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Analysis of radial growth responses to changes in stand density for four tree species

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Abstract

Enhancement of radial-growth by reducing stand density is a common silvicultural practice. Traditional methods of analysis based on stand level variables, such as stand mean diameters, overestimate the effects of reduced density on radial-growth due to 'technical growth', i.e. increases in the mean diameter caused by the thinning operation itself through removal of small trees. A new method for analyzing radial-growth responses in forest stands based on samples of the largest trees within populations is proposed, and the hypotheses tested that: (1) reducing stand density enhances radial-growth; (2) radial-growth response varies with site and changes with the release period, i.e. the period of time after thinning; (3) radial-growth response varies among tree species. Based on studies of *Picea abies* (L.) Karst. it is suggested that water supply influences radial-growth responses significantly. Tree species differ greatly in their ability to enhance radial-growth when stand density is reduced. For *Pinus sylvestris* L. and *Acer pseudoplatanus* L. the responses are very limited. *P. abies* (L.) Karst. showed the greatest response to thinning while *Fagus sylvatica* L. showed an intermediate response. These differences may be ascribed to differences in strengths of intraspecific competition, strategies of photosynthate allocation or inherent growth inertia. The method of analysis applied in this study can be used to quantify radial-growth responses of tree species relative to the length of release periods and site.

Keywords: Optimal stocking; Density management; Competition; Radial growth; Dendrometry; Thinning; *Picea abies* (L.) Karst.; *Fagus sylvatica* L.; *Pinus sylvestris* L.; *Acer pseudoplatanus* L.

1. Introduction

Competition is now considered the primary pattern of interaction among tree species (Oliver and Larson, 1996), and thinning is widely carried out to minimize the slowing of growth of individual stems that follows from increasing competition among trees as they become bigger (Sheriff, 1996). Thus, objectives of controlling forest stand density include: optimizing the yield of merchantable timber volume by reductions in stand density that enhance diameter growth (Smith et al., 1997), and controlling stand stability through height–diameter ratios (Wilson and Oliver, 2000; Wonn and O'Hara, 2001). However, objectives are usually a compromise between maximum volume production and maximum individual tree growth (Long, 1996), and between maximum individual tree growth and wood quality properties such as wood density (Danborg, 1994; Cameron, 2002). Responses to reduced stand density have been carefully examined in even-aged monospecific forest stands, but plant

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growth has usually been studied at the level of the population or of the average individual including variables such as stand volume production, stand mean diameter and stand basal area (Stoll et al., 1994). However, applying mean tree variables when comparing artificially thinned forest stands may veil important information and result in misinterpretation, because they are a mix of biological and mathematical properties. When forest stands are thinned through removal of the small or suppressed trees, referred to as thinning from below (Nyland, 1996; Smith et al., 1997), the mean diameter increases immediately, not because competition is reduced or resources are more readily available, but simply because trees below the mean are removed and therefore the mean diameter after thinning is greater than before thinning. This has been referred to as 'technical growth', cf. Montero et al. (2001). To uncover responses to silvicultural treatments, measures that are biologically interpretable, and studies of the growth of individuals within populations are needed (Stoll et al., 1994). Ideally, for such purposes a density measure for individual trees that accounts for distances to neighboring trees and their size, e.g. Johann (1993), should be used. However, such density measures require information on tree stem positions, which are rarely available in research data. The distribution of sizes within a population has been applied as a statistical bridge between individual- and population-level results (Knox et al., 1989). In the case of radial-growth responses to thinning, distributions of diameters are shifted upwards as a result of reduced density. Comparison of distributions from unthinned populations with those of thinned populations may reveal information on radial-growth responses to density. In the case of thinning from below the largest cohorts of trees are not directly influenced by the thinning operation itself. Hence, the cohorts of largest trees in thinned and unthinned forest stands are comparable and differences between them can be ascribed to reductions in stand density. The need for biologically meaningful measures is underscored by the current trend towards continuous cover forestry or uneven-aged forestry, cf. Kerr (1999), Christensen and Emborg (1996), Schütz (1999) and O'Hara (2001). These silvicultural systems tend to require a stronger focus on individual trees, and density management in mixed-species and uneven-aged stands presents a more complex challenge than that of single species and even-aged stands (Long and Daniel, 1990; O'Hara et al., 2001). It is possible, however, that from analysis of growth responses in even-aged monospecific stands, valuable information on site–species and growth–density interactions can be extracted—provided that the method of analysis is biologically meaningful. The purpose of this paper is to reframe a classic question in silviculture in terms of ecology and to test a new method of analysis. The following hypotheses are investigated: (1) reducing stand density enhances radial-growth; (2) the extent of the radial-growth response varies with site, age and the period of release, i.e. the period of time after reducing stand density; (3) the radial-growth responses to density are tree species dependent.

2. Material and methods

2.1. Study area

Data were compiled from seven thinning experiments including a total of 51 permanent plots in Denmark, between 54°37′N–56°48′N and 9°20′E–12°18′E. Experiments are located at elevations of 0–150 m. Precipitation for the entire study area ranges from 500 to 850 mm per year and 300 to 450 mm in the growing season (May–September) (Sundberg et al., 1999). Mean annual temperature is 8 °C, with a monthly average minimum of 0 °C and an average maximum of 16 °C. Average plot size varied between 0.18 and 0.24 ha and periods of observation were in the range of 20–60 years (Table 1). The topography is generally flat with slopes <10%.

The site quality varied among experiments (Table 1). Generally site quality in terms of nutrient status and water holding capacity is low at experiment Picea3, Pinus1, intermediate–high at Picea1, Fagus1 and high at Picea2, Acer1 and Acer2.

2.2. Treatments

Each thinning experiment comprises one or more unthinned plots and two or more plots with stand density reduced, thinned, to different levels. Reductions in stand density were done by relative basal area, i.e. basal area relative to the unthinned plot (Nyland, 1996; Smith et al., 1997). Thus, the unthinned plots

Table 1
General information about the experiments[a]

Record ID at DFLRI[b]	Experiment number	Number of plots	Initial density (m^2/ha)	Average plot size (ha)	First observation, age (years)	Most recent observation, age (years)	Site description[c]
P. abies (L.) Karst.							
IS	Picea3	20	25.6	0.21	44	104	Sandy soil (acc = 1–2%), well drained
KO	Picea1	4	28.2	0.24	21	54	Sandy loam (acc = 8%), well drained
KI-KK	Picea2	8	21.6, 24.8	0.18	19	51	Clay loam (acc = 25%), water-logged with gley
F. sylvatica L.							
EB	Fagus1	4	20.8	0.2	21	55	Sandy loam (acc = 20%), well drained but with a few low wet areas
A. pseudoplatanus L.							
LZ	Acer1	4	20.0	0.21	18	44	Clay loam (acc = 20%), occasional water-logging
L@	Acer2	3	13.6	0.23	17	37	Clay loam (acc = 20%), occasional water-logging
P. sylvestris L.							
SG	Pinus1	8	25.9, 24.5	0.24	26	58	Sandy soil (acc = 1–2%), well drained

[a] Experiments Picea2 and Pinus1 have four different density levels with two plots for each density. The remaining experiments have one plot for each density level, including Picea3, which has a range of 20 different density levels.

[b] Danish Forest and Landscape Research Institute.

[c] acc: average clay content.

have 100% relative basal area and thinnings generally reduced densities to approximately 85, 65 and 50% relative basal area. Densities at experiment establishment varied from 13.6 to 28.2 m^2 basal area per hectare for the unthinned plots (Table 1) and stand densities for the other plots were reduced relative to their respective unthinned plots every fourth year. Thus, densities were reduced successively to the initially determined relative density. Plots were measured at every thinning incidence, and diameters of all trees were determined by cross-calipering to the nearest millimeter. Thinnings were conducted from below, i.e. removal of small trees. In the initial thinnings some dominant trees of low quality, e.g. due to crooked stems or branchiness were also removed. Experiments were considered to be homogenous in terms of site quality and trees were distributed regularly within the individual plot areas.

2.3. Analyses

2.3.1. The independent variable: density-competition

Competition in single species populations of plants is a function of the density and the mean plant size, and relations between density and mean plant size have been intensely studied to determine what should constitute maximum density (Reineke, 1933; Yoda et al., 1963; Westoby, 1984; Zeide, 1995). However, in even-aged forest stands, of similar height with little or no site variation between plots, the relative strength of competition largely depends on the number of trees present within a given area (Barnes et al., 1998, p. 387). However, as trees grow the area needed to maintain growth increases, and consequently the area available to individual trees should be determined relative to the size of the tree. In this study, the strength of competition is described as the average growing area available per tree relative to tree size represented by the dominant stand height, see also Handler (1984), Henriksen (1988), Jack and Long (1991) and Avery and Burkhart (1994):

$$\mathrm{RTD}\,(\%) = \frac{\sqrt{10.000/N}}{H_{100}} \times 100 \qquad (1)$$

where RTD is the relative tree distance, 10.000 correspond to the area of 1 ha in m^2, N the number of trees/ha, H_{100} the stand height (determined as height of the largest 100 trees/ha).

2.3.2. A meaningful growth-response variable: limiting the sample

Since stand mean values are biased by ‘techncal growth’, a sample should be identified that is biologically meaningful and unbiased. As stated above, the cohorts of largest trees within populations are not affected by the thinning operation, provided that thinning is conducted from below. Therefore, it is suggested that the samples are drawn from the cohorts of largest trees and that it is limited in absolute terms, i.e. the sample size should be the same disregarding the size of the population from which it was sampled. When determining the sample size the number of trees that are left in the thinned stand can be compared with the same number of largest trees in the unthinned stand. Differences in mean diameter of these two cohorts would be the result of reduced stand density. Thus, $D_{L\chi}$ is a meaningful response variable, where $D_{L\chi}$ is the arithmetic mean diameter of the largest trees in the stand and χ denotes the number of trees included in the sample. In a preliminary study 150, 200, 250 and 300 of the largest trees per hectare were included in the calculations. Meanwhile, in some plots, particularly in the case of heavily thinned old plots, these stem numbers exceeded the actual number of trees per hectare and in those cases the plots were excluded from the calculation. However, the number of trees included in the calculations was found not to influence the results significantly, which suggests that the number of trees included in the analysis (within this range) is not important. What is important is that the number of trees included is the same for all plots, and that they are sampled from the largest cohort of trees. Other studies have concentrated analysis on the largest 100–250 trees/ha to avoid influence from suppressed trees, e.g. see Reukema (1979) and Wilson and Oliver (2000). To increase the course of time where the radial-growth responses can be calculated D_{L150} values (arithmetic mean diameter of the largest 150 trees) are used in the analysis. For each plot all diameters were rounded to the nearest centimeter, and D_{L150} values were calculated for each plot by per-hectare expansion factors because all plots were less than one hectare. For each experiment plot values of D_{L150} were plotted against their respective RTD, and the slope and intercept of a linear model (2) were calculated for each experiment (based on all plots in that experiment):

$$D_{L150} = \alpha + \beta(\text{RTD}) \qquad (2)$$

The slope β of this line is a measure of the radial-growth response to reductions in stand density, i.e. improved resource availability. However, β is likely to change with site quality, reflecting site–tree species interactions, and with the release period. Thus, β reflects competition history and disturbances of the stands, expressing the cumulative diameter response to changes in stand density.

All analyses were conducted in SAS using the general linear models (GLM) and frequency (FREQ) procedures (SAS, 1989a,b).

3. Results

3.1. *Reducing stand density enhances radial-growth*

Comparing diameter-distributions of plots within experiments (Figs. 1A–C and 2A–D) shows that the tree species in this study, at the respective tested sites, are capable of enhancing radial-growth when density is reduced, i.e. to some extent the distributions of diameters are shifted upwards. However, the distributions of diameters of experiment Acer2 indicate very limited responses.

The β values calculated are in agreement with what would be expected from a qualitative analysis of distributions of diameters. β values between 0.02 and 0.84 were calculated. The response variable D_{L150} against RTD showed strong linear relationships, generally with R^2 around 0.90 (Table 2). In addition, large plots (0.18–0.24 ha) and complete enumeration reduce the influence of random errors.

3.2. *Radial-growth responses varies with release period and site quality*

For experiments Picea1, Picea2 and Picea3, β values were calculated at three ages each (Picea1 at 33, 41 and 54 years; Picea2 at 32, 40 and 51 years; Picea3 at 69, 82 and 90 years). The three ages for each experiment were selected to allow comparison among experiments with regard to development of dominant stand height and release periods. In experiment Picea3 stand development was delayed due to severe frost die back. The β values varied greatly with the length of the release period for *Picea abies* (L.) Karst. Values of β are in the range of 0.34–0.84 (age 33–54), 0.30–0.53 (age 32–51) and 0.51–0.69 (age 69–90) for experiment

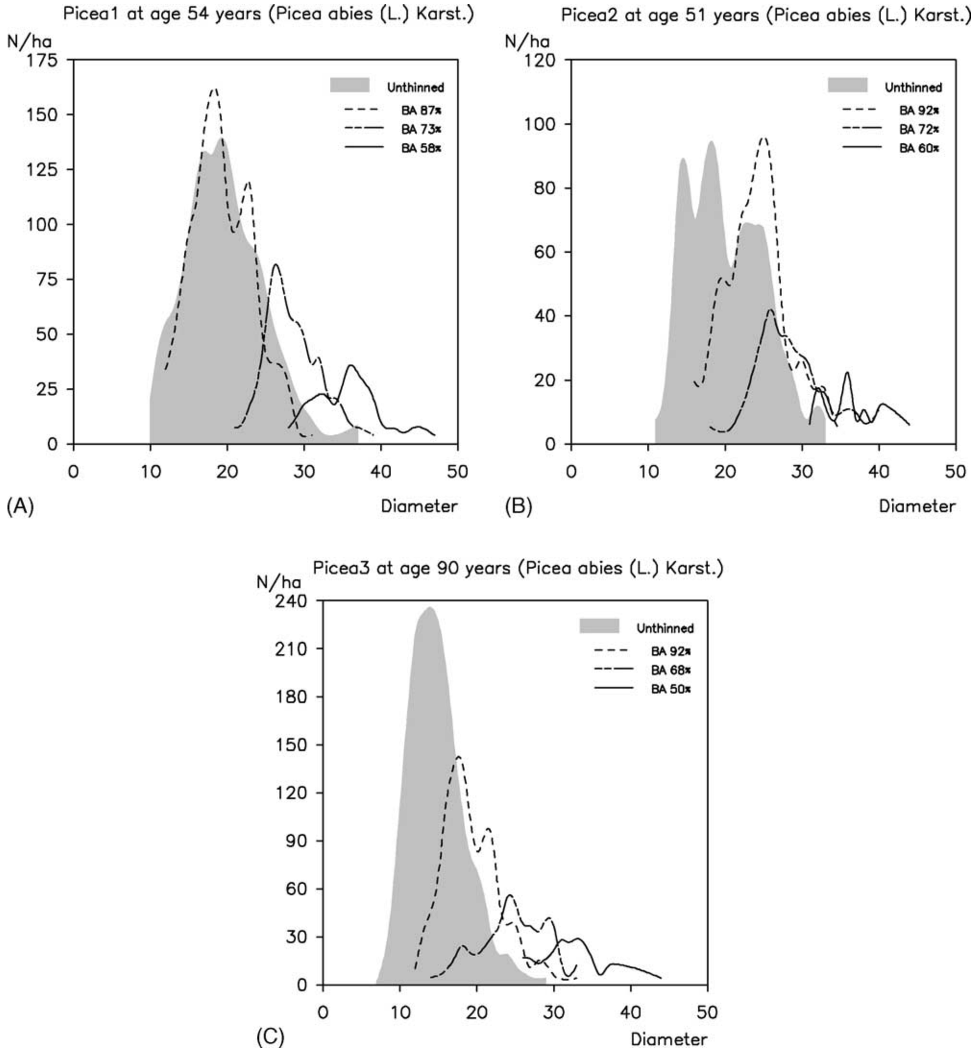

Fig. 1. Number of trees distributed to diameter classes at four different thinning intensities for each of the three experiments in *P. abies* (L.) Karst. BA (%) denotes basal area relative to the unthinned plot after thinning. Diameter classes are defined at 1 cm intervals, but data are shown as curve fitted lines instead of histograms to make interpretation easier. (A) Picea1 age 54: basal area of unthinned plot, 52.6 m^2/ha. (B) Picea2 age 51: basal area of unthinned plots, 35.1 (53.6) and 37.5 m^2/ha (49.15). (C) Picea3 age 90: basal area of unthinned plot, 36.5 m^2/ha (44.1). Note that the unthinned plots of Picea2 and Picea3 had partly disintegrated at this point and numbers in parentheses are the maximum densities for these plots.

Picea1, Picea2 and Picea3, respectively (Fig. 3A–I and Table 2).

The β values of Picea2 (age 32) and Picea1 (age 33) represent the accumulated diameter response approximately 14–15 years after the first thinning, whereas Picea3 (age 69) is 25–26 years after the first thinning. From this period to the next, i.e. Picea2 (age 40), Picea1 (age 41) and Picea3 (age 82), β values increased significantly for all three experiments. However, from the second to the third period, i.e. Picea2 (age 51), Picea1 (age 54) and Picea3 (age 90), only experiment Picea1 continues to increase its β value. Experiments Picea2 and Picea3 show slightly reduced values of β, but remain at a similar level.

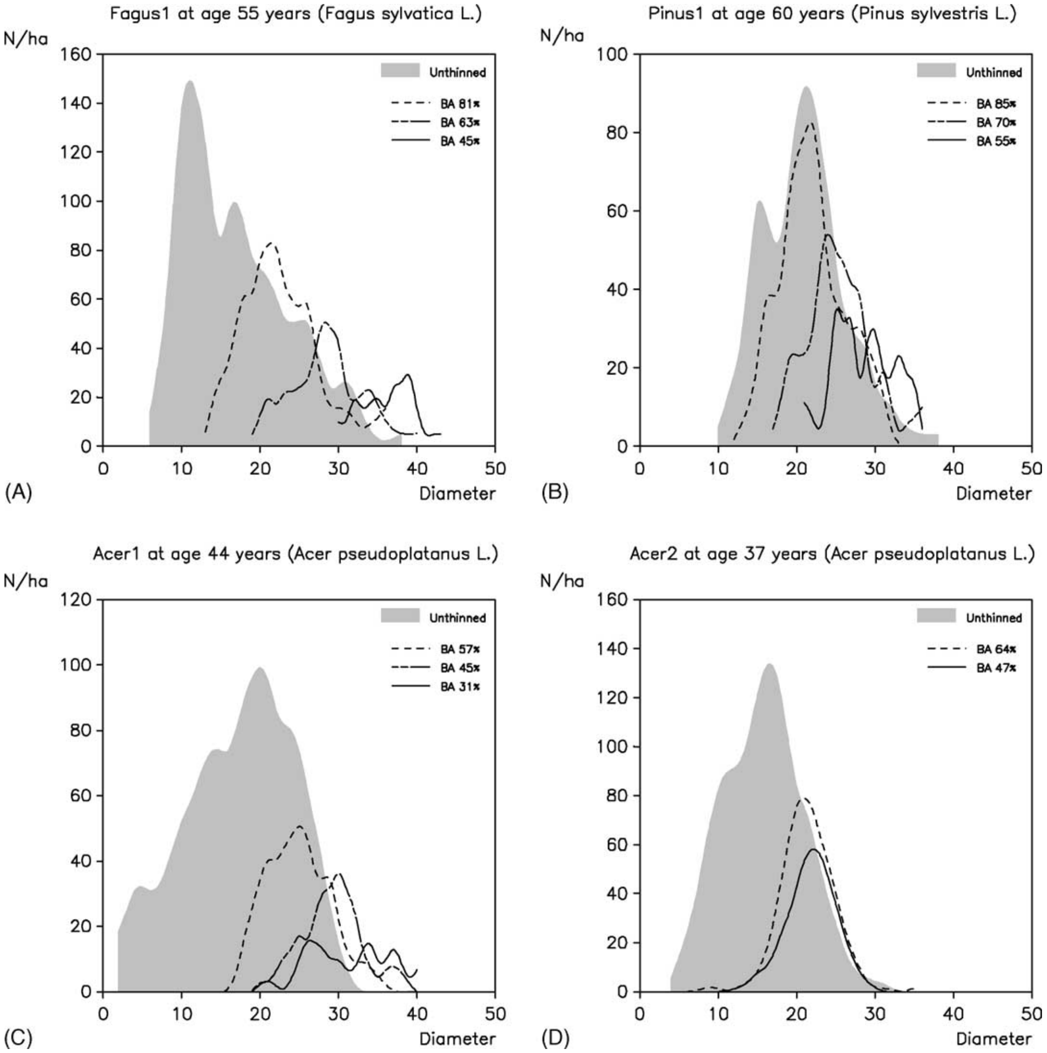

Fig. 2. Number of trees distributed to diameter classes at different thinning intensities for Pinus1, Fagus1, Acer2 and Acer1 thinning experiments in *P. sylvestris* L., *F. sylvatica* L., *A. pseudoplatanus* L. and *A. pseudoplatanus* L., respectively. BA (%) denotes basal area relative to the unthinned plot after thinning. Diameter classes are defined at 1 cm intervals, but data are shown as curve fitted lines instead of histograms to make interpretation easier. (A) Pinus1 age 60: basal area of unthinned plot, 36.7 m^2/ha. (B) Fagus1 age 55: basal area of unthinned plot, 47.1 m^2/ha. (C) Acer2 age 37: basal area of unthinned plot, 35.8 m^2/ha. (D) Acer2 age 44: basal area of unthinned plot, 46.2 m^2/ha.

3.3. Radial-growth responses varies among tree species

Comparison of β values among tree species can only be done comparatively to the length of the release period. However, even considering release periods it is clear that *P. abies* (L.) Karst. has higher β values at all sites than the other tree species. *Fagus sylvatica* L. at experiment Fagus1 (until the age of 55) produced a β value of 0.54 slightly below *P. abies* (L.) Karst. at the site of the Picea1 experiment, but at the level of the Picea2 site (similar ages). The impression of limited radial-growth responses to density in *Pinus sylvestris* L. (Fig. 2B) agrees with the β value of 0.27 (Fig. 4B). For *Acer pseudoplatanus* L. the radial-growth responses to density are very

Table 2
Linear regressions of radial-growth responses to density according to model (2) ($D_{L150} = \alpha + \beta(\mathrm{RTD})$) dependent variable is D_{L150} (mean diameter of the 150 largest trees) and independent variable is RTD (average distance between trees relative to dominant stand height)[a]

Tree species	Experiment number	Age	n	Estimate, β	$S_{y/x}$	R^2	P
P. abies (L.) Karst.	Picea1	33	4	0.3431	0.0620	0.939	0.0312
P. abies (L.) Karst.	Picea1	41	4	0.5922	0.1199	0.924	0.0387
P. abies (L.) Karst.	Picea1	54	4	0.8355	0.1817	0.914	0.0442
P. abies (L.) Karst.	Picea2	32	8	0.3034	0.1058	0.578	0.0285
P. abies (L.) Karst.	Picea2	40	8	0.5803	0.0644	0.931	0.0001
P. abies (L.) Karst.	Picea2	51	6	0.5250	0.0778	0.919	0.0025
P. abies (L.) Karst.	Picea3	69	17	0.5109	0.0365	0.929	<0.0001
P. abies (L.) Karst.	Picea3	82	20	0.7314	0.0473	0.930	<0.0001
P. abies (L.) Karst.	Picea3	90	19	0.6858	0.0739	0.835	<0.0001
F. sylvatica L.	Fagus1	55	4	0.5444	0.1250	0.905	0.0489
A. pseudoplatanus L.	Acer2	37	3	0.0023	0.0364	0.004	0.9605
A. pseudoplatanus L.	Acer1	44	4	0.1545	0.0350	0.907	0.0477
P. sylvestris L.	Pinus1	60	8	0.2745	0.0411	0.881	0.0005

[a] The estimate for β is proposed as a measure of radial-growth responses; β values are calculated for each experiment at the specified age; n is the number of plots from each experiment included in the calculation, i.e. number of observations. $S_{y/x}$ is the standard error of the estimate, R^2 the percent of the variation in β that is associated with density (RTD). P is the level of significance.

limited with β values of 0.15 for experiment Acer1 and 0.02 for experiment Acer2 (Fig. 4C and D, respectively).

4. Discussion

4.1. Site–species interactions

Comparison of Picea1 (medium–high productivity) to Picea3 (low productivity), in terms of β values, indicate that there is a positive influence of site productivity on radial-growth responses to changes in density. However, the relatively high β value of experiment Picea3 (low productivity) and the lower β value of Picea2 (high productivity) suggest that radial-growth responses are determined by other site–tree species interactions as well. Experiment Picea2 is located at a highly productive site, which however is subject to occasional waterlogging. Tree roots develop less well in wet soils such as gleys (Cameron, 2002) potentially causing water-stress that may cause stomata to close thereby stopping xylem production (Kozlowski and Pallardy, 1997). Consequently, waterlogged or gley soils may be the cause of poor radial-growth responses to changes in stand density, see also Skovsgaard (1997), because root development is restricted by anaerobic conditions rather than resource availability in terms of nutrients.

4.2. Influence from the length of the release period

The influence of successive reductions in stand density (approximately 4-year thinning intervals) is clearly seen (Fig. 3A–I), i.e. there is generally an increase in β. However, there is a slight reduction in β from Picea3 age 82–90 and from Picea2 age 40–51. This means that within these last growth periods the absolute growth rate of the 150 largest trees has been approximately the same independent of density. The explanation for this observation may be that the radial-growth responses to reduced density decreases with age or that there is a size related decrease in growth. As stated by Schwinning and Weiner (1998) plant growth, even in the absence of competition, is sigmoidal, and this means that the relative growth rate of plants decreases with size. Therefore, the absolute growth rates determining β could be changing as a result of differences in size rather than a decreased ability to respond to reductions in density with age. This is supported by the observation that slopes changed positively and significantly in experiment Picea3 from age 69–82, and changes were comparable to changes in experiment Picea2 from age 32–40.

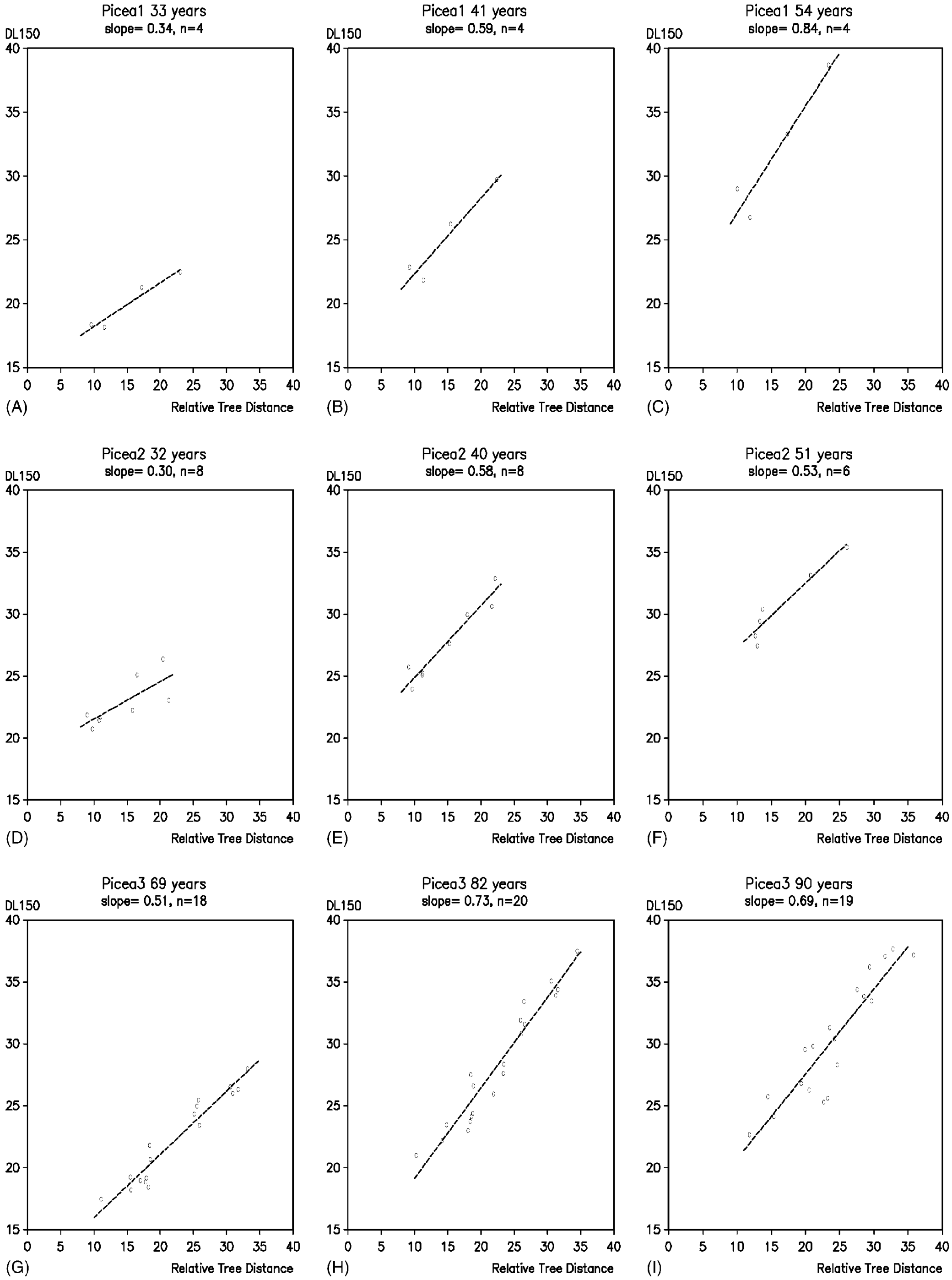

Fig. 3. Mean diameter of the largest 150 trees (D_{L150}) versus RTD after thinning shown for each plot (n) in three experiments (Picea1, Picea2 and Picea3). For each experiment the development over time is shown; reflecting successive thinning at 4-year intervals. Differences in the number of plots included in the calculations are due to stem numbers being lower than 150 (Picea2), and that not all plots were measured the same year (Picea3). c denotes plot values of D_{L150} at different densities and (- - -) are the fitted lines from linear regressions (summary statistics in Table 2).

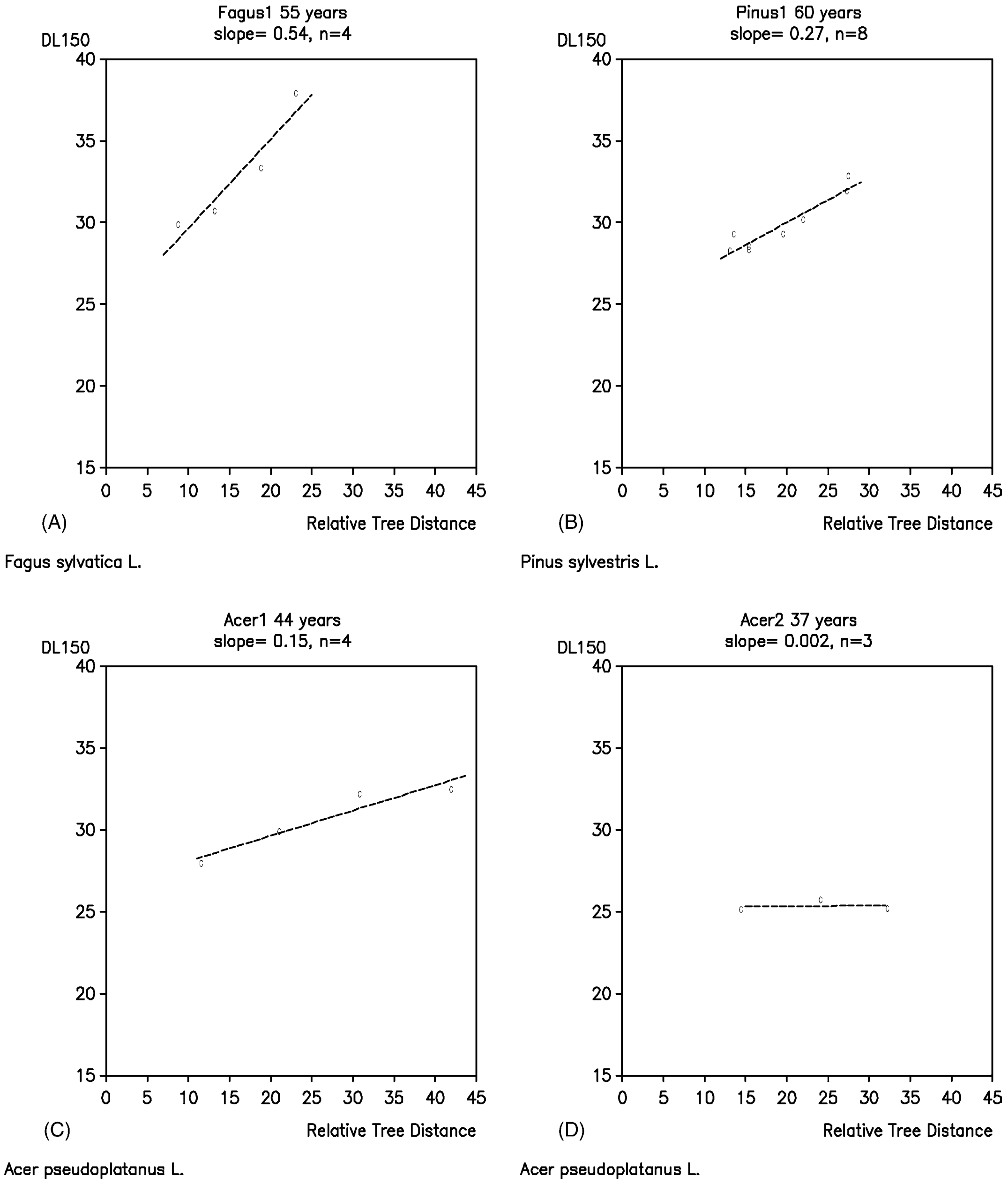

Fig. 4. Mean diameter of the largest 150 trees (D_{L150}) versus RTD after thinning shown for each plot (n) in four experiments (Pinus1, Fagus1, Acer2 and Acer1). c denotes plot values of D_{L150} at different densities and (- - -) are the fitted lines from linear regressions (summary statistics in Table 2).

4.3. Variation in radial-growth responses among tree species

This study shows that radial-growth responses resulting from thinning forest stands varies greatly among tree species. *P. abies* (L.) Karst. showed significant responses to reductions in density and *F. sylvatica* L. showed intermediate responses. However, for the tree species *A. pseudoplatanus* L. and *P. sylvestris* L. the enhancement of radial-growth was very limited. These differences may be attributed to one or more of the following:

1. If competition is very weak before thinning, then decreasing the density will have no or little effect because tree growth is not limited by competition.
2. It could be that tree species have different strategies of photosynthate allocation. Stem wood growth may have greater relative priority in some tree species compared to others and vice versa. Therefore, even tree species that show limited radial-growth responses may in effect increase resource uptake as density is reduced. However, because resources are allocated elsewhere, e.g. roots or foliage, the response in radial-growth is very limited. Differences among species in terms of competition-allocation strategies has been reported in other studies, e.g. Latham (1992), Cannel and Dewar (1994) and Orwig and Abrams (1997).
3. The trees would have shown greater radial-growth if they had grown at the lower density from the beginning, but a sort of ‘‘growth inertia’’ or ‘‘growth memory’’ means that they cannot respond to reductions in density. The amount of foliage and the size of the root system at a given time may condition the growth through an extended period of time.

Weak intraspecific competition, i.e. competition within species, may be part of the explanation for the results of Acer1 and particularly Acer2, however, for both experiments β values are calculated after the onset of natural mortality in the unthinned stands with basal areas of 46.2 and 35.8 m^2/ha, respectively. For Pinus1 the unthinned plots had basal areas of 36.7 and 36.5 m^2/ha with natural mortality corresponding to a basal area of 7.3 and 3.7 m^2/ha. respectively in the latest 4-year period. By comparison, Fagus1 had a basal area of 47.1 m^2/ha in the unthinned plots, and Picea1, Picea2 and Picea3 had basal areas of 52.6, 35.1–37.5 (53.6–49.15) and 36.5 m^2/ha (44.1) in unthinned plots at the last measurement (note that unthinned plots in Picea2 and Picea3 had partly disintegrated due to pathogens at the last measurement and numbers in parentheses are the maximum densities that are considered better indicators of the relative strength of competition). Therefore, Acer1 and Fagus1 experienced similar relative strengths of competition, not much different from the Picea experiments. Acer2 and Pinus1 had lower basal areas in the unthinned plots, however, in both experiments natural mortality occurred. Hence, differences in the relative strength of competition may explain some of the differences in responses, but they are not the full explanation. It seems likely that the results are the combined effects of points 1 and 2 and/or 3. These mechanisms are currently not well understood, however, recognizing that some tree species show limited radial-growth responses to reductions in stand density may improve density management.

5. Conclusion

The method applied in this study can be used to quantify radial-growth responses to reductions in density in forest experiments with thinning from below. It escapes the influence of ‘technical growth’ that is involved in analysis of stand mean diameter responses to density, causing significant bias. Moreover, the method can be applied to typical thinning and spacing experiments without the requirement of tree stem positions.

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