Differential modulation of crown allometry and stem growth at gap edges in five European tree species by drought conditions

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ABSTRACT

Background: In Central Europe, forests are increasingly affected by various disturbances, resulting in an increasing gap formation in the canopy. In order to support goal-oriented management, more knowledge is required about the acclimation of the crown and its effects on the basal area growth of trees at the edge of a gap.

Methods: This work compared trees' growth and crown structure at the edge of a transient gap, with a gap size of more than 80 m^2, with trees in the stand that were at least 30 m away from the gap. A total of 249 European beeches (*Fagus sylvatica* L.), Norway spruces (*Picea abies* L. Karst), Scots pines (*Pinus sylvestris* L.), oaks (*Quercus* spp.; *Quercus petraea* (Matt.) Liebl., *Quercus robur* L.), and silver firs (*Abies alba* Mill.) were examined on long-term experimental plots in southern Germany. Various crown measures were developed and calculated using high-resolution terrestrial laser scanning (TLiDAR) to capture the three-dimensional crown structures. Growth responses to edge conditions were measured based on tree rings. Using linear mixed models, we predict the basal area increment of edge trees relative to trees in the stand under wet and dry soil moisture conditions after the gap formation.

Results: We identified i) species-specific acclimation of the crown of edge trees after the gap formation, ii) under wet soil moisture conditions a growth increase of 25%–45% for beech, pine, and oak edge trees and growth losses of 5%–60% for spruce and fir and iii) coniferous tree species benefited from the edge position regarding their basal area increment under dry soil moisture conditions and deciduous tree species grew regardless of the soil moisture conditions at the edge of a gap.

Conclusion: Gaps have a species-specific effect on the habitus and growth of edge trees and can have both positive and negative impacts on silviculture.

1. Introduction

In Central Europe, forests are increasingly affected by gaps in the canopy (Kucbel et al., 2010; Seidl et al., 2014; McDowell et al., 2020). Natural disturbances such as storms, fires, or insects (Turner, 2010; Lindner et al., 2010; Seidl et al., 2014, 2018), as well as human interventions, lead to canopy gaps (Yaffee, 1999; Senf and Seidl, 2021). Forest management focused on structurally rich stands (Vepakomma et al., 2011), and increasing wood utilisation has also exacerbated these openings (Palahí et al., 2021). As a result, 17% of the forest area in Europe was disturbed within the last 30 years (1986–2017), leading to a large amount of forest edges (Senf and Seidl, 2021).

Gaps in the canopy reduce competition pressure for trees at the edge of the gap and provide them with more light for photosynthesis (Bugmann, 2001; Schliemann and Bockheim, 2011; Muscolo et al., 2014). Trees grow toward light to maximise their photosynthesis rate (Pretzsch et al., 2015; Wimalasekera, 2019). Consequently, edge trees extend their growth toward the gap and can even close smaller gaps (Stenberg et al., 1994; Vepakomma et al., 2011; Richards and Hart, 2011). Within five years, trees of boreal mixed deciduous coniferous forests can grow up to 2 m into the gap and gap edge trees respond to canopy gaps with an increase in height growth (Vepakomma et al., 2011). Nevertheless, how the crown structure of gap trees changes in detail and gets structurally acclimated to the gap is still to be determined. Since the 21st century, laser measurement systems based on LiDAR (Light Detection And Ranging), such as terrestrial laser scans (TLS), have been used in forestry science and enable non-destructive, three-dimensional measurements of trees in the millimetre range (Disney, 2019; Calders

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et al., 2020). Metrics that go beyond the description of crown expansion still have to be developed in some cases (Fernández-Sarría et al., 2013; Reich et al., 2021). Analysing the crown structure of trees at the edge of a gap is particularly important. Denser crowns can enhance light absorption and increase a tree's productivity (Pretzsch, 2014). Pretzsch et al. (2022) have shown that the external characteristics of tree crowns are closely linked to the internal stem structure. Within gaps, edge trees particularly benefit from increased water and nutrient availability (Ritter et al., 2005; Schliemann and Bockheim, 2011). Depending on the tree species, this favours their growth and results in 15%–30% (Biber and Pretzsch, 2022) or 39% (Gray et al., 2012) higher growth rates than trees in a closed stand.

Various studies have examined the drought stress response of trees in stands and have concluded that particularly younger trees growing at lower densities are less susceptible to drought (D'Amato et al., 2013; Bottero et al., 2017; Diaconu et al., 2017). However, the forest interior climate is disturbed in gaps, leading to a microclimate characterized by higher top soil temperatures and wind speeds (Abd Latif and Blackburn, 2010; Gaudio et al., 2017; Gromke and Ruck, 2018). Based on current climate projections, an increase in the frequency, duration, and intensity of droughts is predicted, which will further exacerbate the climate conditions in the gap (Samaniego et al., 2018; Szejner et al., 2020; IPCC, 2022). These conditions may enhance the drought stress response of trees at forest edges. In contrast to stands, less is known about the drought stress response of trees on forest edges. A few studies investigate the drought stress response of edge trees in Amazonas (e.g. Laurance et al., 2001; Albiero-Júnior et al., 2021) and Buras et al. (2018) investigate the drought-induced mortality of Scots pines at permanent edges (between forests and other land cover classes). As far as we know, no study has investigated the drought stress response of different tree species at transient edges (temporarily unstocked forest areas that usually close again through forest regeneration) in temperate forests. The research on forest gaps has mainly focused on the climatic and soil physiological conditions in gaps (Vilhar et al., 2015; Gaudio et al., 2017), seedling regeneration (Coates, 2000) and mortality of edge trees (Keane et al., 2001). Less is still known about how the crown structure development of edge trees after the gap formation, how individual tree species benefit from a transient edge in their growth and how drought affects the growth of edge trees. Given this lack of knowledge, the hypothesis of this research were:

  i) Crown metrics of edge trees differ significantly from stand trees after the gap formation and are species-specific.
  ii) Compared to trees in the stand, edge trees benefit tree species specifically from the gap formation in their basal area increment under wet soil moisture conditions.
  iii) During dry soil moisture conditions, edge trees reduce their basal area increment more than the stand trees

The five tree species, Norway spruce (*Picea abies* L. Karst), European beech (*Fagus sylvatica* L.), Scots pine (*Pinus sylvestris* L.), oak (*Quercus* spp.; *Quercus petraea* (Matt.) Liebl., *Quercus robur* L.), and silver fir (*Abies alba* Mill.) were investigated on long-term experimental plots in Germany. Terrestrial laser scans (TLS) were used to capture the three-dimensional crown structure, and the basal area increment (bai) was analysed through tree rings. This work compared trees at the edge of a transient gap with a gap size of more than 80 m^2 with trees in the stand that were at least 30 m away from the gap. In order to exclude a significant influence of the gap on the stand during the analysis, a minimum distance of 30 m from the gap was chosen for the selected stock trees according to Vepakomma et al. (2011) and Sandoval and Cancino (2008). In the following, we would refer to the examined trees at the edge of a gap as edge trees and the trees in the stand as stand trees.

2. Material and methods

2.1. Long-term experimental plots as database

Overall, 249 trees were selected, 110 trees at transient edges (edge trees) and 139 trees in the stand (stand trees). Twelve long-term experimental sites in southern Germany were selected that have been disturbed by calamity or heavy thinning in recent decades (Fig. 1b). The experimental sites are between 400 and 800 m above sea level and are predominantly located in the main distribution areas of the respective tree species (Fig. 1a). The mean annual temperature ranged between 5.0 °C and 7.7 °C, and the total annual precipitation ranged between 600 and 1,200 mm. Predominant soil types were Luvisols, Podsole and Cambisols, with different nutrient supplies and water balances (Table S1). The experimental plots were established between 1934 and 1994 and have been measured every 5–9 years since then. The plots represent pure and mixed stands. Most sites experienced several droughts during this study period, while recent years have been characterised by increasingly drier conditions (Fig. 1c).

Individual plots of the experiment were affected by a calamity such as storm, snow or insects or by heavy thinning/releasing during the experiment, resulting in gaps and transient edges in the forests. In this work, we follow Biber and Pretzsch (2022) and define edge trees as trees adjacent to a transient gap larger than 80 m^2. Thanks to regular surveys and close contact with local foresters, it was possible to define the year of gap formation for each edge tree from the records of the experimental plots and the stem distribution maps. In this study, we selected edge trees at the edge of a transient gap and stand trees at least 30 m distance from the edge of a gap in the stand. Sandoval and Cancino (2008) and Vepakomma et al. (2011) found a significant influence of the edge on the growth of trees, which extended up to 30 m into the stand. During the measurement campaign (November 2021–March 2022), a total of 249 trees were selected. The 139 stand trees are composed of 65 Norway spruce, 43 European beech, 14 Scots pine, 10 Oak and 7 silver fir. The 110 edge trees are divided into 57 Norway spruce, 24 European beech, 14 Scots pine, 10 Oak and 7 silver fir. The data set for the pine, oak and fir species is smaller because there were fewer appropriate experimental plots to choose from. The diameter at breast height, tree height and crown height of all 249 study trees were measured with measuring tapes and the Vertex (Haglöf, Sweden). In addition, each tree was drilled from two sides at breast height with a 5-mm increment borer (Haglöf, Sweden). The cores were taken at a 90° angle in the north and east direction when the slope was less than 5%. Otherwise, parallel to the slope to reduce the influence of reaction wood.

The plots and their surroundings were laser scanned with the RIEGL VZ-400-i (RIEGL, 2022) in the same measurement campaign on windless, rainless and broadleaved tree species leafless conditions. Depending on the visibility of the study trees, the tree height, stand density and the complexity of the canopy, several scans were carried out in succession inside as well as outside the plots in the form of a grid with a repeating pattern. A scan was made approximately every 10–15 m, and on average we have five different scan positions for each tree of interest. The Supplementary Material S1 contains a more detailed description of the settings of the terrestrial laser scanner and the following post-processing.

2.2. Tree ring processing

Overall, 498 cores were extracted, air-dried, glued onto a wooden slide, and sanded with increasingly finer grit sandpaper (120–400 grit) to highlight annual ring boundaries. Subsequently, the cores were measured to the nearest 0.01 mm using the digital positioning table Lintab 5 and the software TsapWin (both Rinntech, Heidelberg). Then, standard dendrochronological techniques were applied and we performed a visual cross-dating (Stokes and Smiley, 1968; Speer, 2010). We averaged the two tree ring series per tree, resulting in 249 tree ring series. For each tree, we calculated the initial basal area (ba) and the following
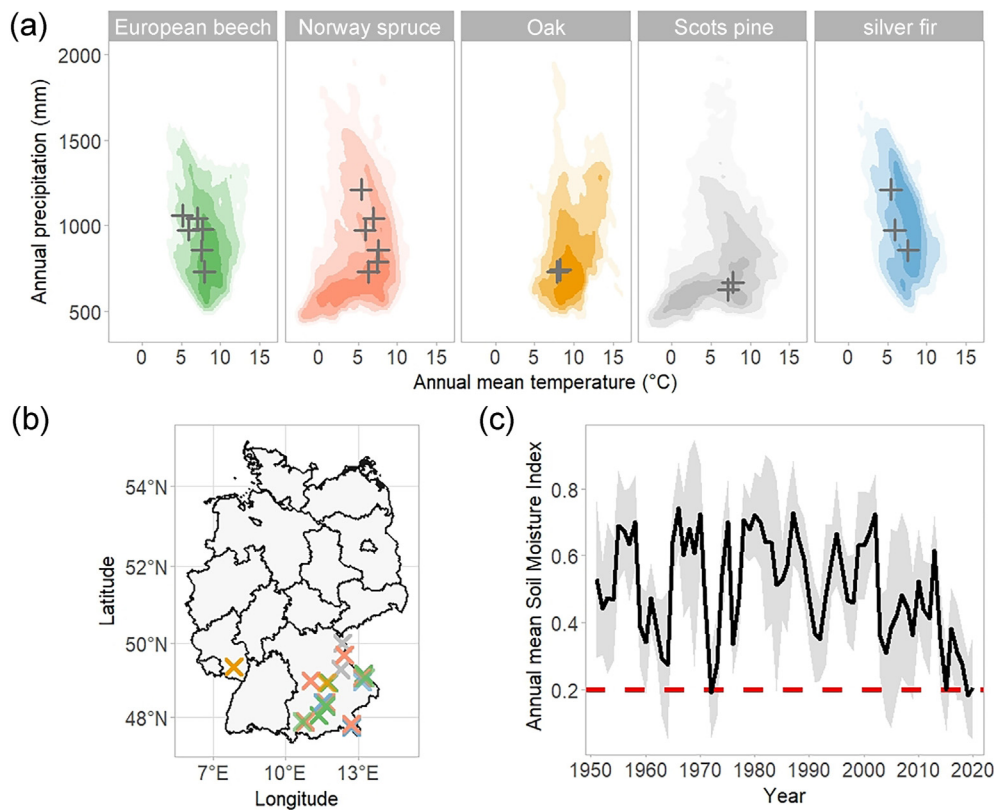
Fig. 1. Climate-space diagrams (a) for European beech (green), Norway spruce (red), Oak (orange), Scots pine (grey) and silver fir (blue). Coloured areas are all forest field observations of the respective species in Europe. Darker coloured areas indicate a higher density of observed occurrences of a species. Grey crosses display the climatic position of the experimental plots. Presence data used in the climate-space diagrams were extracted from Mauri et al. (2017), and the temperature and precipitation data were from WorldClim 2 (Fick and Hijmans, 2017) for the study sites. The geographic location of the study sites in Germany is shown in (b), and the annual mean soil moisture index (SMI) (Marx, 2017) for the period 1951–2020 is given in (c). Details are given in Section 2.3. The black line shows the overall average, while the grey ribbon indicates the site variation.

basal area increment (bai) for each year (Bunn, 2008, 2010; Bunn et al., 2023). On site 804, we did not retake cores from investigation trees that had already been measured in April 2018. The tree ring series ended for ten oaks and three beeches in 2017. Table 1 provides an overview of the examined species groups, split into edge trees and stand trees. The diameters at breast height (dbh) refer to the year of recording (measurement campaign) and the calculated basal area increment (bai) to the entire measured time series.

2.3. Drought identification with soil moisture index (SMI)

The Soil Moisture Index (SMI) was calculated to quantify the soil water supply of the trees. The SMI is calculated from the Helmholtz Center for Environmental Research (UFZ) and based on the mesoscale Hydrologic Model (mHM) according to Beven and Kirkby (1979) (Samaniego et al., 2010). The mHM includes various climate variables (e.g. precipitation) and morphological (e.g. canopy interception) and physiographic (e.g. surface runoff) data and does not require additional

local soil samples (Samaniego et al., 2013). A detailed model description can be found in the Supplementary Material S4, in Samaniego et al. (2010) and Kumar (2010). In this work, the monthly SMI data for the entire soil in Germany was downloaded from the UFZ (https://www.ufz.de/index.php?de=37937), and the SMI value was extracted based on the coordinates of the long-term experimental plots (Zink et al., 2016). For each site the annual mean SMI is calculated (Table 2). The range of the SMI values is 0–1, and a value < 0.2 is considered a drought (Marx, 2017).

Olano et al. (2023) have shown that the weather and especially water availability have direct and lagged effects on the growth of a tree. In various works such as Anderegg et al. (2015) or Wu et al. (2018), legacy effects on tree growth were found in the past 3–4 years, with a decreasing strength of the effect with further events back in the past. To consider this, we assumed a linear decreasing effect and calculated a weighted soil moisture index (smooth SMI) over four years, for each year. The current year (i) is fully included in the evaluation, while the previous years in succession are weighted 25 percentage points less (Eq. 1). The range of

Table 1
Overview of the tree ring measurements per tree species. Note that the examined trees in the stand (edge tree = no) include the data from the edge trees until the gap formation. The number of examined trees ("n_{trees}") in the stand corresponds to the sum of the edge trees and stand trees. The stand age and diameter at breast height (dbh) refer to the stand age and diameter during data collection, and the basal area increment refers to the tree's lifespan of the tree up to 1951.

Species	Stand age (min – max)	n_{trees}	Edge tree	Tree rings	dbh (cm)			Basal area increment (cm²·yr⁻¹)		
					min	mean	max	min	mean	max
Norway spruce	47–161	122	no	6994	22.1	45.2	74.3	0.1	13.6	79.2
		57	yes	569	20.7	46.5	73.9	1.2	15.7	58.0
Silver fir	77–161	12	no	767	38.2	47.8	54.4	0.9	10.5	34.7
		5	yes	73	34.9	51.2	61.0	2.1	11.9	36.9
Scots pine	53–129	28	no	1191	19.8	32.6	42.5	1.0	6.8	24.7
		14	yes	516	16.2	32.4	42.9	0.2	7.3	22.3
European beech	62–173	67	no	4173	21.7	40.4	58.0	0.2	9.9	50.8
		24	yes	345	28.8	45.3	58.8	2.2	14.8	42.3
Oak	135–146	20	no	1158	24.4	54.7	75.6	1.4	12.1	33.8
		10	yes	178	28.6	56.9	80.6	3.2	16.4	36.9

Table 2

Overview of the calculated smooth soil moisture index (smooth SMI) and the annual mean soil moisture index (SMI year) for each site.

Site	Location	smooth SMI (1954–2020)			SMI year (1951–2020)			
		min	mean	max	min	mean	max	*n* drought years
88	Waldleiningen	0.16	0.49	0.90	0.05	0.50	0.95	8
91	Starnberg	0.25	0.50	0.73	0.18	0.50	0.87	2
111	**Zwiesel**	0.26	0.51	0.68	0.20	0.50	0.75	1
113	Ruhpolding	0.28	0.50	0.72	0.24	0.50	0.86	0
134	**Zwiesel**	0.20	0.51	0.70	0.12	0.50	0.77	2
233	Denklingen	0.17	0.50	0.76	0.10	0.50	0.88	5
256	Waldsassen	0.21	0.52	0.76	0.04	0.50	0.87	6
309	**Bodenwöhr**	0.11	0.50	0.75	0.07	0.49	0.86	6
613	**Weißenburg**	0.19	0.50	0.77	0.09	0.50	0.88	5
622	**Vohnstrauß**	0.16	0.48	0.75	0.08	0.49	0.84	3
804	**Kelheim**	0.32	0.51	0.64	0.25	0.50	0.72	0
813.1	**Freising**	0.11	0.50	0.80	0.06	0.49	0.84	9
813.2	Grafendorf	0.09	0.49	0.76	0.05	0.49	0.86	9

values of the index remains the same as described above. An overview of the average annual SMI and smooth SMI per site is provided in Table 2.

$$\text{smooth SMI}_i = \frac{(1 \times \text{SMI}_i + 0.75 \times \text{SMI}_{i-1} + 0.5 \times \text{SMI}_{i-2} + 0.25 \times \text{SMI}_{i-3})}{2.5}$$

(Eq. 1)

2.4. TLS data

2.4.1. TLS data post-processing

The point clouds of the individual scan positions were first registered (merged) into a local coordinate system. To improve the quality of the registered point cloud, scatter and noise points were cleaned by filtering (Pfennigbauer and Ullrich, 2010). In addition, the point cloud was voxelised to a 5-cm grid. This point reduction enables a uniform point cloud independent of the scanner and the density of the scan positions. The study trees were then explicitly identified by reflectors and manually cut out of the scans. All processing steps were carried out using the software Riscan Pro 2.14.1 (http://www.riegl.com/products/software-packages/riscan-pro/) with the respective programs (RIEGL, 2022). Supplementary Material S1 contains a more detailed description of the TLS post-processing.

2.4.2. Variables for gap characterisation

We calculated the gap age and the gap size to characterise a gap. The years of the gap formation could be taken from the long-term experimental plots' records and verified with the local forest managers (see Table S2). The leading causes of the gap formation were thinnings, storms and insect calamities. The observed gap age covers periods of up to 31 years for spruce, 23 years for beech, 62 years for pine, 19 years for fir and 21 years for oak. Due to the large shape variation of the gaps, we decided to calculate the gap size instead of the gap width. For calculating the gap size, we used the point clouds of the stand to create a crown height model with a horizontal grid width of 1 m. Sections of the stand, where the canopy height was below 10 m above ground, were defined as gaps, the size of which was determined with the polygon-based approach of Silva et al. (2019). In this work, we follow Biber and Pretzsch (2022) and define gap trees as trees adjacent to a gap larger than 80 m². Table S2 gives an overview of the number of identified gaps and their sizes.

2.4.3. Crown variables from point clouds

To describe the shape and structure of the crown, we derived various metrics from the tree point clouds. Crowns are mainly described two-dimensionally based on standard lengths, widths or area measurements (e.g. crown length, crown radius and crown projection area). Point clouds make it possible to divide the crown into different height layers and to analyse individual height layers separately (see Fig. 2a). Further information about the crown structure can be obtained by repeatedly calculating, for example, the crown radii in different height layers. For

this reason, in addition to various known crown metrics (upper part of Table 3), we also developed new crown measurements (lower part of Table 3). In this work, 18 different crown variables were calculated, of which 13 have already been described in various publications (see Table 3 for references), and five were developed in this work. The developed metrics are mainly based on known width and area measurements, which were applied to individual height layers of the crown. We describe the developed crown metrics in the following text. Table 3 summarizes all metrics and is divided into the known and developed crown metrics. Some metrics are also shown in Fig. 2 and Table S3 gives an overview of the value range of the individual crown variables.

2.4.3.1. Degree of crown solitarity.
The crown solitarity degree compares the tree's convex canopy projection area to the theoretical canopy projection area of a solitaire. We assume that the maximum crown radius (CR) of a tree in the stand corresponds to that of a solitary tree. However, when viewed from above, a solitary tree forms an almost uniform and
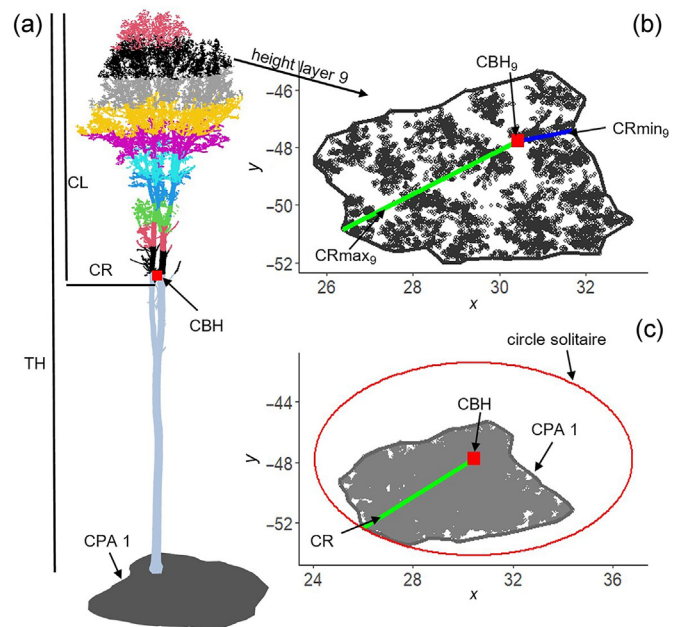

Fig. 2. Display of various crown variables that were calculated. a) shows the tree point cloud of a beech. The crown is divided into ten height classes by colour. The abbreviations resemble Table 3 (TH = Tree Height, CL = Crown Length, CR = Crown Radius, CBH = Crown Base Height, CPA 1 = Convex Crown Projected Area). In b), the calculation approach for the crown concentricity 3D in the height layer nine is shown graphically. In c), the calculation approach for the degree of crown solitarity is shown graphically.

Table 3

Overview of the calculated crown variables from the point clouds. Divided into known (upper) and developed crown metrics (lower).

Variable and metric name	Abbreviated form	Explanation or calculation
Crown length	CL	Vertical distance between the tree height (TH) and crown base height (CBH) (TH-CBH) (Reich et al., 2021)
Crown radius	CR	Maximum distance from the outer crown to the centre of the CBH (Seidel et al., 2015)
Crown radius to crown length ratio	ratio CL CR	ratio between crown radius (cr) and crown length (cl) (cr/cl)
Crown percent	CP	Ratio crown length (cl) to tree height (th) (cl/th) (Martin-Ducup et al., 2016)
Crown displacement	displacement	Projected deviation of crown tip from crown base, viewed from above (Reich et al., 2021)
Convex crown projection area	CPA 1	Projected canopy area on the ground with an alpha value of 1 (Jacobs et al., 2021)
Concave crown projection area	CPA 0.1	Projected canopy area on the ground with an alpha value of 0.1 (Jacobs et al., 2021)
Space capture index	SCI	Ratio between the concave crown projection area to the convex crown projection area (Fleck et al., 2011)
Sinuosity	sinuosity	Is calculated as the sum of the distance between the symmetry axis and the centre of the 3D polygon for each height layer and divided by the crown length (Martin-Ducup et al., 2016)
Crown volume	CV	Sum of the area of a polygon with an alpha value of 1 in 0.2 m height classes of the crown (Fernández-Sarría et al., 2013; Barbeito et al., 2017)
Branch volume	BV	Sum of the area of a polygon with an alpha value of 0.1 in 0.2 m height classes of the crown (Fernández-Sarría et al., 2013; Barbeito et al., 2017)
Crown density	C density	Ratio between branch volume (BV) to crown volume (CV) (BV/CV) (Martin-Ducup et al., 2016)
Crown perforation	perforation	Ratio between the length of the crown projection area ($a = 0.1$) in dependency of the crown projection area polygon ($a = 1$) and the length of the crown projection area polygon ($a = 1$) (Jacobs et al., 2022)
Degree of crown solitarity	solitarity	Ratio between CPA 1 and the area of a circle with the radius of CR
Degree of crown solitarity 3D	solitarity 3D	Mean ratio between CPA 1 and the area of a circle with the radius of CR in 10 relative height layers
Crown concentricity	concentricity	Ratio between min. crown radius (CR min.) to max. crown radius (CR max.) (CR min./CR max.)
Crown concentricity 3D	concentricity 3D	Mean ratio between min crown radius (CR min) to max crown radius (CR max) in 10 relative height layers
Space capture index 3D	SCI 3D	Mean ratio between the concave crown projection area to the convex crown projection area of 10 height classes. Based on SCI of Fleck et al. (2011)

round crown (Pretzsch, 2014). We calculate the study tree's theoretical crown projection area (tCPA) by placing a circle through the maximum CR of the study tree (entire crown) and determining its circular area. The study tree's convex crown projection area (CPA 1) is determined by fitting a slack polygon (α-value of 1) around the two-dimensional point cloud of the crown viewed from above. An α-value of 1 was chosen to obtain the roundest possible adjustment of the crown projection area to compare it with the tCPA. The degree of crown solitaire is calculated by relating the theoretical crown projection area to the actual convex crown projection area (Eq. 2). An index between 0 and 1 results. The closer the

value is to one, the more the convex corresponds to the theoretical crown projection area and the rounder the crown projection area of the examination tree is.

$$\text{Degree of crown solitarity} = \frac{\text{CPA 1}}{\text{tCPA}} \qquad \text{(Eq. 2)}$$

2.4.3.2. Degree of crown solitarity 3D. The index of the degree of solitarity can be calculated not only for the entire crown but also for individual crown areas (light/shadow crown) or individual height layers of a crown. This allows further three-dimensional information about the crown structure to be collected. The degree of solitarity 3D is calculated in the same way described previously for degrees of crown solitarity. However, the crown is divided vertically, e.g. into ten relative height layers (i_{1-10}). For each height layer, the maximum crown radius (CR_i), the theoretical crown projection area ($tCPA_i$) and the convex crown projection area ($CPA 1_i$) are calculated. The results are summarized, and the mean value is calculated (Eq. 3).

$$\text{Degree of crown solitarity 3D} = \frac{\sum(\text{CPA 1}_i/\text{tCPA}_i)}{\sum \text{height layer}_i} \qquad \text{(Eq. 3)}$$

2.4.3.3. Crown concentricity. Crown concentricity calculates the ratio between the entire crown's minimum and maximum crown radius. The smaller the difference, the more uniform the crown is. This variable can be used to compare the crown shape of a pinched crown (e.g. flag-shaped) with that of a round one (solitary). The examined tree's longest (CR max) and shortest crown radius (CR min) are calculated. The crown concentricity is the ratio between CR min and CR max (Eq. 4). The result is between zero and one. The closer the result is to one, the more even the two CRs are or the rounder a crown is.

$$\text{Crown concentricity} = \frac{\text{CR min}}{\text{CR max}} \qquad \text{(Eq. 4)}$$

2.4.3.4. Crown concentricity 3D. The crown concentricity 3D is the ratio between the minimum $CR \, min_i$ and maximum crown radius $CR \, max_i$ for multiple height layers (i). This enables more detailed information about the structure of the crown. The $CR \, min_i$ and $CR \, max_i$ is calculated for each height layer (e.g. ten; i_{1-10}). The ratio between $CR \, min_i$ and $CR \, max_i$ per height layer is then determined (Eq. 5). The results are summed up, and the average is calculated.

$$\text{Crown concentricity 3D} = \frac{\sum(\text{CR min}_i/\text{CR max}_i)}{\sum \text{height layer}_i} \qquad \text{(Eq. 5)}$$

2.4.3.5. Space capture index 3D. The space capture index 3D basically corresponds to the space capture index of Fleck et al. (2011) and is only applied to the individual height layers of the crown (e.g. ten; i_{1-10}). The mean ratio between the concave crown projection area (CPA 0.1) to the convex crown projection area (CPA 1) for each crown height layer (i) is calculated (Eq. 6). The result is between zero and one. The closer the result is to one, the more even/regular is the crown overall.

$$\text{Space capture index 3D} = \frac{\sum 1 - \frac{\text{CPA 1}_i - \text{CPA 0.1}_i}{\text{CPA 0.1}_i}}{\sum \text{height layer}_i} \qquad \text{(Eq. 6)}$$

2.5. Statistical modelling

2.5.1. Crown development after the gap formation (Question 1)

Related to the first research question, we investigate which crown variables differ significantly between the edge and stand trees. For this, we use the previously calculated crown variables (see 2.4.3), the basal area (ba) and the age of the gap at the time of field measurement. We investigated if the crown variable of interest differs significantly among edge and stand trees (dummy variable gap; 0 = stand tree, 1 = edge tree)

and if it correlates with tree basal area and gap age. In our first statistical approach, we use the following mixed linear model:

$$\text{crown variable}_{ijl} = a_0 + a_1 \times \text{gap}_{ijl} + a_2 \times \text{gap\_age}_{ijl} + a_3 \times \ln(\text{ba}_{ijl}) + a_4$$
$$\times \text{gap}_{ijl} \times \text{gap\_age}_{ijl} + b_i + b_{ij} + \varepsilon_{ijl}$$

(model 1)

where the indexes i, j and l represent the site, the plot and the single observation. Gap is a dummy variable that indicates the gap tree status and takes the value 1 for gap trees, otherwise 0. The tree's basal area (cm^2) of the tree is ba, and gap_age is the age of the gap in 2021. We also considered the interaction between the dummy variable gap and gap_age to determine a different temporal development of the respective variable between edge and control trees. The parameters a_0, ..., a_4 are for the fixed effects. The parameters $b_i \sim N(0, \tau_1^2)$, and $b_{ij} \sim N(0, \tau_2^2)$ denote random effects at the site and plot level to account for the nested data structure, also covering the climate variation on site and plot level. The $\varepsilon_{ijl} \sim N(0, \sigma^2)$ are identically and independently distributed errors.

The model was adapted separately for each crown variable and tree species: Norway spruce, European beech, Scots pine, Oak and silver fir. If individual dependent variables or interactions, except the dummy-variable gap, were insignificant, they were removed from model 1, and the reduced model was adjusted again.

2.5.2. Calculation of the relative basal area increment

For hypotheses ii) and iii), we required a reference model that estimated the basal area increment of the stand trees to quantify the relative changes of basal area increment between edge and stand trees. These estimates were in a second step, compared to the actual growth of the gap trees. This makes it possible to investigate the influence of the gap position of a tree on tree growth in relation to the trees in the stand. In our second statistical approach, we examined the basal area increment (bai) of the trees in the stand, depending on their ba and smooth SMI of the respective year. To estimate the bai of the trees in the stand, we formulated a mixed linear model as follows:

$$\ln(\text{bai}_{ijl}) = a_0 + a_1 \times \ln(\text{ba}_{ijl}) + a_2 \times \ln(\text{SMI\_smooth}_{ijl}) + a_3$$
$$\times \ln(\text{SMI\_smooth}_{ijl}) \times \ln(\text{ba}_{ijl}) + b_i + b_{ij} + \varepsilon_{ijl} \quad \text{(model 2)}$$

where the indexes i, j and l represent the site, the plot and the single observation. The annual basal area increment (cm$^2 \cdot a^{-1}$) of a tree per year is bai, and ba is the tree's basal area (cm^2). SMI_smooth is the weighted soil moisture index over four years per site and per year. We also used an interaction between ba and SMI_Smooth to account for different tree size-dependent growth responses to weather conditions. The entire function was log-transformed to homogenize variances and normalize residuals. Assumptions about random effects are as in model 1. The model was adapted separately for the trees in the stand of the species Norway spruce, European beech, Scots pine, oak and silver fir. If an interaction turned out insignificant, it was removed from the model, and the reduced model was adjusted again.

The model was then applied to the dataset of the edge trees to estimate their expected increment under control conditions. The relative basal area increment (rel bai) was calculated by dividing the measured bai by the predicted bai (pred bai) (Eq. 7). In the following we would refer to the relative basal area increment as relative increment. A result of 1 means no difference in relative increment between edge and stand trees. However, a value of 1.4, for example, means that the trees at the edge grow relatively 40% more than in the stand, and a value of 0.7 means that the edge trees grow 30% less.

$$\text{rel bai (\%)} = \left(\frac{\text{bai}}{\text{pred bai}} \right)$$

(Eq. 7)

2.5.3. Growth effect to gap formation and under low water supply (Question 2 and 3)

Using the previously calculated relative increment (rel bai) of the edge trees, we examine the deviation of the basal area increment from the edge to the stand trees as a function of gap age, gap size, SMI and basal area in our third statistical model. For this purpose, we formulated a mixed linear model as follows:

$$\ln(\text{rel bai}_{ijkl}) = a_0 + a_1 \times \text{gap age}_{ijkl} + a_2 \times \text{gap size}_{ijkl} + a_3 \times \text{SMI smooth}_{ijkl}$$
$$+ a_4 \times \ln(\text{ba}_{ijkl}) + a_5 \times \ln(\text{ba}_{ijkl}) \times \text{gap age}_{ijkl} + a_6$$
$$\times \ln(\text{ba}_{ijkl}) \times \text{SMI smooth}_{ijkl} + a_7 \times \text{gap age}_{ijkl}$$
$$\times \text{SMI smooth}_{ijkl} + a_8 \times \text{gap size}_{ijkl} \times \ln(\text{ba}_{ijkl}) + b_i + b_{ij}$$
$$+ b_{ijk} + \varepsilon_{ijkl}$$

(model 3)

where the indexes i, j, k, l represents the site, plot, and tree, and a single tree-ring measurement, respectively. SMI and ba have the same meaning as previously in model 2. Gap_age is the progressive age of the gap in years, starting with the value 1 for the first growing period at the gap. As described above, gap_size is calculated from the point clouds of the terrestrial laser scanner. We also considered interactions between the tree size (ba) and the individual parameters, such as gap_age, gap_size and the weighted SMI, to investigate different tree sizes depending on growth reactions. The parameters $b_i \sim N(0, \tau_1^3)$, $b_{ij} \sim N(0, \tau_2^3)$ and $b_{ijk} \sim N(0, \tau_3^3)$ denote random effects at the site, plot and tree level to account for the nested data structure, also covering the climate variation on site and plot level. The $\varepsilon_{ijkl} \sim N(0, \sigma^2)$ are identically and independently distributed errors.

The model was fitted separately for the edge trees Norway spruce, European beech, Scots pine, Oak and silver fir. If an interaction turned out insignificant, it was removed from the model, and the reduced model was adjusted again.

We used statistical environment R, version 4.3.0, for all analyses and visualizations (R Core Team, 2022). In Supplementary Material S2, the supplement is a more detailed overview of the packages used in this work. All variables were scaled (centred) based on the mean and standard deviations in each model.

3. Results

3.1. Crown development after the gap formation (Question 1)

We found significant differences between edge and stand trees in terms of crown shape/crown structure, except for oak. Of the crown variables, the space capture index 3D and crown density most often showed significant differences between edge and stand trees. Model 1 was adjusted individually for each variable and tree species. The results of the model 1 are presented in Supplement Tables S4–S8 due to the extent of the single tree species and crown variables (a total of 95 models).

For spruce, ten crown variables with significant differences between edge trees and trees in the stand were identified (Table S4). Except for crown perforation, all significant crown variables in the spruce models have a positive coefficient for the gap parameter. Edge trees of spruce have significantly broader and longer crowns. On average the crown radius is 40 cm wider, the crown projection areas (CPA 1 and CPA 01) are ~5 m^2 larger, and the living crown is 2.4 m longer. Compared to the stand, edge trees have significantly denser and less transparent crowns. The branch volume is 15.4 m^3 higher, and the crown perforation is −1.5% lower. For beech, eight crown variables with significant differences were identified (Table S5). Beech trees have 2.7 m longer crowns at the edge of a gap and a more even side profile (Sinuosity). The crown volume differs not significantly, while the branch volume increases significantly. The variables space capture index 3 d, degree of crown

solitary 3 d and crown concentricity 3 d showed that the crown projection area become more uniform in the individual height layers and rounder towards the trunk axis. No significant lateral expansion of the crown could be determined. This indicates an acclimation of the beech crown by expanding the crown structure. Some variables (e.g. C density or BV) have a significant negative interaction between edge trees and gap age (see Table S5). This indicates an opposite crown development, which converges over time.

For pine edge trees, only three significant changes to the crown could be determined (see Table S6). A significant increase in the crown radius and a more uniform side profile of the crown were observed. The space capture index 3 d indicates an overall more regularly shaped crown. Although the crown radius is 55 cm wider, the pine tree does not have a significantly larger crown projection area. The acclimation of the concave to the convex crown projection area in the individual height layers (SCI 3D) indicates a closure of the gaps in the crown structure. However, it is not sufficiently pronounced to detect significant differences in branch volume, crown density or transparency compared to the trees in the stand. In the case of fir, only the crown density was higher at the edges than trees within the stands (Table S7). No significant differences were observed for oaks in the crown development of edge trees (Table S8).

3.2. Growth reaction to the gap formation (Question 2)

We found species-specific model fits (model 3) for the examined tree species and predicted in Fig. 3 the relative increment (relative basal area increment, the difference between the predicted and measured basal area increment of the edge trees, see 2.5.2) for an average-sized tree per species group (except for pine) under average smooth soil moisture conditions (smooth SMI = 0.5, see 2.3 and Table 2). The model was applied to a pine tree with a basal area of 600 cm^2 and a gap size of 1,000 m^2. The dashed line represents the growth of the stand tress. Table 4 summarizes the statistical results for model 3. In the first year after the gap formation, edge beech, pine, and oak trees can benefit from the formation with a 45%, 35% and 26% higher relative growth. Spruce trees

had a comparable growth (−5% relative increment) as the trees in the stand, and firs had 60% lower relative basal area growth than in the stand after gap formation. However, the gap age had a strong negative impact on the relative increment of all tree species, except for fir (see Table 4), and resulted in a declined growth in the following decades (Fig. 3). The coefficient of gap age is lowest for pine compared to the other tree species and shows the largest decrease in growth with gap age in Fig. 3. After 60 years, the relative increment of pines was 80% less than in the stand (0.2 relative increment). Edge beech and oaks can profit over 20 years after the gap formation, while spruce grows after 30 years, 47% less compared to the stand. Based on model 3, fir is the only species that recovers and reaches, after 20 years, the relative growth of the stand trees again. The results of model 3 also show that smaller spruce and pine trees have significantly higher relative growth than those with larger basal areas (Table 4). Conversely, larger pines benefit more from the edge position with higher relative increments. The size of the gap had a positive effect on the growth of beech and fir trees (Table 4). In interaction with the basal area, larger pine trees benefit more from larger gaps, while smaller fir trees benefit from larger gaps.

The results of reference model 2, which estimates the basal area increment of the trees in the stand, and the results of the calculated relative increment are described together in Supplementary Material S3 and Table S9. In model 3, different interactions are non-significant depending on the tree species. These were removed from the model for the corresponding tree species, and the reduced model was readjusted. In the case of spruce, pine, fir and oak, the random effect had to be omitted at the site or plot level to achieve convergence (see Table 4).

3.3. Growth of edge trees under low water supply (Question 3)

Using model 3, we could determine significant tree species-specific growth responses in dry soil moisture of gap trees after the gap formation. Table 4 provides an overview of the statistical results for model 3. In Fig. 4, we predicted the relative increment for an average-sized tree per species group (except for pine, see 3.2) under dry soil moisture conditions (smooth SMI = 0.2). The dashed line represents the growth of the
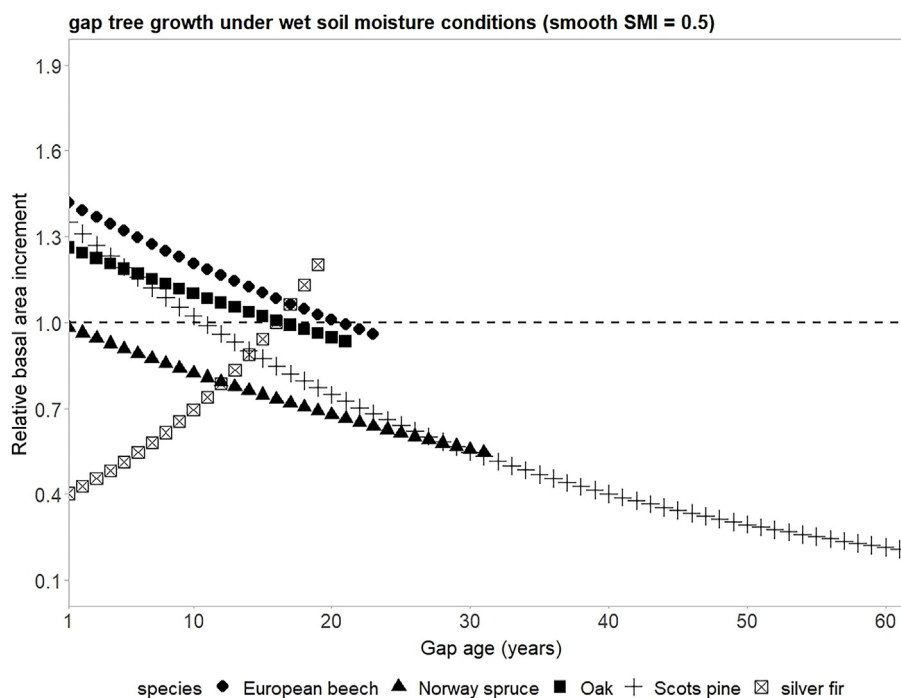

Fig. 3. Model prediction (with the fixed effects of the fitted model 3) for an average-sized edge tree in wet (smooth SMI = 0.5) soil moisture conditions over gap age for European beech (filled circle), Norway spruce (filled triangle), Oak (filled square), Scots pine (plus) and silver fir (square cross). The dashed horizontal line represents the average growth of the trees in the stand. See Table 4 for statistical properties of the fitted models.

Table 4
Results of fitting model 3 with the data set for the trees at the gap for spruce, beech, pine, oak and fir. Significant values are bold.

| Fixed effect variables	Norway spruce			European beech			Scots pine			silver fir			Oak		
	Estimate	Std. Error	*p*	Estimate	Std. Error	*p*	Estimate	Std. Erro	*p*	Estimate	Std. Error	*p*	Estimate	Std. Erro	*p*
Intercept	−0.017	0.084	0.844	0.222	0.160	0.291	−0.067	0.146	0.653	2.021	0.340	**0.035**	0.110	0.097	0.287
ln(ba)	−0.136	0.065	**0.043**	0.057	0.084	0.505	0.621	0.110	**0.000**	−2.127	0.274	**0.000**	–	–	–
gap_age	−0.149	0.028	**0.000**	−0.108	0.031	**0.001**	−0.568	0.062	**0.000**	0.264	0.048	**0.000**	−0.081	0.021	**0.000**
SMI_smooth	−0.166	0.023	**0.000**	−0.040	0.028	0.152	−0.223	0.025	**0.000**	−0.162	0.055	**0.005**	−0.013	0.022	0.549
gap_size	–	–	–	0.195	0.082	**0.046**	0.144	0.146	0.346	4.187	0.559	**0.000**	–	–	–
ln(ba) × gap_age	0.052	0.020	**0.010**	–	–	–	−0.078	0.039	**0.049**	0.333	0.035	**0.000**	–	–	–
ln(ba) × SMI_smooth	–	–	–	0.082	0.023	**0.000**	−0.101	0.026	**0.000**	–	–	–	–	–	–
ln(ba) × gap_size	–	–	–	–	–	–	0.410	0.061	**0.000**	−3.034	0.434	**0.000**	–	–	–
Random effects	Std. Dev.			Std. Dev.			Std. Dev.			Std. Dev.			Std. Dev.		
Site	–			0.247			–			0.311			–		
Plot	0.290			0.243			0.473			–			–		
Tree	0.309			0.293			–			0.301			0.302		
Residuals	0.361			0.329			0.419			0.228			0.237		
AIC	667.842			453.920			631.021			61.386			87.890		
R^2 **(conditional)**	0.638			0.719			0.717			0.919			0.633		
R^2 **(marginal)**	0.140			0.184			0.356			0.627			0.037		
Observations	569			345			516			73			178		
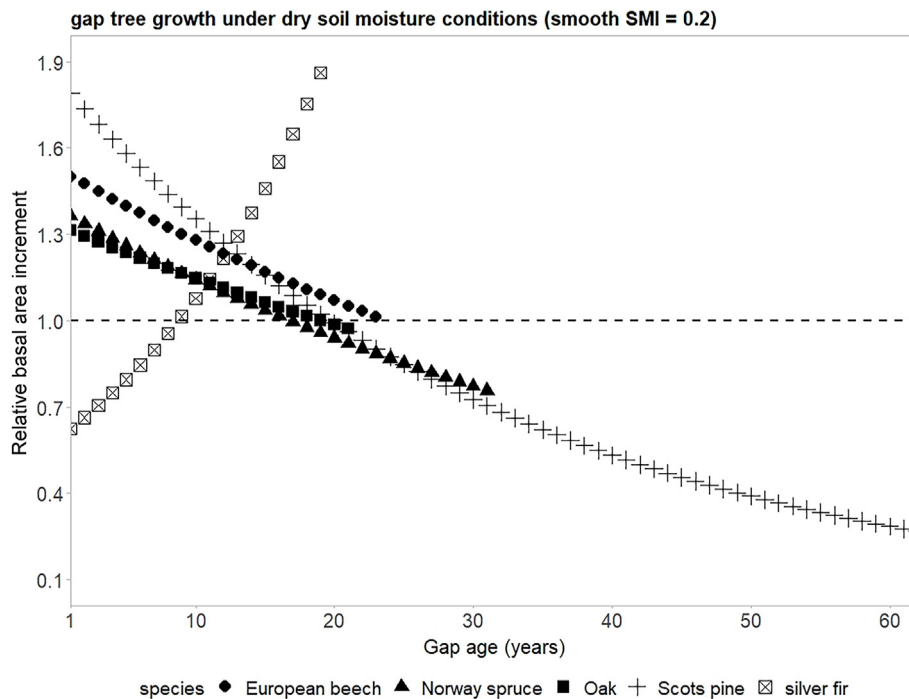
Fig. 4. Model prediction (with the fixed effects of the fitted model 3) for an average-sized edge tree in dry (smooth SMI = 0.2) soil moisture conditions over gap age for European beech (filled circle), Norway spruce (filled triangle), Oak (filled square), Scots pine (plus) and silver fir (square cross). The dashed horizontal line represents the average growth of the trees in the stand. See Table 4 for statistical properties of the fitted models.

stand stress. Under dry soil moisture conditions, edge trees of spruce, beech, pine, and oak exhibit 35%, 45%, 79%, and 26% greater relative increments, and fir trees exhibit 40% lower relative increments compared to the stand (Fig. 4). In model 3, the coefficient for the smooth SMI has a significantly negative effect for all conifer species and leads to higher relative increments under drier soil moisture conditions (Table 4). Regardless of water supply (smooth SMI), the two deciduous tree species benefit from the gap formation with higher relative growth (see 3.2 and Table 4). Compared to the averaged water supply (Fig. 3), the relative increment decreases more for spruce and pine under low water supply and increases more for fir. After 30 years, spruce trees show 25% lower growth with a low water supply, and pine trees show a 73% lower relative increment after 60 years than the stand trees (Fig. 4). Under dry conditions, fir trees show comparable growth to stand trees after just ten years and an 80% higher relative increment after 20 years. The conifer species' relative increment is significantly higher with a low water supply than a high one. The relative increment of beech and oak does not differ significantly between average and low water supply (Fig. 4). The basal area and smooth SMI interaction are significant for beech and pine trees

(Table 4). Larger beech trees benefit significantly from moist conditions, and smaller pines show significantly higher relative increments under low water supply.

4. Discussion

Our results indicate that i) tree species-specific acclimations of the crown to the gap occur and mostly lead to changes in the structure of the crown, ii) there are growth reactions particular to tree species that can have a gap-age-dependent positive or negative impact on the basal area increment and iii) the examined coniferous tree species can benefit from the edge location under low water supply compared to stand trees, whereas the examined deciduous tree species showed no differences. Table 5 provides an overview of all results discussed in the following chapters.

4.1. Crown development after the gap formation

Edge trees acclimate their crown structure and shape to the edge

Table 5
Summary of the identified acclimations of the individual tree species to the gap. The results of the three hypotheses and the consequences for silviculture are listed in the rows. The growth trends illustrate the edge trees' growth development compared to the stand trees. The symbols used for the growth trends mean: + stands for higher growth compared to the stand trees, 0 stands for no change in growth compared to the stand trees and – stands for lower growth compared to the stand trees.

Acclimation after the gap formation	Norway spruce	European beech	Scots pine	silver fir	Oak
crown development	• longer • wider • denser	• longer • denser • more regular shape	• wider • more regular side profile	• denser	• no significant differences
growth trend under average water supply	0 30 years −	+ 20 years 0	+ 60 years −	−20 years +	+ 20 years −
growth trend under low water supply	+ 30 years −	• not significant • trees with higher basal areas profit from higher water supply	+ 60 years −	−20 years +	• not significant
Consequences for silviculture	• Different development of the crown and growth between edge trees and trees in the stand • Gaps can temporarily positively affect the drought stress of the examined conifers • Negatively affect saw timber quality				

position. Various crown variables, calculated from point clouds, show significant differences between edge trees (trees at the edge of a transient gap) and stand trees (trees in the stand, min. 30 m far away from the gap). Species-specific acclimation reactions were identified (Table 5). Spruce trees respond to the gap by expanding the crown laterally and horizontally, forming a denser crown structure. Beeches strengthen their crown structure without developing significantly wider crowns. Pine trees grow their crown radius and create more regular crowns in the side profile. Firs have significantly denser crowns at the edge of a gap, but no clear acclimation strategy can be determined. Other works have found that firs expand their existing crown space after being exposed or at edges of gaps (Szwagrzyk et al., 2012; Dobrowolska et al., 2017), and oaks have more even spatial crown distributions (Longuetaud et al., 2008).

The fact that the spruce forms a denser crown structure when located at a gap edge was evident from various crown structure variables. This can be explained by the formation of internode branches between the branch nodes of the living crown, which was observed by Seifert (2003). In addition, we found a significant horizontal and vertical expansion of the crown space of spruce at gap edges, as also observed by Vepakomma et al. (2011). A significantly longer crown, in contrast to beech, is solely due to increased height growth. This was also observed by Seifert (2003) on exposed spruce trees. Spruce trees are not able to expand their crown through stem shoots (epicormic branches) below the living crown but can only extend their crown space horizontally and vertically above the living crown (Rittershofer, 1994). This expansion probably represents the spruce's key acclimation strategy to a gap. The needles of Norway spruce that are newly formed every year are acclimated to the current lighting conditions (Kubínová et al., 2018) and, depending on the altitude and latitude, remain on the branch for the following eight years before they are shed (Reich et al., 1995, 1996). After a gap is created, the competitive situation changes the lighting conditions for the individual needles. The tree must acclimate to the edge by developing new needles and branches. Spruce trees, therefore, significantly expand their crown space horizontally and vertically and compact it with additional branches and leaves.

Deciduous tree species such as beech can form new leaves every year, which are acclimated to the current lighting conditions or competitive conditions in their shape and size (Petriţan et al., 2009; Weithmann et al., 2022; Zhu et al., 2022). This makes beech trees more flexible in their acclimation to changing lighting conditions. However, shade tree species are more acclimated to closed stands (Petriţan et al., 2009; Barbeito et al., 2014). Various works (e.g. Muth and Bazzaz, 2002; Pedersen and Howard, 2004; Bayer and Pretzsch, 2017) have observed a horizontal expansion of the beech tree crown into gaps, but this could not be confirmed in the study at hand. Vepakomma et al. (2011) found that hardwood tree species such as beech expand into the gap by approximately 21 cm annually. In contrast to the work of Bayer and Pretzsch (2017) or Vepakomma et al. (2011), we did not carry out repeated crown measurements. We were, therefore, unable to directly measure expansion. In a study on *Quercus petraea* (Matt.) Liebl., Longuetaud et al. (2008) showed that crown eccentricity and plasticity stabilized over time after thinning, resulting in a more regular spatial distribution of the crown. We conjecture that this kind of stabilization causes our results for beech due to lower competition and higher light availability in the edge position (Bugmann, 2001; Schliemann and Bockheim, 2011; Muscolo et al., 2014).

The results we obtained for Scots pine showed that this species had a significantly larger crown radius when located at gap edges. Similar reaction patterns were seen by Ackerman et al. (2013) in their research on *Pinus patula* (Schltdl. et Cham.), which they attributed to the impact of one-sided competition. Trees grow toward light and expand primarily into areas with less competition (Ackerman et al., 2013). This has also resulted in less pinched and more even crown shape. As a pioneer tree species, Scots pine is adapted to high light conditions (Durrant et al., 2016). Pine trees in managed forests are primarily thinned to increase growth (Mäkinen and Isomäki, 2004). Overall, only a few significant changes to the crown could be detected for pines. A lack of significance

could indicate that the crown is already acclimated to the light conditions at the gap. Presumably, the crown of the pines in thinning stands is already better acclimated to the gap and only changes slightly.

Overall, various acclimations of the crown to the edge of the different tree species could be observed. Spruces and beeches show a variety of acclimations of the crown to the gap, while the pine makes only a few acclimations. The acclimation varies depending on the tree species and is species-specific. We showed that point clouds from terrestrial laser scans can be used to calculate various metrics to describe the crown shape and structure. The developed variables in this work have shown further variations in crown development.

4.2. Growth reaction to the gap formation

The basal area increment response for the examined tree species is species-specific under average soil moisture conditions after the gap formation. Compared to the stand, different tree species can temporarily benefit from the gap in their relative increment (basal area increment of edge trees in relation to stand trees), while some decline in growth. The average growth profits immediately after gap formation (26%–45%) are comparable to the results found in other studies in Europe and North America (Pedersen and Howard, 2004; Roberts and Harrington, 2008; Gray et al., 2012; Biber and Pretzsch, 2022). Due to the reduction of competitors, edge trees have more light available, allowing them to have a higher photosynthesis rate (Wimalasekera, 2019). In addition, after the gap is formed, the solar radiation and water input into the gap is increased, which may mineralize the upper soil layers and create nutrient hotspots (Ritter et al., 2005; Scharenbroch and Bockheim, 2007; Muscolo et al., 2010; Schliemann and Bockheim, 2011). Furthermore, due to the unstocked gap, less water is removed from the soil for photosynthesis (transpiration & evapotranspiration), which is potentially available to the edge trees (Ritter et al., 2005; Dalsgaard, 2007; Abd Latif and Blackburn, 2010; Vilhar and Simončič, 2012). These conditions allow edge beech, pine and oak trees to achieve higher growth rates than the trees in the stand and benefit from the gap. However, these conditions also depend on the size of the gap, as found by Abd Latif and Blackburn (2010) or Amolikondori et al. (2021). Larger gaps increase light availability and can enhance the microclimatic conditions in the gap. As a result, edge beech, pine and fir trees can benefit from larger gaps in their relative increment.

In contrast to other studies, we found species-specific adverse growth reactions to gap formation. Compared to the trees in the stand, spruce and fir trees reduce their basal area increment by −5% and −60% after the gap formation. This adverse growth reaction of the two conifer species can be attributed to their high shade tolerance, long coniferous leave lifespan, and the crown's expansion described above (Dobrowolska et al., 2017; Kubínová et al., 2018; Zhu et al., 2022). In contrast to the examined two deciduous tree species, the needles of the three coniferous trees are acclimated to the respective light conditions of the previous years (Petriţan et al., 2009; Weithmann et al., 2022; Zhu et al., 2022). By expanding the crown through the formation of new needles and branches, at least fir trees can slowly acclimate to the gap and reach the growth level of the stand trees again after two decades. This crown expansion was also noted by Seifert (2003) and Bayer and Pretzsch (2017) and indicates an acclimation to the gap through an accumulation of biomass in the crown, especially for spruce trees (see 4.1). Of the conifers, pine is the only tree species that can benefit from the gap and have higher growth in the first decades. As a light-demanding tree species, its needles are already acclimated to the high light conditions in the gap (Durrant et al., 2016). The crown of pines only needs to acclimatize slightly and the tree benefits from the gap in growth (see 4.1). After years, the growth level decreased below that of the trees in the stand. This development indicates that the growth of the tree species has been exhausted, so the growth is declining compared to the stand. This development is also known as the growth acceleration effect (Assmann, 1956). It describes the early achievement of maximum growth due to

changes in the environment or competitive conditions, especially in young stands (Pretzsch, 2019).

In addition to pine, we also found a negative growth trend over the gap age for spruce, beech and oak. This negative effect of the gap age could be explained by continuous nutrient leaching on the gap and diminishing advantages of the gap position with developing vegetation. Due to the increased solar radiation, soil moisture and mineralization of the topsoil in the gap, more pioneer tree species can develop (Vilhar et al., 2015; Jankovska et al., 2015). Over time, this developing vegetation might increasingly compete with the edge trees for light, water and nutrients. In addition, depending on the soil type, exposure and slope, nutrients could be washed out of the soil (Bauhus and Bartsch, 1995; Ritter and Vesterdal, 2006; Vilhar and Simončič, 2012). As the gap age increases, the conditions in the gap change and edge trees can no longer benefit from the gap to the same extent. After around 20 years, beech, pine, fir and oak reached the growth level of the trees in the stand again, and spruce showed −40% less growth than the trees in the stand.

In addition to the previously discussed generally positive effect of the gap size and the negative effect of the gap age, we also found a tree species-specific effect of tree size (basal area) on the relative increment of edge trees. Spruce and fir edge trees with a smaller basal area have a higher relative increment than those with larger basal areas. However, their advantage in growth decreases slowly with increasing gap age for larger spruce and fir trees. This response suggests a greater potential for earlier developmental stages to acclimate their crown and growth to environmental changes (Biber and Pretzsch, 2022). Our analysis of beech and pine trees reveals that larger individuals profit more from their gap edge position than smaller ones. For beech, this reaction can be explained by the tree species' high shade tolerance and favoured growth under a closed canopy especially in younger stands (Dusan et al., 2007; Petritan et al., 2007; Petriţan et al., 2009; Barbeito et al., 2014). Pines probably need to develop their root system and crown structure to be competitive and benefit more from the gap (Mickovski and Ennos, 2002; Finér et al., 2007). Overall, a variety of growth reactions of the trees to the formation of gaps could be determined. These depend primarily on the age of the gap and the size of the tree. In addition, reduced basal area growth of gap edge trees does not automatically indicate low acclimation but can also represent a redistribution of resources, e.g. into the crown or roots.

4.3. Growth of gap edge trees under low water supply

Our models of relative increment showed that the conifer species Norway spruce, Scots pine, and silver fir were better acclimated to low water supply than to wet conditions when they were located at gap edges. This was not the case for the deciduous species European beech and oak, where the location (gap edge or closed stand) did not seem to make a difference. We found that both conifer species (Norway spruce, Scots pine) had a higher relative increment after the gap formation than the trees in the stand. Our results suggest that, after the gap is formed, spruces grow 35% more, pines 79% more, and firs 40% less under low water supply than the stand trees. This finding can be explained by the lower competition for water at the edge of a gap. In the gap, the edge trees have, even during a drought, a higher water supply and, therefore, lower stress than trees in the closed stand (Dalsgaard, 2007). Due to the vegetation that develops in the gap, the relative growth decreases more with increasing gap age when the water supply is low than when the water supply is average. The emerging vegetation in the gap increases water competition over time (Vilhar and Simončič, 2012). In various studies on the drought stress response of spruce (e.g. Laurent et al., 2003; Kohler et al., 2010; Gebhardt et al., 2014) and pine (e.g. Martín-Benito et al., 2010; Sohn et al., 2016; Sankey and Tatum, 2022) a positive effect was found at lower stand densities. This effect was also primarily explained by lower competition and higher water availability in lower stand densities. However, the effectiveness of lower stand densities to reduce drought stress is discussed controversially and depends on tree species, mixture and structure of the stands (Mathes et al., 2024). Buras

et al. (2018) observed higher vulnerability to drought for Scots pine trees at permanent forest edges. Although we found that pine benefited from a gap edge position under drought stress for the first decades after the gap formation, the growth fell below the level of the trees in the stand during subsequent decades. This development confirms the results of Buras et al. (2018) and indicates a higher vulnerability to drought for Scots pine trees with increasing gap age.

The two deciduous tree species benefit from gap edge situations with higher growth regardless of soil moisture conditions which underlines their anisohydric character (Pretzsch et al., 2018, 2023). A positive growth effect during drought stress, such as reported by Bréda et al. (1995) after the thinning of oak trees, cannot be confirmed by our results. Overall, different drought stress responses of gap edge trees were identified. While spruce and pine edge trees, show higher growth under drought stress compared to the stand after gap formation, the two deciduous tree species show no significant growth effect under drought stress. Fir trees show higher relative growth with low water supply compared to average water supply, but had a lower relative increment than in the stand in the first decade.

4.4. Consequences for silviculture

We showed that edge position had a tree species-specific influence on the crown and basal area increment under average and low water supply (Table 5). This results in different consequences for silviculture. In general, we were able to show that tree species can acclimate to the gap in their crown and growth. However, depending on the management objective, gaps can also have a negative impact. Trees acclimate their crown structure to the light conditions, which, as with spruce, can lead to an accumulation of biomass in the crown (4.1). On the other hand, beech, pine, and oak could benefit from the gap formation in their growth time-wise (4.2). A strip- and group-cutting system could help individual tree species reach the target diameter earlier. Growth declines may also arise in the long term compared to the stand trees. Therefore, the gap age has a direct impact on the consequences for silviculture. In addition, the results indicate that the examined conifer species react less to drought stress in their growth at the edge of a gap (4.3). A gap or general reduction in stand density could positively affect the drought stress response of edge trees. However, as mentioned in the previous section 4.3, the effectiveness of lower stand densities in reducing drought stress is controversially discussed (Mathes et al., 2024).

Furthermore, acclimatization of the crown of edge trees, e.g., through epicormic branches or a secondary crown, could negatively impact wood quality (Seifert, 2003; Longuetaud et al., 2008). Lateral crown expansion combined with lower basal area increments could result in an unfavourable height-diameter ratio and make edge trees more vulnerable to subsequent storm calamities (Wallentin and Nilsson, 2014). Timber distortion could also increase with the heterogeneity of the ring width pattern (Pretzsch and Rais, 2016). Different measures for silviculture arise after the gap formation, depending on the tree species, diameter, location, and gap age.

5. Conclusion

With this study, we were able to contribute to a better understanding of the development of trees at transient forest edges. Due to forests increasingly being affected by gaps in the canopy, this study has a high practical relevance. In addition, the topic has hardly been investigated from the perspective of drought stress, until now. We identified tree species-specific developments in the crown and growth of edge trees under drought stress. Further variations in crown development were revealed by the crown variables developed in this work. These crown variables can be calculated in other studies and therefore have a high application value. Our study provided new insight into the effect of drought events on the growth of edge trees. In addition, the results have a high practical application value and can be used as a basis for

management decisions. However, it remains unclear how the edge trees will develop in their phenotype and growth in the long term and what effects this will have on the stand. Including dead trees in the data set could provide a deeper understanding and reflect more significant variation. More extensive studies are required for understanding the resilience and recovery properties of edge trees to individual drought events. Future studies could use our developed crown metrics to examine the tree crown structure dynamics over longer time periods.

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CRediT authorship contribution statement

Luke Bohnhorst: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Peter Biber:** Writing – review & editing, Validation, Methodology, Formal analysis, Conceptualization. **Torben Hilmers:** Writing – review & editing, Methodology, Formal analysis. **Enno Uhl:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Hans Pretzsch:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2024.100219.

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