

Individual-tree growth dynamics of mature *Abies alba* during repeated irregular group shelterwood (Femelschlag) cuttings

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Abstract: This study investigated the individual-tree diameter response of mature silver fir (*Abies alba* Mill.) to reproduction harvests (Femelschlag: an irregular group shelterwood method) on six sites in the Black Forest, Germany. On each site, four different treatments were applied, including a control treatment and short-, medium, and long-term regeneration periods aimed at the complete removal of overstory trees within 20, 35, and 50 years, respectively. These treatments created a wide variety of growing conditions for individual trees. Relationships between relative diameter growth and stand-level and neighborhood interaction indices were evaluated. Growing conditions for individual trees in control conditions were best characterized using Lorimer's index for a 16 m radius neighborhood. Equations predicting tree growth in control stands underpredicted initial growth of trees after harvesting operations, suggesting a release effect that is not captured by postharvest density. This effect was larger for smaller trees and influenced by removal intensity. Growth response to density reductions was also influenced by previous harvests. Our results suggest that the growth response of mature trees to reproduction harvests may become an important consideration when increased emphasis is placed on managing for long-term regeneration periods.

Résumé : Nous avons étudié la réaction en diamètre d'individus matures d'*Abies alba* Mill. à des coupes de reproduction (Femelschlag : une méthode de coupe progressive irrégulière par groupe) appliquées sur six stations de la Forêt Noire, en Allemagne. Sur chaque station, quatre traitements différents ont été appliqués, dont un traitement témoin et des coupes progressives visant la récolte entière du couvert dominant à la suite de périodes de régénération s'étalant sur des horizons temporels court (20 ans), moyen (35 ans) et long (50 ans). Ces traitements ont créé une large gamme de conditions de croissance pour les arbres résiduels. Nous avons établi des relations entre la croissance relative en diamètre des arbres et des indices à l'échelle du peuplement et des interactions entre arbres voisins. La meilleure caractérisation des conditions de croissance des arbres individuels dans les traitements témoins a été obtenue à l'aide de l'indice de Lorimer pour un rayon de voisinage de 16 m. Les équations de prévision de la croissance des arbres des peuplements témoins sous-estimaient la croissance initiale des arbres après les opérations de récolte, ce qui implique qu'un effet de dégagement n'a pu être pris en compte par la densité après coupe. Cet effet était plus important chez les plus petits arbres et variait selon l'intensité de la récolte. La réaction de croissance à la suite des réductions de densité a aussi été influencée par les récoltes précédentes. Nos résultats indiquent que la réaction de croissance des arbres matures aux coupes de reproduction peut devenir un facteur important à considérer lorsqu'on met l'accent sur un aménagement faisant intervenir de longues périodes de régénération.

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Introduction

Management of stand density is a common silvicultural practice for achieving various management objectives. Density reductions through thinnings are intended to improve the growth and vitality of the residual trees, whereas reproduction cuttings are final harvest operations that typically focus on lowering overstory densities to provide suitable conditions for establishment and growth of tree regeneration.

Research into the effects of density manipulations in older stands has generally focused on tree regeneration; however, studies have shown that older trees of many but not all species can respond to reductions in stand density (Youngblood 1991; Latham and Tappeiner 2002; Beber et al. 2004). With the recent interest in longer rotations and in reproduction methods that maintain an overstory cover for extended periods, understanding how older, mature trees respond to density manipulations has gained importance (Kenk and

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Guehne 2001). Furthermore, harvesting operations in these settings are frequently applied as repeated target-diameter or diameter-limit cuts, raising questions regarding how trees of smaller sizes and associated lower crown classes respond to release. Also, the gradual removal of the overstory through multiple harvest operations raises questions about the impacts of repeated, frequent stand density reductions on the growth of residual trees.

Most information about the impacts of density management comes from studies in which manipulations are planned, implemented, and analyzed at the stand scale. When applied in fairly homogenous stands, the performance of stand-level competition or interaction indices typically has not justified the additional effort of calculating distance-dependent neighborhood indices (Bigging and Dobbertin 1995; Rivas et al. 2005). With the recent increased emphasis on variable-density treatments and multiple age-classes within stands, indices that incorporate spatial variation have received more interest (Lorimer 1983; Wagner and Radosevich 1998; Canham et al. 2004; Roberts and Harrington 2008). These indices are based on the assumption that local conditions within the vicinity of a tree are more important for its growth than average stand conditions. The performances of interaction indices have been compared in a variety of settings and can provide information about the scales, patterns, and results of plant interactions (e.g., D'Amato and Puettmann 2004; Roberts and Harrington 2008). Nonetheless, the usefulness of these indices and the potential insight they provide into tree responses in the context of silvicultural manipulations, such as reproduction harvests, have received limited attention, even though such evaluations would provide basic information for selecting trees for retention and removal.

Much research has focused on how tree growth responds to different stand densities; however, less attention has been paid to the transition phase, when trees gradually adjust to the modification of their local environment from the preharvest to the postharvest density (Bebber et al. 2004; Jones and Thomas 2004). Investigations into young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands showed an adjustment period during which the diameters of trees at breast height (1.3 m; DBH) grew faster after thinning than would have been expected based on the residual density (Hann et al. 2003; Roberts and Harrington 2008). On the other hand, older Douglas-fir showed a delayed growth response, which was only detectable during the second decade after thinning (Yerkes 1960; Williamson 1982). Despite these trends, little information is available about potential mechanisms explaining thinning responses, such as decreased sapwood permeability (Reid et al. 2003), stomatal constraints (Renninger et al. 2007), increased water availability (Stogsdill et al. 1992), and shifts in carbon allocation after thinning.

The overall objective of this study was to improve our understanding of tree interactions among older trees, as influenced by density reductions during the regeneration phase. As specific objectives, we developed a list of hypotheses (Table 1) that addressed the following questions about DBH growth of mature trees: (i) Are growing conditions for individual trees acting at local neighborhood or stand-level scales? (ii) Is current density sufficient for representing

growing conditions after stand density reductions, or is tree performance better predicted by also considering the influence of preharvest densities and harvest intensities? (iii) Is DBH growth of individual trees following multiple harvest operations solely influenced by the latest density reduction or do previous density reductions have a lingering influence? Furthermore, we tested whether the results of investigations of these questions are influenced by target tree size.

Materials and methods

Study area and design

The data that formed the basis for this analysis were from a long-term research project initiated by Weise (Forest Research Institute of Baden-Wuerttemberg) in the late 1970s aimed at investigating tree and regeneration response to Femelschlag operations. Femelschlag is a traditional reproduction method used to regenerate mixed-species mountain forests with silver fir (*Abies alba* Mill.) in central Europe; it could be described as an irregular group shelterwood reproduction method (Röhrig et al. 2006). The experiment compared treatments with different lengths of the regeneration phase and thus speeds of tree removal (Weise 1995). Experimental treatments included one control and three Femelschlag treatments. In the control, only 50% of the periodic volume increment was harvested every 10 years, maintaining basically a fully stocked stand. In contrast, the short-, medium-, and long-term Femelschlag treatments were aimed at the complete removal of the overstory trees within 20, 35, and 50 years, respectively (Fig. 1). To calibrate the Femelschlag treatment areas, all units, with the exception of the control units, were cut to approximately 75% of the volume of a fully stocked stand when setting up the research installations. For calibration purposes, the density of a fully stocked stand was defined as the average volume of an installation. The treatments were assigned to approximately 0.25 ha square plots.

Tree removal in the short-term regeneration treatments were scheduled every 5 years to residual volume of 65%, 50%, 30%, and 0% of fully stocked stands (Fig. 1). After the initial density reduction to 75% at installation, the medium-term regeneration treatments were further thinned 10 years after installation to 70%, then every 5 years to 60% and 45% of fully stocked stands (Weise 1995). In the long-term regeneration treatments, a stocking level of 75% of fully stocked stands was maintained for the first 20 years, before additional density reductions took place. The range of treatments allowed the evaluation of individual-tree growth responses to a wide range of growing conditions and release intensities.

Trees were marked according to Femelschlag principles (Röhrig et al. 2006). Thus, harvests combined the creation of group shelterwood openings with subsequent enlargement of these openings and removal of shelter trees. Furthermore, selection criteria included financial maturity of trees as determined by the landowner's specific criteria (e.g., target DBH, quality). However, in contrast to strict target-diameter cutting, trees are also selected for spatial and stand structural considerations, such as to open up gaps or to remove trees of poor quality or health. For these reasons, the typical harvesting operations in Femelschlag are quite variable. The

Table 1. List of objectives and associated hypotheses that were evaluated for each objective using the corrected Akaike information criterion.

Objective <i>i</i> : Determine which factors influence diameter growth under control conditions, i.e., without the impact of stand density reductions.	
Growth in unthinned stands is best predictable by:	
H ₀	Null model: Tree–tree interactions are not important for predicting diameter growth rates. The null model states that growth is solely a function of the spatial and temporal correlation among trees.
H ₁	Neighborhood model: Neighborhood conditions (as quantified by Lorimer’s interaction index) influence growth of target tree. Different neighborhood sizes will be tested.
H ₂	Stand model: Tree growth is independent of neighborhood conditions but reflects a tree’s “position” within populations (as quantified by Glover’s index), and overall population density (as quantified by Wykoff’s index).
H ₃	Initial size: The size of a tree in relation to the mean tree size is the best determinant of individual-tree growth.
Objective <i>ii</i> : Determine the impact of density reductions on diameter growth.	
Growth after harvesting is best predictable by:	
H ₀	Null model: Density reductions have no effect on tree growth. Tree performance is solely a function of current density (i.e., best performing models from objective <i>i</i>) and initial tree size.
H ₁	Preharvest conditions: Pretreatment neighborhood conditions and initial tree size best predict tree growth after harvesting treatments.
H ₂	Harvesting intensities and initial tree size: Tree growth following density reductions is a function of neighborhood-scale harvesting intensity and initial tree size.
H ₃	Harvesting type (such as high-intensity versus low-intensity thinnings): Tree growth following thinnings is best predicted by harvesting type.
Objective <i>iii</i> : Determine the impact of multiple density reductions on diameter growth.	
Growth after multiple harvesting operations is best predictable by:	
H ₀	Null model: Only conditions after last harvest entry (best model or models from objective <i>ii</i>) and initial tree size are important to tree growth.
H ₁	Harvesting frequency: Tree growth is a function of the number of past and present harvesting operations within a stand and initial tree size.
H ₂	Cumulative harvesting intensity: The cumulative intensity of past harvesting operations and initial tree size are the best predictors of diameter growth.
H ₃	Weighted cumulative harvesting intensity: Recent harvests have the greatest effect on diameter growth; however, previous harvests are also important for predicting growth response (measured using weighted cumulative treatment intensity in which the most recent harvests are weighted more than previous harvests).

Note: A detailed description of interaction indices is presented in the text. The full set of variables used to assess the support for each hypothesis is listed in Table 3.

treatment-level d/D (quadratic mean diameter of trees removed divided by quadratic mean diameter of trees before harvesting within the whole treatment area) for the harvest operations in this study ranged from 0.22 to 1.77 throughout the study period, with a mean of 0.96 (standard deviation = 0.22). Our analysis followed the underlying approach of Femelschlag treatments that focuses on managing growing conditions on a small spatial scale, rather than stand-level scales. We used the experimental setup as a unique opportunity to investigate individual-tree responses to a wide variety of growing conditions (Figs. 1 and 2).

The research sites were established between 1979 and 1981 to cover the north–south extent of the natural range of silver fir in southwestern Germany (mostly the Black Forest region). Specific details about site and stand characteristics at the time of establishment are provided in Table 2. The selected stands had not undergone harvesting operation in the decade prior to study establishment and presented homogeneous full stocking conditions (maximum deviation in volume of any plot from mean stocking within an installation was less than 15%).

Limited snow breakage, windthrow, and bark-beetle-induced mortality occurred in the study sites, and total mortality from sources other than harvesting was less than 9% during the study period despite two rather serious gale events hitting the forests of Baden-Wuerttemberg in 1990 and 1999. Changes in density due to these disturbances were treated in the analysis in the same way as stand density reductions through harvesting (except when addressing objective *iii*, see below); however, natural disturbance events were not included in the calculation of the number of harvest operations. Generally, tree mortality due to natural disturbances, such as wind or snow breakage, was reported by local forestry personnel, and the actual year of tree death was reported in the data set. However, if mortality had gone unnoticed, the actual year of mortality could not be assigned to the trees. In these few cases, the year of the next measurement was assigned as the mortality year. Since these incidences represent only a few minor reductions in density, the measurement error should not influence our study results and conclusions.

Harvesting operations were coordinated with the measure-

Fig. 1. Size (a), preharvest growing conditions and harvesting intensities for all study trees, as reflected in diameter distributions (a), preharvest densities in 16 m radius neighborhoods (b), and the percentage of basal area in the 16 m radius neighborhoods removed in the harvesting operations (c). Data in Figs. 1a and 1b are separated for trees without any harvesting operation within the last decade and trees with harvesting operation within the last decade to highlight that trees and growing conditions for both populations are comparable. Data in Fig. 1c are separated by the Femelschlag treatments, that is, short-, medium-, and long-term regeneration period.

ment schedule to obtain accurate information about preharvest and postharvest conditions. Measurements were typically taken at 5 year (4 to 6 years) intervals. The DBHs of trees >4 cm (excluding advanced regeneration newly established during the experiment) were measured with calipers to the nearest millimetre in two directions and averaged. Stem locations were mapped, and linear distances between all trees were calculated to determine the tree neighborhoods.

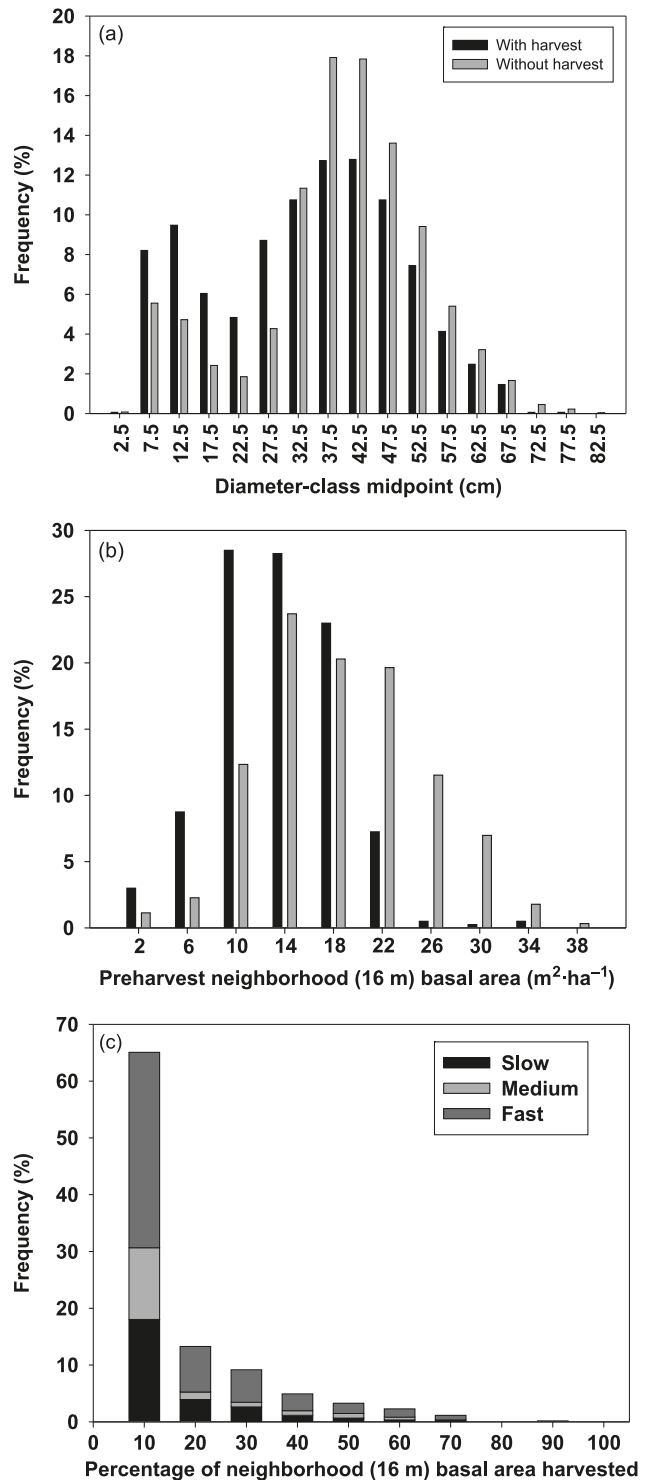
The tree population used in the neighborhood analysis varied with neighborhood size, as only trees for which the whole neighborhood was within the plot boundaries were included as target trees. To keep sampling sizes and populations comparable, we limited our analysis to trees for which all three indices could be calculated (Fig. 2). Thus, stand-level indices were only calculated for the trees for which a neighborhood index could be calculated, that is, trees close to the edge and potentially influenced by conditions outside the measurement plots were excluded from selection as target trees. The data set for objective *i* included only trees that had not undergone a major density reduction, such as a Femelschlag harvest, within the last decade. For objective *ii*, trees and measurement periods were also selected from plots in which a single harvest had recently occurred. Similarly, trees and measurement periods that followed single and multiple harvesting operations were selected for objective *iii*.

Data management and statistical analysis

The vast majority of trees across the study sites were silver fir, although silver fir was not the dominant species by volume in all plots (Table 2). Because this species is known to be responsive to release operations (Weise 1995, 1996), it was exclusively chosen as target trees in our analyses. Neighboring trees included mainly silver fir, Norway spruce (*Picea abies* L.), and European beech (*Fagus sylvatica* L.). For calculation of indices (see below), neighboring trees were grouped into conifers and hardwoods and labeled as intraspecific and interspecific interactions, respectively. As an indicator of individual-tree performance, relative growth rate (RGR) was calculated for each measurement period using the formula by Fisher (1921):

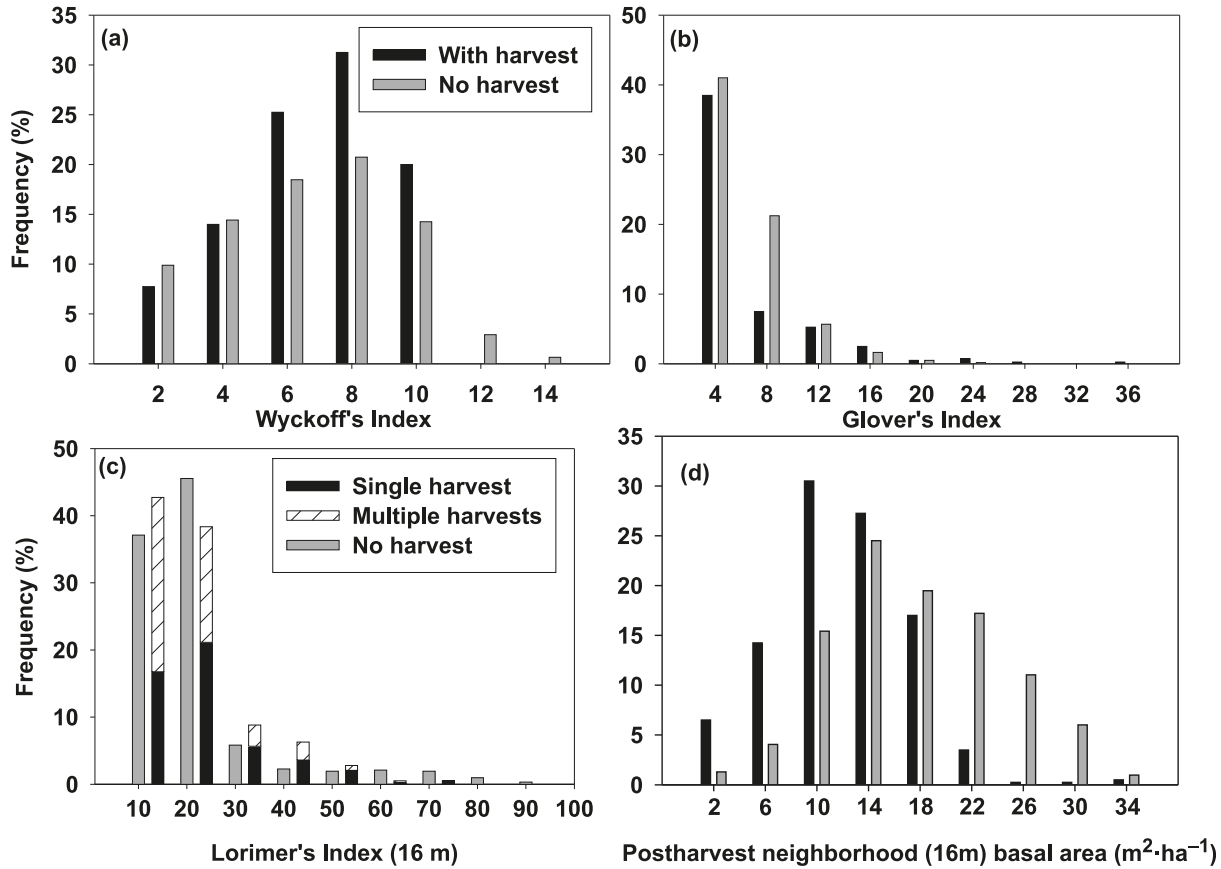
$$\text{RGR} = \frac{\ln D_2 - \ln D_1}{t_2 - t_1}$$

where D_1 and D_2 are the diameters at the beginning (t_1) and end (t_2) of measurement period 1. Diameter growth has been shown to be a very sensitive indicator of growing conditions (e.g., Zhao et al. 2004) and has been commonly used by ecologists to investigate competitive relationships (e.g.,



Cannell et al. 1984; Ramseier and Weiner 2006). By accounting for initial diameter, RGR allows an assessment of the relative importance and intensity of tree–tree interactions for a wide range of tree sizes (Ford and Sorrensen 1992) and site productivities (Yue et al. 2008). Since RGR has been under scrutiny by forest scientists (South 1995) and may not account for size-related growth differences when growth curves are not exponential (South 1991), initial diameter was also included as an independent variable in the first set of models. However, models including initial

Fig. 2. Description of initial stand densities for all measurement periods, as represented by distribution of Wykoff's (a) (Wykoff et al. 1982), Glover's (b) (Glover and Hool 1979), and Lorimer's (c) (Lorimer 1983) indices and postharvest basal areas (d). Lorimer's index and the postharvest basal area were calculated based on densities within 16 m radius neighborhoods. Data are separated for trees with and without harvesting operation in the last decade and for Lorimer's index for trees with single and multiple harvest operations.



diameter were not well supported by our data, suggesting that RGR successfully account for size-related differences (see results for objective *i*; Table 4).

Data were summarized, and the following interaction indices were calculated for each target tree and each measurement period. Conditions within the vicinity of individual trees were represented by a neighborhood interaction index (also labeled “proximity indices” by Weigelt and Jolliffe 2003) developed by Lorimer (1983; hereafter referred to as “Lorimer’s index”). This index was calculated for circles with radii of 10, 13, 16, and 20 m around target trees to allow for a determination of appropriate neighborhood sizes (D’Amato and Puettmann 2004). Glover and Hool’s (1979) index assumes the principle of perfect size symmetry (Schwinning and Weiner 1998) within stands. It is solely based on size hierarchies and does not include measures of absolute densities. In contrast, Wykoff et al.’s (1982) index quantifies absolute densities of trees larger than the target trees. It has the reputation of being a “behaved density variable under all types of thinnings” and is especially recommended when comparing thinnings from above and below and single-tree selection (Monserud and Sterba 1996; p. 62). These indices were selected from the vast possible list of indices (e.g., see Bigging and Dobbertin 1995) using two criteria. First, they represented the range of hypotheses of interest (see Table 1). Second, they were computable

based solely on available information and did not require additional assumptions and interim calculations.

Lorimer’s index (Lorimer 1983) was calculated as

$$L_i = \left[\sum_{j_1=1}^{n_1} \left(\frac{D_{j_1}}{D_{i_1}} \right) \right] + \left[\sum_{j_2=1}^{n_2} \left(\frac{D_{j_2}}{D_{i_1}} \right) \right]$$

Glover’s index (Glover and Hool 1979) was calculated as

$$G_i = \left[\left(\frac{B_{i_1}}{\bar{B}_1} \right) + \left(\frac{B_{i_1}}{\bar{B}_2} \right) \right] / 2$$

and Wykoff’s index (Wykoff et al. 1982) was calculated as

$$W_i = \left[\sum_{\substack{j_1=1 \\ D_{j_1} > D_i}}^{p_1} (D_{j_1})^2 \cdot 0.00007854 \right] + \left[\sum_{\substack{j_2=1 \\ D_{j_2} > D_i}}^{p_2} (D_{j_2})^2 \cdot 0.00007854 \right]$$

where \bar{B} is the basal area of tree with mean D within a stand; B_i is the basal area of target tree i ; D_i is the diameter

Table 2. General characteristics of study sites at which Femelschlag treatments were applied, Black Forest, Germany.

	Study sites						
	Ta220	Ta221	Ta222	Ta223	Ta224	Ta225	Ta225
Elevation (m a.s.l.)	830	720	1020	1020	520	700	700
Annual rainfall (mm)	860	860	1840	1840	1070	1340	1340
Mean annual temperature (°C)	6.5	7	6.5	6.5	7	7.5	7.5
Parent material	Limestone	Sandstone	Gneiss	Granite	Sandstone	Sandstone	Sandstone
Slope, aspect	Level, na	Steep, south	Moderate, south	Moderate, northeast	Moderate, south	Moderate, southwest	Moderate, southwest
Site index* (m)	31	22	29	24	29	26	26
Pretreatment volume (m ³ ·ha ⁻¹)	598–707	524–602	460–580	452–625	468–656	463–578	463–578
Mean age (<i>A. alba</i> , <i>P. abies</i>)	103, 91	120, 126	95, 92	116, 107	108, 103	98, 91	98, 91
Species volume mixture (% at installation); fir, spruce, beech	79, 17, 4	38, 62, —	61, 24, 16	33, 47, 20	42, 58, —	52, 46, 2	52, 46, 2

*Estimated height of silver fir at 100 years according to the yield table of Hauser (1956) (Landesforstverwaltung 1993).

at breast height of target tree i ; D_j is the diameter at breast height of neighbour tree j ; n is the total number of neighbours; p is the total number of trees in the population; and 1 and 2 represent species, whereby 1 is used for all conifers (spruce, fir, pine), and 2 is used for all hardwoods (e.g., beech, maple)

The indices by Glover and Hool (1979) and Wykoff et al. (1982) were scaled to a per-hectare basis to avoid confounding effects of minor differences in plot size and to render the index comparable among sites and plots.

The base main statistical model used was

$$RGR_i = \beta_0 + \beta_1 \ln(\Pi_{aa}) + \beta_2 \ln(\Pi_{ab}) + \beta_3 \ln(\Pi_{aa} \times \Pi_{ab}) + \varepsilon$$

where Π_{aa} and Π_{ab} are the calculated intraspecific and interspecific interactions (Π) at the beginning of the growth interval, $\Pi_{aa} \times \Pi_{ab}$ is the intraspecific \times interspecific interaction, and ε is the remaining error. Various forms of this model reflecting the hypotheses (for a detailed listing of variables and their use in testing specific hypotheses see Tables 1 and 3) were constructed and were evaluated for each growth interval and interaction index (Π). Mixed linear regression analyses were performed in SAS (PROC MIXED; SAS Institute Inc. 1999) and accounted for the nested structure of the study setup (trees are nested in plots that received a plot-level treatment, sets of plots nested within sites). For the majority of models, nonlinearity and nonhomogeneous variance were corrected by logarithmic transformation of each independent variable. Spatial correlation among trees in each plot was accounted for by including a power spatial correlation structure in each of the models (SP(POW); SAS Institute Inc. 1999). In addition, a repeated measures structure was included in the error covariance matrix to account for temporal correlation among repeated diameter measurements for each subject tree.

The hypotheses were evaluated by comparing models with the corrected Akaike information criterion (AIC_c) (Burnham and Anderson 1998). To rank the models according to their relative fit, AIC_c rewards models for goodness of fit and penalizes them for multiple parameters. AIC_c values are assessed according to the difference between the value for a model i (AIC_{ci}) and the value for the best fitting model, that is, the lowest AIC_c value (AIC_{cmin}):

$$\Delta_i = AIC_{ci} - AIC_{cmin}$$

where Δ_i provides an indication of the strength of evidence that model i is the best approximating model in the set, whereby higher Δ_i values correspond to lower strength of evidence (Anderson et al. 2001). Akaike weights (w_i) were calculated to assess the probability of a model i being the best model in the set (Burnham and Anderson 1998):

$$w_i = \frac{\exp(-\Delta_i/2)}{\sum_{i=1}^R \exp(-\Delta_i/2)}$$

where w_i is the Akaike weight for model i , and R is the number of models in the set. The w_i values provide information about how model i relates to the overall set of models. Weight values range between 0 and 1, with 1 having the highest probability that model i is the best model in the set.

Table 3. Variables used in the regression equations.

	Variable	Objective	Hypothesis	Definition	
Independent variable	RGR	All		Relative diameter growth rate (Fisher 1921)	
General site description	elevation	R		Elevation above sea level (m)	
	age	R		Year, separate for species	
	slope	R		Label	
	rainfall	R		Annual average (mm)	
	temperature	R		Annual average (°C)	
	site productivity	R		Average yield table volume growth over 100 years (m ³ ·ha ⁻¹ ·year ⁻¹)	
General stand description	measurement year	R		Initial year of growth period	
	initden	R		Precalibration relative stocking density	
	harvest	iii	1, 2, 3	No. of previous harvest operations	
	year of origin	R		Year of germination (by species)	
Stand conditions					
Density	gloverconci, gloverhdwpci	<i>i</i>	2	Glover and Hool's index, calculated for conifers and hardwoods, respectively	
	wconif, whdwd	<i>i</i>	2	Wycoff's index, calculated for conifers and hardwoods, respectively	
	ba	<i>i</i>	2	Basal area (m ² ·ha ⁻¹)	
	<i>n</i>	<i>i</i>	2	Tree density (trees·ha ⁻¹)	
	Pretreatment density	nbefore	<i>ii</i>	1	Trees per acre before harvesting operation
babefore		<i>ii</i>	1	Pretreatment basal area (m ² ·ha ⁻¹)	
Treatment intensity	perba	<i>ii</i>	2	Percent basal area removed	
	perN	<i>ii</i>	2	Percentage of trees removed	
	Lorcondiff	<i>ii</i>	2	Pretreatment minus posttreatment Lorimer's index	
Treatment type	<i>d/D</i>	<i>ii</i>	3	Quadratic mean diameter (qmd) of cut trees divided by pretreatment qmd (all species) for 16 m radius neighborhoods	
	Relative tree size	reldiam	<i>i</i>	Diameter of target tree divided by average tree diameter	
Neighborhood conditions	Initial density	lorconci, lorhwci	<i>i</i>	1	Lorimer's index at beginning of measurement period, for trees without previous harvesting in the last decade
	Posttreatment density	lorconpostci, lorhwpostci	<i>ii</i>	1	Lorimer's index after harvesting, calculated for hardwood and conifers, respectively
			<i>iii</i>	1	
	Pretreatment density	Lorconpreci, lorhwpreci	<i>ii</i>	2	Lorimer's index before harvesting, calculated for hardwood and conifers, respectively

Note: Variables were used in regression equations representing the listed objectives and hypotheses, as described in Table 1. R indicates variables with limited replications that were used solely in residual analyses.

As a measure of model fit, the AIC_c approach compares all models to a null model, whereby the model fit is indicated by the difference between the AIC_c value of model *i* and the AIC_c value of the null model. Thus, a null model was included in the set of models to determine the importance of tree interactions on relative growth rates. The null model stated that the relative growth rate was not a function of tree interactions but of the spatial autocorrelation (diameter growth of trees is similar because they are in the same vicinity), temporal correlation (diameter growth of trees is solely related to past diameter growth) among trees, and measurement year (see below). Correspondingly, no terms describing tree–tree interactions were included in the null models. Models with lower Δ_{*i*} values than the null model indicated that tree interactions were more important than other unmeasured factors (Anderson et al. 2001), such as random chance, genetic variation, and environmental hetero-

geneity (Welden and Slauson 1986). To provide another measure of goodness of fit a pseudo-*R*² was calculated as the proportion of variance explained by the best supported model versus the proportion of variance explained by the null model (Klienbaum et al. 1998).

An initial analysis of the data suggested a time trend that has been shown in several other studies in central Europe (e.g., Spiecker et al. 1996). During the 1980s and early 1990s, tree growth was better than the long-term average, presumably because of favorable environmental conditions. However, since the early 1990s tree growth has shown a decrease in southwestern Germany, even before the exceptional drought year of 2003 (Forest Research Institute of Baden-Württemberg, unpublished data). To account for this time effect, we added measurement year (time) as a quadratic fixed effect to all models. The residual analyses indicated that this fixed effect successfully removed the time trend in our data.

Results

Growth patterns in environments without recent density reductions

In mature silver fir dominated stands, both intraspecific and interspecific interactions within local neighborhoods were important determinants of silver fir growth. Models using neighborhood interaction indices consistently showed a superior fit than models based on stand-level indices (Table 4). A comparison of different neighborhood sizes suggested that a neighborhood within a 16 m radius of the target tree provided the best predictive power for diameter growth of individual trees. Concerns that these results may be an artifact of spatial autocorrelation appear unwarranted, as inclusion of terms accounting for spatial autocorrelation among trees did not influence model selection results.

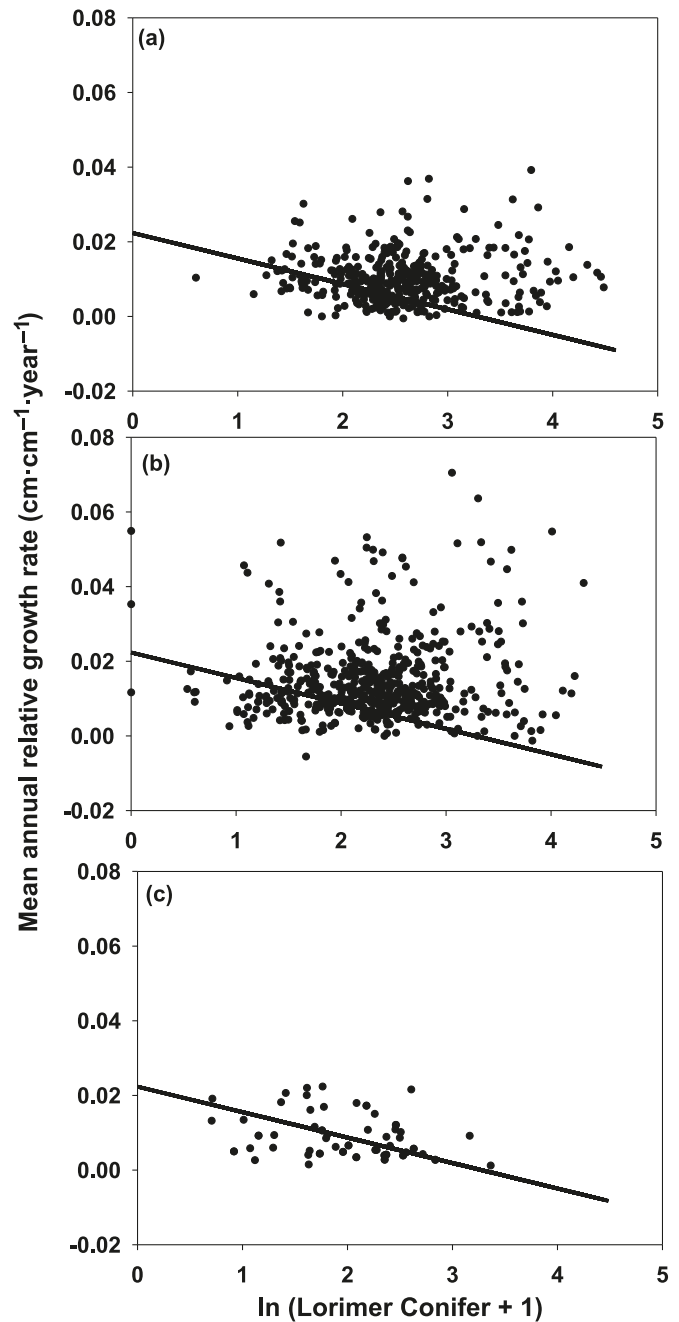
Models with a term for relative size had some support for being the best approximating model. However, models solely including terms describing neighborhood interactions had much greater support (pseudo- R^2 of the best model was 0.45). As expected, larger trees (in terms of diameter) had higher relative growth rates than smaller trees in higher density stands. Hardwood trees (European beech) were only present in a few installations, but where they were found, their presence reduced target tree growth to a greater degree than the presence of same-sized conifers.

Models containing stand-level indices (Wykoff's and Glover and Hool's) also received higher support than the null model (Table 4), suggesting that they can be useful indicators of growing conditions, if spatial information is not available to calculate neighborhood indices. Nonetheless, models for both stand-level indices had a weight of 0.01 or less, suggesting that tree growth is much better predicted based on neighborhood models.

Effects of density reductions on diameter growth

The hypothesis that current growing conditions are the only factors influencing tree growth suggests that equations developed for trees in untreated neighborhoods (Table 4) should also apply to trees in neighborhoods that have undergone harvesting operations, if Lorimer's index is calculated for postharvesting densities. However, trees responded to density reductions in the 16 m radius neighborhood with a release response that was larger than predicted by information about postreduction density alone (Fig. 3). Equations developed for predicting growth in stands that had previously been undisturbed for a decade consistently underpredicted growth for trees in stands after density reductions. This bias was less pronounced in the initial growth period after density reduction than in the second 5 year growth period (starting 4 to 6 years after the density reduction; Fig. 3). This release effect basically disappeared within a decade. Trees in the third growth period (9 to 14 years after harvest) were represented quite well by the equation that was developed from stands that had been undisturbed for at least a decade. Effectively acting as validation data set, the fit for trees in the third growth period after harvesting confirmed the generality of the best equations for objective *i*. It also supported our decision to use 10 years without harvest operations as a cutoff to determine whether trees were growing in environments not influenced by recent density reductions.

Fig. 3. Plots indicating that trees experienced a "release" effect beyond the effects of neighborhood densities. Equations developed to predict annual tree growth as a function of neighborhood conditions in stands without recent density reductions (trend line) generally underpredict growth of trees in neighborhoods of the same condition that experienced recent density reductions (*a*) during the initial measurement period, that is, from 0 or 1 year postharvest to 4, 5, or 6 year postharvest and (*b*) from 4 or 5 to 9 or 10 years postharvest. The release effect was not obvious in the growth period from 9 to 14 years postharvest (*c*).



Evidence for a possible release effect was also provided by the fact that pretreatment conditions and the degree of density reduction in the neighborhood of target trees were the most powerful indicators of relative growth rates during the initial release period (pseudo- R^2 of the best model was

Table 4. Statistics and parameter estimates of approximating models for objectives *i*, *ii*, and *iii*.

Objective	Model	AIC _c	Δ _i	w _i
<i>i</i>	RGR = 0.021644 - 0.00378 × lorconci16 - 0.00007 × time ²	-497.2	0	0.32
	RGR = 0.022245 - 0.00392 × lorconci16 - 0.00258 × lorhwci16 + 0.000532 × lorconci16 × lorhwci16 - 0.00006 × time ²	-496.9	0.37	0.27
	RGR = 0.04314 - 0.01365 × lorconci16 - 0.02113 × reldiam + 0.009881 × lorconci16 × reldiam - 0.00007 × time ²	-494.6	2.62	0.09
	RGR = 0.020433 - 0.00217 × wconif + 0.04117 × whdwd - 0.01129 × wconif × whdwd - 0.00007 × time ²	-490.0	7.20	0.01
	RGR = 0.01046 + 0.006543 × gloverconci - 0.00008 × time ²	-489.3	7.93	<0.01
	Null model ^{iv}	-481.3	15.96	<0.01
<i>ii</i>	RGR = 0.05367 - 0.01515 × nbefore16 - 0.02489 × babefore16 - 0.05831 × reldiam16 + 0.05257 × babefore16 × reldiam16 + 0.02322 × nbefore16 × reldiam16 + 0.01071 × nbefore16 × babefore16 - 0.0229 × nbefore16 × reldiam × babefore16 - 0.00004 × time ²	-3287.8	0	0.62
	RGR = 0.03065 - 0.0518 × nbefore16 - 0.01299 × reldiam16 + 0.003150 × nbefore16 × reldiam16 - 0.00004 × time ²	-3285.9	1.91	0.24
	RGR = 0.01494 + 0.03927 × percentbacut16 - 0.00288 × reldiam16 - 0.04141 × percentbacut16 × reldiam16 - 0.00003 × time ²	-3282.5	5.28	0.04
	RGR = 0.05175 - 0.05282 × lorcondiff16 - 0.04080 × reldiam16 + 0.05447 × lorcondiff16 × reldiam16 - 0.00003 × time ²	-3279.4	8.43	<0.01
	RGR = 0.01682 - 0.00116 × lorconpre16 - 0.00414 × lorhwpre16 + 0.001574 × lorconpre16 × lorhwpre16 - 0.00004 × time ²	-3276.1	11.66	<0.01
	RGR = 0.01682 + 0.000317 × lorconpost16 - 0.00131 × reldiam - 0.00173 × lorconpost16 × reldiam16 - 0.00004 × time ²	-3272.9	14.91	<0.01
<i>iii</i>	RGR = 0.01389 + 0.001932 × lorhwpost16 + 0.000506 × reldiam16 - 0.00396 × lorhwpost16 × reldiam16 - 0.00004 × time ²	-3269.4	18.34	<0.01
	Null model ^{iv}	-3112.2	34.89	<0.01
	RGR = 0.04946 - 0.04083 × wtlorconpostci16 + 0.002003 × wtlorhwpostci16 - 0.01665 × reldiam16 + 0.03455 × wtlorconpostci16 × reldiam16 - 0.00486 × wtlorhwpostci16 × reldiam16 + 0.009366 × wtlorconpostci16 × wtlorhwpostci16 - 0.00775 × wtlorconpostci16 × reldiam16 × wtlorhwci16 - 0.0016 × time ²	-1701.2	0	0.99
	RGR = 0.02409 + 0.005110 × wtba16 - 0.00682 × wtm16 - 0.00118 × reldiam16 + 0.003289 × wtba16 × wtm16 - 0.00248 × reldiam16 × wtba16 × wtm16 - 0.00551 × wtba16 × reldiam16 + 0.004073 × wtm16 × reldiam16 - 0.00012 × time ²	-1690.6	10.59	<0.01
	RGR = 0.02192 - 0.0123 × wperba16 + 0.006111 × wperba16 + 0.003052 × wperba16 × wperba16 - 0.00012 × time ²	-1674.7	26.50	<0.01
	RGR = 0.01873 + 0.001477 × wtharvest + 0.001853 × reldiam16 - 0.00178wtharvest × reldiam16 - 0.00013 × time ²	-1664.3	36.87	<0.01
Null model ^{iv}	RGR = 0.01561 + 0.003588 × harvest + 0.006938 × reldiam16 - 0.00534 × harvest × reldiam16 - 0.00012 × time ²	-1661.4	39.78	<0.01
	Null model ^{iv}	-1647.5	53.73	<0.01

Note: Only the best approximating models, the null model, and best model for a given hypothesis are presented. Models with the lowest corrected Akaike information criterion (AIC_c) and Δ_i (difference between model AIC_c and minimum AIC_c) have the highest support from the data. The weight (w_i) provides information about the likelihood (from 0 to 1, with 1 being the highest likelihood) that model *i* is the best supported model in the set. Variables are described in Table 3. A “wt” at the beginning of a variable name indicates that the variable was weighted (first harvest, 1; second harvest entry, 2; and so on). A number at the end of a variable name indicates the radius (m) of the neighborhood that was used to calculate the variable. Variables without a number were calculated based on the whole treatment plot.

^{iv}Null model stated that relative growth rate was not a function of tree interactions but solely the spatial and temporal correlation among trees and a quadratic function of the measurement year (time²).

0.23). Rather than variables reflecting current neighborhood conditions, pretreatment densities and reduction in basal area and tree density were prevalent in the best fitting equations (Table 4). In contrast to stands without density reductions, trees with smaller initial sizes showed greater relative diameter growth responses to density reductions than larger trees.

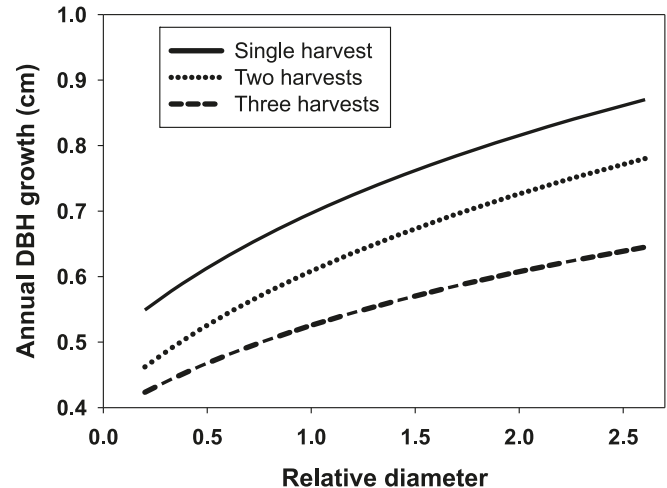
Effects of multiple density reductions on diameter growth

In stands receiving multiple density reductions treatments, growth performance was by far best predicted by the additive, weighted intensity of tree removal expressed as Lorimer's index within the 16 m radius neighborhood (pseudo- R^2 was 0.47). Our weighting scheme placed the most weight on the latest density reduction, while earlier density reductions were still influential, but their relative importance diminished linearly with the number of subsequent harvesting operations. These results suggest that previous conditions are still influential after multiple density reductions, even when stand density changed repeatedly and dramatically during those years. The equations for objective *iii* in Table 4 suggest that in stands with less intense density reductions over time, larger trees responded better than smaller trees. On the other hand, in stands with heavier density reductions smaller trees showed a stronger response in relative diameter growth, supporting the findings regarding objectives *i* and *ii*. For visualization of the impact of multiple harvests, Fig. 4 presents absolute growth over relative tree size for trees after the first, second, and third density reduction.

Discussion

Our findings lend further support to the notion that even at older ages conifers may be responsive to density reductions — a phenomenon well established and exploited for management of European beech (von Teuffel and Hein 2004). The results of an earlier analysis of preliminary data from the same study sites indicate similar findings for silver fir as well as for Norway spruce (Weise 1995, 1996). Schmitt (1994) even suggested that overstory release through harvesting operations that removed overtopping of suppressed Norway spruce may result in a shift in growth patterns. In particular, he suggested that the culmination of diameter increment may be delayed for such trees. Even in previously unmanaged stands, long-term growth responses to density reductions were also documented in approximately one-century-old stands of white spruce (*Picea glauca* (Moench) Voss) (Youngblood 1991), white pine (*Pinus strobus* L.) stands (Bebber et al. 2004), and Douglas-fir stands (Williamson 1982). Investigations in Douglas-fir old-growth stands ranging from 158 to 650 years old showed that two-thirds of the trees responded positively to density reductions, and only a few trees (about 1%) showed growth declines (Latham and Tappeiner 2002). Our results suggest that patterns of density reductions during the regeneration phase may have a substantial influence on growth patterns of the residual trees. This finding is of special economic interest in stands where ownership objectives have resulted in adoption of practices with longer regeneration periods. These implications support the empirically developed traditional propensity of forest practitioners in southwestern Germany

Fig. 4. Visualization of the impact of multiple harvest operations. Annual DBH growth for a 5 year period was simulated for a tree with an initial DBH of 40 cm. Harvest intensities for the first, second, and third entries used mean values for the data set. Note that the y axis presents absolute diameter growth, and simulating growth for a tree of 40 cm DBH implies that the tree has a more dominant position as relative diameter increases.



and Switzerland to favor long-term regeneration regimes, particularly in the management of stands with silver fir (e.g., Kenk and Guehne 2001). However, it must be kept in mind that our and the other cited studies based their conclusions on diameter increment, rather than volume growth, thus ignoring any potential change in tree taper.

Evidence is mounting that tree interactions are a spatially explicit process (e.g., Wagner and Radosevich 1998; D'Amato and Puettmann 2004; Roberts and Harrington 2008). In contrast to even-aged, even-spaced stands, the spatial variability in growing conditions within stands with high spatial variability renders stand-level indices less suitable for predicting growth of individual trees (Bigging and Dobbertin 1995). Furthermore, relevant scales at which neighborhood interactions influence tree growth increase with tree size from a few centimetres for seedlings (Wagner and Radosevich 1998; Hofmann and Ammer 2008) to 5–10 m for saplings (D'Amato and Puettmann 2004; Roberts and Harrington 2008) to more than 15 m for adult trees (D'Amato and Puettmann 2004), corresponding with the lateral extension of crowns and root systems.

The documentation of a “release effect” suggests that growth simulators that model density reductions simply by predicting tree growth at lower densities will underpredict diameter growth in stands after harvests. Similar release responses were documented in younger Douglas-fir stands in neighborhoods that varied in density as a result of variable density thinning (Roberts and Harrington 2008) and in fairly evenly spaced, homogenous stands (Hann et al. 2003). The release effect was greater with a higher proportion of basal area removed (Wang 1990) and with a lower d/D ratio (i.e., ratio of diameter of trees removed to diameter of the trees before harvesting). Furthermore, Yue et al. (2008) demonstrate that relative growth ratios of trees in age-class type stands of Norway spruce are governed by the trees' diameter rank as well as by stand density.

We did not have an annual resolution of tree growth to investigate the adjustment period in more detail. However, in contrast to our study, where the release effect was most evident 5 to 10 years postharvest, the release effect in young Douglas-fir stands declined in an exponential function over time (Hann et al. 2003). In all instances where a release effect was documented, it practically disappeared within a decade. Hypotheses supporting such an effect include a preferential removal of damaged trees in harvesting operations, higher crown length after thinning (when compared with trees in unthinned stands), and increased soil moisture and nutrient availability due to dynamic responses of the fine-root systems and root grafting, which would allow stomata to remain open longer during the day (Hann et al. 2003; Sala et al. 2005).

The high support for models including pretreatment conditions confirms that previous growing conditions and thus previous growth rates have a lingering effect after harvesting or disturbances (Fraver and White 2005). For most harvesting intensities, smaller trees responded with higher relative growth rates (and higher increases in absolute growth; data not shown) to density reductions than larger trees. These findings support the relative dominance hypothesis (D'Amato and Puettmann 2004), which predicts that growth of larger, dominant trees is less influenced by neighborhood conditions than growth of smaller trees. For direct comparison with other findings (e.g., Weise 1995; Simard et al. 2004), it must be noted that in our study, such as in Yue et al. (2008), we calculated relative growth rate, which accounts for differences in initial size. Especially in stands with a history of density management, even the smaller trees apparently have sufficient leaf area to be able to respond to increased light, moisture, and nutrient levels. However, at higher density reduction levels the differences due to initial size diminish (see also absolute diameter growth rate in Simard et al. 2004). At low stand densities, smaller trees tend to exhibit higher relative growth rates. (Yue et al. 2008). However, at extremely high thinning intensities, smaller trees can suffer a thinning shock potentially resulting from an initial loss in foliage owing to desiccation of needles (Harrington and Reukema 1983).

Postharvest growth reductions are not solely limited to smaller trees, as following intensive thinning or reproduction harvests temporary growth reductions in large trees has also been documented. For example, small-sized trees responded more rapidly to thinning, whereas medium- to large-sized trees suffered reductions in diameter growth following heavy reductions in stand density in single-tree-selection forests in southwestern Germany (Spiecker 1986). Reasons for this pattern may include increased transpirational stress, physiological adaptation of leaves or needles to high radiation levels, or problems with sunscald in more open settings (Tucker et al. 1987; Skov et al. 2004). Carbon allocation patterns may be at least partially responsible for a slow or negative response of tree diameter growth to abrupt reductions in stand density (Lacointe 2000). Under intense competition, trees will have allocated proportionally less carbon to roots and reserves, as reflected in lower root-to-shoot ratios of suppressed trees when compared with those of dominant trees (e.g., Bolte et al. 2004). Increased carbon allocation to structural roots may also result from the in-

creased wind loading and swaying of trees following density reductions (Urban et al. 1994).

The trend of smaller growth responses in stands that had been thinned previously has also been documented in young Douglas-fir stands after two (Roberts and Harrington 2008) or more thinning events (Hann et al. 2003). However, any direct evaluation of the impact of multiple harvest entries needs to be viewed with caution, as many factors will vary simultaneously among the first versus the second or third entries. For example, for the purpose of visualization of our results (Fig. 4), preharvesting stand densities, tree age, and tree sizes were kept constant.

Overall, our study suggests that reproduction harvests can have a considerable impact on growth patterns of residual trees and thus on economic evaluation of harvesting practices. Where retained trees have long, branch-free boles, are free of defects, and do not develop epicormic branches following harvesting, the additional increment is likely to produce timber of high value. Our results suggest that heavier stand reductions in mature stands would result in reduced growth response of the residual trees. Thus, for optimal growth of the residual stand, heavy density reductions should be avoided in older stands, especially if the stand includes numerous trees that were suppressed prior to harvesting. This recommendation is of special importance in instances where regeneration periods make up to a quarter or more of the production period or rotation. Also, our findings suggest that the clear distinction between intermediate stand treatments, such as thinnings and reproduction harvests, typically found in silviculture textbooks is not warranted when using extended regeneration periods. Instead, our findings suggest a need for an integrated approach to reproduction harvests that addresses residual tree growth and seedling establishment patterns simultaneously.

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