KeAi

Contents lists available at ScienceDirect

# Forest Ecosystems

journal homepage: www.keaipublishing.com/cn/journals/forest-ecosystems



# Optimizing competitor definitions for the sustainable management of dominant silver fir trees (*Abies alba* Mill.) in uneven-aged mixed Dinaric forests



Milan Kobal<sup>a</sup>, Tom Levanič<sup>b,c,\*</sup>

- a Department for Forestry and Renewable Forest Resources, Biotechnical Faculty, University of Ljubljana, Ljubljana 1000, Slovenia
- <sup>b</sup> Slovenian Forestry Institute, Department of Yield and Silviculture, Ljubljana 1000, Slovenia
- c Faculty of Mathematics, Natural Sciences and Information Technologies, University of Primorska, Koper 6000, Slovenia

#### ARTICLE INFO

# Keywords: Sustainable forest management Dinaric silver fir-European beech forests Competition indices (CIs) Optimal search distance Optimal diameter at breast height (DBH)

#### ABSTRACT

Understanding competition between trees is essential for sustainable forest management as interactions between trees in uneven-aged mixed forests play a key role in growth dynamics. This study investigated nine competition indices (CIs) for their suitability to model the effects of neighboring trees on silver fir (Abies alba) growth in Dinaric silver fir-European beech (Fagus sylvatica) forests. Although numerous competition indices have been developed, there is still limited consensus on their applicability in different forest types, especially in mature, structurally complex forest stands. The indices were evaluated using the adjusted coefficient of determination in a linear model wherein the volume growth of the last five years for 60 dominant silver fir trees was modeled as a function of tree volume and competition index. The results demonstrated that distance-dependent indices (e.g., the Hegyi height-distance competition and Rouvinen-Kuuluvainen diameter-distance competition indices), which consider the distance to competitors and their size, perform better than distance-independent indices. Using the optimization procedure in calculating the competition indices, only neighboring trees at a distance of up to 26-fold the diameter at breast height (DBH) of the selected tree (optimal search radius) and with a DBH of at least 20% of that of the target tree (optimal DBH) were considered competitors. Therefore, competition significantly influences the growth of dominant silver firs even in older age classes. The model based solely on tree volume explained 32.5% of the variability in volume growth, while the model that accounted for competition explained 64%. Optimizing the optimal search radius had a greater impact on model performance than optimizing the DBH threshold. This emphasizes the importance of balancing stand density and competition in silvicultural practice.

## 1. Introduction

Competition is among the most studied topics in forest research (Biging and Dobbertin, 1992, 1995; Woodall et al., 2003; Das, 2012; Fraver et al., 2014); however, several questions remain unresolved (Weiskittel et al., 2011; Seifert et al., 2014). These include understanding how competition varies between different species, forest types, and environmental conditions, and how competition can best be quantified. Another challenge is to reconcile competition with other stress factors such as climate change, pests, and natural disturbances. Competition is crucial to gain insights into fundamental forest processes, such as resource allocation (Men et al., 2023; Chen et al., 2024), species

interactions (Hrivnák et al., 2022; Seifert et al., 2014), and successional dynamics (D'Amato and Puettmann, 2004; Puettmann et al., 2009), as well as to predict forest development under changing environmental conditions (Verdonck et al., 2025). In addition, it is instrumental in optimizing various silvicultural measures, including stand density regulation (Luu et al., 2013), species selection (Wagner and Radosevich, 1998; Castagneri et al., 2008), and growth modeling (Pretzsch, 2009), which are essential for sustainable forest management (Mizunaga et al., 2010; Bončina, 2011; O'Hara, 2014).

Competition occurs because of limited resources (Grams and Andersen, 2007). An important division in competition is above ground, where trees compete for light, and below ground, where trees compete

Peer review under the responsibility of Editorial Office of Forest Ecosystems.

<sup>\*</sup> Corresponding author. Slovenian Forestry Institute, Department of Yield and Silviculture, Ljubljana 1000, Slovenia. E-mail address: tom.levanic@gozdis.si (T. Levanič).

for water and nutrients (Weiskittel et al., 2011). Studies on below-ground competition are rare for obvious reasons, e.g., inaccessibility and complexity of roots, intertwined root systems, lack of clear spatial boundaries, and various measurement problems (Lei et al., 2012; Bolte et al., 2013).

Most studies on competition have been conducted in even-aged forest stands and/or plantations (Lorimer, 1983; Daniels et al., 1986; Tomé and Burkhart, 1989; Wagner and Radosevich, 1998; Larocque, 2002; Béland et al., 2003; Hynynen and Ojansuu, 2003; D'Amato and Puettmann, 2004; Corral Rivas et al., 2005; Castagneri et al., 2008; Boivin et al., 2010; Contreras et al., 2011; Sabatia and Burkhart, 2012; Luu et al., 2013), and much less in uneven-aged forest stands (Mailly et al., 2003; Woodall et al., 2003; Richards et al., 2008; Duduman et al., 2010; Fichtner et al., 2012; Pedersen et al., 2012). The awareness of the benefits of uneven-aged forests is growing (Mizunaga et al., 2010; Bončina, 2011; Pukkala et al., 2011; Schütz et al., 2012; O'Hara, 2014), considering that various studies have shown that competition in these forests differs significantly from that in even-aged forests (Oliver and Larson, 1996). Additionally, the stand structure of uneven-aged forests can be very diverse, as knowledge about competition in such forests remains insufficient (Seydack et al., 2011). In particular, the response of older trees in uneven-aged stands is poorly understood (Fichtner et al.,

To analyze competition, researchers have proposed several indicators, among which competition indices (CIs) stand out as a more practical alternative to direct assessments of resource availability, which are usually very labor-intensive and involve measurements of many variables such as light, water, and nutrient availability (Seifert et al., 2014). CIs can be defined as the effect of neighboring trees on the growth of the subject tree and are usually expressed using mathematical equations that represent how much the subject tree is influenced by its neighboring trees (Burkhart and Tomé, 2012). The number of CIs described is very high (Pretzsch, 2009), whereby we can distinguish groups of distance-independent CIs (Munro, 1974), distance-dependent CIs (Lorimer, 1983; Tomé and Burkhart, 1989) and, more recently, a group of semi-distance-independent CIs (Stage and Ledermann, 2008; Ledermann, 2010).

One of the most used parameters in CI calculations to assess competition is the diameter at breast height (DBH). However, CIs vary in complexity depending on their applicability (Pretzsch, 2009; Burkhart and Tomé, 2012). While some indices rely solely on DBH or basal area, several also incorporate the spatial relationships between trees. Several well-established indices consider both DBH and the distance between the subject tree and its neighboring trees (DIST $_{ij}$ ) (Hegyi, 1974; Lorimer, 1983; Martin and Ek, 1984). More complex CIs may additionally consider tree height (H), crown dimensions, and light availability, which require extensive calculations and field measurements (Stadt et al., 2007).

Some CIs have been further refined by including a relationship between the DBH of the subject tree (DBH<sub>i</sub>) and that of its neighboring trees (DBH<sub>i</sub>). This modification considers the fact that the competitive effect of a neighboring tree increases with its DBH<sub>i</sub>, indicating that larger trees compete more strongly with the subject tree. In calculating the CI, some studies consider only neighboring trees with a DBH equal to or greater than that of the subject tree as competitors (Fichtner et al., 2012). In addition, some indices refine the competition assessment by including a distance-dependent weighting factor in which the influence of neighboring trees decreases with increasing  $DIST_{ij}$ . While some studies assume a fixed threshold for DISTij (Hegyi, 1974; Mailly et al., 2003; Woodall et al., 2003; Coomes and Allen, 2007; Stadt et al., 2007; Contreras et al., 2011; Szwagrzyk et al., 2012), others investigated variable DIST; based on the dimensions of the subject tree to determine the distance at which neighboring trees act as competitors (Lorimer, 1983; Béland et al., 2003; Puettmann et al., 2009; Oheimb et al., 2011; Das, 2012; Sabatia and Burkhart, 2012; Luu et al., 2013).

Two important questions arise in connection with CI calculation in uneven-aged forests: How large must a neighboring tree be to act as a competitor to the subject tree, and at what distance does a neighboring tree exert significant competitive influence? These considerations are crucial for precisely defining CIs, as they determine which trees should be included in their calculation. Determining appropriate DBH $_j$  and DIST $_{ij}$  thresholds is particularly important in complex stand structures, where variations in tree size, spacing, and species composition influence competitive interactions. It is, therefore, reasonable to define both the limiting DBH $_j$  and DIST $_{ij}$  relative to the dimensions of the subject tree. This implies that the minimum competitive diameter (DBH $_{j_{min}}$ ) and maximum competitive distance (DIST $_{ij_{max}}$ ) are not fixed values but instead depend proportionally on the DBH $_j$  of the subject tree.

This study aimed to refine the methodology for calculating CIs for dominant silver fir trees in uneven-aged forests by considering two key aspects: the  $\mathrm{DBH}_{j_{\min}}$ , at which a neighboring tree acts as a competitor, and  $\mathrm{DIST}_{ij_{\max}}$ , at which it still exerts competitive influence. Considering the complexity of stand structure in uneven-aged forests, where differences in tree size, spacing, and species composition significantly affect competitive interactions, we sought to develop a more dynamic approach to defining competition. By considering the proportional relationship between the  $\mathrm{DBH}_i$  of the subject tree and  $\mathrm{DBH}_j$  and  $\mathrm{DIST}_{ij}$ , we aimed to improve the accuracy of competition assessment and its usefulness for forest growth modeling and silvicultural decision-making in uneven-aged forests with diverse forest structures.

#### 2. Materials and methods

#### 2.1. Study area

The study was conducted in the Dinaric Mountains in southwest Slovenia (14°26′ E, 45°35′ N) at an elevation of 850 m where silver fir (*Abies alba*)-European beech (*Fagus sylvatica*) forests are dominant (Fig. 1). Topography in the area is diverse, with abundant sinkholes and limestone outcrops typical of the high karst geology in the region. Various soils are developed from the limestone parent material, primarily litosols, leptosols, cambisols, and luvisols. The soil depth varies between 0 and 300 cm depending on micro-topographic position (FMP,

Precipitation is evenly distributed throughout the year, with a mean annual sum of precipitation of 2,150 mm. The mean yearly temperature averages 6.5 °C, and late spring and early autumn frosts are common. The Dinaric silver fir-European beech forest type (*Omphalodo-Fagetum*) is the dominant forest community in the study area. These forests primarily comprise silver fir and European beech, with varying proportions of Norway spruce (*Picea abies*), sycamore (*Acer pseudoplatanus*), and elm (*Ulmus glabra*). Stands are managed using selection (single-tree or group) systems or irregular shelterwood, leading to considerable withinstand variation in tree age and species composition (FMP, 2012).

In the middle of the 19th century, forests of European beech and silver fir predominated in the wider study area, and the young trees under the canopy consisted primarily of silver fir, which regenerated well due to the low ungulate densities. Older beech trees were intensively harvested until the mid-20th century (firewood and charcoal production), while silver fir became a dominant tree species (Gašperšič, 1967; Bončina et al., 2003).

Over time, its share has declined due to silver fir mortality between the 1960s and late 1990s. Recent studies suggest that the decline of silver fir is a consequence of interactions of various influences (e.g., air pollution, acid rain, drought effects, extensive ungulate browsing) (Tikvić et al., 2008; Diaci et al., 2010; Nagel et al., 2015). During this period, European beech gained considerable importance, while Norway spruce was promoted as its primary substitute. As a result of these forest dynamics, today's stands are more mixed and structurally diverse than in the past and have greater species diversity (Kobal et al., 2017). Tree

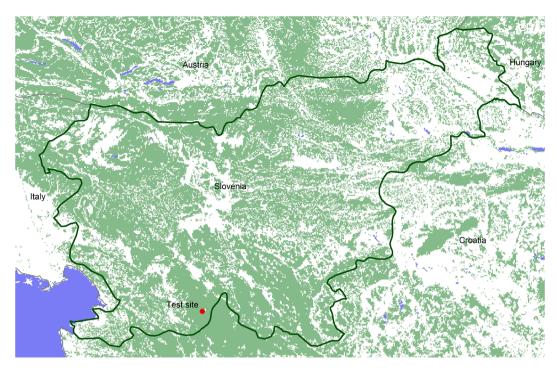


Fig. 1. Locations of the Leskova dolina study area in Slovenia.

species now occur more frequently in mixed patterns, either as individual trees or in small groups. Size differentiation has become more pronounced, with a wider range of smaller and larger trees. Consequently, the vertical and horizontal diversity of stands has increased, indicating a higher degree of differentiation and spatial complexity in the current forest structure (Kobal and Hladnik, 2009). Most stands are managed by selective felling (single trees or groups) or by irregular shelterwood management, which leads to considerable differences in tree age and species composition within stands. The close-to-nature forest management prevents clear-cutting or intensive forest conversion, which makes these forests very suitable for studying the structure and dynamics of forest communities. The ingrowth of trees is largely due to natural processes and not to the planting of trees (Fig. 2).

#### 2.2. Fieldwork

#### 2.2.1. Plot establishment and subject silver fir selection

In 2008, a systematic sampling grid was established with a spacing of 50 m  $\times$  50 m. On each grid intersection, a circular sampling plot of 500  $m^2$  was established and served as the basis for selecting the dominant silver fir trees. In each plot, all live trees with a DBH  $>\!\!10$  cm were measured, and the data on tree species and DBH were recorded.

Dominant trees were defined as those with the largest diameter in the plot, corresponding to 100 largest diameter trees per hectare or five largest diameter trees per 500 m $^2$ . To ensure representative selection, the third-largest silver fir tree in each plot was selected as the subject tree to represent the average dominant tree for further analysis. A total of 60 subject trees were selected.



Fig. 2. Typical uneven-aged mixed structure of silver fir-European beech forests.

#### 2.2.2. Stem analyses of subject silver firs

The selected subject trees were felled to enable a detailed stem analysis. Each stem was then divided into 15–20 sections, depending on the tree's total H. The diameter was measured at each section, and stem discs were taken for tree-ring width measurements. The first stem disc was obtained from the stump (0.15 m above the ground), followed by one at breast height (1.3 m) and then at regular intervals of 4.1 m up to a diameter of 30 cm. For the tree top, where the diameter of the stem was <30 cm, the stem was divided into 1 m sections. Overall, 992 stem discs were collected from all sampled trees, allowing a thorough analysis of stem growth patterns.

#### 2.3. Laboratory work

Stem discs were air-dried for at least three months before being prepared for tree-ring measurements. From each disc, a central block was extracted, carefully excluding the reaction wood. The bottom surface was sanded with progressively finer grades of sandpaper. Tree-ring widths were measured in two directions along the block, with a precision of 0.01 mm using ATRICS (Slovenian Forestry Institute, Slovenia; Levanič, 2007) and WinDendro software (Regent Instruments Inc., Canada). Each ring width series was checked, corrected, and dated both visually and statistically using PAST software (SCIEM, Austria). A standard arithmetic mean function was used to obtain the individual tree-ring width series.

#### 2.4. Data analysis

#### 2.4.1. Stem analysis: tree volume and volume increment measurement

The tree stem volume (V) was calculated as the sum of the volumes of all sections of the stem, treated as truncated cones. The volume in 2008 (the year of felling) marked as  $V_{2008}$  was computed using the following equation (Eq. 1):

$$V_{2008} = \frac{\pi \cdot h_{\rm s}}{3} \cdot \left( r_{2008}^2 + R_{2008} \cdot r_{2008} + R_{2008}^2 \right) \tag{1}$$

where  $h_{\rm s}$  represents the height of the truncated cone (length of the section), and  $R_{\rm 2008}$  and  $r_{\rm 2008}$  denote the radii of the stem at the bottom and top of the section, respectively.

We also calculated the V of the tree in the past to calculate the volume increment ( $V_{\rm incr}$ ). As we have analyzed, five-year  $V_{\rm incr}$  in this analysis, the 2003 volume  $V_{2003}$  was calculated using Eq. 1, while  $R_{2003}$  and  $r_{2003}$  were calculated by subtracting  $R_{2008}$  and  $r_{2008}$  from the sum of tree-ring widths (radial increment) between 2003 and 2008, respectively, which was obtained from detailed stem analysis at the bottom and top of the section separately.

The  $V_{\text{incr}}$  over the five years was then determined as per Eq. 2.

$$V_{\rm incr} = V_{2008} - V_{2003} \tag{2}$$

where  $V_{\rm incr}$  is the volume increment between 2003 and 2008,  $V_{2008}$  represents the volume of the tree in 2008, and  $V_{2003}$  represents the volume in 2003.

A detailed stem analysis was performed using a software package written specifically for our study in the R programming language (R Foundation for Statistical Computing, Austria) (R Development Core Team, 2013). Among its various capabilities, the software allowed for the reconstruction of the past growth history of tree stems. We used the correction proposed by Carmean (1972) to estimate the height growth of each subject tree. This method assumes that the annual height growth within a given stem section is constant and that crosscuts occur in the middle of the given annual height growth.

# 2.4.2. Measurement of neighboring trees

The measurements used to determine competition intensity were conducted after cutting and removing discs from the selected dominant silver fir trees (subject trees). All live neighboring trees with a DBH >10 cm were measured, and the data on tree species, DBH, and H with radii of 25.23 m from the subject tree (area = 2,000 m $^2$ ) were recorded. The H and horizontal distances between the subject tree and its potential competitors were measured using a Vertex IV instrument (Haglöf Sweden AB, Sweden). In total, 4,454 trees were measured.

#### 2.4.3. CIs

We quantified the level of competition using nine different CIs (Table 1). The first three CIs (CI1–CI3) are distance-independent, whereas the remaining six CIs (CI4–CI9) are distance-dependent. The CIs (CI5–CI9) include a relative component in their calculations by considering the ratio of the size of the competitor to the subject tree (DBH or *H*). In addition, CI5–CI9 decreased the influence of a competitor with increasing distance, which further refines the assessment of competition intensity.

2.4.3.1. Parameter optimization for competition index computation. This analysis aimed to optimize the calculation of CIs in uneven-aged forests using threshold values that determine whether a neighboring tree acts as a competitor. We applied the optimization procedure described previously by Miina and Pukkala (2000) and Vanclay (2006), as this approach ensures that competition is assessed dynamically based on the size of the subject and neighboring trees. To achieve this, we used the following threshold values.

- DBH<sub>j<sub>min</sub></sub>, which defines the minimum DBH above which a neighboring tree is considered a competitor (DBH<sub>j</sub> > DBH<sub>j<sub>min</sub></sub>).
- DIST<sub>ijmax</sub>, which defines the maximum distance within which a neighboring tree is still considered a competitor (DIST<sub>ij</sub> < DIST<sub>ijmax</sub>).

Unlike fixed threshold values,  $\mathrm{DBH}_{j_{\mathrm{min}}}$  and  $\mathrm{DIST}_{ij_{\mathrm{max}}}$  are dynamic and scale in proportion to  $\mathrm{DBH}_i$ . Their values are determined by two parameters— $\alpha$  and  $\beta$ , which are used to be multiplied by  $\mathrm{DBH}_i$  to calculate the relative value of  $\mathrm{DBH}_{j_{\mathrm{min}}}$  and  $\mathrm{DIST}_{ij_{\mathrm{max}}}$ , respectively (Fig. 3).

For each subject tree, the  ${\rm DBH}_{j_{\rm min}}$  for neighboring trees was calculated as follows (Eq. 3).

$$DBH_{i_{min}} = \alpha \cdot DBH_{i} \tag{3}$$

where  $\alpha$  determines how thick a neighboring tree needs to be relative to the subject tree to be a competitor and be included in the CI calculation. For instance, if  $\alpha=0.25$ , only neighboring trees with DBH $_j>25\%$  of the DBH $_i$  of the subject tree (DBH $_{j_{min}}>0.25\times$  DBH $_i$ ) qualify as competitors, and if  $\alpha=1.00$ , only neighboring trees with DBH $_j>100\%$  of the DBH $_i$  of the subject tree (DBH $_{j_{min}}>1.00\times$  DBH $_i$ ) qualify as competitors.

Additionally, for each subject tree,  $DIST_{ij_{max}}$  for neighboring trees was calculated as Eq. 4.

$$DIST_{ij_{max}} = \beta \cdot DBH_i$$
 (4)

where  $\beta$  determines how far a neighboring tree has to be from the subject tree to be a competitor and be included in the CI calculation. For instance, if  $\beta=5$ , only trees within a distance of five times the DBH $_i$  of the subject tree qualify as competitors (DIST $_{ij_{max}}>5\times$  DBH $_i$ ), and if  $\beta=35$ , only trees within a distance of 35-fold the DBH $_i$  of the subject tree qualify as competitors (DIST $_{ij_{max}}>30\times$  DBH $_i$ ).

Both  $\mathrm{DBH}_{j_{\min}}$  and  $\mathrm{DIST}_{ij_{\max}}$  are dynamic and depend on the  $\mathrm{DBH}_i$  of the subject tree. The values of  $\alpha$  and  $\beta$  are crucial, as they determine how strict the criteria for competitor definition are, since a higher  $\alpha$  value results in fewer competitor trees, as only larger trees qualify, and a higher  $\beta$  value increases the competition radius, allowing more distant trees to be included as competitors. By adjusting  $\alpha$  and  $\beta$ , the model can be fine-tuned to reflect diverse and heterogeneous stand structures, ensuring that competition is assessed dynamically rather than with fixed thresholds.

 Table 1

 Nine tested competition indices were used in the study.

Abbreviation	Index	Source	Variable	Equation
CI1	Sum of the basal areas of the competitors	Steneker and Jarvis (1963)	$DBH_j$	$\sum_{n}^{\infty} \frac{\pi \cdot DBH_{j}^{2}}{n}$
CI2	Sum of ratios of competitors to subject tree DBH	Lorimer (1983)	$\mathrm{DBH}_{j}$ $\mathrm{DBH}_{i}$	$\frac{\sum_{j=1}^{j=1} \overline{40000}}{\overline{\text{DBH}_i}} \sum_{j=1}^{n} \overline{\text{DBH}_j}$
CI3	Sum of ratios of competitor to subject tree basal area	Corona and Ferrara (1989)	DBH <sub>i</sub> DBH <sub>i</sub>	$\frac{1}{DBH_i^2} \sum_{j=1}^{n} DBH_j^2$
CI4	Sum of distances between competitors to subject tree	Staebler (1951)	$\mathrm{DIST}_{ij}$	$\sum_{i=1}^{n} \text{DIST}_{ij}$
CI5	Hegyi diameter-distance competition index	Hegyi (1974)	$\mathrm{DBH}_{i}$ $\mathrm{DBH}_{i}$	$\sum_{j=1}^{n} \frac{\mathrm{DBH}_{j}/\mathrm{DBH}_{i}}{\mathrm{DIST}_{ij}}$
CI6	Hegyi height-distance competition index	Braathe (1980)	$DIST_{ij}$ $H_j$ $H_i$	$\sum\nolimits_{j=1}^{n}\frac{H_{j}/H_{i}}{\mathrm{DIST}_{ij}}$
CI7	Rouvinen-Kuuluvainen diameter-distance competition index	Rouvinen and Kuuluvainen (1997)	DIST <sub>ij</sub> DBH <sub>j</sub> DBH <sub>i</sub>	$\sum\nolimits_{j=1}^{n} \left( \frac{\mathrm{DBH}_{j}}{\mathrm{DBH}_{i}} \right) \mathrm{arctan} \left( \frac{\mathrm{DBH}_{j}}{\mathrm{DIST}_{ij}} \right)$
CI8	Rouvinen-Kuuluvainen height-distance competition index	Rouvinen and Kuuluvainen (1997)	$DIST_{ij} \ H_j \ H_i$	$\sum_{j=1}^{n} \left( rac{H_{j}}{H_{i}}  ight) rctan \left( rac{H_{j}}{ ext{DIST}_{ij}}  ight)$
CI9	Pukkala-Kolström height-distance competition index	Pukkala and Kolström, 1987	$egin{aligned}  ext{DIST}_{ij} \ H_i \  ext{DIST}_{ij} \end{aligned}$	$\sum\nolimits_{j=1}^{n}\arctan\left(\frac{H_{j}-H_{i}}{\text{DIST}_{ij}}\right)$

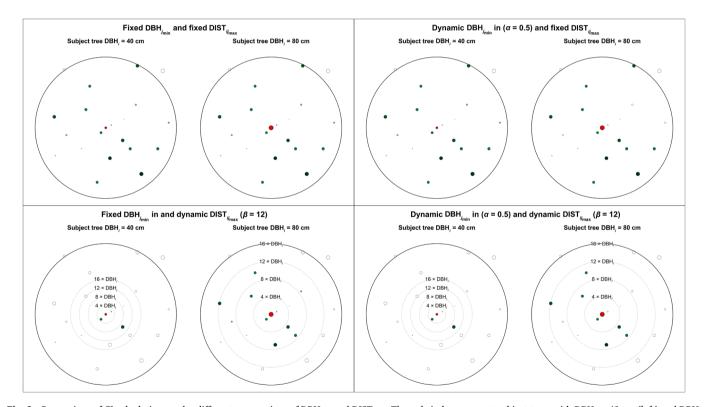


Fig. 3. Comparison of CI calculations under different assumptions of  $DBH_{j_{min}}$  and  $DIST_{ij_{max}}$ . The red circles represent subject trees with  $DBH_i = 40$  cm (left) and  $DBH_i = 80$  cm (right). Neighboring trees are included in the CI calculation based on their  $DBH_j$  and  $DIST_{ij}$  relative to the  $DBH_i$  of the subject tree. The four panels illustrate different combinations of fixed vs. dynamic  $DBH_{j_{min}}$  ( $\alpha \times DBH_i$ ) and  $DIST_{ij_{max}}$  ( $\beta \times DBH_i$ ).  $\alpha = 0.5$ ,  $\beta = 12$ . The size of the circles represents the DBH of a tree and the intensity of the green color indicates a higher  $DBH_j$ . Empty circles represent trees not included in the CI calculation.

2.4.3.2. Optimization of  $\alpha$  and  $\beta$  and calculations of the effect of competition on volume increment. The optimization of  $\alpha$  and  $\beta$  was conducted using a linear regression model, where the  $V_{\text{incr}}$  of the subject tree was the dependent variable, while the volume of the subject tree ( $V_i$ ) and calculated CIs were independent variables. The regression model was formulated as Eq. 5.

$$V_{\text{incr}} = b_0 + b_1 \cdot V_i + b_2 \cdot \sum_j I \left( \text{DBH}_j > \text{DBH}_{j_{\text{min}}}, \text{ DIST}_{ij} < \text{ DIST}_{ij_{\text{max}}} \right) \cdot \text{CI}_j$$

where  $V_{\text{incr}}$  represents the increase in volume over a specified period and CI incorporates both the minimum competitive diameter (DBH $_{j_{\min}} = \alpha \text{DBH}_i$ ) and maximum competitive distance (DIST $_{ij_{\max}} = \beta \text{DBH}_i$ ).

The parameters  $\alpha$  and  $\beta$  were iteratively varied to explore various possible values, with  $\alpha$  tested between 0.25 and 1.00 and  $\beta$  tested between 5 and 35. Four approaches were used.

1. Neighboring trees were considered as competitors, using a fixed threshold  ${\rm DBH_{\it j_{min}}}>10$  cm and maximum distance  ${\rm DIST_{\it ij_{max}}}=25.25$  m

- 2. Neighboring trees were considered competitors if  $DBH_j > DBH_{j_{min}}$  (where  $DBH_{j_{min}} = \alpha \times DBH_i$ ), whereas we fixed the maximum distance  $DIST_{ij_{max}}$  at 25.25 m.
- 3. Neighboring trees were considered competitors if  $DIST_{ij} < DIST_{ij_{max}}$  (where  $DIST_{ij_{max}} = \beta \times DBH_i$ ), whereas we fixed the minimum diameter  $DBH_{i_{min}}$  at 10 cm.
- 4. Neighboring trees were considered competitors if  $DBH_j > DBH_{j_{min}}$  (where  $DBH_{j_{min}} = \alpha \times DBH$ ) and  $DIST_{ij} < DIST_{ij_{max}}$  (where  $DIST_{ij_{max}} = \beta \times DBH_i$ ).

To determine the optimal values for each CI, we selected the combination that resulted in the highest explanatory power of the linear regression model in terms of the maximum adjusted coefficient of determination (Adj.  $R^2$ ). This approach ensures that the selected  $\alpha$  and  $\beta$  values maximize the ability of the CI to explain the growth variation in subject trees. Statistical analyses were conducted using the R2.9.3 software environment (R Development Core Team, 2016).

#### 3. Results

#### 3.1. General data on forest structure and subject trees

Silver fir dominated the analyzed forests with 83.4% of the total growing stock, with the largest average DBH (41.3  $\pm$  0.76 cm), H (26.0  $\pm$  0.39 m), and V (2.70  $\pm$  0.10 m³), indicating its dominance in the forest structure. European beech, which accounted for 10.2% of total growing stock, was the second most common tree species, but with an average DBH of 19.3  $\pm$  0.47 cm, a H of 18.90  $\pm$  0.30 m, and V of 0.46  $\pm$  0.03 m³, it had the lowest dimensions among the measured trees (Fig. 4).

The subject silver fir trees were between 144 and 209 years old, with an average of 178 years. The DBH ranged from 43.4 to 72.1 cm, with a mean of 59.2 cm. The H of the trees ranged from 26.45 to 39.69 m. The  $V_{\rm incr}$  was the most variable and ranged from 1.91 to 8.08 m<sup>3</sup>.  $V_{\rm incr}$  in the

last 5 years ranged from 0.036 to 0.720 m<sup>3</sup>. The linear model for the  $V_{\text{incr}}$  of silver fir related to its one V explained 32.5% of the variability in tree  $V_{\text{incr}}$ . Summary data are listed in Table 2.

#### 3.2. Tree growth in terms of tree volume and competition

Four approaches were tested (see Supplemental Materials). Here, we focus only on the 4th approach, where we use dynamic  $\mathrm{DBH}_{j_{\min}}$  and dynamic  $\mathrm{DIST}_{ij_{\max}}$ . Fig. 5 illustrates the variation in  $\mathrm{Adj}$ .  $R^2$  for different linear models where  $V_{\mathrm{incr}}$  serves as the dependent variable and V and various CIs are the independent variables. The results indicated that  $\mathrm{Adj}$ .  $R^2$  values varied among CIs with changes in both  $\alpha$ , which defines the  $\mathrm{DBH}_{j_{\min}}$  based on  $\mathrm{DBH}_i$  ( $\mathrm{DBH}_{j_{\min}} = \alpha \times \mathrm{DBH}_i$ ), and  $\beta$ , which determines  $\mathrm{DIST}_{ij_{\max}}$  based on the same diameter ( $\mathrm{DIST}_{ij_{\max}} = \beta \times \mathrm{DBH}_i$ ). The overall pattern of  $\mathrm{Adj}$ .  $R^2$  variation was consistent across different CIs (Fig. 5).

Among the indices, CI6 and CI8 had the highest Adj.  $R^2$  (0.647 and 0.642, respectively), indicating their greater ability to explain the effects of competition in the dynamic  $\mathrm{DBH}_{j_{\mathrm{min}}}$  and dynamic  $\mathrm{DIST}_{ij_{\mathrm{max}}}$  approach. Conversely, CI9 had the lowest Adj.  $R^2$  (maximum 0.428), indicating lower efficiency compared to the other indices. Indices such as CI2, CI4, and CI7 showed moderate performance, with a maximum Adj.  $R^2$  between 0.621 and 0.636. Most CIs achieved a higher Adj.  $R^2$  when  $\alpha$  was between 0.27 and 0.39, while the optimal value of  $\beta$  was generally between 19 and 30.5 (Table 3).

Table 2 Summary information for 60 subject silver fir trees, including values for age, DBH, H, V, and  $V_{\rm incr}$ .

Value	Age	DBH	Height	Volume	Volume increment
Unit	years	cm	m	$m^3$	$m^3$
Min.	144	43.4	26.45	1.91	0.036
Mean	178	59.2	34.23	4.82	0.260
Max.	209	72.1	39.69	8.08	0.720

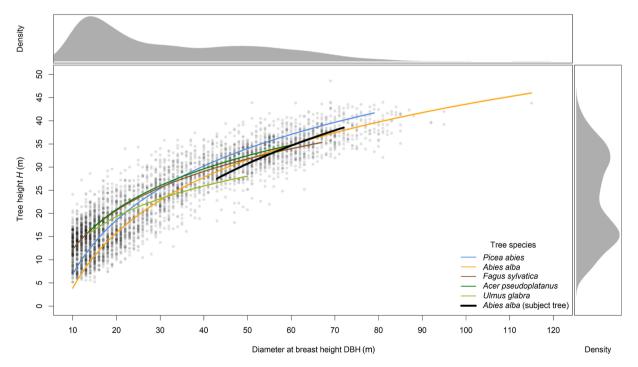


Fig. 4. Height curve of neighboring trees in the study area by tree species. The plot above shows the density distribution of DBH for all three species combined, while the density plot on the right side shows the height density for all trees together.

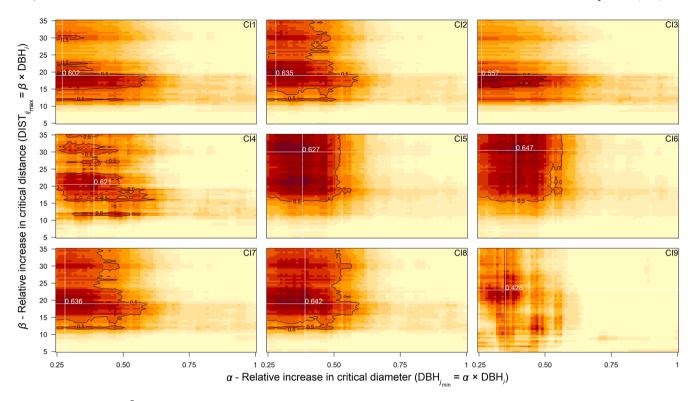


Fig. 5. Changes in adjusted  $R^2$  values for the nine competition indices (CI1–CI9) under the optimal search radius and optimal DBH approaches. Each panel represents a different competition index, with heatmaps illustrating the relationship between  $\alpha$  (relative increase in critical diameter) and  $\beta$  (relative increase in critical distance). Darker areas on the heat maps indicate higher adjusted  $R^2$  values.

**Table 3** Adjusted  $R^2$  values and corresponding *p*-values for various CIs in the linear model, indicating the explanatory power of each index under the fixed search radius and optimum DBH approach.

Model	Adj. R <sup>2</sup> value	<i>p</i> - value	Optimal $\alpha$ value	Optimal $\beta$ value
$V_{ m incr} = b_0 + b_1 \cdot V + b_2 \cdot \text{CI1}$	0.602	0.0000	0.27	19.0
$V_{ ext{incr}} = b_0 + b_1 {\cdot} V + b_2 {\cdot}  ext{CI2}$	0.635	0.0000	0.28	19.0
$V_{ ext{incr}} = b_0 + b_1 {\cdot} V + b_2 {\cdot}  ext{CI3}$	0.557	0.0000	0.26	19.0
$V_{ ext{incr}} = b_0 + b_1 {\cdot} V + b_2 {\cdot}  ext{CI4}$	0.621	0.0000	0.39	20.5
$V_{ ext{incr}} = b_0 + b_1 \cdot V + b_2 \cdot  ext{CI5}$	0.627	0.0000	0.38	30.0
$V_{ ext{incr}} = b_0 + b_1 \cdot V + b_2 \cdot \text{CI6}$	0.647	0.0000	0.39	30.5
$V_{ ext{incr}} = b_0 + b_1 \cdot V + b_2 \cdot  ext{CI7}$	0.636	0.0000	0.28	19.0
$V_{\text{incr}} = b_0 + b_1 \cdot V + b_2 \cdot \text{CI8}$	0.642	0.0000	0.39	19.0
$V_{ ext{incr}} = b_0 + b_1 \cdot V + b_2 \cdot \text{CI9}$	0.428	0.0023	0.35	23.0

# 4. Discussion

## 4.1. Focus on the growth of dominant trees in Dinaric beech-fir forests

In this study, we focused on the growth of the dominant silver fir in heterogeneous Dinaric beech-silver fir forests. Silver fir was the predominant tree species in the study area, accounting for 85.4% of the total growing stock, whereas European beech dominated in terms of tree numbers. When calculating competitiveness, it was, therefore, assumed

that silver fir and the other tree species are equal competitors, although some studies reported that interspecific competition in silver fir stands is more important than intraspecific competition. For instance, Puettmann et al. (2009) found that even a small proportion of European beech in stands has a greater influence on silver fir growth than the presence of other conifers of similar size. Similarly, Pinto et al. (2007) found that the radial increment of silver fir decreased with increasing proportions of Norway spruce in the stand. While our results confirmed similar decreasing trends in growth, the proportion of other tree species (primarily Norway spruce and European beech) in the growing stock at our study site was relatively low (the proportion of silver fir in the growing stock ranged from 55% to 96% per plot level). Due to the limited presence of other tree species, we could not reliably assess the role of interspecific competition.

## 4.2. Significant effect of tree volume on the growth of dominant trees

The  $V_{\text{incr}}$  over the last five years ranged from 0.036 to 0.720 m<sup>3</sup>, indicating considerable variability in the growth of dominant silver fir trees. Although the relationship between V and  $V_{incr}$  was statistically significant (p < 0.001), the relatively low value of Adj.  $R^2$  (0.325) indicates that V explains only a fraction of V<sub>incr</sub> and that other factors such as heterogeneous topography (Kobal and Hladnik, 2021), numerous sinkholes (Kobal et al., 2015), variable soil properties (Kobal et al., 2014), and diverse micro-site conditions (Kobal et al., 2015) play an important role in tree growth. In addition, the forests are characterized by uneven-aged stand structures (Gašperšič, 1967; Bončina et al., 2003), diverse tree species mixtures (Kobal and Hladnik, 2009; Kobal et al., 2017), and spatial mingling and size differentiation of trees (Kobal and Hladnik, 2009) resulting from selective and irregular shelterwood management systems are likely to influence  $V_{incr}$  in a way that they might interact with or mask the effect of competition, reducing the predictive accuracy of the model.

#### 4.3. Significance of competition on the growth of dominant trees

Our results confirmed that competition between trees has a significant negative influence on the growth of dominant and older silver fir trees, consistent with several other studies (Lorimer, 1983; Tomé and Burkhart, 1989; Biging and Dobbertin, 1995; Pretzsch et al., 2002; Mailly et al., 2003; Corral Rivas et al., 2005; Hasenauer, 2006; Stadt et al., 2007; Seifert et al., 2014). Although our study focused on older and dominant individuals, previous research has shown that measures of competition between neighbors can better explain variation in the growth of younger trees (Cannell et al., 1984; Kubota and Hara, 1995; McLellan et al., 1997). However, this may not be true for immature canopy trees growing in the understory, as they did not appear to respond to the calculated CIs, suggesting that the CIs may not adequately reflect the resource conditions experienced by these trees (Seifert et al., 2014).

Despite focusing on older trees, our results showed that neighbor competition remains relevant even at later stages of development (Prévosto and Curt, 2004; Fox et al., 2007), consistent with findings from other studies. For example, older silver fir trees have been shown to respond to reduced stand density with increased radial growth (Puettmann et al., 2009), and similar patterns were observed in uneven-aged old-growth reserves in Romania (Duduman et al., 2009), where the strongest correlation between competition and tree-ring width occurred when only the two nearest neighbors were considered. These results suggest that even minimal local crowding can significantly affect the growth of older silver fir trees. Our findings align with this, as competition indices in our study retained explanatory power even for dominant silver fir trees. Although our analysis focused on silver fir, studies of old conifers, such as black spruce (Picea mariana) (Mailly et al., 2003) and Norway spruce (Castagneri et al., 2008; Fraver et al., 2014) have reported similarly strong responses to competition and stand composition.

# 4.4. Comparison of the performance of CIs

In this study, we used different types of competition indices (Table 1), which differ in which variables are included and whether distance is considered in the calculation. CI1–CI3 are based on tree diameter but do not consider DIST $_{ij}$ , limiting their ability to accurately model competition in structurally heterogeneous forest stands. CI2 and CI3, which use the ratio of the competitor tree diameter to the subject tree diameter, perform relatively well, emphasizing the importance of relative tree size for competition modeling. Indices based solely on the diameter of the trees (CI1–CI3) failed to fully capture the effects of competition (Steneker and Jarvis, 1963; Lorimer, 1983; Corona and Ferrara, 1989). CI4, which considers spatial arrangement, also reflected the role of spatial distribution in competition (Staebler, 1951) but was less effective

In contrast, CI5-CI9 considers both the distance and relative size of neighboring trees (DBH or H), allowing a more realistic assessment of competition intensity. Among these indices, CI6, which considers both Hand distance, was the most effective competition index to emphasize the role of vertical competition in tree growth (Braathe, 1980). It achieved the highest Adj.  $R^2$  (0.647, p < 0.0001), confirming that the integration of distance and *H* significantly improves the performance of the model. This is consistent with the findings that size relationships remain important in modeling competition (Hegyi, 1974) and confirms that models incorporating H and distance better reflect competitive dynamics in vertically complex stands representative of our research site (Kobal and Hladnik, 2009). We can conclude that competition indices integrating multiple factors—size (i.e., DBH or H) and distance—provide the most accurate predictions of tree growth (Hegyi, 1974; Braathe, 1980; Rouvinen and Kuuluvainen, 1997), although some studies suggest that no CI could be identified as the general best option to characterize competition, especially in complex, species-rich, and

highly structured forest ecosystems (Seifert et al., 2014).

These findings can be directly linked to the structural complexity of the forest stands analyzed. As a result of historical management (Gašperšič, 1967; Bončina et al., 2003) and natural regeneration (Diaci et al., 2010), today's Dinaric European beech-silver fir forests exhibit high variability in terms of tree size, spatial arrangement, and tree species composition (Kobal and Hladnik, 2009; Kobal et al., 2017). Under such heterogeneous conditions, distance- and height-based competition indices, such as CI6 and CI8, better capture competitive interactions. This is in line with Lorimer (1983), who emphasized the importance of relative tree size for competition dynamics, and Hegyi (1974), who showed that the combination of size and distance improves the realism of competition modeling.

# 4.5. Use of critical distances and critical tree diameter threshold to determine CIs

To improve competition modeling, we used dynamic thresholds for the definition of competitors and adjusted both  $\mathrm{DBH}_{j_{\min}}$  and  $\mathrm{DIST}_{ij_{\max}}$  based on the size of the subject tree ( $\mathrm{DBH}_i$ ). By varying  $\alpha$ -value within a dynamic modeling approach, we determine the optimal  $\mathrm{DBH}_{j_{\min}}$  ( $\mathrm{DBH}_{j_{\min}}$ ) and  $\alpha$ -values make inclusion of smaller trees possible. By varying the  $\beta$ -value, we were able to dynamically model  $\mathrm{DIST}_{ij_{\max}}$  ( $\mathrm{DIST}_{ij_{\max}} = \beta \times \mathrm{DBH}_i$ ) and define the spatial extent of the competition.

For all models, the optimal  $\alpha$ -values ranged from 0.26 to 0.39, suggesting that tree growth is best explained when both smaller and larger competitors are included. Previous studies consider both, thinner trees than the subject tree (Biging and Dobbertin, 1995; Stadt et al., 2007; Béland et al., 2003; Seifert et al., 2014) and thicker trees than the subject tree (Tomé and Burkhart, 1989; Biging and Dobbertin, 1995; Mailly et al., 2003; Fichtner et al., 2012) when calculating the competition index. However, more recent research emphasizes the role of smaller trees, especially in dense stands (Das, 2012), although their influence may be limited in older or structurally more complex forests (Aakala et al., 2013).

The values of  $\beta$  ranged from 19.0 to 30.5, indicating that competition extends beyond immediate neighbors. These results are consistent with Puettmann et al. (2009), who observed responses of fir growth to the distance of beech trees up to 18 m away. Similarly, Bella (1971), Daniels et al. (1986), and Das (2012) found that wider zones of influence increased modeling accuracy. Lorimer (1983) suggested a critical distance corresponding to 3.5 times the crown radius of the tree, which in our case would be 11.2 m for the silver fir with a diameter of 50 cm and crown radius of 3.2 m (calculated from crown radius measurements at 12 points around the tree; not shown). Das (2012) investigated the competition in old forests and found strong competitive responses in four coniferous species with influence radii ranging from 7.5 to 19.5 m, which is similar to our findings.

Our results show that optimizing  $\mathrm{DIST}_{ij_{\mathrm{max}}}$  had a stronger effect on model performance than optimizing  $\mathrm{DBH}_{j_{\mathrm{min}}}$  alone, suggesting that the spatial arrangement of trees plays a more important role in explaining growth variability than size ratio alone. This is consistent with the results of Canham et al. (2004), who showed that distance-weighted competition indices provide better predictions of tree growth in different forest types.

Although this study provides valuable insights into the effects of competition on the growth of dominant silver fir in Dinaric beech-fir forests, some limitations should be noted. It focused exclusively on the dominant silver fir, which limits the generalisability of the results to other community classes and tree species. Due to the low proportion of other species in most plots, the role of interspecific competition could not be assessed. Competition indices were based on structural variables (tree size and distance), which do not reflect the full range of ecological interactions, such as belowground competition or light interception, and

the narrow range of other ecological factors. Growth was assessed over a five-year period, which may not capture long-term or delayed responses to competition. Future research that incorporates longer-term monitoring, a broader range of species, and functional ecological variables will help deepen our understanding of competition in complex forest ecosystems.

#### 5. Conclusions

Competition significantly affects the growth of dominant silver fir trees in Dinaric beech-fir forests, with tree Vincr being influenced by competition even in older trees. Distance-dependent competition indices improve accuracy, as indices incorporating both distance and tree size (CI5-CI8) outperformed those based solely on basal area or diameter ratios (CI1-CI3). The Hegyi height-distance index (CI6) proved to be the best predictor (Adj.  $R^2 = 0.647$ ). Optimizing competition thresholds enhanced model performance, with the dynamic  $DBH_{i_{min}}$  and  $DIST_{ij_{max}}$ approach improving competition assessment and suggesting the inclusion of smaller competitors (optimal  $\alpha = 0.26-0.39$ ). Competition effects extend beyond immediate neighbors, as the optimal  $\beta$  values (19.0-30.5) suggested that competition influences tree growth over greater distances. Additionally, H is a stronger predictor than DBH, as height-based indices (CI6 and CI8) better explained competition, emphasizing the importance of light availability. These results emphasize the need to incorporate spatial and vertical stand structures into forest growth models and silvicultural planning. Future studies should investigate how these relationships evolve over time, for different species and under different site and climatic conditions in order to improve forest management strategies.

#### CRediT authorship contribution statement

Milan Kobal: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. Tom Levanič: Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Funding acquisition, Formal analysis.

#### Data availability

The data will be available upon reasonable request to the first author.

# Funding

This research was funded by the Slovenian Research and Innovation Agency (https://www.aris-rs.si/sl/) Program and Research Core Funding No. P4-0107 (TL) and No. P4-0059 (MK), and Young Researcher Program Grant (MK). The APC was funded by the Slovenian Forestry Institute (P4-0107).

# Declaration 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.

# Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.fecs.2025.100346.

#### References

Béland, M., Lussier, J.M., Bergeron, Y., Longpré, M.H., Béland, M., 2003. Structure, spatial distribution and competition in mixed jack pine (*Pinus banksiana*) stands on

- clay soils of eastern Canada. Ann. For. Sci. 60, 609–617. https://doi.org/10.1051/
- Bella, I.E., 1971. A new competition model for individual trees. For. Sci. 17, 364–372. https://doi.org/10.1093/forestscience/17.3.364.
- Biging, G.S., Dobbertin, M., 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For. Sci. 38, 695–720. https://doi.org/10.1093/forestscience/38.3.695.
- Biging, G.S., Dobbertin, M., 1995. Evaluation of competition indices in individual tree growth models. For. Sci. 41, 360–377. https://doi.org/10.1093/forestscience/ 41 2 360
- Boivin, F., Paquette, A., Papaik, M.J., Thiffault, N., Messier, C., 2010. Do position and species identity of neighbours matter in 8–15-year-old post-harvest mesic stands in the boreal mixedwood? For. Ecol. Manag. 260, 1124–1131. https://doi.org/ 10.1016/j.foreco.2010.06.037.
- Bolte, A., Kampf, F., Hilbrig, L., 2013. Space sequestration below ground in old-growth spruce-beech forests – signs for facilitation? Front. Plant Sci. 4, 322. https://doi.org/ 10.3389/fpls.2013.00322.
- Bončina, A., Gašperšič, F., Diaci, J., 2003. Long-term changes in tree species composition in the Dinaric mountain forests of Slovenia. For. Chron. 79, 227–232. https://doi. org/10.5558/tfc79227-2.
- Bončina, A., 2011. History, current status and future prospects of uneven-aged forest management in the Dinaric region: an overview. Forestry 84, 467–478. https://doi. org/10.1093/forestry/cpr023.
- Braathe, P., 1980. Height increment of young single trees in relation to height and distance of neighboring trees. Mitt. Forstl. VersAnst. 130, 43–48.
- Burkhart, H.E., Tomé, M., 2012. Modeling Forest Trees and Stands. Springer, Dordrecht. https://doi.org/10.1007/978-90-481-3170-9.
- Cannell, M.G.R., Rothery, P., Ford, E.D., 1984. Competition within stands of *Picea sitchensis* and *Pinus contorta*. Ann. Bot. 53, 349–362.
- Carmean, W.H., 1972. Site index curves for upland oaks in the central states. For. Sci. 18, 109–120. https://doi.org/10.1093/forestscience/18.2.109.
- Castagneri, D., Vacchiano, G., Lingua, E., Motta, R., 2008. Analysis of intraspecific competition in two subalpine Norway spruce (*Picea abies*) stands in Paneveggio (Trento, Italy). For. Ecol. Manag. 255, 651–659. https://doi.org/10.1016/j. foreco.2007.09.041.
- Chen, B., Liu, K., Wang, C., Guo, J., Lu, J., Chen, L., Zhao, Z., Zeng, J., 2024. Tree allometry responses to competition and complementarity in mixed-species plantations of *Betula alnoides*. For. Ecosyst. 11, 100207. https://doi.org/10.1016/j. fecs.2024.100207.
- Contreras, M.A., Affleck, D., Chung, W., 2011. Evaluating tree competition indices as predictors of basal area increment in western Montana forests. For. Ecol. Manag. 262, 1939–1949. https://doi.org/10.1016/j.foreco.2011.08.031.
- Coomes, D.A., Allen, R.B., 2007. Effects of size, competition and altitude on tree growth. J. Ecol. 95, 1084–1097. https://doi.org/10.1111/j.1365-2745.2007.01280.x.
- Corona, P., Ferrara, A., 1989. Individual competition indices for conifer plantations. Agric. Ecosyst. Environ. 27, 429–437. https://doi.org/10.1016/0167-8809(89) 90103-5.
- Corral Rivas, J.J., González, J.G.Á., Aguirre, O., Hernández, F.J., 2005. The effect of competition on individual tree basal area growth in mature stands of *Pinus cooperi* Blanco in Durango (Mexico). Eur. J. For. Res. 124, 133–142. https://doi.org/10.1007/s10342-005-0061-y.
- D'Amato, A.W., Puettmann, K.J., 2004. The relative dominance hypothesis explains interaction dynamics in mixed-species *Alnus rubra/Pseudotsuga menziesii* stands. J. Ecol. 92, 450–463. https://doi.org/10.1111/j.0022-0477.2004.00888.x.
- Daniels, R.F., Burkhart, H.E., Clason, T.R., 1986. A comparison of competition measures for predicting growth of loblolly pine trees. Can. J. For. Res. 16, 1230–1237. https://doi.org/10.1139/x86-218.
- Das, A., 2012. The effect of size and competition on tree growth rate in old-growth coniferous forests. Can. J. For. Res. 42, 1983–1995. https://doi.org/10.1139/x2012-142
- Diaci, J., Roženbergar, D., Bončina, A., 2010. Stand dynamics of Dinaric old-growth forest in Slovenia: are indirect human influences relevant? Plant Biosyst. 144, 194–201. https://doi.org/10.1080/11263500903560785.
- Duduman, G., Roibu, C.C., Duduman, M.L., Miron-Onciul, M., 2010. The influence of competition and dimensional-spatial characteristics of trees on their radial growth in Old-Growth Slătioara forest, Romania. Adv. Environ. Sci. Int. J. Bioflux Soc. 2, 215–230
- Fichtner, A., Sturm, K., Rickert, C., Härdtle, W., Schrautzer, J., 2012. Competition response of European beech (*Fagus sylvatica*) varies with tree size and abiotic stress: minimizing anthropogenic disturbances in forests. J. Appl. Ecol. 49, 1306–1315. https://doi.org/10.1111/j.1365-2664.2012.02196.x.
- FMP, 2012. Forest Management Plan for Forest Management Region Postojna 2011–2020. Slovenia Forest Service, Postojna (in Slovene).
- Fox, J.C., Bi, H., Ades, P.K., 2007. Spatial dependence and individual-tree growth models I. Characterising spatial dependence. For. Ecol. Manag. 245, 10–19. https://doi.org/ 10.1016/j.foreco.2007.04.025.
- Fraver, S., D'Amato, A.W., Bradford, J.B., Jonsson, B.G., Jönsson, M., Esseen, P.-A., 2014. Tree growth and competition in an old-growth *Picea abies* forest of boreal Sweden: influence of tree spatial patterning. J. Veg. Sci. 25, 374–385. https://doi.org/10.1111/jvs.12096.
- Gašperšič, F., 1967. Razvojna dinamika mešanih gozdov jelke-bukve na Snežniku v zadnjih 100 letih. Gozdarski vestnik 7–8, 202–237 (in Slovene).
- Grams, T.E.E., Andersen, C.P., 2007. Competition for resources in trees: physiological versus morphological plasticity. In: Esser, K., Lüttge, U., Beyschlag, W., Murata, J. (Eds.), Progress in Botany, 68. Springer, Berlin, Heidelberg, pp. 281–304. https://doi.org/10.1007/978-3-540-36832-8\_16.

- Hegyi, F., 1974. A simulation model for managing jack-pine stands. In: Fries, J. (Ed.), Growth Models for Tree and Stand Simulation. Royal College of Forestry, Stockholm, 22, 74, 00.
- Hrivnák, R., Bošeľa, M., Slezák, M., Lukac, M., Svitková, I., Gizela, J., Hegedüšová, K., Hrivnák, M., Kliment, J., Knopp, V., Senko, D., Ujházyová, M., Valachovič, M., Wiezik, M., Máliš, F., 2022. Competition for soil resources forces a trade-off between enhancing tree productivity and understorey species richness in managed beech forests. Sci. Total Environ. 849, 157825. https://doi.org/10.1016/j. scitotenv.2022.157825.
- Hynynen, J., Ojansuu, R., 2003. Impact of plot size on individual-tree competition measures for growth and yield simulators. Can. J. For. Res. 33, 455–465. https://doi. org/10.1139/x02-173
- Kobal, M., Bertoncelj, I., Pirotti, F., Dakskobler, I., Kutnar, L., 2015. Using LiDAR data to analyse sinkhole characteristics relevant for understory vegetation under forest cover—case study of a high karst area in the Dinaric Mountains. PLoS One 10, e0122070. https://doi.org/10.1371/journal.pone.0122070.
- Kobal, M., Gréman, H., Zupan, M., Levanič, T., Simončič, P., Kadunc, A., Hladnik, D., 2014. Influence of soil properties on silver fir (*Abies alba Mill.*) growth in the Dinaric Mountains. For. Ecol. Manag. 337, 77–87. https://doi.org/10.1016/j. foreco.2014.10.017.
- Kobal, M., Hladnik, D., 2009. Stand diversity in the Dinaric fir-beech forests. Zbornik gozdarstva in lesarstva 90, 25–42. http://www.dlib.si/?URN=URN:NBN:SI: DOC-UNKMF4OC.
- Kobal, M., Kastelec, D., Eler, K., 2017. Temporal changes of forest species composition studied by compositional data approach. iForest 10, 729–738. https://doi.org/ 10.3832/ifor2187-010.
- Kobal, M., Hladnik, D., 2021. Tree height growth modelling using LiDAR-derived topography information. ISPRS Int. J. Geo-Inf. 10, 419. https://doi.org/10.3390/ iigi10060410
- Kubota, Y., Hara, T., 1995. Tree competition and species coexistence in a sub-boreal forest, northern Japan. Ann. Bot. 76, 503–512. https://doi.org/10.1006/ anbo.1995.1126.
- Larocque, G.R., 2002. Examining different concepts for the development of a distance-dependent competition model for red pine diameter growth using long-term stand data differing in initial stand density. For. Sci. 48 (1), 24–34. https://doi.org/10.1093/forestscience/48.1.24.
- Ledermann, T., 2010. Evaluating the performance of semi-distance-independent competition indices in predicting the basal area growth of individual trees. Can. J. For. Res. 40, 796–805. https://doi.org/10.1139/X10-026.
- Lei, P., Scherer-Lorenzen, M., Bauhus, J., 2012. Belowground facilitation and competition in young tree species mixtures. For. Ecol. Manag. 265, 191–200. https://doi.org/10.1016/j.foreco.2011.10.033.
- Levanič, T., 2007. ATRICS—a new system for image acquisition in dendrochronology. Tree-Ring Res. 63, 117–122. https://doi.org/10.3959/1536-1098-63.2.117.
- Lorimer, C.G., 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manag. 6, 343–360. https://doi.org/10.1016/0378-1127(83)90042-7.
- Luu, T.C., Binkley, D., Stape, J.L., 2013. Neighborhood uniformity increases growth of individual Eucalyptus trees. For. Ecol. Manag. 289, 90–97. https://doi.org/10.1016/ j.foreco.2012.09.033.
- Mailly, D., Turbis, S., Pothier, D., 2003. Predicting basal area increment in a spatially explicit, individual tree model: a test of competition measures with black spruce. Can. J. For. Res. 33, 435–443. https://doi.org/10.1139/x02-122.
- Martin, G.L., Ek, A.R., 1984. A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. For. Sci. 30, 731–743. https://doi.org/10.1093/forestscience/30.3.731.
- McLellan, A.J., Law, R., Fitter, A.H., 1997. Response of calcareous grassland plant species to diffuse competition: results from a removal experiment. J. Ecol. 85, 479–490. https://doi.org/10.2307/2960571.
- Men, X., Yue, Y., Gu, H., Wang, X., Chen, X., 2023. Effects of tree competition on biomass allocation of stump and coarse roots of *Larix olgensis* of different site classes. Forests 14, 1431. https://doi.org/10.3390/f14071431.
- Miina, J., Pukkala, T., 2000. Using numerical optimization for specifying individual-tree competition models. For. Sci. 46, 277–283. https://doi.org/10.1093/forestscience/ 46.2.277
- Mizunaga, H., Nagaike, T., Yoshida, T., Valkonen, S., 2010. Feasibility of silviculture for complex stand structures: designing stand structures for sustainability and multiple objectives. J. For. Res. 15, 1–2. https://doi.org/10.1007/s10310-009-0177-x.
- Munro, D.D., 1974. Forest growth models a prognosis. In: Fries, J. (Ed.), Growth Models of Tree and Stand Simulation. Royal College of Forestry, Research Note no. 30, Stockholm, pp. 7–21.
- Nagel, T.A., Diaci, J., Jerina, K., Kobal, M., Roženbergar, D., 2015. Simultaneous influence of canopy decline and deer herbivory on regeneration in a coniferbroadleaf forest. Can. J. For. Res. 45, 266–275. https://doi.org/10.1139/cjfr-2014-2016.
- O'Hara, K.L., 2014. Multiaged Silviculture: Managing for Complex Forest Stand Structures. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198703068.001.0001.
- Oheimb, G., Lang, A.C., Bruelheide, H., Forrester, D.I., Wäsche, I., Yu, M., Härdtle, W., 2011. Individual-tree radial growth in a subtropical broad-leaved forest: the role of local neighbourhood competition. For. Ecol. Manag. 261, 499–507. https://doi.org/ 10.1016/j.foreco.2010.10.035.

- Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics, Update Edition. John Wiley & Sons, New York.
- Pedersen, R.Ø., Bollandås, O.M., Gobakken, T., Næsset, E., 2012. Deriving individual tree competition indices from airborne laser scanning. For. Ecol. Manag. 280, 150–165. https://doi.org/10.1016/j.foreco.2012.05.043.
- Pinto, P.E., Gégout, J.C., Hervé, J.C., Dhôte, J.F., 2007. Changes in environmental controls on the growth of *Abies alba* Mill. in the Vosges Mountains, northeastern France, during the 20th century. Global Ecol. Biogeogr. 16, 472–484. https://doi. org/10.1111/j.1466-8238.2007.00310.x.
- Pretzsch, H., 2009. Forest Dynamics, Growth and Yield. Springer-Verlag, Berlin Heidelberg. https://doi.org/10.1007/978-3-540-88307-4.
- Prévosto, B., Curt, T., 2004. Dimensional relationships of naturally established European beech trees beneath Scots pine and Silver birch canopy. For. Ecol. Manag. 194, 335–348. https://doi.org/10.1016/j.foreco.2004.02.020.
- Puettmann, K.J., D'Amato, A.W., Kohnle, U., Bauhus, J., 2009. Individual-tree growth dynamics of mature *Abies alba* during repeated irregular group shelterwood (Femelschlag) cuttings. Can. J. For. Res. 39, 2437–2449. https://doi.org/10.1139/ V00\_158
- Pukkala, T., Kolström, T., 1987. Competition indices and the prediction of radial growth in Scots pine. Silva Fenn. 21, 55–67. https://doi.org/10.14214/sf.a15463.
- Pukkala, T., Lähde, E., Laiho, O., Salo, K., Hotanen, J.-P., 2011. A multifunctional comparison of even-aged and uneven-aged forest management in a boreal region. Can. J. For. Res. 41, 851–862. https://doi.org/10.1139/x11-009.
- Richards, M., McDonald, A.J.S., Aitkenhead, M.J., 2008. Optimisation of competition indices using simulated annealing and artificial neural networks. Ecol. Model. 214, 375–384. https://doi.org/10.1016/j.ecolmodel.2008.03.008.
- Rouvinen, S., Kuuluvainen, T., 1997. Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scots pine forest. Can. J. For. Res. 27, 890–902. https://doi.org/10.1139/x97-012.
- Sabatia, C.O., Burkhart, H.E., 2012. Competition among loblolly pine trees: does genetic variability of the trees in a stand matter? For. Ecol. Manag. 263, 122–130. https:// doi.org/10.1016/j.foreco.2011.09.009.
- Seydack, A.H.W., Durrheim, G., Louw, J.H., 2011. Spatiotemporally interactive growth dynamics in selected South African forests: Edaphoclimatic environment, crowding and climate effects. For. Ecol. Manag. 261, 1152–1169. https://doi.org/10.1016/j. foreco.2010.12.017.
- Seifert, T., Seifert, S., Seydack, A., Durrheim, G., von Gadow, K., 2014. Competition effects in an afrotemperate forest. For. Ecosyst. 1, 13. https://doi.org/10.1186/ s40663-014-0013-4.
- Schütz, J.-P., Pukkala, T., Donoso, P.J., von Gadow, K., 2012. Historical emergence and current application of CCF. In: Pukkala, T., von Gadow, K. (Eds.), Continuous Cover Forestry, Managing Forest Ecosystems, second ed., 23. Springer, Dordrecht, pp. 1–29. https://doi.org/10.1007/978-94-007-2202-6 1.
- Stadt, K.J., Huston, C., Coates, K.D., Feng, Z., Dale, M.R.T., Lieffers, V.J., 2007.
  Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. Ann. For. Sci. 64, 477–490. https://doi.org/10.1051/forest:2007025.
- Staebler, G.R., 1951. Growth and Spacing in an Even-Aged Stand of Douglas Fir. Master's thesis. University of Michigan.
- Stage, A.R., Ledermann, T., 2008. Effects of competitor spacing in a new class of individual-tree indices of competition: semi-distance-dependent indices computed for Bitterlich versus fixed-area plots. Can. J. For. Res. 38, 890–898. https://doi.org/ 10.1139/X07-192
- Steneker, G.A., Jarvis, J.M., 1963. A preliminary study to assess competition in a white spruce-trembling aspen stand. For. Chron. 39, 334–336. https://doi.org/10.5558/ tfc39334-3
- Szwagrzyk, J., Szewczyk, J., Maciejewski, Z., 2012. Shade-tolerant tree species from temperate forests differ in their competitive abilities: a case study from Roztozce, south-eastern Poland. For. Ecol. Manag. 282, 28–35. https://doi.org/10.1016/j. foreco.2012.06.031.
- Tikvić, I., Seletković, Z., Ugarković, D., Posavec, S., Španjol, Z., 2008. Dieback of silver fir (*Abies alba* Mill.) on northern Velebit (Croatia). Period. Biol 110, 137–143.
- Tomé, M., Burkhart, H.E., 1989. Distance-dependent competition measures for predicting growth of individual trees. For. Sci. 35, 816–831. https://doi.org/ 10.1093/forestscience/35.3.816.
- Vanclay, J.K., 2006. Spatially-explicit competition indices and the analysis of mixed-species plantings with the Simile modelling environment. For. Ecol. Manag. 233, 295–302. https://doi.org/10.1016/j.foreco.2006.05.020.
- Verdonck, S., Geussens, A., Zweifel, R., Thomaes, A., Van Meerbeek, K., Muys, B., 2025. Mitigating drought stress in European beech and pedunculate oak: the role of competition reduction. For. Ecosyst. 13, 100303. https://doi.org/10.1016/j. fecs.2025.100303.
- Wagner, R.G., Radosevich, S.R., 1998. Neighborhood approach for quantifying interspecific competition in coastal Oregon forests. Ecol. Appl. 8, 779–794. https:// doi.org/10.1890/1051-0761(1998)008[0779:NAFQIC]2.0.CO;2.
- Weiskittel, A.R., Hann, D.W., Kershaw, J.A., Vanclay, J.K., 2011. Forest Growth and Yield Modeling. Wiley-Blackwell, Oxford. https://doi.org/10.1002/ 9781119998518.
- Woodall, C.W., Fiedler, C.E., Milner, K.S., 2003. Intertree competition in uneven-aged ponderosa pine stands. Can. J. For. Res. 33, 1719–1726. https://doi.org/10.1139/ x03-096.