap cutting can be regarded as a regeneration tool of close-to-nature forestry. However, very little is known about the gap-phase regeneration of sessile oak. This paper examines height growth of sessile oak (*Quercus petraea*) and hornbeam (*Carpinus betulus*) seedlings, as well as, spread of blackberry (*Rubus fruticosus*) in circular gaps of various sizes.

Material and methods:
Three gaps of 15 m (G15), three gaps of 30 m (G30) and two gaps of 45 m (G45) in diameter were cut in a sessile oak-hornbeam forest. Height of sessile oak and hornbeam seedlings, as well as, cover of soil moisture indicator plants and that of blackberry were monitored until the fourth year of the regeneration.

Results and conclusions:
Sessile oak grew faster in G30 than in G15, but the two larger gap types did not differ in this aspect. Intensity of hornbeam seedling development increased with gap size. Proliferation rate of blackberry was the highest in G45. Within the gaps, both sessile oak and hornbeam were the tallest in the centres. In the northern parts, competition ability of hornbeam decreased relatively to that of sessile oak. For spread of blackberry, the west locations were the most optimal. Development of both of sessile oak and hornbeam seedlings was related to soil moisture as indicated by the herb layer. It was concluded that regeneration of sessile oak could be made more secure if starting it with cutting small gaps (e.g. 0.5 tree height) and if these gaps are enlarged then gradually.

Keywords:
***Quercus petraea, Carpinus betulus, Rubus fruticosus*, regeneration, gap, soil moisture**

INTRODUCTION

Studying gap dynamics is essential in order to work out close-to-nature regeneration methods since temperate deciduous forests often regenerate themselves by spontaneous gap formation if forestry operations do not influence the natural processes (1). Thus, gap cutting can be regarded as a basic tool of continuous cover forestry (2).
Site conditions inside the gaps are spatially heterogeneous due to the differential shading by the neighbouring trees. South parts of the gaps are more shaded and cooler than the north parts therefore soil moisture content of the former is higher. However, fine-scale pattern of soil attributes may modify this phenomenon (3, 4, 5, 6, 7, 8). East locations can be drier than the west ones because they are exposed

to the warm west sunlight (5). Thus, a site gradient often occurs inside the gaps and affects tree seedling density and growth, as well as, spatial pattern of the herbaceous vegetation. It was hypothesized that various species grow differently at different location along this environmental gradient (9, 10). Therefore, gap-phase regeneration processes of mixed stands are especially important to understand (11).

Shading effects of the mother trees depend on the size of the gap. Larger gaps are more illuminated but relations between gap size and soil moisture content are less evident (6, 12, 13). Interception of the canopy and root concurrence of the parent stand decrease with gap area while soil temperature increases (12).

Although pedunculate and sessile oak (*Quercus robur* L. and *Q. petraea* (Mattuschka) Liebl.) are major tree species in many forest types throughout Europe, very little is known about their gap-phase regeneration (e.g. 14, 15, 16, 17, 18). High weed abundance and competition of fast growing associated tree species can make pedunculate oak regeneration in gaps rather difficult, similarly to the more traditional regeneration methods (18). Bobiec (16) found that in natural gaps of various sizes of a mixed deciduous forest (*Tilio-Carpinetum*) lime (*Tilia cordata* Miller) and hornbeam (*Carpinus betulus* L.) could regenerate well but pedunculate oak could regenerate hardly.

In mesic sites, gap formation or gap cutting promotes spread of blackberry (*Rubus fruticosus* agg.) (19, 20). Blackberry is known as one of the strongest competitors of sessile or pedunculate oak (19, 21, 22), though some results showed that pedunculate oak could grow over the blackberry layer (23). By contrast, Tobisch (19) noticed the opposite in a Central-European sessile oak-hornbeam forest.

So far, it has been not clarified how gap size influences the height growth of sessile oak and hornbeam seedlings, as well as, blackberry proliferation. It has been not studied, either, how differently seedlings of sessile oak and hornbeam grow and how cover of blackberry changes in various topographical positions within gaps of a given size. This paper addresses these questions by studying circular gaps of 15, 30 and 45 m in diameter (i.e., approximately 0.5, 1 and 1.5 tree length) in a sessile oak-hornbeam stand. Furthermore, spatial differences of seedling height were related to blackberry cover and soil moisture content as indicated by the herb layer.

It was hypothesized a priori that height growth of both of sessile oak and hornbeam, as well as, blackberry abundance increase with the size of the gap due to the higher illumination, smaller canopy precipitation interception and weaker root concurrence of the parent stand. For sessile oak and hornbeam seedling development, the central part of the gaps was supposed to be the most optimal which is well-illuminated and have high soil moisture content. Blackberry was assumed to spread most slowly in the dry north and east parts. Moreover, positive relation was thought between soil moisture content and height growth of the analyzed tree species seedlings, negative relation was hypothesized between development of sessile oak seedlings and blackberry cover. However, due to their fast growth, hornbeam seedlings were assumed to be able to grow over the blackberry layer, thus, no significant relations were foreseen between blackberry abundance and seedling growth.

MATERIAL AND METHODS

The experimental site (47°09’ N, 17°00’ E) occurs at 220 m a.s.l. on a slight (5°) northeast slope. The forest is located near river Rába in southwestern Hungary. The soil is acidic brown forest soil with medium (70 cm) rootable depth developed on gravel. The annual precipitation is 700 mm of which 237 mm falls during the main growing period (1st May - 31st July). The mean annual temperature is 9.4°C.

The study stand is a typical sessile oak-hornbeam forest in which the upper layer is dominated by sessile oak beneath which hornbeam forms a lower canopy layer. Turkey oak (*Quercus cerris* L.) can be also found in the upper layer in small amounts. The stand was 107 years old in 2004 when the regeneration was started. No shrub layer had developed before the intervention and the herb layer was very sparse.

The regeneration was based on the crop of 2003. The study forest was fenced in 2004, before starting the experiment. During the winter of 2004-2005, eight circular gaps were cut. Three of them were 15 m (i.e., 0.5 tree length; G15), three gaps were 30 m (i.e., 1 tree length; G30) and the remaining two were 45 m (i.e., 1.5 tree length; G45) in diameter. Distances between two adjacent gaps were at least 30 m.

In the first year of the regeneration, number of sessile oak seedlings greatly decreased. Under the Hungarian site conditions, sessile oak mass crops are infrequent, therefore in order to increase sample sizes, two-year-old seedlings were planted in each gap with density of 1 seedling/m^2 in November 2005. Before planting, blackberry was removed manually and mechanically from all of the gaps. Despite these artificial influences, gaps and topographical positions within the gaps remained comparable because planting and blackberry removal were done identically in all gaps. Since the autumn of 2005, natural processes have not been disturbed by any other human operations.

Sampling was carried out annually from the initial stage (2004) to the fourth year of the regeneration (2008), except for 2007 when it was not performed. Height of all sessile oak and hornbeam seedlings was measured and cover of blackberry and total cover of soil moisture indicator plants was assessed visually in 1 x 1 m quadrats distributed along two transects in each gap. The transects were oriented N-S and E-W and intersected in the middle of the gaps. The quadrats were continuously placed along the transects hence the number of the quadrats depended on the size of the gaps (Table 1). Cover values were estimated

Table 1
Sampled area (in m²) of various topographical positions within the experimental gaps of different sizes. Method – regeneration technique applied; Location – topographical position inside the gaps; One gap – sampled area within one gap of a given size; Total – total sampled area in all gaps of a given size; transect – sampled area of the 1-m-wide transects (which equals the number of the 1 x 1 m sampling quadrats distributed along the transects); additional – sampled area of the additional 0.5 m-wide sampling units placed at both sides of the 1-m-wide transects; G15, G30, G45 – gaps of 15 m, 30 m and 45 m in diameter, respectively; S, C, N, E, W – south, central, north, east and west parts of the gaps, respectively. Note that the intersection area of the transects was sampled only once during a sampling occasion hence sampled area of the central part is not simply twice as big as that of the other parts (see Figure 1).

Method	Location	One gap		Total	
		transect	additional	transect	additional
G15	S	5	5	15	15
	C	9	7	27	21
	N	5	5	15	15
	E	5	5	15	15
	W	5	5	15	15
G30	S	10	10	30	30
	C	19	17	57	51
	N	10	10	30	30
	E	10	10	30	30
	W	10	10	30	30
G45	S	15	15	30	30
	C	29	27	58	54
	N	15	15	30	30
	E	15	15	30	30
	W	15	15	30	30

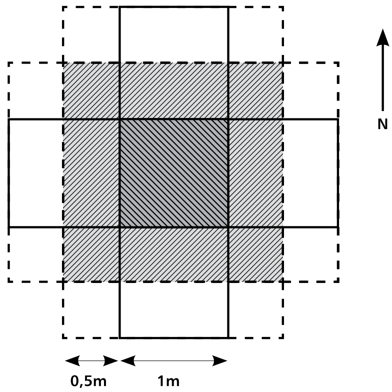


Figure 1
Intersection of the two transects in the middle of the gaps. The 1-m-wide transects are marked with solid lines, whereas the additional 0.5 m-wide sampling units are indicated by dashed lines.

during the spring and the summer aspect. Height of seedlings was measured in autumn by when growth had stopped. Soil moisture indicators were defined according to soil moisture requirements of the species presented by Borhidi (24). Thus, species with an indicator value of WB ≥ 7 (estimated on a scale of 1-12) were regarded as soil moisture indicators.

In order to increase sample sizes, sessile oak seedlings were sampled in additional 0.5-0.5 m-wide areas at both sides of each 1 x 1 m quadrat from 2005 to 2008 (Figure 1, Table 1). However, for some analyses, data of seedlings occurred within the original 1 x 1 m quadrats were used only (see data analyses section).

Temporal and spatial changes of seedling height were analysed by single classification ANOVA-s. However, assumptions of parametric ANOVA could not be met therefore the F statistics were tested by randomization (25, 26, 27). The randomization tests were performed by randomly permuting the assignment of observations to the groups. The sizes of the groups were fixed. Resampling number was 1000 in each case. Two types of tests were carried out. On the one hand, gap sizes were compared. On the other hand, differences between topographical positions within the gaps were examined for each gap size. Both types of tests were done for every sampling year.

Effects of gap size were studied in a planned manner. That is, the smallest and the largest gaps were related to the medium-size ones. Within a given gap size, five topographical locations (south, centre, north, east and west) were distinguished by dividing each transect into three equally-long parts (Table 1). Spatial differences between the locations were analyzed in an unplanned way which means that every possible comparison was performed. Thus, significance level was modified by the Bonferroni-Holm method (26). It must be noted, that the Bonferroni-Holm method makes significance tests rather conservative, thus, the probability of type II error increases. Therefore, the power (the probability of rejecting the null hypothesis when it is false) of the tests decreases and the null hypothesis is accepted too often. However, there were no reasons to make a priori decided (planned) comparisons. To investigate the competition between sessile oak and hornbeam more thoroughly, height of the tallest sessile oak seedling was subtracted from that of the tallest hornbeam seedling (or sapling) by 1 x 1 m quadrats for the fourth year of the regeneration. In the case of sessile oak, only data of seedlings occurred within the original quadrats were used for this type of examinations. Values of height differences (VHD) were evaluated similarly to the height data. It should be taken into consideration that sample sizes are equal to the numbers of those quadrats in which at least one sessile oak and one hornbeam seedling were found. However, unfortunately, in the largest and in the smallest gaps number of these quadrats was very small in some topographical positions. Despite this fact, results on spatial differences of VHD are shown for these gap types, too, in order to achieve a better understand of the data.

Spread of blackberry was characterized by 'change in cover' values (CCV) which were calculated simply by subtracting the cover values estimated in given sampling years from those assessed in the following sampling years (CCV = C_{t2}-C_{t1}). CCV were determined for each quadrat. Summer abundance of blackberry was used for the analyses since it was higher than the spring cover. CCV were evaluated similarly to the height data of seedlings. Multiple regression analyses were applied to relate height of sessile oak and hornbeam seedlings to cover of blackberry and to soil moisture as indicated by herbaceous species. The dependent variables were the height of the tallest sessile oak seedlings within the original 1 x 1 m quadrats (!) and that of the tallest hornbeam seedlings. Blackberry cover and abundance of soil moisture indicators were used as independent variables. The spring and the summer cover values were combined. That is, each species was characterized by the higher value. The reason for not studying light indication of the vegetation was the fact that the amount of light reaching the herbaceous layer is strongly influenced by the growth and closure of the regeneration. Thus, light intensity which seedlings and saplings are exposed to may greatly differ from that which can be utilized by the herbs. Colinearity between the independent variables was studied by variation inflation factors (VIF; 26). If the independent variables are uncorrelated, the largest VIF is close to 1. If the largest VIF is higher than 100, the computation becomes inaccurate (26).

Regression analyses were done for the fourth year of the regeneration since it was supposed that spatial differences in height of seedlings and in cover of various species increase with time. Altogether six regression analyses were performed according to the two tree species and three gap sizes. Observation numbers equalled the numbers of those quadrats in which at least one sessile oak or hornbeam seedling could be found. Residuals were analyzed in order to check the goodness of fit and to detect the outliers (26). Outliers were determined by the method of Hoaglin and Welsch (28) which applies the leverage coefficients and the standardized residuals simultaneously. If it was necessary, the computation was repeated after omitting the outliers. By the multiple regression analyses, coefficients of multiple determination (R^2) and standard partial regression coefficients were calculated.

The square roots of the former ones are the multiple correlation coefficients. The significance of the coefficients of multiple determination was checked by a randomization procedure during which the relationship between the dependent and the independent variables was randomly permuted but the relationships between the independent variables remained unchanged. This type of tests gives good results according to Manly (29).

Resampling number was 1000 in every test. The standard partial regression coefficients showed to what extent each independent variable explained the variance of seedling height. Species names follow Flora Europaea (30). The applied software was the Biomstat 3.3 (31) package.

Table 2

Number of seedlings measured during the sampling period. Abbreviations are explained at Table 1.

Species	Method	Year	S	C	N	E	W	Total
Q. pet.	G15	2004	10	15	7	32	6	70
		2005	20	11	5	35	27	98
		2006	46	62	42	74	56	280
		2008	46	68	42	74	56	286
	G30	2004	57	100	86	50	78	371
		2005	92	91	67	66	52	368
		2006	119	131	133	150	81	614
		2008	119	131	133	150	81	614
	G45	2004	6	193	20	109	72	400
		2005	23	134	35	84	75	351
		2006	49	133	58	184	81	505
		2008	49	113	58	184	81	485
Car. bet.	G15	2004	28	115	89	39	109	380
		2005	314	337	188	235	178	1252
		2006	453	443	221	257	231	1605
		2008	234	184	108	146	107	779
	G30	2004	208	338	132	76	255	1009
		2005	861	1078	592	1139	583	4253
		2006	892	606	566	744	505	3313
		2008	316	423	289	472	263	1763
	G45	2004	22	205	129	100	61	517
		2005	71	309	357	180	184	1101
		2006	249	324	266	304	232	1375
		2008	114	151	131	128	131	655

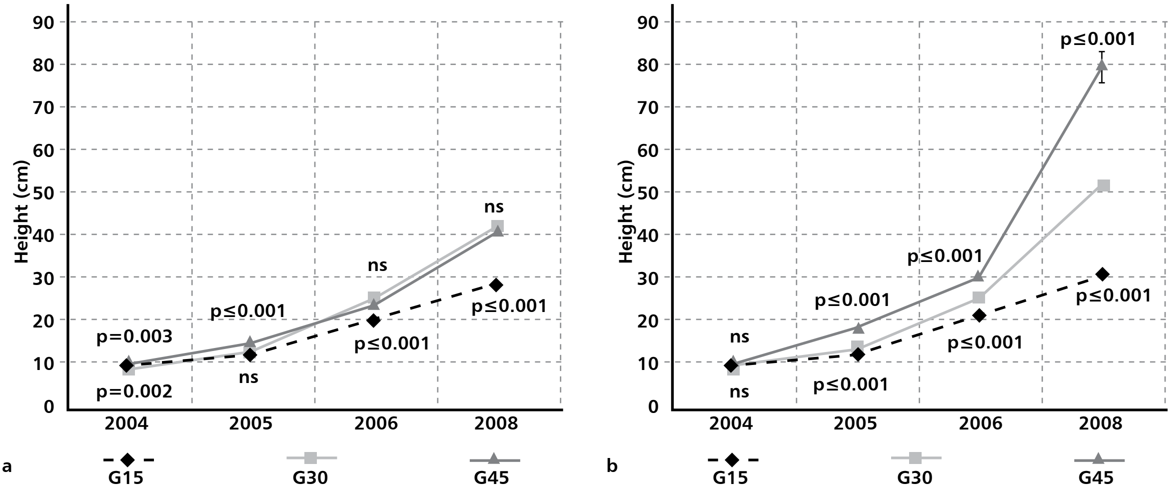


Figure 2
Height of sessile oak (a) and hornbeam (b) seedlings before (2004) and after cutting gaps of various sizes. Medium-size gaps were compared to the largest and to the smallest ones. Significance levels are given at the markers of the latter gaps. Standard errors are shown by whiskers. Where they are not indicated, standard errors were smaller than the size of the markers. Observation numbers are included in Table 2. The legend is shown on Figure 2a. ns – not significant; other abbreviations are explained at Table 1.

RESULTS

Although differences between gap sizes in height of sessile oak seedlings were very small (< 0.5 cm) before starting the regeneration, they were significant (Figure 2, Table 2). However, from 2006 to 2008, differences between G30 and G45 were insignificant. Oak seedling development was the most slowly in the smallest gaps. Intensity of hornbeam seedling growth increased with the size of the gaps. During the first four years of the regeneration, hornbeam grew over sessile oak to the lowest extent in G15, whereas at $p \leq 0.05$, G30 and G45 did not differ significantly in this aspect ($p = 0.07$; Figure 3, Table 3).
Speed of blackberry proliferation was similar in the smaller (G15 and G30) gaps while it was significantly higher in G45 than in G30 (Figure 4, Table 4).
Height of both sessile oak and hornbeam seedlings was spatially homogeneous at the initial stage (Figure 5). In the case of hornbeam, there was only one significant difference at this time but in absolute value, even it was rather small (< 1cm; Table 5).

Table 3
Number of those 1 x 1 m quadrats in which both sessile oak and hornbeam occurred in the fourth year of the regeneration (2008). Abbreviations are given at Table 1 and 2.

Method	S	C	N	E	W	Total
G15	9	21	6	9	11	56
G30	22	35	26	20	22	125
G45	10	30	8	23	18	89

No considerable spatial differences evolved in height of sessile oak seedlings of G15 during the first four years of the regeneration. Although some positions differed significantly in some years, by the autumn of fourth year, differences between them had become insignificant. In the larger gaps, development of

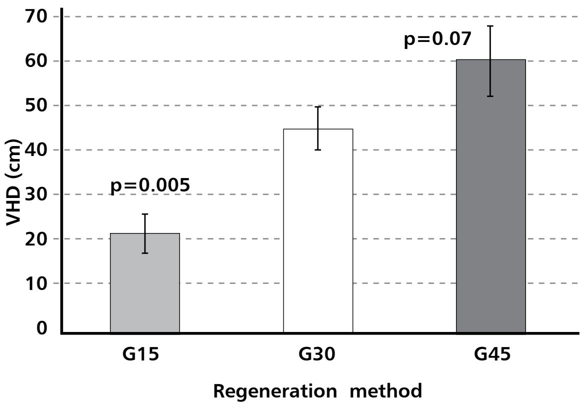


Figure 3
Differences between height of the tallest hornbeam and that of the tallest sessile oak seedlings (VHD) in the fourth year of the regeneration (2008). Height of the tallest sessile oak seedling was subtracted from that of the tallest hornbeam seedling (or sapling) by 1 x 1 m quadrats. Medium-size gaps were compared to the largest and to the smallest ones. Significance levels are given at the bars of the latter gaps. Standard errors are shown by whiskers. Observation numbers are included in Table 3. Abbreviations are given at Table 1.

Table 4
*Spread of blackberry following cutting gaps of various sizes. The cells contain average values (in %) of change in cover during a given period. Standard errors are shown in brackets. By the significance tests, medium-size gaps were compared to the largest and to the smallest ones. Significance levels are indicated by asterisks in the upper index of values of the latter gaps. Observation numbers equal the numbers of the 1 x 1 m quadrats (Table 1). *** - p ≤ 0.001. Abbreviations are given at Table 1.*

Period	G15	G30	G45
2004-5	0.38(0.17)	0.39(0.18)	3.03(0.79)***
2005-6	0.90(0.35)	1.33(0.55)	6.38(1.15)***
2006-8	4.30(0.82)	6.01(1.21)	19.87(1.94)***

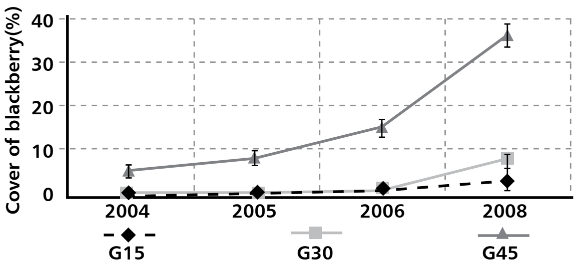


Figure 4
Spread of blackberry following cutting gaps of various sizes. For results of significance tests, see Table 4. Explanations are given at Table 1 and Figure 2.

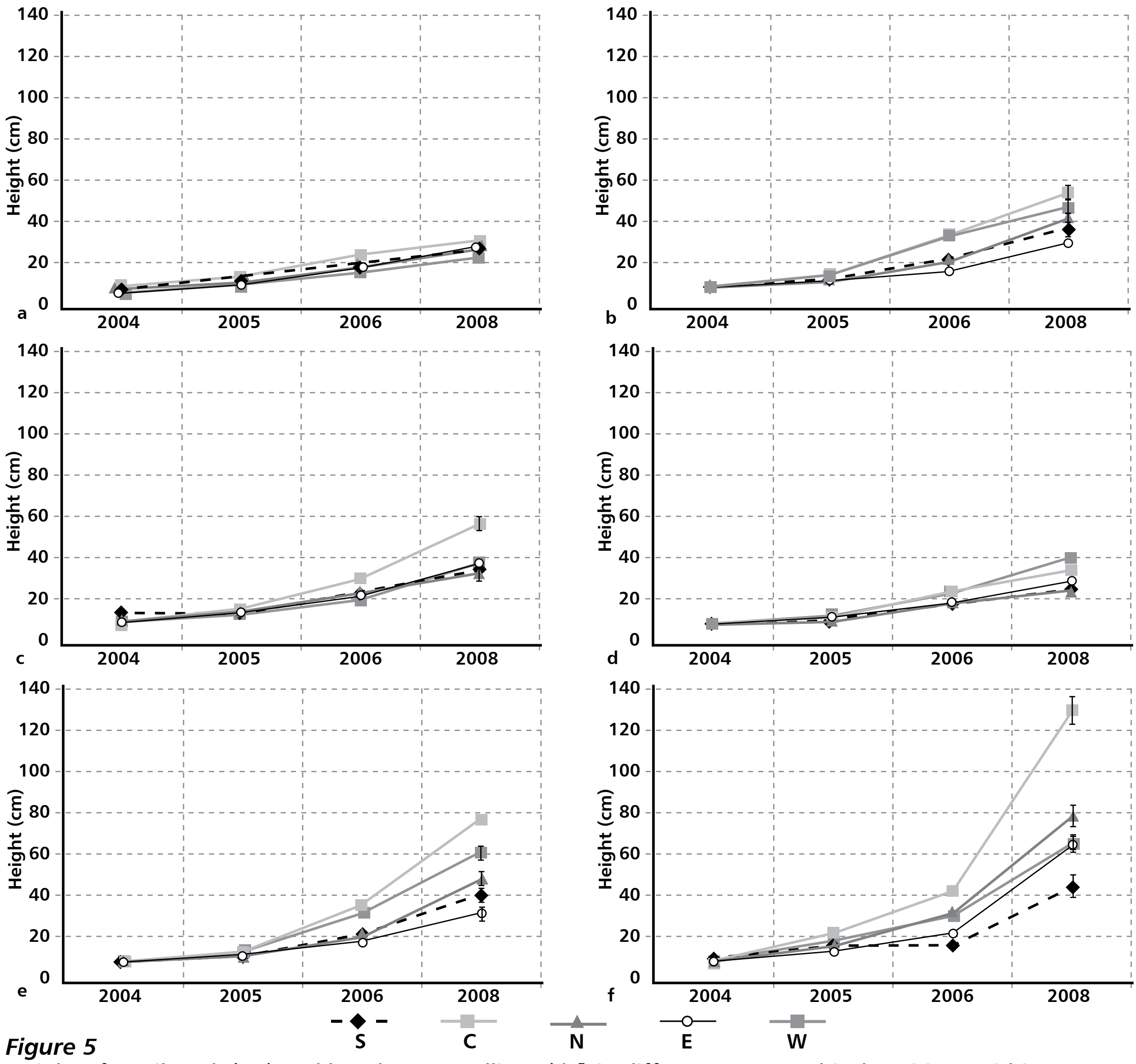


Figure 5
Height of sessile oak (a-c) and hornbeam seedlings (d-f) in different topographical positions within gaps of 15 m (a, d), 30 m (b, e) and 45 m (c, f) in diameter before (2004) and after gap cutting. Observation numbers are included in Table 2. Results of significance tests are described in Table 5. The legend is shown on Figure 5a. Other explanations are given at Table 1 and Figure 2.

Table 5
Results of significance tests carried out on height data of sessile oak and hornbeam seedlings (spatial analyses). The cells contain the numbers of those years of the regeneration period in which the corresponding two locations were significantly different at p ≤ 0.05 (i.e. 0 – 2004; 1 – 2005; 2 – 2006; 4 – 2008; none – the two locations were not significantly different in any of the sampling years). The table consists of six half-matrices. Three of them refer to sessile oak (upper half-matrices) and the other three refer to hornbeam (lower half-matrices). To make the results clearer, the backgrounds of the former matrices are shaded. Abbreviations are given at Table 1 and Figure 2.

Method	Location	S	C	N	E	W
G15	S	-	none	none	none	none
	C	2,4	-	2	1,2	none
	N	1	1,2,4	-	none	none
	E	1	1,2	none	-	1,2
	W	2,4	none	1,2,4	1,2,4	-
G30	S	-	1,2,4	1	1,2,4	1,2
	C	1,2,4	-	2,4	1,2,4	none
	N	ns	1,2,4	-	2,4	2
	E	2,4	1,2,4	1,2,4	-	1,2,4
	W	1,2,4	0,4	2,4	1,2,4	-
G45	S	-	1,2,4	none	none	none
	C	1,2,4	-	4	2,4	2,4
	N	2,4	1,2,4	-	none	none
	E	2,4	1,2,4	1,2	-	none
	W	2,4	2,4	none	1,2	-

sessile oak seedlings was the fastest in the centres. Independently from the gap size, hornbeam seedlings grew at the highest speed in the middle of the gaps. Furthermore, development was intensive also in the west parts of G15 and G30. In G15, the difference between the central and the west parts was not significant at all during the whole sampling period. Hornbeam grew over sessile oak to the lowest extent in the north parts of the gaps (Figure 6). However, VHD differed significantly only in G30.

Blackberry cover increased mostly in the west parts of the gaps, regardless the size of the gaps (Figure 7, Table 6). This result proves that the phenomenon that spread of blackberry was the fastest in G45 is

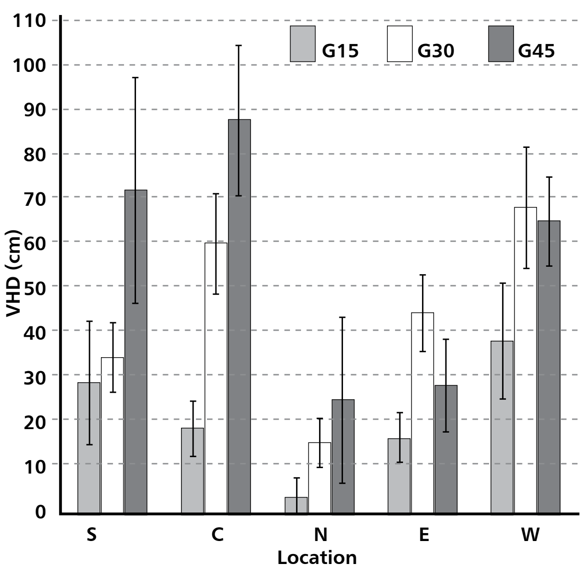
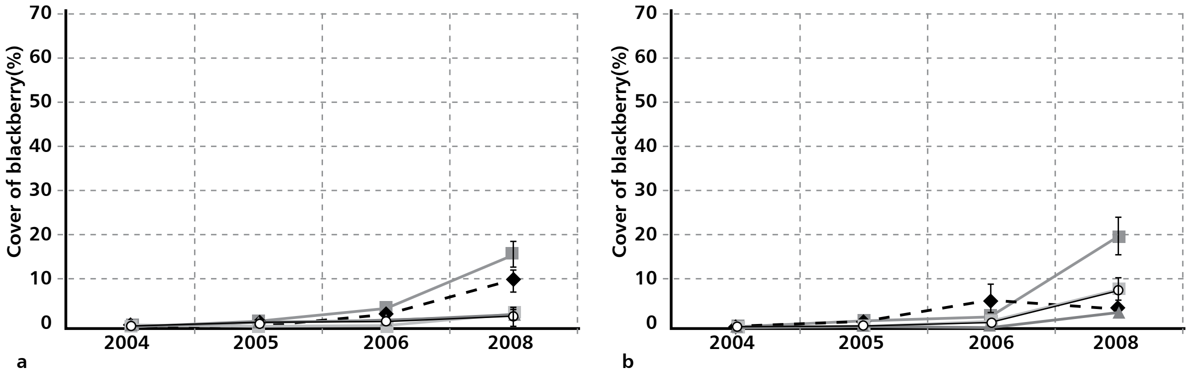


Figure 6
Differences between height of the tallest hornbeam and that of the tallest sessile oak seedlings (VHD) in different locations of gaps of various sizes in the fourth year of the regeneration (2008). Height of the tallest sessile oak seedling was subtracted from that of the tallest hornbeam seedling (or sapling) by 1 x 1 m quadrats. Observation numbers are included in Table 3. VHD was significantly smaller in the northern part than in all other parts but the southern position in G30. The other comparisons did not give any significant results. Further explanations are given at Table 1 and Figure 3.



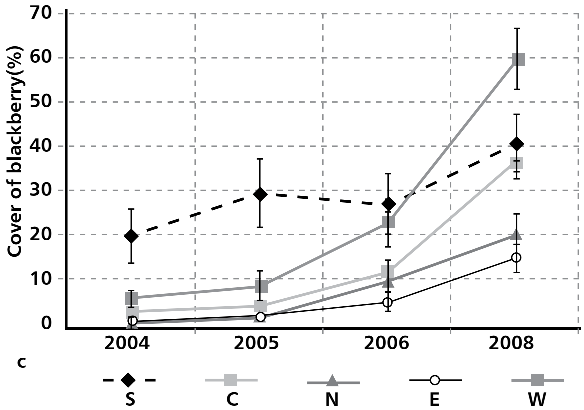


Figure 7
Spread of blackberry in gaps of 15 m (a), 30 m (b) and 45 m (c) in diameter. For results of significance tests, see Table 6. The legend is shown on Figure 7a. Explanations are given at Table 1 and Figure 2.

not only a consequence of the higher initial cover in these gaps. The higher abundance before starting the regeneration was primarily due to blackberry dominance in the south parts where, in turn, proliferation was less intensive than in the west positions.
The relations between the dependent and independent variables were significant in most cases but low (Table 7). The only exception is the analysis of height of sessile oak seedlings in the largest gaps the result of which was not significant. Height of the tallest sessile oak and hornbeam seedlings was related mainly to the cover of soil moisture indicator herbs (Table 8). Blackberry abundance did not influence considerably the development of the seedlings.

Discussion

The results show that even in the smallest gaps, soil moisture and light conditions were sufficient for sessile oak seedlings to grow continuously during the first four years of the regeneration, though seedling

Table 6
Spread of blackberry in different locations of gaps of various sizes (spatial analyses). The cells contain average values (in %) of change in cover during a given period. Standard errors are shown in brackets. The significantly different values ($p \leq 0.05$) are marked with different letters in the upper indices. Observation numbers equal the numbers of the 1 x 1 m quadrats (Table 1). Abbreviations are given at Table 1.

Method	Period	S	C	N	E	W
G15	2004-5	0.60(0.32)	0.00(0.00)	1.00(0.74)	0.00(0.00)	0.67(0.66)
	2005-6	1.93(1.21)^{ab}	0.27(0.27)^{a}	-0.47(0.89)^{ab}	0.20(0.20)^{ab}	3.20(1.18)^{b}
	2006-8	8.07(1.89)^{ab}	2.40(1.13)^{bc}	1.13(1.60)^{bc}	0.20(0.35)^{c}	11.60(2.67)^{a}
G30	2004-5	0.50(0.52)	0.42(0.28)	0.10(0.10)	0.00(0.00)	0.93(0.80)
	2005-6	4.73(3.11)	0.77(0.43)	0.17(0.17)	0.20(0.14)	1.33(0.62)
	2006-8	-1.67(2.30)^{b}	7.13(2.40)^{ab}	3.40(1.85)^{b}	2.37(1.13)^{b}	17.70(3.61)^{a}
G45	2004-5	9.53(3.73)^{a}	1.23(0.55)^{b}	2.23(1.13)^{ab}	1.23(0.54)^{ab}	2.73(2.21)^{ab}
	2005-6	-2.30(2.59)^{a}	7.82(2.00)^{b}	7.07(2.36)^{ab}	3.57(1.44)^{ab}	14.30(3.71)^{b}
	2006-8	13.40(3.06)^{b}	24.57(3.89)^{ab}	10.93(3.85)^{b}	9.53(2.90)^{b}	36.20(5.18)^{a}

Table 7
*Results of multiple regression analyses. R^2 – coefficient of multiple determination; R – multiple correlation coefficient; n – number of observations (quadrats where at least one sessile oak or one hornbeam seedling occurred); WB – standard partial regression coefficient of cover of soil moisture indicator herbs; RUB – standard partial regression coefficient of blackberry cover; VIF – the largest variation inflation factor; * - 0.01 ≤ p ≤ 0.05; ** - 0.001 ≤ p ≤ 0.01; *** - p ≤ 0.001. Further explanations are given at Table 1.*

Method	Regression	*Q. pet.*	*Car. bet.*
G15	R^2	0.308***	0.227***
	R	0.555	0.476
	n	67	72
	WB	0.557	0.475
	RUB	0.019	-0.008
	VIF	1.015	1.014
G30	R^2	0.065*	0.112***
	R	0.254	0.334
	n	129	168
	WB	0.255	0.333
	RUB	-0.002	0.009
	VIF	1.014	1.008
G45	R^2	0.023	0.092**
	R	0.15	0.301
	n	95	144
	WB	0.145	0.281
	RUB	-0.008	-0.056
	VIF	1.107	1.11

development was slower than that in the larger gaps. However, it can be supposed that due to the strong competition of hornbeam, sessile oak could not utilize the advantages caused by the larger size of the gaps (i.e., stronger illumination, lower canopy precipitation interception and lower root concurrence of the parent stand) if increasing gap size over one tree length. Although differences between the heights of the tallest seedlings did not differ significantly between G30 and G45, hornbeam grew faster in the latter case if considering data of all seedlings. Thus, shading effect of hornbeam was presumably higher in G45. Competition pressure of hornbeam was the lowest in G15.

The spatial analyses on seedling development suggest that even in the smallest gaps, differences in site conditions between the topographical positions influenced the regeneration processes. The reason for the fact that it could be recognized only in the case of hornbeam may be partly the slower development of sessile oak. Thus, more time would have been needed for evolution of significant spatial differences in height of oak seedlings. Another reason can be that variability of light conditions was smaller within G15 than those within the larger gaps (4).

In the centres of the gaps, soil moisture became probably higher compared to the other parts (5, 6) and this facilitated height growth of both tree species.

Table 8
Soil moisture indicator herbaceous species occurred in the gaps. No. of quadrats – number of those 1 x 1 m quadrats in which the given species occurred.

Species	No. of quadrats
Cardamine impatiens **L.**	**278**
Urtica dioica **L.**	**230**
Solidago gigantea Aiton	**193**
Galium aparine **L.**	**180**
Festuca gigantea **(L.) Vill.**	**141**
Carex divulsa Stokes	**89**
Erigeron annuus **(L.) Pers.**	**81**
Lapsana communis **L.**	**63**
Athyrium filix-femina **(L.) Roth**	**58**
Stachys sylvatica **L.**	**38**
Juncus effusus **L.**	**12**
Cucubalus baccifer **L.**	**6**
Polygonum minus Hudson	**5**
Dryopteris carthusiana **(Vill.) H.P. Fuchs**	**4**
Epilobium obscurum Schreber	**4**
Polygonum hydropiper **L.**	**4**
Echinochloa crus-galli **(L.) Beauv.**	**2**
Eupatorium cannabinum **L.**	**2**
Juncus tenuis Willd.	**2**
Leontodon autumnalis **L.**	**2**
Rumex sanguineus **L.**	**2**
Solidago canadensis **L.**	**2**
Poa trivialis **L.**	**1**
Polygonum lapathifolium **L.**	**1**
Epilobium hirsutum **L.**	**1**
Lycopus europaeus **L.**	**1**

Influence of canopy precipitation interception and root concurrence of the parent stand is the lowest in the middle of the gaps. Considering hornbeam, this hypothesis is further supported by the intensive development in the west parts because soil moisture content of these parts is higher than that of the east or north positions (5). In the south parts, low light intensity could decrease growth of hornbeam. However, it is not clear why west parts of G45 are much less favourable for hornbeam development than the centres of these gaps. It was reported in earlier studies that fine-scale spatial pattern of soil attributes could modify the effects of differential shading by the parent stand on soil moisture in larger gaps more than in smaller ones (6).

The relatively good properties of west parts of G15 and G45 cannot be recognized in the case of sessile oak, presumably because of the above-mentioned reasons (slower growth rate of oak, competition pressure of hornbeam, less variable site conditions in the smallest gaps and fine-scale pattern of soil attributes in the largest gaps). However, in G30, the central and the west parts did not differ significantly in any of the sampling years, though differences between the west and some other parts were also insignificant in the fourth year of the regeneration. This result implies that for sessile oak growth, site conditions of the west parts were of transitional character between the centres and the other peripheral positions. The key role of soil moisture content in regeneration is confirmed by the results of the multiple regression analyses, too. The reason for the weak relationship is not clear but suggests that many – presumably sometimes stochastic – factors may influence regeneration processes simultaneously. Another explanation for the low values of the coefficients can be that light and soil moisture act synergistically therefore examining only one of these factors may be not sufficient enough to explain the spatial variance occurred in seedling development. In G45, the high hornbeam concurrence could further decrease the relationship between soil moisture and the height of the tallest sessile oak seedlings. Dryness and high illumination of the north parts of the gaps increased the competition ability of sessile oak relative to that of hornbeam in gaps of one tree height in diameter. Hornbeam is a mesophilous species contrarily to sessile oak that is more dry-tolerant and light-demander. Thus, differences between heights of the tallest sessile oak and hornbeam seedlings were the smallest here. The insignificant differences in VHD between various locations in the smallest and in the largest gaps may be the consequences partly of the low observation numbers and partly of the conservative character of the significance tests (see the description of the applied methods). Presumably, the latter is the

explanation of the insignificance of the quite large difference between the south and north parts of G30, too. Despite the insignificant results, the trend that VHD are the smallest in the north parts can be recognized also in G15 and in G45. The data suggest that although optimal conditions for both sessile oak and hornbeam occurred at the same positions inside the gaps, the outcome of their competition varied along the environmental (soil moisture and light) gradient. Schütz (11) reported that hornbeam development was the most intensive at the edge of the gap studied. The differences between results of Schütz (11) and those of the present experiment are consequences of the considerable differences of site conditions of the study stands. The annual precipitation that the beech forest studied by Schütz (11) received was 1190 mm, contrarily to the 700 mm that can be utilized by the sessile oak-hornbeam stand of the present experiment. Thus, it can be assumed that soil moisture content played a more important role in determining hornbeam growth in the latter case. Similarly to hornbeam, blackberry was also favoured by the increasing gap size due to the modified site conditions. For spread of blackberry, both of the strongly illuminated (north) and the relatively dry (east) locations were more or less unfavourable. Regardless the size of the gaps, the west parts seem to be the most optimal for proliferation, whereas in G30 and G45, the central location is of a transitional character between the west and the other peripheral parts. The results also show that in the larger gaps, shadiness of the south parts inhibited blackberry growth, too. The reason for the phenomenon that in G15, blackberry cover increased in the south positions more than in the centres is not clear. In contrast to the initial hypothesis, blackberry cover was not negatively related to sessile oak seedling development. However, this observation is in accordance with studies of Evans (23) and Harmer et al. (21) which showed that blackberry did not definitely decrease the growth of pedunculate oak seedlings. Instead, seedling establishment and survival are inhibited mainly by high blackberry abundance (21, 22). At the same time, in another sessile oak-hornbeam forest, Tobisch (19) found that spread of blackberry impeded regeneration of sessile oak in gaps of one tree height in diameter during the first five years of the regeneration. Tobisch (19) concluded that intensive weed control operations are needed to regenerate sessile oak successfully in the applied gap type. Again, the contradictions between the present experiment and the study of Tobisch (19) can be explained by the differences of the site conditions of the forests examined. The soil of the stand investigated by Tobisch (19) was of a transitional type between ranker and some brown forest soil (i.e., clay migration was noticeable but to a lower extent than in the case of brown forest soils). Furthermore, the mean annual precipitation was 790 mm and seepage water occurred, too. Due to these factors, blackberry proliferation was much more intensive.

Summarizing the results it can be concluded that under the studied site conditions, concurrence of the associated tree species could be reduced during the first years of the regeneration period if cutting as small gaps as 0.5 tree height in diameter. According to former experiments (32, 33), during the period when competition pressure is relatively low, sessile oak seedlings strengthen. However, if cutting larger gaps, concurrence of the associated tree species increases suddenly and sessile oak seedlings do not have time to prepare for the intense competition. If seedlings have time to strengthen, their competition ability increases due to two reasons. They will have strong roots which will facilitate height growth intensity (32, 33) after enlarging the gaps. Furthermore, seedlings with stronger root systems are more biotic and abiotic damage-resistant (34).

Another advantage of the smaller gaps is that their area is more easily reached by sessile oak acorns from trees surrounding the gaps than the area of the larger (e.g. at least one tree height in diameter) gaps because of the low dispersion ability of the heavy oak acorns (19, 22). It is very important since even if the gaps are cut above dense sessile oak regeneration, seedling number may decrease considerably after gap creation due to the disturbance effects caused by felling and harvesting, as well as, by microclimatic changes (19). Thus, regeneration of sessile oak can be made more secure if starting it with cutting small (e.g. half tree height in diameter) gaps and if these gaps are enlarged then gradually according to seedling development (see also 18). The present experiment shows that ecological characteristics of different locations of the circular gaps are markedly different and this influences height growth of sessile oak and hornbeam seedlings. A practical regeneration method may be choosing a position which seems to be suitable for silvicultural aims and then lengthening the gap in order to increase the proportion of the chosen part. For example, in the northern parts of the gaps, both competition of hornbeam and blackberry proliferation were low. Thus, the northern zone may be chosen and the gaps may be lengthened in east-west direction. In addition to decrease the initial size of the gaps, cutting elliptical gaps may be also an effective close-to-nature regeneration technique. However, it should be taken into consideration that if increasing the northern part of the gaps, more stems of sessile oak trees may produce epicormic branches since trees at the north edge of the gaps are exposed to direct sunshine for the longest time (19). Moreover, ecological characteristics of the elliptical gaps cannot be derived directly from those of circular ones because shading effect or root concurrence of the parent stand may prevail differently. Studies on dynamics of elliptical gaps would be very useful either from scientific or from silvicultural point of view.

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