Sustainable regeneration in uneven-aged mixed deciduous forests managed by selection silviculture: the role of demographic structure

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Selection silviculture aims to create and maintain uneven-aged forests with a diameter at breast height (DBH) structure that is balanced at small spatial scales such that the stem number in each DBH class is high enough to replace the harvested and outgrowing trees over time by ingrowth from the next lower class. In these forests, natural regeneration of shade-tolerant species is at an advantage over shade-intolerant species. This is particularly pronounced in continuous-cover stands dominated by European beech (*Fagus sylvatica* L.), which develops its crown laterally as a reaction to release events. The conditions necessary to sustain a mixture with less shade-tolerant species, e.g. sycamore (*Acer pseudoplatanus* L.), have been little studied. Therefore, we explored growth patterns and stand structures in mixed deciduous forests with light availability quantified using vegetation height models. Harvesting and growth patterns were derived from inventory data of beech-dominated selection forests in Thuringia, Germany and long-term forest monitoring plot data from four stands in Switzerland. Based on these data, models of stem number distributions confirmed that stand basal area in deciduous forests dominated by beech should not exceed 21–25 m² ha⁻¹ to maintain a sustainable structure. In these forests, a total of ~90–120 stems per ha are needed in the ingrowth DBH class (DBH 8–11.9 cm) to ensure demographic sustainability. At canopy light transmittance <10 per cent, total stem number required in the thicket stage (DBH < 8 cm) is 800–1700 ha⁻¹. Under such shady conditions, only a small proportion of sycamore was observed (<25 per cent) in the thicket stage, as the species is likely to require canopy gaps >400 m² (gap diameter > 22.5 m) to recruit successfully. Selection silviculture with shade-intolerant species therefore requires much lower stocking volume and larger canopy openings created by group selection cutting than what is routinely applied in practical forest management using single-tree selection principles.

Introduction

The sustainable provisioning of forest ecosystem services (ES) is a major goal of forestry. Different silvicultural systems have emerged to maintain specific forest structures to maximize certain ES, such as protection against natural hazards, recreational value or timber supply, while others are used for multifunctional objectives to promote a multitude of ES simultaneously (Schütz, 1999; Brang *et al.*, 2014). A prominent example of silvicultural systems that simultaneously provide multiple ES is continuous-cover forestry (CCF), where the maintenance of a permanent canopy cover is sought (Pukkala and von Gadow, 2012). Interest in this system has increased tremendously in central Europe during the last decades (Pommerening and Murphy, 2004).

Within the framework of CCF, selection silviculture specifically aims to create and maintain uneven-aged forest structures by the regular cutting of single trees or small groups of trees (Nyland, 2016). Regeneration, tending and harvesting take place

in the same intervention, and each harvest typically provides some timber revenue. To ensure the permanent and long-term provisioning of ES, different concepts for controlling the stocking were developed (O'Hara and Gersonde, 2004; O'Hara *et al.*, 2007). An early concept was the so-called 'check method' (in French: 'méthode du contrôle') dating back to 1878, which aims to optimize wood production by repeatedly assessing and evaluating stem number frequencies by diameter at breast height (DBH) classes. These are then used to adapt the subsequent silvicultural intervention (Biolley, 1901, 1887). This foundation of adaptive ecosystem management was further developed by explicitly quantifying the stem numbers based on negative exponential distributions (De Liocourt, 1898; Meyer, 1952; Kerr, 2014).

However, negative exponential functions alone do not reveal conditions of demographic sustainability, as the decay rate may not be constant over DBH (O'Hara, 1998; Rubin *et al.*, 2006). To maintain a sustainable distribution, there needs to be sufficient trees recruited into each DBH class to compensate for mortality,

harvesting and outgrowth, i.e. when a tree grows from one size class into the next larger size class (Schütz, 2006). If the latter condition is met for the entire distribution, the stand is in a demographic equilibrium that depends on stand basal area (BA), climatic variability or other factors that influence the success of regeneration and the growth rates of recruitment via the light transmitted to the respective canopy layers. It is more important to identify the conditions of this demographic sustainability than to identify any single component, such as the best function describing a hypothesized equilibrium structure (Schütz, 2006).

The conditions of sustainability have been met successfully in the context of the recruitment of shade-tolerant coniferous tree species (*Picea abies* (L.) H. Karst.; *Abies alba* Mill.) in single-tree selection systems, even at high stand BA of up to 40 m² ha⁻¹ (e.g. Bachofen, 1999; Schütz, 2006; Lundqvist, 2017). For the less shade-tolerant Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), stand BA at demographic equilibrium was calculated to be 27.4 m² ha⁻¹ (Schütz and Pommerening, 2013). There are also examples of shade-intolerant species under selection silviculture, e.g. loblolly shortleaf pine (*Pinus taeda* L. – *Pinus echinata* Mill.) at a residual BA of 14 m² ha⁻¹ (Baker, 1986; Guldin, 2006; Guldin et al., 2017).

Single-tree selection silviculture with deciduous species has proven to work well with European beech (*Fagus sylvatica* L.) at a target stand BA of 22–24 m² ha⁻¹ (Schütz, 2006; Hessenmöller et al., 2018). However, it remains unclear under what conditions the selection system may be suitable for maintaining mixtures of tree species with contrasting shade tolerance within the optimum of beech, i.e. the recruitment of less shade-tolerant tree species in the desired amount and quality. Such knowledge is needed for managing mixed deciduous forests towards higher tree species richness, which is important for enhancing the adaptation potential of forests in the face of ongoing global changes (Brang et al., 2014).

In central Europe, beech is the naturally dominant tree species on mesic sites up to an elevation of ~900–1000 m a.s.l. It is known for its high shade tolerance and competitiveness (Packham et al., 2012). In beech-dominated forests, management interventions directly determine tree species diversity by the intensity of the initial canopy opening (Barna and Bosela, 2015). In single-tree selection silviculture, typically only small canopy gaps in the extent of one or two mature tree crowns are opened and thus often only beech is able to establish and survive as advance regeneration (Madsen and Hahn, 2008). Although juvenile beech trees develop plagiotropic branches when suppressed (Packham et al., 2012), the species retains a remarkable ability to react to release events (Trotsiuk et al., 2012). Unlike coniferous species, upperstorey individuals are able to access newly available canopy space by quickly expanding lateral branches (Emborg, 1998), thus closing the window of opportunity for the regeneration of gap specialists such as sycamore (*Acer pseudoplatanus* L.).

Less shade-tolerant tree species are therefore often outcompeted by beech (e.g. Petriřan et al., 2007; Ligot et al., 2013), which renders the management of such mixtures using selection silviculture a major challenge. There is evidence for a decline of tree species richness in single-tree selection forests (e.g. Klopčic and Boncina, 2012; Barna and Bosela, 2015; Nolet et al., 2018; Schall et al., 2018; Brüllhardt et al., 2020b), thus questioning the

appropriateness of the system for maximizing the provisioning of multiple ES that depend on tree species richness, or for increasing forest resilience that partly depends on tree species richness as well (Zhang et al., 2012; Silva Pedro et al., 2015). As many questions remain about the influence of single-tree selection silviculture on the forest structure, stand density and BA that warrant a certain tree species diversity (O'Hara et al., 2007), it is important to evaluate the growth rates of less shade-tolerant species in the typical light environments of uneven-aged mixed deciduous forest stands.

In the specific case of the Swiss Plateau, single-tree selection silviculture is inspired by the classical systems applied to upper montane coniferous forests characterized by very low light availability in the understorey (Schütz, 2001a). Often, canopy gap size is in the range of a single tree crown, and stand BA may be too high to provide recruitment rates that are sufficient to maintain the stand in demographic equilibrium (Schütz, 2006). Clearly, light availability reaching the trees in the lower diameter classes needs to be high enough to ensure a diameter increment corresponding to sustainable ingrowth rates. To date, however, the quantification of such light levels in mixed deciduous forests is lacking.

Therefore, we aim to explore the conditions that are necessary to sustain a demographic equilibrium with the presence of two contrasting species with respect to their shade tolerance, so as to gain insights into the possibilities and limitations of admixing light-demanding species in selection forests dominated by beech. The central research questions for our study thus were:

- What diameter growth rate corresponds to a sustainable stem number ingrowth rate of sycamore and beech?
- What light availability is necessary to attain these ingrowth rates?
- What minimal gap size ensures the ingrowth of sycamore?

To answer these questions, we assessed annual diameter increment of juvenile beech and sycamore in regeneration cohorts typically found in selection forests. Combined with harvesting patterns of beech selection forests in Thuringia, Germany and growth patterns from long-term monitoring plots in Switzerland, models of stem number frequencies at demographic equilibrium were derived to evaluate sustainable recruitment conditions.

Materials and methods

Study area

The study focused on beech forest types across the Swiss lowlands and in the Hainich region of Thuringia, Germany, which are representative for a wide range of central European forests (Figure 1). The elevation of the studied forests ranged from 300 to 860 m a.s.l. mean annual precipitation was 890–1300 mm at the Swiss sites and 600–750 mm in Thuringia. Mean annual temperature was 8°C to 11°C in the Swiss lowlands and 6–8°C in Thuringia.

Soils at the study sites in the Swiss lowlands are slightly acidic to highly alkaline, and mesic to be classified mainly as Luvisols or Cambisols. Soil types at the Thuringia study sites are dominated by a loess cover on a limestone bedrock characterized by a high

Figure 1 Study areas in the Swiss lowlands (46.9–47.6 N/6.6–9.4 E) and Thuringia (51.1 N/10.4 E). Small circles representing EFM plots and field sites from Brüllhardt *et al.* (2020b), triangles representing only the latter. The lower right map shows the natural distribution range of beech, *F. sylvatica* (green vertical lines) and sycamore, *A. pseudoplatanus* (red 45° hatched lines). Distribution maps by EUFORGEN (2009), www.euforgen.org.

loam-clay content, resulting in a high water-holding capacity classified as Luvisols, Stagnosols and Cambisols (cf. Hessenmöller *et al.*, 2018).

Datasets

We used several datasets from three sources to study uneven-aged forests with natural regeneration initiated by a periodic

selection cutting of individuals or small groups of trees. Stem disc data to reconstruct single tree growth patterns were available from the extensive field campaign presented in Brüllhardt *et al.* (2020b). Growth data were available from four long-term monitoring plots of mixed deciduous forests within the experimental forest project (Forrester *et al.*, 2019) and used to model stem number distributions to study demographic sustainability in

uneven-aged mixed deciduous forests. These were further combined with harvesting patterns from a large repeated inventory of a balanced uneven-aged beech forest in Thuringia.

Growth rates from stem disc analysis

We selected 14 study sites across the Swiss lowlands where single-tree selection cutting is applied, typically with a frequency of 5–10 years. Regeneration cohorts in small gaps ($n = 240$) with different sizes of canopy openings were selected on site types of the sub-alliance *Galio-odorati-Fagenion* (mull beech forests) and *Luzulo-Fagenion* (moder beech forest) (cf. Leuschner and Ellenberg, 2017). Within each cohort, dominant or co-dominant individuals of sycamore ($n = 178$) and beech ($n = 196$) were harvested between 2015 and 2018 for stem disc analysis to reconstruct annual growth rates based on tree-ring analysis. Annual ingrowth rates per DBH class were calculated using the average diameter increment of the last five years divided by the width of the respective DBH class.

The sample trees covered a DBH range of 1–19 cm growing in light environments of 2–60 per cent of above-canopy radiation. Gap size was defined as the extended gap by the two distances from the stem of canopy trees in the south to the north and from the west to the east. Around each of the sampled trees, circular plots of 2 and 15 m radius were set up to record all tree species of DBH < 8 cm and DBH > 8 cm, respectively.

Light availability was estimated for each of the sample trees using a novel approach mimicking hemispherical photographs derived from vegetation height models (VHM). We took highly overlapping aerial photographs of each study site to assess forest geometry photogrammetrically as a 3D point cloud using structure-from-motion (SfM) and multi-view-stereo (MVS) processing. Plotting VHM point clouds in polar coordinates results in a synthetic hemispherical picture (Moeser et al., 2014; Zellweger et al., 2019; Brüllhardt et al., 2020a), which was analysed using Hemisfer 2.2 (Schleppi et al., 2007; Thimonier et al., 2010) to estimate light transmission, plant area index, canopy openness and canopy coverage. As a measure of light availability, we used the gap light index (GLI), which is defined as the average transmission of direct and diffuse light during the growing period. Canopy cover was calculated by subtracting the total gap fraction from the theoretical maximum cover of 100 per cent. A complete description of the workflow can be found in Brüllhardt et al. (2020a).

Experimental forest management data

The experimental forest management (EFM) project maintains a network of permanent monitoring plots across Switzerland (Forrester et al., 2019). We selected four plots from that network in mixed deciduous uneven-aged forests of the Swiss lowlands that are managed by selection silviculture and are located in the same stands as those sampled for the stem disc analysis. The plots were located at Deinikon (plot number 2050000), Adlisberg (3025000), Basadingen (2048000) and Muttentz (3021000). These EFM plots are between 1.3 and 2.5 ha in size and are measured every 5 or 6 years according to the local cutting cycle. The plots were established in (respectively) 1998, 1999, 2003 and 2004, and all trees with a DBH > 8 cm are measured.

Inventory data of uneven-aged beech forests in Thuringia

In north-western Thuringia, Germany, selection cutting in cooperative community forests has a long tradition that led to uneven-aged forests dominated by beech. In the forest of the cooperative Hainich, permanent concentric inventory plots were established on a 1 ha grid in 1994 and reassessed in 2004 and 2014 (cf. Hessenmöller et al., 2018). In total, we analysed 1118 plots of 500 m² where all trees with a DBH > 30 cm were measured. Smaller trees were assessed on subplots of 200 m² (DBH 20–29 cm) and 100 m² (DBH 7–19 cm).

Ingrowth and harvesting rates

The repeated measurements of the EFM plots and the Hainich plot inventory served as the basis to calculate annual harvesting and mortality as well as ingrowth rates to higher DBH classes. DBH class width was set to 4 cm and the data were summarized accordingly. Ingrowth rates were defined as the proportion of trees per diameter class growing annually to the next diameter class and were calculated directly from the annual diameter increment divided by the DBH class width (Schütz, 2006). All tree individuals that were not assessed in a consecutive survey were counted as removal by thinning, and we assumed natural mortality to be zero under the high management intensity in these selection forests.

To analyse ingrowth and removal patterns, we used multiple logistic regression to model the probability that a tree grows to the next diameter class or is removed in a certain year. A binomial distribution with a logit link was used, with the general form of the model according to James et al. (2017):

$$\log\left(\frac{p_i}{1-p_i}\right) = \beta_0 + \beta_1 \text{DBH} + \beta_2 \text{DBH}_d^2 + \dots + \beta_n \text{DBH}_d^n \quad (1)$$

where p_i is the response probability for each observed tree i in DBH class d to be harvested or growing to the next DBH-class, and n is the degree of the polynomial function. Estimation of the regression coefficients ($\beta_0 - \beta_n$) was performed using an iteratively reweighted least squares (IRLS) algorithm and maximum likelihood estimation (MLE) (Venables and Ripley, 2002).

We fitted ingrowth and harvesting models with different degrees of the polynomial function and selected the models with the lowest value of the Akaike Information Criterion (AIC). The selected models were then used to predict the respective ingrowth and harvesting rates as a basis for the modelling of stem number distribution (cf. eqs (2) and (3)).

Furthermore, we analysed the ingrowth rates of juvenile trees at different light availabilities and compared beech and sycamore using mixed linear effects models with a nested random intercept given by the study site and the sample tree. To assess pairwise differences, estimated marginal means were calculated and adjusted by the Bonferroni method (Lenth, 2021). To evaluate the differences in the proportion of the two species at different light availabilities, a binomial general linear mixed model was fitted using study site as a random intercept. The P -values from the computed pairwise comparisons of the estimated marginal

Figure 2 Annual ingrowth rates of juvenile trees calculated from the average diameter increment of the five last years at different light availabilities given by the GLI. DBH classes were defined by a width of 4 cm (1 = 0–3.9 cm, 2 = 4–7.9 cm, 3 = 8–11.9 cm, 4 = 12–15.9 cm). Similar letters indicate non-significant differences between groups and different letters stand for significant differences between groups on a $P < 0.05$ level from post-hoc pairwise Bonferroni test.

means of the factors tree species and light availability classes were adjusted using the Tukey's method (Length, 2016).

Modelling of stem number distribution

In uneven-aged forests, trees in many different diameter classes are present on small areas, and it is assumed that demographic sustainability can be achieved at the stand scale (O'Hara and Gersonde, 2004; Schütz, 2006). A model of the demographic equilibrium on the basis of stem number distributions was suggested by François (1938) and further developed by Schütz (2006, 1975). The basic assumption is that a demographic steady state is reached when trees migrating to a higher DBH class replace the trees that were harvested and migrated out of the considered class (Schütz, 2006):

$$n_i * p_i = n_{i+1} * p_{i+1} + n_{i+1} * e_{i+1} \quad (2)$$

where n_i is the stem number in diameter class i , p_i is the out-growth rate and e_i is the removal rate consisting of harvesting and mortality. Based on eq. (2), it is possible to model stem number distributions step by step forward from the lowest to the highest DBH class, or backwards from the highest to the lowest DBH class, as

$$n_{i-1} = n_i * \frac{p_i + e_i}{p_{i-1}} \quad (3)$$

For DBH < 8 cm, tree-ring based growth rates were used (Figure 2) to model a case for trees growing at light availabilities below 10 per cent GLI (lower boundary) and between 10 and 20 per cent GLI (upper boundary). To model the stem number distributions for DBH > 8 cm, we used the lower and upper boundaries of the confidence intervals of the prediction of harvesting and growth rate (Figure 3) as input. Annual removal rates below the calipering

Figure 3 Annual ingrowth (violet circles) and harvesting rates (orange triangles) per DBH class in the EFM plots and the beech selection forest Hainich, Thuringia, with predictions (ingrowth: solid violet line; harvesting: solid orange line) and confidence intervals (dashed lines) from the logistic models (Table 1).

limit were estimated to be within the range of 6–10 per cent (DBH 4–8 cm) and 16–25 per cent (DBH < 4 cm), based on mortality data from Bachofen (2009).

Determination of the demographic equilibrium

Starting from any arbitrary number of stems theoretically growing into the lowest diameter class of, say, 8–12 cm, different stem number distributions were modelled based on equation (2). Comparing the modelled relationship between stand BA and stem numbers in the lowest DBH class with observed numbers indicates the range of the target BA to maintain for demographic sustainability.

As a basis for the determination of the equilibrium, we exclusively used data from our field-campaign and Thuringia inventory plots that featured a stem number distribution with a positive skewness, so as to exclude even-aged stands. The plots were grouped in terms of their BA using a class width of 2 m². Stem numbers were then averaged per BA class while stem number BA classes with <10 observations were not considered due to the high variability.

Harvesting rates were assumed to remove the total periodic increment required to maintain equilibrium conditions. Taking the harvesting pattern in equilibrium-like forests of Thuringia as a baseline, the absolute harvesting rates were multiplied by the proportion of the difference in increment between Thuringia and the respective EFM plot.

All data analysis and statistical work was conducted using R version 3.6.2 (R Core Team, 2019).

Results

Ingrowth rates and harvesting patterns

Annual ingrowth rates in the smallest diameter classes were highly variable with a positive trend along the light availability gradient. This trend differed between sycamore and beech. Below a light availability of 40 per cent, ingrowth rates of juvenile beech <8 cm DBH were almost constant (Figure 2). In contrast, sycamore of DBH > 4 cm showed lower annual ingrowth rates at light availability <10 per cent compared to beech and followed a clear trend towards higher values under better light conditions (Figure 2).

Patterns of annual ingrowth rates of trees with DBH > 8 cm were different at the EFM sites and the selection forest in Thuringia, where diameter increment was smaller (Figure 3). There was an increase of the ingrowth rates up to the diameter classes of 26–30 cm followed by a small decrease in the mid-sized trees at the Deinikon, Adlisberg and Hainich sites, where increasing rates were found for the larger size classes, culminating at a DBH of 80–86 cm. In Basadingen, a bell-shaped curve peaking at 54 cm DBH represented ingrowth rates best, while the data for Muttentz were matched best by a monotonically increasing model (Figure 3, Table 1).

Harvesting patterns at the selection forest in Hainich were best represented by a U-shaped function (Figure 3, Table 1). At the Deinikon site, the harvesting patterns resembled those at Hainich but were not as high in the smallest classes. In contrast, at Adlisberg, Muttentz and Basadingen, harvesting rates followed

different and more site-specific patterns, which were characterized by a steady increase (Muttentz), a steep increase from DBH 8 to DBH 24 cm followed by a decrease towards the large timber (Basadingen) and a small increase towards the small-sized timber at Adlisberg followed by a decrease in the mid-sized timber and an increase in the large timber.

Demographic equilibrium

The modelled stem number distributions suggested 95–110 trees ha⁻¹ to be present in the 8–11.9 cm DBH class to sustain an equilibrium at a stand BA of 21.2–24.5 m² ha⁻¹ in the beech selection forests of Thuringia (Figure 4). For the EFM plots, the range of uncertainty in the corresponding equilibrium BA values per ha differed among sites and was 24.4–28.4 m² ha⁻¹ (102–118 ingrowth stems) for Basadingen, 19–29.2 m² (93–142) for Adlisberg, 22.1–26.8 m² (144–174) for Deinikon and 17.5–24 m² (60–85) for Muttentz (cf. Figure 4).

Stem number distributions

Modelled equilibrium stem number distributions followed a typical shape characterized by a sharp decrease of stem numbers in the small diameter classes that flattened out in the mid-sized diameter classes and increased again for the largest dimensions (Figure 5). This pattern was more pronounced at sites with decreasing or constant growth rates in the mid-sized classes (Deinikon, Adlisberg and Hainich). The stem numbers of ingrowth in the DBH class 8–11.9 cm that are required to sustain this structure were between 95 and 174 per hectare, which in most study sites was congruent with current measured forest properties (cf. Figure 5).

While the observed stem number distributions for DBH < 40 cm corresponded well to the sustainability model at Hainich, observed stem numbers for DBH > 40 cm were higher. The forest stands at Deinikon, Muttentz and Adlisberg featured an excess in the stem numbers of the large timber (DBH > 50 cm), reflecting the ongoing transformation from former even-aged to uneven-aged stands. Modelled stem number distributions were approximated well by the EFM data from Basadingen (cf. Figure 5).

In the lowest diameter class (DBH < 4 cm), the stem number necessary to sustain a demographic equilibrium was between 500 and 3000 per hectare. At light availabilities below 10 per cent GLI, growth rates of trees with DBH < 8 cm were small (Figure 2), and therefore stem numbers at the respective DBH class needed to be larger to sustain a demographic equilibrium than at higher light availability, as reflected by the stronger decrease of the upper bound of the equilibrium range at DBH < 8 cm (Figure 5). At light availabilities between 10 and 20 per cent GLI, stem numbers of trees with a DBH < 8 cm sustaining the equilibrium were between 500 and 1000 ha⁻¹.

Light availability and canopy cover

Annual diameter increment of sycamore and beech was lowest under the highest canopy cover, leading to high modelled stem numbers in the thicket stage (DBH < 8 cm) that would be

Table 1 Regression coefficients of the binomial logistic models with standard errors and *P*-values for the log-odds ratios to predict ingrowth and harvesting rates. The amount of deviance that the models account for is given as *D*² which is equivalent to the *R*² in linear models

Ingrowth rates							
Area	β_0	β_1	β_2	β_3	β_4	β_5	D^2
Adlisberg	-5.388 ± 0.993 ($P = 0.5381$)	0.374 ± 0.132 ($P = 0.0046$)	$-1.249 \cdot 10^{-2} \pm 5.741 \cdot 10^{-3}$ ($P = 0.0296$)	$1.666 \cdot 10^{-4} \pm 9.718 \cdot 10^{-5}$ ($P = 0.0864$)	$-7.652 \cdot 10^{-7} \pm 5.573 \cdot 10^{-7}$ ($P = 0.1697$)	-	0.968
Basadingen	-2.904 ± 0.265 ($P < 0.0001$)	0.046 ± 0.016 ($P = 0.0029$)	$-4.259 \cdot 10^{-4} \pm 1.868 \cdot 10^{-4}$ ($P = 0.0226$)	-	-	-	0.637
Deinikon	-4.626 ± 1.003 ($P < 0.0001$)	0.296 ± 0.130 ($P = 0.0223$)	$-1.046 \cdot 10^{-2} \pm 5.439 \cdot 10^{-3}$ ($P = 0.0544$)	$1.527 \cdot 10^{-4} \pm 9.092 \cdot 10^{-5}$ ($P = 0.0931$)	$-7.529 \cdot 10^{-7} \pm 5.218 \cdot 10^{-7}$ ($P = 0.1491$)	-	0.869
Muttenz	-2.632 ± 0.225 ($P < 0.0001$)	$9.582 \cdot 10^{-3} \pm 5.384 \cdot 10^{-3}$ ($P = 0.0751$)	-	-	-	-	0.355
Hainich	-4.896 ± 0.528 ($P < 0.0001$)	0.238 ± 0.060 ($P < 0.0001$)	$-7.316 \cdot 10^{-3} \pm 2.252 \cdot 10^{-3}$ ($P = 0.0012$)	$9.283 \cdot 10^{-5} \pm 3.407 \cdot 10^{-5}$ ($P = 0.0064$)	$-4.088 \cdot 10^{-7} \pm 1.793 \cdot 10^{-7}$ ($P = 0.023$)	-	0.467
Harvesting rates							
Adlisberg	0.630 ± 1.039 ($P = 0.5381$)	-0.515 ± 0.187 ($P = 0.0059$)	$3.599 \cdot 10^{-2} \pm 1.148 \cdot 10^{-2}$ ($P = 0.0017$)	$-1.005 \cdot 10^{-3} \pm 3.071 \cdot 10^{-4}$ ($P = 0.0011$)	$1.205 \cdot 10^{-5} \pm 3.703 \cdot 10^{-6}$ ($P = 0.0011$)	$-5.149 \cdot 10^{-8} \pm 1.647 \cdot 10^{-8}$ ($P = 0.0012$)	0.418
Basadingen	-8.064 ± 1.191 ($P < 0.0001$)	0.818 ± 0.018 ($P < 0.0001$)	$-3.713 \cdot 10^{-2} \pm 1.019 \cdot 10^{-2}$ ($P = 0.0003$)	$7.573 \cdot 10^{-4} \pm 2.446 \cdot 10^{-4}$ ($P = 0.0019$)	$-7.087 \cdot 10^{-6} \pm 2.633 \cdot 10^{-6}$ ($P = 0.0071$)	$2.455 \cdot 10^{-8} \pm 1.032 \cdot 10^{-8}$ ($P = 0.0173$)	0.413
Deinikon	-1.481 ± 0.438 ($P = 0.0007$)	-0.113 ± 0.048 ($P = 0.0189$)	$3.014 \cdot 10^{-3} \pm 1.326 \cdot 10^{-3}$ ($P = 0.0230$)	$-1.680 \cdot 10^{-5} \pm 1.071 \cdot 10^{-5}$ ($P = 0.1168$)	-	-	0.252
Muttenz	-3.584 ± 0.401 ($P < 0.0001$)	$3.457 \cdot 10^{-2} \pm 2.015 \cdot 10^{-2}$ ($P = 0.086$)	$-3.717 \cdot 10^{-5} \pm 2.231 \cdot 10^{-4}$ ($P = 0.8677$)	-	-	-	0.232
Hainich	-0.428 ± 0.135 ($P = 0.0015$)	$-9.437 \cdot 10^{-2} \pm 1.287 \cdot 10^{-2}$ ($P < 0.0001$)	$1.762 \cdot 10^{-3} \pm 3.340 \cdot 10^{-4}$ ($P < 0.0001$)	$-7.364 \cdot 10^{-6} \pm 2.554 \cdot 10^{-6}$ ($P = 0.0039$)	-	-	0.221

Figure 4 Determination of the demographic equilibrium based on the site-specific relationship between stand BA and the stem number of ingrowth (DBH class of 8–11.9 cm; dashed line with standard errors). The solid line indicates all theoretical model equilibrium states calculated based on equation (2). The theoretical optimum for the demographic equilibrium is where the lines intersect.

needed to warrant demographic sustainability, i.e. a stem number of 110 ha^{-1} in DBH class 8–11.9 cm (Table 2). In the smallest canopy gaps, sycamore exhibited smaller diameter increment than beech. In DBH class 4–7.9 cm, sycamore had higher diameter increment than beech in gaps $>395 \text{ m}^2$ (Table 2).

At low light availability (GLI < 10 per cent), there was a trend towards lower proportions of sycamore and higher proportions of beech (Figure 6) in the thicket class (1–8 cm DBH). At light availabilities between 10 and 29.9 per cent GLI, the median of the proportions from the total number of thicket trees was in a similar range, i.e. between 40 and 50 per cent for both species (cf. Figure 6).

Discussion

Ingrowth rates

Patterns of ingrowth rates reveal important stand growth characteristics because they reflect management history, stand structure and species composition. In deciduous vs coniferous forests and in monocultures vs mixtures, stand development and dynamics differ (Pretzsch et al., 2017). Especially in view of the emerging popularity of selection cutting it is crucial to analyze the respective ingrowth patterns (Pommerening and Murphy, 2004; Brang et al., 2014). For uneven-aged forests managed by regular single-tree selection cuttings dominated

by *P. abies* and *A. alba*, annual ingrowth rates were reported to follow a unimodal-shaped function of DBH (Bachofen, 1999), similar to site Basadingen in Figure 3 with a culmination in the mid-timber and large timber classes (DBH $> 54 \text{ cm}$). However, in three of the five uneven-aged mixed deciduous forests studied here, ingrowth rates are not unimodal, but feature a plateau between DBH 30 and 60 cm followed by a second maximum in the large size classes, thus resembling a bimodal function (Figure 3). The different patterns observed can be explained by species composition shaped by past even-aged management and are not only important for our understanding of growth dynamics in selection silviculture, but also as a foundation of dynamic vegetation modelling (Schelhaas et al., 2018).

The predicted ingrowth patterns were more reliable for the smaller size classes than the larger size classes due to the rare occurrence of larger trees on small sample plots although their growth variability was smaller compared to mid-sized size classes. These large size classes exhibited the largest diameter growth as the deciduous beech can expand its crown continuously (Forrester et al., 2017), and thus quickly occupy more canopy space (Emborg, 1998). From that perspective, the competitive environment created by trees that are laterally closing the canopy and thus shade smaller recruits (Forrester, 2014) in combination with crowding effects helps to explain the plateau or slight decrease of ingrowth rates in the mid-sized classes (Canham et al., 2004; Bartkiewicz and Paluch, 2019).

Figure 5 Observations from the EFM plots, the Hainich inventory and the circular plots assessed in this study along with modelled stem number distributions (green shading) in a range of possible demographic equilibria. The upper dashed line for the DBH classes with midpoints of 2 and 6 cm represents growth rates at GLI < 10 per cent, while the lower line represents GLI 10–19.9 per cent.

It is unclear, however, to what extent phenotypic plasticity causes the large variability in the observed ingrowth rates, and how this is linked to resource availability and ontogenetic

limitations (Ishii *et al.*, 2013). Although it would be interesting to derive species-specific ingrowth rates of canopy trees to complement those reported for juvenile trees in our study, the sample

Table 2 Tree ring-based annual diameter increment ($\pm$ standard deviation) in DBH classes 1 and 2 (<8 cm) and DBH class 3 (8–11.9 cm) of beech and sycamore at different light availabilities based on the GLI, canopy cover and gap size ($\pm$ standard error) with respective modelled stem numbers to sustain an ingrowth of 110 stems to DBH class 3.

GLI [%]	Canopy cover [%]	Gap size [m ²]	Annual diameter increment [cm yr ⁻¹]				Total stem number		
			<i>A. pseudoplatanus</i>		<i>F. sylvatica</i>				
			DBH class		DBH class		DBH class		
			1	2	1	2	1	2	3
< 10	91.3 ± 4	269 ± 32	0.13 ± 0.07	0.19 ± 0.11	0.17 ± 0.07	0.20 ± 0.08	797–1663	202–305	110
10–19.9	83.6 ± 7	395 ± 24	0.16 ± 0.06	0.22 ± 0.11	0.15 ± 0.08	0.17 ± 0.06	674–2062	279–378	110
20–29.9	74.9 ± 8	457 ± 38	0.17 ± 0.08	0.23 ± 0.08	0.17 ± 0.07	0.19 ± 0.08	522–1271	237–293	110
30–39.9	57.1 ± 21	742 ± 111	–	0.32 ± 0.14	–	0.20 ± 0.04	315–941	169–256	110
40–49.9	48.2 ± 14	1602 ± 400	–	0.46 ± 0.17	–	0.39 ± 0.11	235–381	151–166	110

Figure 6 Proportion of sycamore and beech trees in the thicket stage (DBH 1–8 cm) at different light availabilities. Significant differences ($P < 0.05$) are indicated by different letters based on the results of the general linear mixed model.

size of sycamore in the inventory and long-term monitoring plots was not representative to allow for reliable modelling. Except at very low light availability (<10 per cent GLI), juvenile sycamore of DBH < 16 cm were observed to grow relatively quickly, but there are indications that they lose vigour in the pole stage (20–30 cm DBH) and small timber classes (30–40 cm DBH) (cf. Hein *et al.*, 2009; Brüllhardt *et al.*, 2020b). Further research should therefore focus on the development of diameter increment of sycamore in uneven-aged forests to better understand the admixing possibilities of this (and possibly other) less shade-tolerant tree species.

Harvesting patterns

Managing uneven-aged forests to maintain demographic sustainability requires the regular harvesting of the accumulated increment using selection cutting. Understanding how these

harvesting patterns influence stem distribution patterns is important not only for maintaining demographic sustainability from a management perspective (O'Hara and Gersonde, 2004), but also for adequately modelling the dynamics of managed forest stands (Lafond *et al.*, 2014). The five examples in this study allow us to better describe and replicate harvesting patterns in mixed deciduous uneven-aged forests.

As harvesting rates per DBH class depend on the respective forest structure, the observed removal rates in the selection forests of Thuringia were assumed to be representative ('state of the art') to maintain sustainable deciduous selection forests that are dominated by beech. These patterns are similar to those in coniferous selection forests (Bachofen, 1999). In comparison, removal rates in the EFM plots are much lower in the small DBH classes due to lower stem numbers in the thicket class, caused by high stand BA. Thus, forest structure in the EFM plots is not in an equilibrium yet and therefore still influenced by the even-aged or coppice-with-standards management history, reflecting the long transformation time until demographic equilibrium structures are achieved (cf. Schütz, 2001b).

Demographic equilibrium

The determination of demographic equilibria revealed important relationships between ingrowth rates and stand characteristics. Due to the site-specific growing conditions, the relationship between stem numbers of the ingrowth (DBH class 8–11.9 cm) and stand BA was different for each site. This leads to the important notion that demographic equilibria depend on site-specific stocking volumes or stand BA (Bachofen, 1999; Schütz, 2006). Knowledge of the optimal target BA is therefore of crucial importance to determine harvesting rates (Cancino and von Gadow, 2002).

The values of target BA from our study that are required to maintain a demographic equilibrium are in line with values reported in the literature. Schütz (2006) calculated an equilibrium BA for the Hainich selection forests of $22 \text{ m}^2 \text{ ha}^{-1}$, while a slightly higher $24 \text{ m}^2 \text{ ha}^{-1}$ was suggested by Hessenmöller *et al.* (2018). In forests dominated by shade-tolerant coniferous species, equilibrium BA was reported to be $28\text{--}32 \text{ m}^2 \text{ ha}^{-1}$ (Bachofen, 1999).

With less shade-tolerant species and on less fertile sites, the target basal area to maintain a balanced structure is smaller, e.g. $16 \text{ m}^2 \text{ ha}^{-1}$ in mixed *P. taeda*—*P. echinata* stands (Guldin, 2006).

In this context, the demographic equilibria determined for the presented sites in the Swiss lowlands have to be interpreted with care due to the unbalanced structure and the presence of large timber *P. abies*. Especially the higher estimations above $26 \text{ m}^2 \text{ ha}^{-1}$ are a result of the ongoing transformation from even-aged (Adlisberg) or coppice-with-standards (Basadingen, Deinikon) forests to uneven-aged stand structures. Although we tried to exclude such plots by filtering out stem number distributions with a negative skewness, the locally clustered occurrence of mature trees strongly influences stand BA and thus may blur the relationship between ingrowth stem number and BA. Therefore, the relationship between stem numbers of the ingrowth (DBH class of 8–11.9 cm) and stand BA varied broadly, and in some strata and particularly at low stand BA the number of observations was low. From a methodological point of view, a circular plot radius greater than 15 m (area $\sim 706 \text{ m}^2$) may have allowed for more reliable assessments of these highly variable properties. Another uncertainty lies in the lag time for trees to grow into the 8–11.9 cm DBH class following thinning (Lundqvist, 2017), which may be of particular relevance for the transformation of stands from an even-aged to an uneven-aged structure. Nonetheless, the relationship we found is based on a more robust foundation compared with other studies (cf. Bachofen, 1999; Schütz, 2006).

Sustainable stem number distributions

Stem number distributions are important to evaluate the sustainability of selection forests, and they are pivotal as a solid and evidence-based foundation to guide forest management (O'Hara and Gersonde, 2004; Rubin *et al.*, 2006). As tree age is of subordinate importance in uneven-aged stands, it is crucial to maintain appropriate tree numbers per diameter class to ensure continuous timber production and other ES. The stem numbers in the lowest diameter classes in particular are determined directly by forest structure via light availability (Canham *et al.*, 2004; Ratcliffe *et al.*, 2015). Therefore, it is essential to have a good understanding of the growth dynamics of ingrowing trees when aiming to develop sustainable stem number distributions.

To ensure the sustainability of the system, the observed ingrowth rates of sycamore in the lowest diameter class, with an average diameter increment of 0.13 cm at light availabilities below 10 per cent GLI (Table 2), suggest that ~ 800 – 1700 trees ha^{-1} of a DBH < 4 cm would need to be present. As these sycamore individuals would be more than 30 years old when growing into the next diameter class, it is questionable whether they would keep their vigour or even survive such a long suppression period, given that their height growth vigour is ontogenetically limited (Hein *et al.*, 2009; Brüllhardt *et al.*, 2020b). Therefore, to maintain sycamore, higher GLI are likely to be required, which are equivalent to a gap size of minimally 400 m^2 .

Conclusion

The demographic structure of uneven-aged forests is mainly driven by the periodic harvesting of the volume increment, thus maintaining a stand BA that ensures continuous ingrowth. In mixed deciduous forests on beech site types, the equilibrium

stand BA varies strongly, depending on site productivity and the proportion of coniferous trees. To maintain sustainable ingrowth of shade-tolerant species in beech forests, a target BA of 21 – $25 \text{ m}^2 \text{ ha}^{-1}$ should not be exceeded.

Within a homogenously spaced deciduous tree stocking of 21 – $25 \text{ m}^2 \text{ ha}^{-1}$ the annual DBH growth rate in the smallest DBH classes is often in the range of 0.1 – 0.2 cm. In these conditions it is perfectly possible to sustain an equilibrium structure as long as: (1) stem numbers are large enough to replace the removals and outgrowing stems in the higher DBH classes and (2) timber quality is guaranteed. These conditions are met well by the growth strategy of shade-tolerant tree species like beech that is tolerating long suppression periods, but they are critical for the less shade-tolerant sycamore.

In terms of light availability, sycamore ingrowth may be promoted by a minimum gap size of 400 m^2 or a maximum canopy cover of approximately 80 per cent to ensure more than 10 per cent of above-canopy light. Therefore, to attain sustainable ingrowth rates and to increase the proportion of sycamore, group selection cuttings should be preferred over single-tree selection cuttings.

Supplementary data

Supplementary data are available at *Forestry* online.

Data availability statement

The growth data from stem disc analysis of beech and sycamore used in this article will be shared on reasonable request to the corresponding author. The data from the EFM are available on the EnviDat online data portal (<https://www.doi.org/10.16904/envi.dat.213>). The inventory data from the beech selection forest were provided by ThüringenForst by permission.

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Conflict of interest statement

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References

- Bachofen, H. 2009 Nachhaltige Verjüngung in ungleichförmigen Beständen | Sustainable recruitment in uneven aged stands. *Schweiz. Z. Forstwes.* **160**, 2–10.

- Bachofen, H. 1999 Gleichgewicht, Struktur und Wachstum in Plenterbeständen | Equilibrium, structure and increment in selection forest stands. *Schweiz. Z. Forstwes.* **150**, 157–170.
- Baker, J.B. 1986 The Crossett farm forestry forties after 41 years of selection management. *South. J. Appl. For.* **10**, 233–237.
- Barna, M. and Bosela, M. 2015 Tree species diversity change in natural regeneration of a beech forest under different management. *For. Ecol. Manage.* **342**, 93–102.
- Bartkiewicz, L. and Paluch, J. 2019 Co-occurrence of shade-tolerant and light-adapted tree species in uneven-aged deciduous forests of southern Poland. *Eur. J. For. Res.* **138**, 15–30.
- Biolley, H. 1901 Le jardinage cultural. *Schweiz. Z. Forstwes.* **52**, 113–132.
- Biolley, H. 1887 Quelques réflexions Sur le Jardinage à propos des publications de Mr. Gurnaud. *Schweiz. Z. Forstwes.* **38**, 189–192.
- Brang, P., Spathelf, P., Larsen, J.B., Bauhus, J., Boncina, A., Chauvin, C., et al. 2014 Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. *Forestry* **87**, 492–503.
- Brüllhardt, M., Rotach, P., Schleppi, P. and Bugmann, H. 2020a Vertical light transmission profiles in structured mixed deciduous forest canopies assessed by UAV-based hemispherical photography and photogrammetric vegetation height models. *Agric. For. Meteorol.* **281**, 1–11.
- Brüllhardt, M., Rotach, P., Bigler, C., Nötzli, M. and Bugmann, H. 2020b Growth and resource allocation of juvenile European beech and sycamore maple along light availability gradients in uneven-aged forests. *For. Ecol. Manage.* **474**, 118314.
- Cancino, J. and von Gadow, K. 2002 Stem number guide curves for uneven-aged forests development and limitations. In *Continuous Cover Forestry: Assessment, Analysis*. K., von Gadow, J., Nagel, J., Saborowski (eds.). Scenarios. Springer Netherlands, Dordrecht, pp. 163–174.
- Canham, C.D., LePage, P.T. and Coates, K.D. 2004 A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Can. J. For. Res.* **34**, 778–787.
- De Liocourt, F. 1898 De l'aménagement des sapinières. *Bulletin trimestriel - Société forestière de Franche-Comté & Belfort* **4**, 396–409.
- Emborg, J. 1998 Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. *For. Ecol. Manage.* **106**, 83–95.
- Forrester, D.I. 2014 A stand-level light interception model for horizontally and vertically heterogeneous canopies. *Ecol. Model.* **276**, 14–22.
- Forrester, D.I., Benneter, A., Bouriaud, O. and Bauhus, J. 2017 Diversity and competition influence tree allometric relationships - developing functions for mixed-species forests. *J. Ecol.* **105**, 761–774.
- Forrester, D.I., Nitzsche, J. and Schmid, H. 2019 *The Experimental Forest Management Project: An Overview and Methodology of the Long-Term Growth and Yield Plot Network*. Swiss Federal Institute of Snow and Landscape Research WSL, Birmensdorf.
- François, T. 1938 La composition théorique normale des futaies jardinées de Savoie. *Rev. Eaux For.* **76**, 101–115.
- Guldin, J.M. 2006 Uneven-aged silviculture of longleaf pine. In *The Longleaf Pine Ecosystem*. S., Jose, E.J., Jokela, D.L., Miller (eds.). Springer New York, New York, NY, pp. 217–249.
- Guldin, J.M., Bragg, D.C. and Zingg, A. 2017 Plenter mit Kiefern-Ergebnisse aus den USA. *Schweiz. Z. Forstwes.* **168**, 75–83.
- Hein, S., Collet, C., Ammer, C., Goff, N.L., Skovsgaard, J.P. and Savill, P. 2009 A review of growth and stand dynamics of *Acer pseudoplatanus* L. in Europe: implications for silviculture. *Forestry* **82**, 361–385.
- Hessenmöller, D., Bouriaud, O., Fritzlar, D., Elsenhans, A.S. and Schulze, E.D. 2018 A silvicultural strategy for managing uneven-aged beech-dominated forests in Thuringia, Germany: a new approach to an old problem. *Scand. J. For. Res.* **33**, 668–680.
- Ishii, H., Azuma, W. and Nabeshima, E. 2013 The need for a canopy perspective to understand the importance of phenotypic plasticity for promoting species coexistence and light-use complementarity in forest ecosystems. *Ecol. Res.* **28**, 191–198.
- James, G., Witten, D., Hastie, T. and Tibshirani, R. (eds.) 2017 *An Introduction to Statistical Learning: With Applications in R, Corrected at 8th. printing* edn. Springer texts in statistics. Springer, New York.
- Kerr, G. 2014 The management of silver fir forests: de Liocourt (1898) revisited. *Forestry* **87**, 29–38.
- Klopčič, M. and Boncina, A. 2012 Recruitment of tree species in mixed selection and irregular shelterwood forest stands. *Ann. For. Sci.* **69**, 915–925.
- Lafond, V., Lagarrigues, G., Cordonnier, T. and Courbaud, B. 2014 Uneven-aged management options to promote forest resilience for climate change adaptation: effects of group selection and harvesting intensity. *Ann. For. Sci.* **71**, 173–186.
- Lenth, R.V. 2016 Least-squares means: the R package lsmeans. *J. Stat. Softw.* **69**, 1–33.
- Lenth, R.V. 2021 Emmeans: estimated marginal means, aka least-squares means. *R package version 1*, 2–1. <https://CRAN.R-project.org/package=emmeans>.
- Leuschner, C. and Ellenberg, H. 2017 *Ecology of Central European Forests: Vegetation Ecology of Central Europe, Volume I*. 1st edn. Springer, Cham.
- Ligot, G., Balandier, P., Fayolle, A., Lejeune, P. and Claessens, H. 2013 Height competition between *Quercus petraea* and *Fagus sylvatica* natural regeneration in mixed and uneven-aged stands. *For. Ecol. Manage.* **304**, 391–398.
- Lundqvist, L. 2017 Tamm review: selection system reduces long-term volume growth in Fennoscandic uneven-aged Norway spruce forests. *For. Ecol. Manage.* **391**, 362–375.
- Madsen, P. and Hahn, K. 2008 Natural regeneration in a beech-dominated forest managed by close-to-nature principles — a gap cutting based experiment. *Can. J. For. Res.* **38**, 1716–1729.
- Meyer, H.A. 1952 Structure, growth, and drain in balanced uneven-aged forests. *J. For.* **50**, 85–92.
- Moeser, D., Roubinek, J., Schleppi, P., Morsdorf, F. and Jonas, T. 2014 Canopy closure, LAI and radiation transfer from airborne LiDAR synthetic images. *Agric. For. Meteorol.* **197**, 158–168.
- Nolet, P., Kneeshaw, D., Messier, C. and Bêland, M. 2018 Comparing the effects of even- and uneven-aged silviculture on ecological diversity and processes: a review. *Ecol. Evol.* **8**, 1217–1226.
- Nyland, R.D. 2016 *Silviculture-Concepts and Applications*. 3rd edn. Waveland Press, Inc, Long Grove, Illinois.
- O'Hara, K.L. 1998 Silviculture for structural diversity: a new look at multi-aged systems. *J. For.* **96**, 4–10.
- O'Hara, K.L. and Gersonde, R. 2004 Stocking control concepts in uneven-aged silviculture. *Forestry* **77**, 131–143.
- O'Hara, K.L., Hasenauer, H. and Kindermann, G. 2007 Sustainability in multi-aged stands: an analysis of long-term plenter systems. *Forestry* **80**, 163–181.
- Packham, J.R., Thomas, P.A., Atkinson, M.D. and Degen, T. 2012 Biological flora of the British isles: *Fagus sylvatica*. *J. Ecol.* **100**, 1557–1608.
- Petrișan, A.M., Von Lupke, B. and Petrișan, I.C. 2007 Effects of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. *Forestry* **80**, 397–412.

- Pommerening, A. and Murphy, S.T. 2004 A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* **77**, 27–44.
- Pretzsch, H., Forrester, D.I. and Bauhus, J. (eds.) 2017 *Mixed-Species Forests: Ecology and Management*. Springer, Berlin Heidelberg, New York, NY.
- Pukkala, T. and von Gadow, K. (eds.) 2012 *Continuous Cover Forestry*, 2nd edn. Managing Forest Ecosystems. Springer, Dordrecht London.
- Core Team, R. 2019 *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ratcliffe, S., Holzwarth, F., Nadrowski, K., Levick, S. and Wirth, C. 2015 Tree neighbourhood matters – Tree species composition drives diversity–productivity patterns in a near-natural beech forest. *For. Ecol. Manage.* **335**, 225–234.
- Rubin, B.D., Manion, P.D. and Faber-Langendoen, D. 2006 Diameter distributions and structural sustainability in forests. *For. Ecol. Manage.* **222**, 427–438.
- Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., et al. 2018 The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *J. Appl. Ecol.* **55**, 267–278.
- Schelhaas, M.-J., Hengeveld, G.M., Heidema, N., Thürig, E., Rohner, B., Vacchiano, G., et al. 2018 Species-specific, pan-European diameter increment models based on data of 2.3 million trees. *For. Ecosyst.* **5**, 21.
- Schleppi, P., Conedera, M., Sedivy, I. and Thimonier, A. 2007 Correcting non-linearity and slope effects in the estimation of the leaf area index of forests from hemispherical photographs. *Agric. For. Meteorol.* **144**, 236–242.
- Schütz, J.-P. 2006 Modelling the demographic sustainability of pure beech plenter forests in eastern Germany. *Ann. For. Sci.* **63**, 93–100.
- Schütz, J.-P. 2001a *Der Plenterwald Und Weitere Formen Strukturierter Und Gemischter Wälder*. Parey Buchverlag, Berlin.
- Schütz, J.-P. 2001b Opportunities and strategies of transforming regular forests to irregular forests. *For. Ecol. Manage.* **151**, 87–94.
- Schütz, J.-P. 1999 Close-to-nature silviculture: is this concept compatible with species diversity? *Forestry* **72**, 359–366.
- Schütz, J.-P. 1975 Dynamique et conditions d'équilibre de peuplements jardinés Sur les stations de la hêtraie à sapin. *Schweiz. Z. Forstwes.* **9**, 637–671.
- Schütz, J.P. and Pommerening, A. 2013 Can Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) sustainably grow in complex forest structures? *For. Ecol. Manage.* **303**, 175–183.
- Silva Pedro, M., Rammer, W. and Seidl, R. 2015 Tree species diversity mitigates disturbance impacts on the forest carbon cycle. *Oecologia* **177**, 619–630.
- Thimonier, A., Sedivy, I. and Schleppi, P. 2010 Estimating leaf area index in different types of mature forest stands in Switzerland: a comparison of methods. *Eur. J. For. Res.* **129**, 543–562.
- Trotsiuk, V., Hobi, M.L. and Commarmot, B. 2012 Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). *For. Ecol. Manage.* **265**, 181–190.
- Venables, W.N. and Ripley, B.D. 2002 *Modern Applied Statistics with S*, 4. ed. edn. Statistics and Computing, Springer, New York.
- Zellweger, F., Baltensweiler, A., Schleppi, P., Huber, M., Küchler, M., Ginzler, C., et al. 2019 Estimating below-canopy light regimes using airborne laser scanning: an application to plant community analysis. *Ecol. Evol.* **9**, 9149–9159.
- Zhang, Y., Chen, H.Y.H. and Reich, P.B. 2012 Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis: *diversity and productivity relationships*. *J. Ecol.* **100**, 742–749.