Do competition-density rule and self-thinning rule agree?

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HAL Id: hal-01284181
https://hal.science/hal-01284181

ORIGINAL PAPER

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Abstract

· *Key message* **Competition-density relationships and self-thinning are major principles in forest growth. They are combined, describing self-thinning as a marginal case of the competition-density relationship. Robust estimation techniques allow parameterizing of both from national forest inventory data even for minor species.**

· *Context* The competition-density principle, which can mathematically be described by the competition-density rule, is an important principle in plant ecology. The border line relationship is the self-thinning rule. Despite the importance of both rules for forest management, they have been fit for few species.

· *Aims* The aim of this study is to compare competition-density rule and self-thinning rule in particular with respect to potential density for 15 species from the Austrian National Forest Inventory (ANFI).

· *Methods* The self-thinning line was estimated using quantile regression. The competition-density rule was fit as four- and as three-parameter model, where the fourth parameter was substituted (a) with a specific slope from the self-thinning line estimated from the ANFI and (b) Reineke's slope (-1.605).

· *Results* Potential density was highest for Austrian pine and Norway spruce, followed by silver fir and Scots pine; it was considerably lower for European larch, stone pine and broadleaf species. Species-specific slopes of the self-thinning line ranged between -1.5 and -2.0 and were significantly different from Reineke's slope for Norway spruce, European larch and European beech.

· *Conclusions* Using robust estimation techniques, both competition-density rule and self-thinning line can also be fit for minor species, providing an important guide for practical forest management.

Keywords Competition-density rule · Self-thinning rule · Maximum basal area · Potential density · Quantile regression · National Forest Inventory

1 Introduction

Competition is a key process affecting plant populations and communities (Drew and Flewelling 1977; Xue et al. 2011). Trees, like other plants, require site resources such as light, water, nutrients and space. As individual trees grow in size, their demand on site resources and growing space increases. When resources are no longer adequate to support full growth of all trees, growth of some trees will decrease and some trees will eventually die (Burkhart and Tomé 2012). The competition-density principle is considered one of the most important principles in plant ecology (Drew and Flewelling 1977). The competition-density rule (Kira et al. 1953) mathematically describes this principle for a variety of densities (Eq. 1). For a given dominant height or age, average tree size decreases as density increases.

As intraspecific competition becomes fiercer, the per capita growth rate slows until the population reaches a stable maximum, the carrying capacity. At the carrying capacity, the rate of change of population density is zero because the population is as large as possible based on the resources available. This density-dependent, species-specific upper frontier is described by the self-thinning rule (Reineke 1933). The rule states, that in logarithmic scales, the relationship between plant size and stand density is a straight line in overcrowded (fully stocked) stands (Eq. 2). Individual stands seldom travel along their self-thinning frontier, but are more likely to converge towards

Contribution of the co-authors Sonja Vospernik performed data analysis and wrote the manuscript. Hubert Sterba contributed ideas, participated in the discussion, evaluated the manuscript and coordinated the research project

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them during the self-thinning phase (Kira et al. 1953; Bi 2001; Vanclay and Sands 2009).

The self-thinning line represents potential density of a particular species across sites. The intercept of the self-thinning line, c_0, varies with species and site, and small variations in c_0 cause considerable differences in density. The slope parameter, c_1, was estimated to be -1.605 by Reineke and varies little with species, age or site quality. There has been much debate, whether the slope of -1.605 is a universal constant. But recent research seems to indicate that there are species-specific differences (e.g. Pretzsch and Biber 2005; Zeide 2010). Also, site productivity has only recently been formally incorporated into the equation. In general, a larger intercept has been found in stands grown on the more productive land (Bi 2001; Weiskittel et al. 2009).

$$d_g = \frac{1}{a_0 \cdot h_{dom}^{a_1} \cdot N + b_0 \cdot h_{dom}^{b_1}} \tag{1}$$

$$\ln(N) = c_0 + c_1 \cdot \ln(d_g) \tag{2}$$

d_g Quadratic mean diameter
N Stem number per hectare
h_{dom} Dominant height
a_0, a_1, b_0, b_1 Coefficients of the competition-density rule
c_0, c_1 Coefficients of the self-thinning line

Competition-density rule and self-thinning rule are expressions of the same ecological principal. However, the competition-density rule is more widely applicable, because it describes the relationship between stem number, quadratic mean diameter and dominant height for different densities. Accordingly, Sterba (1987) showed that the coefficients of the self-thinning rule can be obtained from the competition-density rule (Eqs. 3 and 4). This provides a convenient way to estimate the parameters of the self-thinning rule from inventory data. Vice versa, the slope coefficient from the self-thinning rule (-1.605) is used as substitute in Eq. 1, reducing the four-parameter competition-density rule to a model with only three parameters to be estimated (Eq. 5). The three-parameter model is more robust than the four-parameter model.

$$c_1 = \frac{a_1}{b_1} - 1 \tag{3}$$

$$c_0 = \frac{b_0}{a_0} \cdot (2b_0)^{c_1} \tag{4}$$

$$d_g = \frac{1}{a_0 \cdot h_{dom}^{a_1} N + b_0 \cdot h_{dom}^{a_{1/-0.605}}} \tag{5}$$

dg Quadratic mean diameter
N Stem number per hectare
h_{dom} Dominant height
a_0, a_1, b_0, b_1 Coefficients of the competition-density rule
c_0, c_1 Coefficients of the self-thinning rule

Further, Sterba (1987) showed that maximum basal area can be obtained from the competition-density rule by calculating basal area from stem number and quadratic mean diameter in Eq. 1 and setting the first derivate to zero. The resulting equation is given below (Eq. 6).

$$G_{max} = \frac{\pi}{16000 \cdot a_0 \cdot b_0} \cdot h_{dom}^{-(a_1 + b_1)} \tag{6}$$

G_{max} Maximum basal area, potential density
h_{dom} Dominant height
a_0, a_1, b_0, b_1 Coefficients of the competition-density rule

Some differences in size-density relationships are introduced by the use of stand diameter, height, volume, or biomass for relating mean plant size to density. In forestry, usually quadratic mean diameter is used due to ease of computation and because it is a direct measure that does not rely on prior relationships. Furthermore, mortality is driven by crown width, which is more closely related to diameter than to height and volume (Zeide 2010).

Initial works on size-density relationships dealt with even-aged pure stands. In mixed and uneven-aged stands, the slope of the maximum density line depends on the skewness of the diameter distribution, which in turn is correlated with species mixture and "unevenagedness" (Sterba and Monserud 1993; Gül et al. 2005). As the diameter distribution becomes increasingly skewed, the slope becomes more flat.

Both, competition-density rule and self-thinning rule, have been extensively used for forest management purposes: for stand density management diagrams and stocking guides (e.g. Drew and Flewelling 1979; Halligan and Nyland 1999; Spathelf and Schneider 2000), yield tables (e.g. Mesfin 1996; Eckmüllner and Vospernik 2005) and in individual tree growth models, where the actual stem numbers are compared to the maximum theoretical number given by the self-thinning line (Mäkelä et al. 2000; Nagel 2009).

Despite the importance of size-density relationships, functions for many species are lacking. To date, for Austria, only functions for common beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.) have been fit (Schnedl 2003); functions for Norway spruce (*Picea abies* Karst.) (Sterba 1975; Eckmüllner and Vospernik 2005) and Stone pine (*Pinus cembra* L.) (Lick and Sterba 1991) have been developed for specific regions.

The aims of this manuscript are (1) to compare two different models (competition-density rule, self-thinning rule) used

to fit size-density relationships. In particular, we want to evaluate maximum densities obtained by the two methods and discuss advantages and disadvantages of the models for practical use and (2) to evaluate intercept and slope of the self-thinning line and compare the resulting potential densities across species, including minor species for which to date such relationships are lacking.

2 Material and methods

2.1 Study area

Austrian forests cover an area of 4.0 mio ha, which is about 48 % of Austria's land area. Elevation ranges from about 100 to 1800 m, thus reaching from collin to subalpine forest. They are comprised in the Alpine as well as in the Continental biogeographic region (European Environmental Agency 2006) and contain the forest types of the alpine coniferous forests and the mesophysic deciduous forests sensu EEA (European Environmental Agency 2006).

2.2 Data

For this research, we selected plots from the third, fourth, fifth, sixth and seventh Austrian National Forest Inventory (ANFI). The ANFI is a systematic permanent forest inventory over all of Austria. Data were collected from 1981 to 1985, 1986 to 1990, 1992 to 1996, 2000 to 2002, and 2007 to 2009. ANFI clusters are located at the nodes of a 3.89x3.89 km^2 grid. Each cluster contains four sample plots, which are located at the corners of a 200×200-m square. On each sample plot, trees with a dbh from 5 to 10.4 cm were sampled on fixed radius plots with a radius of 2.6 m which is the critical distance for a 10.4-cm tree in angle counts with a basal area factor (BAF) of 4 m^2/ha; trees with a dbh >10.4 cm were selected by angle count sampling with BAF=4 m^2/ha. We selected plots from the ANFI which were situated entirely in the forest and were undivided by forest roads.

Models were calculated for 15 species that were found on more than 50 plots in pure stands. Pure stands were defined as stands where the relevant species constituted more than 80 % of basal area at the respective inventory. Norway spruce, with 11,881 plots, is by far the most frequent species; other important tree species, which occur on 1091 to 101 plots (Table 1), are European beech, Scots pine, European larch, oak, Austrian pine, silver fir, ash, stone pine and hornbeam. Sycamore, grey alder, birch, black locust and black alder are found on less than 100 plots. The dataset encompasses a large range of dominant heights, quadratic mean diameters and densities. Summary statistics and scientific names for the species are given in Table 1.

2.3 Methods

To estimate the coefficients of the self-thinning rule, we used linear quantile regression (Koenker and Bassett 1978). Quantile regression is a method for estimating functional relationships for all proportions of the probability distribution, i.e. equations estimate the conditional median or quantiles of the response variable. Quantile regression is especially useful when extremes are important and for data with unequal variance. Unequal variance implies that there is more than a single slope (rate of change) between a response variable and a predictor variable. Quantile regression makes no distributional assumption about the error term and therefore offers considerable model robustness against outliers (Cade and Noon 2003). Since the self-thinning line is a limiting boundary, we fit models to the 0.9, 0.95 and 0.99 quantile. Slopes obtained at the extremer quantiles were then tested against slopes at the median (Koenker and Bassett 1982).

The coefficients of the competition-density rule were estimated using nonlinear regression. We estimated the four-parameter model according to Eq. 1. To obtain the three-parameter competition-density rule, we inserted (a) Reineke's slope, −1.605, and (b) the species-specific slopes obtained from quantile regression (quantile=0.95) into Eq. 1. We estimated the remaining parameters by the generalized method of moments (Hansen 1982) in the three-parameter competition-density rule. Generalized method of moments is an estimation procedure that allows models to be specified, while avoiding unwanted assumptions, such as specifying a particular distribution. Generalized method of moments is a robust procedure and is recommended for heteroscedastic data, where a particular weighting scheme is difficult to determine. The four-parameter model was fit using least squares estimation—the model contained too many parameters to be estimated by generalized method of moments (GMM). Both, three- and four-parameter models were weighted by stem number. From the four-parameter model, we calculated intercept (Eq. 3) and slope (Eq. 4) of the Reineke rule as proposed by Sterba (1987) and compared the results to slopes obtained by quantile regression.

3 Results

3.1 Self-thinning rule

Because we were seeking the self-thinning boundary line, the highest quantile that had significant parameters was chosen. Models were fit to the 0.99 quantile for the six most frequent species, which are Norway spruce, European beech, Scots pine, European larch, oak and Austrian pine. Models were fit to the 0.95 quantile for the following four species: silver fir, ash, stone pine and hornbeam. For the remaining five species,

Table 1 Summary statistics of the data

Species	Number	Dominant height (m)				Quadratic mean diameter (cm)				Density (trees/ha)			
		Min	Max	Mean	Std	Min	Max	Mean	Std	Min	Max	Mean	Std
Norway spruce *Picea abies* Karst.	11,881	2.4	48.9	23.0	8.7	5.0	81.5	26.0	12.6	8	10,185	1125	1087
Silver fir *Abies alba* Mill.	179	4.8	44.0	26.4	10.0	6.5	84.8	30.8	15.9	15	3608	733	803
European larch *Larix decidua* Mill.	505	3.9	43.9	20.1	7.5	5.3	81.1	32.7	15.8	8	4427	461	658
Scots pine *Pinus sylvestris* L.	848	3.1	32.7	19.4	6.1	5.1	49.8	22.8	7.9	21	6741	1183	1048
Austrian pine *Pinus nigra* Arnold	205	8.6	29.2	16.4	4.3	11.2	47.8	24.3	6.7	57	5021	1199	827
Stone pine *Pinus cembra* L.	102	4.1	23.5	15.1	4.5	6.5	67.4	38.0	12.1	18	1266	294	235
European beech *Fagus sylvatica* L.	1091	3.5	41.9	23.4	7.9	5.0	85.5	28.2	13.6	9	6224	866	952
Oak *Quercus spp.*	394	4.3	34.4	18.1	6.2	5.1	79.5	26.1	15.6	9	3663	739	652
Hornbeam *Carpinus betulus* L.	101	5.3	30.1	13.4	4.8	5.3	48.1	13.4	7.1	22	8494	2047	1744
Ash *Fraxinus excelsior* L.	118	5.3	37.7	20.0	7.5	5.1	66.2	23.2	14.7	12	6478	991	1251
Sycamore *Acer spp.*[a]	68	5.6	30.6	17.7	5.9	5.3	76.6	27.1	15.0	9	3103	737	874
Black locust *Robinia pseudoacacia* L.	64	6.4	25.6	15.3	4.6	5.2	24.6	13.1	3.5	284	5238	1252	723
Birch *Betulus spp.*	66	4.1	25.3	13.1	5.0	5.1	52.2	14.1	9.4	19	5511	1479	1380
Black alder *Alnus glutinosa* Gaertn.	60	3.3	31.8	16.8	6.9	5.0	32.4	17.4	7.2	49	4749	1150	1014
Grey alder *Alnus incana* Moench	68	4.8	22.9	12.5	4.6	5.7	34.7	13.9	5.6	42	5505	1671	1153

[a] Acer spp., predominantly *Acer pseudoplatanus* L.

which occur on less than 100 plots, we were not able to fit a model to the extreme quantiles. Model coefficients are given in Table 2. The quantile regression models fitted the data well. As an example, the models for Norway spruce and ash are shown in Fig. 1.

In order to be able to compare the models of all ten species for which models could be fit, we compared the self-thinning line at the 0.95 quantile. For all species except stone pine (intercept=11.62; slope=−1.50), the intercept ranged between 12.41 and 13.25 and the slope ranged between −1.63 and −2.00 (Table 2). Slopes for Norway spruce, European larch and European beech were significantly different from Reineke's slope. Maximum (potential) stem number (Fig. 2) and maximum (potential) basal area (Fig. 3) for different tree species are also compared at the 0.95 quantile. In the left panels, the conifer species (Figs. 2a and 3a) and in the right panels broadleaf species (Figs. 2b and 3b) are plotted. For a given quadratic mean diameter, potential density (stem number, basal area) is highest for Austrian pine and Norway spruce, followed by silver fir and Scots pine. Potential density is considerably lower for European larch, stone pine and all broadleaf species. For the broadleaf species beech, ash and hornbeam have higher potential stem numbers and basal areas than oak. For larch and broadleaf species, the maximum basal area is almost constant over quadratic mean diameter, because of the very steep slope of the self-thinning rule estimated for these species—a slope of −2 means a constant basal area over the whole range of quadratic mean diameters. As would be expected, the intercept slightly increases with increasing quantile. These small differences in intercept however cause large differences of 5–21 m^2 ha^{-1} in maximum basal area.

Slopes of the self-thinning lines estimated at the 0.95 quantile were steeper than the slopes at the median except for oak and Scots pine. These differences were however only significant for Norway spruce and European beech.

3.2 Competition-density rule

The competition-density rule (Tables 3 and 4) estimates the relationship between stem number and quadratic mean diameter for a variety of densities. In smaller stands (dominant height=15 m), quadratic mean diameter decreases nearly linearly with increasing density. In larger stands (dominant height=35 m), competition acts more severely even with lower stem numbers, and therefore, the decrease is more sharp, till it levels off at higher densities (Fig. 4).

To compare the potential densities estimated by the competition-density rule to those obtained from the self-thinning rule, we calculated maximum basal areas. For the three-parameter competition-density rule, the rate of increase in maximum basal area with quadratic mean diameter depends on the slope of the self-thinning line inserted into the model. For most species, the slope estimated from the Austrian National Forest Inventory is steeper than Reineke's slope (−1.605) (Table 2). The increase in maximum basal area with quadratic mean diameter is therefore smaller than with Reineke's slope. Reineke's slope corresponds more closely to the slope estimated at the median or to the slope estimated from the four-parameter competition-density rule.

Plotting the maximum basal areas by species results in a similar ranking as for the self-thinning rule. Obvious

Table 2 Shade tolerance on a 1 (=shade tolerant) to 9 (=shade intolerant) scale and coefficients of the self-thinning rule at the median, at the 0.95 quantile, at the 0.99 quantile and coefficients for the self-thinning rule obtained from the competition-density rule according to Sterba (1987). For sample size, see Table 1

Species	Shade tolerance[a]	Q 0.5		Q 0.95		Q 0.99		CD rule	
		c_0	c_1	c_0	c_1	c_0	c_1	c_0	c_1
Norway spruce	(5)	11.57	−1.542	12.86	−1.753	12.94	−1.716	12.19	−1.589
Silver fir	(3)	11.45	−1.574	12.41	−1.633				
European larch	(8)	11.27	−1.744	13.00	−1.936	13.60	−2.053	11.04	−1.352
Scots pine	(7)	12.30	−1.764	12.77	−1.750	12.93	−1.762	11.52	−1.375
Austrian pine	(7)	12.37	−1.711	13.20	−1.845	12.25	−1.488		
Stone pine	(7)	9.92	−1.194	11.62	−1.500				
European beech	(3)	11.86	−1.701	13.25	−1.941	13.28	−1.891	12.56	−1.791
Common oak	(7)	12.07	−1.904	12.62	−1.800	12.93	−1.850	12.08	−1.739
Hornbeam	(4)	10.36	−1.184	13.33	−2.000				
Ash	(4)	11.22	−1.705	13.22	−1.939				
Birch	(7)	11.58	−1.883						
Grey alder	(6)	9.27	−0.753						

[a] Shade tolerance according to Ellenberg et al. (2003) on a 1 to 9 scale. Shade tolerance for all tree species is given in parenthesis to indicate that shade tolerance refers to shade tolerance during regeneration but may differ in mature stands

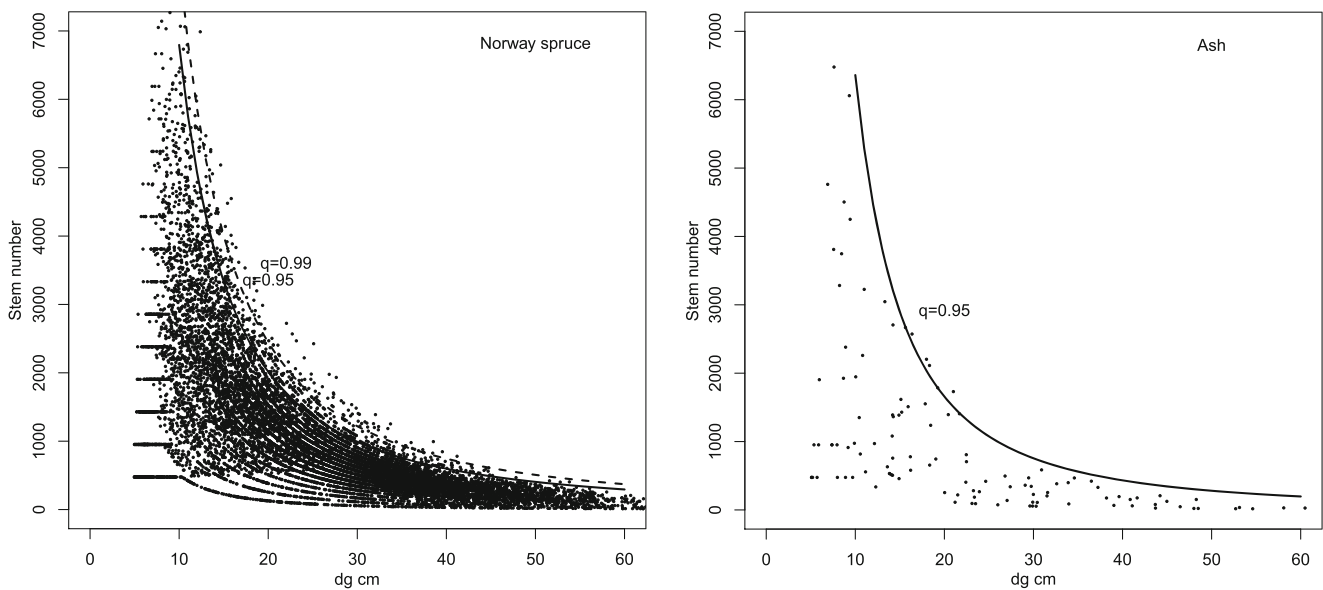INRA SCIENCE & IMPACT Springer

Fig. 1 Plot of stem number over quadratic mean diameter for Norway spruce and ash. *Dots* indicate the observations of the Austrian National Forest Inventory. The *lines* show the self-thinning line (Reineke rule), fit using quantile regression. *Solid line*, q=0.95; *dashed line*, q=0.99

differences in ranking are however the ranking of stone pine and ash and hornbeam in the three-parameter model fit using Reineke's slope in comparison to the other two models (self-thinning rule with quantile regression, three-parameter competition-density rule using the slope from the ANFI). In that model, stone pine attains as high basal areas as Scots pine, whereas ash has a lower basal area than oak in that model. For a number of broadleaf species, maximum basal areas could only be attained from the three-parameter competition-density rule using Reineke's coefficient. The ranking in maximum basal area of broadleaf species for that model were high basal areas for a given dominant height for grey alder, hornbeam,

black alder, and birch. However, all four species seldom reach dominant heights of more than 20 m. Followed by sycamore, European beech, oak and black locust. As mention before, the smallest basal area for that model is obtained for ash.

4 Discussion

4.1 Self-thinning rule

The intercept and slope estimated from the Austrian National Forest Inventory represents the species boundary line, i.e. the
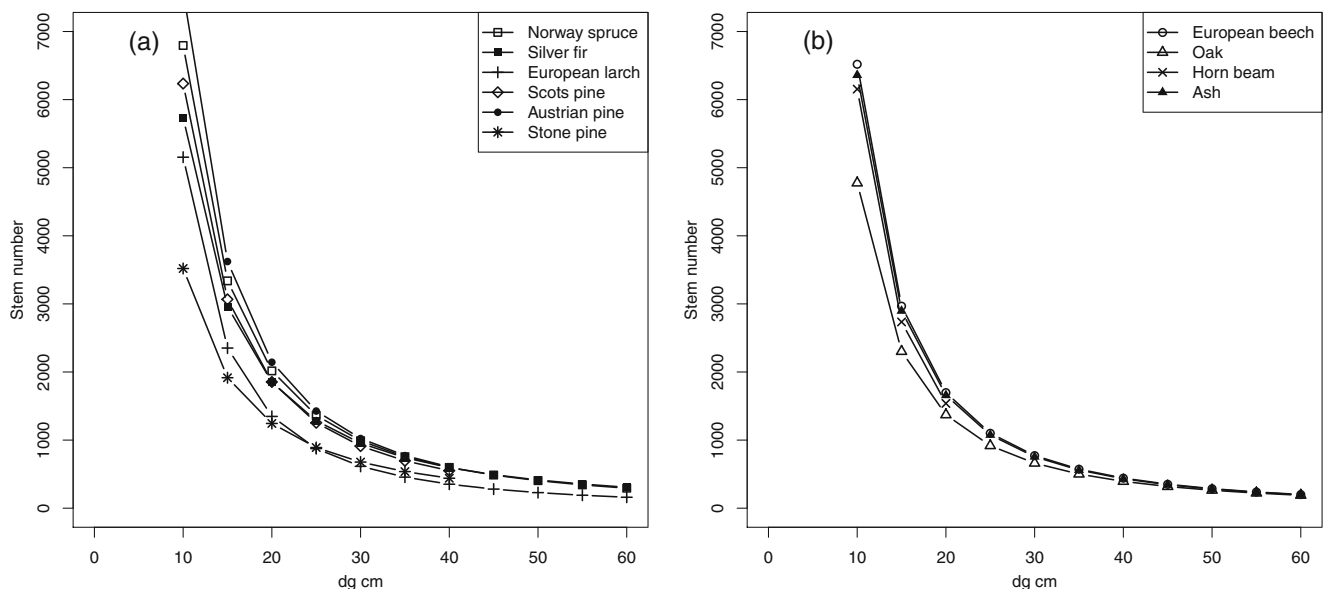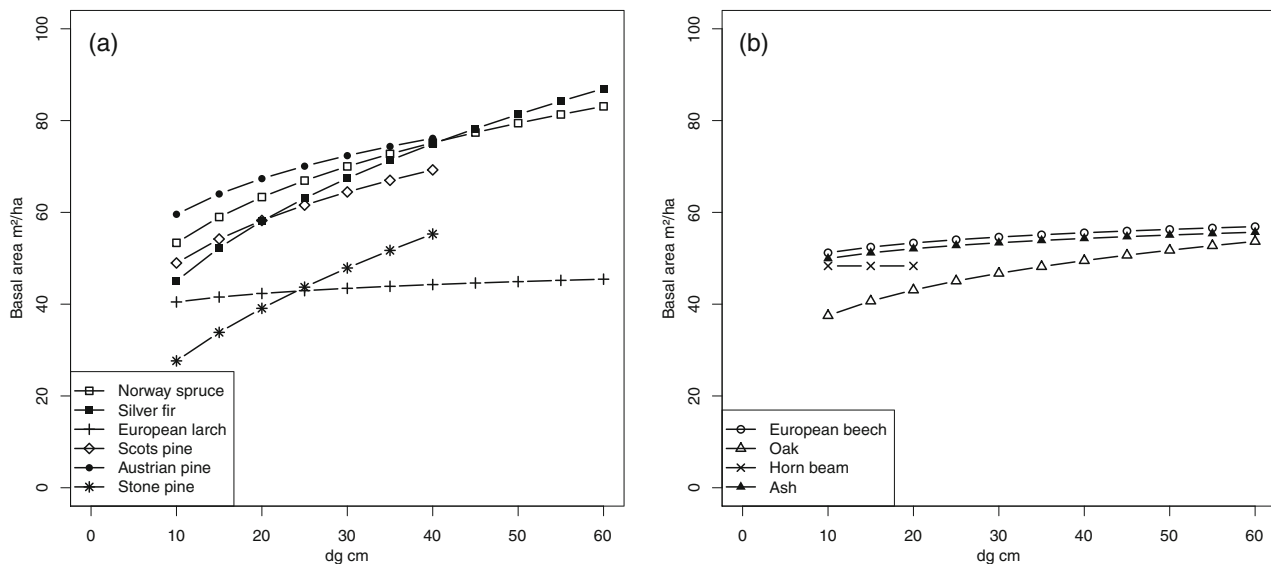

Fig. 2 The self-thinning rule (Reineke rule) fitted from the Austrian National Forest Inventory using quantile regression (q=0.95). The *plot* shows maximum stem numbers over quadratic mean diameter for conifer (**a**, *left panel*) and deciduous (**b**, *right panel*) species

Fig. 3 The self-thinning rule (Reineke rule) fitted from the Austrian National Forest Inventory using quantile regression (q=0.95). The *plot* shows maximum basal area over quadratic mean diameter for conifer (**a**, *left panel*) and deciduous (**b**, *right panel*) species

"overall" maximum density of that species in Austria. This overall maximum is remarkably similar over large geographic areas or sampling methods (inventory, permanent research plots). For example, maximum densities (basal area, SDI) obtained for Norway spruce and Scots pine from inventory data in Austria are almost identical to those obtained from permanent research plots for spruce in Bavaria (Pretzsch and Biber 2005) or Scots pine in Spain (Del Rio et al. 2001). Similarly, Zhang et al. (2013) evaluated the self-thinning line of ponderosa pine using inventory data and permanent research plots. They found both dataset to be adequate, although the inventory data yielded higher intercepts and more negative slopes.

Since the intercept of the self-thinning line increases with productivity (Bi 2001; Weiskittel et al. 2009), the self-thinning line thus estimated may be adequate for the most productive stand in the group, but for many stands, it is certainly overestimated (Bi 2001). Bi (2001), for example, found that changes with site productivity were 11 % of magnitude of the range for species. Differences in site productivity (poorer soil or climate conditions) might also explain why maximum basal area obtained from Finnish stands (Hynynen 1993) is not as high as obtained for Austria. Site index has been identified as a key factor affecting the intercept of the self-thinning line. Other factors associated with significant changes in the intercept were stand origin or purity of stands (Weiskittel et al. 2009).

Table 3 Coefficients of the three-parameter competition-density rule using Reineke's coefficient (−1.605). For sample size, see Table 1

Species	a_0	a_1	b_0	Root MSE	R^2	Adj. R^2
Norway spruce	1.522 10-6	0.6493	0.8882	96.4	0.90	0.90
Silver fir	1.917 10-6	0.6670	0.9215	99.8	0.88	0.88
European larch	2.526 10-6	0.6961	0.8278	87.3	0.87	0.87
Scots pine	2.682 10-6	0.5600	0.4717	89.1	0.86	0.86
Austrian pine	3.778 10-6	0.4382	0.2113	100	0.80	0.80
Stone pine	3.471 10-6	0.6940	0.4645	85.7	0.82	0.81
European beech	1.806 10-6	0.6921	1.0364	93.1	0.89	0.89
Common oak	2.733 10-6	0.5922	0.6260	112	0.71	0.71
Hornbeam	1.061 10-6	0.6689	1.1904	82.7	0.78	0.78
Ash	8.719 10-7	0.9370	4.0332	87.9	0.86	0.85
Sycamore	1.195 10-6	0.8475	1.9154	97.3	0.80	0.79
Black locust	2.004 10-6	0.5696	0.8257	63.1	0.75	0.74
Birch	1.630 10-6	0.5913	0.8692	73.9	0.69	0.68
Black alder	1.136 10-6	0.7777	1.6379	95.8	0.81	0.80
Grey alder	1.326 10-6	0.6109	0.7958	82.5	0.80	0.79

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Table 4 Coefficients of the three-parameter competition-density rule using species-specific coefficients estimated from the data of the Austrian National Forest Inventory using quantile regression (quantile=0.95). For sample size, see Table 1

	a_0	a_1	b_0	Root MSE	R^2	Adj. R^2
Norway spruce	8.828 10-7	0.8374	1.0570	95.6	0.90	0.90
Silver fir	1.401 10-6	0.7685	1.0487	99.0	0.88	0.88
European larch	5.602 10-7	1.2205	1.2948	90.3	0.86	0.86
Scots pine	9.961 10-7	0.9188	0.7845	93.8	0.85	0.85
Austrian pine	2.349 10-6	0.6160	0.2736	101	0.79	0.79
Stone pine	9.432 10-6	0.3108	0.3228	85.2	0.82	0.82
European beech	2.247 10-7	1.3975	2.2454	93.3	0.89	0.89
Common oak	1.308 10-6	0.8536	0.7991	110	0.72	0.72
Hornbeam	2.338 10-7	1.2802	1.5925	81.4	0.79	0.78

Our results did again confirm the hypothesis of species-specific slopes, the range of coefficients is however small. Species-specific slopes have been attributed to differences in shade tolerance and the ability to colonize space and the huge diversity in the geometry of trees (Pretzsch and Biber 2005; Charru et al. 2012). However, in our dataset, we could not find a ranking of slopes with shade tolerance (Table 2). However, in accordance with other studies, we found steeper slopes for broadleaf species than for conifer species (Pretzsch and Biber 2005; Charru et al. 2012). A species that does not fit into this general pattern is larch with a slope as steep as for broadleaf species. Note again that a steep slope results in almost constant maximum basal areas over a wide range of quadratic mean diameters.

In general, the slopes estimated from this study are steeper than the slope of −1.605 proposed by Reineke. This agrees well with many other studies which find steeper slopes, which are at least for some species significantly different from Reineke's

coefficient (Sterba 1987; Del Rio et al. 2001; Pretzsch and Biber 2005). These results are not surprising, since even the re-analysis of Reineke's data using standard statistical methods provided a steeper slope, −1.707, than originally proposed by Reineke (MacKinney and Chaikenen 1935 in Zeide 2010). Furthermore, the slopes found in this study are within the range of slopes found in the literature (Table 5).

Although the slopes vary a little, the intercept which controls maximum density varies by species. To date, species-specific intercepts for many species were lacking. This might have been partly due to the methodology. Historically, the self-thinning line has first been fit by hand due to the lack of computing tools. Later approaches selected plots at maximum density and OLS regression was fit to the data points. The choice of appropriate plots is however an arbitrary one. Newer statistical techniques, such as quantile regression or statistic frontier functions, provide a more objective way of fitting the self-thinning line. With these methods, all plots can be kept whatever their density and because these techniques use the whole range of data, functions for many species can be fit. Both techniques have previously been successfully applied to fitting the self-thinning line (Bi 2001; Zhang et al. 2005, 2013; Weiskittel et al. 2009; Charru et al. 2012).

In this study, we were interested in the species self-thinning boundary. Statistically, this corresponds to fitting a marginal model, for which linear quantile regression is an appropriate choice. Because the data of the Austrian National Forest Inventory was remeasured five times, also conditional models
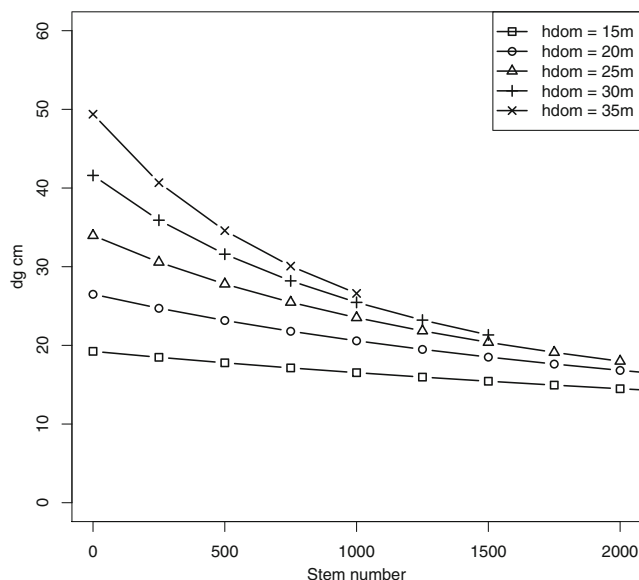

Fig. 4 Competition-density lines for Norway spruce obtained by fitting the competition-density rule to the data of the Austrian National Forest Inventory. The *plot* shows the decrease in quadratic mean diameter with increasing stem number for a given dominant height

Table 5 Slopes of the self-thinning rule found in the literature

Species	Min	Mean	Max
Norway spruce	−1.30	−1.61	−1.88
Silver fir		−1.78	
Scots pine	−1.55	−1.71	−1.84
European beech	−1.60	−1.79	−1.94
Oak	−1.34	−1.70	−1.92

Literature used: Hynynen 1993; Del Rio et al. 2001; Pretzsch and Biber 2005; Rivoire and Le Moguede 2012; Charru et al. 2012
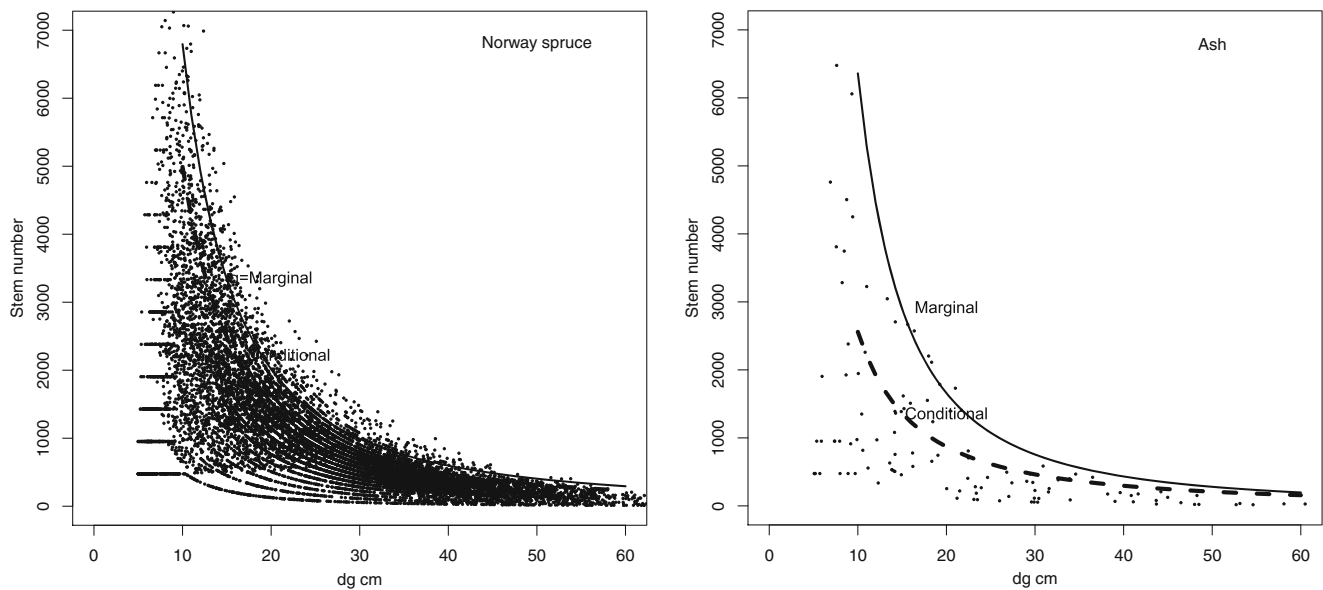
Fig. 5 Plot of stem number over quadratic mean diameter for Norway spruce and ash. *Dots* indicate the observations of the Austrian National Forest Inventory. The *lines* show the self-thinning line (Reineke rule).

Solid line, fit using linear quantile regression *q*=0.95; *dashed bold line*, fit using linear quantile regression with random plot effect

using quantile mixed models (Geraci and Bottai 2007) including a random plot effect could be fit to the data. Figure 5 compares the two methods for Norway spruce and ash. From the figure, it can be seen that the borderline relationship is better described by the marginal model.

We estimated the self-thinning model of Reineke. One important reason is that it can be directly linked to the competition-density rule, i.e. the parameters are required to

estimate the three-parameter competition-density rule. Also, Reineke's rule is the most popular model for self-thinning. Slightly but consistently more precise models are the models presented by Nilson (1973, 2006 in Zeide 2010). Other approaches model directly the self-thinning trajectory of individual stands (Vanclay and Sands 2009). A comprehensive overview of different approaches to model self-thinning is given by Zeide (2010).
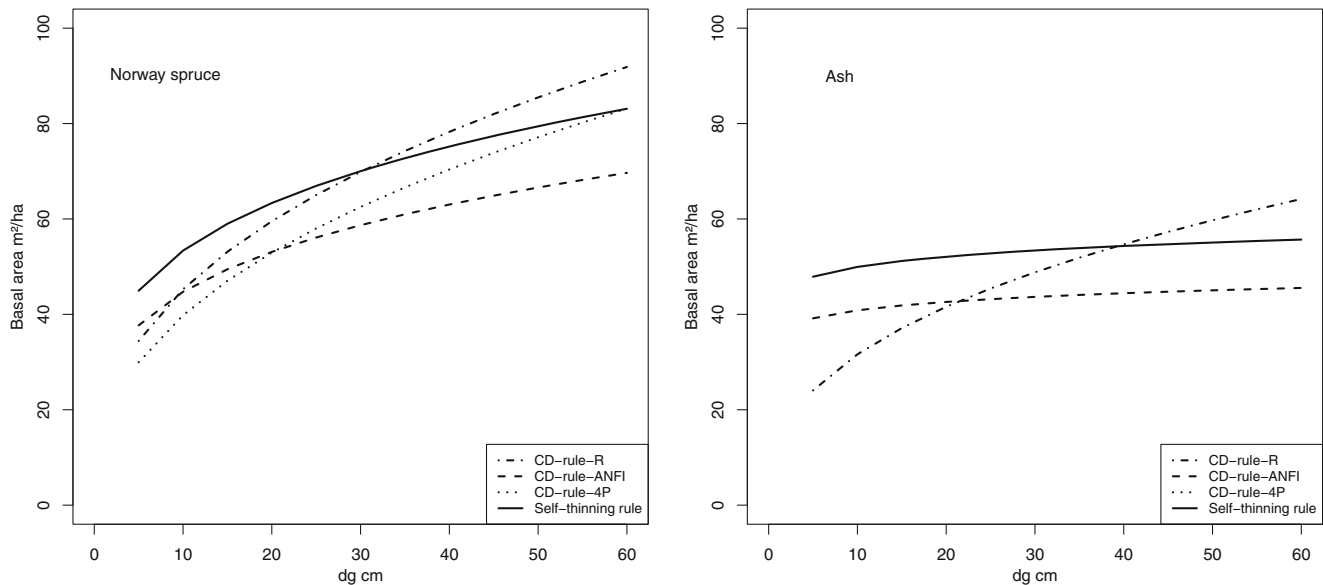

Fig. 6 Comparison of potential density obtained from different models fit to the data of the Austrian National Forest Inventory. The self-thinning line was fit using quantile regression. The competition-density rule was fit as three-parameter model using Reineke's slope (CD-rule-R), as three-parameter model using the slope of the self-thinning line estimated from

the Austrian National Forest Inventory (CD-rule-ANFI) and as four-parameter model (CD-rule-4P). The *left panel* shows the models for Norway spruce, the *right panel* shows the models for ash. For ash, the four-parameter model could not be fit, because of insufficient data

4.2 Competition-density rule

The competition-density rule represents the average decrease in quadratic mean diameter with increasing stem number for a given dominant height. It can therefore be used in stand density management diagrams as well as for the construction of yield tables. When fitting the four-parameter competition-density rule, the high inter-correlation of the parameters, in particular of a_0 and a_1, is an obstacle. To fit the four-parameter competition-density rule, a large number of plots is required for fitting and it is impossible to fit it for minor species. With the three-parameter model and a robust estimation technique, such as the generalized methods of moments estimation, the competition-density rule can also be fit for minor species. One problem however is the choice of an appropriate self-thinning slope for the competition-density rule. Species-specific slopes from the Austrian National Forest Inventory seem to be the best choice because then the slope of the competition-density rule and self-thinning rule agree at potential density. However, there are a number of species such as sycamore, black locust, birch and alder for which the self-thinning rule could not be fit, because there was insufficient data. Here, using Reineke's slope might be an appropriate choice.

In comparison to other models' fit for Norway spruce (Döbbeler 2004; Eckmüllner and Vospernik 2005; Sterba 1975), silver fir (Döbbeler 2004), European larch (Tumler 1992), Scots pine (Döbbeler 2004; Schnedl 2003), stone pine (Lick and Sterba 1991), European beech (Schnedl 2003; Döbbeler 2004) and oak (Döbbeler 2004), the three-parameter model fit from the Austrian National Forest Inventory yields higher maximum basal areas. The only exception is a model for Norway spruce in south-eastern Germany (Döbbeler 2004). These higher basal areas might be partly due to the yield level of the region and partly to the estimation method. Yield level as defined by Assmann (1970) is the phenomenon that stands at a given site index, age and treatment still may vary considerably in growth. This is a result of varying potential densities at given site indices (Franz 1967; Sterba 1987). Thus, higher potential basal areas as they result for the competition-density rule indicate a higher yield level, which is a well-known fact for Austrian sites, compared to many German ones. Similarly, south-eastern Germany, where maximum basal areas obtained for Norway spruce are higher than those for Austria, is a region known for its especially high yield level (Assmann 1970, p. 171).

In most other studies, the competition-density rule was estimated using OLS. Differences in estimated parameters, R^2 and MSE between OLS and GMM are very small, and both models result in almost identical maximum stem numbers and basal areas. The major advantage of GMM is that it is more robust and that models can be fit for minor species, where otherwise OLS estimation may result in illogical model

behaviour. In contrast to the estimation method, weighting with stem number considerably influences estimation results. Maximum basal areas from the weighted models are 0–11 m^2 ha^{-1} higher.

4.3 Comparison between self-thinning rule and competition-density rule

Potential density can be obtained from both self-thinning rule and competition-density rule. Figure 6 shows maximum basal areas for Norway spruce and ash obtained for the two species. In detail, it compares the self-thinning line at the 0.95 quantile to (i) the three-parameter competition-density model using Reineke's slope, (ii) the three-parameter competition-density model using the slope from the Austrian National Forest Inventory and (iii) the four-parameter competition-density rule. Obviously, if the slope of the ANFI is inserted into the competition-density rule, the resulting maximum basal area line is parallel to the maximum basal area line obtained from the self-thinning slope. As noted in the discussion on the competition-density rule, the slope obtained from the four-parameter model is usually steeper than the slope obtained from the ANFI, and therefore, the increase in maximum basal area with quadratic mean diameter is higher and more similar to the three-parameter model using Reineke's slope. The ranking of intercepts of different modelling approaches varies between species, and there is no evidence that any of the models consistently yields higher maximum basal areas. Thus, we assume that, if both rules are fit from the same dataset and if the competition-density rule is set equal to the self-thinning rule at potential density, as we do, it is reasonable to assume that both ways to characterize potential density are valid. Similarly, Huber et al. (2014) also found both ways to characterize potential density to be adequate. An important difference between the two models is the variables in the model: in the self-thinning model, the only variable is quadratic mean diameter (Eq. 2). Since it is the only variable in the model, it is a combined measure of age, site quality and stand treatment (Pretzsch 2005). Variables in the competition-density model are dominant height and quadratic mean diameter. Dominant height is largely independent of stand density. Therefore, at a given site, it is a good indicator of age, and quadratic mean diameter can then be interpreted as a measure of stand treatment. From a practical point of view, the competition-density rule is more widely applicable. It does provide not only estimates of potential density but also estimates of mean dimensions at a given dominant height for stand densities deviating from the potential density. These mean dimensions are for example required for yield tables, stocking guides and assortment tables (e.g. Sterba 1983; Eckmüllner and Vospernik 2005; Castedo-Dorado et al. 2009). If the major interest is in potential densities, the self-thinning line might be more easy to fit. Also it does not require height measurements.

5 Conclusions

The self-thinning rule is a well-known model of potential density. The self-thinning boundary line can be fit using quantile regression. In principle, the highest quantile that can be fit to the data is closest to the boundary. However, high quantiles can only be fit for few tree species, for which sufficient data is available. Fitting a model to the 0.95 quantile is therefore useful for practical applications, e.g. potential densities for the calculation of species proportions, because it facilitates the comparison between species. Self-thinning boundaries would be even more useful, if the self-thinning frontier could be estimated for individual stands. The competition-density rule is the more flexible and more broadly applicable model. It does provide not only potential densities but also mean dimensions required for many practical applications. However, unless the dataset is large, it cannot be fit without knowledge of the self-thinning slope. To assure consistency between self-thinning rule and competition-density rule, the same slope should be used for both models.

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