Are Self-Thinning Constraints Needed in a Tree-Specific Mortality Model?

Robert A. Monserud, Thomas Ledermann, and Hubert Sterba

ABSTRACT. Can a tree-specific mortality model elicit expected forest stand density dynamics without imposing stand-level constraints such as Reineke's maximum stand density index (SDI_{max}) or the $-3/2$ power law of self-thinning? We examine this emergent properties question using the Austrian stand simulator PROGNAUS. This simulator was chosen specifically because it does not use stand density constraints to determine individual tree mortality rates. In addition, it is based on a probability sample of the population that includes the span of the data being used to test the hypothesis. Initial conditions were obtained from 27 permanent research plots that were established in young pure stands of Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.) in Austria. A growth period of 250 years was simulated. We conduct our test in two parts. First, we compare our simulated results to Reineke's theory of maximum density and stand density index by examining the self-thinning relationship between stem number per hectare and quadratic mean diameter (log-log scale). Second, we compare our results to Sterba's full competition density rule, which incorporates dominant height along with stem number and quadratic mean diameter. From the results for Norway spruce, we conclude that stand-level density constraints are not necessary to obtain Reineke's maximum size-density relations. Norway spruce results confirm that the maximum size-density relationship reflects reasonable and stable stand dynamics and conforms to that expected by Reineke's theory. Results from simulation of Scots pine also display reasonable and stable stand dynamics, except that they greatly exceed Reineke's maximum stand density index determined empirically from the literature. This Scots pine result argues for stand-level constraints (such as specifying SDI_{max}) to ensure that the appropriate intercept for the maximum density line is used. Our second test revealed that the estimated maximum stand density index according to Sterba's theory was too high for both species, but that the relative rankings across plots were correct. Thus, we are left with ambiguous results. First, that a density-dependent individual-tree mortality model, developed on an adequate data set, is sufficient for the desired stand-level behavior of Reineke to emerge. Second, that stand-level constraints on SDI_{max} need to be imposed if the underlying mortality modeling database is not adequate. FOR. SCI. 50(6):848–858.

Key Words: Self-thinning, maximum size-density relationship, mortality model, stand simulation, PROGNAUS, Reineke.

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D OES SELF-THINNING at a higher level (forest stand) emerge from the behavior of lower-level tree models? Specifically, is a tree-level mortality model sufficient to elicit stand self-thinning dynamics without resorting to a density constraint at the stand level? This can be viewed as a question of emergent properties: will the desired property (self-thinning) simply emerge from the lower-order interaction of the individual units (trees), or does it need to be explicitly mandated with constraints at the next higher level (stand)? We begin by examining two concepts (the self-thinning law and mortality modeling in stand simulators) that will allow us to examine this question.

Self-Thinning

The mortality caused by competition among trees within a stand is called self-thinning (Yoda et al. 1963, Hynynen 1993). Foresters and plant ecologists have long known the strong negative relationship between the number and average size of trees in a given area. Trees at a competitive disadvantage die from crowding and suppression as crowns expand and tree size increases (Johnson et al. 2002). Thus, self-thinning refers to the reduction in tree numbers over time due to density-dependent mortality as the plants increase in size (Yoda et al. 1963). One result is an upper limit to the average size of a given number of trees or plants that occupy an area.

Reineke (1933) observed a linear relationship (on the log–log scale) between number of trees N and quadratic mean diameter dg in even-aged stands of full density:

$$\ln(N) = k + q \cdot \ln(dg). \qquad (1)$$

Reineke (1933) then found that the slope q behaved as a constant (-1.605) over a range of species. He further noticed that the intercept k varied across species, but not within species, regardless of site quality and stand age (Hynynen 1993). Thus, maximum stem number at a given dg is

$$N = C \cdot dg^{-1.605}, \qquad (2)$$

where $C = e^k$. For convenience, Reineke referred to this maximum number of trees at a dg of 10 in. (25 cm) as stand density index (SDI). This was the first stand density index that quantified self-thinning. The SDI of an observed stand at a given dg_{obs} relates the stand density N_{obs} to the maximum possible stand density, and expresses this relative density as the stem number that could have been observed if the stand's dg value were 25 cm (Sterba 1981):

$$SDI = N_{obs}(25/dg_{obs})^{-1.605}. \qquad (3)$$

Working with a variety of agricultural crops and weed species, Yoda et al. (1963) examined mean plant mass across a range of densities and thereby uncovered what they referred to as the $-3/2$ power law of self-thinning. This principle describes a maximum plant size/density relationship that dictates competition-related self-thinning within a stand of relatively uniform plants (Farnden 1996). Yoda et al. (1963) plotted mean plant mass versus density (number/area) on the log–log scale, and repeatedly observed

a constant slope close to -1.5. The relation held across all species examined. They observed that in pure even-aged stands there is a maximum population density that is dependent on the plants' stage of development; as time increases, these upper limits tend to converge on a fixed density level (Drew and Flewelling 1977).

These parallel and seminal ideas, Reineke's (1933) stand density index and the $-3/2$ power law formalized by Yoda et al. (1963), have received both great praise (White and Harper 1970, Hutchings and Budd 1981, Westoby 1984) and enormous scrutiny (Weller 1987, Zeide 1987). Robinson (1998) considers the $-3/2$ power law to be "a rigid manifestation" of the self-thinning property. Biologists have difficulty accepting theories that some call "laws," as the comprehensive review articles by Weller (1987) and Zeide (1987) make clear. The $-3/2$ exponent of the relationship between mean plant mass and plant density in overcrowded monocultures was once considered a universal constant (Hutchings 1983), but recent analyses examine deviations (Osawa 1995). Sources of variation include species differences, shade tolerance, and site quality (Weller 1987, Zeide 1987). Examining the effects of stand conditions on the thinning exponent, Zeide (1987) suggested that steeper slopes of the self-thinning line are associated with stands of optimal conditions, while flatter slopes are related to those of suboptimal conditions. Therefore, variation in the thinning exponent is not necessarily species-specific, but it may be site-specific (Osawa 1995). Sterba and Monserud (1993) generalized the concept to uneven-aged mixed-species stands, and tied their results to Assmann's (1970) idea of potential density (the variation in potential density across stands with the same site index, due to different carrying capacities). They then found that the slope of the maximum density line became flatter as stand structure (the diameter distribution) became more skewed and uneven-aged.

Although the self-thinning law was meant to describe unmanaged conditions, foresters have used the maximum size-density relationship inherent in self-thinning to good advantage, in the form of stand management diagrams (Farnden 1996). These are graphical representations of stand development which, in various formats, illustrate the interactions between density or some other measure of stocking, and various stand parameters such as mean diameter, top height, and volume (Farnden 1996). Often, the plant mass variable of Yoda et al. (1963) is replaced by mean volume (Drew and Flewelling 1979) or even mean diameter (Long 1985). Note that the $-3/2$ power law exponent relating volume to stem number is equivalent to Reineke's -1.6 exponent relating quadratic mean diameter dg to stem number only when volume is proportional to $dg^{2.4}$.

Sterba's Maximum Stand Density Index

Based on the Japanese ideas of Kira et al. (1953), Yoda et al. (1963), Ando (1968), and Ando et al. (1968), and an earlier development by Reineke (1933), Sterba (1987) derived a competition-density rule for even-aged stands. Considering a number of stands on the same site at the same age

(and thus the same dominant height), but different in density, Sterba (1987) described the relationship between stem number N and the quadratic mean diameter dg as a hyperbola when dominant height is constant,

$$dg = 1/(A \cdot N + B), \qquad (4)$$

with parameters A and B. These parameters are not used to make projections of quadratic mean diameter over time, but only to define maximum density at a given dominant height (Sterba and Monserud 1993). This approach is similar to a hyperbolic function used by Kira et al. (1953). The corresponding stand basal area G is

$$G = N \cdot dg^2 \cdot \frac{\pi}{4} = \frac{N\pi}{4(A \cdot N + B)^2} \cdot \qquad (5)$$

The stem number producing maximum basal area $(N_{G\max})$ is obtained by setting the derivative with respect to N equal to zero:

$$\frac{dG}{dN} = \frac{\pi(B - A \cdot N)}{4(A \cdot N + B)^3} = 0. \qquad (6)$$

Solving Equation 6 for N gives the maximum density line,

$$N_{G_{\max}} = B/A. \qquad (7)$$

The corresponding quadratic mean diameter is

$$dg_{G_{\max}} = 1/(2B). \qquad (8)$$

At a constant dominant height, these values describe the asymptotic density of Yoda et al. (1963) (Sterba 1987).

Ando (1968) and Ando et al. (1968) pointed out that the parameters A and B are power functions of dominant height h. Thus, the full Competition Density Rule then describes quadratic mean diameter as a function of dominant height h and stem number N,

$$dg = \frac{1}{a_0 h^{a_1} \cdot N + b_0 h^{b_1}}, \qquad (9)$$

with parameters a_0, a_1, b_0, b_1. This derivation allows for estimating the points of maximum density from a number of plots that need not be fully stocked, but rather vary in density and dominant height (Sterba and Monserud 1993). The corresponding maximum density and quadratic mean diameter are then

$$N_{G_{\max}} = \frac{b_0}{a_0} h^{b_1 - a_1}, \qquad (10)$$

and

$$dg_{G_{\max}} = \frac{1}{2b_0} h^{-b_1}. \qquad (11)$$

Expressing height as a function of mean diameter at this maximum density yields

$$h = (2b_0 dg_{G_{\max}})^{-1/b_1}. \qquad (12)$$

Substituting h in Equation 10 for this expression gives

$$N_{G_{\max}} = \frac{b_0}{a_0}(2b_0 dg_{G_{\max}})^{a_1/b_1 - 1}. \qquad (13)$$

This is of the form of Reineke's SDI. Thus, Reineke's slope q and intercept C of the maximum density line are

$$q = \frac{a_1}{b_1} - 1 \qquad (14)$$

and

$$C = \frac{b_0}{a_0}(2b_0)^q. \qquad (15)$$

Therefore, SDI and $N_{G_{\max}}$ at an index diameter of 25 cm are

$$\text{SDI} = C \cdot 25^q = N_{G_{\max}} = \frac{b_0}{a_0}(2b_0 25)^{a_1/b_1 - 1} = \text{SDI}_{\max}. \qquad (16)$$

Thus, by estimating the coefficients a_0, a_1, b_0, b_1 from Equation 9 for different site classes and referring to an index diameter of 25 cm, Sterba (1987) characterized the potential densities of these site classes in terms of $\text{SDI}_{\max}$.

Mortality Models in Stand Simulation Models

Individual-tree stand simulation models have served as both research tools and forest management aides for nearly 40 years (Dudek and Ek 1980, Ek et al. 1988, Vanclay and Skovsgaard 1997). Both the $-3/2$ power law of self-thinning (Yoda et al. 1963) and Reineke's (1933) SDI have been used in several forest stand growth models as density-dependent stand level constraints (e.g., FVS—Wykoff et al. 1982, Wykoff 1986, Hamilton 1986, Hamilton 1990; STAND—Pukkala and Miina 1997; BWIN—Nagel 1999; MELA—Hynynen et al. 2002).

Usually, the main motivations for imposing stand-level constraints in individual-tree stand simulation models are (1) to ensure proper stand density dynamics sensu Reineke's (1933) rule or the $-3/2$ power law (Yoda et al. 1963); and (2) to set the intercept of the self-thinning line, which is a measure for site productivity in terms of Assmann's (1970) potential density. Wykoff et al. (1982), for example, used maximum basal area to set this intercept, as Assmann (1970) recommended. In addition, Hamilton (1990) uses stand-level constraints to extend the area of applicability of the mortality model.

We now focus on how tree mortality is modeled in two of these individual-tree stand simulators. The first (FVS) uses stand-level mortality constraints, and the second (PROGNAUS) does not.

The forest vegetation simulator (FVS) is an individual-tree nonspatial forest growth model built around a set of empirically derived equations of diameter growth, height growth, crown ratio, regeneration, and mortality (Teck et al. 1997, Crookston and Havis 2002). The core model of the western variants of FVS was originally known as Prognosis (Stage 1973), and covers northern Idaho and western Montana (Wykoff et al. 1982). Typical stands in the northern Rockies are mixed-species and uneven-aged, often with

diverse stand structures. Because such irregular stands do not satisfy the pure monoculture assumption underpinning the $-3/2$ power law of self-thinning of Yoda et al. (1963), a rather complex series of stand-density constraints is used to model mortality. To begin, an individual-tree mortality rate is predicted as a function of diameter. Three stand-density adjustments are then made to this rate (Wykoff et al. 1982). The first is an approach to normality (full stocking) adjustment, which depends on quadratic mean diameter dg, density (trees/area), and predicted change in dg. The second density-dependent mortality rate adjustment is based on the assumption that there is a maximum basal area that a site can sustain and that this maximum varies by site quality. The third adjustment is intended to reflect the increased probability of mortality that is associated with advanced age in overmature trees; diameter (size) is used as a surrogate for age. Thus, the probability of mortality is increased for large-diameter trees in stands with a large mean diameter. Finally, all three stand-level adjustments are combined in a composite estimate of individual-tree mortality rate. There are currently 20 different geographic variants of FVS (Teck et al. 1997, Crookston and Havis 2002), each with their own parameterization. Most of them use this same three-step formulation to impose stand-density constraints on predicted tree mortality.

Hamilton (1990) carefully examined the structure of the mortality model in FVS. He began with the mortality model developed by Hamilton (1986) for Version 5.1 of the Stand Prognosis Model (Wykoff 1986). This initial model (termed "the new model") was a typical individual-tree mortality model without stand-level constraints. Hamilton (1990) then systematically introduced six assumptions intended to increase the applicability of the mortality model when it is used outside the range of conditions represented in the original development data set. These six mortality assumptions amount to the three-step procedure used by Wykoff et al. (1982) to introduce stand-level constraints (outlined above). Hamilton (1990) concluded that incorporating these assumptions (stand-level constraints) increased model performance and extended its range of applicability.

PROGNAUS (PROGNosis for AUStria, Monserud et al. 1997) is a forest stand growth model designed to simulate the growth and development of both pure even-aged and mixed-species uneven-aged stands in Austria using a nonspatial individual-tree methodology (Monserud et al. 1997). The current version of the forest stand growth model PROGNAUS comprises the following basic submodels: a basal area increment model (Monserud and Sterba 1996, for coefficients cf. Hasenauer 2000), a height increment model (Gschwantner 2004), a crown ratio model (Hasenauer and Monserud 1996), an ingrowth model (Ledermann 2002), and a mortality model (Monserud and Sterba 1999, for coefficients cf. Hasenauer 2000). All submodels were developed from remeasured permanent plot data from Austrian National Forest Inventory data (the first inventory cycle, 1981–1990), and supplemented by permanent research plots. The basal area increment model (Monserud

and Sterba 1996) does not use site index or age to determine productivity.

In contrast to the stand-level mortality constraints in FVS, PROGNAUS uses only an individual-tree mortality model (Monserud and Sterba 1999). This mortality model is a logistic function with the same general form for all species, which were modeled independently:

$$P = \left(1 + \exp\left[b_0 + \frac{b_1}{D} + b_2\,\mathrm{CR} \right.\right.$$
$$\left.\left. + b_3\mathrm{BAL} + b_4D + b_5D^2\right]\right)^{-1}, \quad (17)$$

where P is the probability of mortality (5 year), D is diameter (cm) at breast height (1.3 m), CR is crown ratio (live crown length to total tree height), BAL is basal area in larger trees (m^2 ha^{-1}), and b_0–b_5 are maximum likelihood estimates of the parameters. Note that BAL contains both tree-specific and stand-specific information.

All parameter estimates conform to biological expectations (Monserud and Sterba 1999). The intercept is positive and the coefficient of D^{-1} is negative in all cases, resulting in decreasing mortality rates with increasing diameter. The coefficients of D and D^2 were significant only for Norway spruce (*Picea abies* L. Karst.), indicating that for this tree species a senescence effect could be detected. Furthermore, the coefficient of CR is positive in all cases, resulting in increasing mortality rates as crown ratio decreases; and the coefficient of BAL is negative in all cases, indicating that mortality rate will be higher as basal area in larger trees increases and a tree's competitive status is less favorable. In general, the species-specific mortality models are all well-behaved and match the observed mortality rates quite well (Monserud and Sterba 1999).

Objective

In this analysis we seek to test whether stand-level constraints such as Reineke's maximum density line and Sterba's full competition density rule are necessary components of an individual-tree model of mortality. Thus, we are using two complementary theories (Reineke's and Sterba's) to test the behavior of the simulation model. If the theory emerges without being explicitly programmed, then it does not need to be forced as a constraint in the mortality model.

Methods

Data and Analysis

We rely on data from permanent research plots that were established in young pure stands of Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.) for thinning and fertilizing experiments. These data represent the northern, eastern, and southern part of Austria and are the two most important tree species (Fig. 1) in these areas.

Although repeated measurements were available from all research plots, we only used data from the very first measurement before any treatment (thinning or fertilizing) had been conducted. In the selection of the research plots, we looked primarily for even-aged, single-species structures. This
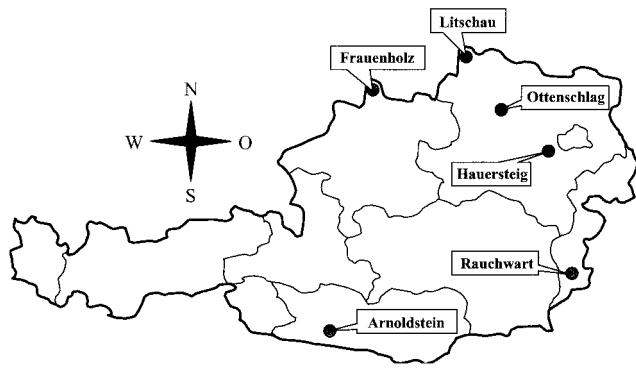
Figure 1. Locations of the research plots in northern, eastern, and southern Austria.

resulted in 27 plots, each showing full crown closure and an SDI value greater than 700 (Table 1). We lack even-aged permanent plots of lower density that are needed to examine low-density stand behavior, and for testing Sterba's (1987) full competition density rule. Thus, we created two additional replicates of these stands and then simulated moderate and heavy thinning in the first period by randomly removing 30% and 85% of the stems in each plot, respectively.

For carrying out the simulation runs, the forest stand growth model PROGNAUS was initialized for each individual plot. The ingrowth model of the simulator was deactivated for all simulation runs to ensure pure species and even-aged stand development. A growth period of 250 years for Norway spruce and Scots pine was simulated. To obtain estimates of Reineke's (1933) slope coefficient q and the maximum stand density index (SDI$_{max}$), we conducted our test in two parts following different approaches.

First, we compared our simulated results to Reineke's (1933) theory of maximum density and stand density index. Thus, from the growth simulations of the unthinned plots we recorded pairs of the quadratic mean diameter dg and the stem number N at each time period. We then determined the time period when the quadratic mean diameter exceeded 25 cm, and calculated the slope q_{25} using dg and N from the beginning and the end of this growth period. This can be considered as a close approximation of the tangent to the plot-specific $\ln(N)$ versus $\ln(dg)$ curve at a dg value of 25 cm. The reference value was based on our assumption that we expected the unthinned plots to reach full site occupancy latest when they reach a dg value of 25 cm. Due to full crown closure and relatively high stand density at the beginning of the simulation runs, this assumption was certainly justified for all our research plots. The estimates of q_{25} were then compared to values from the literature. Proceeding in the analysis we replaced Reineke's slope of -1.605 by q_{25} in Equation 3, and calculated the SDI value at each time period from

$$\mathrm{SDI} = N_{\mathrm{sim}}(25/dg_{\mathrm{sim}})^{q_{25}}, \tag{18}$$

where N_{sim} and dg_{sim} are the simulated stem number and the simulated quadratic mean diameter, respectively. The maximum stand density index of a plot was then determined by

inspection for each stand simulation, and referred to as SDI$_{maxR}$. Usually, this SDI$_{maxR}$ value was found close to $dg = 25$ cm.

Second, we were also interested in estimating Sterba's (1987) full competition density rule from the behavior of the simulation model. Thus, for all plots (i.e., the unthinned, the moderately thinned, and the heavily thinned plots), we recorded triplets of the simulated quadratic mean diameter dg, stem number N, and dominant height h. From Equation 14 we can express parameter a_1 as

$$a_1 = (q + 1)b_1. \tag{19}$$

By reformulating Equation 16, we obtain parameter a_0 as

$$a_0 = (b_0/\mathrm{SDI}_{\max})(2b_0 25)^q. \tag{20}$$

Substituting both parameters in the full competition density rule (Equation 9), we can write

$$dg = \cfrac{1}{\cfrac{b_0}{\mathrm{SDI}_{\max}}(50b_0)^q h^{(q+1)b_1}N + b_0 h^{b_1}}. \tag{21}$$

Hence, using Equation 21 as the objective function and nonlinear regression (PROC NLIN, Gauss-Newton iterative method, SAS Institute 1989), we estimated both q and SDI$_{max}$ along with parameters b_0, b_1 based on all three thinning trials of the respective plot. These estimates of q and SDI$_{max}$ we referred to as q_{ST} and SDI$_{maxST}$, respectively. Both the calculation of SDI$_{maxR}$ along with q_{25} and the estimation of SDI$_{maxST}$ along with q_{ST} were done separately for each stand (plot), because the stand density index can vary with site productivity.

Test Criteria

We are primarily interested in determining whether stand dynamics over time is stable and reasonable. Specifically, this includes the following criteria:

1. Reineke's slope of the maximum density line (-1.605) should be approximated when the unthinned stands reach full site occupancy, which we expect to occur at a dg value close to 25 cm.

2. The maximum density should not be exceeded.

3. Differences in the intercept or SDI$_{max}$ due to different potential densities (site productivity) at a given dominant height are expected and should conform to ecological expectations.

4. If stand density is low, mortality rates will be low and stand development will be below the maximum density line until full occupancy is reached (Zeide's (1987) young stage of development).

5. If the stand is old (and not regenerating), stand development will drop below the maximum density line (Zeide's (1995) "gappiness" as large trees die).

The individual-tree diameter growth model and the individual-tree mortality model are the key functions for the first test, Reineke's theory of maximum density. The second test,

Table 1. Stand characteristics of the research plots at the beginning of the simulation runs.

Species and Location	Plot no.	Plot size (ha)	dg[a] (cm)	h_{dom}[b] (m)	N[c] (ha^{-1})	BA[d] (m^2 ha^{-1})	SDI[e]
Norway spruce							
Litschau	019	0.0400	10.8	15.1	3125	28.6	812
	021	0.0400	8.9	12.5	5575	34.7	1062
Frauenholz	111	0.1207	18.3	20.4	1939	51.0	1175
	112	0.1040	18.5	20.5	1923	51.7	1186
	213	0.0968	18.3	20.2	2097	55.2	1271
	214	0.1331	17.7	18.8	2119	52.1	1217
Ottenschlag	121	0.0890	17.5	22.0	2135	51.4	1204
	222	0.0886	17.1	22.3	2167	49.8	1178
	123	0.0893	17.1	22.6	2172	49.9	1181
	224	0.0918	17.1	21.8	2004	46.0	1089
Hauersteig	001	0.2500	8.3	11.6	5124	27.7	873
	002	0.2500	10.1	11.9	3236	25.9	756
Arnoldstein	005	0.0225	12.7	13.3	2578	32.7	869
	006	0.0225	12.6	13.0	2400	29.9	799
	012	0.0227	10.8	14.9	2819	25.8	733
	015	0.0225	9.3	12.9	3467	23.6	709
	016	0.0100	9.0	12.1	3700	23.5	718
Scots pine							
Arnoldstein	001	0.0222	13.1	13.7	3649	49.2	1293
	002	0.0230	15.9	15.4	2348	46.6	1136
Rauchwart	305010	0.1000	8.7	8.4	4380	26.0	805
	305020	0.1000	8.9	8.0	5170	32.2	985
	305030	0.1000	8.5	8.1	5030	28.5	890
	306010	0.1000	8.7	8.7	5430	32.3	998
	306020	0.1000	8.8	8.8	5710	34.7	1069
	307030	0.1000	9.0	9.0	5720	36.4	1110
	308040	0.1000	9.5	9.4	5520	39.1	1168
	308050	0.1000	9.4	10.0	5310	36.9	1105

[a] dg is the quadratic mean diameter.
[b] h_{dom} is the dominant height.
[c] N is the stem number.
[d] BA is the basal area.
[e] $SDI = N(25/dg)^{-1.605}$, Stand Density Index (Reineke 1933).

Sterba's full competition density rule, is stronger and requires proper interaction of all tree-specific models (viz., diameter growth, height growth, mortality, and crown ratio) for simulating full dynamics. PROGNAUS is well suited for this test because (1) these maximum density relations were not used to model mortality, and (2) it is based on a probability sample of the population that includes the span of the data being used to test the hypothesis in question.

Results

Based on the simulations of the unthinned plots, we found for both species that the relationship between maximum stem number per hectare N and quadratic mean diameter dg of a simulated stand development generally follows the Reineke rule (Fig. 2). Stand dynamics over the 250-year simulations are stable and reasonable. Basically, the trajectories proceed from left to right (Fig. 2). None of the displayed lines strictly follows a straight line; Norway spruce shows definite curvature, while Scots pine shows minor curvature (Fig. 2).

The heavy 85% thinning simulations resulted in a prolonged period of low mortality rates as stand density increased. Eventually, the thinned and unthinned simulations became coincident for large quadratic mean diameters. The 30% thinning (not displayed) is intermediate between the unthinned simulations and 85% thinnings in Figure 2.

In Table 2 we display the slope q_{25} determined from the unthinned plots when a dg value of 25 cm was reached. Note that Sterba's theory was not yet used in these determinations. Estimates of q_{25} range from -1.3 to -1.9 for Norway spruce, with a mean of -1.56. Estimates of the slope range from -1.5 to -2.0 for Scots pine, with a mean of -1.82. This range of slopes coincides closely with those listed by Sterba (1981, 1987) for the same regions in Austria.

Next, we examine our results of SDI_{maxR}, the overall maximum SDI found by inspection of the unthinned plots using q_{25} as the exponent. Estimates of SDI_{maxR} range from 1,057 to 1,571 for Norway spruce, with a mean of 1,366 (Table 2). Estimates of SDI_{maxR} range from 1,397 to 1,582 for Scots pine, with a mean of 1,459.

From the studies of Sterba (1981, 1987, 2003), we have estimates of potential density in terms of SDI_{max} for several collections of research thinning plots that either are the same plots that we used for simulation (Hauersteig and Rauchwart) or are from the same locality and vegetation type (Frauenholz and Ottenschlag) (see Table 1). We begin with Norway spruce. The Litschau plots are located in a
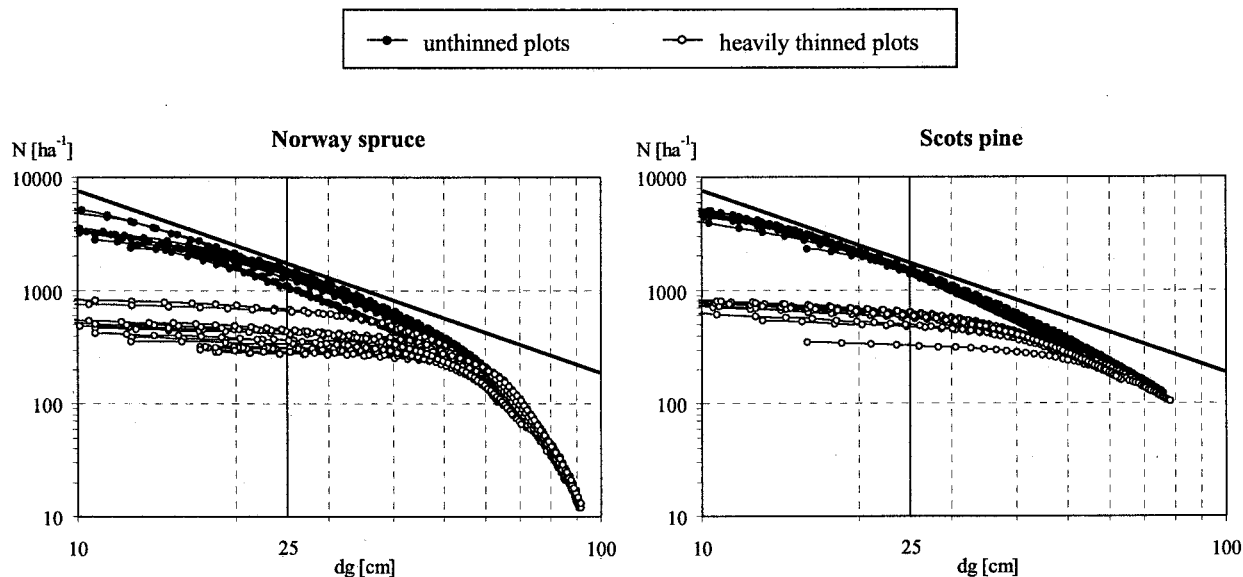
Figure 2. Relationship between stem number per hectare (*N*) and quadratic mean diameter (*d_g*) on the log-log scale for stands of Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.). Stand development has been simulated for 250 years using the forest stand growth model PROGNAUS. The bold lines follow the slope of −1.605 postulated by Reineke (1933). On heavily thinned plots 85% of the trees were removed randomly before the simulation runs had been started. Plots with moderate thinning are not displayed in this graph.

region where usually the yield table "Weitra" is used. For this region Sterba (1981) found an SDI_{max} value of 1,310 on medium sites. This compares closely to our average estimate of 1,320 (Table 2). The plots in Arnoldstein are situated in a region for which the yield table "Bayern" is recommended. Sterba (1981) found a mean of 1,280 for this region. Our estimates for Arnoldstein averaged 1,272. Plots in Frauenholz and Ottenschlag are in the *Oxalis acetosella* vegetation type, and the Wald- and Mühlviertel region. They correspond to good sites in the "Weitra" yield table. Sterba (1981) lists the SDI_{max} as 1,410. Our eight plots average 1,430. For Hauersteig, Sterba (2003) lists the SDI_{max} as 1,028; our estimates are much higher at 1,442. For Scots pine in Rauchwart, Sterba (2003) lists SDI_{max} as 893; our estimates average 1,440, considerably higher. For Scots pine in Arnoldstein, our estimates average 1,539, again considerably higher than Sterba's (2003) overall average of 921. Schnedl (2003) found that SDI_{max} averaged 1,152 for Scots pine across all of Austria and 1,124 in eastern Austria. In summary, SDI_{maxR} was quite close to published values for Norway spruce, except for Hauersteig. In contrast, SDI_{maxR} greatly exceeded published values for Scots pine.

We then examined model predictions in relation to Sterba's theory. For Norway spruce, slope q_{ST} varied from −1.3 to −1.9, with a mean of −1.59 (Table 2). With a standard error of 0.10, slope q_{ST} is not significantly different from Reineke's −1.605. For Scots pine, mean slope q_{ST} varied from −1.5 to −1.9, with a mean of −1.76 (Table 2). With a standard error of 0.13, mean slope q_{ST} is also not significantly different from Reineke's −1.605.

Stand density index SDI_{maxST} told a rather different story. Estimates of SDI_{maxST} range from 1,523 to 2,385 for Norway spruce, with a mean of 1927 (Table 2). Estimates of

SDI_{maxST} range from 1,954 to 3,299 for Scots pine, with a mean of 2,242. SDI_{maxST} exceeds SDI_{max} by 561 for Norway spruce, and by 813 for Scots pine (Table 2). Clearly, SDI_{maxST} estimated from Sterba's full competition density rule greatly exceeded both published values and estimates of SDI_{maxR}, although the slope q_{ST} was close to published values.

Discussion

Let us begin with our criteria.

Criterion 1—Reineke's slope q of the maximum density line (−1.605) was approximated fairly well by q_{25} of the unthinned plots once they reached a dg value of 25 cm. Estimates for Norway spruce averaged −1.56 and estimates for Scots pine averaged −1.82 (Table 2). The maximum density line served almost as a tangent to the unthinned simulations both for Norway spruce and for Scots pine (Fig. 2). Basically, no evidence appeared to suggest that the slope q was poorly approximated. We also estimated the slope using Sterba's full competition density rule. Again results were very close to Reineke's slope: the average slope q_{ST} was −1.59 for Norway spruce and −1.76 for Scots pine (Table 2). Mean slope q_{ST} was not significantly different from Reineke's −1.605 for either species.

Criterion 2—We estimated the level of Reineke's maximum density line by using stand density index, which is related to the intercept. Our estimates of SDI_{maxR}, the overall maximum SDI found by inspection of the unthinned plots (Table 2), were very close to estimates found in the literature for Norway spruce, except for one installation (Hauersteig). Estimates of SDI_{maxR} for Scots pine considerably exceeded estimates found in the literature (by 50%). We also estimated SDI_{maxST} simultaneously with slope q_{ST}

Table 2. Estimates of Reineke's (1933) slope coefficient q and of potential density in terms of SDI_{max} obtained by two different methods.

| Species and Location | Plot no. | Inspection | | Sterba (1987) | | | |
		q_{25}[a]	SDI_{maxR}[b]	q_{ST}[c]	Std. error	SDI_{maxST}[d]	Std. Error
Norway spruce							
Litschau	019	−1.525	1289	−1.507	0.100	1761	69
	021	−1.780	1351	−1.646	0.099	1745	84
Frauenholz	111	−1.424	1418	−1.681	0.109	2176	73
	112	−1.323	1396	−1.824	0.118	2180	81
	213	−1.545	1429	−1.758	0.150	2385	125
	214	−1.497	1463	−1.780	0.116	2236	82
Ottenschlag	121	−1.472	1428	−1.495	0.105	2086	79
	222	−1.542	1412	−1.392	0.107	2076	84
	123	−1.499	1419	−1.460	0.096	2021	71
	224	−1.281	1379	−1.371	0.098	1985	66
Hauersteig	001	−1.878	1454	−1.773	0.043	1534	20
	002	−1.624	1430	−1.875	0.056	1523	27
Arnoldstein	005	−1.462	1571	−1.712	0.059	1917	31
	006	−1.462	1515	−1.636	0.064	1970	36
	012	−1.683	1057	−1.454	0.132	1683	116
	015	−1.686	1113	−1.442	0.117	1589	98
	016	−1.824	1104	−1.292	0.135	1891	156
Mean		−1.559	1366	−1.594	0.100	1927	76
Scots pine							
Arnoldstein	001	−1.704	1582	−1.465	0.239	3299	351
	002	−1.475	1496	−1.748	0.127	2392	88
Rauchwart	305010	−1.809	1397	−1.715	0.105	2025	93
	305020	−1.981	1455	−1.797	0.111	2074	107
	305030	−1.936	1443	−1.803	0.100	1954	86
	306010	−1.942	1430	−1.817	0.109	2035	108
	306020	−1.950	1446	−1.896	0.100	1924	91
	307030	−1.826	1454	−1.845	0.129	2106	136
	308040	−1.821	1450	−1.778	0.144	2298	178
	308050	−1.786	1441	−1.745	0.141	2314	175
Mean		−1.823	1459	−1.761	0.130	2242	141

[a] Slope coefficient determined from the $\ln(N)$ versus $\ln(dg)$ trajectory when the dg value exceeded 25 cm.
[b] Overall maximum SDI found by inspection of the unthinned plots; $SDI = N(25/dg)^{q25}$.
[c] Slope coefficient determined by Sterba's (1987) full competition density rule.
[d] Potential density in terms of SDI_{max} obtained by Sterba's (1987) full competition density rule.

and two other parameters of Sterba's full competition density rule. SDI_{maxST} exceeds SDI_{max} by more than 500 for Norway spruce and 800 for Scots pine (Table 2). These greatly exceeded values found in the literature. Clearly, the PROGNAUS simulations are not in accordance with Sterba's full competition density rule.

Criterion 3—Variation existed from stand to stand, likely a result of differing potential densities (Assmann 1970). This is usually reflected in different values of SDI_{max} for different regions and vegetation types. For Norway spruce, the relative ranking of both SDI_{maxR} and SDI_{maxST} across the different locations met expectations, even though SDI_{maxST} estimates were 500–600 too large. Arnoldstein illustrates this (Table 2): the first two plots (005, 006) are on rich soils in the floodplain (mean $SDI_{maxR} = 1,543$), and the other three (012, 015, 016) are on poor soils with low water holding capacity (mean $SDI_{maxR} = 1,091$). This means that a constant correction term across all sites seems to be sufficient to adjust the model for region-specific maximum density.

Criterion 4—Some stands are stocked with relatively small-diameter trees (e.g., $dg < 10$ cm in Table 1) at the beginning of the simulations. These stands initially are not fully occupying the site, and begin below the maximum density line. This effect is more pronounced for Norway spruce than Scots pine. The thinning simulations showed a low mortality rate as the stands grew and approached the maximum density line (Fig. 2). The thinning simulations clearly show this effect. Mortality rates are very low as the stands grow and begin to approach full occupancy. Once this is reached, the thinned and unthinned simulations are essentially coincident.

Criterion 5—As the stands age in the 250-year simulations, stand development drops below the maximum density line (Fig. 2). Old stands do not show asymptotic density because of the increasing proportion of gaps due to two reasons: (1) higher mortality rates for older trees due to senescence effects, and (2) a reduced ability of neighboring trees to close these gaps (Zeide 1995). Regarding the first point, recall that Monserud and Sterba (1999) were able to fit a U-shaped mortality function for Norway spruce, because their sample was large enough to detect the sharp increase in mortality rates for trees larger than 70 cm; no such effect was detected for Scots pine. Regarding the

second point, recall that we intentionally turned off the ingrowth submodel so that the stands would remain pure and even-aged. This precludes the recruitment of trees to fill the gaps. Zeide (1995) assumed that the line would be straight without these gaps. Clearly, the drop-off below the maximum density line as fully stocked stands continue to grow and age is due to senescence mortality and a lack of ingrowth.

In conclusion, criteria 1, 3, 4, and 5 were met for both species. Criterion 2 was met for Norway spruce for the level of Reineke's maximum density line, but was not met for Sterba's full competition density rule. Criterion 2 was not met for Scots pine under either theory.

The results of the simulation runs for both tree species show that the logarithmic relationship between stem number N and quadratic mean diameter dg does not follow a straight line, but shows a more or less well-pronounced curvature (Fig. 2). Recall that Reineke's (1933) rule was designed only for "fully stocked" stands. The curvature in our $\ln(N)$ versus $\ln(dg)$ relations over time results from young stands that do not exhibit asymptotic density because they have not reached crown closure, and from old stands that do not show asymptotic density because of the increasing mortality rates for older trees due to senescence effects (Norway spruce) and a lack of ingrowth to close these gaps.

As an aside, we did in fact turn on the natural regeneration submodel in PROGNAUS for a third set of simulations, not illustrated here. The result was that the even-aged assumption underpinning the maximum density theory became increasingly violated. Sterba and Monserud (1993) addressed this problem and found that Reineke's maximum density slope became increasingly flatter as stands became more uneven-aged.

This deviation (i.e., curvature) from Reineke's (1933) rule has been repeatedly observed (Zeide 1987). Meyer (1938) had to use a curve concave downward instead of Reineke's (1933) straight line to fit his data on ponderosa pine (*Pinus ponderosa*). Sterba (1981) presented similar results when he calculated $\ln(N)$ versus $\ln(dg)$ relationships from Assmann and Franz's (1965) stand model for maximum basal area. Hamilton's (1990) demonstrations do not follow a straight line either.

Hamilton (1990) further proposed additional assumptions (constraints) when the range of applicability of an individual-tree mortality model needs to be extended. He justified these assumptions with the fact that on some habitat types, very small trees and very dense stands were rare in the data set used for parameterization of the mortality model. He also demonstrated the effects when no assumptions were made (see Figure 1 in Hamilton 1990). The result of his demonstration is similar to our results for Scots pine: stands exceed the maximum stand density. Basically, this overestimation of the intercept amounts to a corresponding overestimation of site productivity. Hence, results for Scots pine would favor the arguments to impose density-dependent stand level constraints in an individual-tree growth simulator. However, our results for Norway spruce show

that this is not necessary for obtaining the expected level of Reineke's maximum density line.

What is the cause of the overestimation of SDI_{max}? One clue is given by Gschwantner (2004). He analyzed the Austrian National Forest Inventory (ANFI) for the past two decades. Recall that the mortality model (Monserud and Sterba 1999) and key growth components in PROGNAUS were built using only the first inventory cycle, 1981–1990. Gschwantner (2004) found that this first period was characterized by unusually high growth rates and low mortality rates relative to subsequent inventory cycles. He uncovered climatic variation as the cause. It follows that the current parameterization of PROGNAUS could lead to overestimation of the level of the maximum density relationship (e.g., SDI_{max}).

A second reason that the maximum density is exceeded in Scots pine could be due to the relatively small data set used for parameterizing the mortality model (approx. 4,000 for Scots pine versus 26,700 for Norway spruce, see Monserud and Sterba 1999). Recall that Monserud and Sterba (1999) tried and failed to estimate a U-shaped mortality model for Scots pine, due to limited data in advanced ages. The only species that they succeeded in estimating this senescence effect was for Norway spruce, with the largest data set.

Sterba's theory depends heavily on the interrelations among dominant height, mean diameter, and stem number. Particularly, Sterba (1987) used dominant height as a surrogate for age, implicitly assuming that stand treatment has no effect on height growth. However, Gschwantner's (2004) height growth model uses annual diameter growth rate as a predictor variable. Hence, the height growth model may be another culprit for why the PROGNAUS simulations could not fully produce his theory. This situation indicates the difficulty of testing a mortality model in isolation. A model can only be examined fully when it is used as a component of the full stand simulation system.

An often-stressed argument for imposing stand-level constraints in an individual-tree growth simulator is the assumption by many modelers that site productivity (potential density) is not reflected properly without density-based adjustment of the intercept of the maximum density line. However, a proper representation of site productivity is certainly not the sole responsibility of the mortality model. In this context, the basal area (Monserud and Sterba 1996) and the height increment model (Gschwantner 2004) are more important in our study because site factors, which definitely determine site productivity, are only considered in these two models. Thus, we implicitly assumed that there is no site effect on mortality besides that already included in the basal area and the height increment model. In fact, a plausible representation of self-thinning and site productivity is the result of the interactions among all submodels implemented in an individual-tree growth simulator, and again indicates the difficulty of testing a mortality model in isolation.

From the results for Norway spruce (Fig. 2, Table 2), we

conclude that stand-level density constraints are not necessary to obtain Reineke's maximum size-density relations. Norway spruce results confirm that the maximum size-density relationship reflects reasonable and stable stand dynamics and conforms to that expected by Reineke's theory. Results from a simulation of Scots pine also display reasonable and stable stand dynamics, except that they greatly exceed the maximum density line determined empirically from the literature. This argues for stand-level constraints (such as specifying SDI_{max}) to ensure that the appropriate intercept for the maximum density line is used. Thus, we are left with ambiguous results: First, that a density-dependent individual-tree mortality model, developed on an adequate data set, is sufficient for the desired stand-level behavior to emerge; and second, that stand-level constraints on SDI_{max} need to be imposed if the underlying mortality modeling database is not adequate.

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