

Response of *Quercus robur* L. seedlings to north-south asymmetry of light within gaps in floodplain forests of Slovenia

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Abstract – To examine *Quercus robur* establishment and growth in low to intermediate light levels, we analysed regeneration in different microsites created by light asymmetry within gaps in two main floodplain forest regions of Slovenia: Dolinsko and Krakovo. Four years after a mast year in 1995, we installed systematic grids of 1×1 m plots in 11 gaps (0.03–0.40 ha) on wet and dry site variants. In 256 plots, seedling species, cover, density, height, height increment, browsing damage, tree architecture, understory vegetation species and cover, and direct and diffuse light were measured. The average seedling density in all gaps was 15/m², but the highest densities were found in gap positions with low diffuse light levels (10–20%). Competing understory vegetation was more abundant in positions with high diffuse light. In gaps on dry site variants a combination of low diffuse and high direct light was favourable for regeneration. The results indicated that *Q. robur* can successfully establish in gaps. Here, both light components were sources of within gap resource heterogeneity, therefore knowledge of light asymmetry can improve regeneration success.

Quercus robur / *Carpinus betulus* / natural regeneration / canopy gaps / north-south asymmetry of light in gaps

Résumé – Réponse des semis de *Quercus robur* L. à l'asymétrie de lumière Nord–Sud dans les trouées des forêts inondables en Slovénie. Pour examiner l'installation et la croissance de *Quercus robur*, sous des niveaux d'éclaircissement faibles à moyens, nous avons analysé la régénération dans différents microsites affectés par l'asymétrie de la lumière dans des trouées en forêts inondables en Slovénie : Dolinsko et Krakovo. Quatre années après une forte glandée en 1995, nous avons installé des placettes d'observation suivant une grille de 1×1 m dans 11 trouées (0.03–0.40 ha) de stations sèches et humides. Les paramètres suivants ont été mesurés sur 256 emplacements : l'espèce des semis, l'abondance relative, la densité, la hauteur, l'accroissement en hauteur, les dommages d'abrutissement, l'architecture des arbres, les espèces du sous-bois, l'éclaircissement direct et diffus. La densité moyenne des semis de toutes les trouées était de 15/m², mais les plus fortes densités ont été trouvées dans les trouées aux expositions caractérisées par des faibles niveaux d'éclaircissement diffus (10–20%). La végétation compétitrice du sous-bois était plus abondante dans les situations à niveau élevé de lumière diffuse. Dans les variantes sèches des trouées, une combinaison de faible niveau de lumière diffuse et de fort éclaircissement direct était favorable à la régénération. Les résultats indiquent que *Quercus robur* peut s'installer avec succès dans les trouées. Ici, les deux composantes de l'éclaircissement ont été sources d'hétérogénéité dans les ressources des trouées, par conséquent la connaissance de l'asymétrie de l'éclaircissement peut améliorer le succès de la régénération.

Quercus robur / *Carpinus betulus* / régénération naturelle / trouées dans la canopée / asymétrie de lumière Nord–Sud dans des trouées

1. INTRODUCTION

Hardwood floodplain forests dominated by pedunculate oak (*Quercus robur* L.) once covered substantial areas of South East (SE) Europe. Later, their area declined significantly due to deforestation for urban and agricultural purposes. In Slovenia, oak floodplain forests make up less than 1.5% (17 275 ha) of the total forest cover. These forests have a restricted and fragmented distribution in Europe, and represent valuable, diverse natural landscape features. Consequently, the management and conservation of these ecosystems has received increased attention. However, declining *Q. robur* populations have posed challenges to traditional oak management. Many factors have contributed to the oak decline, including absence

of flooding, air and water pollution, a lower ground water table, climatic extremes, non-adapted silvicultural practices, and biotic factors, especially insects and fungi [14, 35]. Furthermore, natural regeneration of *Q. robur* can be hindered by sparse seed years, heavy seed predation, powdery mildew, browsing pressure, and competition from dense understory vegetation, making it one of the most difficult tasks of modern silviculture in Central Europe [26, 31, 39].

Many studies have examined large-scale natural regeneration processes within traditional silviculture of pedunculate oak in CE and SE Europe [17, 25]. Natural regeneration is induced under slightly opened canopies of mature trees, which are then successively removed in two to three regeneration fellings, which form the oak shelterwood system. The time interval between the last two is short (2–6 years) in order to improve the height growth of oak [25, 30, 39]. To optimally

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exploit seed years and achieve uniformity of regeneration, which should lead to high commercial quality, whole compartments (up to 40 ha) are typically regenerated in this way. However, there are several disadvantages of the traditional system. It triggers an abrupt change in the local climate, which disrupts nutrient cycling and promotes growth of understory vegetation [22, 30]. Also, it makes it difficult to take advantage of individual trees with exceptional quality. Finally, it is becoming increasingly costly due to the required site preparation, protection against rodents, and control of understory vegetation [25, 39]. It is also very likely that regeneration under the traditional system significantly deviates from regeneration under the natural disturbance regime. While there is evidence of small-scale gap dynamics in the few old-growth remnants left [1, 5, 16], it is likely that flooding also played a role in these ecosystems. For example, in North America both flooding and windthrow have been noted as important disturbance agents in bottomland hardwood forests [4, 15].

The deficiencies of traditional silviculture have promoted research into alternative methods [19, 22, 26, 31]. Natural oak regeneration with permanent canopy cover has been successfully applied in the past within the coppice and standards system [30] and selection felling [25]. Still, there are several disadvantages associated with oak regeneration in small gaps. These include higher browsing pressure, inferior competition of oaks compared to other shade tolerant trees, underutilization of mast years, formation of epicormic branches on gap edge trees, and saplings that have large height/diameter ratios and heliotropic (non-vertical) growth, both of which can lead to lower stability and quality of stands.

Past studies have documented advantages of oak regeneration in smaller patches [22, 28, 30, 38, 40], but there is still relatively little information on the effects of within-gap environmental heterogeneity on *Q. robur* regeneration. For example, spatial variation in understory light levels is an important source of heterogeneity within gaps [8, 27, 36]. Furthermore, the partitioning of light into diffuse and direct components creates additional heterogeneity due to north-south asymmetry of direct light (Fig. 1). This partitioning is ecologically meaningful. The photon flux density is substantially different for each component, and plants are differently equipped to cope with predominantly direct, diffuse, or both components of light [20]. Many other abiotic (e.g. soil and air temperature, humidity, incidence of frost) and biotic factors (e.g. humus quality, crown and root competition, abundance of insects) are directly linked to the distribution of light components [3, 6, 18, 32]. Hence, both light components are useful for describing environmental heterogeneity within gaps [12, 27]. The distribution of diffuse and direct light within gaps can be predicted and described (Fig. 1). Therefore, knowledge of the influence of light components on regeneration patterns could help silviculturists to design optimal gaps in space and time [3, 6, 10, 11, 32]. The purpose of this study was: (1) to examine natural regeneration patterns in two major oak floodplain forests in Slovenia, (2) to evaluate regeneration and understory vegetation competition in low light environments, and (3) to analyse the response of seedlings to north-south asymmetry of light in gaps.

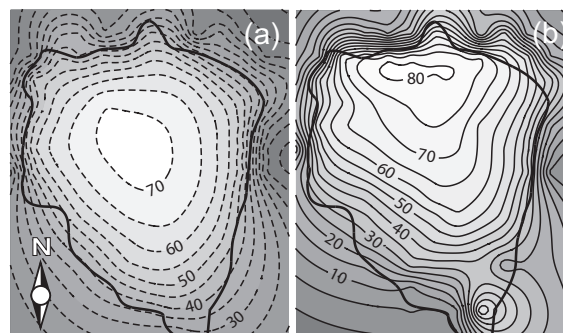


Figure 1. Contour map of solar radiation asymmetry in a forest gap projection (gap border shown with a thick black line) in a silver fir-beech forest in Slovenia (gaps size: 0.23 ha, gap edge tree mean height: 30 m, method: fish-eye [12], 89 sampling points interpolated by Krigging using the linear model for the semivariogram [29]). (a) Distribution of the relative diffuse radiation (DIFF in %) in dotted contour lines. (b) Distribution of the potential relative direct radiation (DIR in %) in solid contour lines. In the temperate region of the northern hemisphere direct light is concentrated in the northern part of gaps.

2. MATERIALS AND METHODS

2.1. Study sites

We conducted this study in Dolinsko and Krakovo, two of the main bottomland, hardwood forest regions in Slovenia. Dolinsko (46.64° N, 16.29° E, elevation 175 m) is located near the Mura and Ledava rivers in southeastern Slovenia. The climate in Dolinsko is continental with an average annual temperature of 9.2 °C and annual precipitation of 815 mm (1961–1990). Rain is abundant in summer, when it falls mostly during heavy showers. The geology is dominated by Pleistocene and Holocene alluvium, comprised of mostly clay and sand at the surface and coarser gravel and conglomerate in deeper layers. Soils are acidic, stagnic gleysols or pseudogleysols of variable depth (20–100 cm). The forest is characterized by a *Quercus roboris-Carpinetum* association s. lat. [33], but local forest structure and composition varies over a moisture gradient. We selected two forest stands; the first was 130 years old (420 m³/ha) and dominated by *Q. robur* (85%), *Carpinus betulus* L. (12%), *Acer campestre* (2%), and *Fraxinus oxycarpa* Willd. (1%) – later referred to as the dry site variant. The second stand (later referred to as the wet site variant) was 90 years old (300 m³/ha) and consisted of *Q. robur* (60%), *C. betulus* (20%), and *F. oxycarpa* (15%). A few *Alnus glutinosa* (L.) Gaertn., *A. campestre*, *Ulmus laevis* Pallas. and *Prunus avium* L. were also present (< 5%).

The Krakovo forest (45.88° N, 15.42° E, elevation 153 m) is located between the Sava and Krka rivers in eastern Slovenia. The climate is subcontinental, with an average annual temperature and precipitation of 10.1 °C and 1210 mm (1961–1990), respectively. The geology consists of Pleistocene alluvium (sands and clay) and soils are primarily stagnic gleysols and pseudogleysols. Vegetation is classified as a *Pseudostellario europaeae-Quercetum roboris* association, and similar to Dolinsko, soil moisture varied over the study region. Selected research stands ranged from 100 year-old private holdings to old-growth remnants over 200 years old, with growing stocks ranging from 400 to 737 m³/ha, respectively. The canopy was dominated by *Q. robur*, which made up 80–85% of the growing stock, followed by

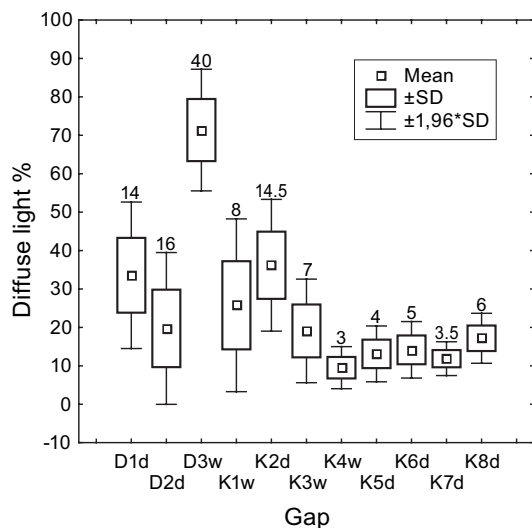


Figure 2. Distribution of relative diffuse light (DIFF) within experimental gaps in Dolinsko (D1d-D3w) and Krakovo (K1w-K8d). Small letters in gap codes indicate site variant (d-dry; w-wet). Numbers above the whiskers represent gap size (100 m²). Gaps D1d and D2d were irregular with some remaining trees in gap interiors.

C. betulus (8–12%). Other species were present, including *A. glutinosa*, *U. laevis*, and *A. campestre* [34]. All species nomenclature follows Martincic et al. [24].

In both study areas, we selected gaps, artificially created during an abundant seed year of *Q. robur* in 1995 or one year after. In Dolinsko, three gaps were formed with the irregular shelterwood system [32] in the spring of 1996. In Krakovo, we selected eight gaps (Fig. 2), which were created from salvage cuts in 1995 and 1996. In both study areas abundant herbaceous vegetation developed 4 years after the gaps were formed. However, this did not become evident until the full development of the understory vegetation, which occurred after we selected gaps for sampling. Therefore, we grouped gaps a posteriori into dry and wet site variants in both forest regions based on diagnostic herbaceous species [1] for the forest communities under research (Braun-Blanquet vegetation school). In Dolinsko, there were two gaps in the dry site variant (D1, D2) and one in the wet site variant (D3; Fig. 2). In Krakovo, five gaps were characterized by a dry site variant (K2, K5, K6, K7, K8), while three were on wet sites (K1, K3, K4; Fig. 2).

2.2. Vegetation and light climate analysis

In the summer of 1999, we established a systematic 5×5 m grid in each gap with 1×1 m plots at the grid intersections in Krakovo. The grid covered entire gaps and the area below the canopy adjacent to the gaps. In Dolinsko, we established a systematic grid (2×2 m) with 25 1×1 m plots at the grid intersections. Here the grid was denser, since only part of the regenerated area in gaps could be excluded from regular silvicultural operations (understory vegetation control and favouring of *Q. robur* seedlings). In all plots understory vegetation cover was scored to the nearest 10% (to the nearest 1% for cover < 10%) for each woody plant species and herbaceous plants separately. All individual seedlings were tallied and the heights of the three tallest *Q. robur* seedlings in each plot were measured to the nearest cm and averaged. *Quercus robur* seedlings were scored as browsed if there

was damage to the terminal shoot or heavy damage to main lateral shoots. In Dolinsko, we also classified *Q. robur* seedling architecture in two classes: (1) monopodial growth with a vertical stem axis and (2) significant stem-inclination and/or a fork with crooked, bowed, or broom-shaped growth [17]. In Krakovo, the annual height increments of the three tallest *Q. robur* seedlings per plot were measured to the nearest 0.5 cm. The measurements were completed in late autumn to account for several growth flushes. In each plot the percentage of diffuse (DIFF) and potential direct light (DIR) were estimated from the start of April until the end of October at 1.3 m above the ground with a horizontoscope [10–12] in Dolinsko and with hemispherical photographs in Krakovo [12]. All photographs were taken beneath a clear sky after sunset or before sunrise with a Nikon F50 camera equipped with a Sigma 8 mm fisheye lens. Commercially processed negatives were scanned using a Nikon LS-30 scanner and analysed using hemIMAGE software [7].

2.3. Statistical analysis

The differences in solar radiation, vegetation and browsing among the forest site variants (dry, wet) within forest regions Dolinsko and Krakovo were assessed with ANOVA, and followed by Fisher's LSD post hoc comparisons. The dry site in Dolinsko was more a transition towards a *Carpinetum* site, therefore the results were evaluated according to four site variants separately. Variables in percentages were transformed with an arcsine square-root equation, while abundance data were square-root transformed to satisfy the requirement for homogeneity of variances, multilinearity, and normality [21]. Microenvironmental estimations of DIFF, DIR and vegetation cover were related to regeneration variables with multiple regression forward stepwise procedures. Since the regeneration response to DIFF and DIR enables locating favourable microsites within gaps [10, 11, 27], we also tested the influence of only DIFF and DIR components on *Q. robur* density and coverage with standard multiple regression. For all the regression models, the same transformation procedures for variables were applied as mentioned above. Examination of the residuals indicated the appropriateness of a linear model. All statistical analyses were conducted using Statistica version 6.0.

3. RESULTS

3.1. Comparison of vegetation and light between forest regions

The mean herbaceous cover was 75% over all the plots ($N = 256$), but differed within the gaps depending on the moisture gradient (Tab. I). Herbs were less abundant (45%) in gaps on the dry site in Dolinsko, with prevalent species including *Solidago gigantea* Aiton, *Festuca gigantea* (L.) Vill., *Fragaria vesca* L., *Carex sylvatica* Huds., and *Carex brizoides* L. In contrast, herbaceous cover was higher in the wet site (90%), and was dominated by *C. brizoides*, *Carex remota* L., *F. gigantea*, *Juncus effusus* L., and *Deschampsia caespitosa* (L.) P. Beauv. In Dolinsko the difference in herbaceous cover in gaps between wet and dry sites was significant (Fisher's LSD, $P = 0.000$), but the difference was not significant in Krakovo (Fisher's LSD, $P = 0.293$). Here, the dominant species in

Table I. Comparison of variables (mean values with 1 SE in parentheses) describing natural regeneration, understory vegetation, and light climate in the research sites within two forest areas (one-way ANOVA).

	Dolinsko		Krakovo		F	P
	Dry	Wet	Dry	Wet		
Number of gaps (total plots)	2 (N = 50)	1 (N = 25)	5 (N = 124)	3 (N = 57)		
Herbaceous cover (%)	44.9 (4.3)	90.0 (4.3)	82.9 (1.7)	79.5 (3.0)	35.04	0.000
Woody cover (%)	32.8 (3.7)	24.1 (5.1)	25.3 (1.8)	29.9 (2.7)	1.62	0.185
Cover of <i>Q. robur</i> (%)	15.6 (2.2)	16.7 (4.8)	21.5 (1.6)	25.4 (2.4)	3.10	0.027
Cover of <i>C. betulus</i> (%)	14.0 (2.8)	3.6 (1.7)	2.8 (0.7)	3.2 (0.9)	17.53	0.000
Density of <i>Q. robur</i> (N/m ²)	8.1 (0.8)	8.8 (1.2)	16.6 (1.3)	19.7 (1.9)	6.38	0.000
Density of <i>C. betulus</i> (N/m ²)	3.6 (0.4)	1.4 (0.3)	0.5 (0.1)	1.3 (0.4)	31.52	0.000
Height of <i>Q. robur</i> (cm)	39.3 (1.9)	48.2 (3.3)	43.6 (1.6)	47.7 (2.6)	2.70	0.046
Browsing of <i>Q. robur</i> (%)	34.2 (4.0)	50.9 (5.9)	16.3 (2.4)	25.1 (2.8)	12.48	0.000
DIR (%)	31.0 (1.6)	40.3 (1.7)	22.6 (1.2)	25.0 (1.8)	16.44	0.000
DIFF (%)	26.7 (1.7)	71.4 (1.6)	22.3 (1.1)	20.5 (1.5)	109.56	0.000

F = F statistic in ANOVA. P = level of statistical significance. Degrees of freedom for all F values are 3 and 254. Factors in percentages were transformed with an arcsine square-root equation, and counts were square-root transformed.

the herb layer in gaps on the wet variant were *D. caespitosa*, *J. effusus*, *Iris pseudacorus* L., *Peucedanum palustre* (L.) Moench, *C. remota*, *C. brizoides*, and *Athyrium filix-femina* (L.) Roth. Herbaceous dominants in gaps on the dry variant were *C. brizoides*, *A. filix-femina*, *Dryopteris carthusiana* (Vill.) H.P. Fuchs, *Circea luetiana* L., and *Scrophularia nodosa* L.

The cover of woody vegetation (seedlings and shrubs) was similar among the sites (Tab. I), yet the species composition varied. The mean cover and density of *Q. robur* seedlings were higher in Krakovo than Dolinsko (Fisher's LSD). The highest mean cover of *Q. robur* seedlings was in wet (25%) and dry sites (22%) in Krakovo, followed by wet (17%) and dry (16%) sites in Dolinsko. The highest mean cover of *C. betulus* was found on dry sites in Dolinsko (14.0%), while it was less abundant on all of the remaining sites (2.8–3.6%). The same seedling pattern was observed for *C. betulus* seedling density. In Dolinsko, aside from *Q. robur* and *C. betulus*, some *A. campestre*, *Robinia pseudacacia* L. (dry site only), and *F. angustifolia* were present (cover 3.4%). In Krakovo, though, seedlings of other tree species and shrubs covered only 1%, including *A. glutinosa*, *A. campestre*, and *F. angustifolia*. Finally, deer browsing was significantly higher in Dolinsko compared to Krakovo.

Diffuse light was significantly higher in the large 0.40 ha gap in Dolinsko compared to the two mid sized gaps (Tab. I and Fig. 2). In Krakovo, where the gaps were smaller (0.03–0.15 ha), light levels were lower. The differences in direct light (DIR) among sites were smaller than for diffuse light (DIFF).

3.2. Light asymmetry in relation to herbaceous and woody vegetation

Due to variation in site conditions in the two study regions, regression analyses were completed separately for the wet and dry sites within each study area (Tab. II). In both the wet and dry sites in each study area, there was a negative relationship between herbaceous cover (VEG%) and *Q. robur* seedling

cover (Q%), suggesting herbaceous cover inhibited *Q. robur* seedling establishment and growth. In regard to light, DIFF and DIR were only included in the model for the Krakovo dry site, where the model predicted a higher Q% in microsites with less VEG%, less DIFF, and more DIR. The regression models explained more variability for *Q. robur* seedling density – NQ (from 8% to 39%). Again, there was a negative relationship between VEG% and NQ on all the sites. Similar to seedling cover, DIFF and DIR were also included in the model for the dry sites in Krakovo.

In Krakovo the highest seedling density was recorded from approximately 10–20% DIFF. In Dolinsko the density for wet and dry types was within the same range regardless of DIFF (Fig. 3a). When all the gaps from both study areas were combined, seedlings were present in all plots below 16% DIFF. When we tested only the influence of DIR and DIFF on NQ and Q% (only NQ is presented in Tab. II), we found similar significant patterns for the dry sites in both forest regions. In gap positions with less DIFF and more DIR, the model predicted both a higher NQ and Q%. The most important predictor of *Q. robur* height (HDOM) on the dry sites in both study areas was DIFF, while on wet sites it was VEG% and DIR, respectively. Browsing percentage of *Q. robur* was positively related to VEG% on the dry site in Dolinsko ($R^2 = 0.112$, $P = 0.019$). In Krakovo, the main predictor was VEG% followed by HDOM on the wet site, whereas the main predictors were HDOM, DIF and –DIR on the dry site ($R^2 = 0.339$ and 0.573 , respectively; $P < 0.000$).

Out of 626 *Q. robur* seedlings in 75 plots in Dolinsko analysed for tree architecture, 348 (54%) showed monopodial growth with a vertical stem axis. The regression model predicted a higher density of poorly shaped seedlings in positions with lower VEG% on both the dry ($R^2 = 0.087$; $P = 0.038$) and wet site ($R^2 = 0.385$; $P < 0.000$). In Krakovo, *Q. robur* seedlings were analysed in gaps with a mean diffuse light of 21.7%, yet many seedlings in the gap centres experienced up to 4 growth flushes. In 1999 the mean height increment in Krakovo was 14.5 cm, with a maximum of 53.0 cm and a

Table II. Regression models of *Q. robur* seedling cover (Q%), density (NQ), height (HDOM) and herbaceous vegetation cover (VEG%) as a function of diffuse (DIFF) and direct light (DIR) in % and variables describing presence of competing species (C% = *C. betulus* seedling cover) in hardwood floodplain forest in E and SE Slovenia. Regression equations are presented in columns for each forest region and site variant separately.

Forest regions with site variants							
Dolinsko – dry (N = 50)		Dolinsko – wet (N = 25)		Krakovo – dry (N = 124)		Krakovo – wet (N = 57)	
Regression equation	R ² (P)	Regression equation	R ² (P)	Regression equation	R ² (P)	Regression equation	R ² (P)
Q% = 0.968*** – 0.170 VEG%*	0.085 (0.039)	n. s.		Q% = 1.838*** – 0.261 VEG%*** – 0.992 DIFF** + 0.636 DIR* + 0.156 C%	0.237 (0.000)	Q% = 1,539*** – 0.237 VEG%*	0.094 (0.020)
NQ = 3.236*** – 0.403 VEG%*	0.083 (0.043)	NQ = 5.557*** – 0.968 VEG%*** – 0.943 C%	0.390 (0.004)	NQ = 8.850*** – 0.972 VEG%*** – 5.798 DIFF*** + 2.739 DIR*	0.366 (0.000)	NQ = 6,368*** – 1.012 VEG%*	0.106 (0.013)
NQ ^a = 1.922** – 2.000 DIFF* + 2.444 DIR*	0.134 (0.034)	n. s.		NQ ^a = 6.770*** – 6.436 DIFF** + 3.059 DIR***	0.290 (0.000)	n. s.	
HDOM = 15.459*** + 18.210 DIFF** + 7.628 C%	0.312 (0.000)	HDOM = 12.642 + 12.135 VEG* + 17.410 C%	0.278 (0.028)	HDOM = 11.242* + 35.222 DIFF***	0.295 (0.000)	HDOM = 21.066** + 26.808 DIR***	0.211 (0.001)
VEG% = 1.943*** – 0.454 Q% + 1.305 DIFF* – 1.331 DIR*	0.180 (0.027)	n. s.		VEG% = 2.269*** – 0.329 Q%*** – 0.862 C%*** + 0.612 DIFF***	0.354 (0.000)	VEG% = 2.243*** – 0.308 Q%* – 0.740 C% ** + 0.587 DIFF*	0.388 (0.000)

All regression models were built with multiple regression forward stepwise procedures. Variables were added to the model if the F statistic for the factor was > 1.0. (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$, n. s. – not significant.)

^a For this test only radiation components (DIFF and DIR) were included and a standard regression procedure was used.

minimum of 3.0 cm (Fig. 3b). The regression model predicted a higher yearly height increment with increasing DIFF for both the dry ($R^2 = 0.356$; $P < 0.000$) and wet sites ($R^2 = 0.211$; $P = 0.003$).

Understorey vegetation (VEG%) was an important competitor with *Q. robur* seedlings (Q%, NQ) on the one hand, while on the other hand indicated favourable positions within gaps for *Q. robur* height growth and seedling architecture. VEG% was positively related to DIFF (on three sites) and negatively to *Q. robur* and *C. betulus* cover on the Krakovo sites. In the Dolinsko dry site VEG% was negatively related to DIR (Tab. II). *Carpinus betulus* is known to be a strong competitor with *Q. robur*, especially on dry sites, yet we did not find any negative relationships with *Q. robur*. On the dry sites in Krakovo, a higher density of *C. betulus* was predicted on microsites with low VEG% and high DIFF, while on the wet sites a higher density was predicted on microsites with low VEG% and low DIR ($R^2 = 0.432$ and 0.327 , respectively; $P < 0.000$ for both).

4. DISCUSSION

Although this study focused on small openings in the canopy layer (0.03–0.40 ha; mean and SE for DIFF 27.5% ± 1.2%), an abundant herb layer developed after the gaps were

formed, except for the dry site in Dolinsko, which could represent a transition site towards *C. betulus* dominated forests. One possibility is that this stand was planted on former agricultural land outside the natural range of *Q. robur*. A second possibility is that the site may have been altered because of drainage changes during the last century, which may also affect oak distribution [9, 33]. In spite of low understorey vegetation cover, the overall seedling success (cover, density, height) on the dry site in Dolinsko was lower compared to the other sites. This can be in part attributed to frequent and abundant seed years of *C. betulus*, and its ability to sprout from stumps. Similar patterns were also observed in Croatia [25, 26]. Within both forest areas the highest mean cover, density, and height were found in gaps on the wet sites. It seems that in these sites, *Q. robur* is able to outcompete other woody species, while competition from herbaceous vegetation may be strong [1, 25]. Although *Q. robur* seedling density was higher in Krakovo, the density in both areas was considerably above recommended values. According to Matic [25], the optimal density of *Q. robur* seedlings on sites with *C. betulus* is between 24 000 and 32 000/ha, while Leibundgut [22] justifies densities as low as 20 000/ha.

In both forest regions understorey vegetation was the main competitor for *Q. robur* seedlings. This has been found in

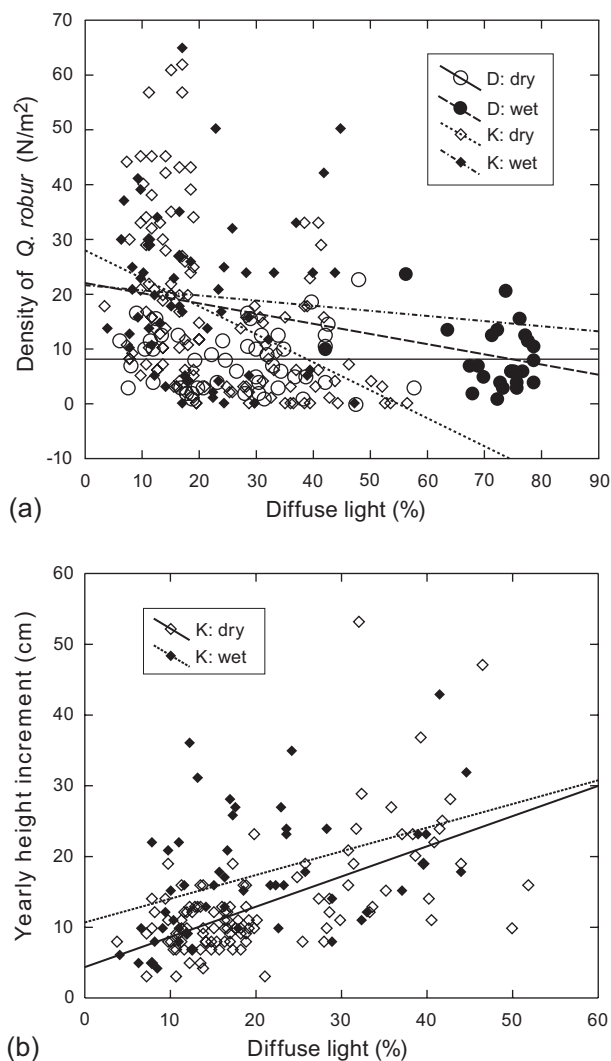


Figure 3. (a) Density of *Q. robur* seedlings for each site variant and (b) yearly height increment of *Q. robur* seedlings in Krakovo in relation to diffuse light and fitted regression lines. For clarity the variables were not transformed.

many floodplain forests in Europe [22, 26, 38]. Understorey vegetation was also positively influenced by DIFF. Therefore, it seems likely that the establishment and early growth of seedlings could be improved with creation of smaller gaps. Moreover, on the dry sites in both forests, a combination of low DIFF and high DIR was favourable for regeneration. These are microsites in the sun exposed northern area of gaps, especially below the canopy adjacent to the gap [3, 10, 18]. Here a combination of direct light, low precipitation due to interception, and root competition could have a drought effect. *Quercus robur* was reported as more sensitive to drought stress [37] compared to *Q. petraea*, but it seems more resistant than competing understorey vegetation. This could be attributed to a deep root system, which can rapidly develop in a few years [13, 17, 23]. Although light components were not directly included in the regression models for *Q. robur* density and cover

on the wet sites, their importance was clear through facilitating growth of competing herbs, especially in Krakovo.

The positive relationship found between dominant height of *Q. robur* and light components was expected and proven in other studies [25, 39]. The same pattern was observed for height increment, which was relatively low compared to traditional regeneration methods. However, the values are equivalent with those given by authors who worked in similar light climates [25, 38, 39]. In contrast to other findings, we recorded a minor decrease in height increment below 10% light. Regarding height and height increment the favourable positions within gaps were in the gap centre and in the sun exposed, northern gap area in the wet sites in Krakovo. Thus, positions within gaps for establishment and further growth of seedlings were not identical in all the gaps, which is often the case for particular tree species [10, 32].

Similar to other studies [17, 30], the results showed more poorly shaped plants outside the gap centre (negative association with VEG%). The poor relationship between tree architecture and light components and more than half of seedlings with straight growth could be a result of young (4 years), short seedlings (mean \pm SE = 42.3 \pm 1.7 cm) and shade tolerance in early growth [22, 25, 39]. Thus, the main causes for growth irregularities in our study are probably linked with other factors, such as competition and fauna. Problems with stability and quality begin with older saplings taller than 2 m, especially in the late thicket phase [30, 40]. Browsing in both forest regions was significant, yet tolerable, and was more intense in the gap centres. Adamic [2] found that oak was regularly present in rumen samples of red (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) in both study areas.

5. IMPLICATIONS AND CONCLUSIONS

This research indicated that *Q. robur* can successfully establish in small gaps (0.03–0.05 ha). Here more than 75% of plots received diffuse light in an interval from 8–18% (Figs. 2 and 3a). Several authors suggest that *Q. robur* can successfully establish and grow under a dense canopy for two years [41, 42], but survival and growth after two years requires a minimum relative light intensity of 3–4% [25]. Further development is only possible in gaps [1, 5], where a minimum relative light intensity of 15–20% is necessary [25, 39]. However, higher light levels are less favourable for regeneration due to intense competition with understorey vegetation and potential frost damage. The small gaps in our study were just below the proposed minimum light intensity. Therefore, in order to promote further survival and growth of the regeneration, the gaps would at least need to be extended to approximately 0.10 ha (Fig. 2) after the first four years. However, *Q. robur* saplings taller than 2 m (thicket) in small-gaps often have an unfavourable height/dbh ratio and a non-vertical stem axis. Small gaps may also generate many unstable cohort edges and result in excessive felling damage on regeneration and a decrease in quality of the remaining trees (epicormic branches). Therefore, Schütz [30] proposed to extend gaps in this stage to a minimum of 0.15 ha or optimal size of 0.25–0.30 ha. Leibundgut [22] advocated

0.10–0.20 ha gaps, which can later be extended or merged up to a hectare. Weinreich [40] studied 3–7 year-old oak sapling quality and found evidence that quality decreased below 32% relative light. Although he emphasized that trees of both superior and poor quality were more frequent in small gaps. This could be due to edge effects in overlapping gaps and high resource variability within gaps. In this study, more than 75% of plots in gaps of 0.15 ha had diffuse light levels above 28% (Fig. 2).

The results of this study, and the findings from oak forests in Switzerland [22, 30], Germany [39, 40], and Croatia [25], suggest that the relationship between gap size, light, and oak regeneration is comparable across large geographic areas. This study has confirmed the importance of DIFF and DIR as a source of within gap resource heterogeneity and for development of silvicultural guidelines. In the first four years of development, regeneration of *Q. robur* in gaps as small as 0.10 ha has many advantages. Further development of the regeneration, especially if high commercial quality trees are desired, is more favourable in gaps larger than 0.15 ha. Our findings suggest that for dry variants of our research sites elliptical gaps with longer northern edges of gaps should be created, while existing gaps should be extended toward the sun exposed northern gap edge. Still, if the commercial quality of trees is of no concern, the entire oak regeneration cycle is probably possible in smaller gaps, as indicated by research in natural forests. However, further studies should focus more on natural disturbance dynamics in SE European old-growth hardwood floodplain forests and consider the entire regeneration cycle, including the recruitment of cohorts into the canopy.

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