REGENERATION AND SAPLING GROWTH OF EUROPEAN HORNBEAM AT ITS NORTHERN LIMIT IN LATVIA

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Abstract
The regeneration of European hornbeam (*Carpinus betulus* L.) has been assessed in the National Gene Reserve Forest near Lukne in the south-western part of Latvia, which is the northernmost point of hornbeam distribution in Europe. In the studied stand, six sampling plots and four transects were established to assess stand structure and the effect of irradiation parameters on stand regeneration. Successful regeneration of hornbeam was shown by its presence in all height and diameter classes. Nevertheless, in the smallest height and diameter classes, an increased abundance of other shade tolerant species (maple (*Acer platanoides* L.) and lime (*Tilia cordata* Mill.) was observed. Norway spruce (*Picea abies* Karst.) mainly formed a scattered second forest floor and, apparently, competed with hornbeam. Light parameters, particularly, the diffuse radiation, had a significant effect (p=0.05) on the distribution and abundance of hornbeam understory. The threshold values of irradiation parameters for hornbeam were notably higher compared to other species. The number and height of hornbeam saplings correlated tightly with the amount of available light. Nevertheless, under sufficient light conditions hornbeam showed good vitality, thus suggesting suitability of growing conditions.
Key words: *Carpinus betulus*, light, saplings, understory, stand structure.

Introduction

Climate is one of the main factors that determine the distribution of species and ecosystems (Maiorano et al., 2013). Under changing climate, shifts in species distribution have been observed (Kullman, 2008) and forecasted (Hickler et al., 2012). In Northern Europe, forest distribution models predict that coniferous forests will migrate northwards and will be partially replaced with deciduous forests (Hickler et al., 2012). Such shift will inevitably cause ecological and economic impact (Hanewinkel et al., 2012), therefore adjustments of forest management, i.e. application of species suitable for future climates and multi-species forestry, might be necessary to maintain stability of forests (Aitken et al., 2008; Thompson et al., 2009). Migration of species is more evident near the borders of species distribution (Kullman, 2008) thus marginal populations are good bioindicators of changes (Harsch et al., 2009).

European hornbeam (*Carpinus betulus* L.), which is common auxiliary forestry species in Central Europe, known for dense and hard wood (Hornbeam …, 2013), in Latvia occurs at its northern boundary (Anderberg and Anderberg, 2013). Considering that northern range of species distribution is usually limited by temperature in the dormant period – spring and by the length of vegetation period (Harsch et al., 2009), warming of climate apparently will improve growing conditions for hornbeam in Latvia. Such improvement of growing conditions and thus competitive ability can be portrayed by successful natural regeneration (Harsch et al., 2009; Szwagrzyk et al., 2012). The aim of this study was to assess the structure and natural regeneration of hornbeam stand in the south-western Latvia. Considering that hornbeam is often found as an understory species, light conditions are crucial for its regeneration (Diekmann, 1994; Modry et al., 2004). Therefore, the subordinate objective was to evaluate the role of irradiation parameters: canopy closure and amount of solar radiation on sapling/seedling density and size.

Material and Methods

The study was carried out in the National Gene Reserve Forest near Lukne in south-western part of Latvia (56°14'40'' N, 21°25'43'' E). The research territory is one of the few hornbeam stands in Latvia, which in total occupy 50 ha of the forest land. According to data from the National Forest Service, the studied hornbeams were up to 145 years old. The relief was a slight slope with southern exposition, the elevation of studied territory ranged from ~ 30 to 35 meters above the see level. Climate is mild, influenced by dominant western winds, which bring cool and moist air masses from the Baltic Sea and the Atlantic. The mean annual temperature is +7.6 °C, February is the coldest and August the warmest month (mean temperatures are -2.0 and +17.6 °C, respectively).

The studied stand was located on dry sites with loamy soils; the forest type was Oxalidosa. It is considered, that European hornbeam has naturally colonised the studied territories since the Atlantic period. However, the area occupied by hornbeam has varied (decreased) during the recent centuries. Since the mid-19th century, the stand has been intensively managed, particularly to release hornbeam from competition with Norway spruce (*Picea abies* Karst.) (Krauklis and Zariņa, 2002).

For the description of stand structure, six stand sampling plots (20 × 20 m) were arbitrarily established in 'typical' parts of stand avoiding ecotones and micro-depressions of relief. Within each stand sampling plot all trees were counted according to five height classes: < 1 m, from 1.01 to 2 m, from 2.01 to 5 m, from 5.01 to 10 m and above 10.01 m. For all trees within stand sampling plots higher than 2 m, the diameter at breast height (DBH) was measured to the nearest cm. Sampling was done in August 2013.

For the assessment of the effect of light conditions on sapling/seedling density and size, four 20 m long transects, crossing groups of hornbeam saplings, were established. Along each transect, ten smaller sampling plots (2 × 2 m) were established. Within each of the sampling plots, the height of all saplings and seedlings was measured with accuracy of 5 cm. At the centre of each sampling plot, the canopy image at 1.3 m height was taken by WinScanopy (Regent Instruments) system (digital camera Nikon Coolpix E8400 equipped with fish-eye lens (fish-eye DSLR 4.9 mm-203)). To capture the canopy image, after the height measurements any understory trees covering camera were bent aside.

The mean frequency of each height and diameter class was determined for all stand sampling plots. The diameter classes used were as follows: < 5 cm, 5 to 10 cm, 11 to 20 cm, 21 to 30 cm and > 30 cm. For each sampling plot established along transects, number, mean height and the total length of saplings/seedlings (mean height × count) of each species was determined. Parameters of irradiation: crown density (gap fraction and openness) and solar radiation (direct, diffuse and total radiation under tree crowns) (Zdors and Donis, 2011) were calculated using WinScanopy2006a software. Whole images (no masks) were used; the vegetation period was considered form April 25 to October 28, standard overcast sky (SOC) model considering 48% fraction of diffuse radiation was applied. The total amount of solar radiation above crowns was estimated as 47.5 mol m^{-2} day^{-1}.

For the assessment of the effect of irradiation parameters on regeneration of hornbeam and other species, the mean values of each parameter were compared between sampling plots according to presence/absence of saplings/seedlings by ANOVA and Tukey HSD test. Data from all transects were used together. Considering that the requirements for available irradiation (light) of seedlings of overstorey species differ (Modry et al., 2004), threshold values of irradiation parameters necessary for the presence of saplings/seedlings were estimated by regression analysis. Logarithmic models were fit to total length of saplings and irradiation parameters. Threshold values of irradiation parameters were estimated according to the model equations. Analysis was conducted for overstorey species present in > 10 sampling plots (hornbeam, maple (*Acer platanoides* L.), lime (*Tilia cordata* Mill.) and ash (*Fraxinus excelsior* L.)), only the data for sampling plots with species present were used. To describe the strength of relationships between parameters of saplings/seedlings (number, mean height and total length) and irradiation, bootstrapped (1000 iterations) Pearson correlation analysis was used. The species present in ≥ 15 sampling plots were analysed; only complete pairs were used. Data analysis was conducted in R (R core team, 2014).

Results and Discussion

For 259 trees, DBH was measured and 1560 understory trees shorter than two meters were accounted (Table 1) in stand sampling plots. The studied stand was mixed and several forest floors were evident as shown by tree heights (Fig. 1). The main canopy species (height > 10 m) were hornbeam, lime and silver birch (*Betula pendula* Roth), while the proportion of spruce (*Picea abies* Karst.) and other species was considerably lower. Spruce was the main species (110 trees per ha) in height class from 2 to 10 thus forming a scattered second floor. Most of the birch trees were in the largest height class. Regarding diameter structure, hornbeam was the most abundant in diameter classes from 10 to 30 cm. Similar density (about 60 trees per ha) of lime, spruce and hornbeam was observed in the second diameter class (from 5 to 10 cm). The thickest of the studied trees were birches, which were mainly in diameter class above 30 cm; only a few trees of other species exceeded DBH of 30 cm. The smallest diameter and height classes (< 5 cm and < 1 m) were mainly formed by maple, lime

Table 1

Number of measured trees (higher that two m), accounted seedlings and the total basal area of sampling plots established for the description of stand

	Sampling plot						
	1	2	3	4	5	6	Total
Measured trees	50	41	35	48	32	53	259
Number of saplings in stand sampling plots	107	146	238	158	788	123	1560
Total number of trees in sampling plot	157	187	273	206	820	176	1819
Basal area of measured trees in stand sampling plots, m^2 ha^{-1}	72	57	67	37	71	53	59

and hornbeam (mean density was ~ 3500, 1200 and 1000 tress per ha, respectively). Other species (grey alder (*Alnus incana* (L.) Moench), aspen (*Populus tremula* L.), ash, silver birch, hazel (*Corylus avellana* L.), oak (*Quercus robur* L.), spruce, alder buckthorn (*Frangula* alnus Mill.), spindle (*Euonymus europaea* L.), rowan (*Sorbus aucuparia* L.) and guelder-rose (*Viburnum opulus* L.)) occurred with considerably lower densities, reaching ~ 340 trees per ha (aspen).

The diversity of diameter and height structure and mixture of species in the studied stand (Fig. 1) suggested that natural processes have been prevailing (Angelstam and Kuuluvainen, 2004), despite management (removal of spruce) during the 20th century (Krauklis and Zariņa, 2002). Continuous regeneration of hornbeam was portrayed by its presence in all height and diameter classes (Fig. 1); however, its abundance in diameter class > 30 cm was low, as expected for understory species (Hornbeam…, 2013). Since the last management events, spruce, which has been considered the main competitor of hornbeam in the studied region (Kiršteins and Eihe, 1933), has been re-establishing itself in the studied stand forming scattered second forest floor or even reaching the canopy (Fig. 1). Apparently, such re-establishment of spruce has burdened regeneration of other species including hornbeam as suggested by inverse relationship of abundance of these species in the height classes from 2 to 10 m. Lime, which is considered a late successional species (Pigott, 1991), was the second most abundant species in the height class > 10 m, and it was present in height classes from 2 to 10 m (Fig. 1), suggesting that the stand has not suffered an intensive large-scale disturbance. Birch,

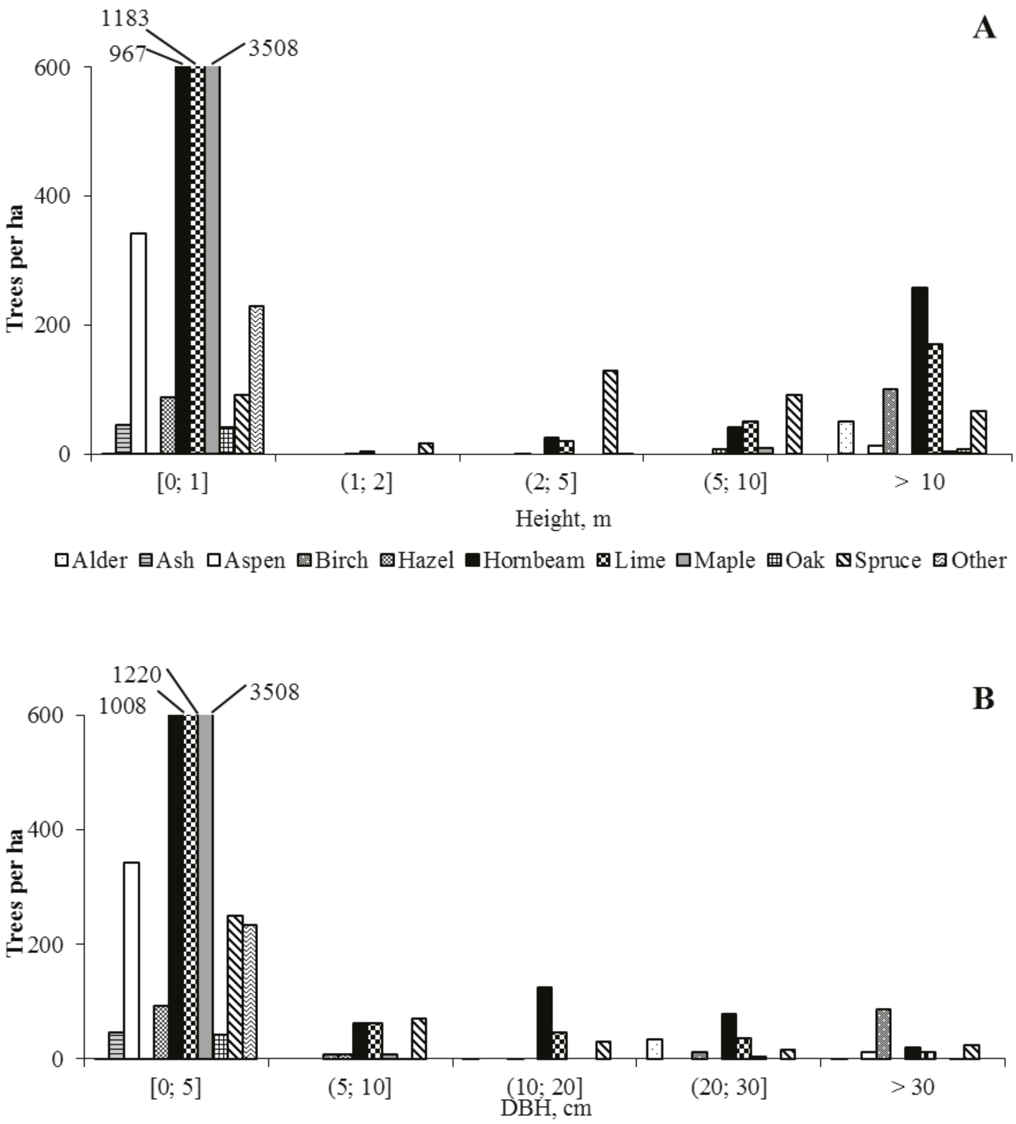

Figure 1. Distribution of studied trees according to height (A) and diameter at breast height (DBH) (B) in stand sampling plots. ‘Other’ corresponds to alder buckthorn, spindle, rowan and guelder-rose.

Table 2

Statistics of the datasets: number, height and total length of saplings and parameters of solar radiation, used for the evaluation of the effect of irradiation parameters on stand regeneration. Occurrence shows the number of sampling plots where species was present (in total 40 sampling plots were established)

	Min	Max	Mean	Median	St. dev.	Number of saplings/ seedlings	Occurrence
Sapling count							
Hornbeam	0	25	9.18	9	7.30	367	35
Hazel	0	4	0.25	0	0.71	10	7
Maple	0	2	0.38	0	0.67	15	11
Ash	0	5	0.88	0	1.30	35	17
Spruce	0	1	0.13	0	0.33	5	5
Oak	0	3	0.20	0	0.65	8	4
Lime	0	8	1.03	0	1.64	41	17
Other	0	4	0.25	0	0.78	23	15
Sapling height, cm							
Hornbeam	5	133	30	20	29		
Hazel	10	410	80	25	147		
Maple	5	120	31	20	33		
Ash	10	41	23	20	9		
Spruce	20	170	76	50	63		
Oak	10	80	35	25	32		
Lime	5	340	51	13	83		
Other	23	105	61	50	36		
Total length of sapling in sampling plot, cm							
Hornbeam	0	1165	277	153	305		
Hazel	0	410	18	0	73		
Maple	0	120	10	0	23		
Ash	0	205	22	0	43		
Spruce	0	170	10	0	32		
Oak	0	160	8	0	30		
Lime	0	470	52	0	123		
Other	0	210	13	0	40		
All species	0	1275	421	363	361		
Irradiation parameters							
Gap fraction, %	1.85	14.20	5.22	4.24	3.03		
Openness, %	2.15	15.21	5.93	4.68	3.39		
Direct radiation, mol $m^{-2}day^{-1}$	0.72	8.17	3.10	2.48	1.80		
Diffuse radiation, mol $m^{-2}day^{-1}$	0.51	3.28	1.49	1.17	0.87		
Total radiation, mol $m^{-2}day^{-1}$	1.43	11.18	4.60	4.19	2.50		

which is considered to be an indicator of disturbance (Angelstam and Kuuluvainen, 2004), was mainly present in the canopy (height > 10 m) and was thick (mean DBH ~ 38 cm) (Fig. 1), suggesting that the studied stand was locally disturbed some time ago, likely by the management activities (Krauklis and Zariņa, 2002).

In the sampling plots established along transects, height of 504 understory trees of 12 species was measured (including 367 hornbeam) (Table 2). The number of species per plot varied from one to four. The presence of species varied from 35 to 4 sampling plots for hornbeam and oak, respectively. The maximum number of individuals per plot was 25. The mean height of samplings/seedlings ranged from ~ 22 to ~80 cm for ash and hazel, respectively. The absolute height of hornbeam ranged from 5 to 550 cm; however, the mean height of all measured hornbeam was ~30 cm. Total length of all measured individuals reached 1275 cm per plot with mean value of 421 cm per plot.

The smallest height and diameter classes were formed by deciduous species (Fig. 1), whose seedlings/ samplings are shade tolerant (Diekmann, 1994), suggesting that canopy in the studied plots has not been notably disturbed during the recent years. Maple was the dominant species, but lime and hornbeam were also abundant (Fig. 1) suggesting that the

Table 3

Significance of difference (p-values) of mean values of irradiation parameters between sampling plots with and without saplings. Differences with p-value <0.05 are in bold

Species	Gap fraction, %	Openness, %	Direct radiation, mol m^{-2} day^{-1}	Diffuse radiation, mol m^{-2} day^{-1}	Total radiation, mol m^{-2} day^{-1}
Hornbeam	**0.02**	**0.01**	0.05	**0.01**	**0.02**
Hazel	0.36	0.38	1.00	0.47	0.8
Maple	0.43	0.42	0.69	0.49	0.6
Ash	0.58	0.57	0.05	0.54	0.11
Spruce	0.78	0.87	0.78	0.8	0.9
Oak	0.49	0.45	0.12	0.37	0.15
Lime	0.36	0.39	0.35	0.6	0.39
Rowan	**0.04**	0.06	0.88	0.15	0.55

Table 4

Estimated threshold values of irradiation parameter for the presence of hornbeam, maple, ash and lime saplings/seedlings and their coefficients of variation. Calculations are based on the total length of saplings within a sampling plot

Species	Gap fraction, %	Openness, %	Direct radiation, mol m^{-2} day^{-1}	Diffuse radiation, mol m^{-2} day^{-1}	Total radiation, mol m^{-2} day^{-1}	df
Hornbeam	1.64	1.77	0.48	0.54	1.36	34
Maple	0.58	0.67	0.55	0.15	0.87	10
Ash	0.96	0.75	0.42	0.49	0.96	16
Lime	0.95	1.05	0.62	0.24	1.01	16
Variation	43%	47%	17%	53%	20%	

studied stand tends to regenerate with broadleaved species. Such regeneration of broadleaves apparently might be related to a disturbed ground cover (Kobayashi and Kamitani, 2000). The abundance of maple seedlings might be explained by higher shade that might provide advantage for maple also in competition with other saplings. However, maple was absent in height classes from 1 to 5 m, suggesting that further development of saplings has been insufficient. Similar density of lime, which occurs in mid-part of its distribution area (Pigott, 1991), and marginal hornbeam suggests that present climatic conditions are suitable for early development of both species. Low abundance of spruce in height classes below 2 m (Fig. 1, A), suggested that its regeneration has decreased during the recent decades (Niklasson, 2002), that might be related to changes of climate (Hickler et al., 2012).

The canopy was mainly closed as from 3 to 23% (mean value 10%) of the amount of total radiation was able to penetrate the crowns. Irradiation parameters varied greatly among sampling plots, suggesting contrasting light conditions (Table 2). Presence of hornbeam in sampling plots was significantly ($p = 0.05$) affected by availability of light as the irradiation parameters were significantly ($p = 0.05$) lower in plots where the species was absent (Table 3). However, no statistically significant ($p = 0.05$) differences in irradiation parameters were found between sampling plots grouped according to presence/absence of other species, except rowan (gap fraction). Although differences were statistically non-significant ($p = 0.05$), presence of ash tended to be positively affected by direct radiation (mean values were 3.75 and 2.63 mol $m^{-2}day^{-1}$ sampling plots where ash was present and absent, respectively).

The observed threshold values of irradiation parameters necessary for presence of saplings/seedlings were similar for the studied species - hornbeam, maple, ash and lime (not shown) and in most cases were the minimal values of the dataset (Table 2). The estimated threshold values (Table 4) reached about 45 to 83% of the observed for maple and hornbeam, respectively. Such differences were likely caused by the uneven sample size. The estimated threshold values of irradiation parameters differed notably among the studied species and these differences were more expressed for openness and amount of diffuse radiation (highest coefficients of variation). Threshold values of direct and total radiation showed the smallest variability among the species. The lowest threshold values of irradiation parameters, except direct solar radiation, were estimated for maple and the highest values for hornbeam. Lime and ash appeared to be the most sensitive and robust species against the amount of direct solar radiation, respectively.

Table 5

Pearson correlation coefficients calculated between count, mean height and the total length of saplings and irradiation parameters

Species	Gap fraction	Openness	Direct radiation	Diffuse radiation	Total radiation	df
Count						
Hornbeam	0.45*	0.46*	0.41*	0.47*	0.47*	35
Ash	0.05	0.10	0.01	0.26	0.09	17
Lime	-0.13	-0.14	-0.31	-0.18	-0.28	17
All species	0.53*	0.53*	0.47*	0.55*	0.53*	39
Mean height						
Hornbeam	0.42*	0.45*	0.25	0.54*	0.38	35
Ash	0.64*	0.67*	0.65*	0.79*	0.71*	17
Lime	0.08	0.08	0.19	0.05	0.15	17
All species	0.39*	0.41*	0.36	0.47*	0.43*	39
Total length						
Hornbeam	0.48*	0.51*	0.30	0.60*	0.43*	35
Ash	0.28	0.32	0.26	0.49*	0.33	17
Lime	-0.15	-0.15	-0.10	-0.17	-0.13	17
All species	0.54*	0.57*	0.41*	0.65*	0.52*	39

*- correlations significant at p=0.05

Parameters of sapling/seedlings of hornbeam, ash and all understory species together were significantly (p = 0.05) affected by irradiation as shown by correlation analysis; however, no significant correlation (p = 0.05) was observed for lime (Table 5). The significant (p = 0.05) correlation coefficients ranged from to 0.39 to 0.79, suggesting medium tight to tight linkage. According to correlation coefficients, hornbeam and ash showed the highest and the lowest sensitivity to irradiation parameters (mean r was 0.44 and 0.15, respectively). Diffuse radiation apparently had the strongest effect and direct radiation had the weakest effect on the development of understory in the studied stand as suggested by correlation coefficients and their significance (mean r was 0.43 and 0.31, significant (p = 0.05) in four and eight cases, respectively). Number of hornbeam in understory correlated significantly (p = 0.05) with most of the irradiation parameters (the effect of direct radiation on mean height and total length was non-significant). The mean height of ash showed the strongest correlation with irradiation parameters, while the count of ash did not show significant relationship (p = 0.05). Total length of ash correlated significantly (p = 0.05) only with the amount of diffuse radiation.

The distribution of hornbeam saplings within the stand was determined by the availability of light, as shown by the differences of irradiation parameters in plots distinguished by the presence of hornbeam (Table 3). It was also affirmed by the highest requirements for light compared to other tested species (Table 4). The distribution of saplings/seedlings of other species were likely determined by stochastic processes as irradiation parameters generally did not differ in plots distinguished by the presence of species (Table 3) and the estimated threshold values of irradiation parameters (Table 4) were notably lower than the observed minimum (Table 2). Variation of threshold values (Table 4) and correlation analysis (Table 5) suggested that diffuse radiation had the strongest effect on parameters of saplings/seedlings. Considering that canopy in deciduous forests is closed as also observed along transects (mean ~ 5.9%) (Table 2), diffuse radiation has been described as one of the significant light sources for the forest understory (Hutchinson and Matt, 1977). Although the amount of direct radiation was higher compared to diffuse radiation (Table 2), it had a weaker effect on sapling parameters (Table 5). This might be explained by seasonality of the effect as the direct irradiation depends on the time of the year.

When all species were analysed together, light conditions had the strongest effect on the count of individuals, suggesting that light mainly affects germination. However, the effect differed amongst species. Regarding hornbeam, irradiation parameters mainly affected the total length, suggesting that light conditions are crucial for the establishment and early growth of the species. In contrast, no significant relationships were found between parameters of lime understory and irradiation, suggesting that lime can establish and grow under various light conditions and its size is likely related to age. Among the tested parameters of ash, the mean length was affected by irradiation parameters, suggesting that light parameters are crucial for its growth, while germination is apparently limited by other factors.

Conclusions

Successful regeneration of hornbeam was observed in the studied site near Lukne as it has been present in all height and diameter classes. Hornbeam was abundant also in the understory where it formed groups, suggesting that conditions are suitable for its germination and early growth. Nevertheless, competition with other deciduous species has been evident, particularly in the lowest height and diameter classes that might be related to light conditions. Although hornbeam is considered an understory species, the requirements of irradiation of hornbeam saplings were higher compared to native species and spatial distribution, abundance and size of hornbeam saplings/seedlings was affected by light conditions, particularly diffuse radiation. Thus some canopy disturbance and/or management is necessary to facilitate a further development of the species. Hornbeam also might develop in stands with lower crown density.

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