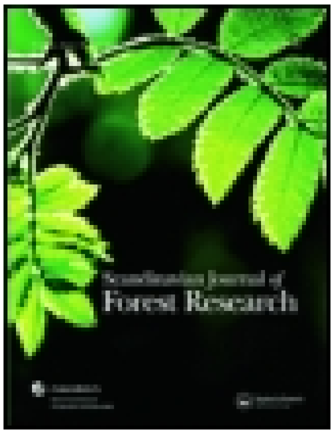


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# Self-thinning models for even-aged stands of Pinus sylvestris, Picea abies and Betula pendula

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# Self-thinning Models for Even-aged Stands of *Pinus sylvestris, Picea abies* and *Betula pendula*

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Self-thinning models were developed to describe the relationship between the stem number and mean diameter of even-aged and monospecific tree stands undergoing self-thinning. The models were developed separately for *Pinus sylvestris* L., *Picea abies* (L.) Karst. and *Betula pendula* Roth. stands. Data from 41 unthinned permanent sample plots were used. According to Reineke's equation and the −3/2 power rule of self-thinning, a log–log plot of average tree size and stem density will give a straight, self-thinning line of constant slope. According to this study, the slope of the line consistent with Reineke's equation varies for different tree species. Within tree species, the intercept of the self-thinning line varies according to site index. *Key words: Scots pine, Norway spruce, birch, self-thinning, prediction.*



## INTRODUCTION

The mortality caused by competition between trees within a stand is called self-thinning. It results in a decrease in tree number along with increasing stand biomass. In forest management planning it is important to know the degree of mortality caused by self-thinning in unthinned stands. Such information is essential when studying different thinning cycles and intensities in order to find the optimal thinning programme. Self-thinning models are used in growth simulators, in addition to growth models, to predict stand development under different treatment schedules.

The rate of self-thinning in even-aged and monospecific stands with complete crown closure has been found to be considerably regular, and it has been modelled on the basis of the relationship between stem number and tree size. Reineke (1933) stated that the relationship between the number of trees ($N$) and the quadratic mean diameter ($D_g$) in stands of full density follows a straight line when plotted on a log–log scale:

$$\ln(N) = p - q \cdot \ln(D_g) \tag{1}$$

According to Reineke's equation, the slope of the line ($q$) is constant, equal to 1.605, irrespective of the tree-species. The intercept ($p$) of the line varies according to tree species, while it is constant within species, regardless of site quality and stand age. Using this reference curve Reineke derived the "stand-density index" as a measure of stocking for forest management applications.

The −3/2th power rule of self-thinning developed by Yoda et al. (1963) describes the general relationship between the maximum attainable average plant weight ($w$) and the number of plants per unit area ($N$) in a monospecific, even-aged plant population with complete crown closure. Like Reineke's equation, the power rule states that the relationship among successive measurements of a stand undergoing self-thinning, plotted on a log–log scale, follows a linear "self-thinning line":

$$\ln(w) = c - (3/2) \cdot \ln(N) \tag{2}$$

According to the self-thinning rule, the slope of the line is a constant, equal to $-3/2$, independent of species, site quality, age, initial density and location.

The $-3/2$th power rule of self-thinning has been widely applied to describe intraspecific, density-dependent regulation in plant populations of a wide range of species (Weller, 1987). The self-thinning rule has been the basis of more complicated models (Smith & Hann, 1984; 1985), and it has also been used in forest management applications (Drew & Flewelling, 1979). Recently it has been demonstrated, based on empirical data, that the parameters of the self-thinning line vary according to tree species of different shade tolerance, locality and site type (Sprugel, 1984; Weller, 1987; Zeide, 1985; 1987). Zeide (1987) has questioned the assumptions of the self-thinning rule, and concluded that the line of self thinning does not have a constant slope, but is generally of a concave form.

The main objectives of this study are (1) to investigate the applicability of Reineke's equation in unthinned pine (*Pinus sylvestris* L.), spruce (*Picea abies* (L.) Karst.) and birch (*Betula pendula* Roth.) stands in Finland, and (2) to develop stand-level self-thinning models for use in forest management planning in predicting the mortality in unthinned stands. The models are restricted to the sort of variables measured in practical forest inventories.



## MATERIAL AND METHODS

### *Study material*

The study material consisted of 41 unthinned permanent plots in experimental stands. The oldest stands have been measured regularly since the 1920s. Nineteen of the sample plots were in pine stands, 11 in spruce stands and 11 in birch stands (Table 1). Sample plot size varied between 800 $m^2$–2500 $m^2$.

The stands were growing on mineral soils in southern Finland. The pine and birch stands had been regenerated by either sowing or natural seeding. Most of the spruce stands were plantations. The stands were even-aged and monospecific; the proportion of dominant tree species was at least 75% of the total volume of the growing stock. The birch stands were dominated by silver birch, but the proportion of pubescent birch (*Betula pubescens* Ehrh.) has not been documented in the oldest experimental stands.

The experimental plots included in the study material were untreated control plots, where no thinnings had been carried out. Only stands where no extensive natural damage (e.g. snow, wind or insect damage) had appeared during the investigated period were accepted in the analysis.

The plots had been measured six times on average, and the study period covered an average of 32 years. The basal area, stem number, mean diameter, dominant height and volume of the growing stock were measured at each measurement. In the analysis of the data, trees belonging to the dominant tree storey, regardless of species, were included in the stem number count.

The dominant height, defined as the average height of the 100 thickest trees $ha^{-1}$ at an age of 100 years ($H_{100}$), was used as the site index for the pine and spruce stands. The site indices were calculated using the models of Vuokila & Väliaho (1980) for artificially regenerated stands, and the models of Gustavsen (1980) for naturally regenerated stands. The site index of the birch stands was depicted as the dominant height at an age of 50 years ($H_{50}$) calculated according to the models of Gustavsen & Mielikäinen (1983).

The self-thinning line is an asymptotic constraint that acts only when stands have become so crowded that crown closure is complete. Estimation of the self-thinning line on the basis of empirical data presupposes that the data used in modelling have been collected from stands in the self-thinning phase. It is therefore necessary to eliminate observations from

Table 1. *General information about the experimental stands*
The stand characteristics refer to the time when the expeiments were established

| Exp. no. | Location | Sample plots, no. | Site type[a] | Site index, m | Age, yr | Stem number, no. ha$^{-1}$ | $D_g$, cm | $H_{dom}$, m | Study period, yrs. | Measurement instances, no. |
|---|---|---|---|---|---|---|---|---|---|---|
| Pine stands | | | | | | | | | | |
| 21 | Vilppula | 1 | OMT | 26.5 | 104 | 555 | 30.2 | 26.5 | 1928–1965 | 5 |
| 23 | Vilppula | 1 | OMT | 27.6 | 35 | 4 816 | 11.2 | 13.0 | 1928–1973 | 7 |
| 15 | Vilppula | 1 | OMT | 27.7 | 79 | 760 | 26.1 | 25.0 | 1928–1964 | 5 |
| 3 | Elimäki | 1 | PyT | 29.7 | 21 | 5 873 | 8.4 | 8.4 | 1926–1936 | 3 |
| 11 | Vesijako | 1 | MT | 28.2 | 26 | 2 476 | 11.4 | 10.0 | 1924–1963 | 7 |
| 46 | Vesijako | 1 | MT | 25.7 | 31 | 8 700 | 7.2 | 11.5 | 1948–1974 | 6 |
| 9 | Evo | 1 | MT | 28.2 | 30 | 3 988 | 10.6 | 11.5 | 1925–1980 | 9 |
| 3 | Evo | 1 | VT | 22.0 | 45 | 4 963 | 9.8 | 12.0 | 1925–1989 | 8 |
| 8 | Evo | 1 | VT | 22.8 | 55 | 2 195 | 14.1 | 17.0 | 1925–1957 | 5 |
| 2 | Parkano | 1 | VT | 26.0 | 34 | 6 170 | 9.8 | 9.6 | 1963–1986 | 4 |
| 2 | Juupajoki | 1 | VT | 18.7 | 77 | 2 737 | 12.4 | 16.0 | 1949–1963 | 3 |
| 7 | Koli | 1 | CT | 19.2 | 94 | 2 140 | 16.5 | 19.0 | 1924–1962 | 6 |
| 18 | Vippula | 1 | CT | 17.2 | 45 | 5 850 | 6.5 | 8.0 | 1928–1973 | 7 |
| 19 | Vippula | 1 | CT | 17.5 | 49 | 10 125 | 6.4 | 8.0 | 1928–1981 | 6 |
| 7 | Pohjankangas | 1 | CT | 15.6 | 90 | 1 484 | 16.3 | 14.0 | 1926–1965 | 4 |
| 1 | Pohjankangas | 1 | CIT | 16.4 | 66 | 2 652 | 11.5 | 12.5 | 1926–1965 | 5 |
| 9 | Pohjankangas | 2 | CIT | 15.2 | 76 | 3 062 | 9.9 | 11.0 | 1926–1965 | 5 |
| 3 | Pohjankangas | 1 | CIT | 15.2 | 55 | 5 987 | 8.0 | 8.0 | 1926–1965 | 4 |
| Spruce stands | | | | | | | | | | |
| 11 | Ruokolahti | 1 | OMaT | 31.4 | 30 | 2940 | 14.1 | 13.0 | 1932–1965 | 6 |
| 2 | Heinola | 1 | OMT | 34.3 | 31 | 2970 | 13.7 | 15.6 | 1962–1988 | 6 |
| 3 | Heinola | 2 | OMT | 33.0 | 36 | 2480 | 15.8 | 16.5 | 1962–1988 | 6 |
| 4 | Heinola | 1 | OMT | 33.7 | 37 | 2060 | 16.2 | 15.3 | 1962–1988 | 6 |
| 5 | Heinola | 1 | OMT | 30.8 | 37 | 3540 | 11.7 | 13.8 | 1962–1988 | 6 |
| 1 | Hauho | 1 | OMT | 29.5 | 27 | 3936 | 9.0 | 10.0 | 1965–1988 | 4 |
| 1 | Heinola | 2 | MT | 29.8 | 41 | 2180 | 13.7 | 14.1 | 1961–1987 | 6 |
| 9 | Punkaharju | 1 | MT | 21.6 | 46 | 3074 | 9.4 | 10.0 | 1924–1955 | 8 |
| 12 | Punkaharju | 1 | MT | 24.5 | 46 | 2735 | 12.0 | 13.0 | 1924–1950 | 4 |
| Birch stands | | | | | | | | | | |
| 1 | Koli | 1 | OMT | 22.5 | 34 | 5334 | 11.6 | 15.0 | 1924–1962 | 7 |
| 1 | Ruotsinkylä | 1 | OMT | 18.5 | 35 | 8996 | 8.6 | 12.5 | 1924–1967 | 8 |
| 13 | Vesijako | 1 | OMT | 21.6 | 70 | 1029 | 21.0 | 27.0 | 1924–1964 | 6 |
| 24 | Vesijako | 1 | OMT | 17.5 | 78 | 1675 | 17.1 | 23.0 | 1925–1954 | 5 |
| 43 | Punkaharju | 1 | MT | 29.0 | 26 | 1880 | 12.9 | 21.4 | 1976–1986 | 3 |
| 2 | Lapinjärvi | 1 | MT | 19.3 | 50 | 2500 | 13.3 | 19.5 | 1950–1969 | 4 |
| 15 | Vesijako | 1 | MT | 17.9 | 70 | 1312 | 16.6 | 22.0 | 1924–1964 | 6 |
| 21 | Vesijako | 1 | MT | 17.6 | 60 | 1592 | 16.3 | 20.0 | 1925–1963 | 6 |
| 22 | Vesijako | 1 | MT | 15.0 | 65 | 2912 | 13.9 | 18.0 | 1925–1963 | 6 |
| 851 | Yli-Kiiminki | 2 | VMT | 18.4 | 38 | 3190 | 11.1 | 15.7 | 1973–1987 | 4 |

[a] According to Cajander (1909).

stands not yet undergoing self-thinning. In this study, an observation from a stand was accepted if the stem number in the plot had decreased during the preceding measurement period. Thus, at least the first measurement of each stand was omitted from the analysis. Nineteen percent of the observations were rejected. The final data consisted of 95 observations from 19 pine stands, 47 observations from 11 spruce stands and 47 observations from 11 birch stands (Fig. 1).

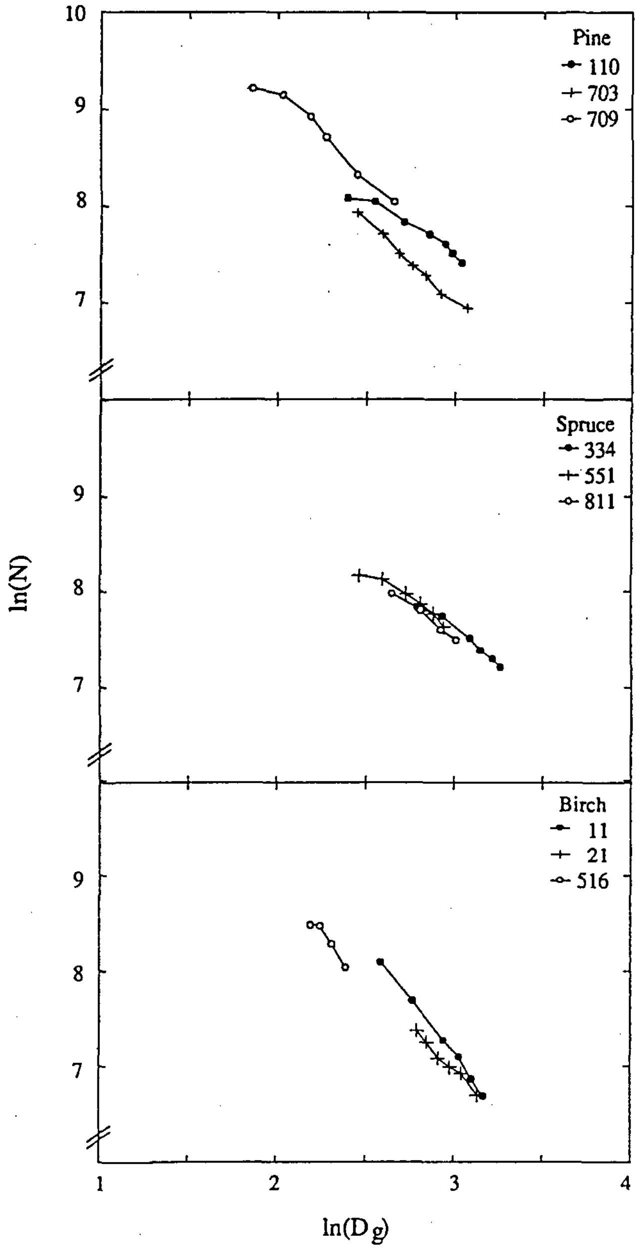


*Fig. 1.* The relationship between mean diameter ($D_g$) and stem number ($N$) on a log–log scale from nine stands belonging to the study material. In every stand the first observation was omitted from the analysis.

*Test material*

The reliability of the models was tested against independent data sets. Unthinned control plots from an experimental series on thinning intensity (HARKAS experiments, Vuokila, 1987) were used as a test material for the self-thinning models for pine and spruce. Observations from 42 unthinned control plots in pine stands and 16 plots in spruce stands were included in the test material. To validate the birch models, 15 unthinned plots from repeatedly measured thinning experiments for birch were used as the test material. Of these plots 5 were pure silver birch stands and 10 were dominated by pubescent birch.

Most of the conifer stands had been thinned at the seedling stage before the experiments were established. Therefore, the control plots where the investigated periods extended for at least 15 years were accepted in the test material. The most recent measurement on each control plot, regarded as being in the self-thinning phase, was used in testing the models.

*Modelling of the self-thinning line*

The mean diameter weighted with the basal area ($D_g$) was chosen as the variable describing the tree size. Tree diameter was considered to have been measured precisely enough, although the accuracy and the methods used for calculating stand and tree volume have changed during the long study periods. From the theoretical point of view, tree diameter is considered to be closely correlated with crown width, which is the primary factor affecting the degree of stand density and crown closure. Diameter is also more sensitive than tree volume to changes in the growing space of a tree (Assmann, 1970; Zeide, 1987).

The strategy adopted in modelling the self-thinning line was to develop separate models for each tree species. The site-independent models were first developed using the number of trees ($N$) and mean diameter ($D_g$) as the only variables (model (3)).

$$\ln(N) = a_0 + a_1 \cdot \ln(D_g), \tag{3}$$

where $a_0$, $a_1$ = parameters. The influence of site quality on the intercept of the self-thinning line was examined by adding the site index ($SI$: $H_{100}$ for pine and spruce, $H_{50}$ for birch) to the model as an independent variable.

$$\ln(N) = a_0 + a_2 \cdot \ln(SI) + a_1 \cdot \ln(D_g), \tag{4}$$

where $a_0$, $a_1$, $a_2$ = parameters. In order to investigate the effect of site quality on the slope of the self-thinning line, the site index was added to the slope, resulting in model (5)

$$\ln(N) = a_0 + a_2 \cdot \ln(SI) + [a_1 + a_3 \cdot \ln(SI)] \cdot \ln(D_g) \tag{5}$$

Mixed linear models were used in estimating the parameters of the self-thinning models. The study material consisted of successive observations from sample plots. Thus, the observations within a given stand, were correlated with each other. Correlations between the observations and the hierarchial data structure can be taken into account by using mixed linear models (e.g. Goldstein, 1986; Lappi & Bailey, 1988).

In the self-thinning models the effects of stem number and site index were considered to be fixed effects. The data had two sources of random variation (i.e. variance components); the variation between stands (random stand effect, $b$) and the variation within a stand between successive measurements (error term, $e$). In the mixed linear model the random effects $b$ and $e$ are assumed to have zero mean and fixed variances. Further, $b$ and $e$ are assumed to be uncorrelated with each other (Searle, 1987). The assumptions also state, when applied to the present data, that the within-stand $e$ values between successive observations should be uncorrelated. Although the observations from a stand were autocorrelated with each other over time, it was assumed that the $e$ values between observations were uncorrelated.

The mixed linear models consistent with models (3), (4) and (5), including fixed and random effects, are as follows:

$$\ln(N_{ij}) = a_0 + a_1 \cdot \ln(D_{gij}) + b_i + e_{ij} \tag{6}$$

$$\ln(N_{ij}) = a_0 + a_2 \cdot \ln(SI_i) + a_1 \cdot \ln(D_{gij}) + b_i + e_{ij} \tag{7}$$

$$\ln(N_{ij}) = a_0 + a_2 \cdot \ln(SI_i) + [a_1 + a_3 \cdot \ln(SI_i)] \cdot \ln(D_{gij}) + b_i + e_{ij} \tag{8}$$

where $N_{ij}$ = stem number in stand $i$ at measurement $j$, no. ha$^{-1}$; $D_{gij}$ = mean diameter (weighted with basal area) in stand $i$ at measurement $j$, cm; $SI_i$ = site index in stand $i$: $H_{100}$

for pine and spruce, $H_{50}$ for birch, m; $b_i$ = random stand effect; $e_{ij}$ = error term in stand $i$ at measurement $j$; $a_0, a_1, a_2, a_3$ = fixed parameters.

The fixed parameters and the random effects were estimated with the restricted maximum likelihood method using BMDP program 3V (General mixed model analysis of variance) (Jennrich & Sampson, 1988). The random stand effects were not predicted in this study.

In model tests against the independent data sets, model (7) was used for the pine and spruce, while the site-independent model (6) was used for birch. The following characteristics were calculated to describe the behaviour of the models when applied to the independent test material:

$$b = \sum_{i=1}^{n} (N_i - \hat{N}_i) \Big/ n \quad \text{(systematic error)} \tag{9}$$

$$b_r = \sum_{i=1}^{n} [(N_i - \hat{N}_i) \Big/ \hat{N}_i]/n \quad \text{(relative systematic error)} \tag{10}$$

$$RMSE = \left[ \sum_{i=1}^{n} (N_i - \hat{N}_i)^2 \Big/ n \right]^{0.5} \quad \text{(root mean square error)} \tag{11}$$

$$RMSEr = \left[ \sum_{i=1}^{n} [(N_i - \hat{N}_i)/\hat{N}_i]^2 \Big/ n \right]^{0.5} \quad \text{(relative RMSE)} \tag{12}$$

where $N_i$ = observed stem number in stand $i$, no. $ha^{-1}$; $\hat{N}_i$ = predicted stem number in stand $i$, no. $ha^{-1}$.

## RESULTS

Site independent models of the self-thinning line, consistent with Reineke's equation, were estimated for the pine, spruce and birch stands. The differences between the tree species as regards the parameter estimates of intercept and slope of the self-thinning lines were statistically significant (Table 2). The residual variance of the models was divided into the

Table 2. *Site-independent self-thinning models*

Dependent variable: $\ln(N)$

| | estimate | standard error | estimate/ std. dev. | 95% confidence intervals |
|---|---|---|---|---|
| Pine | | | | |
| constant | 12.669 | 0.123 | 103.25 | [12.425, 12.913] |
| $\ln(D_g)$ | −1.844 | 0.042 | −44.34 | [−1.927, −1.761] |
| $\hat{\sigma}_b$ | 0.195 | | | |
| $\hat{\sigma}_e$ | 0.077 | | | |
| Spruce | | | | |
| constant | 11.414 | 0.164 | 69.82 | [11.084, 11.744] |
| $\ln(D_g)$ | −1.301 | 0.006 | −23.15 | [−1.313, −1.289] |
| $\hat{\sigma}_b$ | 0.082 | | | |
| $\hat{\sigma}_e$ | 0.043 | | | |
| Birch | | | | |
| constant | 13.891 | 0.192 | 72.24 | [13.504, 14.278] |
| $\ln(D_g)$ | −2.331 | 0.066 | −35.22 | [−2.464, −2.198] |
| $\hat{\sigma}_b$ | 0.141 | | | |
| $\hat{\sigma}_e$ | 0.065 | | | |

List of variables: $N$: stem number, $D_g$: mean diameter (weighted with basal area), $\hat{\sigma}_b$: between-stand standard deviation, $\hat{\sigma}_e$: within-stand standard deviation.

Table 3. *Site-dependent self-thinning models*

Dependent variable: $\ln(N)$

| | estimate | standard error | estimate/ std. dev. | 95% confidence intervals |
|---|---|---|---|---|
| Pine | | | | |
| constant | 11.213 | 0.448 | 25.02 | |
| $\ln(H_{100})$ | 0.489 | 0.146 | 3.35 | |
| $\ln(D_g)$ | −1.855 | 0.041 | −45.45 | [−1.936, −1.774] |
| $\hat{\sigma}_b$ | 0.154 | | | |
| $\hat{\sigma}_e$ | 0.074 | | | |
| Spruce | | | | |
| constant | 10.059 | 0.474 | 21.22 | |
| $\ln(H_{100})$ | 0.446 | 0.149 | 2.99 | |
| $\ln(D_g)$ | −1.354 | 0.057 | −23.81 | [−1.469, −1.239] |
| $\hat{\sigma}_b$ | 0.058 | | | |
| $\hat{\sigma}_e$ | 0.043 | | | |
| Birch | | | | |
| constant | 13.645 | 0.697 | 19.57 | |
| $\ln(H_{50})$ | 0.085 | 0.231 | 0.37 | |
| $\ln(D_g)$ | −2.332 | 0.066 | −35.21 | [−2.465, −2.199] |
| $\hat{\sigma}_b$ | 0.140 | | | |
| $\hat{\sigma}_e$ | 0.065 | | | |

List of variables: $N$: stem number, $D_g$: mean diameter (weighted with basal area), $H_{100}/H_{50}$: site index, $\hat{\sigma}_b$: between-stand standard deviation, $\hat{\sigma}_e$: within-stand standard deviation.

variance between stands ($\sigma_b^2$) and the variance within a stand ($\sigma_e^2$). Most of the random variation for all three tree species was due to the variation between the stands.

The effect of site index on the values of the intercept of the self-thinning lines (model (7)) proved to be significant in the pine and spruce stands (Table 3). Adding the site index to the model as an independent variable significantly diminished the variance between the stands ($\sigma_b^2$) in the pine and spruce models. In the birch stands the effect of site index on the intercept was nonsignificant, and adding the site index to the model had no effect on the amount of between-stand random variation.

The parameter estimates of the slopes differed at the 95% confidence level between tree species (Table 3). Adding the site index in connection with the slope parameter according to model (8) was nonsignificant, and did not improve the model compared with (7).

According to both models (6) and (7), the slopes of the self-thinning lines of each tree species differed at the 99% confidence level from the constant slope value (−1.605) of Reineke's equation.

*Validation of the models*

The relative systematic error of the predicted stem number per hectare ($N$) was −13.1% in the pine stands, −8.7% in the spruce stands, and −8.8% in the birch stands (Table 4). The residual variance of the predicted values was evenly distributed for all tree species (Fig. 2). In the birch stands dominated by pubescent birch the relative systematic error was −14.8%. In the pure silver birch stands the error was only 2.8%.

Table 4. *Statistics describing the applicability of the self-thinning models to the independent test material from permanent sample plots*

| | Tree species—(model number) | | |
|---|---|---|---|
| | Pine (7) | Spruce (7) | Birch (6) |
| Number of observations | 28 | 16 | 15 |
| Mean of the predicted stem number, no. $ha^{-1}$ | 2385 | 1904 | 4226 |
| Systematic error, no. $ha^{-1}$ | −327 | −164 | −638 |
| Relative systematic error, % | −13.1 | −8.7 | −8.8 |
| RMSE, no. $ha^{-1}$ | 437 | 245 | 1399 |
| $RMSE_r$, % | 17.4 | 13.4 | 15.9 |

## DISCUSSION

Mixed linear models were used in the analysis of the data. The assumptions underlying the applicability of mixed linear models to the data set were fulfilled, except for the assumption concerning the noncorrelation between the errors of successive observations, which was not verified. However, the effect of the possible uncertainty in the estimation of the within-stand variance component, $\hat{\sigma}_e^2$, is likely to be negligible. The main aim of the present study was to estimate the values of the fixed parameters of the self-thinning models. The amount of total random variation in the models, and especially the amount of $\hat{\sigma}_e^2$, remained comparatively small. Thus the effect of $\hat{\sigma}_e^2$ on the values of the fixed parameter is likely to be of minor importance.

Testing the models against the independent data sets confirmed their ability to predict self-thinning in unthinned stands with considerable accuracy. There was no noticeable trend in the amount of bias with the dependent variable. The predictions were slightly positively biased for all tree species. In other words, the observations from the stands lay below the predicted self-thinning line. Since most of the conifer stands had been thinned in the seedling stage, it is possible that they had not reached the phase of self-thinning by the end of the 15-year investigation period. When considering the test results from the birch stands, it should be noted that most of the test material was from pure pubescent birch stands, while the model was based on the data from stands dominated by silver birch. Applying the model to independent data from pure silver birch stands resulted in an almost unbiased prediction.

The results from the present study argue against the assumptions of Reineke's equation concerning the constancy of the slope of the self-thinning line. The slope values varied with tree species, and for each species the slope differed from the constant value of Reineke's equation, equal to −1.605, to a statistically significant degree at the 99% confidence interval. The rate of self-thinning under intraspecific competition with increasing average tree size was slowest in spruce stands and fastest in birch stands. Based on these results, the slope of the self-thinning line could be interpreted as a measure of self-tolerance, as Zeide (1985) has stated.

The results for Scots pine and Norway spruce indicate that the intercept of Reineke's equation also varies with site index. In the birch stands the intercept was independent of site

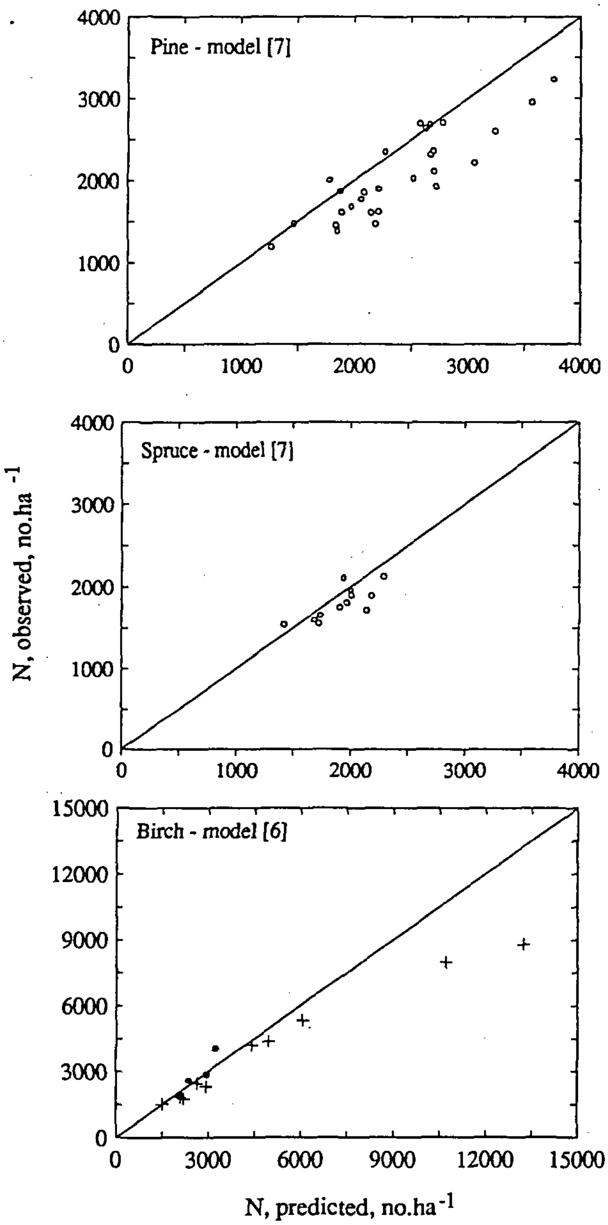


*Fig. 2.* Predicted and observed stem numbers from the stands included in the test material. ○ = pine and spruce; ● = silver birch; + = pubescent birch.



index. The possible mixture of the two birch species could have affected these results, since the birch stands most likely consisted of two birch species (silver birch and pubescent birch), which are known to have different site requirements. The change in slope with site index cannot be confirmed on the basis of this study.

The connection between Reineke's equation and the $-3/2$th power rule of self-thinning is based on the relationship between the diameter and biomass (or volume) of the average tree. If model (6) is transformed to describe the relationship between biomass and stem number using the diameter-biomass allometric exponent of 2.5, as Yoda et. al. (1963), the slope of the self-thinning line changes with tree species and deviates from the theoretical constant slope value. However, the relationships after transformation can be regarded as only approximative. Results that argue against the constant slope value, equal to −3/2, have earlier been reported by e.g. Kellomäki & Nevalainen (1983), Zeide (1985, 1987), Weller (1987) and Verwijst (1989).

Zeide (1985, 1987) has pointed out that the self-thinning line does not have any constant slope, but changes according to the stage of stand development. The relationship between average tree size and tree number on a log–log scale is linear only in the intermediate stage of development with complete canopy closure and constant self-tolerance. In the present study the relationship between mean diameter and tree number on a log–log scale was found to be linear between the stand ages of 20–140 years for pine, 30–80 years for spruce and 30–110 years for birch. Models (6) and (7) should not be applied to stands with a stand age far beyond the above age limits.

This study does not try to confirm or disprove the assumption of linearity or nonlinearity of the self-thinning relation during the whole lifespan of a stand. This would not have been possible on the basis of the study material, because the material did not consist of data measured precisely enough in the seedling stage, nor in the oldest development stages of the stands. However, a linear relation existed during the period covering stand development between the pole stage up until the maturity of commercial forests in Finland. This is the most important period of stand development as regards the management of forests, as well as application of the models developed in this study.



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