



The effect of gap size on the establishment and initial development of natural regeneration of Scots pine (*Pinus sylvestris* L.) in oligotrophic sites

Marcin Czacharowski¹ · Leszek Bolibok¹

Received: 20 December 2024 / Revised: 23 September 2025 / Accepted: 27 September 2025 / Published online: 30 October 2025
© The Author(s) 2025

Abstract

Artificial canopy gaps represent an effective tool for promoting natural regeneration, increasing structural diversity in forest ecosystems. However, the influence of specific gap characteristics on regeneration success remains insufficiently understood. This is especially important for the transformation of even-aged, single-layered Scots pine (*Pinus sylvestris* L.) stands on oligotrophic sites, where there is a clear need for evidence-based silvicultural recommendations. This study investigated the effects of gap size (0.05 ha vs. 0.30 ha), soil cover type, microtopography, and within-gap position on the establishment and early development of naturally regenerated Scots pine. To assess these factors, generalised additive models were applied to data from a regeneration experiment established in a 98-year-old pine stand during the winter of 2013/2014. Regeneration density was recorded after the 2nd and 8th growing seasons, and in the latter inventory, seedling height and proportions of soil cover types were also measured. Initial findings showed that seedling density in large gaps was over three times higher than in small gaps (3.42 vs. 1.04 seedlings·m⁻²). However, after 8 years, this difference had disappeared, and the gap size no longer significantly affected either seedling density or height. Dwarf shrubs and grasses negatively influenced regeneration density, while lichens and litter had a positive effect on seedling density but were negatively associated with seedling height. The results suggest that both gap sizes may be suitable for regeneration cuttings under similar site conditions.

Keywords Continuous cover forestry · Canopy opening · Soil cover · Microtopography · Soil scarification

Introduction

One of the most important forest tree species in European forests is Scots pine (Andrzejczyk and Żybura 2012; Krakau et al. 2013). Due to the numerous utility properties of pine timber, this species has historically been strongly promoted in forestry. For more than 200 years, various forms of clear-cutting have been the predominant method of managing Scots pine stands in most European countries. Clear-cutting is usually, but not always, associated with

artificial regeneration, preceded by soil preparation, which most commonly involves the creation of furrows using a double mouldboard plough.

Classical silvicultural literature, both in Poland and abroad, is ambivalent about clear-cut systems (Bernadzki 2000; Jaworski 2011; Ashton and Kely 2018). On the one hand, numerous advantages are emphasised, such as the ability to regenerate tree species with high and moderate light requirements outside the shading influence of the overstory. It is also noted that the even-aged, dense stands created by clearcutting, consisting of trees of similar size growing under conditions of intense interspecific competition, are a source of valuable medium- and large-size timber that can be obtained through periodic thinning's and final cuttings. Many authors also recognise the positive role of clear-cutting in developing modern forestry, highlighting it as a method that halted the unplanned and exploitative use of forests in Europe during the period of rapid industrial

Communicated by Enno Uhl.

✉ Marcin Czacharowski
marcin_czacharowski@sggw.edu.pl

¹ Department of Silviculture, Institute of Forest Sciences, Warsaw University of Life Sciences, Nowoursynowska 159, 02-776 Warsaw, Poland

growth (Johann 2006; Lundmark et al. 2013; Remeš 2018). This approach has significantly contributed to the restoration of forest resources, which are now at a very high and continuously increasing level.

On the other hand, an important disadvantage of clear-cutting is the susceptibility of the resulting stands to various biotic and abiotic disturbances, such as insects and fungi, or pressure from vegetation and ungulates in the early stages of development. For example, the frequent heat waves and droughts during the last decade, as observed in 2015, 2018, 2019, and 2023, have severely weakened the stability of many Scots pine stands in Poland. In 2016–2017, the pine sharp-toothed bark beetle (*Ips acuminatus* Gyll.) caused considerable damage to pine stands by infesting mature trees weakened by drought (Plewa and Mokrzycki 2017). Bark beetle outbreaks not only contribute significantly to forest mortality but also play an important role as natural gap creators, initiating regeneration processes and increasing structural heterogeneity in affected stands. Therefore, their impact should be considered both in the context of forest health and natural disturbance dynamics.

In recent years, Scots pine has also been increasingly affected by mistletoe (*Viscum album*), leading to severe weakening and, in extreme cases, the death of individual trees or even entire stands (Iszkuło et al. 2020; Walas et al. 2022). Increased pine mortality rates have been observed in many regions of Europe (Bigler et al. 2006; Vila-Cabrera et al. 2012; Vacchiano et al. 2012; Kunert 2020), affecting even healthy and dense stands. Sanitary cuttings performed to control pest outbreaks often result in numerous gaps and varying-sized patches within affected stands. Many authors predict that these negative phenomena, already observed today, will intensify in the future due to ongoing climate change. Coniferous species, mainly spruce and pine, are expected to gradually retreat from Central Europe as the climate will become warmer and drier (Hanewinkel et al. 2013; Matías and Alistair 2014; Zajączkowski et al. 2013; Dyderski et al. 2018).

These challenges, combined with increasing public criticism of clear-cutting (due to its negative impact on landscape aesthetic), especially in forests used for recreational purposes (Gołos 2018; Koivula et al. 2020), have prompted forestry in Poland and other countries to explore alternative methods of managing Scots pine stands. In this context, the concept of Closer-to-Nature Forest Management (CNFM) (European Commission 2023) is gaining increasing attention. This approach encompasses a set of principles and practices aimed at increasing stand stability and biodiversity. Fundamental principles of CNFM include: (i) avoiding clear-cuts larger than 0.25 ha (Pommerening and Murphy 2004); (ii) promoting mixed-species stands (Pretzsch et al. 2013); (iii) ensuring gradual turnover of forest generations

(Schütz et al. 2016); and (iv) favouring single-tree and group selection cutting methods (Mlinšek 2006).

Examples of applying these principles to Scots pine management can be found in Germany, where target diameter harvest methods are used (Drozdowski 2018). In Spain, where uniform shelterwood cutting remains the predominant method for Scots pine regeneration (Pardos et al. 2007), although alternative approaches, including selection systems and other close-to-nature methods, are also increasingly applied (Gallo et al. 2020). In Poland, despite the predominance of clear-cutting, there are also examples of alternative regeneration methods for Scots pine stands, including shelterwood, group selection, strip cutting and even selection-cutting systems (Andrzejczyk 2000, 2006, 2007; Barzdajn and Zientarski 2007; Andrzejczyk and Żybura 2012; Szmyt 2025). These and other locally applied, non-standard silvicultural approaches encourage the exploration of alternatives to traditional clear-cutting methods in the management of Scots pine stands (Ciancio et al. 2006; Czacharowski and Drozdowski 2021).

One of the most promising methods for the regeneration and, at the same time, the diversification of the structure of pine stands is gap cutting (Rouvinen and Kouki 2011). Gaps are small areas, either naturally occurring or artificially created serve as regeneration sites for species that require protection from frost or excessive sunlight during early developmental stages (Yamamoto 2000). In Poland, gap cuts are typically used to convert pure pine, oak, or beech stands into mixed ones. Nevertheless, knowledge of using such cuts for obtaining natural Scots pine regeneration is relatively limited and comes mainly from Fennoscandia and the Mediterranean region.

Existing research in this area has focused on topics such as the effect of gap size on drought resistance during regeneration (Barbeito et al. 2009a, b; Calama et al. 2015; Çoban et al. 2018; Frutos et al. 2024), the optimal gap size for successful regeneration (de Chantal et al. 2003; Axelsson et al. 2014; Pasanen et al. 2016; Hallikainen et al. 2019), and the potential of gap cutting to shape uneven-aged stand structures (Rouvinen and Kouki 2011; Pasanen et al. 2016; Hjältén et al. 2017). However, in Central Europe, where Scots pine is one of the main forest-forming species, knowledge on the suitability of small and large gaps for its regeneration is much more limited, and the number of publications addressing this issue is relatively low (Mierzejewski and Niedźwiedzki 1954; Andrzejczyk 2000; Paluch 2004; Bolibok and Andrzejczyk 2008).

Taking this into account, this study focuses on the natural regeneration establishment and early development in artificial small and large gaps in mature Scots pine stands. The research questions addressed in this study include:

1. How do various characteristics of small and large gaps, including soil cover types, microtopography (furrows and ridges), and distance from gap edge, influence the dynamics of natural Scots pine regeneration two and eight growing seasons after the regeneration cuts?
2. What are the most significant factors affecting the success of Scots pine regeneration during the early stages of its development in gaps of varying sizes?

Methods

Study area

The study was conducted in the Janowskie Forest (39,100 ha) in southeastern Poland (50°36' N, 22°36' E, 230 m a.s.l.), located on flat lowland terrain within the Małopolska region and the Solska Forest mesoregion (Zielony and Kliczkowska 2012). The majority (85%) of stands grow on oligotrophic podzolic sandy soils and are predominantly composed of Scots pine, admixed by Norway spruce (*Picea abies* (L.) H. Karst), silver fir (*Abies alba* Mill.), and silver birch (*Betula pendula* Roth). The prevailing silvicultural system for mature pine stands in this forest, as in the rest of Poland, is clear-cutting, with harvest areas of up to 4 ha. To mitigate the adverse effects of large open spaces created during clear-cutting, so-called “retention patches” of mature trees (with a minimum area of 0.06 ha, occupying up to 5% of the mature stand) are often retained within the harvested area. Additionally, groups or individual trees of high ecological value, characterized by the presence of dendromicrohabitats (e.g., woodpecker cavities), are also preserved.

Climate and weather conditions

The study area is located in a temperate climate zone, exhibiting features of both continental and oceanic climates (Okolowicz 2000). The mean annual air temperature for the reference period 1986–2021 is 8.3 °C. The coldest month is January, with an average temperature of −2.2 °C, while the warmest month is July, averaging 19.2 °C (Fig. 1a). The mean annual precipitation totals approximately 645 mm. The growing season begins in late April and ends in early November, lasting about 160 days. Snow cover persists for approximately 70 days yearly (Tomczyk and Bednorz 2022).

The climatic conditions during the study period (2014–2021) are illustrated in Fig. 1b, c. Both average temperature and precipitation during this period exceeded the long-term averages; however, two extremely dry years (2015 and 2019) and four years with exceptionally high precipitation (2014, 2016, 2017, and 2021) were recorded (Fig. 1).

To characterise the water supply conditions for pine regeneration, the de Martonne aridity index (MI) was used, calculated as $MI = \text{annual precipitation (mm)} / (\text{mean annual temperature (°C)} + 10)$ (De Martonne 1926). During the study period, MI values ranged from 28.8 to 40.9 mm·°C, with the average for this period slightly exceeding the long-term mean at 36.3 mm·°C (Fig. 1). According to Baltas (2007), these values indicate conditions classified as semi-humid to very humid. The MI can also be calculated for individual months. According to the World Meteorological Organization (1975), months with $MI < 20$ are characterised by significant water deficits. During the study, such months occurred 12 times in the growing season (April–October), representing 21% of the total 56 months analysed.

Study object

The study object was a 98 year-old Scots pine stand covering an area of 27.82 ha, composed of two compartments (38-a-00 and 51-a-00) located in the Zdzisławice Forest Range, in Janów Lubelski Forest District. The stand represents a moist coniferous forest site (Plan Urządzania Lasu 2020). Before the initiation of the regeneration experiment, 31 permanent circular sample plots, each with an area of 0.05 ha, were established within the stand in autumn 2012. The plots were arranged in a regular 100 m × 100 m grid. Based on data collected from these plots, the average stand parameters were as follows: tree density: 470 ± 28 trees ha^{−1}, basal area: 30.3 ± 1.1 m²·ha^{−1}, and standing volume (under bark): 349 ± 12.5 m³·ha^{−1}. The share of Scots pine, calculated by volume, was 97%. Stand stocking was 0.8, and canopy closure was classified as moderate. The mean diameter at breast height (DBH) and tree height were 33.4 cm and 26.9 m, respectively, while the top DBH and height were 45.9 cm and 29.7 m, respectively. The stand quality was good and typical for the Solska Forest mesoregion.

In addition to Scots pine, the stand contained minor admixtures of Norway spruce and silver birch. The understorey and shrub layers covered approximately 50% of the area, consisting mainly of younger individuals of Scots pine and Norway spruce, along with occasional black cherry (*Prunus serotina* (Ehrh.) Borkh.), silver fir, and common juniper (*Juniperus communis* L.). The ground vegetation layer included dwarf shrubs, mosses, grasses, and lichens. From a phytosociological perspective, the studied stand represented the moist pine forest *Molinio caeruleae-Pinetum* W. MAT. (Matuszkiewicz 2013).

Experimental design

In the winter of 2013/2014, a total of 25 small gaps (0.05 ha each) and 5 large gaps (0.30 ha each) were created within

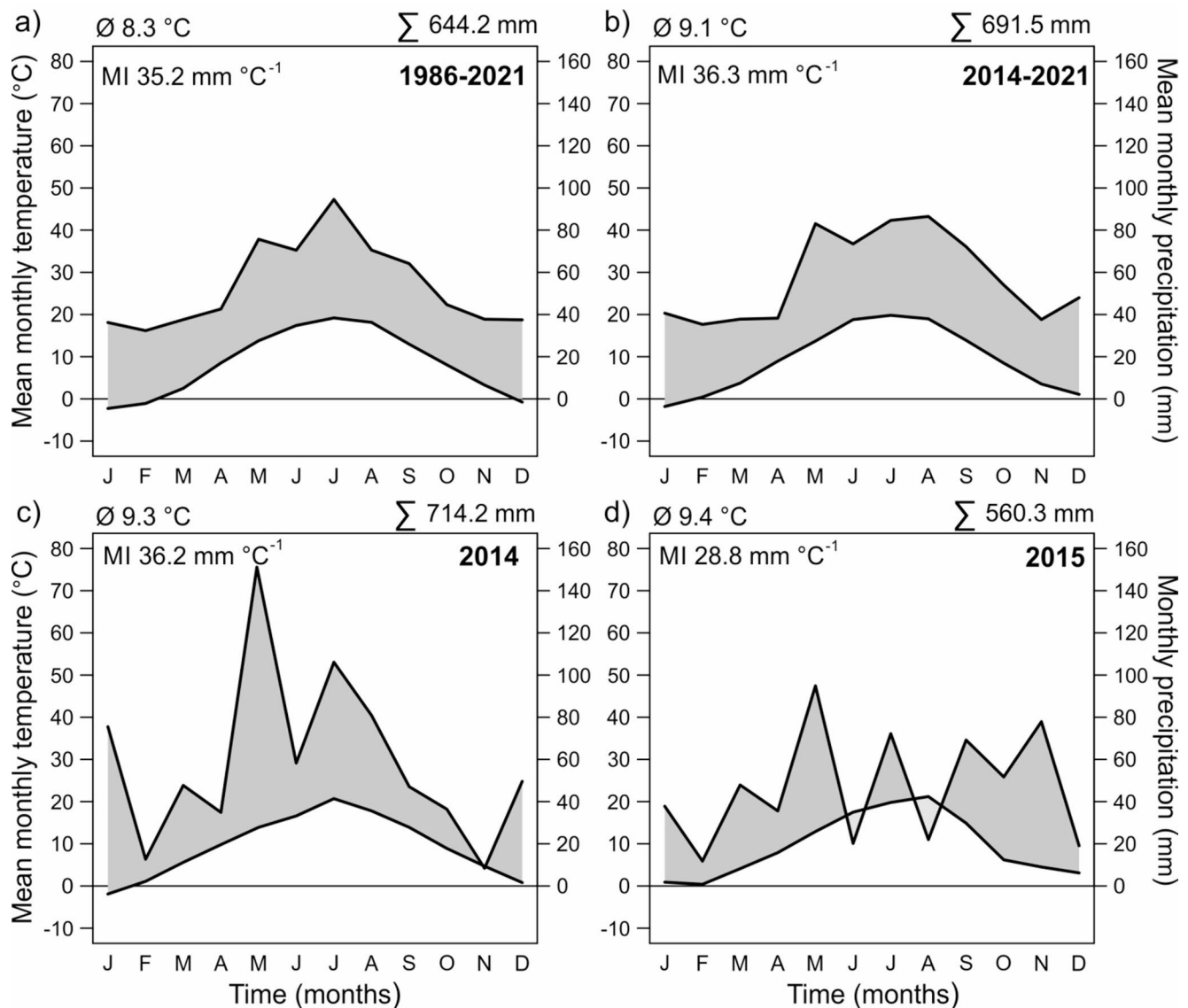


Fig. 1 Walter climate diagrams showing: **a** the long-term climatic conditions, typical for the Janów Forest; **b** average climatic conditions during the study period (2014–2021); **c** conditions during the first, fairly wet, year of the experiment, and **d** conditions during the second,

extremely dry, year of the experiment. Data source: the Jarocin meteorological station located ~20 km from the study site (Instytut Meteorologii i Gospodarki Wodnej 2023). MI—de Martonne Aridity Index

the studied stand. The shape of the gaps was circular, where the ratio of the diameter (d) of the gap to the height (h) of the tree stand was 2.0 for large gaps and 1.0 for small gaps. The diameter of large gaps was 62 m, and that of small gaps was 25 m. The trees of all species within the border of the gaps were felled by clear-cutting and removed from the area. The approximate distance between the gaps was 35 m for the small gaps and 40 m for the large gaps. The total area of the gaps was 2.5 ha, accounting for about 10% of the stand's total area. In April 2014, standard soil scarification was conducted within the small and large gaps to expose mineral soil and improve conditions for seed germination and early seedling growth. The scarification involved ploughing

furrows approximately 15 cm deep and 70 cm wide using an LPz-75 double-mouldboard forestry plough (otljarocin.lasy.gov.pl) (Fig. 2). Furrows were spaced 1.5 m apart, measured from their centres. During ploughing, the top 15 cm of ground vegetation and forest litter were displaced to the sides, forming ridges consisting of the upper soil layer, litter, and plant cover. No further silvicultural treatments were carried out in the stand during the experiment. Only a few trees infected by the pine sharp-toothed bark beetle were removed as part of sanitary cuts.

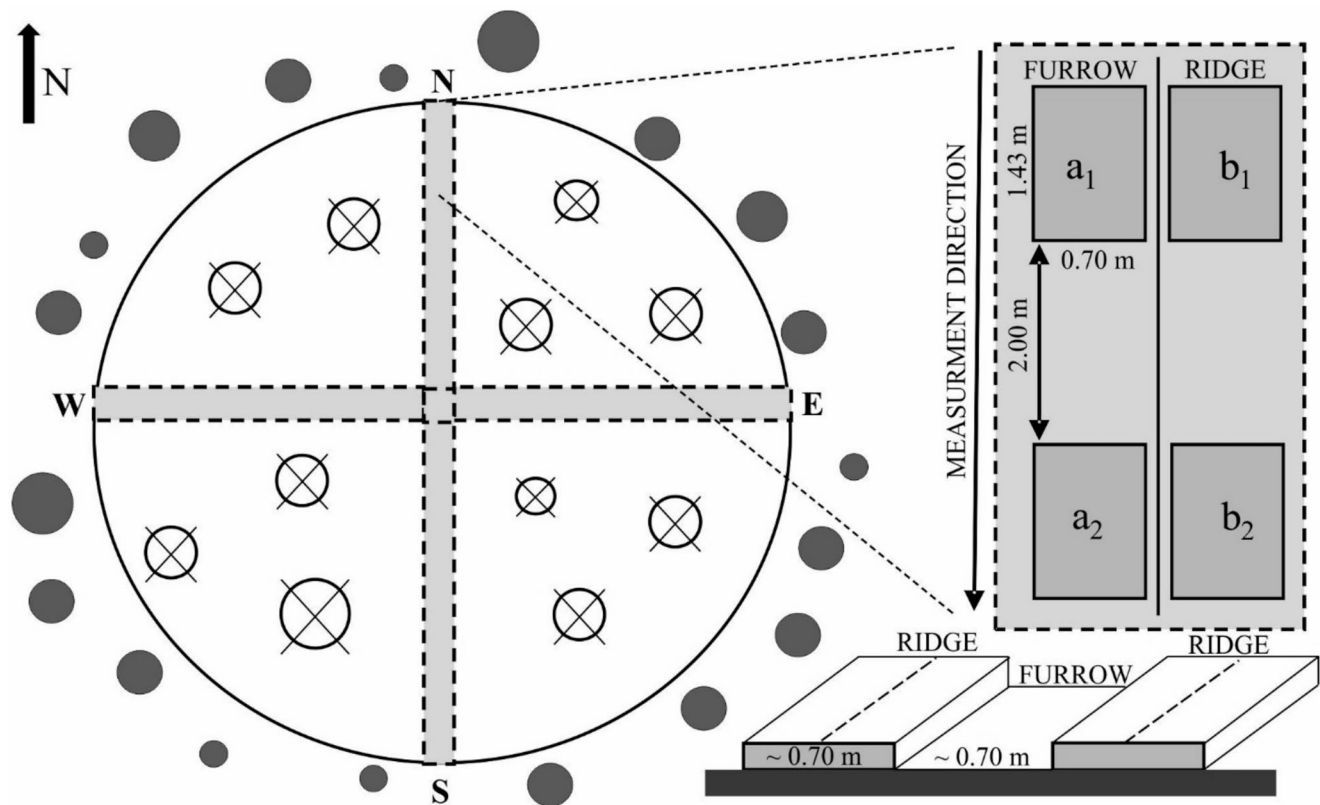


Fig. 2 The sampling design within a gap. Sample plots were established along 4 transects (N, E, S, W) joining in the central point of the gap. Empty circles represent stumps inside the gap, while grey circles show trees surrounding the gap

Field measurements

Field measurements were conducted on five randomly selected small gaps (0.05 ha each) and three randomly selected large gaps (0.30 ha each). Regeneration parameters were assessed using pairs of adjacent sample plots measuring 70×143 cm (1 m^2 each), arranged along four virtual transects corresponding to the main cardinal directions (N, E, S, W) (Fig. 2). One plot in each pair represented the conditions of the furrow (type "a" – exposed mineral soil), while the other represented the ridge conditions (type "b" – the upper soil layer, litter, and ground vegetation displaced during ploughing). The distance between successive pairs of sample plots along the transects was 2 m, measured from their edges. The number of plot pairs within a single transect depended on the size of the regeneration site: on average, there were 8 pairs in small gaps and 17 pairs in large gaps.

The first regeneration inventory was conducted in late August 2015, following the second growing season after gap cutting. This inventory involved counting all tree seedlings present in the sample plots. A seedling is defined as a tree older than one year. The second inventory was carried out in late August 2021, after the eighth growing season. During this inventory, the height of all Scots pine individuals was

measured, and seedlings of all tree species in the plots were counted. Although some measured individuals exceeded 50 cm in height (which is commonly referred to as saplings), we did not distinguish them as a separate class, and all trees were analysed together and referred to as seedlings. Additionally, in 2021, the percentage cover (estimated to the nearest 1%) of different soil cover types within the sample plots was assessed. The following categories were distinguished: 1) Bare (exposed) soil; 2) Litter (dead needles, bark, small branches); 3) Coarse woody debris (pieces with a mid-length diameter > 5 cm); 4) Stumps, and 5) Ground vegetation, further divided into subcategories: 5a) Dwarf shrubs: bilberry (*Vaccinium myrtillus* L.), lingonberry (*Vaccinium vitis-idaea* L.), and heather (*Calluna vulgaris* (L.) Hull), 5b) Mosses: red-stemmed feather moss (*Pleurozium schreberi* (Willd. ex Brid.) Mitt.), broom fork moss (*Dicranum scoparium* Hedw.), and juniper haircap moss (*Polytrichum juniperinum* (Willd.) Hedw.), 5c) Herbaceous plants, mainly cow-wheat (*Melampyrum pratense* L.), 5d) Sedges and grasses, including hairy wood-rush (*Luzula pilosa* (L.) Willd.) and wavy hair-grass (*Deschampsia flexuosa* (L.)), and 5e) Lichens (*Cladonia* spp.).

Statistical analysis

To describe the relationships between dependent/response variables (a density of Scots pine seedlings in 2015 and 2021 and a maximum seedling height on sample plots in 2021) and the explanatory variables, generalized additive models (GAMs; Wood 2006) were used. The choice of GAM models was motivated by their ability to uncover non-linear effects of the continuous explanatory variables, which has been proven to occur in other research regarding natural regeneration in canopy gaps (Downey et al. 2018).

In the beginning, in the models describing the effects of environmental variables on seedling density, a Poisson distribution for the response variable was assumed. However, the dispersion parameter calculated for the Pearson residuals was markedly above one. For this reason, in the final models, a negative binomial distribution with the logarithmic link function was used. In turn, in the case of maximum seedling height, a Gaussian distribution of response variable was assumed. As it led to acceptable residual plots (Wood 2006), it was used in the final model version.

The model-building process relied on the analysis of correlations between the available explanatory and response variables, supported by the visual inspection of their spatial variability in different gap fragments (i.e., the comparison of trend lines for N, S, E, and W transects). The final models were built in a forward stepwise manner. In the model-building process, subsequent variables were added one by one and they were retained in the model only when the ANOVA test proved their significance ($p < 0.05$). To decide which of two highly correlated variables (correlation coefficient > 0.5) should be included in the final model, two separate models, containing only one of the two variables, were built. The “right” variable was chosen based on amount of deviance explained. If the visual assessment suggested that the continuous predictor distinctly differs for different transect orientations (N, S, E, W), models with two versions of smoother were compared. The first simple model assumed that the relationship between the response and the explanatory variable is independent with respect to transect orientation [s(variable)] and the second one assumed that transect orientation influences the shape of relationship [s(variable, by=transects)]. Similar comparisons were made if bigger differences between two types of microtopography (furrow, ridge) were observed. In such a case, the smoother in the second model had the following form: s(variable, by=microtopography).

Observations gathered on one gap tend to be more similar than observations coming from two different gaps representing the same size class. Thus, it could violate the assumption of independence of observations. To deal with this problem, all developed models were converted into

general additive mixed-effect models. Initially selected variables were used as fixed effects. The random effects were included as additional smoothers in the way described by Wood (2006). Three types of random effects parametrization were compared. First, random intercept, which adjusts model terms with the constant value depending on gap.id [s(gap.id, bs=“re”)]. Second, which adjusts the slope of the trend of numeric predictor (distance from gap edge) [s(gap.id, distance, bs=“re”) and the third in which random intercept and random slope are combined. The final model (the form of random effect parametrization) was chosen based on the lowest Akaike information criterion (AIC) scores.

A total of 4 models were constructed. In the first and second model (Eqs. 1 and 2), the effect of the gap size, the location within the gap (geographic orientation of the transect) and the type of microtopography (furrow/ridge) on the density of pine regeneration in 2015 and 2021 was assessed. In the third model (Eq. 3), additional explanatory variables, recorded during the second inventory conducted in 2021, including the cover (in %) of different types of ground vegetation (dwarf-shrubs, mosses, herbaceous plants, grasses, lichens) and types of soil cover (exposed mineral soil, litter, dead wood, stumps) were included. The last, 4th model was constructed to examine which types of soil cover and types of microtopography have the greatest influence on the maximum height of pine seedlings within individual sample plots (Eq. 4).

The final form of the model, in which the dependent variable was the density of natural regeneration of Scots pine (E(Ps)), measured in 2015, i.e. after 2 growing seasons from the moment of cutting down the regeneration gaps, was as follows:

$$\begin{aligned} \text{Log}[E(Ps)] = & \beta_0 + \beta_1 \cdot \text{transect} + \beta_2 \cdot \text{gap size} \\ & + \beta_3 \cdot \text{microtopography} \\ & + f_1(\text{distance}|\text{size}) + f_2(\text{id.gap, bs} = \text{“re”}) \end{aligned} \quad (1)$$

where: $\text{Log}[E(Ps)]$ - the natural logarithm of the expected number of seedlings (Ps) (the response variable), β_0 - the intercept term, representing the expected number of seedlings in the reference category for the variable transect (e.g., transect 1, north), β_1 , β_2 and β_3 - the coefficients for the categorical variables transect, gap size, and microtopography, respectively. These terms reflect linear relationships between the predictors and the number of seedlings, holding other variables constant, $f_1, f_2, \dots$ - smooth functions that capture potentially nonlinear relationships between the explanatory variables and the response variable (i.e., the number of seedlings Ps).

The final model for the number of Scots pine seedlings (E(Ps)), measured in 2021, i.e. after eight growing seasons from gap cutting, was:

$$\begin{aligned} \text{Log}[E(Ps)] = & \beta_0 + \beta_1 \cdot \text{transect} \\ & + \beta_2 \cdot \text{gap size} \\ & + \beta_3 \cdot \text{microtopography} \\ & + f_1(\text{distance}|\text{microtopography}) \\ & + f_2(\text{distance, id.gap, bs} = \text{"re"}) \end{aligned} \quad (2)$$

The final model for the number of Scots pine seedlings ($E(Ps)$), measured in 2021, i.e. after eight growing seasons from gap cutting, including data on microtopography and soil cover types, was:

$$\begin{aligned} \text{Log}[E(Ps)] = & \beta_0 + \beta_1 \cdot \text{transect} \\ & + \beta_2 \cdot \text{gap size} \\ & + \beta_3 \cdot \text{microtopography} \\ & + f_1(\text{distance}|\text{transect}) \\ & + f_2(\text{shrubs}|\text{transect}) \\ & + f_3(\text{shrubs}|\text{microtopography}) \\ & + f_4(\text{litter}|\text{transect}) \\ & + f_5(\text{lichens}) + f_6(\text{glasses}) \\ & + f_7(\text{distance, id.gap, bs} = \text{"re"}) \end{aligned} \quad (3)$$

The final model for the maximum height of Scots pine seedlings ($E(H_{\max})$), after eight growing seasons from gap cutting, including data about microtopography and soil cover types, was:

$$\begin{aligned} \text{Log}[E(H_{\max})] = & \beta_0 + \beta_1 \cdot \text{transect} \\ & + \beta_2 \cdot \text{microtopography} \\ & + f_1(\text{distance}|\text{microtopography}) \\ & + f_2(\text{litter}|\text{transect}) \\ & + f_3(\text{lichens}) + f_4(\text{mosses}) \\ & + f_5(\text{herbs}) \\ & + f_6(\text{distance, id.gap, bs} = \text{"re"}) \end{aligned} \quad (4)$$

Meaning of symbols in Eqs. (2)–(4) are as in Eq. (1).

All analyses were conducted in the R environment (version 3.6.2; R Core Team 2014), using the mgcv package for GAM modelling (Wood 2011), and the itsadug (van Rij et al. 2017) and ggeffects (Lüdtke 2018) packages for model visualizations.

Results

Overall characteristics of regeneration parameters and soil cover types

The average natural regeneration density within the studied gaps was relatively low. Scots pine was the most frequently regenerating species, while other species were found sporadically (Table 1). After the first two growing seasons,

the regeneration density of Scots pine in small gaps ($1.04 \text{ seedlings} \cdot \text{m}^{-2}$) was significantly (more than three times) lower than in large gaps ($3.42 \text{ seedlings} \cdot \text{m}^{-2}$). However, after eight growing seasons, the regeneration densities in small gaps ($2.16 \text{ seedlings} \cdot \text{m}^{-2}$) and large gaps ($2.13 \text{ seedlings} \cdot \text{m}^{-2}$) were nearly equal. The proportion of empty sample plots (those without natural regeneration) was high, particularly during the first inventory (47.0%). By the second inventory, this proportion had decreased to 27.2%.

Among the types of soil cover assessed after the eighth growing season, dwarf shrubs had the highest percentage on the sample plots. On average, they covered more than half of the plot area, both in small and large gaps. Mosses ranked second, covering approximately one-quarter of the plot area. Forest litter also accounted for a relatively large share (6–8%). Other types of soil cover occurred much less frequently.

The number of Scots pine seedlings as a function of multiple factors

The density of Scots pine regeneration in 2015 was mainly influenced by the gap size, the microtopography and, to a lesser extent, the geographical orientation of the transects (Fig. 3a; Table 2). In large gaps, regeneration density gradually decreased from the edge towards the centre, whereas in small gaps, the opposite trend was observed. Regeneration density was significantly higher in furrows than on ridges. The lowest and most similar regeneration densities were found on the western and northern transects. The predictive accuracy of the constructed model for the first inventory results was very high (62.5%).

In contrast to the results obtained in 2015, the gap size (large gaps compared to small gaps) did not significantly affect the density of Scots pine regeneration in 2021 (Fig. 3b; Table 4). However, the transects' geographical orientation and microtopography type significantly influenced regeneration density in 2021. After eight growing seasons, there was a significant change in regeneration numbers growing in furrows, observed along a gradient from the edge to the centre of the gap. In both small and large gaps, regeneration density decreased noticeably from the stand edge towards the gap centre (Fig. 3b). In the central part of the gaps, regeneration density dropped almost to zero, regardless of the geographical orientation of the transects. In contrast to the results for furrows, the regeneration growth data on ridges showed an opposite trend. In the case of small gaps, a slight upward trend in regeneration density was observed as one approached the central part. For large gaps, the highest regeneration density ($1\text{--}3 \text{ seedlings} \cdot \text{m}^{-2}$) occurred at a distance of 15–20 m from the stand edge. The model's

Table 1 Overview of the study's variables measured after the 2nd and 8th growing seasons

Variable	Unit	Small gaps (0.05 ha)				Large gaps (0.30 ha)			
		Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
2015									
Density of natural regeneration									
<i>Pinus sylvestris</i>	number·m ⁻²	1.04	1.35	0.00	6.00	3.42	3.75	0.00	15.00
Frequency of empty plots	%	51.59	8.33	36.36	66.67	31.18	0.82	30.21	32.22
2021									
Density of natural regeneration									
<i>Pinus sylvestris</i>	number·m ⁻²	2.16	2.54	0.00	22.00	2.13	2.56	0.00	13.00
<i>Prunus serotina</i>	number·m ⁻²	0.13	0.72	0.00	9.00	0.07	0.61	0.00	9.00
<i>Betula pendula</i>	number·m ⁻²	0.10	0.41	0.00	4.00	0.07	0.31	0.00	2.00
<i>Frangula alnus</i>	number·m ⁻²	0.02	0.14	0.00	2.00	0.03	0.18	0.00	2.00
<i>Sorbus aucuparia</i>	number·m ⁻²	0.00	0.04	0.00	1.00	0.00	0.05	0.00	1.00
<i>Picea abies</i>	number·m ⁻²	0.00	0.06	0.00	1.00	0.00	0.05	0.00	1.00
Frequency of empty plots	%	22.68	5.64	13.73	28.89	34.72	3.56	30.33	39.05
Maximum height of <i>Pinus sylvestris</i> seedlings/plot	(cm)	46.66	37.29	5.00	173.00	34.68	27.00	5.00	173.00
Types of ground cover									
Bare mineral soil	%	0.29	1.21	0.00	10.00	4.16	8.85	0.00	70.00
Litter	%	6.21	11.33	0.00	65.00	8.03	10.99	0.00	55.00
Deadwood	%	0.22	1.76	0.00	18.00	0.01	0.11	0.00	2.00
Stumps	%	0.39	2.13	0.00	15.00	0.65	3.30	0.00	40.00
Dwarf shrubs	%	51.30	17.00	10.00	85.00	58.92	22.66	5.00	100.00
<i>Vaccinium myrtillus</i>	%	26.85	15.38	0.00	66.50	7.01	11.74	0.00	56.00
<i>Vaccinium vitis-idea</i>	%	9.29	9.54	0.00	56.00	13.38	13.30	0.00	64.00
<i>Calluna vulgaris</i>	%	15.16	18.09	0.00	75.65	38.53	31.66	0.00	100.00
Mosses	%	36.19	15.68	0.00	79.00	23.23	16.48	0.00	65.00
<i>Pleurozium schreberi</i>	%	26.06	14.15	0.00	79.00	14.71	12.91	0.00	57.00
<i>Dicranum scoparium</i>	%	7.07	9.09	0.00	49.30	7.30	9.39	0.00	53.00
<i>Politrichum juniperum</i>	%	0.90	4.86	0.00	52.50	0.78	2.45	0.00	14.95
Other mosses	%	2.17	5.83	0.00	45.75	0.44	3.84	0.00	65.00
Herbs	%	3.72	5.57	0.00	68.00	1.09	3.65	0.00	50.00
Grasses	%	1.55	6.54	0.00	70.00	3.46	9.45	0.00	70.00
Lichens	%	0.15	1.04	0.00	10.00	0.43	1.75	0.00	20.00

Density of tree regeneration, by species (seedlings·m⁻²); types of soil cover and ground vegetation types (given in % at the plot level); SD—standard deviation; Min. and Max.—minimum and maximum value of a given variable per sample plot, respectively

predictive accuracy for the data obtained during the second inventory was relatively low (17.9%).

A significant improvement (from 17.9 to 32.3%) in the predictive accuracy of the model constructed for the 2021 inventory data was achieved by incorporating additional explanatory variables, specifically the types of soil cover (see Eq. 3). According to the extended version of the model, the density of Scots pine in gaps was influenced by the geographical orientation of the transects and the type of soil cover (Fig. 4; Table 3). Cover of shrubs and grasses was negatively correlated with pine regeneration density, while the opposite was true for mosses and litter. All these relationships were statistically significant. Even a small increase in shrub cover in the ploughed furrows and on the ridges resulted in a significant reduction in seedling density.

Maximum height of Scots pine seedlings as a function of multiple factors

The maximum height of pine seedlings within individual sample plots was strongly correlated with the geographical orientation of the transect and the microtopography (Fig. 5; Table 4). The highest seedlings were found in the northern part of the gaps, while the lowest were found in the eastern part. The relationship between the maximum height of pine regeneration and the distance from the gap edge was unclear. The tallest specimens were located 8–10 m from the forest's edge. Seedlings in furrows reached greater heights than those on ridges, especially in the central part of the regeneration sites. Seedlings' height was negatively

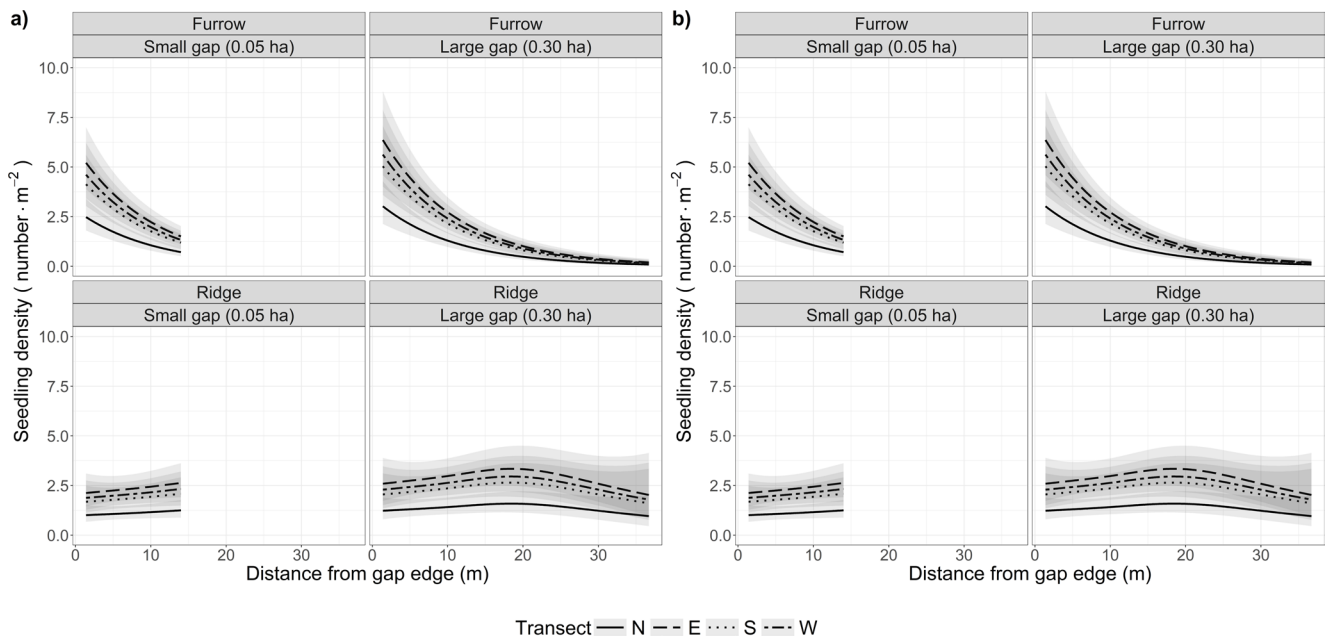


Fig. 3 Number of Scots pine seedlings (number·m⁻²) in 2015 (**a**) and 2021 (**b**) as a function of GAM covariates (size of canopy openings (small vs. large gaps), type of microtopography (furrows vs. ridges), distance from gap edge). Shaded bands indicate the 95% confidence intervals

Table 2 Summary of the GAM model for the expected number of Scots pine seedlings (number·m⁻²) in 2015 (A) and 2021 (B), respectively

A. Negative binomial model. R ² =0.607					B. Negative binomial model. R ² = 0.139				
Parametric coefficients:	Estimate ^a	SD ^b	Error z value ^c	Pr(> z) ^d	Parametric coefficients:	Estimate ^a	SD ^b	Error z value ^c	dPr(> z) ^d
(Intercept)	0.6415	0.1304	4.918	<0.0001	(Intercept)	-0.2060	0.1512	-1.362	0.1731
transect E	0.2837	0.1077	2.634	0.0084	transect E	0.7433	0.1446	5.142	<0.0001
transect S	0.2314	0.1076	2.151	0.0315	transect S	0.5105	0.1515	3.37	<0.0001
transect W	0.0005	0.1117	0.005	0.9964	transect W	0.6206	0.1449	4.282	<0.0001
Size large gap	1.0472	0.1366	7.668	<0.0001	Size large gap	0.1984	0.1257	1.579	0.1144
Microtopography ridge	-2.1600	0.1043	-20.705	<0.0001	Microtopography ridge	0.3875	0.1013	3.824	<0.0001
Smooth term	E. df ^e	Chi.sq ^f	p-value ^g	Ref.df ^h	Smooth term	E. df ^e	Chi.sq ^f	p-value ^g	Ref.df ^h
s(distance): size small gap	1.00	4.02	0.04	1	s(distance): microtopography furrow	1.00	66.09	0.0000	1.00
s(distance): size large gap	1.05	0.6	0.44	1.09	s(distance): microtopography ridge	1.98	2.23	0.3200	2.49
s(id.gap)	2.3	5.43	0.04	6	s(distance,id.gap)	1.93	5.45	0.0300	7.00
No. of observations	502				No. of observations	571			
Deviance explained (%)	62.5				Deviance explained (%)	17.9			

^aEstimate – the estimated coefficient for each parametric term, indicating its average effect on the response variable; ^bSD – standard deviation of the estimated coefficient; ^cError z value – test statistic calculated by dividing the Estimate by its Standard Error; ^dPr(>|z|) – *p*-value for testing the statistical significance of the parametric term; ^eE.df – estimated degrees of freedom for the smooth term, reflecting its complexity (higher values indicate greater flexibility); ^fChi. sq – test statistic for assessing the significance of the smooth term, based on the model's deviance; ^g*p*-value – significance level for the smooth term, indicating whether it contributes to the model; ^hRef. df – reference degrees of freedom used in the hypothesis test for the smooth term

correlated with the presence of mosses and lichens. A similar pattern was observed for litter, although in this case, the geographical orientation of the transect played a significant role. This relationship was strongest in the western part of the regeneration sites and weakest in the northern part.

Discussion

This study presents the results of an eight-year regeneration experiment conducted in a mature Scots pine stand on oligotrophic sites in Poland, using small and large gaps. Our considerations are based on the assumption that creating both small and large canopy openings mimics the natural

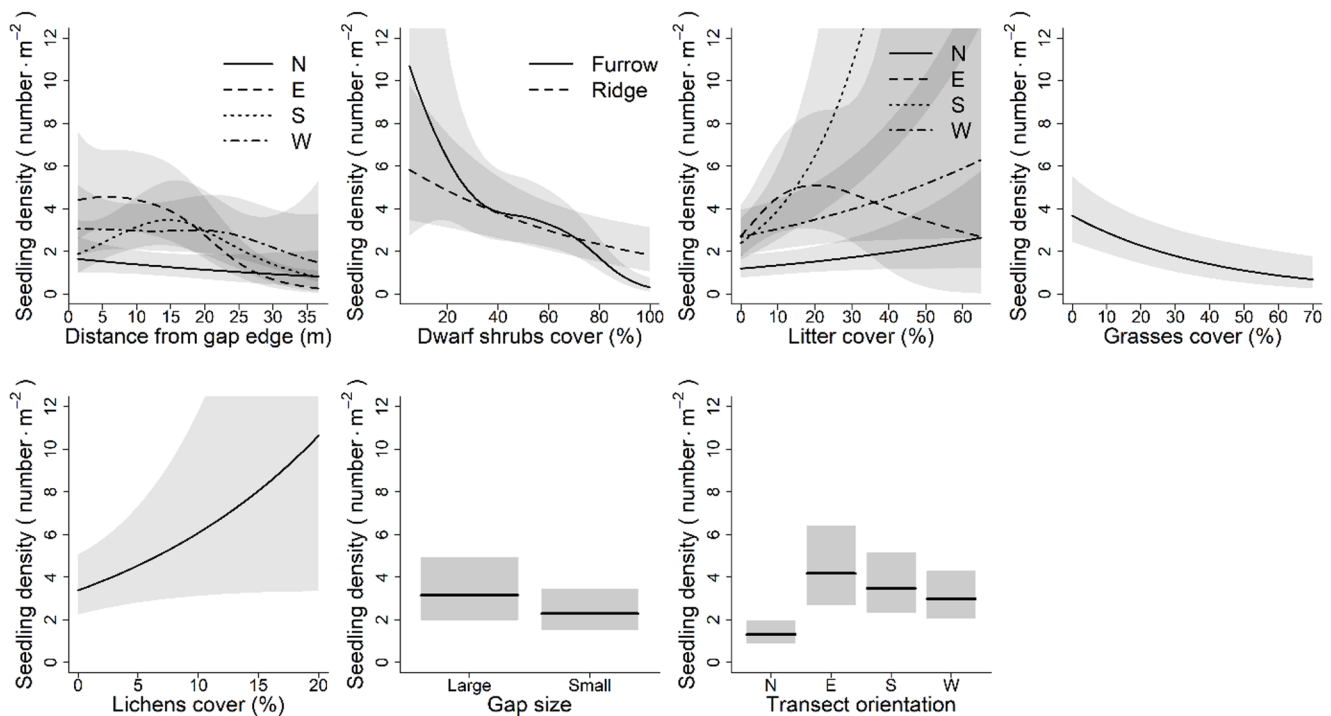


Fig. 4 Number of Scots pine seedlings (number · m⁻²) after the 8th growing season as a function of GAM covariates (extended version). Shaded bands indicate the 95% confidence intervals

Table 3 Summary of the GAM model for the expected number of Scots pine seedlings (number · m⁻²) in 2021, i.e. after the 8th growing season

Parametric coefficients	Estimate	SD	Error z value	Pr(> z)
(Intercept)	-0.23533	0.16029	-1.468	0.1421
transect E	0.70299	0.15603	4.505	<0.0001
transect S	0.68888	0.16637	4.141	<0.0001
transect W	0.79281	0.15238	5.203	<0.0001
Gap size	0.31958	0.13527	2.363	0.0181
Microtopography ridge	0.08561	0.10036	0.853	0.3936
Smooth term	E. df	Chi.sq.	Ref.df	p-value
s(distance): transect N	1.000	1.468	1.000	0.2256
s(distance): transect E	2.510	22.878	3.154	<0.0001
s(distance): transect S	2.171	5.433	2.715	0.1087
s(distance): transect W	1.977	1.488	2.472	0.4503
s(dwarf shrubs): microtopography furrow	3.401	44.722	4.241	<0.0001
s(dwarf shrubs): microtopography ridge	1.000	8.648	1.000	0.0831
s(litter): transect N	1.000	3.003	1.000	0.0616
s(litter): transect E	1.958	7.442	2.400	0.0290
s(litter): transect S	1.000	15.851	1.000	<0.0001
s(litter): transect W	1.000	3.363	1.000	0.0667
s(lichens)	1.031	4.325	1.061	0.0387
s(grasses)	1.000	13.153	1.000	0.0003
s(distance, id.gap)	2.735	10.627	7.000	0.0023
No. of observations	571			
Deviance explained (%)	32.3			

Meaning of symbols as in Table 2

disturbance dynamics that are typical of coniferous forests (Kuuluvainen 1994; Shorohova et al. 2011). This approach is highlighted in the principles of CNFM as a means of promoting natural regeneration and enhancing structural diversity within forest stands (European Commission 2023). Due to the limited number of documented applications of this method, our study aimed to address this knowledge gap by providing empirical evidence of its effectiveness in oligotrophic pine stand conditions.

After eight growing seasons, the average regeneration density in small and large gaps was just over two individuals per square metre or approximately 20,000 individuals per hectare. This is twice the initial density typically achieved in artificial regeneration. However, it is worth noting that the initial density of pine seedlings and saplings obtained by lateral (or combined) natural seeding on clearcuts often exceeds 100,000 individuals per hectare (Andrzejczyk 2000; Brichta et al. 2020). The uneven distribution of pine regeneration within the regeneration openings studied also influences the negative results. This is evidenced by the high percentage of empty sample plots, which was about 40% after the first two growing seasons and about 30% eight years after the start of the regeneration process. Therefore, the regeneration experiment cannot be unequivocally regarded as a success when evaluated in the context of Polish silvicultural practices.

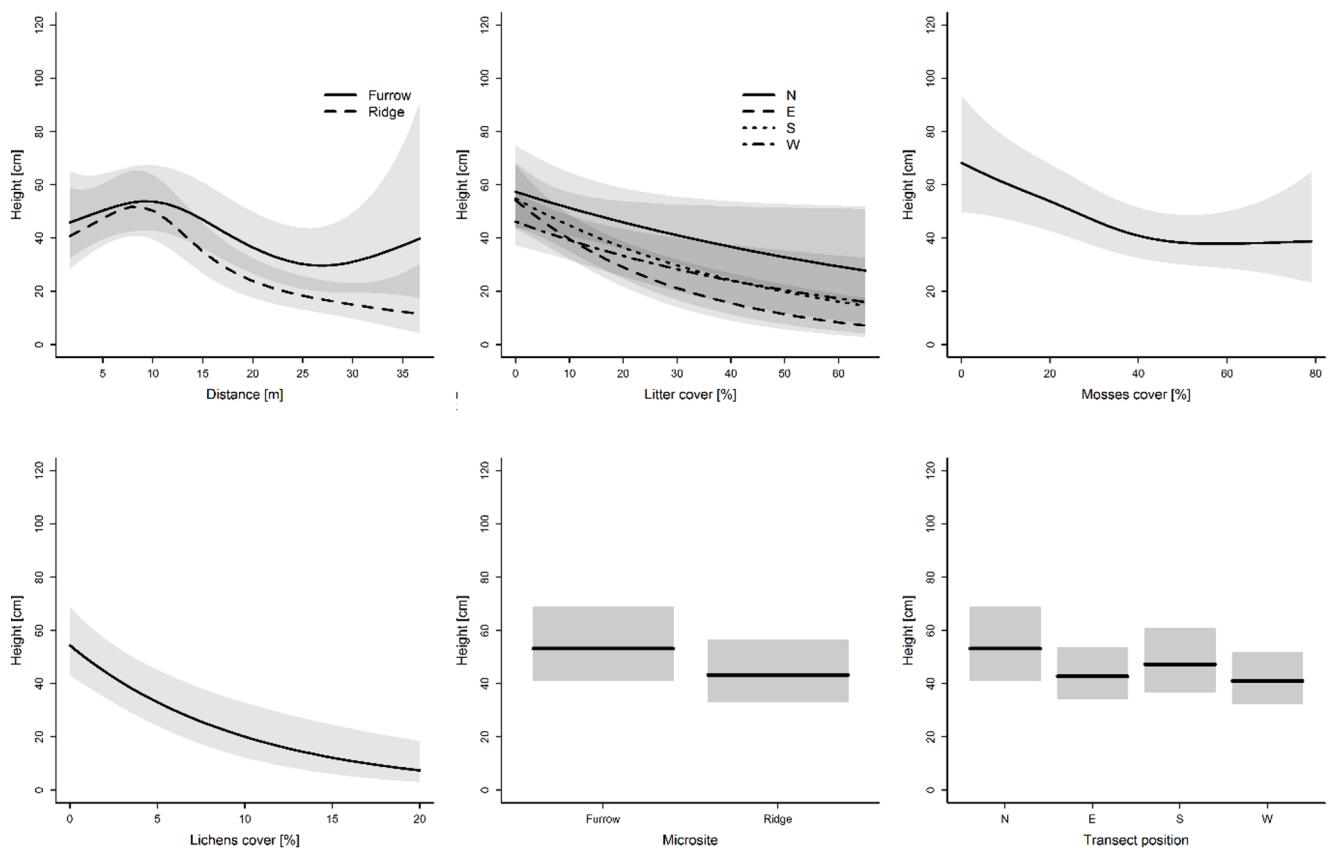


Fig. 5 Estimated maximum height (cm) for Scots pine seedlings on sample plots after the 8th growing season as a function of GAM covariates. Shaded bands indicate the 95% confidence intervals

Table 4 Summary of the GAM model for the maximum height of Scots pine seedlings after the 8th growing season

Parametric coefficients	Estimate	SD	Error z value	Pr(> t)
(Intercept)	3.86711	0.10120	38.211	<0.0001
transect E	−0.21729	0.11626	−1.869	0.0624
transect S	−0.11884	0.12699	−0.936	0.3499
transect W	−0.25853	0.11175	−2.313	0.0212
microtopography ridge	−0.19349	0.07427	−2.605	0.0095
Smooth term	Est. df	Chi.sq.	Ref.df	p-value
s(distance): microtopog- raphy furrow	2.943	3.679	3.421	0.0174
s(distance): microtopog- raphy ridge	3.203	3.996	12.201	<0.0001
s(litter): transect N	1.001	1.003	3.965	0.0473
s(litter): transect E	1.000	1.000	16.899	<0.0001
s(litter): transect S	1.000	1.000	3.956	0.0474
s(litter): transect W	1.000	1.000	7.887	0.0052
s(lichens)	1.000	1.000	18.745	<0.0001
s(mosses)	2.184	2.775	6.923	0.0003
s(distance,id.gap)	1.440	7.000	0.729	0.0076
No. of observations	380			
Deviance explained (%)	30			

Meaning of symbols as in Table 2

However, when viewed as the initial stage in the long-term development of structurally diverse forests, the obtained outcomes may be considered acceptable from an ecological perspective and aligned with the core principles CNFM. The clear spatial and height differentiation of the seedlings obtained is characteristic of the initial transition from even-aged to uneven-aged stands in a regime of minor disturbance on a small scale (Kuuluvainen 1994; Axelsson and Östlund 2001; Shorohova et al. 2011). These stands are more structurally complex than traditional uneven-aged stands and create a greater supply of ecological niches, favouring the preservation of microhabitat richness for biota (Lust et al. 2001; Zaniewski et al. 2014). They are also characterised by greater genetic diversity and adaptability to changing climatic conditions (Brang et al. 2014). Scots pine from Polish provenances shows a genetically determined tendency to produce strong lateral branches and to develop multi-stemmed forms under conditions of loose or uneven stand density (Giertych and Oleksyn 1992; Kowalczyk and Wojda 2019). From this perspective, the variation in seedling density observed across different parts of the gaps, particularly in the larger ones, may be considered unfavourable, as it could promote irregular growth forms and reduced stem quality. However, this issue may be less

relevant for other Scots pine provenances, such as those from Scandinavia, which exhibit a lower tendency to produce vigorous lateral shoots.

The average maximum height of seedlings, approximately 50 cm after eight growing seasons, considerably lower than expected when compared to both artificial and natural regeneration on large open areas, where trees of similar age often exceed 200 cm (Korzeniewicz et al. 2014; Barzdajn et al. 2019). Nonetheless, the reduced height growth observed in gaps is less problematic than it would be in clear-cut areas, where strong competition from light-demanding herbaceous species often poses a major obstacle to seedling establishment. In gaps, lower light availability slows down pine height growth, but it also helps suppress the development of aggressive weeds.

Considering the results obtained, which from a silvicultural perspective may pose challenges to maintaining continuous forest cover and developing a high-quality forest stand, it is necessary to examine the factors contributing to this outcome. Many authors studying the regeneration of pine stands emphasise that one of the most critical factors influencing the establishment and initial development of pine seedlings is adequate light conditions (de Chantal et al. 2003; Gaudio et al. 2011). It is generally accepted (Coates 2000; Malcolm et al. 2001; Pasanen et al. 2016) that the larger the opening in the forest canopy, the better the conditions for the regeneration of light-demanding species such as pine. Malcolm et al. (2001) suggest that the minimum size of regeneration gaps for pine should be at least 0.20 ha, and the ratio of gap diameter (d) to mature stand height (h) should be at least 2.0. However, more recent studies indicate that satisfactory regeneration of shade-intolerant pine species may also occur in gaps with a lower d/h ratio. For example, Wang et al. (2017) showed that natural regeneration of *Pinus tabulaeformis* was successful in gaps where the d/h ratio was approximately 1.5. Similarly, de Frutos et al. (2024) reported the establishment of *Pinus pinaster* under comparable conditions. These findings suggest that although larger gaps generally provide better light conditions, the threshold for successful regeneration may vary depending on species-specific light requirements, local site conditions, and competition pressure from ground vegetation.

However, studies on pine regeneration with canopy openings of different sizes do not always give consistent results. Rouvinen and Kouki (2011), who studied pine regeneration in forest gaps in eastern Finland, found no significant differences in seedling density or height between gaps of different diameters (h/d ratio between 0.5 and 2.0). Furthermore, a study by Hallikainen et al. (2019) in central Lapland showed that the correlation between pine seedling density and gap size was negative five years after the start of

regeneration. This suggests that gap size, correlated with the amount of light reaching the regeneration, does not always play a decisive role in establishing and further developing pine regeneration. The literature and this study show that regeneration success depends on the size of openings and other factors, which are often difficult to identify.

Many authors argue that the main reason for regeneration failures within gaps is the shading effect of the surrounding stand (Canham et al. 1990; Wayne and Bazzaz 1993). However, such situations rarely occur in pure pine stands, even those with high basal area values, such as the stand analysed in this study (basal area = 28 m²). This is because the open crowns of pine trees allow significant amounts of diffuse and direct light to reach the forest floor. As noted by Aaltonen (1919), pine seedlings can even establish in gaps created by the death of a single tree, provided the surrounding stand is not overly dense. The spatial analysis of regeneration density variability carried out in this study did not show a clear negative effect of the neighbouring stand on this characteristic. On the contrary, in large gap, regeneration density was significantly higher near the edge of the stand than in the centre of the gaps (Fig. 3). This finding contrasts with previous studies suggesting that regeneration develops best in the centre of gaps, where competition from the surrounding stand is reduced and both light and precipitation levels are highest (Gray and Spies 1996; Bolibok and Andrzejczyk 2008; Rouvinen and Kouki 2011; Pasanen et al. 2016).

In our case, the primary factor influencing the observed pattern was probably soil moisture, which plays a critical role in seed germination and seedling establishment. This study showed that regeneration density varied with the orientation of transects. The highest density was in the eastern parts of the gaps, consistent with the 'rain shadow' theory, as prevailing westerly winds in Poland result in more precipitation in these areas (Puchalski and Prusinkiewicz 1975; Bolibok et al. 2011). During the dry year of 2015 (Fig. 1d), the high light availability in the gap centre also resulted in elevated temperatures, which further dried the soil and made this area particularly unfavourable for seedling emergence.

Another factor considered in this study was the diverse microtopography of the site, resulting from the applied soil preparation method. The results showed that seedlings' density and local maximum height were higher in furrows than in ridges. Many publications indicate that soil preparation positively affects seedling density and subsequent growth during the initial regeneration phase (Béland et al. 2000; Karlsson and Örlander 2000). Furrows provide a more favourable microsite for seedling establishment due to direct seed contact with mineral soil, which is crucial for initial root development in dry years (Aleksandrowicz-Trzcńska et al. 2017; Tiebel and Karge 2025). Furthermore,

the microclimate within furrows is more favourable to seedling growth as the surrounding ridges provide partial protection from direct solar radiation, which stimulates evaporation and desiccation of germinating seeds (Andrzejczyk and Drozdowski 2003; Hansson et al. 2018).

An additional factor that may influence the response of regeneration to furrow-based site preparation is the subsequent accumulation of litter in the furrows. This litter layer can reduce evaporation and improve seedling survival and growth under drought conditions (Tiebel and Karge 2025). This effect is likely to be more pronounced in smaller gaps, where a greater proportion of the area lies within the reach of litterfall from the surrounding stand. In our study (Fig. 3), we did not observe a higher number of seedlings in furrows on small gaps, either during the initial assessment in 2015 or in the final one in 2021. However, this does not exclude the possibility that, with ongoing climate warming, the use of smaller gaps may become more beneficial (Tiebel and Karge 2025).

With regard to the influence of soil cover on Scots pine regeneration, our results for lichen and grass cover are consistent with earlier findings. An increase in lichen cover was positively correlated with seedling density, as reported in previous studies (Gmyz and Skrzyszewski 2010; Steijlen et al. 1995; Nystuen et al. 2019). In contrast, the negative effect of grass cover on pine seedling establishment and growth, previously highlighted by others (Picon-Cochard et al. 2006; Sewerniak 2016a, b; Huth et al. 2022), was also evident in our data.

The effects of lichen and grass cover on Scots pine seedling density were consistent across different positions within the gap and microtopographic features (furrows and ridges), with no statistically significant interactions observed. In contrast, the influence of the subsequent soil cover types discussed in the study showed statistically significant interactions with gap position and microtopography. Numerous studies have demonstrated the negative effect of dwarf shrub cover on Scots pine regeneration (Hyppönen et al. 2013). In our study, we detected a statistically significant interaction between microtopography and dwarf shrub cover in shaping seedling density. Although furrows generally provided more favourable microsites for seedling emergence compared to ridges, this effect diminished when dwarf shrub cover exceeded approximately 30% (Fig. 4).

Our study indicates a positive correlation between litter cover and the density of naturally regenerated Scots pine seedlings. This pattern may reflect the mechanism proposed by Tiebel and Karge (2025), in which litterfall occurring after seedling emergence improves microsite conditions. However, we observed that the position within the gap strongly modulates this effect. The positive relationship was most pronounced in the southern part of the gap, weakest

in the northern part, and intermediate in the eastern and western sections. These differences are likely related to the influence of direct solar radiation, which is most intense in the northern portions of gaps. While litter may reduce soil evaporation and improve seedling growth conditions in the southern part of the gap, the high levels of heat delivered by direct sunlight in the northern part likely offset this benefit.

The lowest density was observed in the northern parts of the gaps, where high sunlight increases evaporation, making conditions unfavourable for seedling establishment (de Chantal et al. 2003; Bolibok and Andrzejczyk 2008). However, seedlings that survived in these areas grew the tallest. This supports the idea that conditions favourable to seedling establishment are not always advantageous to subsequent development and vice versa (Gray and Spies 1996; Hyppönen et al. 2013). A similar pattern was observed for two other soil cover variables: litter cover and lichen cover. Both were positively correlated with seedling density but negatively associated with the local maximum height of Scots pine seedlings. This is likely due to the fact that lichens tend to colonise areas where herbaceous vegetation is absent, and litter remains more visible and decomposes more slowly in patches not occupied by ground vegetation (Wardle and Zackrisson 2005; Hyppönen et al. 2013). These areas are probably among the most nutrient-poor within the study site, where seedling height growth is more limited over the long term compared to more productive microsites.

Implications for management

In light of these findings, great caution is advised when considering the replacement of clear-cutting with small-scale regeneration cuts in mature pine stands. The optimal strategy may involve closely monitoring stand dynamics at each site and, above all, making full use of naturally occurring gaps – both small and large – that emerge in dense canopy conditions, along with the regeneration that establishes within them. Careful analysis of such naturally regenerated gaps can help determine the key parameters for purposefully designed openings, ensuring they are tailored to local conditions, which may vary greatly depending on geographic location, soil fertility, moisture regime, and other environmental factors. At the same time, such observations may help identify cases in which alternatives to clear-cutting (e.g., shelterwood systems) should be considered – or even confirm that a modified form of clear-cutting, aligned with current silvicultural guidelines, remains the most appropriate solution.

Conclusion

An urgent challenge for forestry in Poland and elsewhere is finding alternatives to clear-cutting systems, especially for pure Scots pine stands on oligotrophic sites. Group cutting with small-scale natural regeneration openings (0.05–0.30 ha) is a promising approach promoted in European forestry guidelines to enhance stand diversity, ecological resilience, and landscape value. Our findings suggest that natural regeneration of Scots pine in small and large gaps on oligotrophic sites is possible but subject to strong microsite variability. However, results from an eight-year experiment indicate that satisfactory outcomes are not always guaranteed. Both small and large gaps showed significant variability in regeneration success, influenced by factors beyond light availability. Key challenges include weather conditions, ground vegetation competition (e.g., *Calamagrostis* spp. and heather), uneven moisture and light distribution, and high seedling mortality in certain gap areas. While soil preparation mitigates some issues, dense initial regeneration (e.g., ~34,000 ind./ha) often declines over time. Additional concerns include the slender growth of seedlings, vulnerability to snow damage, and increased browsing by ungulates.

Acknowledgements Sincere gratitude is extended to colleagues from the Department of Silviculture, Institute of Forest Sciences, Warsaw University of Life Sciences, Stanisław Drozdowski, Bogdan Brzeziecki, Tadeusz Andrzejczyk, Kamil Bielak and Bohdan Kolisnyk for their support and guidance in writing this article.

Author contributions M.C. conceived the ideas, designed the methodology, collected the data, analyzed the data and wrote the manuscript. L.B. statistical analyzes. All authors critically reviewed the drafts and approved the final version for publication.

Funding This research was financially supported by the General Directorate of State Forests in Poland (GA No. OR.271.3.16.2017).

Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright

holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Aaltonen VT (1919) Über die natürliche Verjüngung der Heidewälder im finnischen Lappland I. Commun Inst for- Est Finl 1:1–319 (In Finnish with German summary)
- Aleksandrowicz-Trzcińska M, Drozdowski S, Wołczyk Z, Bielak K, Żybura H (2017) Effects of reforestation and site preparation methods on early growth and survival of Scots pine (*Pinus sylvestris* L.) in South-Eastern Poland. Forests 8:421. <https://doi.org/10.3390/f8110421>
- Andrzejczyk T (2000) Wpływ odległości od ściany drzewostanu na zagęszczenie i przeżywalność nalotów sosny zwyczajnej (*Pinus sylvestris* L.) na zrębach zupełnych i gniazdach. Sylwan 144(1):27–42 (in Polish)
- Andrzejczyk T (2006) Rębna przerębowa w drzewostanach sosnowych. Sylwan 8:52–60 (in Polish)
- Andrzejczyk T (2007) Wpływ przerzedzenia okapu górnego na rozwój podrostów sosny zwyczajnej (*Pinus sylvestris* L.) w pogradacyjnych drzewostanach w lasach pilskich. Sylwan 1:20–29. <https://doi.org/10.26202/sylvan.2006009>. (in Polish)
- Andrzejczyk T, Drozdowski S (2003) Rozwój naturalnego odnowienia sosny zwyczajnej na powierzchni przygotowanej plugiem dwuodkładnicowym. Sylwan 5:28–35. <https://doi.org/10.26202/sylvan.2003952>. (in Polish)
- Andrzejczyk T, Żybura H (2012) Sosna zwyczajna: odnawianie naturalne i alternatywne metody hodowli. PWRiL, Warszawa (in Polish)
- Ashton MS, Keltly MJ (2018) The practice of silviculture: applied forest ecology, 8th edn. Wiley, Hoboken, p 174
- Axelsson AL, Östlund L (2001) Retrospective gap analysis in a Swedish boreal forest landscape using historical data. For Ecol Manage 147(2–3):109–122. [https://doi.org/10.1016/S0378-1127\(00\)00470-9](https://doi.org/10.1016/S0378-1127(00)00470-9)
- Axelsson EP, Lundmark T, Högborg P, Nordin A (2014) Belowground competition directs spatial patterns of seedling growth in boreal forests in Fennoscandia. Forests 5:2106–2121. <https://doi.org/10.3390/f5092106>
- Baltas E (2007) Spatial distribution of climatic indices in northern Greece. Meteorol Appl 14:69–78. <https://doi.org/10.1002/met.7>
- Barbeito I, Fortin MJ, Montes F, Cañellas I (2009a) Response of pine natural regeneration to small-scale spatial variation in a managed Mediterranean mountain forest. Appl Veg Sci 12:488–503. <https://doi.org/10.1111/j.1654-109X.2009.01043.x>
- Barbeito I, Fortin MJ, Montes F, Cañellas I (2009b) Response of pine natural regeneration to small-scale spatial variation in a managed Mediterranean mountain forest. Appl Veg Sci 12:488–503. <https://doi.org/10.1111/j.1654-109X.2009.01043.x>
- Barzdajn W, Kowalkowski W, Tomczak R (2019) Porównanie odnowień sosny zwyczajnej powstałych z siewu i sadzenia w różnych terminach. Leśne Prace Badawcze 80(3):213–217 (in Polish)
- Barzdajn W, Zientarski J (2007) Wielogeneracyjne drzewostany sosnowe jako forma ochrony siedlisk leśnych. Studia i Materiały Centrum Edukacji Przyrodniczo-Leśnej, 9(2–3 [16] cz. 2). (in Polish)
- Béland M, Agestam E, Ekö PM, Gemmel P, Nilsson U (2000) Scarification and seedfall affects natural regeneration of Scots pine under two shelterwood densities and a clear-cut in southern Sweden. Scand J Forest Res 15(2):247–255. <https://doi.org/10.1080/028275800750015064>

- Bernadzki E (2000) Półnaturalna hodowla lasu. Biblioteczka leśniczego 129 (in Polish)
- Bigler C, Bräker OU, Bugmann H, Dobbertin M, Rigling A (2006) Drought as an inciting mortality factor in Scots pine stands of the Valais. *Swiss Ecosyst* 9(3):330–343
- Bolibok L, Andrzejczyk T (2008) Analiza zagęszczenia samosiewów brzozy i sosny na gniazdach na podstawie modelu promieniowania słonecznego. *Sylvan* 2:10–19. <https://doi.org/10.26202/sylvan.2006017>. (in Polish)
- Bolibok L, Andrzejczyk T, Drozdowski S, Szeligowski H (2011) Wysokość siedmioletnich odnowień dębowych na gniazdach w różnych warunkach siedliskowych. *Leśne Prace Badawcze* 72(2):163–170. <https://doi.org/10.2478/v10111-011-0016-7>. (in Polish)
- Brang P, Spathelf P, Larsen JB, Bauhus J, Boncina A, Chauvin C, Drossler L, Garcia-Guemes C, Heiri C, Kerr G, Lexer MJ, Mason B, Mohren F, Muhlethaler U, Nocentini S, Svoboda M (2014) Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. *Forestry* 87:492–503
- Brichta J, Bilek L, Linda R, Vítámvás J (2020) Does shelterwood regeneration on natural Scots pine sites under changing environmental conditions represent a viable alternative to traditional clear-cut management? *Cent Eur Forestry J* 66:104–115
- Calama R, Manso R, Barbeito I, Cañellas I, Pardos M (2015) Is natural regeneration a bottleneck in the performance of *Pinus sylvestris* mountain forests? Mountain Forest Management in a Changing World, Proceedings of the conference, 6–9 July 2015, Smokovce, Slovakia
- Canham CD, Denslow JS, Platt WJ, Runkle JR, Spies TA, White PS (1990) Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can J Forest Res* 20(5):620–631. <https://doi.org/10.1139/x90-084>
- Ciancio O, Iovino F, Menguzzato G, Nicolaci A, Nocentini S (2006) Structure and growth of a small group selection forest of Calabrian pine in Southern Italy: a hypothesis for continuous cover forestry based on traditional silviculture. *For Ecol Manage* 224:229–234
- Coates KD (2000) Conifer seedling response to northern temperate forest gaps. *For Ecol Manage* 127:249–269. [https://doi.org/10.1016/S0378-1127\(99\)00135-8](https://doi.org/10.1016/S0378-1127(99)00135-8)
- Çoban S, Çolak AH, Rotherham ID, Özalp G, Çalışkan A (2018) Effects of canopy gap size on the regeneration of Scots pine (*Pinus sylvestris* L.) in Eskişehir-Çatacik region of Turkey. *Austrian J Forest Sci* 3:183–212
- Czacharowski M, Drozdowski S (2021) Zagospodarowanie drzewostanów sosnowych (*Pinus sylvestris* L.) w zmieniających się uwarunkowaniach środowiskowych i społecznych. *Sylvan* 165(5):355–370. <https://doi.org/10.26202/sylvan.2021030>. (in Polish)
- De Chantal M, Leinonen K, Kuuluvainen T, Cescatti A (2003) Early response of *Pinus sylvestris* and *Picea abies* seedlings to an experimental canopy gap in a boreal spruce forest. *For Ecol Manage* 176:321–336
- De Martonne E (1926) Une nouvelle fonction climatologique: L'indice d'aridité. *Meteorologie* 2:449–458
- Downey M, Valkonen S, Heikkinen J (2018) Natural tree regeneration and vegetation dynamics across harvest gaps in Norway spruce dominated forests in southern Finland. *Can J Forest Res* 48:524–534. <https://doi.org/10.1139/cjfr-2017-0358>
- Drozdowski S (2018) Rębnia stopniowa [Irregular shelterwood system]. Biblioteczka leśniczego, Wydawnictwo Świat Warszawa, p 319 (in Polish)
- Dyderski MK, Paź S, Frelich LE, Jagodziński AM (2018) How much does climate change threaten European forest tree species distributions? *Glob Change Biol* 24:1150–1163
- European Commission (2023) Directorate-General for Environment, Guidelines on closer-to-nature forest management, Publications Office of the European Union, <https://doi.org/10.2779/731018>
- Frutos SD, Manso R, Roig-Gómez S, Ruiz-Peinado R, Río MD, Bravo-Fernández JA (2024) Height increment patterns in *Pinus pinaster* seedlings emerging in naturally regenerated gaps. *For Int J* 97(4):635–648. <https://doi.org/10.1093/forestry/cpae002>
- Gallo J, Bilek L, Šimůnek V, Roig S, Bravo-Fernández JA (2020) Uneven-aged silviculture of Scots pine in Bohemia and Central Spain: comparison study of stand reaction to transition and long-term selection management. *J Forest Sci*. <https://doi.org/10.1722/1/147/2019-JFS>
- Gaudio N, Balandier P, Perret S, Ginisty C (2011) Growth of understorey Scots pine (*Pinus sylvestris* L.) saplings in response to light in mixed temperate forest. *Forestry* 84:187–195. <https://doi.org/10.1093/forestry/cpr005>
- Giertych M, Oleksyn J (1992) Studies on genetic variation in Scots pine (*Pinus sylvestris* L.) coordinated by IUFRO
- Gmyz R, Skrzyszewski J (2010) Wpływ zróżnicowania mikrosiedliskowego boru świeżego na liczebność odnowienia naturalnego sosny zwyczajnej (*Pinus sylvestris* L.). *Sylvan* 154(03):173–181 (in Polish)
- Gołos P (2018) Społeczne i Ekonomiczne Aspekty Pozaprodukcyjnych Funkcji Lasu i Gospodarki Leśnej – Wyniki Badań Opinii Społecznej. Wydawnictwo Instytut Badawczy Leśnictwa, Sękocin Stary, Poland (in Polish)
- Gray AN, Spies TA (1996) Gap size, within-gap position, and canopy structure effects on conifer seedling establishment in forest gaps. *J Ecol* 84:635–645
- Hallikainen V, Hökkä H, Hyppönen M, Rautio P, Valkonen S (2019) Natural regeneration after gap cutting in Scots pine stands in northern Finland. *Scand J for Res* 34(2):115–125. <https://doi.org/10.1080/02827581.2018.1557248>
- Hanewinkel M, Cullmann D, Schelhaas MJ, Nabuurs GJ, Zimmermann NE (2013) Climate change may cause severe loss in the economic value of European forest land. *Nat Clim Chang* 3:203–207. <https://doi.org/10.1038/nclimate1687>
- Hansson LJ, Ring E, Franko MA, Gärdenäs AI (2018) Soil temperature and water content dynamics after disc trenching a sub-xeric Scots pine clearcut in central Sweden. *Geoderma* 327:85–96. <https://doi.org/10.1016/j.geoderma.2018.04.023>
- Hjältén J, Hägglund R, Löfroth T, Roberge JM, Dynesius M, Olsson J (2017) Forest restoration by burning and gap cutting of voluntary set-asides yield distinct immediate effects on saproxylic beetles. *Biodivers Conserv* 26:1623–1640. <https://doi.org/10.1007/s10531-017-1321-0>
- Huth F, Wehnert A, Wagner S (2022) Natural regeneration of Scots pine requires the application of silvicultural treatments such as overstorey density regulation and soil preparation. *Forests* 13(6):817
- Hyppönen M, Hallikainen V, Niemelä J, Rautio P (2013) The contradictory role of understory vegetation on the success of Scots pine regeneration. *Silva Fenn* 47:1. <https://doi.org/10.14214/sf.903>
- Instytut Meteorologii i Gospodarki Wodnej (2023). Online: https://danepubliczne.imgw.pl/data/dane_pomiarowo_obserwacyjne. Accessed 15 Oct 2025
- Iszkulo G, Armatus L, Dering M, Ksepko M, Tomaszewski D, Ważna A, Giertych MJ (2020) Jemiola jako zagrożenie dla zdrowotności drzewostanów iglastych. *Sylvan* 164(03):226–236
- Jaworski A (2011) Hodowla lasu: Sposoby zagospodarowania, odnowienie lasu, przebudowa i przemiana drzewostanów. PWRiL, Warszawa (in Polish)
- Johann E (2006) Historical development of nature-based forestry in Central Europe. In Nature-based forestry in Central Europe. Alternatives to industrial forestry and strict preservation. Diaci J (ed.). Proceedings, Univ. of Ljubljana, pp. 1–18

- Karlsson C, Örlander G (2000) Soil scarification shortly before a rich seed fall improves seedling establishment in seed tree stands of *Pinus sylvestris*. *Scand J for Res* 15(2):256–266. <https://doi.org/10.1080/028275800750015073>
- Koivula M, Silvennoinen H, Koivula H, Tikkanen J, Tyrväinen L (2020) Continuous-cover management and attractiveness of managed Scots pine forests. *Can J Forest Res* 50(8):819–828
- Korzeniewicz R, Skoczylas M, Szmyt J, Wawro T (2014) Charakterystyka biometryczna rozpięrczy w młodnikach sosnowych w Nadleśnictwie Kalisz. *Zarządzanie Ochroną Przyrody w Lasach* 8:126–137. [https://doi.org/10.5604/20811438.1158035\[inPolish\]](https://doi.org/10.5604/20811438.1158035[inPolish])
- Kowalczyk J, Wojda T (2019) Wyniki 35-letniego doświadczenia proweniencyjnego z sosną zwyczajną z serii IUFRO 1982 na powierzchniach w Wyszowie i Sękocinie. *Sylvan* 163(07). (in Polish)
- Krakau UK, Liesebach M, Aronen T, Lelu-Walter MA, Schneck V (2013) Scots pine (*Pinus sylvestris* L.). In: Pagues LE (ed.) *Forest tree breeding in Europe: current state-of-the-art and perspectives. Managing forest ecosystems*, vol 25, pp 267–323. https://doi.org/10.1007/978-94-007-6146-9_6
- Kunert N (2020) Preliminary indications for diverging heat and drought sensitivities in Norway spruce and Scots pine in Central Europe. *iForest - Biogeosci for* 13(2):89–91. <https://doi.org/10.3832/for3216-012>
- Kuuluvainen T (1994) Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. *Ann Zool Fenn* 31:35–51
- Lüdtke D (2018) ggeffects: tidy Data Frames of Marginal Effects from Regression Models. *J Open Source Softw* 3:772. <https://doi.org/10.21105/joss.00772>
- Lundmark H, Josefsson T, Östlund L (2013) The history of clear-cutting in northern Sweden – Driving forces and myths in boreal silviculture. *For Ecol Manag* 3007:112–122
- Lust N, Geudens G, Nachtergale L (2001) Aspects of biodiversity of Scots pine forests in Europe. *Silva Gandavensis*, 66
- Malcolm DC, Mason WL, Clarke GC (2001) The transformation of conifer forests in Britain—regeneration, gap size and silvicultural systems. *For Ecol Manag* 151(1–3):7–23
- Matias L, Alistair SJ (2014) Impacts of predicted climate change on recruitment at the geographical limits of Scots pine. *J Exp Bot* 65(1):299–310. <https://doi.org/10.1093/jxb/ert376>
- Matuszkiewicz W (2013) *Przewodnik do oznaczania zbiorowisk roślinnych Polski*. Państwowe Wydawnictwo Naukowe, Warszawa, p 297 (in Polish)
- Mierzejewski W, Niedźwiedzki P (1954) Z badań nad przebiegiem odnowienia w rębni gniazdowej. *Sylvan* 98(1):51–58 (in Polish)
- Mlinšek D (2006) Close to nature forestry as the only true culture of a man's activity. In: Diaci J (Ed.), *Nature-based forestry in central Europe. Alternatives to industrial forestry and strict preservation*. Studia Forestalia Slovenica, Ljubljana, vol 126, pp 91–103
- Nystuen KO, Sundsdal K, Opedal ØH, Holien H, Strimbeck GR, Graae BJ (2019) Lichens facilitate seedling recruitment in alpine heath. *J Veg Sci* 30(5):868–880
- Okolowicz W (2000) *Strefy klimatyczne [świata]*. W: *Atlas geograficzny* (Wyd. XXXII), PPWK, Warszawa (in Polish)
- Paluch R (2004) Stan, warunki i problemy odnowienia naturalnego sosny w Puszczy Białowieskiej. *Sylvan* 11:9–21 (in Polish)
- Pardos M, Montes F, Aranda I, Cañellas I (2007) Influence of environmental conditions on germinant survival and diversity of Scots pine (*Pinus sylvestris* L.) in central Spain. *Eur J for Res* 126(1):37–47
- Pasanen H, Rouvinen S, Kouki J (2016) Artificial canopy gaps in the restoration of boreal conservation areas: long-term effects on tree seedling establishment in pine-dominated forests. *Eur J Forest Res* 135(4):697–706. <https://doi.org/10.1007/s10342-016-0965-8>
- Picon-Cochard C, Coll L, Balandier P (2006) The role of below-ground competition during early stages of secondary succession: the case of 3-year-old Scots pine (*Pinus sylvestris* L.) seedlings in an abandoned grassland. *Oecologia* 148:373–383
- Plan Urządzania Lasu (2020) *Opis Ogólny Lasów Nadleśnictwa Janów Lubelski sporządzony na okres od 1 stycznia 2020 do 31 grudnia 2029 roku, na podstawie stanu lasu w dniu 1 stycznia 2020 roku*. Biuro Urządzania Lasu i Geodezji Leśnej Oddział w Lublinie (in Polish)
- Plewa R, Mokrzycki T (2017) Occurrence, biology, and economic importance of the sharp-dentated bark beetle *Ips acuminatus* (Gyllenhal, 1827) (Coleoptera, Curculionidae, Scolytinae) in Poland. *Sylvan* 161(8):619–629. <https://doi.org/10.26202/sylvan.2017077>
- Pommerening A, Murphy S (2004) A review of the history, definitions, and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* 77:27–44. <https://doi.org/10.1093/forestry/77.1.27>
- Pretzsch H, Schütze G, Uhl E (2013) Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by interspecific facilitation. *Plant Biol* 15:483–495
- Puchalski T, Prusinkiewicz Z (1975) *Ekologiczne podstawy siedliskoznawstwa leśnego*. PWRiL, Warszawa (in Polish)
- R Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Remeš J (2018) Development and present state of close-to-nature silviculture. *J Landsc Ecol* 11:17–32. <https://doi.org/10.2478/jleco-1-2018-0010>
- Rouvinen S, Kouki J (2011) Tree regeneration in artificial canopy gaps established for restoring natural structural variability in a Scots pine stand. *Silva Fenn* 45(5):1079–1091. <https://doi.org/10.14214/sf.88>
- Schütz JP, Saniga M, Diaci J, Vrška T (2016) Comparing close-to-nature silviculture with processes in pristine forests: lessons from Central Europe. *Ann for Sci* 73:911–921. <https://doi.org/10.1007/s13595-016-0579-9>
- Sewerniak P (2016a) Differences in early dynamics and effects of slope aspect between naturally regenerated and planted *Pinus sylvestris* woodland on inland dunes in Poland. *iForest* 9(6):875–882. <https://doi.org/10.3832/for1728-009>
- Sewerniak P (2016b) Differences in early dynamics and effects of slope aspect between naturally regenerated and planted *Pinus sylvestris* woodland on inland dunes in Poland. *iForest* 9:875–882. <https://doi.org/10.3832/for1728-009>
- Shorohova E, Kneeshaw D, Kuuluvainen T, Gauthier S (2011) Variability and dynamics of old-growth forests in the circumboreal zone: implications for conservation, restoration, and management. *Silva Fenn* 45:785–806
- Steijlen I, Nilsson M-C, Zackrisson O (1995) Seed regeneration of Scots pine in boreal forest stands dominated by lichen and feather moss. *Can J Forest Res* 25(5):713–723
- Szmyt J (2025) Group-selection system as alternative management of Scots pine (*Pinus sylvestris* L.) forests facing climate change. *Eur J Forest Res* 144(1):133–148. <https://doi.org/10.1007/s10342-024-01746-1>
- Tiebel K, Karge A (2025) Influence of drought stress on the seed germination and seedling survival of *Pinus sylvestris* and *Larix decidua*. *For Ecol Manag* 591:122852
- Tomczyk AM, Bednorz E (2022) *Atlas of Climate of Poland 1991–2020*. Bogucki Wydawnictwo Naukowe, Poznań, Poland, p 126 (in Polish)
- Vacchiano G, Garbarino M, Borgogno Mondino E, Motta R (2012) Evidences of drought stress as a predisposing factor to Scots pine decline in Valle d'Aosta (Italy). *Eur J Forest Res* 131(4):989–1000

- van Rij J, Wieling M, Baayen RH, van Rijn H, van Rij MJ (2017) Package ‘itsadug’
- Vilà-Cabrera A, Rodrigo A, Martínez-Vilalta J, Retana J (2012) Lack of regeneration and climatic vulnerability to fire of Scots pine may induce vegetation shifts at the southern edge of its distribution. *J Biogeogr* 39(3):488–496
- Walas Ł, Kędziora W, Ksepko M et al (2022) The future of *Viscum album* L. in Europe will be shaped by temperature and host availability. *Sci Rep* 12:17072. <https://doi.org/10.1038/s41598-022-21532-6>
- Wardle DA, Zackrisson O (2005) Effects of species and functional group loss on island ecosystem properties. *Nature* 435(7043):806–810
- Wayne PM, Bazzaz FA (1993) Morning vs. afternoon sun patches in experimental forest gaps – consequences of temporal incongruency of resources to birch regeneration. *Oecologia* 94:235–243. <https://doi.org/10.1007/BF00341324>
- Wood S (2006) Generalized additive models: an introduction with R, 1st edn. Chapman and Hall/CRC, Boca Raton, FL
- Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc Ser B (Stat Methodol)* 73:3–36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>
- Yamamoto SI (2000) Forest gap dynamics and tree regeneration. *J Forest Res* 5:223–229
- Zajączkowski J, Brzeziecki B, Perzanowski K, Kozak I (2013) Impact of potential climate changes on competitive ability of main forest tree species in Poland. *Sylvan* 157(4):253–261. <https://doi.org/10.26202/sylvan.2012134>. (in Polish)
- Zaniewski PT, Bernatowicz A, Kozub Ł, Truszkowska E, Dembicz I, Wierzbicka M (2014) Traditionally managed patch of *Cladonia*-Scots pine forest in the Biebrza valley—specificity of the protected forest community shaped by human activity. *Ecol Quest* 20:45–52
- Zielony R, Kliczkowska A (2012) Regionalizacja przyrodniczo-leśna Polski 2010. Centrum Informacyjne Lasów Państwowych, Warszawa, p 356 (in Polish)
- Wang Z, Yang H, Dong B, Zhou M, Ma L, Jia Z, Duan J (2017) Effects of canopy gap size on growth and spatial patterns of Chinese pine (*Pinus tabulaeformis*) regeneration. *Forest Ecology and Management*, 385, 46–56.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.