The Self-Thinning Surface

Huiquan Bi

ABSTRACT. This article introduces a generalized expression of the self-thinning rule, $B = KS^\alpha N^\beta$, where B is stand biomass per unit area, N is stand density, S is relative site index, and K, α and β are parameters. On log scales, this equation becomes a self-thinning surface that defines a density-dependent upper frontier of stand biomass over a gradient of site productivity for a given species. This equation is formulated for parameter estimation as a stochastic frontier function with two error components that have different distributional properties. As an example, maximum likelihood estimates of the self-thinning surface and its confidence envelope were shown for *Pinus radiata* (D. Don). Furthermore, site occupancy was estimated through one of the error components of the stochastic frontier function. The conditional response of mortality at any given site occupancy was revealed by using regression quantiles. Light mortality was associated with increases in site occupancy, while heavy mortality caused a reduction in site occupancy. Changes in the estimated site occupancy had a linear relationship with changes in log stand density. The dynamic interplay between site occupancy and mortality, together with the random external effects on the self-thinning frontier, was suggested to drive the growth trajectories of individual stands during stand growth and self-thinning. Consequently, individual stands seldom travel along their self-thinning frontiers but are more likely to converge toward them during the self-thinning phase of stand development. For. Sci. 47(3):361–370.

Key Words: Stochastic frontier function, site productivity, site occupancy, mortality regression quantile, stand dynamics, *Pinus radiata.*

THE SELF-THINNING RULE defines a density-dependent upper frontier of stand biomass for even-aged pure plant stands in a given environment with a power function:

$$B = KN^\beta \qquad (1)$$

where B is the total stand biomass per unit area, N is stand density, K is a species-specific and environment-specific constant, and $\beta = -0.5$ is the hypothesized self-thinning exponent (Yoda et al. 1963, White and Harper 1970, White 1980, 1981, 1985, Westoby and Howell 1981, Westoby 1984, Whittington 1984). On log scales, Equation (1) becomes a line with a slope of –0.5. A vast amount of literature has appeared on self-thinning since the pioneer work of Yoda et al. (1963). However, there has not been general agreement in the literature on the invariability of β among species and on the variability of K across environmental gradients within one species as reviewed recently by Jack and Long (1996)

and Bi et al. (2000). The lack of a consensus calls for a generalized expression of Equation (1):

$$B = KS^\alpha N^\beta \qquad (2)$$

where S represents a measure of site productivity that indicates the level of resource supply in a given environment, and α is a coefficient. K in this generalized expression becomes a species-specific constant. On log scales, Equation (2) becomes a self-thinning surface that defines a density-dependent upper frontier of stand biomass over a gradient of site productivity for any given species. Under this surface, a self-thinning frontier can be determined for any individual stand within the range of site productivity represented by S.

Despite the vast amount of literature on self-thinning, no attempt has been made to define the self-thinning surface for any species. Studies so far have mostly focused on the estimation of a single self-thinning line [i.e., Equation (1) in

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the log transformed form] that lies over a group of growth trajectories of a number of even-aged stands growing on different sites. Site productivity has not been formally incorporated in the equation. If the intercept increases with productivity, the self-thinning line thus estimated may be adequate for the most productive stand in the group, but for many other stands it is certainly an overestimation. The self-thinning rule has well-demonstrated applications in developing stand density management regimes and yield models for even-aged forest stands (Tadaki 1964, Ando 1968, Yin et al. 1978, Drew and Flewelling 1977, 1979, Long 1985, Hibbs 1987, Zhao et al. 1993, Tang et al. 1994, Tang et al. 1995, Jack and Long 1996, Newton 1997). However, these applications have largely remained a tool for making strategic decisions concerning silvicultural regimes rather than for detailed growth and yield analysis (Jack and Long 1996). Likely this is because the self-thinning frontier has not been accurately estimated on a site-specific basis. The potential of the application of the self-thinning rule in the management of even-aged forest stands is much restricted unless the self-thinning frontier can be accurately estimated for individual stands.

Recently, Bi et al. (2000) introduced stochastic frontier functions for estimating the self-thinning frontier in the case of Equation (1) and proposed a measure of site occupancy relative to the self-thinning frontier for stands undergoing self-thinning. However, as with most studies, they estimated a single self-thinning line for a number of even-aged *Pinus radiata* (D. Don) stands growing on different sites. Here I present the statistical model specification of Equation (2) and its log-likelihood function by using relative site index as an indicator of site productivity. As an example, the estimated self-thinning surface and its confidence envelope are shown for *P. radiata*. In addition, I demonstrate how estimating the self-thinning surface rather than estimating a single self-thinning line can reveal greater insight into the dynamics of self-thinning stands.

Data

The data for this work are from experiments in *P. radiata* tree farms established in the 1950s and owned by A.P.M. Forests Pty Ltd. (now Amcor Pty Ltd.) in the Gippsland region of Victoria, Australia. This region is ranked medium in terms of site productivity among the main *P. radiata* regions of the Southern Hemisphere (Lewis and Ferguson 1993). The experiments were designed to test the effect of different thinning regimes on stand growth across the tree farms. The data is an expanded data set from that used by Bi et al. (2000). More recent measurements of some of the 12 plots used by Bi et al. (2000) and data from 6 other plots were recently provided by Amcor Pty Ltd. These 18 control plots underwent self-thinning and provided a total of 153 plot measurements for analysis in this article. The initial planting densities of these plots were unknown. When plots were first measured at the age of 10 to 12 yr, stand density ranged generally from 1,220 to 2,112 trees/ha (Table 1). Plot area varied from 0.0512 to 0.0973 ha. These plots were generally measured every 2 yr or less, and the last measurement was taken between age 22 and 38 yr. At each measurement,

diameter at breast height and height of individual trees were obtained. The death or removal of trees was recorded in three categories: (1) unidentified natural mortality, (2) removed because of *Sirex noctilio* attack, and (3) removed for unknown reasons. Natural mortality varied from 24.1% to 50.5% of the number of live trees at first measurement, and removal because of *Sirex* attack varied between 0.6% and 22.6% among the 18 plots (Table 1). Trees removed for unknown reasons were generally less than 5%, except for one plot where 7% of the trees was removed after the first measurement. The age of imminent mortality (i.e., the age of the plot measurement just before natural mortality occurred) ranged from 10 to 14 yr (Table 1). The biomass equations developed by Baker et al. (1984) for *P. radiata* in the study area were used to calculate tree and total stand biomass as described by Bi et al. (2000).

A relative index of site productivity was derived using the mean height of 50 largest diameter trees per hectare at age 20, similar to the approach of Bi and Jurskis (1996). Since no measurements were taken exactly at age 20 for all stands, stand height at age 20 was estimated using local regression, *loess* (Cleveland 1993). Assuming identically distributed Gaussian errors, a local linear fitting with a smoothing parameter of 0.3 was used after some iterative fitting and visual examination of the smoothed height-age curves and data. The maximum observed stand height at age 20 from all empirical data available in the study area was nearly 35 m. No single stand in the inventory database of *P. radiata* plantations in the region exceeded this maximum stand height at age 20, although a small number of stands at a particular site could reach up to 40m at older ages. The ratio of stand height at age 20 to this maximum stand height was taken as the site productivity index for each stand. This index is different from the conventional site index, i.e., stand height at an index age (Clutter et al. 1983). It provides a relative measure of site productivity. Stand height at age 20 varied from 19.3 to 32.3 m, and so the relative index varied from 0.552 to 0.921 among the 18 stands (Figure 1). Estimation of site quality from empirical stand height data has a long history in forestry (Clutter et al. 1983), while the theoretical basis for such an indirect approach came only recently through the work of Tilman (1988), who showed that the allocation to height growth increases with the availabilities of soil resources and light.

The Self-Thinning Surface: Specification, Estimation and Confidence Envelope

Equation (2) can be formulated as a stochastic frontier function by extending the work of Bi et al. (2000) as follows:

$$B = KS^\alpha N^\beta e^v e^{-u} \qquad (3)$$

where B, K, and N are as previously defined, S is relative site index, α and β are parameters. The variables v and u are two random variables. The first random variable v is assumed to have a normal distribution with a zero mean and constant variance σ_v^2. The second random variable $0 \leq u \leq \infty$ takes the absolute values of a normally distributed variable with zero

Table 1. A data summary of the 18 plots used for the estimation of the self-thinning surface. Age, stand density, average diameter at breast height overbark (dbhob), stand height and stand biomass were shown for the first and last measurements only.

Plot no	Age (yr)	Stand density (trees/ha)	Mean dbhob (cm)	Stand height (m)	Stand biomass (tons/ha)	No. of measurements	Stand height at age 20 (m)	Age of imminent mortality (yr)	Natural mortality	Removed for Sirex	Removed reason not known	Total mortality
									............................(%)............................			
1	12	1,507	15.4	13.0	104	13	19.3	14	42.6	0	3.5	46.1
	35	813	26.4	29.0	268							
2	11	1,336	16.6	15.4	116	10	21.1	11	49.2	0	7.0	56.2
	31	585	31.2	26.0	263							
3	11	1,880	15.1	15.1	133	11	22.1	11	36.4	0	1.1	37.5
	33	1,026	26.4	27.5	323							
4	12	1,220	15.9	14.7	103	14	23.8	12	33.0	8.5	4.7	46.2
	37	667	31.1	33.4	346							
5	11	1,476	14.6	15.3	96	7	23.9	13	24.1	0	0	24.1
	22	1,120	20.4	25.5	197							
6	12	1,979	14.4	17.6	139	13	24.9	14	39.2	0.6	2.4	42.2
	38	1,132	25.9	35.1	397							
7	11	2,112	14.1	17.2	135	11	25.0	11	33.9	0	0	33.9
	30	1,254	23.2	29.4	328							
8	11	1,788	15.1	17.1	134	7	25.3	11	25.6	0	0	25.6
	22	1,344	20.3	27.6	254							
9	11	1,429	16.2	15.7	123	7	26.1	13	25.6	0	0	25.6
	22	1,063	23.0	27.8	253							
10	11	1,505	15.7	16.4	120	7	26.4	11	27.0	0	0	27.0
	22	1,099	21.9	28.5	244							
11	11	1,480	14.9	14.9	105	7	27.1	11	43.1	0	0	43.1
	22	843	22.4	29.6	204							
12	11	1,576	13.6	15.7	93	7	27.2	13	34.4	0	0	34.4
	22	1,021	21.3	29.1	225							
13	10	2,038	13.8	14.6	126	9	27.7	10	34.9	22.6	1.9	59.4
	26	827	28.7	34.8	378							
14	10	1,239	16.5	16.2	115	9	29.4	10	47.0	2.4	0	49.4
	26	627	32.9	33.6	361							
15	10	1,973	13.7	16.4	129	9	30.2	10	50.5	13.9	1	65.4
	26	684	29.4	35.6	327							
16	10	803	14.1	15.2	120	9	30.8	10	47.8	0	3.5	51.3
	26	878	28.1	32.3	374							
17	10	1,583	15.6	16.5	125	9	30.9	10	33.0	18.2	0	51.2
	26	773	29.8	35.2	377							
18	10	1,327	17.2	15.9	132	9	32.2	10	36.0	8.1	3.5	47.6
	26	694	33.5	39.2	432							

mean and constant variance σ_μ^2 and is assumed to be half normal. As in Bi et al. (2000), the term $0 \le e^{-u} \le 1$ represents site occupancy, i.e., the extent to which plant stands have occupied the growing space and utilized the available resources on a given site for growth. At full site occupancy when $e^{-u} = 1$, stands have accumulated the maximum attainable biomass at a given stand density on that site. Any further growth will incur mortality. The maximum attainable biomass at any stand density represents the biomass frontier for that site, which is not directly observable from empirical data (Zeide 1991). The random effects of external factors on the biomass frontier such as climatic variations, insect attacks, diseases or other changes in the environment specific to each site are represented by v.

The interpretation of e^{-u} in Equation (3) as site occupancy, a much-used term in plantation silviculture, can be understood by observing the ratio of the actual stand biomass to the corresponding maximum attainable biomass at the frontier:

$$e^{-u} = \frac{B}{KS^\alpha N^\beta e^v} \qquad (4)$$

Clearly this is a measure relative to the self-thinning frontier. Conceptually equivalent measures of site occupancy are the yield index of Ando (1968) and the relative stand density indices of Tadaki (1964) and Drew and Flewelling (1979). All these indices are constructed using a line of maximum attainable mean tree volume and stand density with a fixed self-thinning slope and an intercept determined by visual placement, largely because of the lack of a proper method of statistical estimation. The relative stand density index (Pr) proposed by Drew and Flewelling's (1979) is the ratio of observed stand density to the maximum stand density attainable in a stand with the same mean tree volume. This index has become widely used particularly in north America in the construction of stand density management diagrams (Jack and Long 1996, Newton 1997).

On logarithmic scales, Equation (3) becomes a stochastic frontier function with the same specification as that of Aigner et al. (1977) for the analysis of maximum potential production and production efficiency in econometrics:

$$\ln B = k + \alpha \ln S + \beta \ln N + \varepsilon \qquad (5)$$
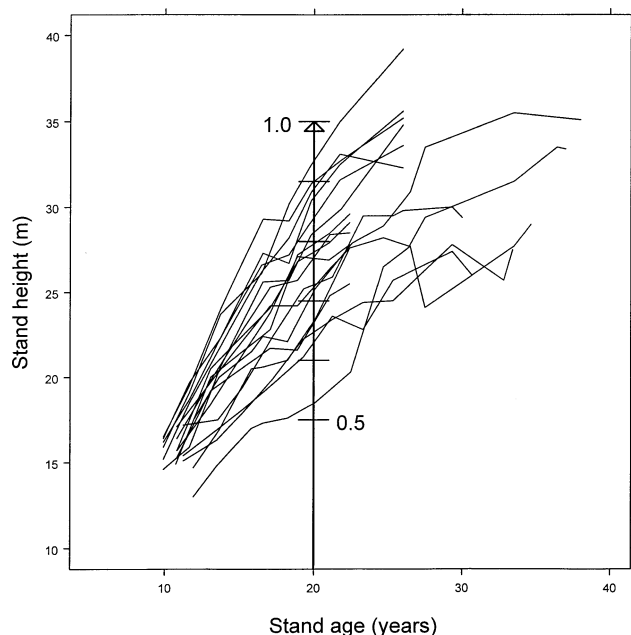
Figure 1. Principle of the site productivity index: growth trajectories of stand height for the 18 plots plotted together with the maximum stand height of 35 m at age 20 for the study area. The site productivity index is the intercept of a trajectory where the maximum stand height is taken as unit measure.

where ln represents natural logarithm, $k = \ln K$, and the error term ε is a compound random variable, $\varepsilon = \nu - u$. The distributional properties of ε and u are well presented in the econometric literature (see Greene 1993, p. 310–311, 1997). The parameters in the model can be estimated by the maximum likelihood methods with the log-likelihood function given by Aigner et al. (1977). The normal equations derived from this log likelihood function have to be solved numerically through iteration. For easier computation, the log likelihood function given by Aigner et al. (1977) can be reparameterized as shown by Battese and Corra (1977):

$$\ln L(\theta) = n \ln \frac{\sqrt{2}}{\sqrt{\pi}} - n \ln \sigma$$
$$+ \sum_{i=1}^{n} \left\{ \ln\left[1 - \Phi\left(\frac{\varepsilon_i}{\sigma}\sqrt{\frac{\gamma}{1-\gamma}}\right)\right] - \frac{1}{2}\left(\frac{\varepsilon_i}{\sigma}\right)^2\right\} \quad (6)$$

where $\theta = (k, \alpha, \beta, \sigma^2, \gamma)'$ denotes the column vector of parameters of the model, n is the number of data points, $\sigma = \sqrt{\sigma_v^2 + \sigma_u^2}$, Φ is the standard normal distribution function, $\varepsilon_i = y_i - x_i\beta$, is the difference between the observed and fitted values of stand biomass for the ith data point, and

$$\gamma = \frac{\sigma_u^2}{\sigma^2} = \frac{\sigma_u^2}{\sigma_u^2 + \sigma_v^2}. \quad (7)$$

The first-order partial derivatives of this log likelihood function with respect to all five parameters can be obtained by following Battese and Corra (1977). The maximum-likelihood estimator denoted by $\hat{\theta}_N$ has the property of consistency and asymptotic normality. The proof of this property is presented by Amemiya (1973) and Battese and

Corra (1977) under some regularity conditions. The variance and covariance matrix of the maximum-likelihood estimator can be estimated by

$$Cov(\hat{\theta}_N) = \sum \left[-\frac{\partial^2 \ln L(\hat{\theta}_N)}{\partial\theta\partial\theta'}\right]^{-1} \quad (8)$$

as shown by Battese and Corra (1977). The practical implication of the above results is that $\hat{\theta}_N$ follows multivariate normal distribution $N(\hat{\theta}_N, \Sigma)$ with large samples, a property useful for making statistical inferences about the parameter estimates.

Once the normal equations are solved by nonlinear search algorithm, the unobservable self-thinning frontier is given by

$$\ln \hat{B} = \hat{k} + \hat{\alpha} \ln S + \hat{\beta} \ln N \quad (9)$$

Site occupancy for the ith observation is estimated as the expectation of e^{-u_i}, $E(e^{-u_i} | \varepsilon_i)$, which is given by Battese and Coelli (1988, 1992):

$$E\left[e^{-u_i} | \varepsilon_i\right] =$$
$$\left[\Phi\left(\frac{u_i^*}{\sigma_*} - \sigma_*\right) \middle/ \Phi\left(\frac{u_i^*}{\sigma_*}\right)\right] \exp\left(-u_i^* + \frac{1}{2}\sigma_*^2\right) \quad (10)$$

where $u_i^* = -\varepsilon_i\gamma$ and $\sigma_*^2 = \gamma\sigma_v^2$.

Following the comments of a reviewer of this article, the self-thinning surface was estimated using data after careful screening and some minor editing. Some stands had trees removed for *Sirex* attack and also for unknown reasons. In addition, five plot measurements occurred before the age of imminent mortality. By definition these plot measurements did not fully represent the self-thinning process. So a total of 29 such measurements were excluded from the analysis, including 21 measurements taken immediately following tree removal, 5 measurements taken before the age of imminent mortality, and 3 data points following the removal of 7% of the trees in plot 2. Since 11 of 18 plots had varying degrees of tree removal (Table 1), excluding these plots from analysis as suggested by the reviewer would result in a great loss of data. All parameter estimates and the variance and covariance matrix of parameter estimates were obtained using FRONTIER 4.1 of Coelli (1996). To be consistent with the previous work of Bi et al. (2000) and much of the literature on self-thinning, the common logarithm of stand biomass, site productivity index and stand density (i.e., logB, logS, and logN) was used in parameter estimation.

The maximum likelihood estimates of the stochastic self-thinning frontier are

$$\log B = 7.076 + 0.357 \log S - 0.509 \log N \quad (11)$$

The estimated values for σ^2 and γ are 0.029 and 0.816, respectively. Since $\sigma^2 = \sigma_v^2 + \sigma_u^2$ and $\gamma = \sigma_u^2 / \sigma^2$, the estimates of σ_μ^2 and σ_v^2 are 0.023 and 0.005, respectively. The estimated variance and covariance matrix of the five parameters is

$$\Sigma = \begin{pmatrix} 0.06127 & 0.00281 & -0.02007 & -0.00025 & -0.00582 \\ 0.00281 & 0.03203 & 0.00020 & -0.00021 & -0.00446 \\ -0.02007 & 0.00020 & 0.00668 & 0.00013 & 0.00274 \\ -0.00025 & -0.00021 & 0.00013 & 0.00005 & 0.00085 \\ -0.00582 & -0.00446 & 0.00274 & 0.00085 & 0.01807 \end{pmatrix}$$

$$(12)$$

Equation (11) and the estimated variance and covariance matrix in Equation (12) defined the self-thinning surface and its confidence envelope (Figure 2). The standard errors of the estimates of k, α, and β were 0.248, 0.179, and 0.082, respectively. Since the t-statistic for the difference between the estimated β and –0.5 was only 0.112, the estimated self-thinning slope was not significantly different from the stated slope of the self-thinning rule at the 95% confidence level. With a *t*-statistic of 1.99, the estimated α was significantly different from zero at the 95% confidence level. As expected, the intercept and slope were negatively correlated, with a covariance of –0.02007 as shown in the estimated variance and covariance matrix.

To obtain the confidence limits of $\log \hat{B}$, random variates were generated 5,000 times from the multivariate normal distribution $N(\hat{\theta}_N, \Sigma)$ using the algorithm for statistical computing given by Tong (1990):

$$\hat{\theta}_N^S = TZ + \hat{\theta}_N \qquad (13)$$

where $\hat{\theta}_N^S$ ($S = 1,2, \ldots , 5,000$) represents a vector of random variates sampled from the multivariate normal distribution $N(\hat{\theta}_N, \Sigma)$, $TT' = \Sigma$ is the Cholesky decomposition of the variance and covariance matrix Σ, $Z \sim N(0, I_5)$ and I_5 is a 5 $\times$ 5 identity matrix. Each sample of random variates $\hat{\theta}_N^S$ provided a set of values for k, α, and β, which was used to obtain the predicted values of $\log B$ over the data space on a 49 $\times$ 71 grid of $\log S$ and $\log N$. The samples provided 5,000
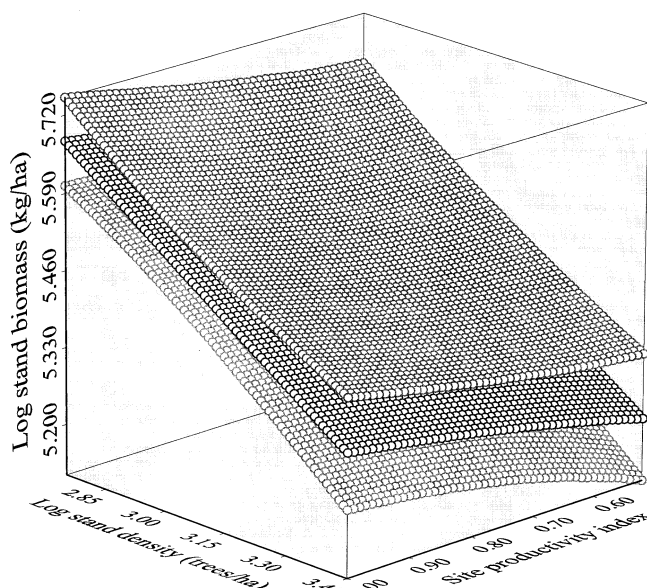

Figure 2. The estimated self-thinning surface (darker surface in the middle) and its upper and lower 95% confidence envelope.

sets of predicted values of $\log B$ over the 49 $\times$ 71 grid, with a total of more than 17 million data points. For each combination of $\log S$ and $\log N$ on the grid, the 2.5th and 97.5th percentiles of the 5,000 predictions of $\log B$ were calculated and taken as the 0.95 confidence limits at that point. The confidence limits for all points on the grid collectively formed a confidence envelope for the estimated self-thinning surface.

Taking a slice from the self-thinning surface and its confidence envelope (Figure 2) at a particular site productivity, the estimated self-thinning frontier and its confidence envelope could be obtained for each stand (Figure 3). The intercept of the estimated self-thinning frontier increased with site productivity, reaching a maximum value of 7.076 when site productivity index $S = 1$. Among the 18 stands, site productivity index varied from 0.552 to 0.921, and the corresponding intercept of the self-thinning frontier increased from 6.984 to 7.063.

Site Occupancy and Mortality During Self-thinning

The estimated site occupancy ranged from 0.705 to 0.973 with an average of 0.888 among the 124 data points. About half of the estimates were greater than 0.90, 90% of the estimates were greater than 0.80, and 97.5% were greater than 0.75. Apart from one stand, plot 2 in Figure 3, which suffered heavy reductions in stand density because of the removal of trees due to unknown reasons, all other stands reached at least site occupancy 0.9 during self-thinning.

To gain further insight into the dynamics of the self-thinning stands, annual mortality rate between successive measurements that were used in the estimation of the self-thinning surface was calculated for each stand. The scatterplot of mortality rate against the estimated site occupancy showed the variation of annual mortality rate increased with site occupancy and the conditional distribution of mortality rate at a given site occupancy seemed to depart markedly from the normal distribution. To highlight such a conditional variation in mortality, the following regression quantile function was chosen for modeling the conditional variation of mortality rate:

$$M_p = a_p + b_p \hat{U}^{c_p} \qquad (14)$$

where M_p represents the mortality regression p-quantile, i.e., the approximate conditional annual mortality rate at a given probability $P \in [0, 1]$, $\hat{U}$ is the estimated f site occupancy, and a_p, b_p, and c_p are parameters of the regression quantile function. Three values of p, 0.5, 0.75, and 0.95, were used in the analysis. For $p = 0.5$ and $p = 0.75$, a_p was restricted to be 0 to avoid the two estimated quantile curves crossing each other within the data range. Parameter estimates were obtained using the estimator of Basset and Koenker (1982). Regression quantiles introduced by Koenker and Basset (1978) and Basset and Koenker (1982) provide a general technique for estimating conditional quantile functions for linear models with independently and identically distributed
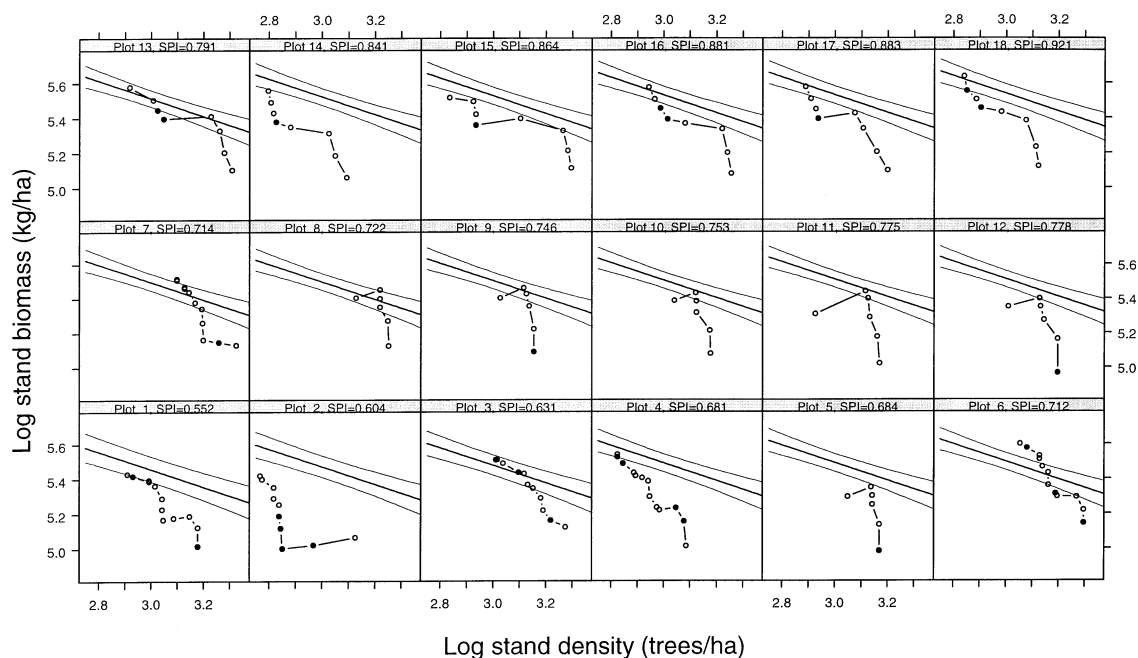
Figure 3. Multipanel display of the self-thinning frontier over the gradient of site productivity. Each panel shows how the observed self-thinning trajectory of a stand approached the estimated self-thinning frontier. The value of the site productivity index is indicated in the strip above each panel. Filled circles show data points not included in the analysis because of tree removal (see text).

(iid) errors. Their estimator of regression quantiles uses the simplest M-function, the absolute value function. The expanded flexibility of this approach has been further developed and widely adopted as a comprehensive approach to statistical analysis of both linear and nonlinear response models (Breckling and Chambers 1988, Efron 1991, Buchinsky 1994, Koenker and Park 1996, Yu and Jones 1998, Cade et al. 1999).

The estimated regression quantile functions corresponding to the three values of p in Equation (14) were

$$M_{0.95} = 2.62 + 30.33\, \hat{U}^{6.43} \qquad (15)$$

$$M_{0.75} = 3.51\, \hat{U}^{0.41} \qquad (16)$$

$$M_{0.50} = 2.06\, \hat{U}^{0.13} \qquad (17)$$

As expected, mortality rates lying above the regression quantile at $p = 0.95$ accounted for about 5% of the observations and data points lying below the regression quantile at $p = 0.50$ accounted for about half of the observations (Figure 4). The regression quantile at $p = 0.95$ represented the near extreme rate of mortality that could take place at any given site occupancy. Mortality rate between the regression quantiles at $p = 0.95$ and $p = 0.75$ were relatively high and accounted for about 20% of the observations. Light mortality could take place well before stands reached full site occupancy (Figure 4). For site occupancy less than 0.85, the annual mortality was mostly less than 5%. As site occupancy increased, much heavier mortality could take place as depicted by the regression quantile at $p = 0.95$. As stands approach full site occupancy, an annual mortality rate greater than 30% is possible, although with a small likelihood.

The three regression quantile functions provided a more comprehensive description of the dependence of

mortality on site occupancy during self-thinning, but they did not reveal the impact of mortality on site occupancy. Bi et al. (2000) found that site occupancy generally increased following light mortality and decreased following heavier mortality in *P. radiata* stands undergoing self-thinning. To explore this qualitative observation, the annual change in the estimated site occupancy and the annual decrease in log stand density between successive measurements used in the estimation of the self-thinning surface were calculated for the stands. The relationship between
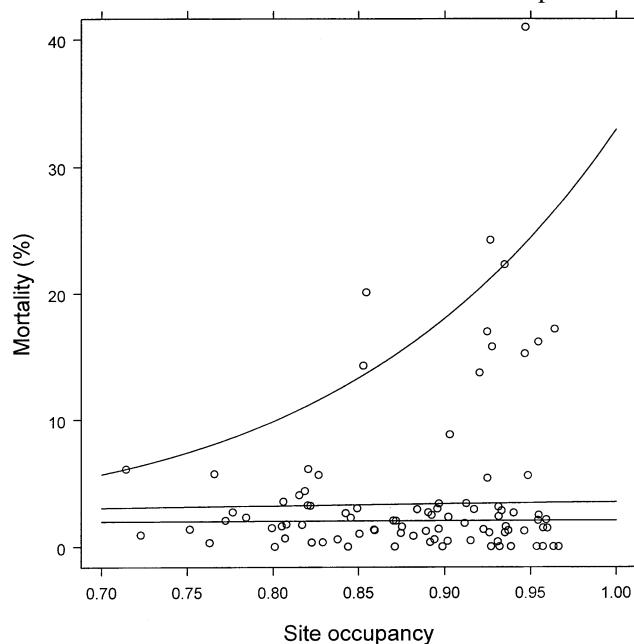
Figure 4. Conditional variation of annual mortality rate upon site occupancy for the 18 stands during self-thinning. The curves are regression quantiles at $p = 0.95$, $p = 0.75$ and $p = 0.50$ from top down.

changes in site occupancy and changes in log stand density was examined using least squares regression.

Mortality had a direct impact on site occupancy. Changes in the estimated site occupancy had the following relationship with changes in log stand density (Figure 5):

$$\hat{U}_{t+1} - \hat{U}_t = 0.020 + 0.624 \log(N_{t+1} / N_t) \qquad R^2 = 0.57 \quad (18)$$

where $\hat{U}_t$ and $\hat{U}_{t+1}$ are site occupancy in year t and $t + 1$, N_t and N_{t+1} are stand density in trees/ha in corresponding years. This relationship shows that on average a mortality rate greater than 3.1% per year resulted in a reduction in site occupancy, while a lighter mortality was associated with increases in site occupancy.

Individual stands approached their self-thinning frontiers along quite different trajectories, and rarely traveled along the self-thinning frontiers (Figure 3). With light mortality taking place during stand growth, site occupancy would not decrease between successive measurements. Stands would gradually approach and converge to the self-thinning frontier. With heavy mortality and reduced site occupancy, stands would fall away from the self-thinning frontier and depart markedly from it. Such movements can be seen clearly from stand trajectories shown in Figure 3. When mixed light and heavy mortalities occurred intermittently during stand growth, large variations in growth trajectories were observed (Figure 3).

Discussion

The results represented an attempt to apply the recently introduced approach of stochastic biomass frontier functions to estimating the self-thinning surface and its confidence envelope. There was little difference in the estimated self-thinning slope β between the results of this work and that estimated previously by Bi et al. (2000). Both estimates were not significantly different from the slope of –0.5 as stated by
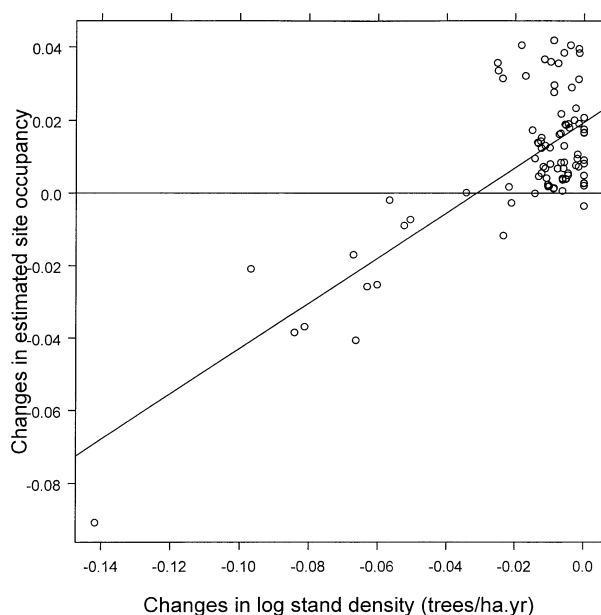
Figure 5. Relationship between the annual change of site occupancy and that of log stand density.

the self-thinning rule. However, this study showed how the intercept of the self-thinning frontier would change over a gradient of site productivity for *P. radiata* in the Gippsland region. The complete range of site productivity index for *P. radiata* in the region varied between 0.523 to 1 based on all available stand height data in the inventory database of plantations around age 20. Over this range, the estimated intercept of the self-thinning frontier increased from 6.976 to a maximum value of 7.076. By comparison, the intercept of the self-thinning frontier for stemwood determined visually by Drew and Flewelling (1977) for 54 *P. radiata* stands in New Zealand is 6.99. This was derived by converting their relationship between mean tree volume and stand density to one that is comparable using the average basic density of stemwood of *P. radiata* in New Zealand (Cown et al. 1991). For a wide range of tree species, the intercept of the self-thinning frontier using the units of kg/ha and trees/ha falls between 6.5 and 7.4, i.e., within one order of magnitude of difference (White 1985). For *P. radiata* in this study, the magnitude of variation in the estimated intercept over the gradient of site productivity is about 11% of the magnitude of variation among the range of tree species given by White (1985).

At a final stocking of 200 trees/ha before harvesting, as is often the case with the density management of *P. radiata* (Lewis and Ferguson 1993), this magnitude of variation in the estimated intercept represents a range of stand biomass from 637 to 803 tons/ha at full site occupancy over the range of productivity gradient for the Gippsland region. This magnitude of variation highlights the need for a careful and more rigorous testing of the assumption in much of the earlier literature that the self-thinning boundary line is species-specific and site-independent (see Westoby 1984). Although not formally tested, this assumed invariability of the self-thinning intercept has been labeled as the *Suckatschew* effect in influential texts of plant population biology and forest stand dynamics (Harper 1977, p. 176–183, Oliver and Larson 1996, p. 342). Growing evidence, however, suggests the contrary (e.g., Furnas 1981, Hozumi 1983, Givnish 1986, Morris and Myerscough 1985, 1991, DeBell et al 1989, Harms et al. 2000). A recent review by Jack and Long (1996) indicates that the concept of a single constant intercept of the self-thinning boundary line for a given species is not fully supported by the literature. As they pointed out, the assumed invariability may be due to the lack of rigorous testing rather than to evidence showing site-independence. Through the model specification in Equation (3), one can incorporate site productivity in the stochastic frontier function through a relative index. Other site, stand, and tree characteristics that affect site productivity (e.g., Harms et al. 1994, 2000) can be incorporated in a similar manner. More importantly, one can test site-dependence of the self-thinning line for a given species.

Another advantage of incorporating site productivity in Equation (3) is that site occupancy can be statistically estimated on a site-specific basis. As a much-used term in plantation silviculture, site occupancy is conceptually defined as a relative measure. It indicates the degree to which a stand has

occupied the growing space and utilized the available resources for growth within the given environment (Bi et al. 2000). The same degree of site occupancy can be achieved by a small number of big trees or a large number of small trees (Baker 1950). Early measures of site occupancy, either in the name of yield index or relative stand density index (e.g., Ando 1968, Tadaki 1964, Drew and Flewelling 1979), are all relative to a single self-thinning line determined largely by visual placement for a given species. Consequently, these measures are neither statistically based nor site-specific.

The relative stand density index (Pr) proposed by Drew and Flewelling (1979) is the ratio of observed stand density to the maximum stand density attainable in a stand with the same mean tree volume. Assuming a single deterministic self-thinning line for a given species by assigning $S = 1$ and $v = 0$ in Equation (4), one can show that the measure of site occupancy (U) proposed here is mathematically related to Pr:

$$U = \frac{B}{B_{max}} = \frac{B}{KN^{\beta}} = \frac{B}{K}N^{-\beta}$$
$$= N_{max}^{\beta}N^{-\beta} = \left(\frac{N}{N_{max}}\right)^{-\beta} = (Pr)^{-\beta} \qquad (18)$$

where B is the observed biomass of a stand with density N, B_{max} and N_{max} are the corresponding values of biomass and stand density on the self-thinning line (Figure 6). For $\beta = -0.5$, $U = Pr^{0.5}$, and $Pr = U^2$. Drew and Flewelling (1977) defined the zone of imminent competition-mortality for *P. radiata* in New Zealand with $0.55 \leq Pr < 1$. The lower limit of the zone with $Pr = 0.55$ was assumed to be correct for all sites (Drew and Flewelling 1979) and subsequently was used in the construction of stand density management diagrams for a range of species in North America (Newton 1997). Although seemingly not unreasonable, the zone represents a relatively wide band, and the lower limit may be more precisely estimated if the self-thinning line is estimated on a site-specific basis for any species.

Since site occupancy was estimated relative to a site-specific self-thinning frontier through Equation (9), the
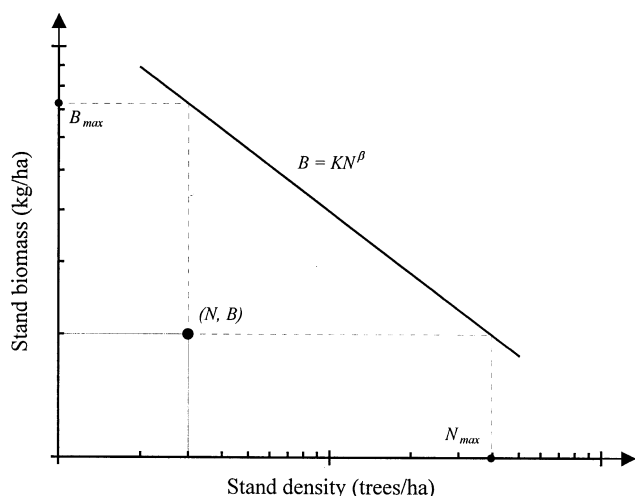
Figure 6. Diagram illustrating the derivation of the proposed measure of site occupancy relative to the self-thinning line in relation to the relative stand density index of Drew and Flewelling (1979) (see text).

estimates of site occupancy were more accurate than that of Bi et al. (2000). The improved estimates of site occupancy made it possible to explore quantitatively the relationship between site occupancy and mortality during self-thinning. The three regression quantile functions [Equations (15), (16), and (17)] and the relationship between annual change of site occupancy and that of log stand density [Equation (18)] provided greater insights into the dynamic interplay between site occupancy and mortality during self-thinning. When site occupany is low, stands suffer only light mortality, probably not all competition-induced. As site occupancy increases, light and heavy mortality take place intermittently. Much heavier mortality could also be expected with a small likelihood. Light mortality is associated with increases in site occupancy. Heavy mortality causes reduction in site occupancy and the growth trajectory of a stand falling back from its self-thinning frontier (Figure 3).

This dynamic interplay between site occupancy and mortality make it unlikely that a stand will grow in a state of full site occupancy throughout the course of self-thinning. Since stands travel along the self-thinning frontier only when site occupancy is one (Bi et al. 2000), plant populations probably seldom travel along their self-thinning frontiers but more likely converge towards them. The growth trajectory of a stand could be further influenced by the random external effects on the self-thinning frontier represented by v. As discussed by Bi et al. (2000), when a stand was approaching full site occupancy (i.e., $u \to 0$ and $e^{-u} \to 1$), and the random effects of external factors represented by v had a positive impact on the biomass frontier such as favorable climatic conditions or fertilization, a positive residual $\hat{\varepsilon}_i$ could be expected. The growth trajectory of the stand could rise and lie above the estimated self-thinning frontier as long as the positive impact lasted.

Previous studies have indicated that the growth and mortality of individuals are size-dependent during competition in plant stands (West and Borough 1983, Cannell et al. 1984, Hara 1985, Schmitt et al. 1987, Bi and Turvey 1996). However, little is known about the extent of variation in mortality rate as stands approach the self-thinning frontier with increasing site occupancy, and even less is known about the impact of mortality on site occupancy in the self-thinning process. The dynamic interplay between site occupancy and mortality in this study is an aspect of the dynamics of self-thinning stands which requires attention. Mortality changes the size distribution and also affects the local variation of growth and mortality of even-aged plant populations (Westoby 1982, Weiner and Thomas 1986, Kenkel 1988, Kenkel et al. 1989, Bi and Turvey 1996, Kenkel et al. 1997). Understanding the dependence of mortality on the size of individual plants as well as the site occupancy of the population will help to explain the dynamics of self-thinning. The practical implication found in this study is that both the site occupancy of a stand and the size of individuals that compose it need to be considered for accurate predictions of the growth and mortality of trees in even-aged pure stands.

Since the data for estimating the self-thinning surface came from multiple measurements of the 18 plots, some degree of autocorrelation may exit among data from the same plot. As discussed by Bi et al. (2000), the parameter estimates of the frontier function would be little affected by such a correlation, although the estimate of the variance and covariance matrix may not be exact. A relevant statistical analysis by Schmidt and Lovell (1980) in a similar context in econometrics showed that there was only a slight increase in the estimated standard errors of parameter estimates when positive correlated productive and allocative efficiencies were permitted in a stochastic frontier model. However, there was no appreciable effect on the inferences concerning the shape and placement of that frontier (Schmidt and Lovell 1980).

Literature Cited

AIGNER, D., K. LOVELL, AND P. SCHMIT. 1977. Formulation and estimation of stochastic frontier production models. J. Econ. 6:21–37.

AMEMIYA, T. 1973. Regression analysis when the dependent variable is truncated normal. Econometrica 41:997–1016.

ANDO, T. 1968. Ecological studies on the stand density control in even-aged pure stand. Gov. For. Ex. Sta., Tokyo, Bull. 210:1–153.

BAKER, F.S. 1950. Principles of silviculture. McGraw-Hill, New York. 414 p.

BAKER, T.G., P.M. ATTIWILL, AND H.T.L. STEWART. 1984. Biomass equations for *Pinus radiata* in Gippsland, Victoria. N. Z. J. For. Sci. 14:89–96.

BASSET, G., AND R. KOENKER. 1982. An empirical quantile function for linear models with iid errors. J. Am. Stat. Assoc. 77:407–415.

BATTESE, G.E., AND G.S. CORRA. 1977. Estimation of a production frontier model: With application to the pastoral zone of eastern Australia. Aust. J. Agric. Econ. 21:169–179.

BATTESE, G.E., AND T.J. COELLI. 1988. Prediction of firm-level technical efficiencies with a generalized frontier production function and panel data. J. Econ. 38: 387–399.

BATTESE, G.E., AND T.J. COELLI. 1992. Frontier production functions, technical efficiency and panel data: With application to paddy farmers in India. J. Prod. Anal. 3:149–169.

BI, H., AND V. JURSKIS. 1996. Yield equations for irregular regrowth forests of *Eucalyptus fastigata* on the south-east tablelands of New South Wales. Aust. For. 59:151–160.

BI, H., AND N.D. TURVEY. 1996. Competition in mixed stands of *Pinus radiata* and *Eucalyptus obliqua*. J. Appl. Ecol. 33:87–99.

BI, H., G. WAN, AND N.D. TURVEY. 2000. Estimating the self-thinning boundary line as a density-dependent stochastic biomass frontier. Ecology 81:1477–1483.

BRECKLING, J., AND R. CHAMBERS. 1988. M-quantiles. Biometrica 75:761–771.

BUCHINSKY, M. 1994. Changes in the U.S. wage structure 1963–1987: Application of quantile regression. Econometrica 62:405–458.

CADE, B.S., J.W. TERRELL, AND R.L. SCHROEDER. 1999. Estimating effects of limiting factors with regression quantiles. Ecology 80:311–323.

CANNELL, M.G.R., P. ROTHERY, AND E.D. FORD. 1984. Competition within stands of *Picea sitchensis* and *Pinus contorta*. Ann. Bot. 53:349–362.

CLEVELAND, W.S. 1993. Visualizing data. AT&T Bell Laboratories, Murray Hill, NJ. 360 p.

CLUTTER, J.L., J.C. FORTSON, L.V. PIENAAR, G.H. BRISTER, AND R.L. BAILEY. 1983. Timber management: A quantitative approach. Wiley, New York.

COELLI, T. 1996. A guide to FRONTIER Version 4.1: A computer program for stochastic frontier production and cost function estimation. Work. Pap. 96/07, Centre for Efficiency and Productivity Analysis, Univ. of New England, Armidale, Australia.

COWN, D.J., D.L. MCCONCHIE, AND G.D. YOUNG. 1991. Radiata pine wood properties survey. FRI Bull. No. 50. For. Res. Inst., Rotorua, NZ.

DEBELL, D.S., W.R. HARMS, AND C.D. WHITESELL. 1989. Stockability: A major factor in productivity differences between *Pinus taeda* plantations in Hawaii and the southeastern United States. For. Sci. 35:708–719.

DREW, T.J., AND J.W. FLEWELLING. 1977. Some recent Japanese theories of yield-density relationships and their application to monterey pine plantations. For. Sci. 23:517–534.

DREW, T.J., AND J.W. FLEWELLING. 1979. Stand density management: An alternative approach and its application to Douglas-fir plantations. For. Sci. 25:518–532.

EFRON, B. 1991. Regression percentiles using squared error. Statistica Sinica 1:93–125.

FURNAS, R.E. 1981. A resource theory of self-thinning in plant populations. Ph.D thesis, Cornell University, Ithaca, NY.

GIVNISH, T.J. 1986. Biomechanical constraints on self-thinning in plant populations. J. Theoret. Biol. 119:139–146.

GREENE, W. 1993. Econometric analysis. Ed. 2. Macmillan, New York. 791p.

GREENE, W. 1997. Frontier production functions. *In* Handbook of applied econometrics: Microeconomics, Pesaran, H., and P. Schmidt (eds.). Blackwell Publishers, Oxford. 453 p.

HARA, T. 1985. A model for mortality in a self-thinning plant population. Ann. Bot. 55:667–674.

HARMS, W.R., D.S. DEBELL, AND C.D. WHITESELL. 1994. Stand and tree characteristics and stockability in *Pinus taeda* plantations in Hawaii and South Carolina. Can. J. For. Res. 24:511–521.

HARMS, W.R., C.D. WHITESELL, AND D.S. DEBELL. 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. For. Ecol. Manage. 126:13–24.

HARPER, J. 1977. Population biology of plants. Academic Press, London. 892 p.

HIBBS, D. 1987. The self-thinning rule and red alder management. For. Ecol. Manage. 18:273–281.

HOZUMI, K. 1983. Ecological and mathematical considerations on self-thinning in even-aged pure stands. III. Effect of the linear growth factor on self-thinning and its model. Bot. Mag. Tokyo 96:171–191.

JACK, S.B., AND J.N. LONG. 1996. Linkages between silviculture and ecology: An analysis of density management diagrams. For. Ecol. Manage. 86:205–220.

KENKEL, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69:1017–1024.

KENKEL, N.C., J.A. HOSKINS, AND W.D. HOSKINS. 1989. Local competition in a naturally established jack pine stand. Can. J. Bot. 67:2630–2635.

KENKEL, N.C., M.L. HENDRIE, AND I.E. BELLA. 1997. A long-term study of *Pinus banksiana* population dynamics. J. Veg. Sci. 8:241–254.

KOENKER, R., AND G. BASSET. 1978. Regression quantiles. Econometrica 46:33–50.

KOENKER, R., AND B.J. PARK. 1996. An interior point algorithm for nonlinear quantile regression. J. Econ. 71:265–283.

LEWIS, N.B., AND I.S. FERGUSON. 1993. Management of radiata pine. Inkata Press, Melbourne, Australia. 404 p.

LONG, J.N. 1985. A practical approach to density management. For. Chron. 61:23–27.

MORRIS, E.C., AND P.J. MYERSCOUGH. 1985. Nutrient level effects on thinning and non-thinning effects in even-aged populations of subteranean clover. Aust. J. Ecol. 10: 469–479.

MORRIS, E.C., AND P.J. MYERSCOUGH. 1991. Self-thinning and competition intensity over a gradient of nutrient availability. J. Ecol. 79: 903–923.

NEWTON, P.F. 1997. Stand density management diagrams: Review of their development and utility in stand-level management planting. For. Ecol. Manage. 98: 251–256.

OLIVER, C.D., AND B.C. LARSON. 1996. Forest stand dynamics. Wiley, New York. 520 p.

SCHIMIDT, P., AND C.A.K. LOVELL. 1980. Estimating stochastic production and cost frontiers when technical and allocative inefficiency are correlated. J. Econ. 13:83–100.

SCHMITT, J., J. ECCLESTON, AND D.W. EHRHARDT. 1987. Dominance and suppression, size-dependent growth and self-thinning in a natural *Impatiens capensis* population. J. Ecol. 75:651–665.

TADAKI, Y. 1964. Effect of thinning on stem volume yield studied with competition-density effect. Gov. For. Exp. Sta., Tokyo, Bull. 166:1–22.

TANG, S.Z., C.H. MENG, F.R. MENG, AND Y.H. WANG. 1994. A growth and self-thinning model for pure even-age stands: theory and applications. For. Ecol. Manage. 70:67–73.

TANG, S.Z., F.R. MENG, AND C.H. MENG. 1995. The impact of initial stand density and site index on maximum stand density index and self-thinning index in a stand self-thinning model. For. Ecol. Manage. 75:62–68.

TILMAN, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton Univ. Press, Princeton, NJ. 360 p.

TONG, Y.L. 1990. The multivariate normal distribution. Springer-Verlag, New York. 271 p.

WEINER, J., AND S.C. THOMAS. 1986. Size variability and competition in plant monocultures. Oikos 47:211–222.

WEST, P.W., AND C.J. BOROUGH. 1983. Tree suppression and the self-thinning rule in a monoculture of *Pinus radiata* D.Don. Ann. Bot. 52:149–158.

WESTOBY, M. 1982. Frequency distributions of plant size during competitive growth of stands: The operation of distribution-modifying functions. Ann. Bot. 50:733–735.

WESTOBY, M. 1984. The self-thinning rule. Adv. Ecol. Res. 14: 167–225.

WESTOBY, M., AND J. HOWELL. 1981. Self-thinning: The effect of shading on glasshouse populations of silver beet (*Beta vulgaris*). J. Ecol. 69:359–365.

WHITE, J. 1980. Demographic factors in populations of plants. P. 21–48 *in* Demography and evolution in plant populations, Solbrig, O.T. (ed.). Univ of California Press, Berkeley, CA.

WHITE, J. 1981. The allometric interpretation of the self-thinning rule. J. Theoret. Biol. 89: 475–500.

WHITE, J. 1985. The thinning rule and its application to mixtures of plant populations. P. 291–309 *in* Studies on plant demography, White, J. (ed.). Academic Press, London.

WHITE, J., AND J.L. HARPER. 1970. Correlated changes in plant size and number in plant populations. J. Ecol. 58: 467–485.

WHITTINGTON, R. 1984. Laying down the –3/2 power law. Nature 311:217.

YIN, T.L., F.Q. HAN, J.C. CHI, AND B.R. WU. 1978. Construction and use of stand density control diagrams (in Chinese). China For. Sci. 3:1–11.

YODA, K., T. KIRA, H. OGAWA, AND K. HOZUMI. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions (Intraspecific competition among higher plants XI). J. Biol., Osaka City Univ. 14: 107–129.

YU, K., AND M.C. JONES. 1998. Local linear quantile regression. J. Am. Stat. Assoc. 93:228–237.

ZEIDE, B. 1991 Self-thinning and stand density. For. Sci. 37:517–523.

ZHAO, S.T., Q.X. YAO, AND L. WEI. 1993. Stand density effects and techniques for quantitative stand density management (in Chinese). Northeast. For. Univ. Press, Harbin, China. 153 p.