Vol 1, No 1, pp. 1–9, 2009
International Journal of
Mathematical and Computational
Forestry & Natural-Resource Sciences

AVAILABLE ONLINE AT HTTP://MCFNS.COM

Submitted: Sep. 26, 2008
Accepted: Oct. 28, 2008
Published: Feb. 28, 2009
Last Correction: Jul. 14, 2009

A SIMPLE AND EFFECTIVE FOREST STAND MORTALITY MODEL

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Abstract. A whole-stand survival model is presented, that is parsimonious and well-behaved when extrapolated, making it particularly useful in data-poor situations. It is argued, on biological and system-theoretical grounds, that a suitable differential equation for the mortality rate should contain number of trees and top height on the right-hand side, avoiding age, mean diameter, or basal area. Following Eichhorn's hypothesis, site quality can be neglected by modelling rates relative to height growth. The proposed model is $\mathrm{d}N/\mathrm{d}H = -aN^bH^c$, where N is number of trees per unit area, H is top height, and a, b and c are parameters to be estimated. The equation can be integrated to predict mortality between any two points in time. Satisfactory performance is demonstrated with a white spruce data set from British Columbia. It is shown that the model generalizes concepts of relative spacing, and mortality models for radiata pine and Douglas-fir used by Beekhuis in New Zealand in the 1960's. Asymptotic behaviour is related to the 3/2, Reineke, and relative spacing self-thinning laws. Limitations of the self-thinning theories and relationships among their various forms are discussed.

Keywords: survival, growth and yield, relative spacing, self-thinning

1 Introduction

The prediction of tree mortality (or more optimistically, survival) is widely recognized as difficult, due to its high variability (e.g., Vanclay 1994). The problem is exacerbated when the available data is limited, and/or does not cover a wide enough range of growing conditions. In that situation, it would be desirable to use a model with few parameters, and that behaves reasonably when extrapolated.

I propose such a robust, whole-stand level model for even-aged stands. As usual, catastrophic mortality is excluded, modelling only regular, density-dependent mortality (Vanclay 1994). The model has been used as a component in a new stand growth model for natural and planted white spruce in the SBS biogeoclimatic zone of British Columbia; the spruce data is used to illustrate its performance (Figure 1).

The following section presents the reasoning behind the new model, and shows the results of fitting the spruce data. Historically, the model derives from one of Beekhuis (1966), and the connection with it and with concepts of relative spacing are presented next. Finally, relationships to self-thinning theories are discussed.

2 Model

2.1 Rate equations. The mortality rate, for a given site quality q, can be predicted by some function of the current values of stand variables such as density, age, top height, basal area, mean dbh, volume per hectare, etc.:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = -f_q(N, A, H, B, D, V, \dots)\ . \tag{1}$$

Equivalently, models are sometimes expressed in terms of the relative mortality rate $(-\mathrm{d}N/\mathrm{d}t)/N = -\mathrm{d}\ln N/\mathrm{d}t$. Variables such as D and V may enter as part of density indices based on self-thinning laws.

2.2 Stem diameter. Tree diameter, basal area, or volume, reflect the amount of xylem accumulated on the stems. Especially in relatively undisturbed stands, these can be good predictors of future development because they tend to summarize past growth conditions. Biologically, however, a causal connection between the mostly dead xylem and stand development is difficult to justify, and the correlations can be expected to weaken or break down when stand density is manipulated. I suggest that these variables should be avoided on the right-hand sides

García (*2009*) (MCFNS 1(1):1–9). ISSN 1946-7664. Manuscript editor: Chris J. Cieszewski

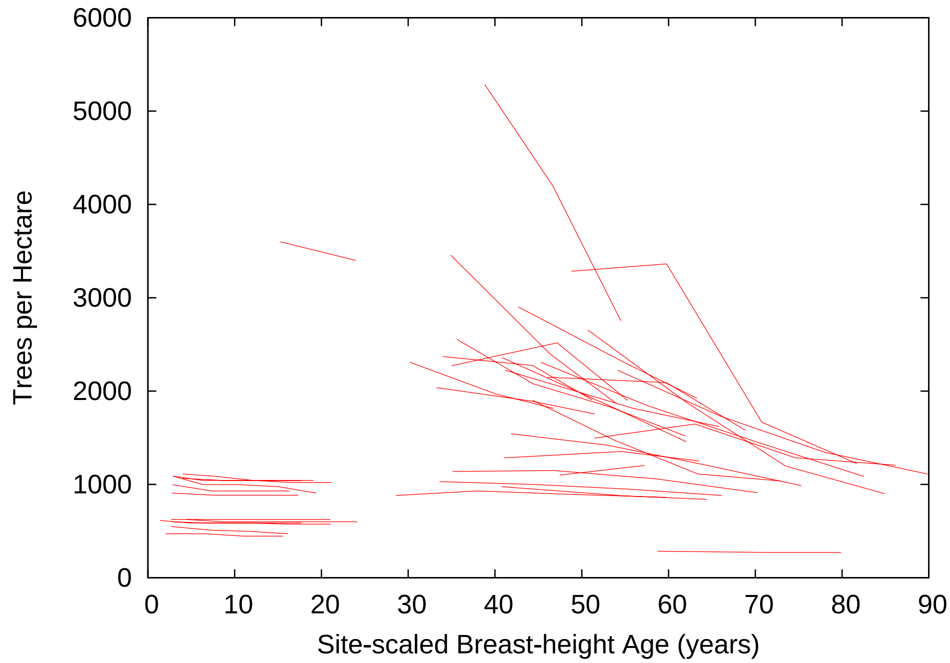

Figure 1: British Columbia white spruce stand density data. Re-measurements in each permanent sample plot are joined by lines. A scaling of breast-height age according to site quality makes the trends comparable across sites. All measurements older than 25 years are in natural stands; except for one high-density plot, all the stands younger than 25 years are planted.

of growth models for managed stands. One is left with

$$\frac{\mathrm{d}N}{\mathrm{d}t} = -f_q(N, A, H) \; . \tag{2}$$

These models are common. Zhao et al. (2007) reviewed 27 models that are all of the form

$$\frac{\mathrm{d}N}{\mathrm{d}t} = -N^a f(A, q) \; , \tag{3}$$

where a is a parameter, and f are various functions of age and site index. Conceptually, it may be useful to distinguish between age, as in $A = 33$ years-old, and time, as in $t = 2008$. It is convenient, however, to substitute $\mathrm{d}N/\mathrm{d}t = \mathrm{d}N/\mathrm{d}A$, using the fact that $\mathrm{d}A/\mathrm{d}t = 1$, i.e., age increases over time at a rate of one year per year. Equation (3) can then be easily integrated as a separable differential equation by writing

$$N^{-a}\,\mathrm{d}N = -f(A, q)\,\mathrm{d}A \; ,$$

and integrating on both sides. As a simple example, the model of Clutter and Jones (1980),

$$\frac{\mathrm{d}N}{\mathrm{d}A} = -aN^b A^c \tag{4}$$

gives

$$\frac{N^{1-b}}{1-b} + a\frac{A^{1+c}}{1+c} = \text{constant} \; . \tag{5}$$

The stand density at any age can then be predicted given the density at any other age from

$$N_2 = [N_1^{1-b} - a\frac{1-b}{1+c}(A_2^{1+c} - A_1^{1+c})]^{1/(1-b)} \; ,$$

provided that there are no management or serious natural disturbances between A_1 and A_2.

2.3 Age or height? Typically, when a forester looks for explanatory variables, the first one that comes to mind is age. But perhaps he/she is actually thinking of size. For a given site, age and height are closely related, and in practice it may not make much difference which one is used. Physiologically, it can be argued that size would dominate over any ageing effects, especially in trees, where meristems are constantly renewed. It will be more convenient here to use top height instead of age, so that (2) reduces to Erratum: 7/14/09

$$\frac{\mathrm{d}N}{\mathrm{d}t} = -f_q(N, H) \; .$$

It is also convenient to divide by the height growth equation $\mathrm{d}H/\mathrm{d}t = h_q(H)$, to obtain a relationship between N and H:

$$\frac{\mathrm{d}N}{\mathrm{d}H} = -f_q(N, H)/h_q(H) \equiv -g_q(N, H) \; . \tag{6}$$

2.4 Eichhorn's hypothesis. Eichhorn (1904) found that graphing yield table predictions over height instead of age produced similar curves for all site qualities. Although not universally accurate, in many instances this so-called Eichhorn's law is a good approximation (Assmann 1970). As a slight extension, the assumption that rates of growth and mortality relative to top height growth are independent of site quality has been successfully used to simplify the development of growth models (e.g., Beekhuis 1966, Mitchell and Cameron 1985). This hypothesis implies that (6) is approximately independent of site quality:

$$\frac{\mathrm{d}N}{\mathrm{d}H} = -g(N, H) \; . \tag{7}$$

A model of this form was used by Evert (1981).

As an example, Figure 2 shows mortality predictions of Zhao et al. (2007) for loblolly pine with several initial densities and site qualities. Using their site index equation, the same predictions are plotted over dominant height in Figure 3. It seems clear that in this case a model like (7) would be satisfactory.

2.5 The model. In view of our objective of estimating mortality with limited data, we want a parsimonious and well-behaved function g for (7). The chosen model is

$$\frac{\mathrm{d}N}{\mathrm{d}H} = -aN^b H^c \; , \tag{8}$$

where a, b and c are parameters to be estimated. Integrating gives (*cf.* equation (5))

$$\frac{N^{1-b}}{1-b} + a\frac{H^{1+c}}{1+c} = \text{constant} \; .$$

The right-hand side of (8) could be justified as a first-order Taylor expansion of $\log g$ in terms of $\log N$ and $\log H$, logarithms being used because the original variables are strictly positive. It is analogous to (4), the model of Clutter and Jones (1980), but with H in place of A, making more plausible the independence of site quality.

An alternative formulation and parametrization using average spacing instead of N may be preferable (Section 3):

$$S^\alpha - (\beta H)^\gamma = \text{constant} \; . \tag{9}$$

Here $S = 100/\sqrt{N}$ is the average square spacing (in meters if N is number per hectare).

The model limiting behavior is shown below to be compatible with generally accepted theories of self-thinning. The three free parameters provide ample flexibility in describing observed trends, but the ratio of γ/α could also be fixed at reasonable values when dealing with sparse data.

2.6 Application to white spruce. Model (8)–(9) was applied to the data of Figure 1. The parameters were estimated by nonlinear least-squares for the logarithm of N (or of S) predicted over pairs of successive observations. The regression was

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$$\ln S_2 = \ln[S_1^\alpha - (\beta H_1)^\gamma + (\beta H_2)^\gamma]/\alpha \; , \tag{10}$$

where (H_1, S_1) and (H_2, S_2) are consecutive data points. It was felt that the nature of the data did not justify procedures based on more elaborate stochastic modelling.

The estimated parameter values were $\alpha = 3.979$, $\beta = 0.07213$, $\gamma = 6.009$. Projections of $\log N$ and S are shown in Figures 4 and 5, respectively. The assumption of asymptotic relative spacing (Section 3) resulted in a significantly worse fit, with $\alpha = \gamma = 4.571$, $\beta = 0.1004$.

3 Beekhuis and relative spacing

Beekhuis (1966) developed a graphical mortality model for radiata pine plantations in New Zealand that is related to the one in Section 2.5. It was based on relative spacing, the ratio of average spacing to stand height. Relative spacing is sometimes used to specify thinning prescriptions, and is also known as the Hart-Becking or Wilson index (Vanclay 1994, Wilson 1951).

Beekhuis' model is reproduced in Figure 6. He used triangular average spacing, which is 1.074 times the average square spacing. The graph was constructed assuming no mortality until the (triangular) relative spacing reaches 30%, and the existence of an asymptotic relative spacing of 11%. In between, the spacing–height curve is an arc of ellipse (García 1981). The graph also shows a thinning regime maintaining a relative spacing above 16%. The same technique, with different threshold and limiting relative spacings, was later used in other models for radiata pine and Douglas-fir.

The exact model was rather cumbersome for computer implementation, and a close approximation was adopted. Noticing that the slope of the S–H curves depends only on the relative spacing $R = S/H$, increasing from 0 to β as R decreases to the limiting relative spacing β, an approximation of the form

$$\frac{\mathrm{d}S}{\mathrm{d}H} = R(\beta/R)^\alpha$$

was found suitable. Integrating,

$$S^\alpha - S_0^\alpha = (\beta H)^\alpha - (\beta H_0)^\alpha$$

(García 1981). With $\alpha = 5.5$ and $\beta = 0.11$ (S being triangular spacing), the approximation differs from Beekhuis' curves by less than 3%. This is a special case of (9), with $\gamma = \alpha$.

A constant limiting value for relative spacing implies that all trajectories tend asymptotically to a straight line

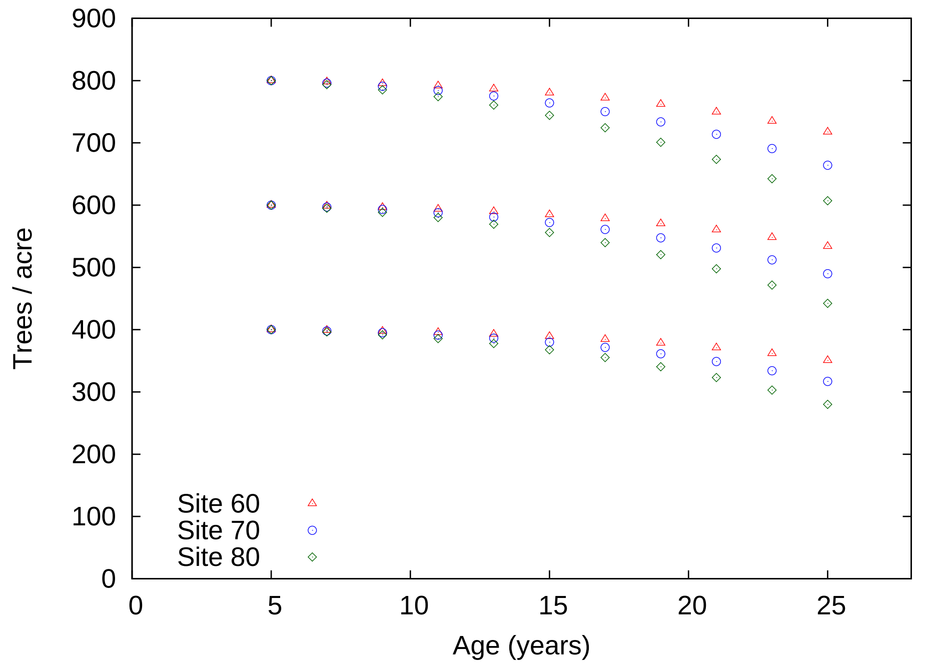

Figure 2: Survival projections for loblolly pine plantations in the Piedmont/Upper Coastal Plain, site indices 60, 70, and 80 (Zhao et al. 2007).

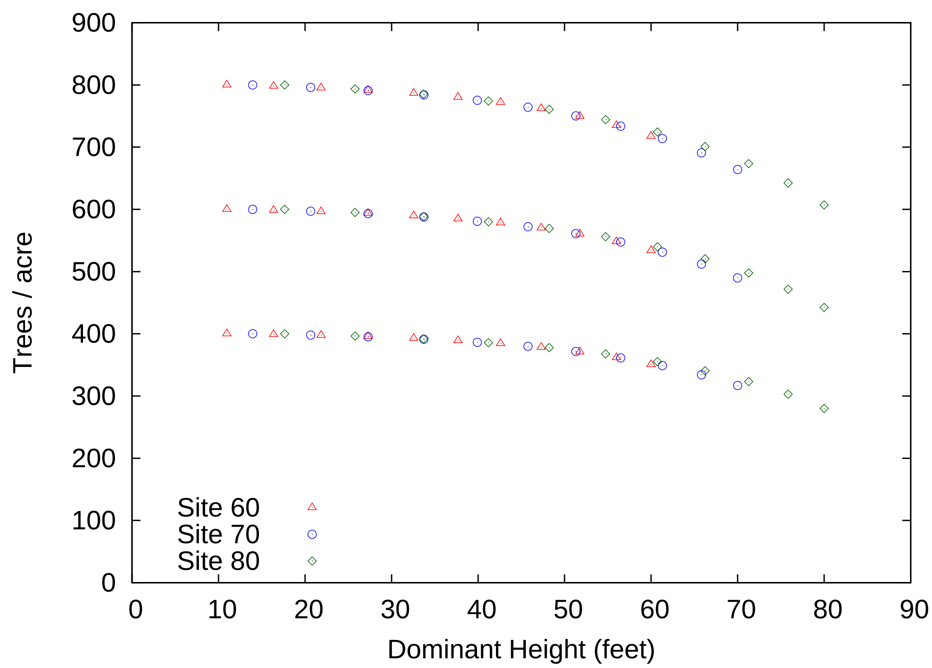

Figure 3: The projections from Figure 2, graphed over dominant height.

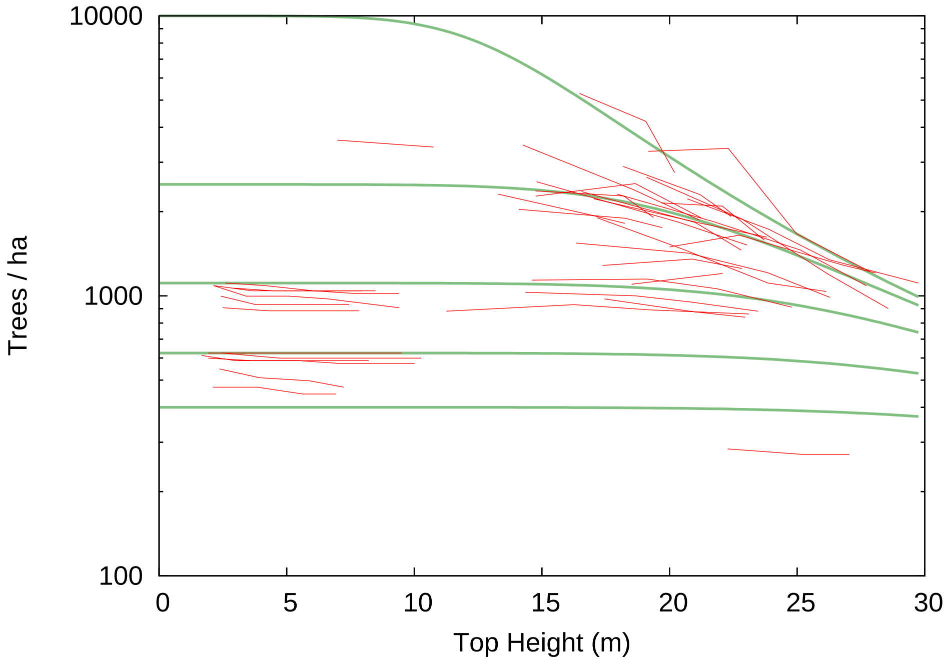

Figure 4: Stand density projections for white spruce from model (8)–(10). Logarithmic N-scale.

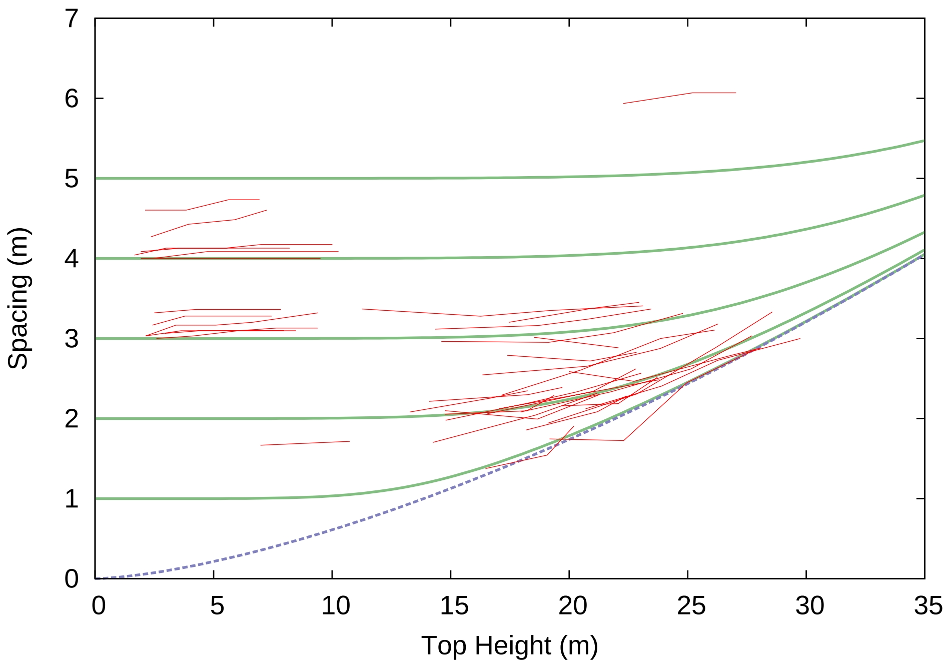

Figure 5: Average spacing projections for white spruce from model (8)–(10). Dashes: limiting self-thinning curve.

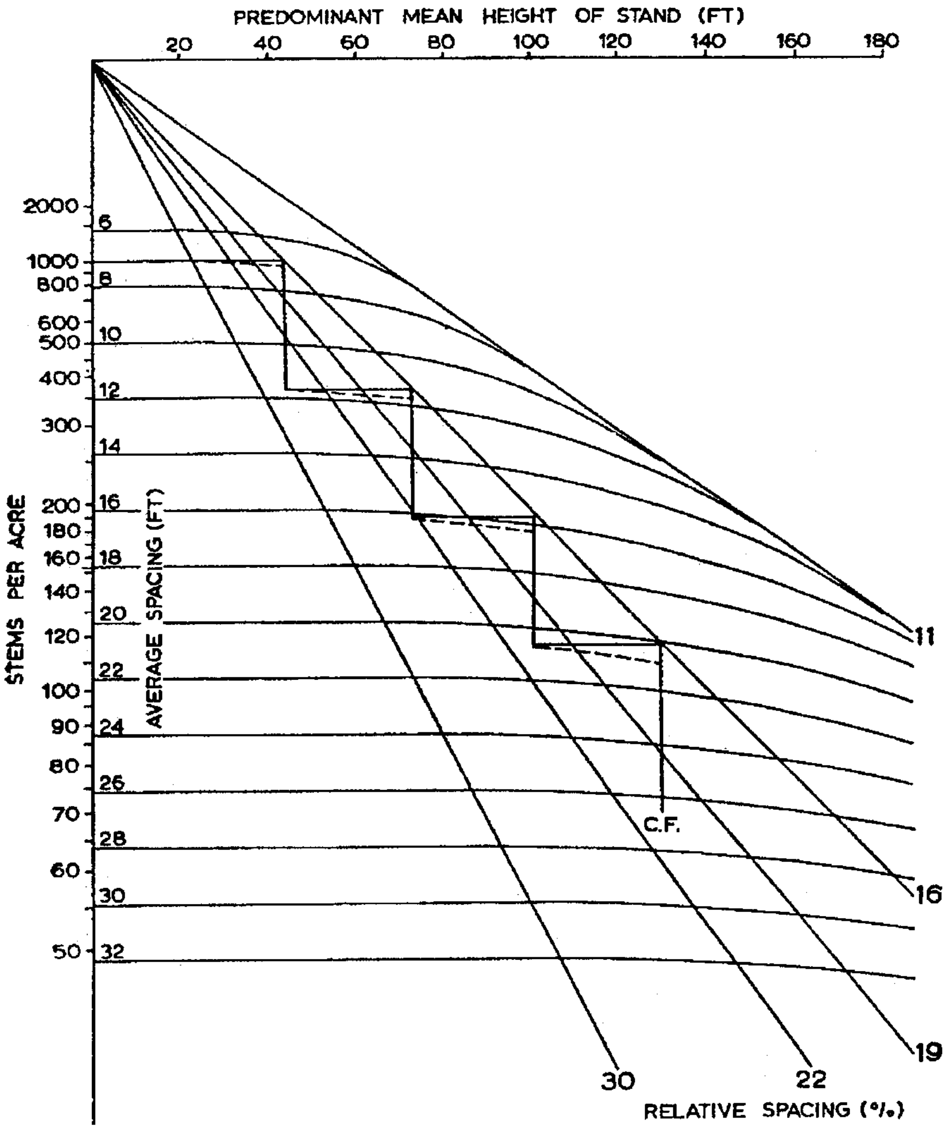

Figure 6: Mortality model from Beekhuis (1966). The triangular average spacing axis is reversed to represent increasing stand density. Predominant mean height is the average of the 40 tallest trees per acre.

through the origin in the S–H plane (Figure 6), rather than to a more general curve as in Figure 5. Unpublished work on radiata pine had suggested that the line through the origin did not always look reasonable, and this also seems to be the case with the spruce data (Section 2.6). The added flexibility of a different γ seems useful, although further research on this topic might be interesting.

4 Self-thinning limits

As mentioned before, our model implies that the S over H trajectories ultimately approach a limiting curve, which is $S = (\beta H)^{\gamma/\alpha}$. Or, taking logarithms and substituting N,

$$\log N + 2\frac{\gamma}{\alpha}\log H = \text{constant} . \tag{11}$$

This, or more specifically the limiting relative spacing case with $\gamma/\alpha = 1$, is an example of *self-thinning law* (Figure 7). The other two self-thinning laws commonly encountered in the literature are Reineke's,

$$\log N + 1.6 \log D = \text{constant} , \tag{12}$$

and the 3/2 law

$$\log w + \frac{3}{2}\log N = \text{constant} , \tag{13}$$

where D is the quadratic mean dbh, and w is mean tree biomass or mean stem volume (e.g., Vanclay 1994).

Although perhaps such "laws" should not be taken too seriously, at least a model that complies with one of them can be trusted to behave reasonably when extrapolated. In view of the widespread interest on these topics, however, some additional observations might be relevant.

First, note that the self-thinning line is only an asymptotic relationship, and does not determine mortality rates over much of the range of interest. In addition, Weller (1987) points out that the distortion caused by the logarithmic transformations, together with the fact that by using an average for diameter or volume the variable N is implicated in both of the graph axes, result in an apparent relationship that is visually stronger than it would otherwise be. To some extent, this idea that self-thinning laws may be partly an optical illusion seems to be supported by a comparison of Figures 1, 4 and 7.

Assuming w approximately proportional to D^2H, (13) can be expressed in terms of the same variables as (11) and (12):

$$2\log D + \log H + \frac{3}{2}\log N = \text{constant} . \tag{14}$$

An undisturbed forest stand follows some trajectory describing a spatial curve in the three-dimensional space $\log D - \log H - \log N$. The self-thinning lines can then be seen as asymptotes for projections of this trajectory on various planes. They can be good approximations for sets of unmanaged stands that do not differ too much in their initial densities, as in the natural stands that have been the subject of most self-thinning research. However, if the stand trajectories are separated due to different initial densities or thinning treatments, the most that can be expected is a limiting plane in the three-dimensional space (Bi 2001, García 1993). Projections may still follow (11)–(14), but in general the constant on the right-hand side will vary across stands. Analysis of data from radiata pine plantations (unpublished) has shown reasonable agreement with the limiting slopes of the Reineke and 3/2 laws, but with levels that depend on initial conditions and treatments. Only projections parallel to the self-thinning plane would produce a unique right-hand side; establishing if (11) is close to one of these would require further research.

Regardless of if the levels vary or not among stands, the slopes of the various self-thinning laws are not necessarily compatible (García 1993, Vanclay 1994). Eliminating D between (12) and (14) gives

$$\log N + 4\log H = \text{constant} .$$

This coincides with (11) if $\gamma/\alpha = 2$, compared to the $\gamma/\alpha = 1$ of the limiting relative spacing hypothesis. The estimated $\gamma/\alpha = 1.510$ from the spruce model can be accommodated by small changes in the nominal coefficients of (12) and (13), and/or in the exponents of the approximation $w \propto D^2H$.

5 Conclusions

Limited or poor-quality data requires simple models with guaranteed "logical" behavior. I suggest that dbh, basal area and age should be avoided as explanatory variables in growth models. Changes relative to height growth are often approximately independent of site quality (Beekhuis 1966, Eichhorn 1904). The mortality model of Section 2.5 followed from these principles. The model generalizes and adds flexibility to models used by Beekhuis (1966) and others. Extrapolation produces expected self-thinning patterns. Future research might suggest appropriate γ/α ratios for use when the available data is particularly poor.

Acknowledgments

The white spruce data was provided by the Forest Analysis and Inventory Branch and by the Forest Sciences Program of the British Columbia Ministry of Forests and Range. It was screened and processed by Zhengjun Hu as part of his Master of Science research

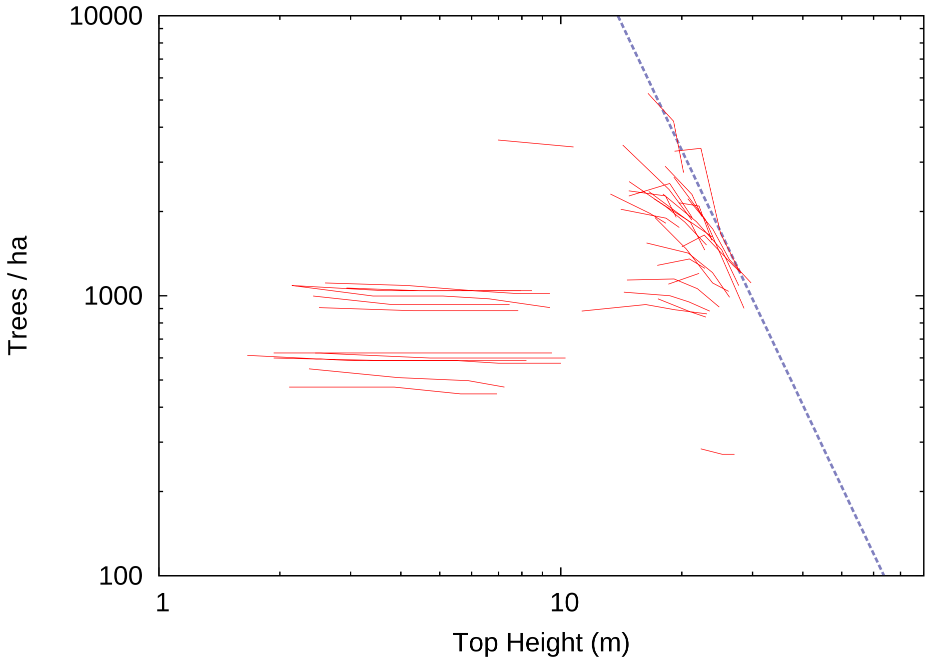

Figure 7: Self-thinning limiting line for the spruce model. Logarithmic axes.

at UNBC. Useful comments from two anonymous referees are gratefully acknowledged.

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Biographical Note

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