Author(s): Daesung Lee, Jouni Siipilehto, Jari Hynynen

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Comparison and analysis of self-thinning models based on diameter-based maximum size-density relationships

Daesung Lee [a,1,*], Jouni Siipilehto [a,2], Jari Hynynen [b,3]

[a] Natural Resources Institute Finland (Luke), Latokartanonkaari 9, Helsinki 00790, Finland
[b] Natural Resources Institute Finland (Luke), Vipusenkuja 5, Savonlinna 57200, Finland

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ABSTRACT

Identifying self-thinning phase is one of the key issues to deal with stand density management and simulate the growth and yield in a forest stand. This study was conducted to figure out the carrying capacity of silver birch plantations and provide the self-thinning zone for practicability. The analyzed data were the stand-wise observations from the experimental plots of silver birch plantations in southern and central Finland, which were established and measured between 1977 and 2020. Models for the diameter-based maximum size-density relationship (MSDR) were fitted only to the censored data after classifying the stand observations undergoing self-thinning phase. The applied diameter-based MSDR in this study were Reineke's self-thinning rule (STR), competition-density (C-D) rule, and Nilson's stand sparsity index (SSI). Model fitting was executed using linear quantile mixed-effect model for Reineke's STR and Nilson's SSI and nonlinear mixed-effect model for the C-D rule. For practical purpose, a lower boundary of the self-thinning zone based on the developed MSDR was analyzed using the concept of relative density (*RD*) according to the ratio of stem number (*N*) to maximum stem number (N_{max}) at quadratic mean diameter (*DQ*). Linear quantile mixed models were fitted well with the 0.99 level for Reineke's STR and with the 0.01 level for Nilson's SSI to find the MSDR between *DQ* and *N*. Among the fitting methods for the C-D rule, the three-parameter method performed better than the four-parameter method or the method with Reineke's slope of −1.605. The fitted slope of Reineke's STR in this study was −1.5848, which was close to the original slope from Reineke's. Our results from the developed models and the observations undergoing self-thinning phase implied that the slope of MSDR is not always invariant. Moreover, a different slope for MSDR was suggested by initial planting density and the stand development stage; a self-thinning phase occurred earlier with lower initial planting density, which meant a steeper slope. When the lower boundary of the self-thinning zone was analyzed applying *RD* to the MSDR models, the results suggested that *RD* 0.7 for Reineke's STR at $DQ \leq 18.65$ cm and *RD* 0.8 for Nilson's SSI at $DQ \geq 18.65$ cm provided adequate level for self-thinning phase. It is considered in this study that the diameter-based MSDR measures were analyzed and examined adequately, and the practical self-thinning zone was provided using *RD* for silver birch plantations.

1. Introduction

Response to silvicultural treatments is closely related to competition, a key process affecting plant populations and communities, for site resources such as light, water, nutrients and space (Drew and Flewelling, 1977; Burkhart and Tomé, 2012). As individual trees grow in size, their demand on site resources and growing space increases (Pretzsch and Biber, 2005; Vospernik and Sterba, 2015). When resources are no longer adequate to support additional growth of all the trees present, the number of trees per unit area will decrease (Burkhart, 2013). The mortality caused by competition between trees within a stand is called self-thinning (Yoda et al., 1963; Hynynen, 1993). At the certain environment, the population size or biomass of a species supported under finite resources reaches a stable maximum and is regarded as carrying capacity (Helms, 1998; VanderSchaaf and Burkhart, 2007; Vospernik and Sterba, 2015). Carrying capacity illustrates how environmental

* Corresponding author.
E-mail addresses: daesung.lee@luke.fi (D. Lee), jouni.siipilehto@luke.fi (J. Siipilehto), jari.hynynen@luke.fi (J. Hynynen).
[1] orcid.org/0000–0003-1586–9385
[2] orcid.org/0000–0002-5661–8972
[3] orcid.org/0000–0002-9132–8612

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factors constrain the size of populations which stabilize at or fluctuate around these limits (Price, 1999). In forestry, stand carrying capacity can be referred to as the maximum possible stocking of trees that a stand can sustain over a long term (Yang and Burkhart, 2017).

In forest management planning it is important to know the degree of mortality caused by self-thinning in unthinned stands (Hynynen, 1993). Quantifying stand density by estimating the self-thinning frontier or carrying capacity is fundamental to developing reliable models for predicting forest growth and yield (Burkhart, 2013). Particularly, such information is essential when studying different thinning cycles and intensities in order to find the optimal thinning programme (Hynynen, 1993). It is not possible to find an optimal level of thinning without the ability to measure density (Zeide, 2005). Reliable measures of self-thinning are used in growth simulators to predict stand development under different treatment schedules (Hynynen, 1993) and to increase forest productivity by controlling competition among trees (Zeide, 2005). In this context, important is one special point of this relationship at which the output of desired products reaches maximum (Zeide, 2004). If the models in a simulator are based on tree-level, the self-thinning constraints may or may not be needed (Monserud et al., 2004). However, together with the stand-level models (e.g. Lee et al., 2024) the self-thinning is fundamental.

As simple and effective indices of competition in forest stands, size-density relationships are critical to estimating stand density and stocking, determining the optimal thinning intensity, and calculating degree of disturbance, rate of self-thinning, and other forest processes (Zeide, 1995; Burkhart, 2013). Several kinds of variables were proposed as density measures: number of trees (*N*), stand basal area (*G*), average distance between trees in proportion to average height or diameter, stand volume, total biomass, crown closure, and leaf area (Zeide, 2005). None of these variables are entirely satisfactory due to the stocking (degree of crowding) or seasonal fluctuation. However, number of trees per unit area can be regarded as the simplest, but still effective, measure of density with an application of Reineke's stand density index. Tree size is an essential component of stand density measures to be useful in quantifying crowding or competition for space (Burkhart, 2013). In this context, several maximum size-density relationship (MSDR) allometry of stands have been developed to study the influence of density on self-thinning (Burkhart, 2013). The best known and most commonly employed of these self-thinning or MSDR are the relationship between numbers of trees per unit area and the quadratic mean diameter (*DQ*) of stands from Reineke (Reineke, 1933), the relationship between mean plant volume (or biomass) and numbers per unit area from Yoda et al. (1963), and the relationship between the average distance among trees and the average height of the dominant canopy from Hart (1926).

By comparing the MSDR measures of three different size variables derived from a common formulated structure, Burkhart (2013) demonstrated while the differences aren't large due to the choice of tree size variable, *DQ* proved most informative and was well ground in theory (Yang and Burkhart, 2017). Zeide (1987, 1995) argued that stem diameter is highly correlated to tree crown size, which is the vital stand size variable representing crowding of trees (Yang and Burkhart, 2017). Because of its closer relationship with crown width, average stem diameter is a better predictor of the number of trees than average height and volume (Zeide, 2010). Accordingly, diameter-based MSDR measures have been substantially studied in many countries, especially with Reineke's self-thinning rule (STR) (Reineke, 1933). In the meantime, the competition-density (C-D) rule (Kira et al., 1953; Shinozaki and Kira, 1956; Sterba, 1975, 1987) and Nilson's stand sparsity index (SSI) (Nilson, 1973, 2006) presented advantages in terms of reasoning, formulation, and performance in several studies. Recent studies continue to examine and compare these three kinds of diameter-based MSDR measures (Zeide, 2010; Gadow and Kotze, 2014; Vospernik and Sterba, 2015; Yang and Burkhart, 2017; Lee and Choi, 2019).

In Fennoscandia, guidelines about maximum stand density were provided targeting on major economic species such as Scots pine, Norway spruce, silver birch and downy birch (Verwijst, 1989; Hynynen, 1993; Nilsson and Albrektson, 1994; Elfving, 2010). These kind of models were incorporated into the forest growth and yield modules and restricted the simulation outputs which enable to have a more reliable prediction (Hynynen, 1993; Hynynen et al., 2002). Recently, the relationship between *DQ* and *N* for Scots pine and Norway spruce in northern Europe was analyzed considering a trend of site index over year (Mäkinen et al., 2021). However, self-thinning models for silver birch are not followed up since a self-thinning model of the species was once developed in the past (Hynynen, 1993; Hynynen et al., 2002). Recently, because of the climate changes and improved breeding techniques which may affect the MSDR, a new self-thinning model is more needed to be used together with new models for stand characteristics of planted silver birch stands (Lee et al., 2024).

Therefore, the objectives of this study were to develop a new self-thinning model for silver birch plantations in southern and central Finland. Specifically, we aimed 1) to analyze the MSDR using managed/unmanaged empirical stands undergoing self-thinning phase, 2) to fit the model parameters using three kinds of diameter-based MSDR approaches, 3) to assess the model reliability by comparing the developed models with previous studies and observations, and 4) to provide practical guidelines of stand density management by estimating a lower boundary of the self-thinning zone.

2. Materials and methods

2.1. Study materials

Data on stands undergoing self-thinning phase are indispensable to develop a self-thinning model. The material is represented as successively measured empirical data from long-term experimental plots in which the trajectory on self-thinning phase is observed when overstocked. The data of this study sufficing for the purpose were from three type of trials in southern and central Finland: thinning, spacing, and tree breeding trials, ranging from 60°5′ N to 65°51′ N in latitude and 24°47′ E to 30°37′ E in longitude. The experimental designs and specifics were different among the trials, but prerequisites met the criteria on a study about density-induced natural mortality with sufficient number of measurement instances and observations (Table 1).

The thinning trials were established between 1977 and 1995, and along with unthinned stands, one to three times of thinning were conducted in thinned stands. An interval year between measurements was usually 5 years. The plots were measured 4–7 times between 1977 and 2020. The spacing trials were established between 1984–1992 and measured similarly at 5-year interval. Initially low- and high-density plots were designed by spacing (400–5000 trees ha^{-1}), and some plots were thinned later. The plots were measured 4–7 times between 1984 and 2016. The breeding trials were established between 1989–2005 to primarily test the genetic improvement of seedlings. The measurement period was relatively less than the other two trials. The time after last thinning varied by plot and the thinned year. More information about the data can be found from Niemistö (1995a, 1995b) and Lee et al. (2024).

All the trials were purely monitored silver birch plantations. In few

Table 1
Descriptive statistics of the dataset for silver birch plantations used in this study.

	Unit	Self-thinning phase (Modeling data)				No self-thinning phase			
		Mean	Std. dev.	Min.	Max.	Mean	Std. dev.	Min.	Max.
Data structure									
Total number of sites		25				43			
Total number of plots		127				354			
Total number of observations		449				1694			
Plot size	m^2	890	268	216	1710	985	616	100	4600
Number of measurements by stand		4.5	1.8	2	9	3.6	2.2	1	9
Observation period by plot	year	26.9	9.8	4	42	19.8	13.2	0	42
Intervals between measurements in year		5	1.4	0	10	5	1.1	2	11
Stand characteristics									
Stand biological age, *AGE*	year	38	11	10	69	30	11	7	69
Quadratic mean diameter, *DQ*	cm	16.6	4.5	5.9	28.2	15.5	5.1	3.3	31.2
Dominant height, *HD*	m	22.8	5.3	8.2	33.0	18.8	5.5	5.3	32.3
Stem number, *N*	trees ha^{-1}	1387.6	777.8	300.0	4246.0	1027.7	749.0	171.4	4523.8
Stand basal area, *G*	m^2 ha^{-1}	24.6	5.3	9.3	39.9	14.8	4.9	2.0	30.5
Relative density[a], *RD*		0.71	0.14	0.30	1.13	0.44	0.14	0.08	0.90
Site characteristics									
Location		Southern and central Finland				Southern and central Finland			
Latitude	degree (°)	62.795	0.928	61.264	64.857	62.429	1.040	60.080	64.857
Longitude	degree (°)	26.694	1.409	24.122	30.479	26.356	1.522	23.791	30.479
Elevation	m	123.3	40.0	70.0	204.0	122.0	40.1	40.0	204.
Temperature sum above 5 °C	degree days	1215.6	68.0	1070.1	1347.7	1236.1	83.9	1070.1	1460.0
Land type		Forest site and abandoned agricultural land				Forest site and abandoned agricultural land			
Site index[b]	m	27.3	2.6	19.4	33.5	27.0	3.2	18.6	41.9

[a] Relative density (*RD*) was calculated based on the finally applied method through Eq. (14) in this study.
[b] Site index was computed based on Lee et al. (2024) with a base age of 50 years.

stands, the understory was covered with naturally grown Norway spruce trees, which were too negligible to compete with dominant silver birch. On each plot, tree diameter at breast height (*dbh*, cm) above 1.3 m from the ground was measured for all trees with the tree status indicating alive, dead, or cut. Tree height (*h*, dm) was measured from sample trees, the number of which was 40 before treatment. Dominant height (*HD*) was defined as 100 thickest trees per ha and site index was based on the model by Lee et al. (2024).

2.2. Censoring self-thinning stand and mortality pattern

Unthinned stands do not always guarantee that the stand density is under self-thinning phase. Therefore, it is an important process to categorize all the measurement instances into either self-thinning phase or not before fitting model parameters. To confirm a self-thinning phase in all observations, the changes of stand and tree variables were checked over time. The number of living and dead trees and those proportions were analyzed, and the trajectory was plotted over time via scatterplots. Plot-level observations with natural mortality were detected in a way of the decreasing number of trees.

To further convince if it's natural mortality instead of other damages such as storm or browsing, diameter distribution was plotted for living and dead trees by plot and year to show the competitive status of dead trees (Appendix A). The relative position of dead trees and degree of natural mortality occurrence from suppressed trees were confirmed to censor the data. To be specific, when the mortality occurred among dominant trees in dbh histogram and/or the proportion of mortality was too low, it was not included in modeling data as doubtful. Additionally, when the mortality only occurred more than 3 % out of total at the measurement instance, the observation was finally categorized as a self-thinning phase for modelling data to prevent the random case caused by other damages.

The first measurements in all plots were parsimoniously excluded from the modelling data no matter how many mortality trees observed because it's difficult to assure that the pre-existing mortality occurred at the stand density level of that time (Hynynen, 1993). In the case of thinned plots, although all of the aforementioned criteria were met for a self-thinning phase, the observations within 15 years since last thinning were dropped out regardless of natural mortality occurrence. It was to ensure that the classified self-thinning phases were not driven by direct or indirect effects of thinning. Consequently, the number of observations at self-thinning phase was 449, which was about one fourth in fraction out of all observations (Table 1). The relevant stand characteristics demonstrated the differences between the censored groups. Most observations at self-thinning level were from unthinned plots as expected. Using these criteria, the data were adequately censored to analyze stand carrying capacity and develop models for self-thinning line.

2.3. Modeling diameter-based maximum size-density relationship (MSDR) measures

On the censored modeling data, three kinds of diameter-based MSDR measures were applied to define the stand carrying capacity of silver birch plantations: Reineke's STR, C-D rule, and Nilson's SSI. These measures follow the ecologically similar principles of stand carrying capacity that is the maximum number of stems or stand basal area. These rules have been widely used for the forest management purpose, e.g., stand density management, relative stocking chart, yield tables, and individual tree growth models, where *N* is compared to the theoretical maximum stem number (N_{max}) proposed by the self-thinning line.

2.3.1. Reineke's self-thinning rule (STR)

The self-thinning rule firstly proposed by Reineke (1933) has a density-dependent, species-specific upper frontier. The rule describes a linear relationship between N_{max} and DQ in fully-stocked even-aged stands on a log-log scale (Eq. 1).

$$\ln N = s_1 \ln DQ + k_1 \quad (1)$$

where ln is natural logarithm, N is the number of trees per ha, DQ is the quadratic mean diameter (cm), s_1 is a slope, and k_1 is an intercept.

The original concept of Reineke's STR is the carrying capacity across sites with the same slope (s_1) of −1.605 regardless of species, stand age, and site quality. Meanwhile, the intercept (k_1) varies by species and sites and gives rise to a substantial variation of stem numbers with a slight difference of the coefficient.

2.3.2. Competition-density (C-D) rule

Competition-density rule was firstly introduced in plant science to explain the competition and carrying capacity using quadratic mean diameter and the number of plants (Kira et al., 1953; Shinozaki and Kira, 1956; Tadaki, 1963; Sterba, 1975, 1987). In forest science, the original equation was devised with dominant height in the relationship between DQ and N_{max} (Eq. 2).

$$DQ = \frac{1}{a_0 HD^{a_1} N + b_0 HD^{b_1}} \quad (2)$$

where DQ is the quadratic mean diameter (cm), HD is the dominant height (m), N is the number of trees per ha, a_0, a_1, b_0, and b_1 are the parameters in the C-D rule.

According to the C-D rule, the N_{max} is derived from a stand having a maximum stand basal area (G_{max}) where an increase of stand basal area is theoretically zero in the primary differential equation of G over N (Sterba and Monserud, 1993; Monserud et al., 2004; Lee and Choi, 2019). As a function of dominant height, N_{max} (Eq. 3) and the minimum DQ (Eq. 4) at that moment is calculated as below (Sterba, 1987).

$$N_{\max} = \left(\frac{b_0}{a_0}\right) HD^{(b_1 - a_1)} \quad (3)$$

$$DQ_{\min} = \frac{1}{2 b_0 HD^{b_1}} \quad (4)$$

where N_{max} is the estimated maximum stem number (trees ha^{-1}), HD is the dominant height (m), $DQ_{\min}$ is the minimum DQ at N_{max}, a_0, a_1, b_0, and b_1 are the parameters estimated by the C-D rule.

To compare the C-D rule with Reineke's STR, the slope and the intercept are expressed as below (Eqs. 5–7) (Vospernik and Sterba, 2015; Lee and Choi, 2019).

$$N_{\max} = \frac{b_0}{a_0} (2b_0)^{\frac{a_1}{b_1} - 1} \cdot DQ_{\min}^{\frac{a_1}{b_1} - 1} \quad (5)$$

$$s_2 = \frac{a_1}{b_1} - 1 \quad (6)$$

$$k_2 = \frac{b_0}{a_0} (2b_0)^{\frac{a_1}{b_1} - 1} \quad (7)$$

where s_2 and k_2 are the slope and the intercept, respectively, of the C-D rule corresponding to each s_1 and k_1 of Reineke's STR, a_0, a_1, b_0, and b_1 are parameters estimated by the C-D rule.

As demonstrated above via Eqs. (1)–(7), Reineke's STR and the C-D rule are algebraically interchangeable and compatible (Sterba, 1987; Vospernik and Sterba, 2015). Moreover, the four-parameter method to estimate the coefficients of Reineke's STR through Eq. (4) can be replaced with the three-parameter method as shown in Eq. (8). This method is widely used because it enables the C-D rule to directly use the slope coefficient (s_1) of Reineke's STR, e.g., −1.605, and because the three-parameter method offers more robust and reliable estimates than the four-parameter method (Sterba, 1987; Vospernik and Sterba, 2015; Yang and Burkhart, 2017; Lee and Choi, 2019).

$$DQ = \frac{1}{a_0 HD^{a_1} N + b_0 HD^{\frac{a_1}{s_1 + 1}}} \quad (8)$$

To substitute the b_1 parameter with s_1 as below, the slope coefficient of Reineke's, −1.605, was applied as in Eq. (9) (Vospernik and Sterba, 2015; Yang and Burkhart, 2017). Additionally, the slope coefficient of Reineke's STR estimated in the present study was analyzed to find the best solution as the three-parameter method (Sterba, 1987; Lee and Choi, 2019).

$$b_1 = \frac{a_1}{s_1 + 1} \quad (9)$$

2.3.3. Nilson's stand sparsity index (SSI)

In plantations where spacing is regular, average distance between planting trees (L) can be approximated by the square root of the area divided by the number of trees per unit area, e.g., 10,000 m^2 (Eq. 10). By focusing the average distance between trees, a minimum distance called stand sparsity was proposed by Nilson (1973, 2006), which is interpreted as a stand carrying capacity for trees to survive. Nilson (1973, 2006) assumed a linear relationship between DQ and L, which of those had the same dimension (Eq. 11).

$$L = \sqrt{\frac{10000}{N}} \quad (10)$$

$$L = s_3 DQ + k_3 \quad (11)$$

where L is the stand sparsity (m) or average distance between trees in a stand, N is the number of trees per ha, s_3 and k_3 are the slope and the intercept, respectively, of Nilson's SSI.

Nilson's SSI is used as an alternative tool of evaluating the MSDR because the equation is expressed with the relationship between DQ and N_{max} as shown in Eq. (12) (Zeide, 2010). Thus, the MSDR was studied especially for plantations with an assumption that it approaches a species-specific line (Gadow and Kotze, 2014; Yang and Burkhart, 2017).

$$N_{\max} = \left(\frac{100}{s_3 DQ + k_3}\right)^2 \quad (12)$$

2.3.4. Model fitting

Model parameters were fitted based on three types of the diameter-based MSDR: Reineke's STR, C-D rule, and Nilson's SSI. To estimate the parameters, Eq. (1) was used for Reineke's STR, Eqs. (2) and (8) for the C-D rule of four- and three-parameter methods, respectively, and Eq. (11) for Nilson's SSI. To fit the model parameters of Reineke's STR and Nilson's SSI, we used linear quantile regression with random effects (Koenker and Bassett, 1978; Bi, 2001; Zhang et al., 2013; Vospernik and Sterba, 2015; Yang and Burkhart, 2017; Mäkinen et al., 2021; Tian et al., 2021). Quantile regression is basically a method to find parameters based on quantile-level of data, not based on ordinary least squared error. In this study, the applied quantile levels were 0.99 for Reineke's STR and 0.01 for Nilson's SSI. Nilson's SSI requires the lower frontier because the essential relationship is consisted of the stand sparsity or L

rather than N_{max}. Meanwhile, a nonlinear mixed-effects modelling was used for the C-D rule with the three- (Eq. 2) and four-parameter (Eq. 8) methods.

All the model fitting was performed using the R statistical software (R Core Team, 2024). Considering the hierarchical design at each experimental site and the longitudinal correlation among repeated measurements, mixed-effects model approaches were applied: the *lqmm* function in the *lqmm* R package for linear quantile mixed models (Geraci, 2014, 2022) and the *nlme* function in the *nlme* R package for nonlinear mixed-effects models (Pinheiro et al., 2024). The nested levels of random effects tested in this study were site (expID) and plot (plotID). In a linear quantile mixed model of Reineke's STR, four kinds of random effect options were examined including the expID and plotID as an intercept and a slope, respectively. In a nonlinear mixed-effects model of the C-D rule, random effects of expID and plotID were both examined and tested by setting intercepts in the a_0 and/or b_0 terms of the Eqs. (2) or (8). Finally, latitude, longitude, elevation, temperature sum (in degree-days, threshold value +5 ℃) for the period 1981–2010 (Venäläinen et al., 2005; Lee et al., 2024), site index and a dummy variable of abandoned agricultural land were tested as an additional fixed-effect in Reineke's STR to find any significance of different site carrying capacity.

Nonlinear quantile regression and the modified Reineke's equation with an additional term were fitted as supplementary information (Cao et al., 2000; Zeide, 2005; Cao and Dean, 2015). The summary of fitting approach and results was provided in Appendix B. This supplementary information was included to provide the pattern of MSDR from the other types of models, to describe the different characteristics from the selected MSDR in this study such as Reineke's STR, C-D rule, and Nilson's SSI, and to support comparative explanations in the discussion section (Appendix B).

2.4. Validation of the developed models

2.4.1. Implication of stand carrying capacity

In addition to the MSDR estimated by the models, predicted stand basal area was calculated for comparison as in Eq. (13).

$$G = N \cdot DQ^2 \cdot q \tag{13}$$

where G is the stand basal area (m^2 ha^{-1}), DQ is the quadratic mean diameter (cm), N is the number of trees per ha, q is a constant, equal to $\pi/40000 \approx 0.00007854$.

The predicted maximum stand basal area (G_{max}) was computed by inserting N_{max} estimated by each model of the diameter-based MSDR to N with an input of DQ in Eq. (13). The applied equations of N_{max} from the MSDR measures were Eq. (1) for Reineke's STR and Eq. (12) for Nilson's SSI. For the C-D rule, Eq. (5) was applied to the finally selected best method among the C-D rule options based on fit statistics and reliable model performance. The equations of implied stand carrying capacity were provided for the N_{max} and G_{max} specifically in Table 2.

After calculating the estimated N_{max}, relative density (RD) was calculated based on the ratio of the observed N to N_{max} (Eq. 14). By applying the RD approach, the lower boundary of the self-thinning zone was suggested for the number of trees (N_{lb}) (Eq. 15) and stand basal area (G_{lb}) (Eq. 16) as below.

$$RD = \frac{N}{N_{\max}} \tag{14}$$

$$N_{lb} = N_{\max} \times RD_{lb} \tag{15}$$

$$G_{lb} = G_{\max} \times RD_{lb} \tag{16}$$

where RD is the relative density, N is the observed number of trees per ha (trees ha^{-1}), N_{max} is the estimated maximum number of trees per ha (trees ha^{-1}), N_{lb} is the lower boundary of the self-thinning zone in stem number (trees ha^{-1}), RD_{lb} is the definite relative density applied for lower boundary of the self-thinning zone, e.g., 0.7 or 0.8. G_{lb} is the lower boundary of the self-thinning zone in stand basal area (m^2 ha^{-1}). G_{max} is the estimated maximum stand basal area (m^2 ha^{-1}).

2.4.2. Model comparison and simulation

To confirm the model performance, consequently, allometries with lnDQ-ln$N$ were examined on natural logarithmic scale and with DQ-N and DQ-G on arithmetic scale using the values calculated from Table 2. Moreover, the self-thinning line proposed in the MELA system from Hynynen et al. (2002), which is similar to Eq. (1), was compared to check the reliability and examine a change from the previous model. Because the MELA system (Hynynen et al., 2002) used a basal area-weighted diameter (DG) at stump height (DGs) as $DGs = 2.0 + 1.25 \times DG$, it was converted to diameter at breast height to apply in this study. In addition, DG was approximated from DQ using formula $DG = 0.987 \times DQ + 0.855$ when calculating results using MELA (2002) for the comparisons (the behavior of MELA (2002) with respect to DQ in Figs. 1–4). Based on the equations offered in Table 2, rearranged slopes and intercepts that are comparable to Reineke's STR in log-log scale were provided for the C-D rule and Nilson's SSI, thus enabling to compare readily under the same dimension. N_{max} at DQ of 15, 20, 25, and 30 cm was offered and checked with the validity in practical forest stands of silver birch.

To validate the level of stand carrying capacity in silver birch plantations, observation trajectories were examined by site type and experimental design. Trajectories from several plots were additionally selected to illustrate the model behavior by initial planting density. To verify an update of a stand carrying capacity, simulations of stand development processes in the MOTTI software (Salminen et al., 2005) were demonstrated by inputting the stand information of the first observation from spacing trials as an initial value in which N ranged from 1100 trees ha^{-1} to 1600 trees ha^{-1}. Finally, by taking the model performance, simulation results, and validity into account, the most desirable model among the MSDR lines was suggested by the stand development stage of silver birch plantations in southern and central Finland. At this point, practical self-thinning lines were proposed with

Table 2
Equations of maximum stem number and stand basal area calculated from diameter-based maximum size-density relationship (MSDR) measures. N_{max} is the maximum stem number (trees ha^{-1}), DQ is the quadratic mean diameter (cm), G_{max} is the maximum stand basal area (m^2 ha^{-1}), HD is the dominant height (m), e is the exponential constant (≈ 2.7183), q is a constant equal to π/40000 (≈ 0.00007854). Other symbols are parameters estimated in this study.

MSDR measures	Maximum stem number (N_{max})	Maximum stand basal area (G_{max})	References
Reineke's self-thinning rule (STR)	$N_{\max} = DQ^{s_1} \cdot e^{k_1}$	$G_{\max} = (DQ^{s_1} \cdot e^{k_1}) \cdot DQ^2 \cdot q$	(Reineke, 1933)
Competition-density (C-D) rule	$N_{\max} = \left(\frac{b_0}{a_0}\right) HD^{(b_1 - a_1)} = DQ^{s_2} \cdot e^{k_2}$	$G_{\max} = \left[\left(\frac{b_0}{a_0}\right) HD^{(b_1 - a_1)}\right] \cdot \left(\frac{1}{2b_0 HD^{b_1}}\right)^2 \cdot q = (DQ^{s_2} \cdot e^{k_2}) \cdot DQ^2 \cdot q$	(Kira et al., 1953; Shinozaki and Kira, 1956; Tadaki, 1963; Sterba, 1975, 1987)
Nilson's stand sparsity index (SSI)	$N_{\max} = \left(\frac{100}{s_3 DQ + k_3}\right)^2$	$G_{\max} = \left(\frac{100}{s_3 DQ + k_3}\right)^2 \cdot DQ^2 \cdot q$	(Nilson, 1973; 2006)

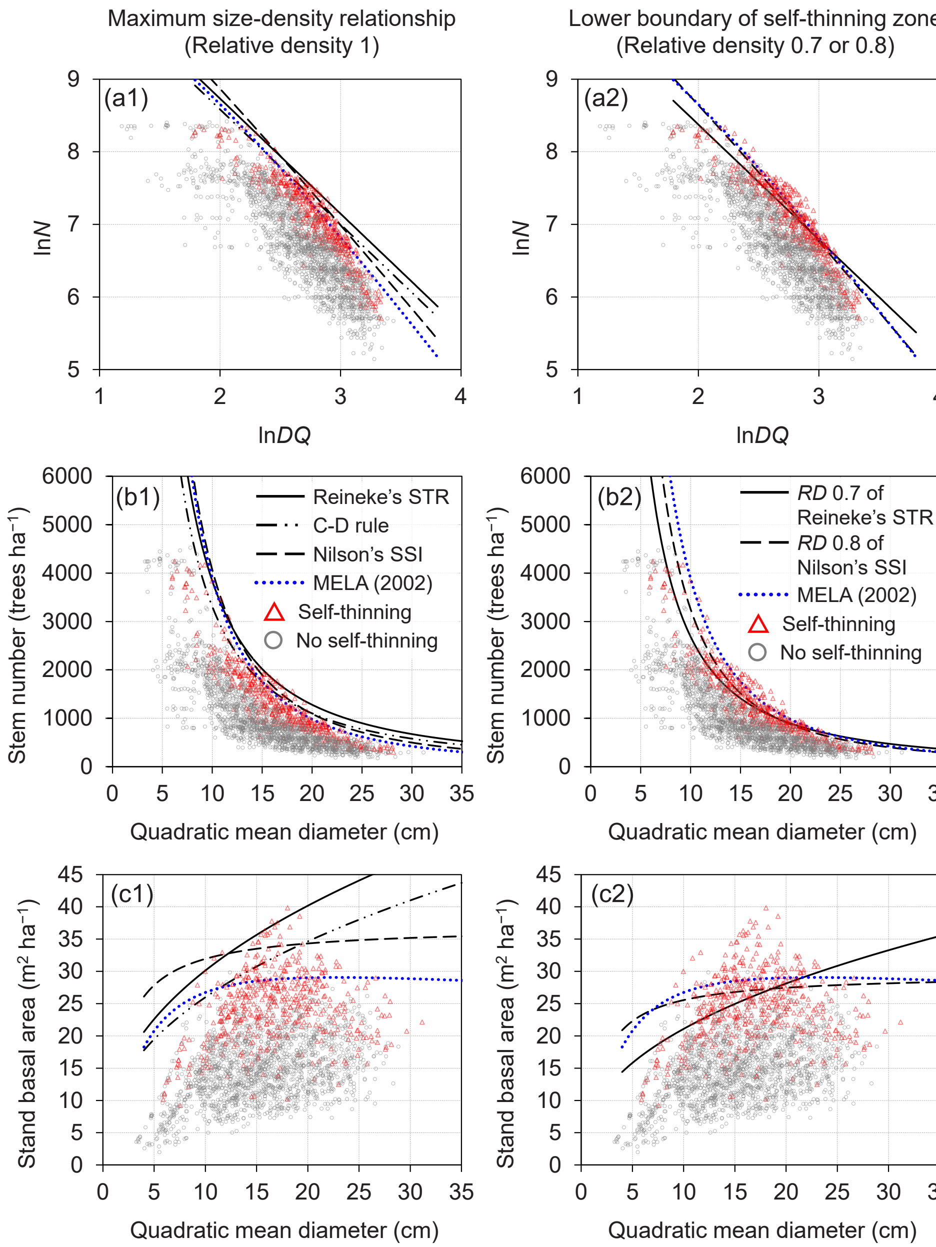

Fig. 1. Maximum size-density relationship lines (plots a1, b1, and c1) and the lower boundary of the self-thinning zone (plots a2, b2, and c2) by measure with scattered observations classified by stand type undergoing self-thinning phases or not on a logarithmic scale of quadratic mean diameter (*DQ*, cm) and stem number (*N*, trees ha^{-1}) (ln*DQ*-ln*N*) (plots a1 and a2), *DQ*-*N* (plots b1 and b2), and *DQ* and stand basal area (*G*, trees ha^{-1}) (*DQ*-*G*) (plots c1 and c2). MELA (2002) is the previous model reported by Hynynen et al. (2002). Maximum size-density relationship lines (plots a1, b1, and c1) are presented using Reineke's self-thinning rule (STR), the competition-density (C-D) rule, and Nilson's stand sparsity index (SSI) with MELA (2002). The lower boundary lines of the self-thinning zone (plots a2, b2, and c2) are presented using the relative density (*RD*) of 0.7 for Reineke's STR and the *RD* of 0.8 for Nilson's SSI with MELA (2002).

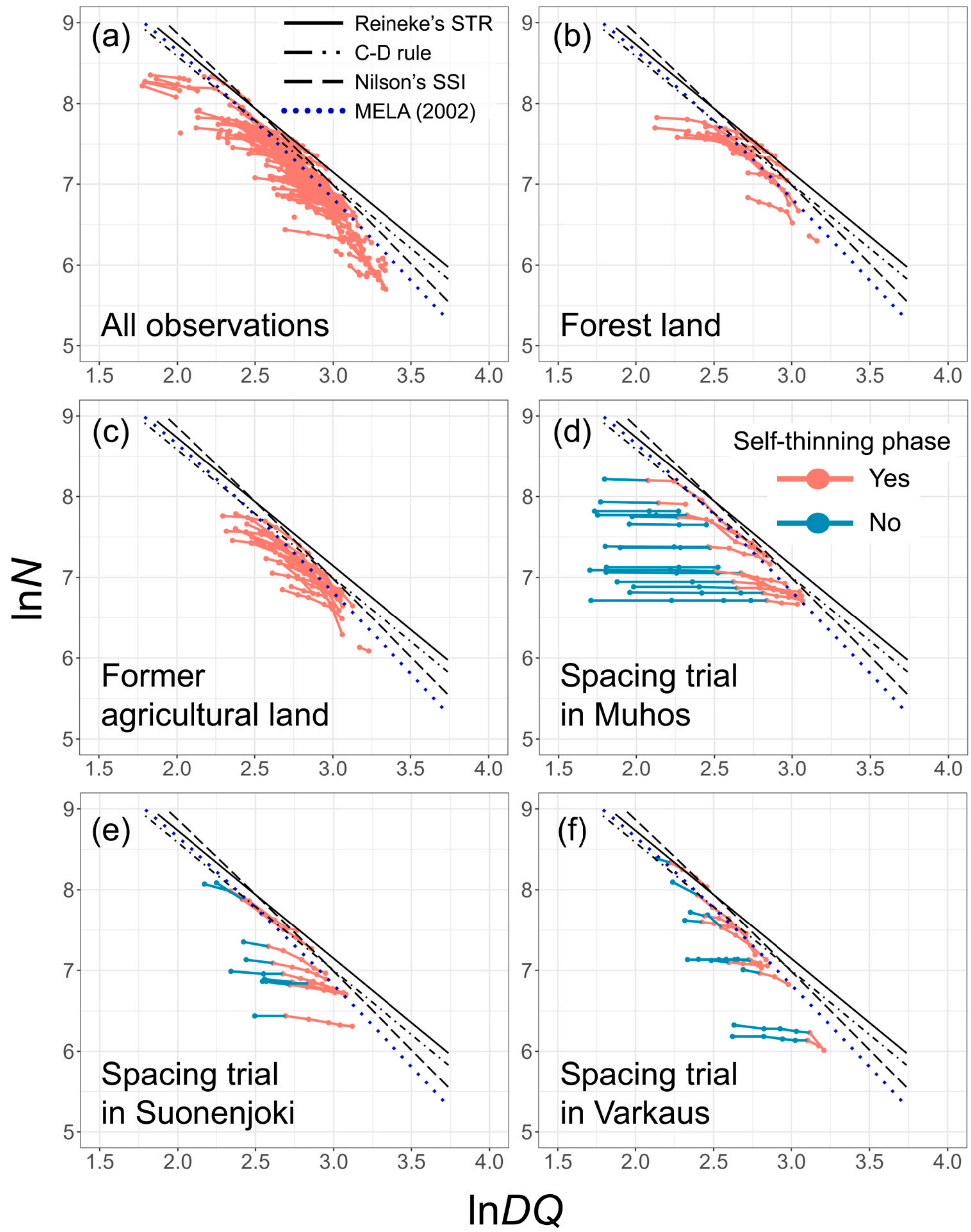

Fig. 2. Maximum size-density relationship lines between quadratic mean diameter (*DQ*, cm) and stem number (*N*, trees ha^{-1}) with observation trajectories on a logarithmic scale by stand types. Reineke's STR stands for Reineke's self-thinning rule, C-D rule stands for the competition-density rule, and Nilson's SSI stands for Nilson's stand sparsity index. MELA (2002) is the previous model reported by Hynynen et al. (2002) in the MELA system. The figures in plots a–c show stand observations that are only undergoing the self-thinning phase: all stands (plot a), stands in forest land (plot b), and stands in former agricultural land except for spacing trials (plot c). Red lines indicate stands undergoing the self-thinning phase while green lines indicate stands that do not reach at this phase in spacing trials of each site (plots d, e, and f). All spacing trials (plots d, e, and f) were located in former agricultural lands.

RD (Drew and Flewelling, 1979; Stout and Larson, 1988; Solomon and Zhang, 2002; Lee and Choi, 2019, 2020) because it's known that self-thinning zone has lower and upper boundaries rather than a solid line (Pretzsch and Biber, 2005; Pretzsch and Mette, 2008; Powell, 2013). An adequate lower boundary of the self-thinning zone would provide more reliable results when simulating the forest growth and yield models by reflecting mortalities at self-thinning phase (Hynynen et al., 2002). The predicted phase of observations based on the finally selected lower boundary of the self-thinning zone was compared with the actual phase of observations to check model performance; that is, the actual vs the predicted classification was compared by calculating the recall (true positive rate) and the precision, e.g., the proportion of actual positives that are correctly identified and the proportion of positive identifications that are actually correct, respectively.

3. Results

3.1. Model fitting of maximum size-density relationship (MSDR)

Upper frontier line with quantile level of 0.99 was fitted to the model on Reineke's STR with a random intercept effect at experiment level. The parameter estimates were all highly significant ($p<0.0001$) and comparable to the original Reineke's slope of -1.605 as the slope parameter of -1.5848 in this study was estimated (Table 3). Nilson's SSI was similarly estimated to Reineke's STR, but the applied quantile level was 0.01 to find a lower boundary line (Table 3). The estimated intercept was insignificant, but the slope parameter was still significant ($p<0.01$) for Nilson's SSI.

Additionally, random intercept and slope effects were further tested

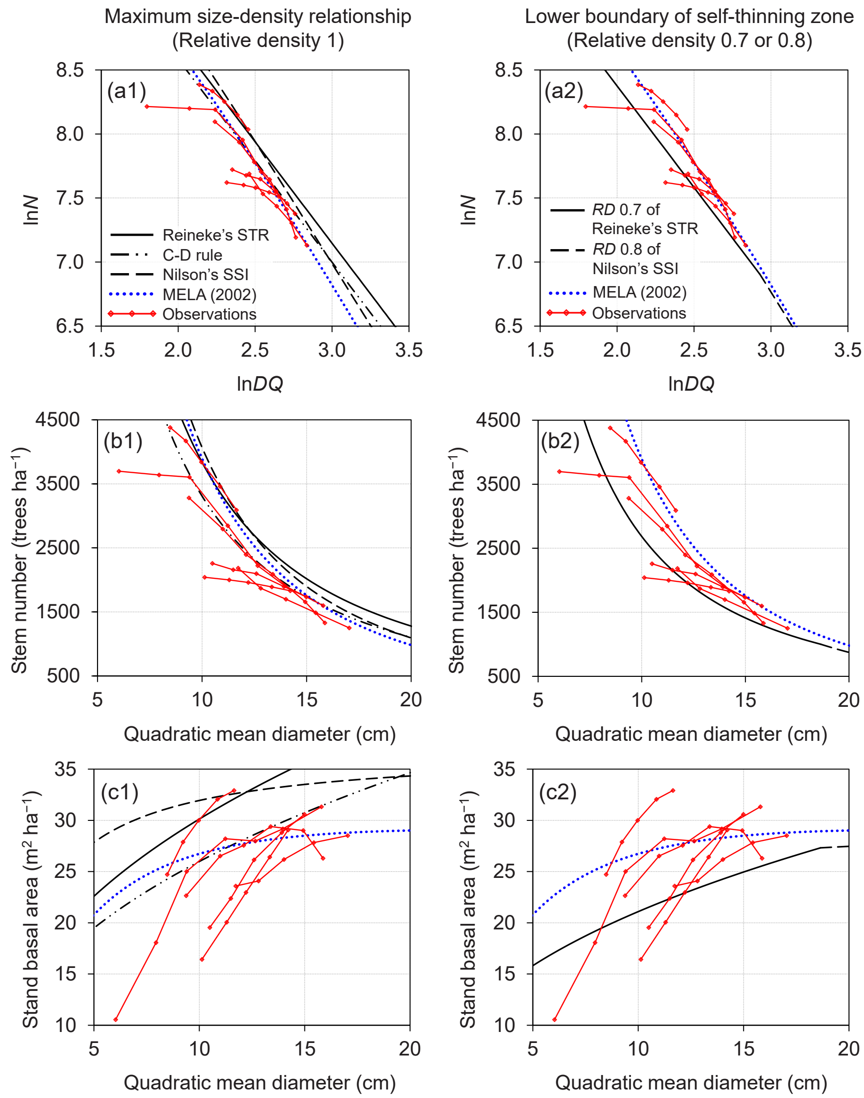

Fig. 3. Maximum size-density relationship lines (plots a1, b1, and c1) and the lower boundary of the self-thinning zone (plots a2, b2, and c2) by measure with exemplary measurement instances from selected five experimental plots in the spacing trials of the Varkaus and Muhos region. MELA (2002) is the previous model reported by Hynynen et al. (2002) in the MELA system. The figure panels describe the estimated lines on a logarithmic scale of quadratic mean diameter (*DQ*, cm) and stem number (*N*, trees ha^{-1}) (ln*DQ*-ln*N*) (plots a1 and a2), *DQ-N* (plots b1 and b2), and *DQ* and stand basal area (*G*, trees ha^{-1}) (*DQ-G*) (plots c1 and c2). Maximum size-density relationship lines (plots a1, b1, and c1) are illustrated using Reineke's self-thinning rule (STR), the competition-density (C-D) rule, and Nilson's stand sparsity index (SSI) with MELA (2002). Lower boundary lines of the self-thinning zone (plots a2, b2, and c2) are presented using the relative density (*RD*) of 0.7 for Reineke's STR and the *RD* of 0.8 for Nilson's SSI with MELA (2002).

at both experiment-level (expID) and plot-level effect within experiment (plotID). The fixed parameters of *DQ* with the random slope effect at both experiment-level and plot-level was not significant with unreasonable estimates. The random intercept effects at plot-level were similar to that at experiment-level in terms of the significance of fixed effects, but the overall fit statistics were not improved. Therefore, it revealed that a random intercept effect at experiment level was the most stable. None of additional fixed effect was significant enough such as latitude, longitude, elevation, temperature sum, site index and a dummy variable of former agricultural land.

Three kinds of the fitting methods were applied for the C-D rule and the estimated parameters were provided in Table 4. The applied b_1 in the three-parameter method (C-D$_{3P}$) of the C-D rule was derived from the estimated parameter of Reineke's STR, which was −1.5848 (Table 3). Also, an original slope coefficient of −1.605 from Reineke's (1933) was tested as the model of C-D$_R$. The estimated parameters of a_0, a_1, and b_0 via Eq. (2) were all significant in C-D$_{3P}$ and C-D$_R$. In the four-parameter method (C-D$_{4P}$) via Eq. (8), the estimated parameter of a_1 was marginally significant. It revealed that the three-parameter fitting method was more stable than the four-parameter fitting method.

An application of random effects on b_0 showed better fit statistics and the residuals were similar when applied to both a_0 and b_0, instead. Among the level for random effect, experiment level was more appropriate for the C-D rule because the parameters with random plot level

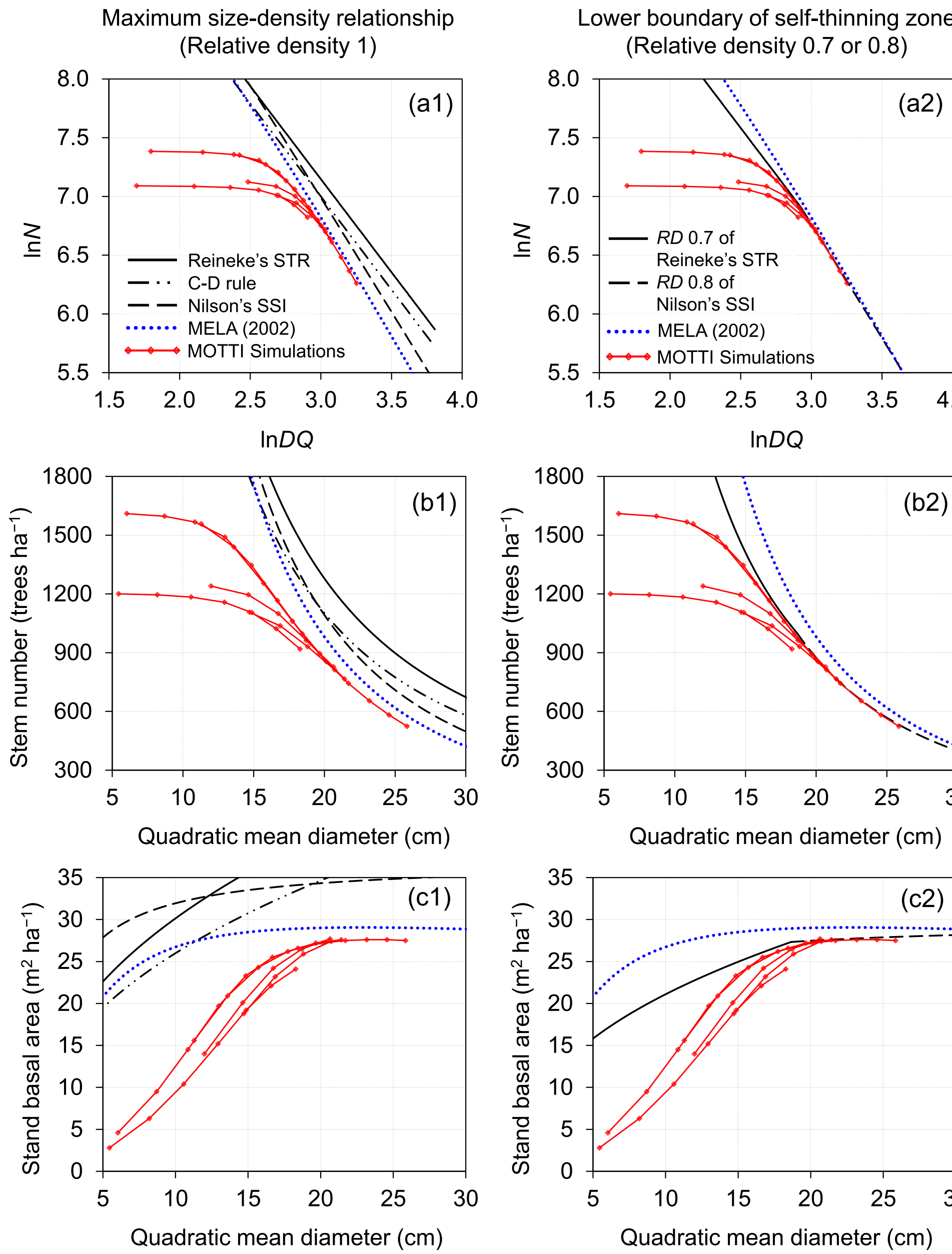

Fig. 4. Maximum size-density relationship lines (plots a1, b1, and c1) and the lower boundary of the self-thinning zone (plots a2, b2, and c2) by measure based on simulation cases from the current MOTTI. MELA (2002) is the previous model reported by Hynynen et al. (2002) in the MELA system. The figure panels describe the estimated lines on a logarithmic scale of quadratic mean diameter (*DQ*, cm) and stem number (*N*, trees ha^{-1}) (ln*DQ*-ln*N*) (plots a1 and a2), *DQ*-*N* (plots b1 and b2), and *DQ* and stand basal area (*G*, trees ha^{-1}) (*DQ*-*G*) (plots c1 and c2). Maximum size-density relationship lines (plots a1, b1, and c1) are illustrated using Reineke's self-thinning rule (STR), the competition-density (C-D) rule, and Nilson's stand sparsity index (SSI) with MELA (2002). Lower boundary lines of the self-thinning zone (plots a2, b2, and c2) are presented using the relative density (*RD*) of 0.7 for Reineke's STR and the *RD* of 0.8 for Nilson's SSI with MELA (2002). The input values of the red lines in the current MOTTI are set up using only the first observation data to simulate the rest of the stand development period.

Table 3
Parameter estimates and standard errors of Reineke's self-thinning rule (STR) and Nilson's stand sparsity index (SSI) using quantile regression with mixed effects for silver birch plantations in southern and central Finland.

Measure	Parameter	Estimate	Std. Err.	t-value	Pr (>|t|)
Reineke's STR (τ=0.99)	k_1	11.9013	0.2601	45.76	<0.0001
	s_1	−1.5848	0.3633	−4.36	<0.0001
	std (expID)	0.7096			
	std(ψ)	0.4493			
Nilson's SSI (τ=0.01)	k_3	0.1112	0.0991	1.12	0.2671
	s_3	0.1457	0.0480	3.04	0.0039
	std (expID)	0.9810			
	std(ψ)	0.5682			

Note: The total number of observations for model fitting was 449. τ is the quantile level. std() represents the standard deviation of the value in parentheses. expID is the random intercept effect at the experiment level. ψ is the residual scale parameter in quantile regression.

effects caused too high slope and intercept parameters of the MSDR. Thus, the random parameter of b_0 at experiment level was finally applied as it was stable (Table 4).

3.2. Estimates of stand carrying capacity and self-thinning zone

Using the estimated parameters in each of the MSDR measures (Tables 3 and 4), the slope and the intercept were computed to compare N_{max} at different DQ through Eqs. (1), (2), (8), and (11) as shown in Table 5. Here, the parameters of the MELA system from Hynynen et al. (2002) were compared together. N_{max} was calculated for each measures using the equations from Table 2. N_{max} from C-D$_{4P}$ was too high compared to other methods especially as DQ increased, e.g., 25 and 30 cm (Table 5). Among the methods of the C-D rules, C-D$_{3P}$ was therefore finally selected considering the significance of estimate parameters and estimated N_{max}. Overall, the slopes and intercepts of this study were gentler and lower, respectively, than those in the MELA system from Hynynen et al. (2002).

A line from each measure was finally selected to present and compare the model performance: Reineke's STR, C-D$_{3P}$, Nilson's SSI, and the approximate MELA from Hynynen et al. (2002). N_{max} among the MSDR measures in a relationship of size-density on a logarithmic plane was similar at certain range, e.g., lnDQ = 2.7, but overall level of the lines presented different upper frontiers based on the different parameters (Fig. 1, Table 5). The line from Reineke's STR displayed the best upper frontier line whereas MELA (2002) was rather situated in the middle of the observed range for self-thinning (Fig. 1, plot a1). More evident differences of the relationship were detected on an arithmetic scale at $DQ \geq 20$ cm. Although Reineke's STR followed the upper frontier line adequately until $DQ = 20$ cm, N_{max} from Reineke's STR was apparently higher than the other MSDR measures when $DQ > 20$ cm (Fig. 1, plot b1).

The plot observations undergoing self-thinning appeared in a wider range when presented with the implied G_{max} (Fig. 1, plot c1). The selected model lines on G over DQ depicted the MSDR patterns more

Table 4
Parameter estimates of the competition-density (C-D) rule from the three different methods using nonlinear mixed effects modeling for silver birch plantations in southern and central Finland.

Measure	Parameter	Estimate	Std. Err.	t-value	Pr (>|t|)	RMSE	R^2	R^2_{adj}
C-D$_{3P}$	a_0	2.4213×10^{-6}	9.1621×10^{-8}	26.43	<0.0001	0.6177	0.9814	0.9628
	a_1	0.6269	0.0109	57.36	<0.0001			
	b_0	1.1453	0.0684	16.73	<0.0001			
	std(expID)	0.0611						
	std(ε)	0.6350						
C-D$_R$	a_0	2.2168×10^{-6}	8.6315×10^{-8}	25.68	<0.0001	0.6192	0.9813	0.9626
	a_1	0.6542	0.0114	57.56	<0.0001			
	b_0	1.1803	0.0707	16.69	<0.0001			
	std(expID)	0.0629						
	std(ε)	0.6365						
C-D$_{4P}$	a_0	1.1025×10^{-5}	2.4979×10^{-6}	4.41	<0.0001	0.6148	0.9815	0.9631
	a_1	0.1570	0.0705	2.23	0.0265			
	b_0	0.6141	0.0719	8.54	<0.0001			
	b_1	−0.8808	0.0357	−24.67	<0.0001			
	std(expID)	0.0337						
	std(ε)	0.6325						

Note: The total number of observations for model fitting was 449. The parameter b_1 for C-D$_{3P}$ was set to the value from Reineke's self-thinning rule in Table 3, and that for C-D$_R$ was set to −1.605 as originally suggested by Reineke (1933). std() represents the standard deviation of the value in parentheses. expID is the random intercept effect at the experiment level. ε is the residuals in model performance.

Table 5
Parameters of diameter-based maximum size-density relationships (MSDR) and stand density indices at each of quadratic mean diameter (DQ) for Reineke's self-thinning rule (STR), competition-density (C-D) rule, and Nilson's stand sparsity index (SSI) of silver birch plantations in southern and central Finland.

MSDR measure		Parameters		Estimated maximum stem number (N_{max})			
Model	Equation	Slope (s_1,s_2,s_3)	Intercept (k_1,k_2,k_3)	DQ = 15 cm	DQ = 20 cm	DQ = 25 cm	DQ = 30 cm
Reineke's STR	1	−1.5848	11.9013	2017	1279	898	673
C-D$_{3P}$	8	−1.5848	11.7534	1740	1103	774	580
C-D$_R$	8	−1.605	11.8067	1738	1095	765	571
C-D$_{4P}$	2	−1.1783	10.6856	1799	1282	985	795
Nilson's SSI	11	0.1457	0.1112	1896	1093	710	498
MELA (2002)	1	−2.2178	14.1979	1613	923	592	408

Note: The equation for MELA (2002) is $\ln N = s_1 \times \ln DG_s + k_1$, where DG_s is the basal area-weighted mean diameter at stump height instead of DQ (Hynynen et al., 2002).

differently and distinctively. Specifically, Reineke's STR line started from the low G, reached 30 m^2 ha^{-1} at $DQ = 10$ cm, and constantly increased with a larger DQ. A pattern of the C-D_{3P} line was similar to Reineke's STR line because of the same slope (s_1, s_2) on a lnDQ-ln$N$ plane, but the implied G_{max} was uniformly lower because the intercept k_2 of C-D_{3P} was lower than that k_1 of Reineke's STR (Table 5, Fig. 1, plot c1). The MSDR lines of Reineke's STR and C-D_{3P} overestimated the upper boundaries of the self-thinning line when $DQ > 25$ cm given that none of the observations suffered a self-thinning phase near 35 m^2 ha^{-1} or in the vicinity of the MSDR lines. On the contrary, Nilson's SSI line presented a gentler level of the upper frontier, which was close to 35 m^2 ha^{-1} when $DQ > 25$ cm (Fig. 1, plot c1). The pattern of MELA was the most similar to that from Nilson's SSI, but the level of the implied G_{max} was lower almost as 5 m^2 ha^{-1} throughout the DQ range (Fig. 1, plot c1).

In addition to the MSDR lines, lower boundary line for self-thinning zone was selected using RD of Reineke's STR and Nilson's SSI (Fig. 1, plots a2, b2, and c2). Reineke's STR was primarily selected instead of the C-D rule because it was all available to estimate the same level of the C-D rule by modifying RD of Reineke's STR. With RD_{lb} 0.7 of Reineke's STR, the observations by self-thinning were categorized adequately as it should be. That is, the lower boundary (lb) line of N_{lb} and G_{lb} was situated as low as for the stands undergoing self-thinning phases and as high as for the stands not undergoing self-thinning phases yet. In other words, the lower boundary line was low enough to include the observations of the self-thinning phases and high enough to exclude the observations of no self-thinning phases. However, as DQ increased and N_{max} decreased, the lower boundary line of N_{lb} and G_{lb} with RD_{lb} 0.7 from Reineke's STR was estimated too high. Specifically, when $DQ >$ 18.65 cm or $N_{lb} <$ 1000 trees, most of the observations failed to be identified as the stands with self-thinning phase. For example, when $DQ \leq$ 18.65 cm or $N_{lb} \geq$ 1000 trees, 52.5 % (160/305) out of the self-thinning observations was categorized as self-thinning phase with the lower boundary line of RD_{lb} 0.7 from Reineke's STR. On the contrary, when $DQ >$ 18.65 cm or $N_{lb} <$ 1000 trees, only 23.6 % (34/144) out of the self-thinning observations was categorized as self-thinning phase, which did not categorize the observations properly, as the implied G_{lb} continuously increased with DQ.

This disadvantage was solved with an application of Nilson's SSI. The selected RD_{lb} 0.8 of Nilson's SSI classified the self-thinning observations the most adequately as DQ increased. To be specific, at $DQ >$ 18.65 cm or $N_{lb} <$ 1000 trees, 29.2 % (42/144) observations of the self-thinning phase were categorized as self-thinning with N_{lb} and G_{lb} from RD_{lb} 0.8 of Nilson's SSI (Fig. 1, plots a2, b2, and c2). DQ of 18.65 cm was the point where RD_{lb} 0.7 of Reineke's STR estimated the same value of RD_{lb} 0.8 of Nilson's SSI as 1000 trees ha^{-1} and the two MSDR lines crossed over. Furthermore, the implied G_{max} and G_{lb} from Nilson's SSI were constant rather than continuously increasing, which is consistent with a concept of the C-D rule.

Overall, for the observations with $DQ >$ 18.65 cm, Nilson's SSI with RD_{lb} 0.8 revealed that it estimated the lower boundary of the self-thinning zone more significantly with N_{lb} and G_{lb} while adequately filtering out the observations that were not from self-thinning. Over the whole range of DQ when the combined RD approach was applied, the recall was 0.4499 (202/449) and the precision was 0.8559 (202/236). In other words, 45.0 % (202/449) observations of the self-thinning phase were categorized as self-thinning and 85.6 % (202/236) out of the predicted values in self-thinning phase was categorized as self-thinning. Almost all the observations were classified properly with the criteria of RD_{lb} 0.8 although it cannot be classified with 100 % for each group using one size variable, DQ, because of variation in reality.

3.3. Model examination

When the trajectories of the self-thinning plots were presented on a lnDQ-ln$N$ plane, the observations were not always situated on the MSDR lines (Fig. 2). There were some variations above and below the lines when the whole measurement period of plots was long term. Moreover, this characteristic was obvious as lnDQ was nearly larger than 3.0 ($\approx$ 20 cm of DQ) (Fig. 2, plot a). The stands in forest sites tended to be resilient to the self-thinning level and retained a higher level of ln$N$ than those in former agricultural lands (Fig. 2, plots b and c). In other words, mortalities from several plots were occurred below the MSDR line in a former agricultural land than in a forest site. However, the dummy variable of former agricultural land was not significant as a fixed-effect in a model fitting for Reineke's STR.

The trajectories of the observations in spacing trials followed the MSDR line adequately when the initial density was relative moderate or dense (e.g., greater than 7.4 of ln$N \approx$ 1600 trees ha^{-1} of N) (Fig. 2, plots d, e, and f). On the other hand, the self-thinning phase below the MSDR lines already occurred at an early stage when initial densities were extremely low with wider spacing (e.g., smaller than 7.0 of ln$N \approx$ 1000 trees ha^{-1} of N). Consequently, a slope and/or an intercept of the self-thinning line were not always constant through the entire range of DQ, and it was rather varied or curved depending on initial planting density.

Example cases of trajectories by initial planting density showed self-thinning phases at different level of density (Fig. 3), but it was located lower than the MSDR lines (Fig. 3, plots a1, b1, and c1). The trajectories mostly experienced self-thinning once it encountered the lower boundary of the self-thinning line. Specifically, the density level of the trajectories tended to be higher with high initial density on lnDQ-ln$N$ or DQ-N planes (Fig. 3, plots a2 and b2). It revealed on DQ-G plane that, when DQ was small, Reineke's STR described self-thinning phases well. When DQ was large, Nilson's SSI estimated it the best (Fig. 3, plot c2). Overall, this analysis indicated that the most appropriate self-thinning line was different by density-related attribute and the stand development stage.

When predicting the trajectory of the size-density relationship with the MOTTI simulator at a five-year interval by setting up the initial values as appeared in our observations of Fig. 3, the simulated lines by stand development were situated below the lower boundary of the self-thinning zone from our model (Fig. 4). The time reaching close to the lower boundary of the self-thinning zone differed along with the initial DQ and N. Nevertheless, the level of the simulated N_{max} and G_{max} maintained equally at any size of DQ once it entered the self-thinning level of the existing MOTTI, which were still lower than the suggested lower boundary of the self-thinning line of this study (Fig. 4). In other words, based on the lower boundary of the self-thinning zone with applying the developed models in this study, the simulated level of N_{max} and G_{max} was a bit higher than those from the existing MOTTI.

4. Discussion

4.1. Evaluation on model fit

In model fitting of Reineke's STR and Nilson's SSI, the quantile level of 0.99 and 0.01 was fitted respectively (Table 3) and considered as an appropriate MSDR lines for each measures (Vospernik and Sterba, 2015;

Yang and Burkhart, 2017). In terms of the random effects amongst the tested ones in Reineke's STR, an intercept of random effect at experiment or site level (expID) was determined in the final model because other options presented unconvincing and unstable results. To be specific, the fixed variable of *DQ* was not significant and showed illogical magnitude of the estimated value with the random slope effect at site (expID) and plot level (plotID). This result is still consistent with the concept of the original Reineke's argument that the slope of the self-thinning rule for a species does not differ by site (Reineke, 1933; Zeide, 2010). Additionally, the random effect of an intercept at plot level (plotID) didn't present any of the improvement compared to the model fit at experiment or site level (expID). In the argument by Reineke (1933), a varying intercept appeared by site or species, not by plot or stand. The results in this study inferred that intercept differed by site, not by plot; an intercept of the self-thinning line is rather invariant and conservative in a site. Hence, an intercept at experiment or site level (expID) was considered as the best random effect option.

There has been much debate whether the slope of −1.605 is a universal constant in Reineke's STR. Recent studies have shown species-specific differences in the slope parameter (Pretzsch and Biber, 2005; Zeide, 2010). Still, the slope parameter, −1.5848, in this study did not differ significantly from the common coefficient postulated by Reineke (Tables 3 and 5). Site productivity has been formally incorporated into the equation (Hynynen, 1993; Mäkinen et al., 2021), but the fixed effect of site index was statistically insignificant in this study. Insignificance of site index could be derived from homogeneous sites or a small spatial range of locations in our data for silver birch compared to the data for Scots pine and Norway spruce in the previous study (Mäkinen et al., 2021). Consistent arguments were found from a previous study (VanderSchaaf and Burkhart, 2008) where the range of site qualities was limited and site quality should not be considered as an indicator on self-thinning in loblolly pine plantations.

A larger intercept has been found in stands grown on the more productive land (Bi, 2001; Weiskittel et al., 2009), and to handle this, Yang and Burkhart (2017) developed the models independently by physiographic region with a dummy indicator variable. Seemingly different MSDR lines were implied between forest sites and former agricultural lands in our study (Fig. 2, plots b and c). Therefore, in addition to *DQ*, a dummy variable of indicating former agricultural land was tested as an additional fixed effect, but the model parameter of the dummy variable was not significant in our study. This result implied that other stand characteristics may override the dummy variable of site type; that is, the real effect may be ascribed to different initial planting densities of three experiments in former agricultural lands (Fig. 2).

Amongst the analyzed methods of the C-D rule, the four-parameter method was less stable, and the estimated N_{max} was too high which was considered as irrational in practice (Tables 4 and 5). Vospernik and Sterba (2015) argued that the three-parameter method is more robust than the four-parameter method. By replacing it with the slope of −1.605 from Reineke's study (1933), the three-parameter method was used in several previous studies (Vospernik and Sterba, 2015; Yang and Burkhart, 2017). However, they also suggested to fit the model for the C-D rule using the slope of the self-thinning line from the independent modeling dataset if the data were large enough (Vospernik and Sterba, 2015). With the argument, C-D_{3P} can be selected as the better one as it presented its own slope independently. The C-D_{3P} method produced a lower MSDR than Reineke's STR (Tables 3 and 4, Fig. 1). This result was consistent to the previous studies from Vospernik and Sterba (2015) and Yang and Burkhart (2017) where the C-D rule estimated a lower MSDR for Norway spruce and ash, and loblolly pine. Therefore, when the number of observations undergoing self-thinning is enough and the potential carrying capacity is the main interest without applying height information as in the present study (Tables 3 and 4, Fig. 1), Reineke's STR is straightforward and more practical than the C-D rule (Vospernik and Sterba, 2015).

The provided quantile level indicated the possible range of MSDR from Nilson's SSI (Tables 3 and 5). The applied levels were considered as stable and applicable in accordance with the previous studies (Gadow and Kotze, 2014; Yang and Burkhart, 2017). By making the slope of Nilson's equation comparable with Reineke's constant slope, Zeide (2010) proposed that the slope of Nilson's self-thinning line differs in kind from that of Reineke's model; it is not constant but becomes steeper with increasing diameter (Zeide, 2010, p. 1124). Because the MSDR line curves fell down along with *DQ* in our study, Nilson's SSI consistently explains better than does Reineke's STR as demonstrated by Zeide (2010). Therefore, based on the findings and arguments, Nilson's SSI can be a better option than Reineke's STR especially for latter stage of stand development also considering senescence.

4.2. Characteristics of the MSDR line

The observation trajectories did not always follow the ln*DQ*-ln*N* line of the MSDR in our study (Fig. 2) and different slopes were implicated along with stand characteristics, e.g., by initial planting density and stand development stage. It indicated the linear slope on a logarithmic scale was not universal for the entire range of *DQ*. For example, it tended to occur more mortality trees when the initial planting density was too high as shown in spacing trials, thus leading to steeper slopes (Fig. 2, plots d–f). Similarly, it was argued that, in loblolly pine stands, the MSDR and the recommended *RD* can be varied by initial planting density (VanderSchaaf and Burkhart, 2012).

Moreover, different slope lines were presented along with stand development stage (Fig. 2, plot a). Zeide (2010) argued that other factors can affect the MSDR along with *DQ*, for example, senescence of trees. As trees become older and larger, the area of the gap created by fallen trees increases, while the ability of neighbors to close it decreases (Zeide, 2005). Therefore, old fully stocked stands cannot be as dense as younger ones (Zeide, 2005). In this perspective, a consistent result was found from the several previous studies where the slope was gentler for small diameters while steeper for large diameters (Meyer, 1938; Stahelin, 1949; Cao et al., 2000; Zhang et al., 2016). These and our results supported the inference that the actual slope of the self-thinning line becomes steeper with increasing age and tree size.

For these reasons, in the previous studies, several approaches were tried to estimate different slopes of the MSDR line by stage and phase of stand development: for example, the segmented regression model for loblolly pine (VanderSchaaf and Burkhart, 2008, 2013) and the nonlinear quantile regression model for slash pine (Cao et al., 2000; Cao and Dean, 2015). Zeide (2005) applied another approach with the modified Reineke's original equation by adding an exponential term to account for a lack of capability in residual trees which cannot completely fill canopy gaps after mortality of neighboring trees as a forest stand matures. In this context, with an agreement on necessity for different slopes of the MSDR lines, our study suggested different slope lines, but the applied approach was different from the previous one. It's because stage and phase of stand development applied with segmented regression was considered as subjective to classify in our data. It's also because nonlinear quantile regression can produce overfitted parameters (Appendix B), which solely rely on the observations, and is not as gradually changing and straightforward in nonlinear slope to provide *RD* as in linear slope. Similarly, the modified Reineke's original equation with an additional term was considered as immoderate trends with an excessive descending slope (Appendix B).

Therefore, the finally applied approach was to combine the self-thinning lines of Reineke's STR and Nilson's SSI by linking two measures when crossed over at a certain *DQ*. Reineke's STR was firstly suggested before the line crossed over Nilson's SSI, but after crossover, Nilson's SSI can explain the self-thinning better at a later stage of stand development. It would be reasonable considering that Nilson's SSI estimates a steeper slope and the lower number of trees than Reineke's STR at a later stage of stand development (Zeide, 2010). With the application the MSDR lines presented different slopes conservatively, which were not volatile depending on definition of self-thinning phases and the number of observations.

Furthermore, it would be plausible to have different MSDR lines between unthinned and thinned stands along with stand development although most observations with large *DQ* were originated from thinned stands where the time since last thinning went a long ago (Table 1, Fig. 2). Hypothetically, stands could react thinnings differently according to the stand density having originally retained because of the adapted root system, fine environment, and microbiome. For example, thinned stands may respond earlier than unthinned stands because thinned stands were not ready to adapt the changed density situation. On the contrary, unthinned stands can withstand and even take advantages of the stand density because the unthinned stands have developed with adjusting the given stand condition (Fig. 2).

4.3. Relative density (RD) and practicability

The phase of self-thinning can be expressed as a range instead of just a solid line because the self-thinning level may hold some variation (Drew and Flewelling, 1979; Stout and Larson, 1988; Solomon and Zhang, 2002; Pretzsch and Biber, 2005; Pretzsch and Mette, 2008; Powell, 2013). As the primary purpose of the MSDR measure in practice is to draw the level of self-thinning that can hold N_{max} and G_{max} rather than finding the maximum stand level without mortality, the highest level was selected amongst the possible results (Table 5). Therefore, Reineke's STR and Nilson's SSI can be used as criteria for N_{max} and G_{max} in this study because the C-D rule presented a relatively lower MSDR line compared to Reineke's STR (Fig. 1, plots a1, b1, and c1) (Vospernik and Sterba, 2015; Yang and Burkhart, 2017).

In the previous studies, the range of RD_{lb} 0.55–0.7 was usually considered as the lower boundary of the self-thinning zone depending on species and region (Long, 1985; Shaw and Long, 2007; Solomon and Zhang, 2002; Powell, 2013; Lee, 2018; Lee and Choi, 2020; Ray et al., 2023). The concept of RD_{lb} was applied similarly in this study, but the different MSDR measure was used by the *DQ* range as discussed in the previous chapter: Reineke's STR at a former phase and Nilson's SSI at a latter phase. Based on the examination in the results of this study with regards to the number of observations and its proportion correctly classified by self-thinning phase, the level of RD_{lb} was finally selected with practical purpose (Fig. 1). Accordingly, RD_{lb} 0.7 of Reineke's STR can be applied as the basic guideline of a lower self-thinning boundary (Eqs. 15 and 16, Fig. 4) especially $DQ \leq 18.65$ cm or $N_{lb} \geq 1000$ trees ha^{-1} based on our results in terms of the percentage and number of observations undergoing self-thinning phase. Later, at $DQ > 18.65$ cm or $N_{lb} < 1000$ trees ha^{-1}, RD_{lb} 0.8 of Nilson's SSI can be applied in the case that the stand density management is preferred below the lower boundary of the self-thinning zone while holding the reliable *G*. In the current study, the selected RD_{lb} and the point of combining Reineke's STR and Nilson's SSI were based on the references such as RD_{lb} 0.55–0.7 and the observation characteristics such as precision and recall. It will be more convincing if any of supporting mathematical or stochastic explanations can be found in future studies to link between Reineke's STR and Nilson's SSI.

In practice, *RD*, RD_{lb}, N_{lb}, and G_{lb} can be effectively used as a tool of diagnosing the level of stand density. In any case, outputs of the models from the current study provided a higher level of *N* and *G* than the MELA system (Hynynen et al., 2002). We considered that the major characteristics were derived from the different data and the number of observations. As our study was conducted with larger data for silver birch plantations with recent progenies, it should reflect the current stand conditions more accurately. The models can be applied without regard to naturally grown Norway spruce understory condition as the small understory trees were found to be insignificant and ineffective to the development of stand characteristics (Lee et al., 2024). Overall, our results are considered to be more favorable in the change of an improved growth and yield conditions.

5. Conclusion

This study analyzed the diameter-based MSDR measures using Reineke's STR, C-D rule, and Nilson's SSI and provided the lower boundary of the self-thinning zone for practical use on silvicultural treatments and growth and yield simulations for silver birch plantations in southern and central Finland. The linear quantile mixed models fitted well for Reineke's STR with quantile 0.99 and Nilson's SSI with quantile 0.01. The nonlinear mixed-effect models fitted for the C-D rules and three-parameter method with the estimated slope (s_1) was the best for the C-D rule in this study based on the fit statistics and reasonable model performance. Based on each of the slope and the intercept of the MSDR, the estimated N_{max} and its rank differed by the MSDR measures according to *DQ*. Still, Reineke's STR showed a higher MSDR than the C-D rule throughout the *DQ* range.

When compared with the observations undergoing self-thinning phase, Reineke's STR estimated the MSDR adequately when *DQ* was small, but Nilson's SSI demonstrated the MSDR better as *DQ* increased in both *N* and *G* variables. This result implied that the slope of the MSDR on ln*DQ*-ln*N* was not constant but variable, and the slope was steeper along with *DQ* as initial planting density increased and stand development progressed. Lastly, the lower boundary of the self-thinning zone for N_{lb} and G_{lb} was suggested using RD_{lb} based on the selected MSDR measures by the *DQ* range. It was evaluated as the most appropriate with RD_{lb} 0.7 of Reineke's STR at $DQ \leq 18.65$ cm or $N_{lb} \geq 1000$ trees ha^{-1} and RD_{lb} 0.8 of Nilson's SSI at $DQ > 18.65$ cm or $N_{lb} < 1000$ trees ha^{-1}. The developed models of MSDR and the self-thinning zone in this study are expected to be informative and useful for managing the stand density and simulating growth and yield in silver birch plantations.

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CRediT authorship contribution statement

Daesung Lee: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **Jouni Siipilehto:** Writing – review & editing, Validation, Methodology, Formal analysis, Conceptualization. **Jari Hynynen:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

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Appendix A. Histogram examples of trees in the stands undergoing the self-thinning phase

To illustrate the characteristics of tree and stand undergoing self-thinning phase, the examples of histogram showed the distribution of mortality trees in dbh class (Fig. A1). It occurred mostly in suppressed trees, and the dbh of dead trees was smaller than the quadratic mean diameter (*DQ*) of living trees. Mortality occurrence did neither increase nor decrease continuously. The number and frequency of dead trees differed by measurement and plot.

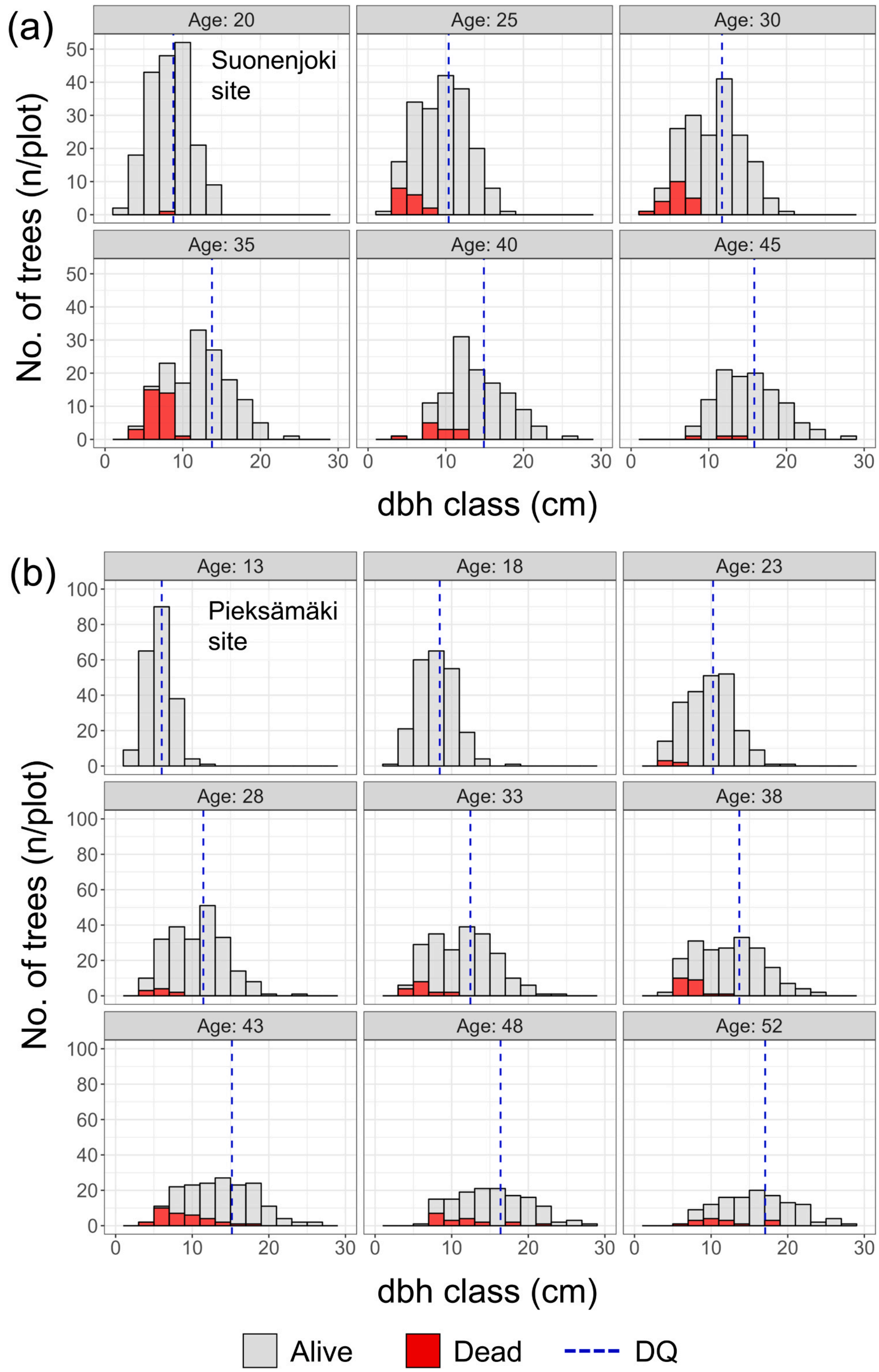

Fig. A1. Tree histogram examples of silver birch stands undergoing self-thinning from the sites of Suonenjoki (a) and Pieksämäki (b). The gray histogram represents living trees, the red histogram represents mortality trees by dbh class of 2 cm, and the blue dashed vertical line indicates quadratic mean diameter (*DQ*, cm) of living trees at each measurement. Note that the measurement instances, at which no mortality was occurred, e.g., early stage, and where the stand carrying capacity was not considered to have reached the self-thinning level were excluded from modeling; only observations at the self-thinning level were included for modeling.

Appendix B. Other examples to estimate a changing slope in the self-thinning rule

Examples of the nonlinear and linear quantile regression based on two kinds of functions were attached as below to illustrate the model performance (Fig. B1). In the first example, the original equation of Eq. (B1) was referenced from Cao et al. (2000) and Cao and Dean (2015) and the estimated parameter of s_1 fitted in this study was applied. The model fitting was performed using *nlrq* function of *quantreg* package in R (Koenker, 2024). Another example for Eq. (B2) was referenced from the modified version of Reineke's original equation (Zeide, 2005). Eq. (B2) was additionally devised in this study by omitting the norm of 10 in., or 25.4 cm, and making it more flexible from the modified version of Reineke's original equation (Zeide, 2005). The model fitting was performed using *lqmm* function of *lqmm* package in R with random effect of experiment (Geraci, 2014, 2022). The applied quantile level for Eqs (B1) and (B2) was 0.95 to obtain the stable model fit. Estimated parameters were shown in Table B1 and the model behavior was illustrated with the predicted lines in Fig. B1.

$$DQ = b_1 \cdot N^{(1/s_1)} \left[1 - \exp\left(b_3 N^{b_4}\right)\right] \tag{B1}$$

$$\ln N = a + b \ln DQ + cDQ \tag{B2}$$

where s_1 is −1.5848 which is provided in Tables 3 and 5, b_1, b_3, and b_4 are the model parameters in nonlinear quantile regression, ln is natural logarithm, N is the number of trees per ha, DQ is quadratic mean diameter (cm). a, b, and c are the model parameters in linear quantile regression, According to Zeide (2005), b is the rate of tree mortality caused by the increase in crown size, and c is the mortality rate due to diminishing canopy closure.

The estimated parameters were not highly significant for certain cases, e.g., b_3 in Eq. (B1) and b in Eq. (B2) (Table B1). Example figures of the nonlinear and linear quantile regression based on two kinds of functions were attached to illustrate the model prediction (Fig. B1). The predicted ln$N$ from the model fits was decreased too dramatically in both cases. It thus led to continuously smaller G nearly after $DQ = 20$ cm as DQ increased. It was considered unrealistic to have excessively small N and G at latter stage, and thus, those equations were not selected as main modeling approaches in this study due to the overfitting and impractical model behavior (Fig. B1).

Table B1
Model parameters of maximum size-density relationships using a nonlinear equation through nonlinear quantile regression and the modified version of Reineke's original equation through a linear quantile mixed model at the 0.95 quantile level.

Model	Parameter	Estimate	Std. Err.	t-value	Pr (>|t|)
Eq. (B1)	b_1	1914.3206	76.4238	25.05	<0.0001
	b_3	−0.0221	0.0091	−2.44	0.0153
	b_4	0.6360	0.0747	8.53	<0.0001
Eq. (B2)	a	8.9659	0.5378	16.67	<0.0001
	b	0.0641	0.3101	0.21	0.8370
	c	−0.1077	0.0324	−3.32	0.0017
	std(expID)	0.9960			
	std(ψ)	0.3734			

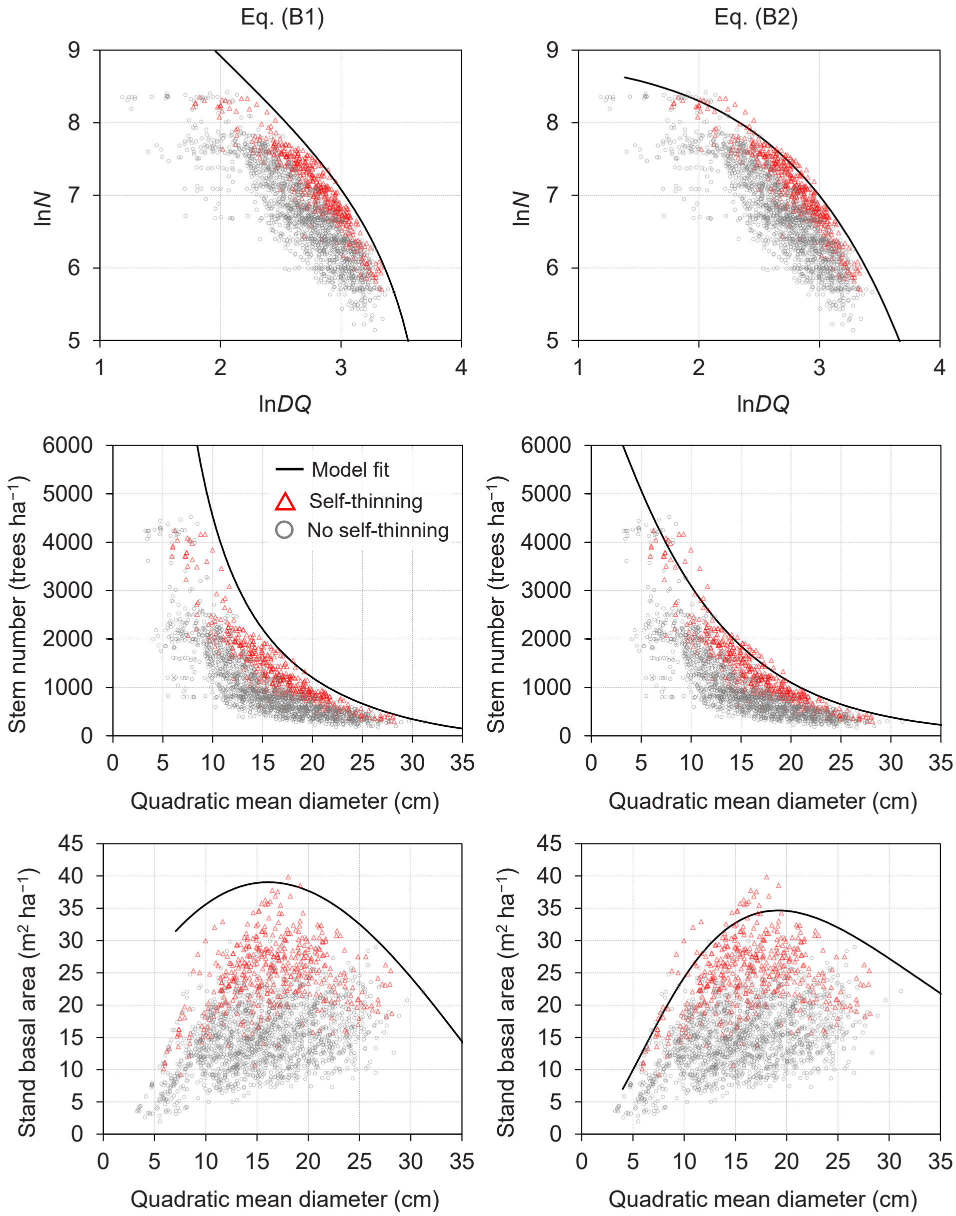

Fig. B1. Maximum size-density relationship lines using a nonlinear equation (Eq. B1) and the modified version of Reineke's original equation (Eq. B2) at the 0.95 quantile level for silver birch plantations in southern and central Finland.

Data availability

Data will be made available on request.

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