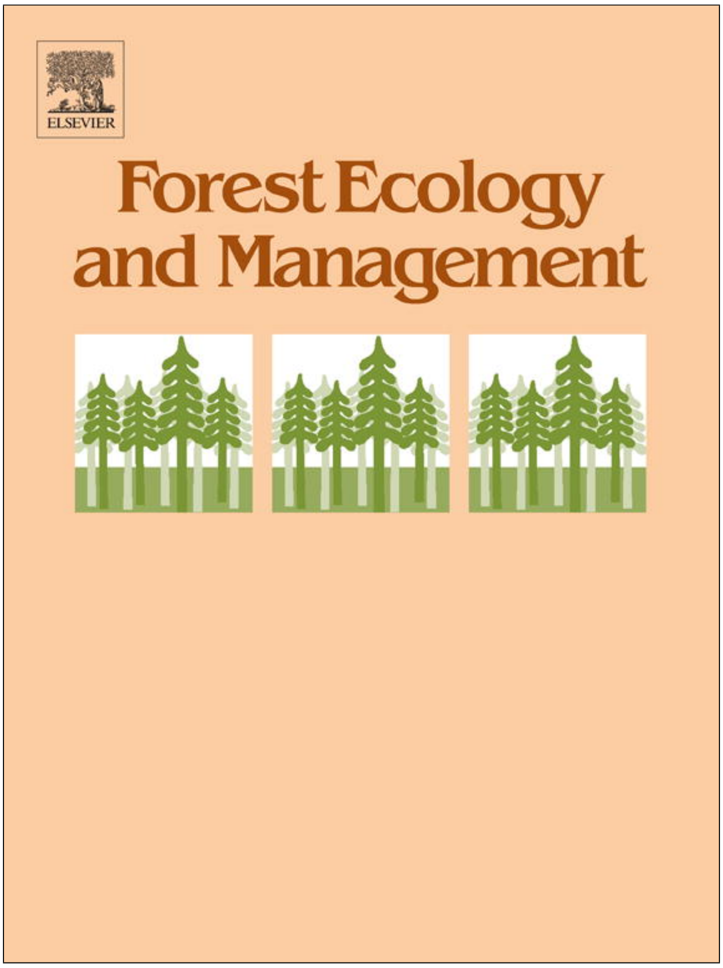
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Can Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) sustainably grow in complex forest structures?

J.P. Schütz [a,*], A. Pommerening [b,c]

[a] Swiss Federal Institute of Technology (ETH) Zürich, Brüggliäcker 37, CH-8050 Zürich, Switzerland
[b] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland
[c] Estonian University of Life Sciences, Institute of Forestry and Rural Engineering, Kreutzwaldi 5, Tartu 51014, Estonia

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ABSTRACT

The sustainability of shade-intermediate tree species such as Douglas fir in complex forest structures (with more than two distinct storeys) has been controversially discussed for a long time and traditionally shade-tolerant tree species have been preferred in plenter forest management. The most critical question in this context is whether recruitment trees of a particular species can survive in the shady conditions of the understorey and whether they can contribute to a demographic continuity. Using data from the unique, replicated monitoring site Artist's Wood in North Wales (UK) we investigated the recruitment dynamics of Douglas fir to address the question whether this species can grow in complex forest structures on a long-term basis. Then we compared the results with those from Norway spruce and silver fir plenter forests in the Swiss Jura. Demographic continuity in complex structures is ensured if all forest development stages are represented in appropriate demographic proportions. We quantified these development stages in terms of stem diameter classes and analysed the corresponding diameter growth, competition and the loss of trees due to mortality and forest management. Based on this analysis we determined demographic equilibrium conditions for Artist's Wood. The results confirmed that Douglas fir at Artist's Wood can indeed grow sustainably in complex forest structures at a stand density of 27.4 m^2 ha^{-1} basal area which corresponds to a standing volume of 342 m^3 ha^{-1}. However, equilibrium conditions for Douglas fir can only be achieved at the expense of a lower overall stand density of approximately 85% of that of Norway spruce. Despite this the corresponding Douglas fir stand volume increment of 15.3 m^3 ha^{-1} $year^{-1}$ is greater than that of Norway spruce. Thus Douglas fir plenter forests are not only possible but are also appealing considering the broad site amplitude of the species in conjunction with ongoing climate change and the potential of the species for CO_2 retention.

1. Introduction

Complex forest structures are currently being discussed a lot in the context of near natural forest management (O'Hara et al., 2007). They are usually defined as forest structures with more than two distinct storeys (Mason and Kerr, 2001). Other definitions refer to all-aged, multi-aged or uneven-aged forests with a high degree of irregularity at small scale. Tree crowns in such structures have the tendency of occupying the whole vertical growing space (Schütz, 1997) and there is a temporal and spatial coexistence of regeneration, young growth, mature trees and old growth, which highly influence each other (Smith et al., 1997).

Research has highlighted the merits of complex forest structures, e.g. their resilience to disturbances, their popularity among forest visitors and the use of biological automation, i.e. employing biological processes such as natural regeneration, natural pruning and self-thinning for silvicultural purposes, which is helpful to reduce management costs (Schütz, 1997, p. 74; Dvořak et al., 2001; Pommerening and Murphy, 2004; O'Hara et al., 2007). Therefore modern forest management based on ecological principles often promotes complex forest structures wherever suitable and possible. In silviculture, the methods for maintaining complex forest structures are collectively referred to as *selection* or *plenter* system (Matthews, 1991; Nyland, 2002; Smith et al., 1997). To avoid confusion with selective forest management (denoting the process of selectively removing individual trees, and particularly the largest ones with best commercial attributes) we use the term *plenter* forest in the remainder of this text.

Important pre-requisites for achieving complex forest structures are tree species that regenerate and develop well at least in semi-shady conditions and their ability to occupy space efficiently due to a space-parsimonious crown morphology (Schütz, 1997).

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* Corresponding author. Tel.: +41 44 321 19 89; fax: +41 32 835 25 08.
E-mail addresses: jph.s@bluewin.ch (J.P. Schütz), arne.pommerening@gmail.com (A. Pommerening).

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For the former it is conventional knowledge that shade-tolerant species can more easily be accommodated in complex structures with medium to high tree densities than the more light-demanding species. As a matter of fact most scientific knowledge as well as practical experience concerning plenter forests has been made in Central European mixed species forests including Norway spruce (*Picea abies* (L.) Karst.), silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.). These three tree species frequently form natural woodland communities in Central European upland forests and there are many successful applications of managing complex structures in this region. All three tree species are rather shade-tolerant, particularly silver fir followed by beech and finally Norway spruce as the most light-demanding of all three species.

Naturally there has been considerable dispute over the question to which degree less shade-tolerant species can successfully and sustainably, i.e. on a long-term basis, be managed in complex structures. This is particularly true for introduced species such as Douglas fir in Europe (Schütz, 1997), because both experience and scientific knowledge concerning these species are still limited. The performance of Douglas fir in the understorey reinitiation phase (Oliver and Larson, 1996) is one of the most critical issues. Until recently there has been no convincing example of complex structures in Douglas fir. However, the replicated monitoring site at Artist's Wood in North Wales has now offered an opportunity to gain more knowledge.

Broadleaved trees have a tendency of laterally enlarging their crowns with increasing growing space (Roloff, 2001) and therefore support the process of vertical structuring less than conifers. Badoux (1949) for example was the first author to demonstrate that beech trees in complex structures need twice the space of conifers with the same stem diameter. As a result, complex structures involving broadleaved trees can only be achieved at lower overall tree densities as opposed to conifer-only plenter forests. For example the calculated equilibrium standing volume of pure beech plenter forests is approximately 250 $m^3\ ha^{-1}$ in Thuringia (Germany). The corresponding basal area is ca. 20 $m^2\ ha^{-1}$ (Schütz, 2006). These values are considerably lower than those listed for conifer plenter forests in Table 1.

In plenter forests, sustainability should be achieved at stand level, because per definition all stem diameter classes coexist at the same spatial level. For the purpose of this study, sustainability is ensured if all stem diameter classes are represented in appropriate demographic proportions. We treat here stem diameter classes as a surrogate for forest development stages.

Early approaches to determining references for sustainability in plenter forests include Gurnaud's and Biolley's control method (Schütz, 2001) as well as de Liocourt's negative exponential model for stem diameter distributions (Liocourt, 1898). The latter was developed to become the *q*-factor model that enjoyed much popularity in the Anglo-American literature (Meyer, 1933; O'Hara, 1996). All variants of the *q*-factor model have in common that they are static, i.e. they do not consider the dynamics of forest demography. Schütz (1975, 2006) developed an approach that takes this into account, particularly by knowledge of tree growth, thinning/harvesting including mortality.

A key process in this context is recruitment, which is comparable to birthrate in general demography. The long-term sustainability of complex forest structures is largely dependent on a sufficient number of recruitments. Browsing and insufficient light levels for example can seriously upset equilibrium conditions. Therefore the determination of realistic minimum recruitment numbers and of associated ingrowth dynamics is crucial for any judgement on the long-term sustainability of complex structures with a given species. In previous studies (Schütz and Röhnisch, 2003) it has been found that this can be achieved with 115–120 trees per hectare in the smallest diameter class and corresponding stem diameter increments, i_d, of 1.0–2.5 mm per year (see also Table 1). This allows a sufficient number of trees to progress to the mid-storey.

The objectives of this study are (1) to investigate the demographic dynamics of Douglas fir and other main species in Artist's Wood (North Wales, UK) including Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and (2) to determine the corresponding equilibrium conditions. Then (3) we discuss the outcomes by contrasting them with results from Norway spruce and silver fir woodlands in the Swiss Jura. Finally (4) we discuss and compare the performance of different tree species in complex forest structures and the potential for management to maintain them in a steady state condition.

2. Materials and methods

2.1. Data

Two forest sites have been considered in this study, Artist's Wood (53°04′35″N and 3°52′30″W) in Gwydyr Forest not far from the village of Betws y Coed in Snowdonia National Park (North Wales) and La Joux Pélichet (47°03′15″N and 6°45′38″E), part of the community forest Le Locle in canton Neuchâtel in the Swiss Jura mountain chain. The data from these two sites form time series.

The geological parent material at Artist's Wood is Ordovician slates, shales and grits. The soil type is iron pan soil and the research plots are located at an altitude of 80 m asl. The coastal climate is influenced by the golf stream and annual precipitation is in access of 1200 mm.

La Joux Pélichet is located in the natural silver fir – beech – forest belt at an elevation of 1000 m asl. The parent rock consists of hard limestone material of the Malm age. The prevailing climatic conditions are temperate oceanic with extended cold and wet periods. Annual precipitation is approximately 1400 mm.

At both sites two monitoring plots have been established. The first plot (0.65 ha) in Artist's Wood was set up in 2002 and a second one (0.36 ha) in 2007. The total area of the Artist's Wood plenter forest is 3.7 ha. The two plots at La Joux Pélichet (0.43 and 0.40 ha) were first surveyed in 1994 and two re-measurements have taken place since. The locations of all trees with a diameter at breast height, *dbh*, larger than 4 cm have been recorded at Artist's Wood. In La Joux Pélichet the measurement is practically identical with a threshold for recruitment even lower, defined by a *dbh* larger than 0 cm and a minimum height of 2 m. At two occasions in

Table 1
Important characteristics of plenter equilibriums with various tree species mixtures at different sites. The equilibriums were determined in the same way as in this paper.

Forests (species)	Country	Basal area (m^2/ha)	Standing volume (m^3/ha)	n_{10}	i_d^{10} (mm)
Artist's Wood (DF)	UK	27.4	342	70.0	4.35
Joux Pélichet (NS)	CH	37.7	421	111.0	3.20
Couvet (NS, SF)	CH	37.3	414	114.8	2.06
Höhronen (NS)	CH	40.6	529	134.0	2.69
Schallenberg (NS, SF, BE)	CH	37.3	482	184.1	1.06
Rougemont les Arses (NS, SF)	CH	31.5	392	142.7	1.97
Langula (BE)	D	20.8	252	98.8	2.19

2007 and 2011 at Artist's Wood and in 2001 and 2005 at La Joux Pélichet diameters have been re-measured.

Artist's Wood was planted in 1921 and established as a Douglas fir plantation with some Sitka spruce in wetter depressions. Western hemlock and broadleaved species later colonised the parts of the understorey, which is still an on-going trend. Initial complex structures developed in response to heavy selective harvesting operations in 1997. This was followed by a deliberate transformation to a plenter forest led by the Tyfiant Coed project (Bangor University, UK). The two research plots located in this forest now allow a detailed analysis. Since the time when the first monitoring plot was set up in 2002, Artist's Wood has been considered as a rare example of best practice in continuous cover forestry with Douglas fir (Helliwell and Wilson, 2012) (see Fig. 1). The standing volume in 2002 before the last plenter treatment (referred to as selection thinning in Europe) was 570 m^3 ha^{-1} and included 88% Douglas fir. The basal area at this time was 34 m^2 ha^{-1}. For the treatment in 2004, 25% of basal area was removed according to conventional cutting principles of European plenter management to result in a residual basal area of 27.7 m^2 ha^{-1}. Tables 2–4 provide an overview of the species composition. Fig. 1 illustrates the *dbh* distributions in Artist's Wood and Fig. 2 at La Joux Pélichet.

La Joux Pélichet is situated in an area with a long-standing tradition of plenter or selection forests. The forest originally stemmed from reafforestation and was established as a plantation. The woodland is now 110 years old and mostly has Norway spruce in the overstorey, which correspond to the native tree composition. From early times on forest management aimed at achieving plenter structures by regular transformation thinnings based on 8–10-years cycles following the plenter concept defined by Biolley and applied for more than 120 year in this region. In 1994 basal area in the two plots were 27.5 and 38.8 m^2 ha^{-1}, respectively, and 29.2 and 37.6 m^2 ha^{-1}, respectively, in 2001. Both plots now visually convey the impression of an acceptable level of complex structure (see Figs. 1 and 2).

2.2. Quantifying competition for light

Competition in plenter forests, particularly in temperate climates, is mostly related to light availability. For an effective quantification of competition for light it is important to identify appropriate characteristics (Pretzsch, 2009). In complex forest structures, it is particularly interesting to compare non-spatially explicit and spatially explicit competition measures. Our hypothesis was that a spatially explicit measure would be more informative. In previous studies (Schütz, 1975, 2006) we used the indicator basal area of larger trees, *BAL*, (Wykoff et al., 1982; Wykoff, 1990), also referred to as overtopping basal area, to characterise competition in forests with complex structures and to accurately determine demographic sustainability. Schütz used the same concept in 1975 and termed it *GCUM*, cumulative basal area. This characteristic has the advantage of being applicable in a non-spatial as well as in a spatial context. It can even be computed from aggregated data such as stem-number distributions or diameter distributions. *BAL* is defined as the sum of cross-sec-

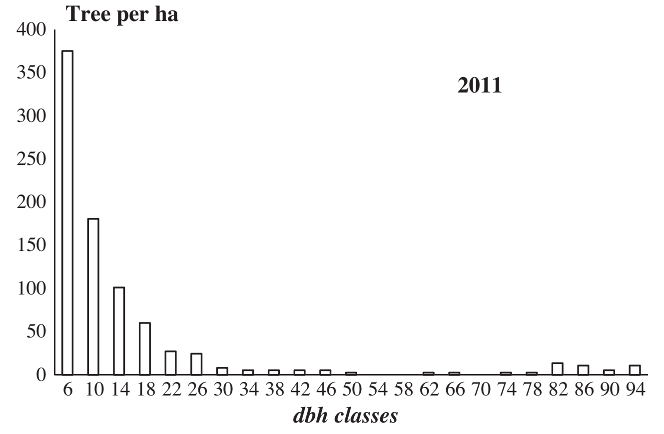

Fig. 1. Diameter distribution of Artist's Wood in 2011. 4 cm-diameter classes were used.

Table 2
Species composition by trees per hectare (*N*) and basal area per hectare (*G*) in Artist's Wood, plot 1.

Species	2002		2007		2011	
	N	*G*	*N*	*G*	*N*	*G*
Douglas fir	258	33.9	234	28.6	258	32.9
Birch	46	0.5	87	0.7	110	0.8
Sitka spruce	25	3.6	28	2.7	31	3.0
Western hemlock	20	0.2	57	0.7	104	1.4
Ash	11	0.2	8	0.1	14	0.2
Other broadleaves	40	0.7	82	0.8	115	1.0
Total	400	39.1	496	33.6	632	39.3

Table 3
Species composition by trees per hectare (*N*) and basal area per hectare (*G*) in Artist's Wood, plot 2.

Species	2007		2011	
	N	*G*	*N*	*G*
Douglas fir	254	33.0	262	38.0
Western hemlock	139	1.3	183	2.1
Beech	55	0.5	57	0.6
Oak	41	1.5	33	1.0
Sitka spruce	30	0.3	38	0.4
Other broadleaves	153	1.8	184	2.1
Total	672	38.4	757	44.2

Table 4
Species composition by trees per hectare (*N*) and basal area per hectare (*G*) in La Joux Pélichet.

Species	2001	
	N	*G*
Silver fir	207	22.5
Norway spruce	327	13.3
Scot pine	2	0.4
Ash and maple	45	2.4
Beech	10	0.5
Other broadleaves	6	0.1
Total	597	39.5

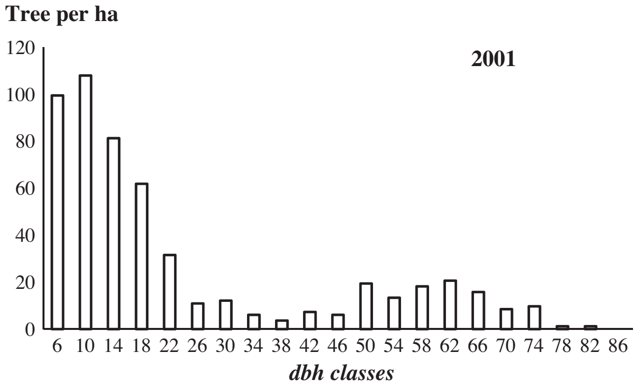

Fig. 2. Diameter distribution of La Joux Pélichet in 2001. 4 cm-diameter classes were used.

tional areas of tree stems (measured at 1.3 m above ground level and termed basal area in forestry) larger than the tree under consideration. If only aggregated data are available, *BAL* is the sum of cross-sectional areas of all diameter classes (multiplied by the frequency in each class) that are larger than the diameter class under consideration. In a spatially explicit context, *BAL* can be computed in the influence zone of each tree of a forest stand.

In general, *BAL* can be interpreted as canopy closure by the size class of the trees used to calculate *BAL*. *BAL* is also an expression of the relative dominance of a tree in a population and is closely related to the concept of basal area percentile. The smaller *BAL* the more the corresponding tree or diameter class dominates the forest stand in terms of its size. *BAL* of the smallest diameter tree or of the smallest diameter class equals the overall stand basal area.

In this study, we tested the spatially explicit characteristic, *SFAC* (short for "shade factor in light cones") in addition to the traditional non-spatial variant of *BAL*. *SFAC* is defined as the sum of tree height segments intercepting an upside-down search cone (Burkhart and Tomé, 2012, p. 206f.) that is set up at the crown tip of the subject tree (see Fig. 3).

The search cone represents the critical zone above a tree where light resources are drawn from. The assumption of this concept is that surrounding competitor trees reduce the amount of available light when parts of them extend into the search cone. A base angle $\alpha = 55°$ of the search cone ensures optimum photosynthetic activity (taking into consideration the position of the sun over the horizon at the end of May/June) (Schütz and Röhnisch, 2003). Other authors use base angles of 60° (e.g. Pretzsch et al., 2002). In contrast to the two versions of *BAL* described before *SFAC* does not primarily depend on area but rather on the height of neighbouring trees. In preliminary simulations we learned that modifying the base angle α between 55° and 65° did not have a great effect on the diameter increment estimation. Therefore we used a value of 55° as in previous studies. Assuming $\alpha = 55°$ and a total tree height of 35 m the corresponding circular influence zone would have a radius of approximately 20 m. In Fig. 3, *SAFC* is the sum of height segments (dashed lines) in meters. Drever and Lertzman (2003) applied a somewhat comparable competition measure, the sum of all tree height, which correlates well with light measurements on the forest floor.

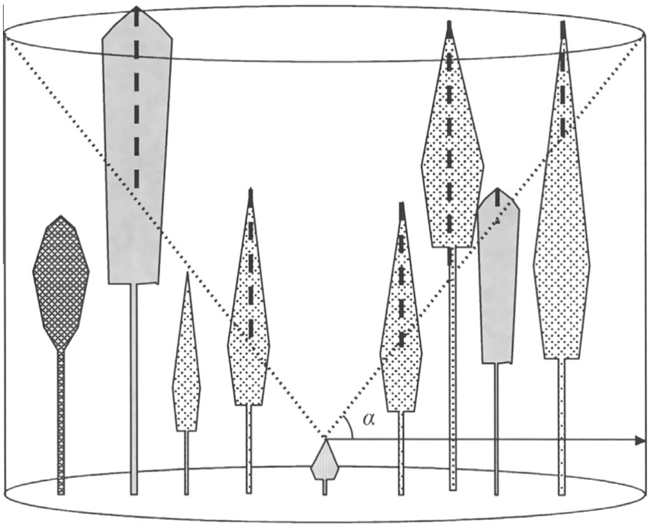

Fig. 3. Reversed search cone using a base angle $\alpha = 55°$ and tree heights intersecting the cone (black dashed lines).

2.3. Estimating diameter increment

In this study we used the following two functions to model diameter increment, i_d (Schütz and Röhnisch, 2003):

$$i_d^1 = \alpha_1 + \beta_1 \cdot BAL^2 + \gamma_1 \cdot \ln(dbh) \quad (1)$$

dbh is the stem diameter at breast height (1.3 m above ground level) and *BAL* is the non-spatially explicit version of this competition measure. Using *SFAC* requires a different model function (Eq. (2)). α_1, β_1, γ_1, α_2 and β_2 are model parameters.

$$i_d^2 = \alpha_2 + \beta_2 \cdot SAFC \quad (2)$$

The relationship between i_d and *SAFC* is linear because of the use of cumulative height segments which are one-dimensional measures.

Since we had spatially-explicit data available in this study, we decided to test the spatial *SFAC* characteristic in addition to the conventional *BAL* measure.

For deriving an equilibrium diameter distribution we fitted Eqs. (1) and (2) to all species regardless of species, since the contribution of species other than Douglas fir (in Artist's Wood) and Norway spruce (at La Joux Pélichet) was small. In addition we also analysed and modelled the species specific growth patterns. As we pooled the data from both plots we had a total of 181 increment records available from Artist's Wood and 209 from La Joux Pélichet.

2.4. Loss rate in sustainable conditions

The loss rate, *l*, (in previous studies by Schütz (e.g. 2006) this function was referred to as *e* as in exploitation) mainly comprises tree removals as part of forest management but also some mortality, i.e. all trees removed by cutting or natural death. This rate is partly based on empirical experience and partly on silvicultural considerations. It should reflect the pattern of tree removals and mortality after the plenter structures have arrived at equilibrium. In this context, 50 cm *dbh* often marks the boundary between different silvicultural tasks which are part of the same plenter thinnings: Trees with a *dbh* smaller than 50 cm (if any) are removed as part of occasional respacing, selection and cleaning operations. According to the authors' experience (Schütz, 1975) *l* curves of many investigated plenter forests are very similar in this diameter range. The shape of the *l* curve beyond 50 cm *dbh* is exponential since larger trees have a greater chance to be removed. This general form has been described on the base of very large records of thinning interventions in Couvet forest. The slope of the exponential *l*-curve, however, can vary depending on local forest management objectives and timber processing constraints. An important condition for determining the loss function is the need to strike a balance between the sum of volume of trees removed and stand volume increment because this is a fundamental pre-requisite of sustainability. To ensure this, the loss function is adapted iteratively, and modelled using a polynomial term

$$l = a_0 + a_1 \cdot dbh + a_2 \cdot dbh^2 + a_3 \cdot dbh^3 \quad (3)$$

a_0, a_1, a_2 and a_3 are model parameters. In a similar way as for diameter increment the data from all plots across the range of species were pooled for every site.

2.5. Identifying a demographically sustainable stem diameter structure

The methods for identifying a sustainable stem diameter structure and the corresponding tree density have been defined by Schütz (1975) and he has applied them to various tree species (Schütz, 1999, 2006). In sustainable conditions, the stem diameter distribution is balanced, i.e. ingrowth in any diameter class equals outgrowth plus losses from natural mortality and forest interventions. Based on the knowledge of diameter increment, i_d, and loss rate (natural mortality, tree removal as part of forest management, see Section 2.4), l, the shape of a balanced diameter distribution can easily be calculated. Steady state conditions are achieved when the number of trees progressing from a smaller diameter class $i-1$ equals outgrowth and loss in the diameter class under study, i (see also Fig. 4):

$$n_{i-1}p_{i-1} = n_i l_i + n_i p_i \tag{4}$$

n_i is the number of trees in diameter class i and n_{i-1} the number of trees in the adjacent smaller diameter class $i-1$. $p = i_d/4$ (assuming 4-cm diameter classes) is the outgrowth rate and $l = f(dbh)$ is the loss rate. $n_{i-1}p_{i-1}$ is the annual ingrowth from diameter class $i-1$ into diameter class i. $n_i l_i$ is the annual loss of trees in class i and $n_i p_i$ is the outgrowth of trees from class i into class $i+1$.

To establish a demographically sustainable stem diameter structure, we used Eq. (5) to assess diameter increment, loss rate, and ingrowth from the two monitoring sites to iteratively calculate the number of trees in successively larger diameter classes.

$$n_{i+1} = \frac{n_i p_i}{p_{i+1} + l_{i+1}} \tag{5}$$

The equilibrium has been identified when the number of trees in the smallest diameter class corresponds to field observations and ensures appropriate demographic proportions across the range of diameter classes.

2.6. Volume calculations

We developed volume functions, restricted to stem volume, from species-specific volume data collected by the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL). These volume functions take the general form

$$v = b_0 \cdot e^{b_1 \cdot \ln dbh + b_2 \cdot \ln^2 dbh + b_3 \cdot \ln h + b_4 \cdot \ln^2 h} \tag{6}$$

v is standing volume, h is total tree height, and b_0, b_1, b_2, b_3 and b_4 are species-specific model parameters.

3. Results

3.1. Performance of competition measures

Using *SFAC* slightly improved the diameter increment estimation ($R^2 = 0.41$ for Douglas fir at Artist's Wood and $R^2 = 0.44$ for silver fir at La Joux Pélichet) compared to *BAL* ($R^2 = 0.39$ for Douglas fir at Artist's Wood and $R^2 = 0.41$ for silver fir at La Joux Pélichet). Overall the improvements were small. The correlation between diameter increment and *SFAC* is even weaker for Norway spruce in La Joux Pélichet, because there is a wide range of tree sizes involved. Fig. 5 shows the relationships between diameter increment and *SFAC* in La Joux Pélichet.

The variation of diameter increment, i_d, was considerable in this study. The corresponding coefficient of variation amounts to 100% for Douglas fir (52% for Western hemlock) at Artist's Wood and 65% for Norway spruce at La Joux Pélichet (151% for silver fir). Even with the same stand density measured by *BAL* we observed a substantial variation of increment. This variation is typical of forest stands and particularly of plenter forests given the interspersion of tree sizes and residual stocking, affecting light and other microclimatic factors that influence diameter growth (Courbeaud et al., 2003; Carter and Klinka, 1992; Wright et al., 1998).

We combined the two competition measures *BAL* and *SFAC* in a multiple linear regression for estimating diameter increment (not reported in detail here) and this again slightly increased the coefficient of determination, but the gains are comparatively small although both measures are significant for almost all species involved.

3.2. Diameter increment

Since the spatially-explicit competition measure did not yield a marked improvement of the increment estimation (see previous section), we decided to proceed the analysis and the modelling using the traditional non-spatial variant of *BAL*. The regression results for Eq. (1) are provided in Table 5.

Interestingly the fitted function for Douglas fir and Norway spruce diameter increment using Eq. (1) was almost the same for *BAL* > 25 m^2/ha regardless whether we used raw data (solid lines in Fig. 6) or aggregated data (dashed lines in Fig. 6). For these levels of *BAL* the function graph approaches the point of diameter increment extinction (=intercept with the abscissa), which is crucial for the survival of recruitment trees and consequently for the sustainability of complex structures.

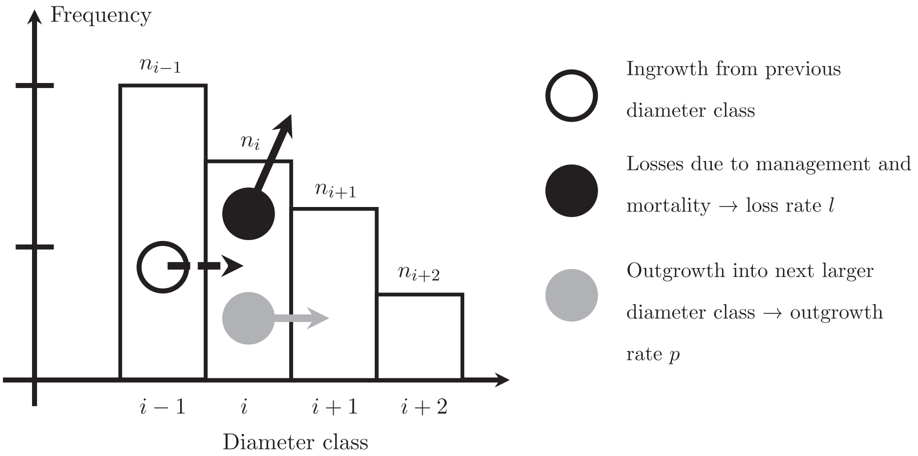

Fig. 4. Main processes of a dynamic stem diameter distribution and the corresponding notations.

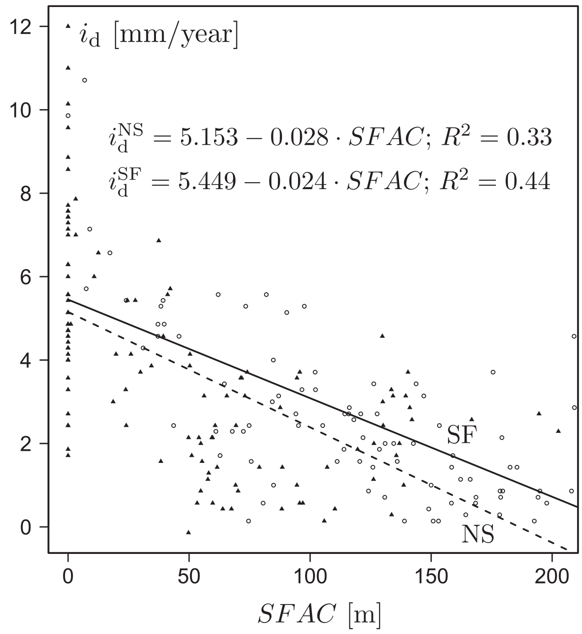

Fig. 5. Diameter increment of Norway spruce (NS) and silver fir (SF) at La Joux Pélichet depending on the competition measure *SFAC*.

Table 5
Regression coefficients relating to Eq. (1) and the relationship between i_d, *BAL* and *dbh* using aggregated data, as well as the coefficient of determination (R^2) as a measure of the goodness of fit.

Species	Parameter values			R^2
	α_1	β_1	γ_1	
Douglas fir	5.23868	−0.00496	1.07691	0.90
Western hemlock	−15.00741	0.00954	5.06713	0.82
Sitka spruce	−30.01527	0.01586	6.65992	1.00
Norway spruce	−1.37412	0.00097	1.68795	0.80
Silver fir	−1.01597	−0.00019	1.92128	0.92

3.3. Demographically sustainable diameter structure

The equilibrium curve indicating sustainable complex structures had to be adjusted to the number of trees in the smallest diameter class (n_6) observed at Artist's Wood. n_6 = 70 Douglas fir trees ha^{-1} observed in the monitoring plots in 2007 and 2011 enabled the equilibrium model to arrive at a basal area of 27.4 m^2 ha^{-1}, a volume of 342 m^3 ha^{-1} and a corresponding volume increment of 15.3 m^3 ha$^{7-1}$ year^{-1} given the loss function in Fig. 7.

The estimated sustainable diameter distribution based on Eqs. (5) and (6) has the shape of a sigmoid curve in a semi-log graph (see Fig. 8) and markedly deviates from a linear relationship as would be implied by the use of a constant *q*-factor. The left- and right-hand ends of the curve have steep slopes with a more gentle middle section. It resembles the rotated-S shape described by Goff and West (1975) for northern hardwoods in North America. If truncated at about 60 cm, the basic shape would resemble a negative exponential form like that proposed by Eyre and Zillgitt (1953) for the same forest community type.

4. Discussion

From a methodological point of view our study reveals that using non-spatial data is sufficient for the analysis and modelling of stem diameter growth dynamics. This outcome is somewhat unexpected but can be explained by the fact that mean relationships and general trends at stand level are of greater importance than single values when assessing long-term sustainability of complex forest structures. Due to the great variability of stem diameter increment, i_d, the shape of the increment function and increment extinction at the point of greatest stand density are more important than increment differences in the overstorey. *BAL* appears to be a compelling measure of competition. Also the comparatively small size of the research plots may have contributed to the lack of effectiveness of spatially explicit competition measures.

This study has clearly confirmed that Douglas fir can sustainably grow in complex forest structures on a long-term basis. Fig. 8 shows a good balance between surplus and deficit in tree numbers along the whole diameter distribution, even if two quite distinctive cohorts are still discernible. This is often the case in forest stands that are still in the process of transformation to complex forest structures. Overall the transformation process is definitely heading into the right direction. The crucial factor here is ensuring that there are sufficient numbers of trees in the smallest size class and not so much the lack of trees in the medium-range *dbh* classes. This guarantees an appropriate progression of Douglas fir trees into the currently still existing gaps between new and older cohorts. At Artist's Wood the amount of small trees is slightly above the required numbers at equilibrium (Fig. 8). In our view this is the most

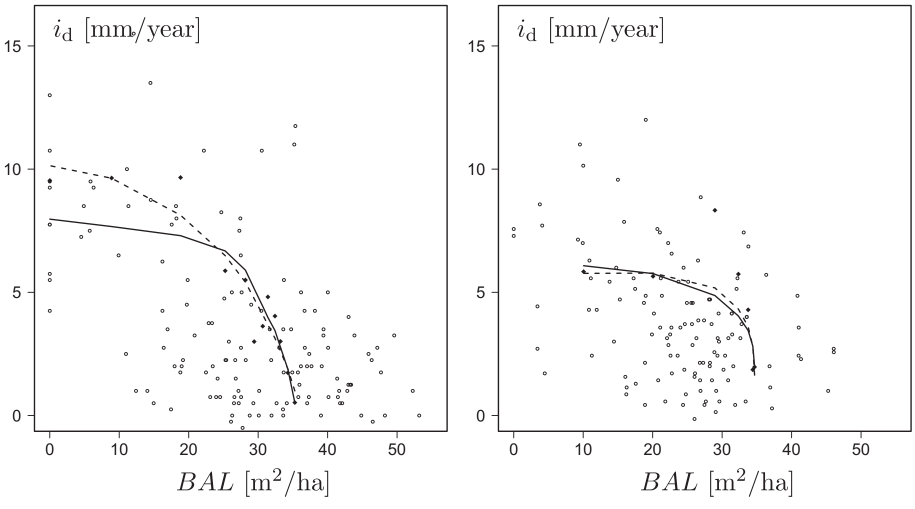

Fig. 6. Individual tree diameter increment (solid lines) over *BAL* for Douglas fir in Artist's Wood (left) and for Norway spruce at La Joux Pélichet (right) with the corresponding model functions from aggregated data (dashed lines) according to Eq. (1).

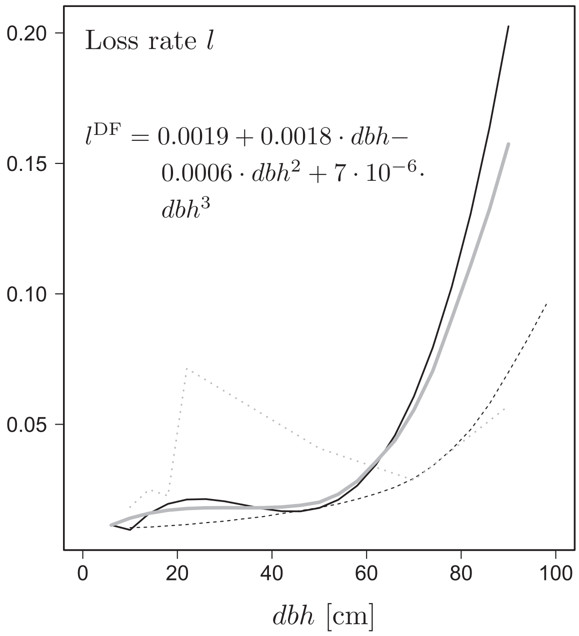

Fig. 7. Loss rate, l, (Eq. (4)) graphs derived from 200 observations of the well-known plenter forest Couvet (dashed line, Schütz, 1975) and of the Höhronen training plot (solid line). The loss rate for Artist's Wood is indicated by the grey curve and by the function equation. DF: Douglas fir.

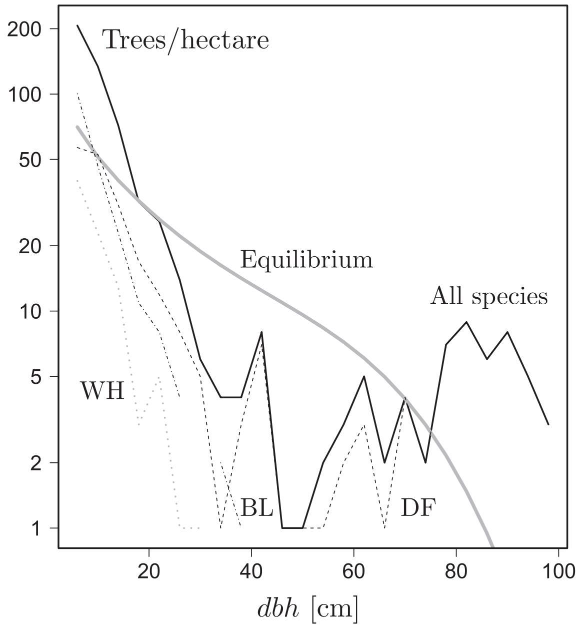

Fig. 8. Observed stem diameter distribution at Artist's Wood in 2007 in comparison to the calculated equilibrium in a semi-log graph. BL: Broadleaves, DF: Douglas fir, and WH: Western hemlock.

important evidence for the feasibility of managing Douglas fir in plenter forest structures. Thus a basal area of 27 m^2/ha marks a sustainable stand density enabling sufficient recruitment in the sense of Bioley's "étale" (stable stand density). According to the understorey light measurements by Drever and Lertzman (2003) this corresponds to approximately 30–40% of full light conditions.

Our findings somewhat contrast earlier conclusions (see for example Spies et al., 1990; Mailly and Kimmins, 1997) stating that gaps of at least 1 ha size are required for successful Douglas fir regeneration. The results of more recent experiments using alternative types of overstorey retention offer new insights (Drever and Lertzman, 2003; Newsome et al., 2010). According to these studies gaps in otherwise fully closed stands have not the same effect on light conditions at the forest floor and therefore on tree seedling and sapling growth than combinations of light shelter and small gaps in the sense of Nyland's patch-selection method (Nyland, 2002, p. 248f.). Such combinations of different retention types have proved to be more efficient methods of light management than more homogeneous types such as the shelterwood method (van Pelt and Franklin, 2000; Coates et al., 2003; Webster and Lorimer, 2005). This is in line with recent work which has also revealed that a shade-intermediate tree species like Douglas fir requires more than 40% of full light for sufficient development (Mailly and Kimmins, 1997; Drever and Lertzman, 2001) achieved with gaps of approximately 0.15 ha size (Kobe and Coates, 1997) or a basal area of 24 m^2 (Lochhead and Comeau, 2012). Following Canham et al. (1994) the effect of different light components, i.e. direct and diffuse light, should also be considered. Artist's Wood clearly shows that Douglas fir can regenerate and is able to form complex forest structures given these stand densities. In general, germination and seedling growth is hardly a problem in plenter forests as can for example be demonstrated in Slovenia, a country with a large area of plenter forests (Klopcic and Bončina, 2012). The limiting factor is light to allow sufficient height and diameter growth, which in turn ensures the required number of trees progressing into larger diameter classes. This requirement is met at Artist's Wood.

The shade tolerance of different tree species forming complex forest structures can be assessed by the location of the i_{d} saturation curve. Tree saplings are required to develop enough growth to eventually progress to the upper canopy. Previous studies have shown that at least 2 mm per year in the smallest diameter class are required for sustainable recruitment and for retaining complex structures, i.e. 50% of the trees in that diameter class move onto the next larger diameter class in 10 years time (Schütz and Röhnisch, 2003).

The extinction of diameter increment, i_{d}, can be interpreted as an indicator of shade tolerance. i_{d} extinction of Douglas fir in Fig. 9 for example occurs at a basal area value which is approximately 6 m^2 smaller than that of Norway spruce at La Joux Pélichet, i.e. Douglas fir at Artist's Wood shows only 85% of the shade tolerance of Norway spruce at La Joux Pélichet measured in terms of stand density. For Sitka spruce at Artist's Wood we can confirm a shade tolerance of 87% of Norway spruce at La Joux Pélichet, i.e. Douglas fir and Sitka spruce have more or less the same light demand. Western hemlock at Artist's Wood and silver fir at La Joux Pélichet exhibit 95% and 105%, respectively, of the shade tolerance of Norway spruce at La Joux Pélichet. These two species are the most shade-tolerant ones of this study. Naturally it must be considered that the two sites can vary in terms of carrying capacity or yield level (in forestry terms), which may have an influence on basal area (Schütz and Zingg, 2010). Therefore this ranking by diameter increment extinction is relative to the carrying capacity of the site. However, also the species-specific spatial efficiency needs to be taken into account. According to a previous study, beech, for example, would score in beech plenter forests in Thuringia (Germany; Schütz, 2006) 55% of the shade tolerance of Norway spruce at La Joux Pélichet and thus would also appear to be less shade-tolerant than Douglas fir at Artist's Wood, although it is well known that beech is more shade-tolerant than the other two species. This seeming contradiction can be explained by the fact that broadleaved trees tend to use space less efficiently than conifers, because their crowns enlarge laterally after release operations (Pretzsch and Schütze, 2009).

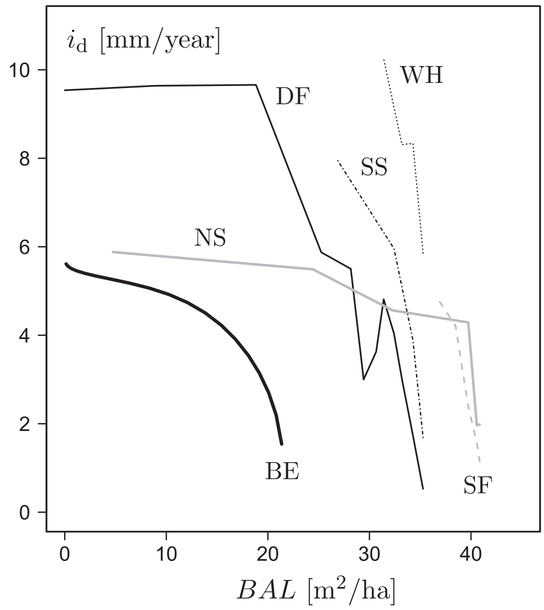

Fig. 9. Diameter increment saturation with decreasing stand density (*BAL* – basal area of larger trees) for the different species at Artist's Wood and La Joux Pélichet according to Eq. (2). For comparison the i_d saturation curve of beech in East German plenter forests (Schütz, 2006) is presented. BE: European beech, DF: Douglas fir, NS: Norway spruce, SF: silver fir, SS: Sitka spruce, and WH: Western hemlock.

Western hemlock is considered to be a shade-tolerant species (Coates and Burton, 1997), which makes it a suitable species for complex structures and plenter forests. In its natural range Western hemlock is mixed with Douglas fir (Spies et al., 1990) and both species form woodland communities. In fact Western hemlock could play a similar role in Douglas fir plenter forests as silver fir in the Norway spruce dominated upland plenter forests of Central Europe. A combination of a shade-intermediate, Douglas fir, and a shade-tolerant species, Western hemlock, could be beneficial in terms of diversity and niche complementarity. In fact, below a relative light level of 20% the growth of Western hemlock exceeds that of Douglas fir (Coates and Burton, 1997).

Silvicultural experience during the transformation process at La Joux Pélichet has highlighted that only silver fir and shade-tolerant shrubs regenerate with a canopy closure larger than 50% (Schütz and Röhnisch, 2003). Due to a lack of sufficient data it is difficult to judge on the ability of Sitka spruce to form complex structures on a sustainable basis. Its sensitivity to shade seems somewhat higher than that of Douglas fir. In its natural range Sitka spruce regenerates abundantly in gaps larger than 0.12 ha (Wright et al., 1998).

It is also interesting to note the differences in terms of productivity. The stem diameter increment of main-canopy Douglas fir trees is approximately 4 mm per year larger than that of Norway spruce (Fig. 9).

The well-known higher productivity of Douglas fir in forests with simple structures also holds in plenter forests despite considerably lower stand densities. Equilibrium basal area per hectare at Artist's Wood is approximately 60% of that of the corresponding yield table reflecting simple structures. Still a stand volume increment of 15.3 m^3 ha^{-1} year^{-1} is achieved. This is 20% more than the yield of Norway spruce at La Joux Pélichet and about the same as the corresponding Douglas fir yield table for Switzerland (Bégin, 1992). Obviously a comparatively heavy reduction of stand density has almost no effect on stand increment. This is an interesting point in the discussion about growing Douglas fir in complex forest structures that also relates to carbon sequestration (Buongiorno et al., 2012).

5. Conclusions

As an outcome of the first debates about plenter systems and complex structures at the end of the 19th century, plenter forests were restricted to uplands, particularly in the silver fir – beech – Norway spruce belt. Since then successful applications in Switzerland have shown that complex structures can also be achieved at lower elevations in the beech vegetation belt so that a total potential plenter forest area of 60% of the Swiss forest area can be estimated (Schütz, 1999). Long-term complex structures in pure beech forest have for a long time been considered as impossible. The beech plenter forests in Thuringia (Germany) prove otherwise (Dittmar, 1990; Schütz, 2006). Now the application of complex forest structures to a shade-intermediate species such as Douglas fir is not only possible but also appealing considering the broad site amplitude of Douglas fir in conjunction with on-going climate change and the species' growth superiority. The latter also means that the species has great potential for carbon sequestration. In addition it has become evident that plenter forests in Switzerland are more resilient to disturbances caused by wind than comparable even-aged forests, i.e. forests with a simple structure (Dvořak et al., 2011), providing yet another incentive for this management method.

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References

Badoux, E., 1949. L'allure de l'accroissement dans la forêt jardinée [The course of increment in the plenter forest]. Mitt. Schweiz. Anst. Forstl. Versuchswes. 26, 9–58.

Bégin, J., 1992. Productivité du Douglas vert (*Pseudotsuga menziesii* (Mirb.) Franco) en relation avec des charactéristiques stationnelles [Yield of Douglas fir in relation to site characteristics]. Mitt. Eidg. Forschungsanst. Für Wald Schnee und Landschaft. 67, 2–313.

Buongiorno, J., Halvorsen, E.A., Bollandsås, O.M., Gobakken, T., Hofstad, O., 2012. Optimizing management regimes for carbon storage and other benefits in uneven-aged stands dominated by Norway spruce, with a derivation of the economic supply of carbon storage. Scand. J. For. Res., http://dx.doi.org/10.1080/02827581.2012.657671.

Burkhart, H., Tomé, M., 2012. Modeling Forest Trees and Stands. Springer, New York, 457p.

Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource heterogeneity in forests; interspecific variation in light transmission by canopy trees. Can. J. For. Res. 24, 337–349.

Carter, R.E., Klinka, K., 1992. Variation in shade tolerance of Douglas fir, western hemlock, and western red cedar in coastal British Columbia. For. Ecol. Manage. 55, 87–105.

Coates, K.D., Burton, P.J., 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. For. Ecol. Manage. 99, 337–354.

Coates, K.D., Canham, C.D., Beaudet, M., Sachs, D.L., Messier, C., 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. For. Ecol. Manage. 186, 297–310.

Courbeaud, B., de Coligny, F., Cordonnier, T., 2003. Simulating radiation distribution in a heterogeneous Norway spruce forest on a slope. Agric. For. Met. 116, 1–18.

Dittmar, O., 1990. Untersuchungen in Buchen-Plenterwald Keula: Ein Vergleich zwischen dem Buchen-Plenterwald Keula und dem gleichaltrigen Buchenhochwald anhand langfristiger Versuchsflächen [Analysis of the beech plenter forest Keula: a comparison between plenter and even-aged stands based on long-term research plots]. For. u. Holz 45, 419–423.

Drever, C.R., Lertzman, K.P., 2001. Light-growth responses of coastal Douglas-fir and western redcedar saplings under different regimes of soil moisture and nutrients. Can. J. For. Res. 31, 2124–2133.

Drever, C.R., Lertzman, K.P., 2003. Effects of a wide gradient of retained tree structures on understory light in coastal Douglas-fir forests. Can. J. For. Res. 33, 137–146.

Dvořak, L., Bachmann, P., Mandallaz, D., 2011. Sturmschäden in ungleichförmigen Beständen [Storm damage in irregular forests]. Schweiz. Z. Forstwes. 152, 445–452.

Eyre, F.H., Zillgitt, W.H., 1953. Partial Cuttings in Northern Hardwoods of the Lake States. U.S. Dept. Agric. Tech. Bull., 1076.

Goff, F.G., West, D., 1975. Canopy–understory interaction effects on forest populations. For. Sci. 21, 98–108.

Helliwell, R., Wilson, E., 2012. Continuous cover forestry in Britain; challenges and opportunities. Quart. J. For., 214–224.

Klopcic, M., Bončina, A., 2012. Recruitment of tree species in mixed selection and irregular shelterwood forest stands. Ann. For. Sci. 69, 915–925.

Kobe, R.K., Coates, K.D., 1997. Models for sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. Can. J. For. Res. 27, 227–236.

de Liocourt, D., 1898. De l'aménagement des sapinières [Management of silver fir forests]. Bull. Soc. For. Franche-Comté et Belfort 4, 396–409.

Lochhead, K.D., Comeau, P.G., 2012. Relationships between forest structures, understorey light and regeneration in complex Douglas-fir dominated stands in south-eastern British Columbia. For. Ecol. Manage. 284, 12–22.

Mailly, D., Kimmins, J.P., 1997. Growth of *Pseudotsuga menziesii* and *Tsuga heterophylla* seedlings along a light gradient: resource allocation and morphological acclimation. Can. J. Bot. 75, 1424–1435.

Mason, W.L., Kerr, G., 2001. Transforming even-aged conifer stands to continuous cover management. In: Forestry Commission Information Note 40. Forestry Commission, Edinburgh, 8p.

Matthews, J.D., 1991. Silvicultural Systems. Oxford University Press, Oxford, 284p.

Meyer, H., 1933. Eine mathematisch–statistische Untersuchung über den Aufbau des Plenterwaldes [A mathematical–statistical analysis of the structure of plenter forests]. Schweiz. Z. Forstwes. 84, 33–46, 88–103, 124–131.

Newsome, T., Heineman, J.L., Nemec, A., 2010. A comparison of lodgepole pine responses to varying levels of trembling aspen removal in two dry south-central British Columbia ecosystems. For. Ecol. Manage. 259, 1170–1180.

Nyland, R.D., 2002. Silviculture. In: Concepts and Applications, second ed. Waveland Press, Long Grove, Illinois, 82p.

O'Hara, K.L., 1996. Dynamics and stocking-level relationships of multi-aged ponderosa pine stands. For. Sci. 42 (4, Suppl. 33), 1–34.

O'Hara, K.L., Hasenauer, H., Kindermann, G., 2007. Sustainability in multi-aged stands: an analysis of long-term plenter systems. Forestry 80, 163–181.

Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics. Update ed. John Wiley & Sons, New York, USA, 520p.

Pommerening, A., 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., 2009. Forest Dynamics, Growth and Yield. Springer, Berlin, 664p.

Pretzsch, H., Schütze, G., 2009. Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanations on individual tree level. Eur. J. For. Res. 129, 183–204.

Pretzsch, H., Biber, P., Ďurský, J., 2002. The single tree-based stand simulator SILVA; construction, application and evaluation. For. Ecol. Manage. 162, 3–21.

Roloff, A., 2001. Baumkronen. In: Verständnis, Zusammenhänge und Anwendung [Tree Crowns. Understanding, Relationships and Applications]. Ulmer Verlag, Stuttgart, 64p.

Schütz, J.P., 1975. Dynamique et conditions d'équilibre de peuplements jardinés sur les stations de la hêtraie à sapin [Plenter stand dynamics and conditions of equilibrium at beech – silver fir sites]. Schweiz. Z. Forstwes. 126, 637–671.

Schütz, J.P., 1997. Sylviculture 2. In: La gestion des forêts irrégulières et mélangées [Management of Irregular and Mixed Forests]. Presses Polytechniques et Universitaires Romandes, Lausanne, p. 78p.

Schütz, J.P., 1999. Praktische Bedeutung der Überführung für die Umsetzung der Plenteridee [Practical significance of transformation for implementing the plenter principle]. In: Hanewinkel, M. (Ed.), Überführung von Altersklassenwäldern in Dauerwäldern. Ber. Freiburger Forstl. Forschung, H. 8, pp. 1–13.

Schütz, J.P., 2001. Opportunities and strategies of transforming regular forests to irregular forests. For. Ecol. Manage. 151, 87–94.

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., Röhnisch, F., 2003. Steuerung des Nachwuchses während der Überführung von gleichförmigen Fichten-Aufforstungsbeständen in Plenterwälder [Steering of recruitment during the transformation of even-aged Norway-spruce forests to plenter forests]. In: Kenk, G. (Ed.), Beiträge zur Jahrestagung 2003. Deutscher Verband forstlicher Forschungsanstalten, Sektion Ertragskunde, Freiburg i. Br., pp. 184–194.

Schütz, J.P., Zingg, A., 2010. Improving estimations of maximal stand density by combining Reineke's size-density rule and the yield level, using the example of spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.). Ann. For. Sci. 67, 507–518.

Smith, D.M., Larson, B.C., Kelly, M.J., Ashton, P.M.S., 1997. The practice of silviculture. In: Applied Forest Ecology, ninth ed. John Wiley & Sons, New York, p. 37p.

Spies, T.A., Franklin, J.F., Klopsch, M., 1990. Canopy gaps in Douglas-fir forests of the Cascade mountains. Can. J. For. Res. 20, 649–658.

van Pelt, R., Franklin, J.F., 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. Can. J. For. Res. 30, 1231–1245.

Webster, C.R., Lorimer, C.G., 2005. Minimum opening sizes for canopy recruitment of midtolerant tree species: a reprospective approach. Ecol. Appl. 15, 1245–1262.

Wright, E.F., Coates, K.D., Canham, C.D., Bartemucci, P., 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. Can. J. For. Res. 28, 871–886.

Wykoff, W.R., 1990. A basal area increment model for individual conifers in the Northern Rocky Mountains. For. Sci. 36, 1077–1104.

Wykoff, W.R., Crookston, N.L., Stage, A.R., 1982. User's guide to the stand prognosis model. USDA For. Serv., Gen. Techn. Rep. INT-133, Ogden, Utah, 112p.