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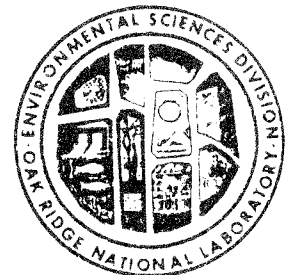
**OAK RIDGE
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MARTIN MARIETTA

**A Mathematical and Statistical
Analysis of the $-3/2$ Power Rule
of Self-Thinning in Even-Aged
Plant Populations**

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ENVIRONMENTAL SCIENCES DIVISION

A MATHEMATICAL AND STATISTICAL ANALYSIS OF THE $-3/2$ POWER RULE
OF SELF-THINNING IN EVEN-AGED PLANT POPULATIONS¹

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Environmental Sciences Division
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LIST OF ABBREVIATIONS AND MATHEMATICAL SYMBOLS

ABBREVIATIONS

| SYMBOL | MEANING |
|------------------------|---|
| ANOVA | analysis of variance |
| BSLA | basal area of tree bole at breast height |
| CI | confidence interval |
| CV | coefficient of variation |
| DBH | diameter of tree bole at breast height |
| EFD | experimental and field data |
| %EV | percentage of the summed variance of two variables explained by bivariate PCA |
| FYD | forestry yield table data |
| GMR | geometric mean regression |
| ln | natural logarithm |
| log, log ₁₀ | common logarithm |
| PCA | principal component analysis |
| RGR | relative growth rate |
| RMR | relative mortality rate |
| RHS | right hand side of an equation or inequality |
| SD | standard deviation |
| SE | standard error |

| SYMBOL | MEANING |
|---------------------|--|
| VOI | volume of influence; space filled |
| ZOI | zone of influence; area covered |
| - | (bar) indicates average value, e.g. \bar{w} , \bar{a} |
| \propto | sign of proportionality |
| ∞ | infinite; without limit |
| $\hat{}$ | indicates a statistical estimate of a parameter, e.g. $\hat{\beta}$, $\hat{\alpha}$ |

MATHEMATICAL SYMBOLS

| SYMBOL | CHAPTER | MEANING |
|------------|---------|--|
| a | 1-3,6-7 | growing surface area occupied by a plant |
| a_{loss} | 3 | area of a plant ZOI lost to a competitor |
| A | 3 | total area covered by a population |
| A_{plot} | 3 | size (area) of a simulated plot |
| b | 1,3 | constant in a power function relating maintenance cost to weight; $cost = b w^q$ |
| B | all | total population biomass; stand biomass |
| B_{max} | 2 | maximum biomass that a population can attain; carrying capacity for biomass |
| c | 2,3,7 | constant in a power function relating ZOI radius to weight |
| c_1 | 2,3,7 | constant defined by $c_1 = \pi c^2$ |
| c_2 | 2 | constant correcting for systematic differences between the $\bar{a}-\bar{w}$ and $a-w$ power relationships |
| c_3 | 2 | constant related to the allowable overlap between plant ZOIs |
| $C(N,B)$ | 2 | function for crowding at given biomass and density |
| $Cov(X,Y)$ | 4 | covariance of variables X and Y |
| d | 3 | density of biomass per unit volume occupied |
| D_{ij} | 3 | distance between the i^{th} and j^{th} plants in a population |
| f | 2 | a constant in the crowding function $C(N,B)$ |

| SYMBOL | CHAPTER | MEANING |
|------------|---------|--|
| F | 5,6 | the variance ratio computed in ANOVA |
| g_0 | 2 | maximum relative growth rate of biomass |
| g_1 | 1,3 | maximum assimilation rate per unit of ground area covered |
| $G(N,B)$ | 2 | function for the growth rate of population biomass |
| $G_r(N,B)$ | 2 | multiplier function reducing RGR_B with increasing crowding |
| H | 5,6 | test statistic from Kruskal-Wallis analysis |
| h | 2-7 | plant height |
| K | all | constant in the self-thinning rule equation |
| m | 2 | mortality constant |
| $M(N,B)$ | 2 | function for population mortality rate |
| $M_r(N,B)$ | 2 | multiplier function producing higher relative mortality with increasing crowding |
| N | all | plant density in individuals per unit area |
| n | 1-7 | size of a sample for statistical analysis |
| n_t | 3 | number of plants remaining in a simulation at time t |
| n_0 | 3 | initial number of plants in a simulation |
| p | 1-7 | power relating ZOI radius to plant weight; $R = c w^p$ |
| p_{est} | 6 | power relating ZOI radius plant weight, estimated by mathematical transformation of a fitted thinning slope; $p_{est} = 0.5 / (1-\beta)$ |

| SYMBOL | CHAPTER | MEANING |
|------------------------------------|---------|---|
| P | 1-7 | statistical significance level; probability of a Type I statistical error |
| q | 3 | power relating maintenance cost to weight; $\text{cost} = b w^q$ |
| r | 3-7 | correlation coefficient |
| r^2 | 3-7 | coefficient of determination |
| r_s | 3,6 | Spearman rank correlation coefficient |
| R | 1-7 | ZOI radius |
| RGR | 1-3 | relative growth rate |
| RGR_B | 1-3 | relative growth rate of total biomass |
| $RGR_{\bar{w}}$ | 1-3 | relative growth rate of average weight |
| RGR_{\min} | 3 | minimum individual RGR allowing survival |
| RMR | 1-3 | relative mortality rate |
| $s_{\bar{w}0}$ | 3 | standard deviation of weights at time 0 |
| $s_{xx},$ $s_{yy},$ s_{xy} | 4 | sums of squares and cross products for X and Y |
| t | 2,3 | time |
| $\text{Var}(X)$ | 4 | variance of variable X |
| v | 1-3,6-7 | volume of an individual plant VOI |
| w | all | weight of an individual plant |
| w | all | average plant weight for a population |

| SYMBOL | CHAPTER | MEANING |
|-----------------|---------|---|
| w_0 | 3 | initial plant weight at time 0 |
| w_{max} | 2 | maximum individual weight |
| X, Y | 4 | general symbols for two variables involved in a bivariate relationship |
| α | 1-6 | common log of K ($\alpha = \log K$); intercept at $\log N = 0$ of the self-thinning line |
| $\alpha_{3.35}$ | 3 | intercept of the self-thinning line at $\log N = 3.35$ |
| β | all | power in the B-N thinning equation $B = K N^\beta$; slope of the $\log B$ - $\log N$ self-thinning line |
| β_t | 2 | instantaneous slope of the self-thinning trajectory at time t |
| β_{yx} | 4 | slope of a linear function giving Y in terms of X |
| γ | all | power in the \bar{w} - N thinning equation $\bar{w} = K N^\gamma$; slope of the $\log \bar{w}$ - $\log N$ self-thinning line |
| $\Delta \log K$ | 2 | difference between the $\log N = 0$ intercepts of the straight lines in the $\log B$ - $\log N$ plane representing the asymptotic population trajectory and the zero isocline of biomass increase |
| Δt | 3 | simulation time step |
| $(\Delta t)_m$ | 3 | simulation time step over which RGR's are averaged to identify plants with untenably low growth rates |
| ϵ | 3 | expansion factor to correct for edge effects in the simulation model |
| η | 3 | sample angle in edge correction equation |
| ζ | 7 | parameter of the lognormal distribution; if w is lognormal, ζ is the mean of $\ln w$ |

| SYMBOL | CHAPTER | MEANING |
|-----------------------|---------|--|
| $\theta_1 - \theta_5$ | 2 | parameters controlling the suddenness of onset of model constraints |
| λ | 4 | ratio of the residual variances in Y and X around a true linear relationship |
| κ | 7 | quantity defined for a stand by $\kappa = B N^{0.5}$; an index of stand shape and biomass density per unit of volume occupied |
| ρ | 7 | ratio of the weights of the largest and smallest individuals in a population |
| σ | 7 | parameter of the lognormal distribution; if w is lognormal, σ is the standard deviation of $\ln w$ |
| τ | 3,7 | ratio of plant height to ZOI radius |
| Φ_0, Φ_1 | 6 | constant and power, respectively, in an allometric power relationship between two plant dimensions |
| Φ_{Bw} | 6 | allometric power relating BSLA to weight; $B \propto w^{\Phi_{Bw}}$ |
| Φ_{dw} | 6 | allometric power relating density to weight; $d \propto w^{\Phi_{dw}}$ (density of biomass per unit of volume occupied) |
| Φ_{Dw} | 6 | allometric power relating DBH to weight; $DBH \propto w^{\Phi_{Dw}}$ |
| Φ_{hB} | 6 | allometric power relating height to BSLA; $h \propto BSLA^{\Phi_{hB}}$ |
| Φ_{hD} | 6 | allometric power relating height to DBH; $h \propto DBH^{\Phi_{hD}}$ |
| Φ_{hw} | 6 | allometric power relating height to weight; $h \propto w^{\Phi_{hw}}$ |

| SYMBOL | CHAPTER | MEANING |
|----------|---------|---|
| Ψ | 2 | slope of a straight line in the log B-log N plane representing points where $d \log B / d \log N = \Psi$ |
| ω | 2 | ratio of mortality and growth constants; $\omega = m / g_0$ |

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ABSTRACT

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A mathematical and statistical analysis of the $-3/2$
power rule of self-thinning in even-aged plant
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Laboratory, Oak Ridge, Tennessee. 262 pp.

The self-thinning rule for even-aged plant populations (also called the $-3/2$ power law or Yoda's law) is reviewed. This widely accepted but poorly understood generalization predicts that, through time, growth and mortality in a crowded population trace a straight thinning line of slope $-3/2$ in a log-log plot of average plant weight versus plant density. The evidence for this rule is examined, then reanalyzed to objectively evaluate the strength of support for the rule. Mathematical models are constructed to produce testable predictions about causal factors.

Major problems in the evidence for the thinning rule include inattention to contradictory data, lack of hypothesis testing, inappropriate curve-fitting techniques, and the use of an invalid data transformation. When these problems are corrected, many data sets thought to corroborate the rule do not demonstrate any size-density relationship. Also, the variations among thinning slopes and intercepts are much greater than currently accepted, many slopes disagree quantitatively with the thinning rule, and thinning slope and intercept differ among plant groups.

The models predict that thinning line slope is determined by the allometry between area occupied and plant weight, while the intercept is also related to the density of biomass per unit of space occupied

and the partitioning of resources among competing individuals. Statistical tests confirm that thinning slope is correlated with several measures of plant allometry and that variations in thinning slope among plant groups reflect allometric differences.

The ultimate thinning line, which describes the overall size-density relationship among populations of many species, is a trivial geometric consequence of packing objects onto a surface. This cause differs from the factors positioning the self-thinning lines of individual populations, so the existence of an overall relationship is not relevant to the thinning rule.

The evidence does not support acceptance of the self-thinning rule as a quantitative biological law. The slopes and intercepts of size-density relationships are variable, and the slopes can be explained by simple geometric arguments.

INTRODUCTION

The title of a recent review article "Ecology's law in search of a theory" (Hutchings 1983) concisely summarizes the status of a hypothesis variously referred to as the self-thinning rule, the $-3/2$ power law, or Yoda's law. This rule states that as growth and mortality proceed in a crowded even-aged plant population, average weight (\bar{w}) and the number of plants per unit area (N) are related by a simple power equation $\bar{w} = K N^\gamma$, where $\gamma = -3/2$ and K is a constant. Widespread acceptance of this rule by plant ecologists is based on many observations of this power relationship in plant populations ranging from mosses to trees, but the reasons for the rule's apparent generality are not well understood (Hutchings and Budd 1981a, Westoby 1981, White 1981, Hutchings 1983).

The theoretical importance of the self-thinning rule is evidenced by the published statements of plant ecologists. White (1981) called it one of the best documented generalizations of plant demography, and further states that its empirical generality is now beyond question. Westoby (1981) considers it the most general principle of plant demography and suggests that it be elevated beyond the status of an empirical generalization to take a "central place in the concepts of population dynamics." Hutchings and Budd (1981a) emphasized the uniqueness of its precise mathematical formulation to a science where most general statements can be stated in only vaguer, qualitative terms. To many ecologists, the rule is

sufficiently well verified to be considered a scientific law (Yoda et al. 1963, Dirzo and Harper 1980, Lonsdale and Watkinson 1982, MalMBERG and Smith 1982, Hutchings 1983). Harper (quoted in Hutchings 1983) called it "the only generalization worthy of the name of a law in plant ecology" and McIntosh (1980) agreed that, if substantiated, a self-thinning law could well be the first basic law demonstrated for ecology. As such, it would help to fill the need for verified laws in a discipline that has been hindered by a lack of laws and other regularities from which to develop the body of comprehensive theory that is the hallmark of a mature science (Johnson 1977, McIntosh 1980).

There have been many proposed extensions and applications of the self-thinning rule. Although it was originally observed in monocultures, evidence now suggests that aggregate measurements of even-aged two-species mixtures (White and Harper 1970, Bazzaz and Harper 1976, MalMBERG and Smith 1982) and many-species mixtures (White 1980, Westoby and Howell 1981) also conform. Some authors have even attempted to apply the thinning rule to animal populations (Furnas 1981, Wethey 1983). The rule can be used to compare the site qualities or histories of plant populations growing at different sites, since relative positions along the curve $\bar{w} = K N^{-3/2}$ give a ranking of the fertilities experienced by equal-aged populations (Yoda et al. 1963), or of population ages if fertility is constant among sites (Barkham 1978). The existence of the $-3/2$ power relationship among a set of population measurements has been interpreted as evidence that natural self-thinning is

occurring, canopies are closed, growth and mortality are ongoing, and competition is the cause of mortality (Barkham 1978), while the absence of the $-3/2$ relationship has been cited as evidence that density independent factors are the important causes of mortality (Schlesinger 1978). The rule can also be a useful management tool in forestry (see Yoda et al. 1963, Drew and Flewelling 1977, and Japanese language papers cited therein), or in other applications requiring predictions of the limits of biomass production for a given species at any density (Hutchings 1983).

In view of the popularity, theoretical importance, and applicability of the self-thinning rule, the troublesome lack of a verified explanatory theory continues to motivate further research. The original objective of the present study was to examine the causes of the self-thinning rule by analyzing a detailed simulation model of a generalized plant population and extracting testable predictions about the effects of different biological parameters on the constants γ and K of the power rule equation. The central question was how the processes of growth and mortality operate to eliminate large among-species variations in size, shape, physiological capability, strategy, and other important factors so that all species obey the same power rule. The model developed for this purpose did not predict such constancy, rather it suggested that the power γ should vary from the idealized value of $-3/2$, with its exact value determined by the relationship between ground area covered and plant weight in a given stand. This hypothesis is

neither new (see Miyanishi et. al 1979) nor well supported in previous studies (Westoby 1976, Mohler et al. 1978, White 1981).

Among the ideas considered after reaching this conclusion was the thought that the previous analyses were somehow wrong. When the evidence behind the self-thinning rule was carefully examined, some troubling problems were discovered. They motivated a new analysis of the data supporting the thinning rule and some new tests of the simple hypothesis suggested by the simulation model. Together, the mathematical models and data analyses evolved into six lines of investigation presented in Chapters 2 through 7 of this report.

Chapter 2. Simple, spatially-averaged models of growth and mortality are developed to formalize in a dynamic model the hypothesis that the power of the self-thinning equation is determined by a relationship between ground area covered and plant weight, and to examine the interaction between this effect and constraints imposed by a carrying capacity and a maximum individual size.

Chapter 3. A detailed, spatially explicit computer simulation model is analyzed to consider the effects of additional population parameters on the power rule relationship, and to verify that the conclusions of the simpler models are not artifacts of spatial averaging.

Chapter 4. Some difficulties in the selection, analysis, and interpretation of self-thinning data are discussed along with the implications for the self-thinning rule. Remedies for some problems are suggested.

Chapter 5. Biomass and density data for 488 self-thinning relationships are statistically analyzed to evaluate support for the self-thinning rule and to estimate the variability of the power equation parameters K and γ . Variations in these parameters among plant groups are considered.

Chapter 6. The biomass and density data from Chapter 5 are combined with plant shape measurements from the same stands and used to test some predictions of the hypothesis that the power of the self-thinning equation is determined by a relationship between ground area covered and plant weight.

Chapter 7. Some hypotheses are presented to explain the overall relationship between size and density. (This relationship emerges when measurements of many crowded plant stands ranging from small herbs to trees are combined to estimate a single power equation relating stand size and stand density across the entire plant kingdom--Gorham 1979, White 1980). The relevance of this overall relationship to the self-thinning rule for individual plant populations is considered.

These efforts are united by an overall goal of developing and testing a unified theoretical framework for understanding observed size-density relationships and evaluating their scientific importance.

CHAPTER 1

LITERATURE REVIEW

Statement of the Self-thinning Rule

The self-thinning rule describes a relationship between size and density in even-aged plant populations that are crowded but actively growing. In the absence of competition from other populations and of significant density-independent stresses (drought, fire, etc.), mortality or "thinning" is caused by the stresses of competition within the population, hence the term "self-thinning." Yoda et al. (1963) observed a general relationship among successive measurements of average weight and density taken after the start of self-thinning. When the logarithm of average weight is plotted vertically and the logarithm of plant density horizontally, the points form a straight line with a slope near $-3/2$ represented by the equation

$$\log \bar{w} = \gamma \log N + \log K, \quad (1.1)$$

where \bar{w} is average weight (in g), N is plant density (in individuals/m²), $\gamma = -3/2$, and K is a constant. Antilogarithmic transformation of this relationship gives the power equation

$$\bar{w} = K N^{\gamma}. \quad (1.2)$$

Since $\bar{w} = B/N$, (where B is total stand biomass or yield in g/m²), these equations relating average weight to density are

mathematically equivalent to the following relationships between stand biomass and density:

$$\log B = \beta \log N + \log K \quad (1.3)$$

and

$$B = K N^\beta, \quad (1.4)$$

with $\beta = -1/2$. The parameters γ and β are related by $\beta = \gamma + 1$.

Yoda et al. (1963) named this relationship the "-3/2 power law of self-thinning" because of the mathematical form of equation 1.2 and the value of the power γ . Any of the above relationships can be referred to as the self-thinning equation, while the linear equations 1.1 and 1.3 give the self-thinning line, or simply the thinning line. γ and β are called self-thinning powers or exponents in reference to equations 1.2 and 1.4, but the names self-thinning slope or thinning slope are also common because these parameters are the slopes of the linear equations 1.1 and 1.3. The logarithm of the constant K is often called the self-thinning intercept because it gives the intersection of the thinning line with the vertical line $\log N = 0$.

The self-thinning rule does not necessarily apply throughout the history of a plant population. When populations are established at combinations of average weight and density well below the self-thinning line, the initial competitive stresses can be absorbed through plastic changes in shape, growth can proceed with little

mortality, and a nearly vertical line is traced in a log-log plot of size versus density. As competition becomes more severe, growth slows and some plants die after exhausting their capacities to adjust to their neighbors' intrusions. The population's path in log size-log density plot bends toward the self-thinning line, then begins to move along it as growth and mortality progress (Hutchings and Budd 1981a, White 1981). The curves traced by populations of differing initial densities converge on the same self-thinning line (Yoda et al. 1963, White 1980, 1981). Movement along the self-thinning line can not continue indefinitely because the population will eventually approach the environmental carrying capacity, which places an upper limit on total stand biomass (Hutchings and Budd 1981a, Peet and Christensen 1980, Lonsdale and Watkinson 1983b, Watkinson 1984). Limits on individual growth, such as a genetically or mechanically defined maximum size or the end of the growing season, can also deflect the population from the thinning line (Harper and White 1971, Peet and Christensen 1980).

The history of an even-aged population can, then, be divided into up to four stages: (1) a period of initial establishment, rapid growth, and low mortality; (2) a period of adherence to the self-thinning rule; (3) a period when constant biomass is maintained at the carrying capacity; and (4) a period of population degeneration, when growth does not replace the biomass lost through mortality. Figure 1.1 shows the idealized representations of these stages as paths in the $\log \bar{w}$ - $\log N$ and $\log B$ - $\log N$ planes.

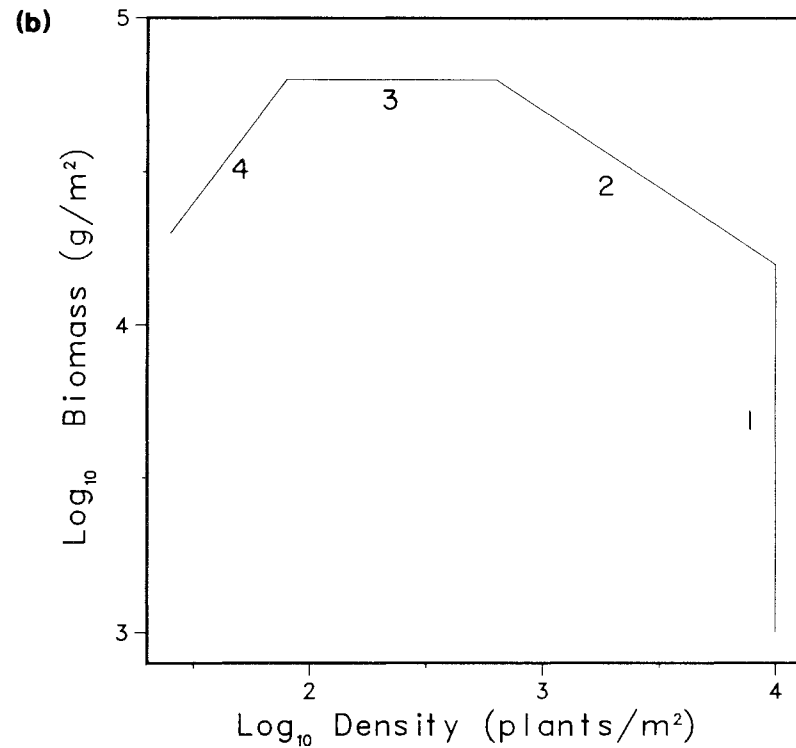
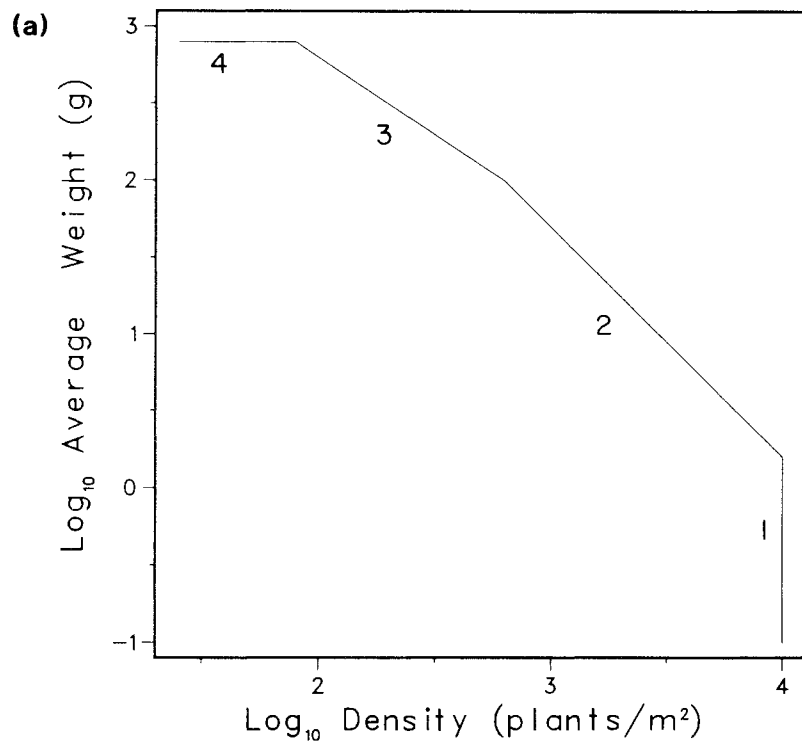


Figure 1.1. Four possible growth stages for an idealized even-aged plant population. (1) initial rapid growth and low mortality, (2) self-thinning rule, (3) constant biomass at carrying capacity, and (4) terminal degeneration or senescence. In the $\log \bar{w}$ - $\log N$ plane, (a) the respective slopes of the last three stages are $-3/2$, -1 , and 0 , while the corresponding slopes in the $\log B$ - $\log N$ plane (b) are $-1/2$, 0 , and $+1$. In both plots, the line representing the first stage is nearly vertical.

The self-thinning rule describes a certain balance between the rates of growth and mortality, which are linked so that the ratio of the relative growth rate to the relative mortality rate is held constant (Harper and White 1971, Westoby and Brown 1980) at the value of the self-thinning slope, that is,

$$\frac{RGR_{\bar{w}}}{RMR} = \frac{d\bar{w} / (\bar{w} dt)}{dN / (N dt)} = \frac{d \log \bar{w}}{d \log N} = \gamma, \quad (1.5)$$

where $RGR_{\bar{w}}$ is the relative growth rate of average weight and RMR is the relative mortality rate (Hozumi 1977). The equivalent relation for the relative growth rate of biomass, RGR_B , is

$$\frac{RGR_B}{RMR} = \frac{dB / (B dt)}{dN / (N dt)} = \frac{d \log B}{d \log N} = \beta. \quad (1.6)$$

Mortality during self-thinning is concentrated among smaller individuals that have been suppressed, possibly because of smaller seed size, later germination, lower growth rate, or close neighbors (Ross and Harper 1972, Kays and Harper 1974, Ford 1975, Hutchings and Barkham 1976, Bazzaz and Harper 1976, Harper 1977, Mohler et al. 1978, Rabinowitz 1979, Hutchings and Budd 1981a, Lonsdale and Watkinson 1983a). These deaths permit a net biomass production among the remaining plants so that total population biomass increases (Ford 1975, Hutchings and Barkham 1976, Westoby 1981).

The self-thinning line can also be interpreted as a constraint separating possible combinations of biomass and density from impossible ones. Biomass and density combinations below or on the

line are possible, while combinations above the line do not occur (Yoda et al. 1963; White 1980, 1981; Westoby and Howell 1981). This means that thinning lines need not be measured by following individual populations through time, rather data for a given population type from several plots of different ages can be used, provided that the plots do not differ in important biotic or environmental factors that would alter the position of the thinning line. This method has been used since the earliest studies (Yoda et al. 1963), and is particularly important for studying long-lived trees (White 1981).

Evidence for the Self-thinning Rule

The self-thinning rule is an empirical statement generalized from repeated observations of linear relationship between $\log \bar{w} - \log N$ with an estimated slope near $-3/2$. The supporting examples include populations ranging in size from small herbs to large trees collected from experimental or natural conditions or from forestry yield tables. Yoda et al. (1963) presented ten data sets which exhibit such a relationship. White and Harper (1970) added five additional examples, plus some evidence from forestry thinning tables. White (1980) presented 36 more examples and mentioned unpublished data for 80 additional cases. White's paper has been widely cited by other authors, along with the study of Gorham (1979), as firmly establishing the generality of the $-3/2$ rule (Hutchings 1979, Dirzo and Harper 1980, Furnas 1981, Westoby

and Howell 1982, Lonsdale and Watkinson 1982, 1983a, Watkinson et al. 1983). Tables A.5 and B.5 give references to studies presenting additional corroborative examples. Most of the weight measurements in these studies are of aboveground plant parts only, but some also include roots. This inclusion raises the value of K but does not affect the slope of the thinning line (Watkinson 1980, Westoby and Howell 1981).

The limited range of variation of thinning line slopes and intercepts are also considered strong evidence for the thinning rule. White (1980) reported that thinning slopes vary between -1.3 and -1.8 when $\log \bar{w}$ is fitted to $\log N$. This range is considered remarkably invariant (Watkinson et al. 1980, Furnas 1981, Lonsdale and Watkinson 1982, Hutchings 1983); however, several exceptions have been reported (Ernst 1979, O'Neill and DeAngelis 1981, Sprugel 1984). The constant K is usually limited to $3.5 \leq \log K \leq 4.4$ and values outside this range are biologically significant (White 1980, 1981). Grasses can give higher $\log K$ values between 4.5 (Kays and Harper 1974) and 6.67 (Lonsdale and Watkinson 1983a), possibly because their erect, linear leaves allow deeper light penetration through the canopy and greater plant biomass per unit volume (Lonsdale and Watkinson 1983a, Watkinson 1984). Some values of $\log K$ greater than 4.4 have also been reported for herbaceous dicots (Westoby 1976, Westoby and Howell 1981, Lonsdale and Watkinson 1983a).

Further support for the self-thinning rule has come from two studies that examined the relationship between size and density among stands of different species (Gorham 1979, White 1980). This relationship is referred to here as the overall size-density relationship to distinguish it from the self-thinning lines of particular populations. Gorham (1979) reported that measurements of 65 stands of 29 species (including mosses, reeds, herbs, and trees) form a straight line of slope -1.5 in the $\log \bar{w}$ - $\log N$ plane, while White (1980) showed that the individual self-thinning lines of 27 different species are closely grouped around a common linear trend of slope -1.5 (see Chapter 7). These results are considered evidence that self-thinning rule applies over a wide range of plant types and growth forms (Gorham 1979, White 1980, 1981, Westoby 1981, Malmberg and Smith 1982, Hutchings 1983). Even some types of plant populations that do not trace straight trajectories in the $\log \bar{w}$ - $\log N$ plane, such as the shoots of clonal perennial species, still seem to be constrained below the ultimate thinning line described by Gorham's study (Hutchings 1979).

Effects of Environmental Factors on Self-thinning Lines

Ecologists have examined the effects of the availability of essential resources, such as light and mineral nutrients, on self-thinning. Plants grown at low levels of illumination thin faster (Harper 1977) and reach maximum biomass levels sooner (Hutchings and Budd 1981b) than populations grown with higher illumination. Decreased illumination also lowers the intercept of

the self-thinning line (White 1981, Hutchings and Budd 1981a, 1981b, Westoby and Howell 1981), possibly due to a decrease in the density of plant matter per unit of occupied space (Lonsdale and Watkinson 1982, 1983a) or to more rapid mortality among shorter plants (Hutchings 1983). The thinning slope is not affected by mild reductions in illumination, but changes from the typical value of $-3/2$ to -1 under severely lowered light treatments have been observed (White and Harper 1970, Kays and Harper 1974, Harper 1977, Furnas 1981). However, other experiments with equally severe light reductions report no change in the thinning slope (Westoby and Howell 1981, Hutchings and Budd 1981b). Possible reasons for these ambiguous results are considered by Westoby and Howell (1982) and Lonsdale and Watkinson (1982). Since the level of illumination affects the position of the thinning line, light has been implicated as the limiting factor whose availability controls the rate of self-thinning (Kays and Harper 1974, Harper 1977, Westoby and Howell 1982, Lonsdale and Watkinson 1982).

High levels of mineral nutrients increase growth and mortality rates and the rate at which populations approach and follow the self-thinning line. The slope and position of that line are insensitive to difference in fertility (Yoda et al. 1963, White and Harper 1970, Harper 1977, White 1981, Westoby 1981, Hutchings and Budd 1981a); however, there is some evidence against this established view. White (1981) mentioned unpublished data which suggests that fertilizer treatments in forest stands may systematically alter $\log K$, while Hara (1984) showed that forestry

yield tables can indicate different thinning lines for stands grown on sites of different quality. Furnas (1981) saw an effect of soil fertility on thinning line position in his own experiments and in those of Yoda et al., which have interpreted as lacking a fertility effect (Yoda et al. 1963, White and Harper 1970).

Explanations for the Self-thinning Rule

Yoda et al. (1963) derived a simple, geometric explanation of the self-thinning from two assumptions: (1) plants of a given species are always geometrically similar regardless of habitat, size, or age; and (2) mortality occurs only when the total coverage of a plant stand exceeds the available area then acts to maintain 100% cover. The first assumption allows the ground area, a , covered by a plant to be expressed mathematically as a power function of plant weight, $a \propto w^{2/3}$, while the second assumption implies that the average area covered is inversely proportional to density, that is, $\bar{a} \propto 1/N$. Combining these two equations and adding a constant of proportionality, K , gives the thinning rule equation $\bar{w} = K N^{-3/2}$. Starting from the Clark and Evans (1954) equation for nearest neighbor distance, White and Harper (1970) developed an alternative derivation that renders the second assumption unnecessary, but still implicitly requires the first.

The assumption that plant shape is invariant is not tenable, so these derivations of the thinning rule are unsatisfactory (White 1981, Furnas 1981). Miyanishi et al. (1979) attempted to reconcile these simple geometric models with the fact of varying plant shapes

in their generalized self-thinning law, which states that the power of the thinning equation depends on the proportionality between plant weight and ground area covered. Their hypothesis can be stated mathematically by setting the area covered proportional to w^{2p} , where p can deviate from $1/3$ to represent changes in shape with increasing size (allometric growth). With this modification, the Yoda logic gives $\bar{w} = K N^{-1/(2p)}$ and the thinning slope is $\gamma = -1/(2p)$, which equals $-3/2$ only if shape is truly invariant (isometric growth, $p = 1/3$). Westoby (1976) used similar logic to predict that the thinning slope should be -1 in the special case of plants that grow radially, but not in height.

The implication of these modified geometric arguments that the self-thinning slope should be dependent on plant allometry has not been supported by experimental tests. Westoby's (1976) experiment with plants that grow only radially gave a thinning slope near $-3/2$, not the expected value of -1 ; however, White (1981) discredited this result, claiming that the species used really does grow in height. Mohler et al. (1978) use allometric data for two tree species to predict thinning slopes of -2.17 and -1.85 , which disagree with the idealized value of -1.5 and with the respective measured slopes of -1.21 and -1.46 . In the most extensive review of the allometric theory to date, White (1981) applied an allometric model to available data for trees and predicted thinning slopes between -2.05 and -0.78 . His discussion of this result implies that the allometric model is faulty in predicting of thinning slopes outside the range -1.8 to -1.3 that he considers acceptably close to

-1.5. White concluded that any theory predicting thinning slopes significantly different from -1.5 is not useful or realistic.

Several non-allometric explanations of explanations of the self-thinning rule have also been proposed. Westoby (1977) hypothesized that self-thinning is related to leaf area rather than to plant weight, but this theory has been discredited (White 1977, Gorham 1979, Hutchings and Budd 1981b). Mohler et al. (1978) suggested that the value of $-3/2$ is maintained by a mutual adjustment of plant allometry and stand structure during self-thinning, while Furnas (1981) proposed that the $-3/2$ value is determined by the fact that limiting resources for plant growth are distributed in a three-dimensional volume. Jones (1982) hypothesized that the $-3/2$ thinning relationship derives from growth and mortality acting to maintain a constant total plot metabolic rate.

Recently, mathematical models have been used to develop even more theories. Pickard (1983) presented three different models deriving the $-3/2$ value from a mixture of allometric theory and physiological considerations, such as the fraction of photosynthate allocated to biomass increase, the amount of structural and vascular overhead incurred by spatial extension, and the rise in proportionate maintenance costs with increasing weight. Charles-Edwards (1984) combined his basic hypothesis that each plant requires a minimum flux of assimilate to grow and persist with additional assumptions about the mathematical representation of growth and mortality to produce an explanation of self-thinning.

Perry (1984) derived the self-thinning curve from a physiological model in which the relationship between leaf area and weight, the decrease in photosynthetic efficiency with crowding, maximum plant size, and age are all important factors that must obey certain mutual constraints if the model is to give thinning slopes and intercepts within the ranges that have been actually observed.

In light of the apparent failure of the allometric theory and the paucity of experimental tests of other theories, no satisfactory explanation of self-thinning rule has yet emerged (White 1980, 1981, Westoby 1981, Hutchings and Budd 1981a, Hutchings 1983). It is a "crude statement of constraint whose underlying rationale remains elusive" (Harper as quoted in Hutchings 1983).

Interpretation of the Self-thinning Constant K

Plant ecologists are also interested in interpreting the constant K and its observed range of variation. K has been presented as a species constant invariant to changes in all environmental conditions except the level of illumination (Hickman 1979, Hozumi 1980, White 1981, Hutchings 1983). Many authors regard K as a parameter related to plant architecture (Harper 1977, Gorham 1979, Hutchings and Budd 1981a, Lonsdale and Watkinson 1983a), but some have proposed that K is insensitive to plant morphology (Westoby 1976, Furnas 1981). White (1981) suggested that K is a rough approximation of the density of biomass in the volume of space occupied by plants and can be considered as a weight to volume conversion, but Lonsdale and Watkinson (1983a) provided evidence

against this hypothesis. Lonsdale and Watkinson (1983a) concluded that plant geometry, particularly leaf shape and disposition, do influence thinning intercepts. Harper (1977) speculated the pyramidally shaped trees have higher intercepts than round crowned trees. Westoby and Howell (1981) and Lonsdale and Watkinson (1983a) have hypothesized that shade tolerant plants should have higher thinning intercepts than intolerant plants. Understanding of K is in a similar status as understanding of the $-3/2$ power: no general theory explaining the variations in K has yet been developed (Hutchings and Budd 1981a).

CHAPTER 2

SIMPLE MODELS OF SELF-THINNING

Introduction

Most proposed explanations of the self-thinning rule have been based on simple geometric models of the way plants occupy the growing surface (Yoda et al. 1963, White and Harper 1970, Westoby 1976, Miyanishi et al. 1979, Mohler et al. 1978, White 1981), but these models suffer from two major limitations. Since they are not related to time dynamics, they can not provide an interpretation of the thinning line as a time trajectory (Hozumi 1977, White 1981). Also, they can not explain deviations from the self-thinning rule, such as the alteration of thinning slopes in deep shade (Westoby 1977).

Two dynamic models are developed here to remedy these deficiencies. A basic model, in which growth is constrained only by the limited availability of growing space, gives an asymptotic linear trajectory in the $\log B$ - $\log N$ plane. The slope and intercept of the model self-thinning line are related to the parameters and assumptions of the model to develop biological interpretations for the slope and intercept. The second model incorporates two additional growth constraints: a upper limit on the size of individuals (Harper and White 1971, Peet and Christensen 1980) and a maximum total population biomass or carrying capacity (Peet and Christensen 1980, Hutchings and Budd 1981a, Lonsdale and Watkinson

1983b, Watkinson 1984). The general behavior of this model is related to observed phases of population growth (White 1980), and the effects of heavy shading on trajectories in the log B-log N plane are considered.

Model Formulation

Basic Model for the Spatial Constraint

The first step in formulating a dynamic model of self-thinning is selecting a set of state variables to represent the plant population at any time t . Animal populations have been successfully modeled with a single state variable, such as the total number of animals, because animals are relatively uniform in size and simple counts provide rough estimates of total biomass, growth rates, and productivity (Harper 1977). However, similar-aged plants can vary up to 50,000-fold in size and reproductive output, so measurements of both numbers and biomass are essential for understanding plant populations (White and Harper 1970, Harper 1977, White 1980, Westoby 1981). Average weight has been the measure of population biomass in most self-thinning analyses, but this popular choice entails some serious statistical difficulties that can be avoided if total biomass is used (see Chapter 4). Accordingly, the models developed here employ two state variables, plant density and stand biomass, as a minimum reasonable representation of a plant population. Density, $N(t)$, and biomass, $B(t)$, are measured in individuals per unit area and weight per unit area, respectively.

In an even-aged population with no recruitment, plant density and stand biomass change only through growth and mortality. If the population is sufficiently large, these processes can be modeled by two differential equations,

$$\frac{dN}{dt} = -M(N,B) \quad (2.1)$$

and

$$\frac{dB}{dt} = G(N,B) , \quad (2.2)$$

where M and G are functions for the rates of mortality and growth when the population state is (N,B) . The simplest choices for these functions would apply to a young population of widely spaced plants. In this case plants would not interfere with one another, growth would be approximately exponential, and mortality would be zero (ignoring density-independent causes of mortality). Equations 2.1 and 2.2 would become

$$\frac{dN}{dt} = 0 \quad (2.3)$$

and

$$\frac{dB}{dt} = g_0 B , \quad (2.4)$$

where g_0 is the exponential growth constant in units of time^{-1} .

The deleterious effects of crowding can be represented in this model by assuming that competition reduces the growth rate and increases the mortality rate. The reduction in growth rate can be modeled by multiplying the exponential growth rate by a function $G_r(N,B) \leq 1$ that decreases as either B or N increases, that is,

$$\frac{dB}{dt} = g_0 B G_r(N,B) . \quad (2.5)$$

To specify a similar function for the increase in mortality with crowding, assume that populations undergoing the same level of crowding stress have the same level of per capita mortality, then define $M(N,B) = m M_r(N,B)$ with m constant. The relative mortality rate is, then,

$$\frac{dN}{N dt} = -m M_r(N,B) , \quad (2.6)$$

which is constant for any given level of crowding stress M_r . M_r is near zero in a widely spaced population and increases as either B or N increases.

Further model development requires some mathematical representation of crowding. A reasonable assumption is that crowding depends on the amount of space actually occupied by the population relative to the total available space. Assume that the

area, a , occupied by an individual is related to its weight, w , by a power function

$$a = c_1 w^{2p}, \quad (2.7)$$

with $0 \leq p \leq 0.5$. Plants that grow only upwards are represented by $p = 0$, while $p = 0.5$ gives pure radial growth. The special case of isometric growth where shape does not vary with size is given by $p = 1/3$. The constant c_1 is inversely related to the density of biomass per unit of occupied space. This constant also depends on initial plant shape, with initially shorter but fatter plants having higher values than taller, thinner ones. Now assume a similar relationship between the average area occupied and the average plant weight

$$\bar{a} = c_2 c_1 \bar{w}^{2p}, \quad (2.8)$$

with constant c_2 correcting for any systematic differences between the \bar{a} - \bar{w} relationship and the a - w relationship for individuals. The total area, A , occupied by N individuals is proportional to the product of N and the average area occupied,

$$A = c_3 N \bar{a} = c_3 c_2 c_1 N \bar{w}^{2p}. \quad (2.9)$$

The constant $c_3 > 0$ is related to the allowable overlap between neighboring plants. If overlap is extensive, c_3 is less than one and the total area occupied is less than the product of the number

of plants and the average area occupied. If plants touch but do not overlap, c_3 is near one and A approximately equals $N \bar{a}$. A shade-intolerant population would have a higher value of c_3 than a shade-tolerant one. Since $\bar{w} = B/N$, the total area covered can also be expressed as

$$A = c_3 c_2 c_1 N^{1-2p} B^{2p} . \quad (2.10)$$

Now divide this expression for the total area occupied by the available area, which is simply one because density is already scaled to individuals per unit area. This gives a general crowding index, $C(N,B)$:

$$C(N,B) = f N^{1-2p} B^{2p} , \quad (2.11)$$

with $f = c_3 c_2 c_1$.

The constant, f , in this crowding function subsumes several factors, including a weight to volume conversion (the density of biomass in occupied space) and information on initial plant shape from constant c_1 of equation 2.7, and a correction from c_2 in equation 2.8 for any systematic differences between the $\bar{a}-\bar{w}$ relationship and the $a-w$ relationship for individuals. Also, f includes information from constant c_3 on how much overlap between the zones of influence of plants is permissible.

The crowding index, $C(N,B)$ can now be used to further specify the functions G_r and M_r by defining

$$M_r(N,B) = C(N,B) \quad (2.12)$$

and

$$G_r(N,B) = 1 - C(N,B) . \quad (2.13)$$

The differential equation model now becomes

$$\frac{dN}{dt} = -m N C(N,B) = -m f N^{1-2p} B^{2p} \quad (2.14)$$

and

$$\frac{dB}{dt} = g_0 B [1 - C(N,B)] = g_0 B [1 - f N^{1-2p} B^{2p}] . \quad (2.15)$$

Two additional parameters can be used to adjust how rapidly the growth and mortality rates respond to changes in crowding. The linear equations 2.12 and 2.13 are special cases of more general power functions of C ,

$$M_r(N,B) = C(N,B)^{\theta_1} \quad (2.16)$$

and

$$G_r(N,B) = 1 - C(N,B)^{\theta_3} , \quad (2.17)$$

where both θ_1 and θ_3 are greater than zero (Figure 2.1). The use of such power functions in plant growth models is discussed in Barnes (1977). With these modifications, equations 2.14 and 2.15 become

$$\frac{dN}{dt} = -m N (f N^{1-2p} B^{2p})^{\theta_1} \quad (2.18)$$

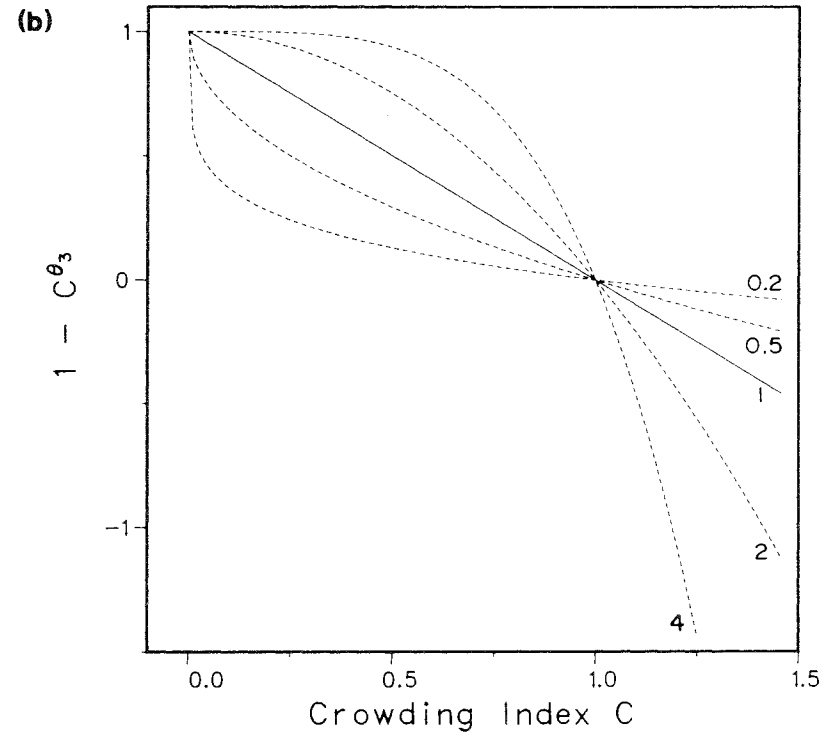
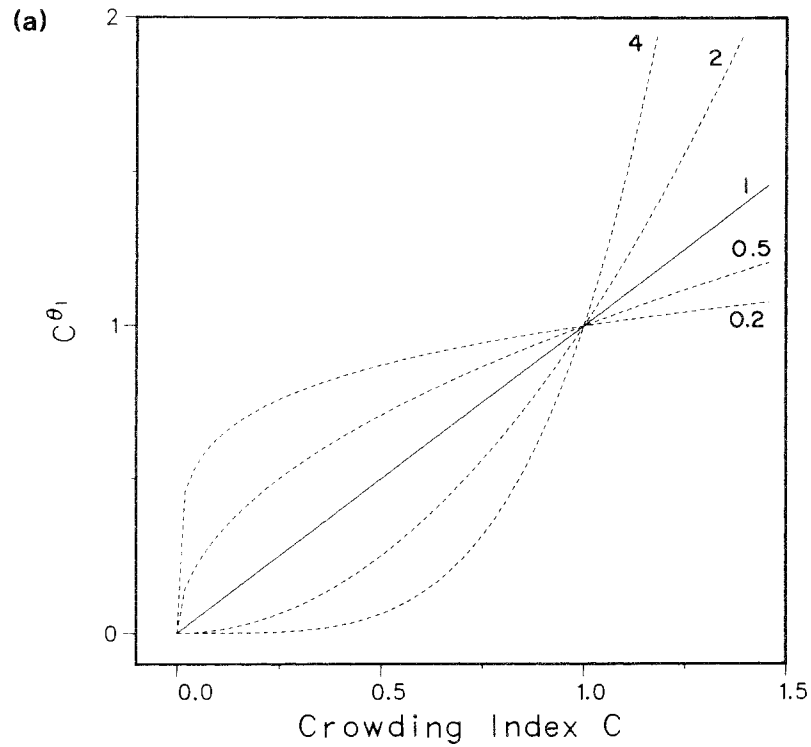


Figure 2.1. Power functions of the crowding index. (a) plots the function $M_r = C^{\theta_1}$ against C for the indicated values of θ_1 while (b) plots $G_r = 1 - C^{\theta_3}$. The powers θ_1 and θ_3 adjust how suddenly each function changes near the critical value $C = 1$.

and

$$\frac{dB}{dt} = g_0 B [1 - (f N^{1-2p} B^{2p})^{\theta_3}] \quad (2.19)$$

Parameters θ_1 and θ_3 allow additional flexibility in representing the plant population. Biologically, they could be related to adaptability to crowding (plasticity) or to initial planting arrangement. Regardless of the exact values of θ_1 and θ_3 , some growth reduction and mortality increase will occur even at low levels of crowding. This is reasonable for natural populations because the random distribution of seedlings places some plants unusually close to their neighbors and competition begins well before the total plot surface is used.

Enhanced Model with Additional Constraints

The basic model can be modified to incorporate other constraints on plant growth. Here, limitations on individual plant weight and total population biomass are added to the basic spatial constraint. It is assumed that approach toward any of the three constraints reduces the population's growth rate, but only the spatial constraint and the carrying capacity affect the mortality rate. Also, the deleterious effects of three constraints are assumed to be additive. The augmented model is

$$\frac{dN}{dt} = -m N \left[(f N^{1-2p} B^{2p})^{\theta_1} + \left(\frac{B}{B_{\max}} \right)^{\theta_2} \right] \quad (2.20)$$

and

$$\frac{dB}{dt} = g_0 B \left[1 - (f N^{1-2p} B^{2p})^{\theta_3} - \left(\frac{B}{B_{\max}}\right)^{\theta_4} - \left(\frac{B}{N w_{\max}}\right)^{\theta_5} \right], \quad (2.21)$$

where B_{\max} is the carrying capacity, w_{\max} is the maximum individual weight, and θ_1 through θ_5 control how abruptly the rates respond to changes in the level of each constrained quantity.

Model Analysis and Results

Basic Model

Although the basic model of equations 2.18 and 2.19 is derived from very simple assumptions, it can not be solved to give explicit equations for $N(t)$ and $B(t)$. However, it is amenable to isocline analysis, a technique discussed in many introductory ecology texts. This method is applied here to the simple case of $\theta_1 = \theta_3 = 1$ represented by equations 2.14 and 2.15. First, note that the growth rate of population biomass is zero when the right hand side (RHS) of equation 2.15 is zero, that is,

$$g_0 B \left[1 - f B^{2p} N^{1-2p} \right] = 0. \quad (2.22)$$

On log transformation and algebraic manipulation, this yields

$$\log B = \left(-\frac{1}{2p} + 1\right) \log N - \frac{1}{2p} \log f, \quad (2.23)$$

the equation of a straight line of slope $\beta = -1/(2p) + 1$ when

ordinate $\log B$ is plotted against abscissa $\log N$. This slope must be negative or zero because $0 \leq p \leq 0.5$, so that $-1/(2p) \leq -1$.

Restrictions on the path of the model population in the $\log B$ - $\log N$ plane (the self-thinning curve) can be deduced from this zero isocline, which divides the $\log B$ - $\log N$ plane into two regions. Below the isocline, population biomass is increasing and trajectories move upward, while above the isocline, biomass is decreasing and trajectories move downward. Since dN/dt is strictly negative, the force of mortality is always decreasing density and moving the population leftward in the plane. Because the isocline slants up toward the left of the plane, it must intercept the downward and leftward path of any population starting above the isocline. Such a population steadily approaches the isocline, then crosses it to enter the lower half of $\log B$ - $\log N$ plane. A population below the zero isocline must move upward ($dB/dt > 0$), but can not grow through the isocline because dB/dt is zero along that line. Three possibilities remain: the population trajectory could approach the zero isocline asymptotically, remain a constant distance from the isocline, or move leftward faster than upward, thus moving away from the isocline.

The potential ambiguity in the behavior of the model population below the zero isocline can be eliminated as follows. The instantaneous direction, β_t , of the population's path at any point in the $\log B$ - $\log N$ plane is given by

$$\frac{d \log B}{d \log N} = \frac{dB / (B dt)}{dN / (N dt)} = \beta_t, \quad (2.24)$$

a relationship that can be used to identify points of the $\log B$ - $\log N$ plane where the slope of the population trajectory is less than or equal to any given value Ψ , that is, where $\beta_t \leq \Psi$. Combining this inequality with equations 2.18 and 2.19 in the ratio of equation 2.24 yields

$$\frac{g_0 [1 - f N^{1-2p} B^{2p}]}{-m f N^{1-2p} B^{2p}} \leq \Psi . \quad (2.25)$$

Algebraic manipulation and log transformation of this expression gives a relationship for $\log B$ in terms of $\log N$:

$$\log B < \left(-\frac{1}{2p} + 1\right) \log N - \frac{1}{2p} \log f + \frac{1}{2p} \log \left(\frac{g_0}{g_0 - m\Psi}\right) . \quad (2.26)$$

The first two terms of the right hand side (RHS) of this equation simply give equation 2.23 for the zero isocline. The third term is a constant added to the intercept of the zero isocline since g_0 , m , and Ψ are constants. The equality in 2.26, which is the locus of points where trajectories take a given slope Ψ , defines a straight line parallel to the zero isocline. In fact, the zero isocline equation 2.23 is the special case of the more general equation 2.26 with $\Psi = 0$.

This general relationship can be used to find regions of the plane below the zero isocline where a population's instantaneous trajectory is steeper (more negative) than the slope of the zero isocline, so that the population is moving closer to the isocline.

Substituting $\Psi = \beta = -1/(2p) + 1$ (the slope of the zero isocline) in equation 2.26 gives

$$\log B \leq \left(-\frac{1}{2p} + 1\right) \log N - \frac{1}{2p} \log f + \frac{1}{2p} \log\left(\frac{g_0}{g_0 - m[-1/(2p)+1]}\right). \quad (2.27)$$

Since $g_0 > 0$ and $m > 0$ while $0 \leq p \leq 0.5$, the third term on the RHS is negative and equality defines a straight line parallel to but below the zero isocline. This lower line is asymptotically approached by all populations. Below this asymptotic trajectory, a population's path is steeper than the asymptotic trajectory, while the path of a population above the asymptotic trajectory is less steep than the asymptotic path. In both cases, the population's trajectory must continuously move closer to the asymptotic trajectory. Thus, the asymptotic trajectory has both attributes of the self-thinning line: populations approach it from any starting point in the $\log B$ - $\log N$ plane, and it is a boundary between allowable and unallowable biomass-density combinations. This second conclusion follows because populations can never grow through the asymptotic trajectory from below, and even if the model was started above the thinning line, mortality and negative growth would drive the population trajectory toward the thinning line and out of the region of the plane representing untenable biomass-density states.

Equation 2.27 also gives the slope and intercept of the self-thinning line in terms of the model parameters. The slope is $-1/(2p) + 1$, a function of the single parameter p which relates area

occupied to plant weight. Only if $p = 1/3$ is the model thinning slope equal to the value of $\beta = -1/2$ predicted by the self-thinning rule. The thinning line intercept is given by the last two terms of equation 2.27

$$\log K = -\frac{1}{2p} \log f + \frac{1}{2p} \log\left(\frac{g_0}{g_0 - m[-1/(2p)+1]}\right). \quad (2.28)$$

The value of $\log K$ depends on all the model parameters, but the first term of the RHS depends only on p and f . If the second term is small relative to the first, then $\log K$ is mainly determined by these two parameters. To determine when this condition is satisfied, define a new quantity, $\Delta \log K$, as the second term of equation 2.28

$$\Delta \log K = \frac{1}{2p} \log\left(\frac{g_0}{g_0 - m[-1/(2p)+1]}\right), \quad (2.29)$$

which is the contribution to the intercept of the self-thinning line of the second term of equation 2.28 and is also the vertical distance between the asymptotic population trajectory and the isocline of zero biomass increase. Since g_0 and m are both constants, m can be expressed as the product of g_0 and a constant ω , that is, $m = \omega g_0$. With this substitution, equation 2.29 gives $\Delta \log K$ in terms of p and ω

$$\Delta \log K = -\frac{1}{2p} \log\left(1 + \omega \left[\frac{1}{2p} - 1\right]\right). \quad (2.30)$$

This expression is negative or zero, so the thinning line is always below the zero isocline or equal to it. Figure 2.2 plots $\Delta \log K$ against $\log \omega$ for several choices of p and shows that most combinations of ω and p give $\Delta \log K \leq 1$. Only when p is small ($p < 1/3$) or ω is large ($\omega > 10$) does $\Delta \log K$ exceed one, and $\Delta \log K$ is much less than one for most reasonable parameter values. Thus, $\log K$ values of four or more are primarily determined by f and p as specified by the first term of equation 2.28.

Several features of this analysis are illustrated in Figure 2.3a, in which equations 2.14 and 2.15 are fitted to a Pinus strobus plantation remeasured nine times between 12 and 51 years after planting (lot 2B, Spurr et al. 1957). By repeated trials, the parameter values $g_0 = 0.5$, $m = 0.0475$, $p = 0.29$, and $f = 0.006$ were found to give a visually good fit to the $\log B$ - $\log N$ data when the model was started at the first data point and solved numerically using the LSODE differential equation solver (Hindmarsh 1980). The resulting solution demonstrates that the model can represent actual population data quite well. Isoleths of equation 2.26 for four values of Ψ are also shown, including the zero isocline of biomass growth ($\log B = -0.724 \log N + 3.83$) given by $\Psi = 0$, and the asymptotic self-thinning line ($\log B = -0.724 \log N + 3.78$) given by $\omega = \beta = -1/(2p) + 1 = -0.724$. The self-thinning line is -0.50 \log units below the zero isocline, that is, $\Delta \log K = -0.05$. Figure 2.3b shows how model solutions for different initial states converge on the asymptotic self-thinning line.

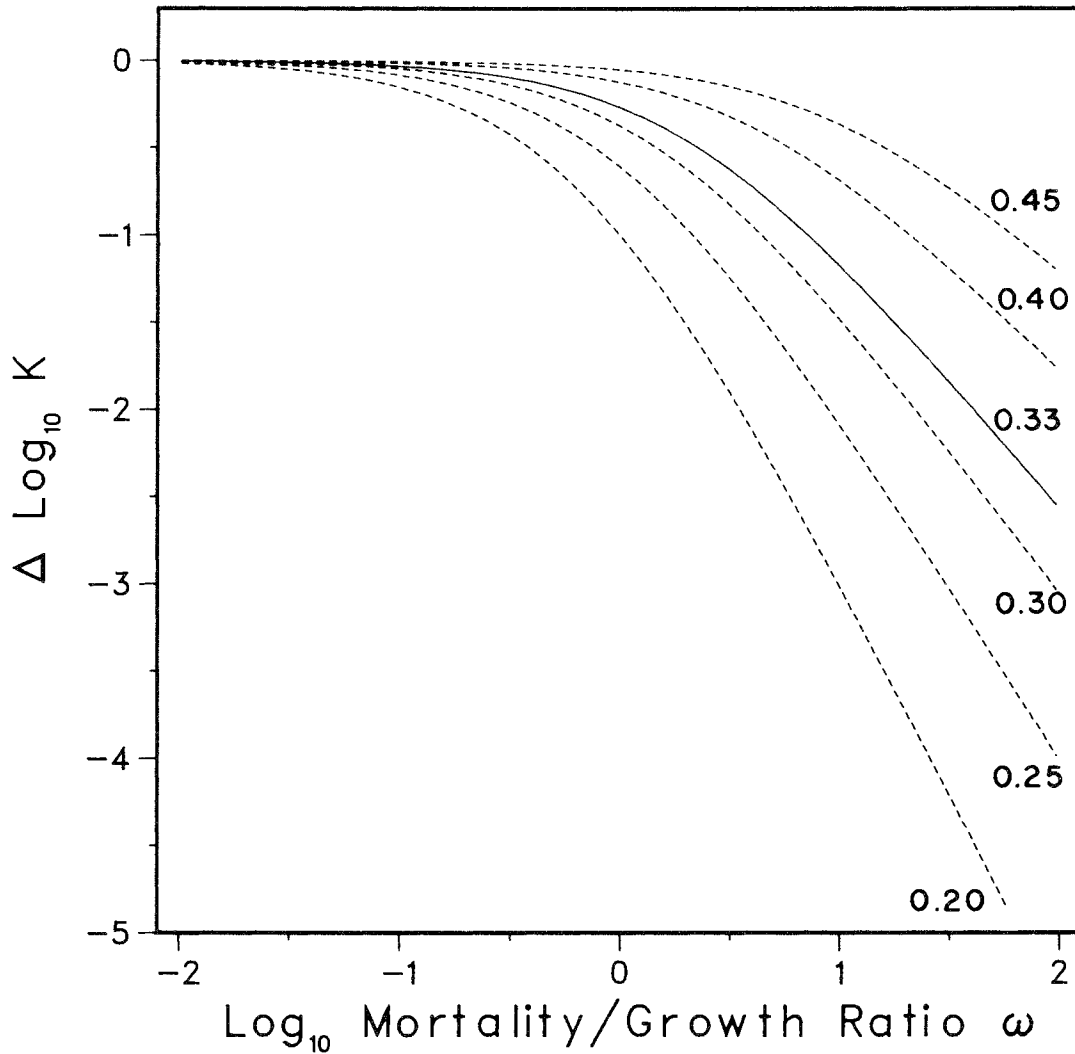


Figure 2.2. Vertical distance between the zero isocline of biomass growth and the self-thinning line. This distance, $\Delta \log K$, is plotted against the ratio, ω , of the mortality constant to the growth constant ($\omega = m/g_0$) for the indicated values of the parameter p . $\Delta \log K$ is the contribution of g_0 and m to the self-thinning intercept and is less than one when $m \leq g_0$.

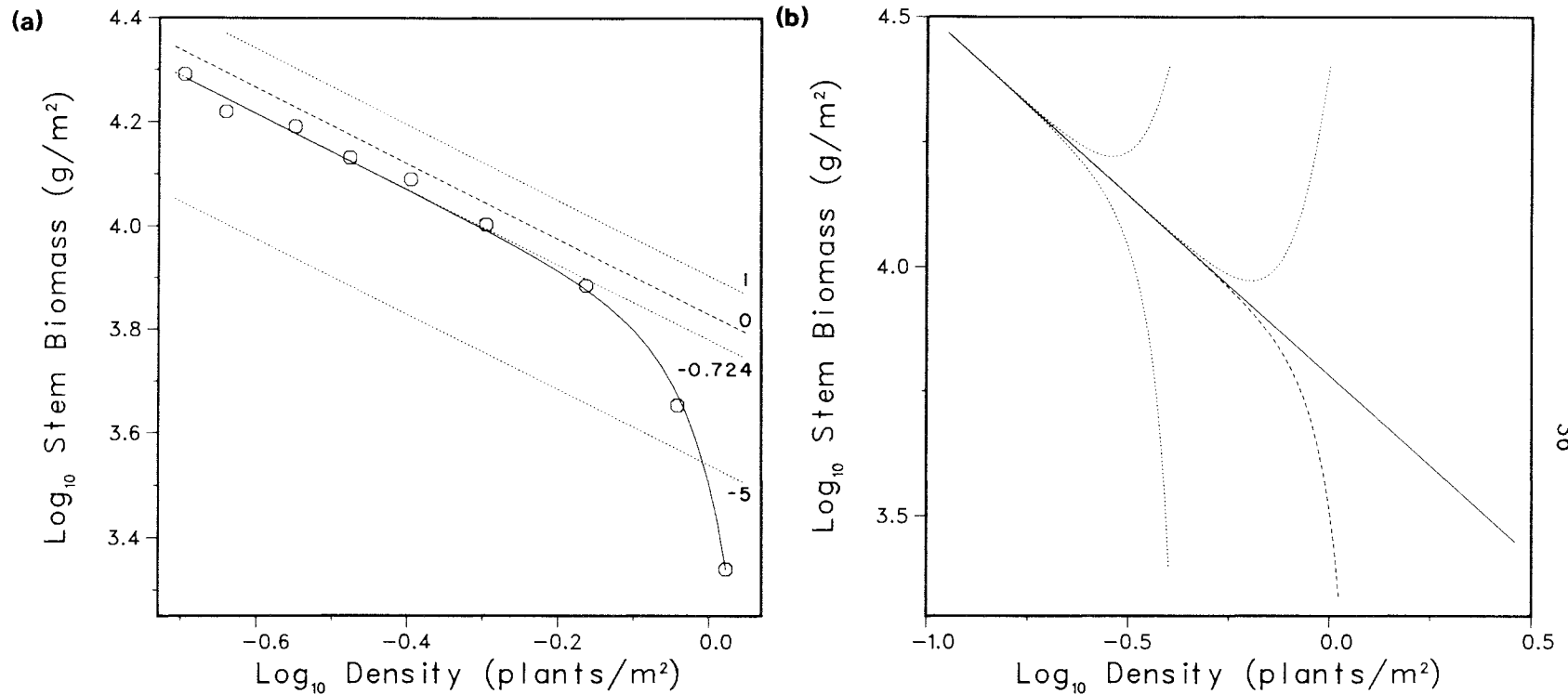


Figure 2.3. Basic model fitted to data from a *Pinus strobus* plantation. Model parameters are $g_0 = 0.5$, $m = 0.0475$, $f = 0.006$, and $p = 0.29$. In (a) data points (Spurr et al. 1957) are circled, the solid line is the solution of the model starting from the first point, the dashed line is the $\text{dB}/\text{dt} = 0$ isocline $\log B = -0.724 \log N + 3.83$, and the dotted lines are loci where trajectories have the indicated instantaneous slopes. The line marked "-0.724" is the model self-thinning line $\log B = -0.724 \log N + 3.78$. In (b), the dotted lines are model solutions starting from different initial conditions and converging on the asymptotic thinning line (solid).

Enhanced Model

Analysis of the model with added constraints on total biomass and individual weight is more difficult, because the equation for the isocline of zero biomass growth,

$$[f N^{1-2p} B^{2p}]^{\theta_3} + \left[\frac{B}{B_{\max}}\right]^{\theta_4} + \left[\frac{B}{N w_{\max}}\right]^{\theta_5} = 1, \quad (2.31)$$

is too complex to solve for $\log B$ in terms of $\log N$. However, the effect of each constraint can be considered independently by removing two of the three terms on the RHS. This analysis gives three straight lines in the $\log B$ - $\log N$ plane. The equation associated with the first term on the RHS is simply equation 2.23 for the zero isocline of the basic model, while the remaining two terms give

$$\log B = \log B_{\max} \quad (2.32)$$

and

$$\log B = \log N + \log w_{\max}. \quad (2.33)$$

The three terms are additive, so the actual zero isocline lies beneath the lowest of the three straight lines in the $\log B$ - $\log N$ plane, and the lowest line dominates the position and slope of the true isocline. Where two of the lines cross, the actual zero isocline undergoes a gradual transition from one slope to another. The abruptness of the transition is controlled by the parameters θ_1 , θ_2 , and θ_3 with higher values giving more abrupt transitions.

These behaviors of the enhanced model are illustrated in Figure 2.4, which was constructed with the parameters estimated for the Pinus strobus plantation, combined with hypothetical values of 10^4 g/m^2 and 10^8 g , respectively, for the new parameters B_{\max} and w_{\max} . Parameters θ_1 through θ_5 were all set to two. The equation of the true zero isocline 2.31 was found numerically using the ZEROIN computer subroutine (Forsythe et al. 1977) to solve

$$\left[f N^{1-2p} B^{2p} \right]^{\theta_1} + \left[\frac{B}{B_{\max}} \right]^{\theta_2} + \left[\frac{B}{N w_{\max}} \right]^{\theta_3} - 1 = 0 \quad (2.35)$$

for B at different values of N. The exact model solution for one set of initial conditions was calculated numerically using LSODE.

Discussion

Basic Model

Analysis of the basic model has shown that the self-thinning rule can be derived in a dynamic model as a consequence of the limited availability of growing area. The power relationship between biomass and density (the straight line relationship between $\log B$ and $\log N$) follows directly from an assumed power relationship between the area occupied by a plant and plant weight. This assumption is reasonable because power functions between plant measurements have been repeatedly demonstrated in many disciplines

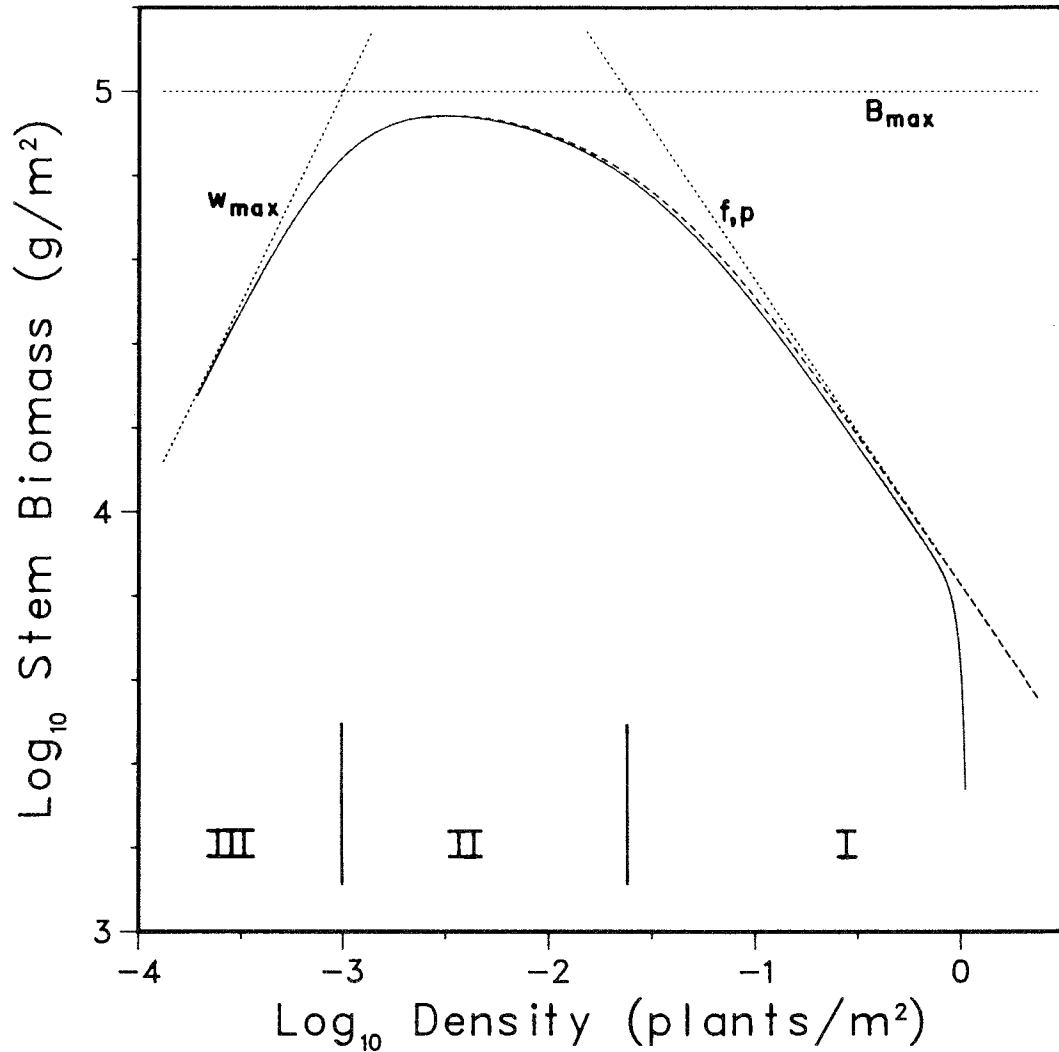


Figure 2.4. Analysis of a model with three constraints on population growth. Parameters g_0 , m , f , and p are as in Figure 2.2, while $B_{\max} = 10^5$, $w_{\max} = 10^8$, and θ_1 through θ_5 all equal 2. Dotted lines are $dB/dt = 0$ isoclines for each constraint considered independently. The maximum individual weight, the carrying capacity, and the spatial constraint are labelled " w_{\max} ", " B_{\max} ", and " f,p ", respectively. The dashed line is the true isocline for all three constraints and the solid line is a model solution for 450 years. Regions I, II, and III are, respectively, portions of the plane where model behavior is dominated by the spatial constraint, the carrying capacity, and the maximum individual weight.

including forestry (Reinke 1933, Curtis 1971) and plant ecology (Whittaker and Woodwell 1968), and such relationships provide the basis for widely used methods of nondestructive sampling of plant populations (see references in Hutchings 1975). When traced to this rather commonplace origin, the power equation form of the self-thinning rule is unremarkable.

The slope of the model thinning line is determined only by the power, p , of the area-weight relationship and equals the classic thinning rule slope of $\beta = -1/2$ only if $p = 1/3$. Plant growth is typically not isometric (Mohler et al. 1978, Furnas 1981, White 1981) so p is not generally $1/3$, and the model predicts that thinning slopes should vary systematically with plant allometry. This hypothesis has not been supported in previous reviews and experimental tests (Westoby 1976, Mohler et al. 1978, White 1981), so the causal mechanisms formalized in the model developed here have been discredited as possible explanations for the self-thinning rule. However, some new analyses presented in Chapters 5 and 6 show that measured self-thinning slopes do vary significantly from the idealized value of the thinning rule, and that these deviations can be correlated with differences in plant allometry, thus verifying a major prediction of the model developed here.

Even for this very simple model, the exact value of the self-thinning constant, K , depends on all the model parameters and can not be interpreted as a function of a single measurement, such as biomass density in space (as discussed in White 1981 and Lonsdale and Watkinson 1983a). Biomass density in space is a component of

the parameter f , but its relationship to $\log K$ is confounded by other components of f , such as initial plant shape and the degree of tolerable overlap between plants, and by the dependence of $\log K$ on the allometric power p . Since thinning slopes do vary with plant allometry (Chapter 6), direct comparisons of thinning intercepts of experimental thinning lines are not clearly interpretable because the comparison of the constants among power relationships is not meaningful unless the relationships have the same power (White and Gould 1965). Experimental interpretation of K will, then, require a careful statistical analysis relating K to several factors, including plant allometry, initial plant shape, the density of biomass per unit of occupied space, and some measure of allowable overlap between plants, such as shade tolerance.

The position of the model self-thinning line is also affected by the rate constants g_0 and m , but these effects are relatively small over a large range of reasonable parameter values. The primary effect in the $\log B$ - $\log N$ plane of g_0 and m is to determine the rate and direction of approach toward the thinning line. By concentrating on the thinning line, these rate dynamics are deemphasized in favor of a focus on the limitations imposed by available growing space and plant geometry.

The model also predicts that the parameters of the self-thinning line are not species constants invariant to changes in all environmental factors except illumination (as proposed by Yoda et al. 1963, Hickman 1979, Hozumi 1980, White 1981, and Hutchings 1983). Any factor that could affect the density of biomass in

occupied space or the degree of allowable overlap between plants would also affect the thinning constant K , while environmental factors affecting plant allometry would also change both K and the self-thinning slope. The remarkable abilities of plants to vary their sizes, shapes, canopy densities, etc. in response to environmental and competitive factors are well-documented (see references in Harper 1977), and allometric relationships for a species also vary significantly among sites (Hutchings 1975). Peet and Christensen (1980) reported that the thinning characteristics of a pine stand could be permanently altered if the initial density is very high and speculated that some aspects of tree geometry were fixed by the initial growing conditions. Such permanent effects of initial density would be another cause for variation in thinning line parameters among populations of a species. The prediction that thinning line parameters are not species constants is tested in Chapters 4 through 6.

Enhanced Model

The model with additional constraints on total biomass and individual plant weight can explain most general features of population dynamics in the $\log B$ - $\log N$ plane. The four phases of population growth that were discussed in Chapter 1 and diagrammed in Figure 1.1, page 9 are reproduced by the model in Figure 2.4, with the sharp corners of idealized behavior replaced by gradual transitions from one growth phase to another. The four phases are explained by the model as the sequential operation of three

constraints on population growth: the spatial constraint, the carrying capacity, and the maximum individual size. The transition from adherence to the self-thinning rule to constant biomass at the carrying capacity, shown by movement from region I to region II of Figure 2.4, has been discussed by White and Harper (1970) and Hutchings and Budd (1981a). Experimental evidence of this transition has been reported by Schlesinger and Gill (1978), Lonsdale and Watkinson (1983b), Watkinson (1984), and Peet and Christensen (1980). The last of these papers also reported that thinning trajectories eventually become even less steep than the constant biomass line, as shown in the transition from region II to region III in Figure 2.4.

The modified model can also explain the ambiguous results of experiments comparing the self-thinning lines of deeply shaded populations to those of populations grown under better illumination. Some investigators have concluded that reduced illumination lowers thinning lines and shifts the slope in the $\log B$ - $\log N$ plane from $-1/2$ to 0 (White and Harper 1970, Kays and Harper 1974, Lonsdale and Watkinson 1982), while others have observed no change in slope when illumination is decreased (Westoby and Howell 1981, Hutchings and Budd 1981b).

The enhanced model (equations 2.20 and 2.21) is used here to investigate the effects of decreased illumination on the $\log B$ - $\log N$ trajectory, but the constraint on individual weight is eliminated to simplify the analysis. It is unlikely that plants would reach their greatest potential size during short experiments under reduced

illumination, so this constraint would be irrelevant. A reduction in illumination could shift the positions of the two remaining constraining lines in the log B-log N plane. As a first approximation, a certain percentage reduction in illumination might be expected to reduce the carrying capacity by the same percentage. It is more difficult to estimate the effect of a light reduction on the spatial constraint line. Lower illumination can stimulate plants to emphasize height growth rather than radial growth (Harper 1977), so that the allometric power p relating area covered to weight might decrease, resulting in a steeper thinning line. However, illumination changes may also alter the density of biomass in occupied space and change the thinning intercept (Lonsdale and Watkinson 1982). Since species differ widely in their shade tolerances, meristem placements, and other important physiological and morphological factors, the actual effect on the spatial constraint line should vary among species. Regardless of these particulars, the carrying capacity will become the dominant constraint over a wider range of plant densities under reduced illumination as long as the spatial constraint line does not drop too drastically.

The consequences for the observed log B-log N trajectory of a drop in total supportable biomass with reduced illumination are shown in Figure 2.5. In this particular example, the carrying capacity drops by one log unit when illumination is reduced by 90%, but the spatial constraint line is not affected. With the light reduction, the lowered carrying capacity dominates model behavior

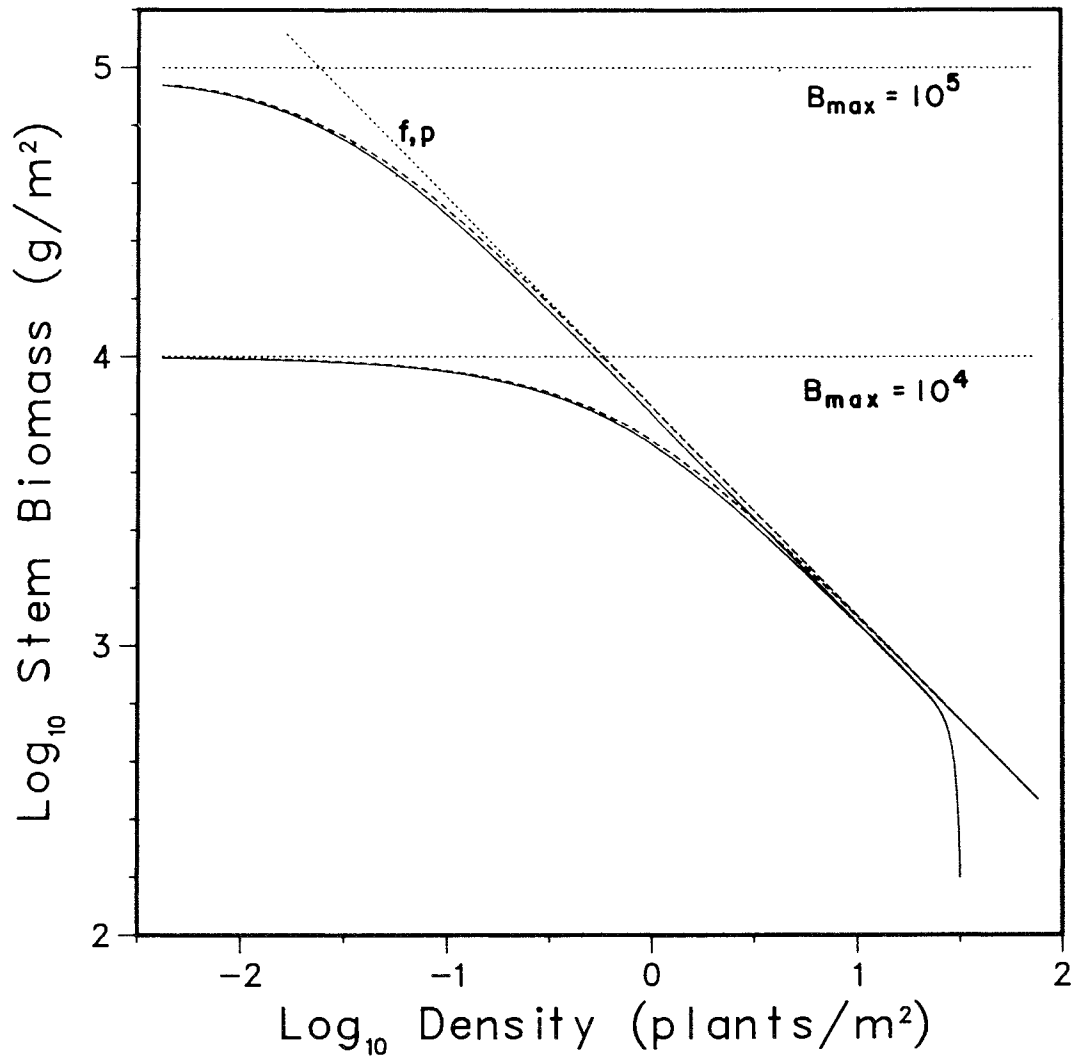


Figure 2.5. Effect of a reduction in illumination on population trajectories in a two-constraint model. A hypothetical 90% drop in illumination changes the carrying capacity from 10^5 to 10^4 (dotted lines labelled " B_{\max} ") but does not affect the spatial constraint line (dotted line labelled "f,p"). Other model parameters are as in Figure 2.4. The dashed line is the true zero isocline for both constraints. Model solutions (solid lines) starting from the same initial conditions are shown for the two values of B_{\max} .

over a wider range of densities when compared to model behavior at the higher light level. This is clear when the complete trajectories are examined over four orders of magnitude of density; however, the response revealed to an experimenter by measurements taken over more limited densities would depend on the range observed. An investigator sampling over $0.5 \leq \log N \leq 1.5$ from populations behaving as shown in Figure 2.5 would see virtually no difference between the high light and reduced light trajectories, but measurements over $-1.0 \leq \log N \leq -0.5$ would reveal a major drop in both the intercept and the slope of a straight line through the data. Thus, the ambiguous and seemingly contradictory results from experiments on reduced illumination are explainable by this model. Confusion has resulted because the various studies have used different plants observed over different densities and so focused on different regions of the overall behavior revealed in Figure 2.5. A similar theory and some supporting evidence were presented by Lonsdale and Watkinson (1982).

CHAPTER 3

SIMULATION MODEL OF SELF-THINNING

Introduction

The models of Chapter 2 yield predictions about the effects of plant geometry and restricted resources on self-thinning, but some of the underlying assumptions merit further consideration since they may be over-simplifications. These highly aggregated and spatially averaged models do not explicitly consider the sizes and locations of individuals or the interactions between them, but plants compete with immediate neighbors not average population conditions (Schaffer and Leigh 1976, Harper 1977). A simulation model which represents these factors in a more realistic, detailed way is analyzed here to check if its responses to variations in plant allometry, the density of biomass in occupied space, and the degree of tolerable overlap between plants are similar to the responses of the simpler models. As in Chapter 2, the principal objective is to discover which model parameters and processes determine the linearity, slope, and intercept of the self-thinning line, then use these results to provide explanations for observed self-thinning relationships.

Model Formulation

The simulation model is based on simple equations for the growth and geometry of an individual plant. Each plant in the

population is represented by separate copies of these equations, and the entire group is united into a single system by some rules for partitioning resources in areas where neighboring plants interact. It is assumed that the growth of a plant is related to the ground area it covers, since this is the region over which light, water, and mineral resources are obtained (Aikman and Watkinson 1980). The basic equation for the growth in weight, w , of a single plant is

$$\frac{dw}{dt} = g_1 a - b w^q, \quad (3.1)$$

where g_1 represents the maximum assimilation rate (in $g/m^2/unit$ time) sustainable per unit of ground area, and a is the area of ground covered by the plant, also called the zone of influence (ZOI--Bella 1971). The second term on the right hand side (RHS) of equation 3.1 represents the cost of maintaining existing plant biomass, which is assumed to be a power function of weight specified by the constants b and q .

To determine the ground area covered by an individual, assume that plants, on the average, occupy cylindrical volumes of space called the volume of influence (VOI). Plant weight can then be related to the dimensions of this cylinder by

$$w = v d = \pi R^2 h d, \quad (3.2)$$

where v , R , and h are the volume, radius, and height of the VOI and d is the average density of biomass in that volume. Changes in

plant geometry with plant size can be modeled by assuming that the radius of the VOI is a power function of weight

$$R = c w^p, \quad (3.3)$$

where c and p are constants. As in Chapter 2, values of p are between 0.0 and 0.5, and c depends on initial plant shape and the density of biomass in occupied space. Assuming that the height to radius ratio, τ , is known for plants of some weight \bar{w}_0 , equations 3.2 and 3.3 can be combined and solved for c to relate this constant to parameters with more direct biological interpretations

$$c = \left[\frac{\bar{w}_0}{\pi \tau d} \right]^{1/3} \frac{1}{\bar{w}_0^p} = \frac{\bar{w}_0^{(1/3 - p)}}{(\pi \tau d)^{1/3}}. \quad (3.4)$$

Thus, c is related to the density of biomass in occupied space, d , and to values of τ and \bar{w}_0 that specify plant shape at a particular weight. Equation 3.3 can be used to develop a formula relating area covered to plant weight

$$a = \pi c^2 w^{2p} = c_1 w^{2p}. \quad (3.5)$$

Since $c_1 = \pi c^2$, c_1 can also be related to \bar{w}_0 , p , τ , and d through equation 3.4. Combining equations 3.1 and 3.5 gives a general equation for the growth rate of an isolated individual

$$\frac{dw}{dt} = g_1 c_1 w^{2p} - b w^q. \quad (3.6)$$

A plant can not fully exploit the resources within its ZOI if some resources are preempted by neighbors attempting to occupy the same area, so the model partitions the resources associated with a particular section of ground among the plants that are competing for it. This is accomplished by a pairwise comparison of all plants. Since the spatial location of each plant and the radius of a ZOI centered at that point are known, simple trigonometry can be used to determine if two plants overlap. If so, the area of ground surface shared is calculated and a fraction of the shared area is subtracted from the ZOI of each member of the pair to represent the loss of resources to its competitor. Equation 3.6 becomes

$$\frac{dw_i}{dt} = g_1 [c_1 w_i^{2p} - \sum_{\substack{j=1 \\ j \neq i}}^{n_t} a_{loss,ij}] - b w_i^q, \quad (3.7)$$

where $a_{loss,ij}$ is the area lost by plant i to plant j and n_t is the number of plants remaining at time t . The model includes six different algorithms for dividing areas of overlap between two plants. Table 3.1 gives names and formulas for all six. The fractions in Table 3.1 are multiplied by the actual area of overlap to obtain the a_{loss} term of equation 3.6 for each pairwise comparison. Since the area controlled by a plant cannot be negative, a_i (the bracketed term in equation 3.7) is set to zero if the total area lost by a plant exceeds the area of its ZOI.

The direct application of equation 3.7 is precluded by edge effects, which can bias the results if the simulated plot is

Table 3.1. Competition Algorithms in the Simulation Model.

| Algorithm Number ^a | Method of Partitioning Contested Areas | Fraction Allocated to | |
|-------------------------------|--|---|---|
| | | Plant i | Plant j |
| 1 | Divided in proportion to weight | $\frac{w_i}{w_i + w_j}$ | $\frac{w_j}{w_i + w_j}$ |
| 2 | Larger plant gets all ^b | 1 | 0 |
| 3 | Neither plant gets any | 0 | 0 |
| 4 | Divided in proportion to height | $\frac{h_i}{h_i + h_j}$ | $\frac{h_j}{h_i + h_j}$ |
| 5 | Divided equally | $\frac{1}{2}$ | $\frac{1}{2}$ |
| 6 | Half divided equally; half in proportion to weight | $\frac{1}{2} + \frac{1}{2} \frac{w_i}{w_i + w_j}$ | $\frac{1}{2} + \frac{1}{2} \frac{w_j}{w_i + w_j}$ |

^aAn arbitrary identification number.

^bFractions are given for the case where plant i is larger than plant j.

intended to represent a sample of a larger population. These effects arise because some of the competitors of plants near the plot edge lie off the plot and are not observed. The linear expansion algorithm of Martin et al. (1977) is used to remove this effect. The calculated area lost by each plant i to its competitor j ($a_{\text{loss},ij}$) is multiplied by an expansion factor

$$\epsilon_{ij} = 2\pi / \eta_{ij} , \quad (3.8)$$

before being summed into equation 3.7. The quantity η_{ij} , called the sample angle, is calculated for each pair of plants by centering on plant i a circle of radius D_{ij} (the distance between plants i and j). The angle subtending the portion of this circle that lies on the simulated plot is η_{ij} . This angle is 2π when the entire circle is on the plot and less than 2π when part of the circle falls outside the plot boundary, so $\epsilon_{ij} \geq 1$.

Multiplication of each observed competitive loss by an expansion factor gives a statistically unbiased estimate of the additional loss to unobserved competitors outside the simulated plot, but this estimate is valid only if the radius of the largest ZOI is less than the plot radius (Martin et al. 1977); therefore, all simulations were halted before this condition was violated.

The persistence of an individual plant requires a favorable balance between the rates of assimilation and respiration. This requirement can be modeled by killing plants whose average relative growth rates over a selected time interval fall below a threshold value, RGR_{min} (Aikman and Watkinson 1980). For the simulations

presented here, the interval was 0.1 time units and the threshold value was 0, that is, all plants not satisfying the inequality

$$\text{RGR}_i = \frac{1}{0.1} \ln \frac{w_{i,t}}{w_{i,t-0.1}} \geq 0 \quad (3.9)$$

were eliminated from the simulation ($w_{i,t}$ is the weight of plant i at time t).

The initial conditions for a simulation were specified by selecting an initial number of plants and a location and weight for each plant. Initial weights for plants were chosen randomly from a normal distribution with mean \bar{w}_0 and standard deviation $s_{\bar{w}_0}$, while plant locations were assigned from a uniform random distribution on a circular plot of specified area. The model was typically started with 200 plants, but 600 was the initial population size when the dynamics of the size distribution were of particular interest and larger sample sizes were needed to obtain accurate estimates of the moments of that distribution.

Model Analysis

The model was analyzed in three steps: (1) verification that the dynamics resemble real self-thinning behavior, (2) estimation of the variations in the self-thinning trajectory strictly due to stochastic model elements, and (3) evaluation of simulation experiments in which a parameter was varied among simulations to determine the effect of that parameter on self-thinning. A reference set of parameters was defined to generate the model

solutions used in steps one and two. The values chosen (Table 3.1) are arbitrary, but within biologically realistic limits. Except for special cases detailed in the results, the model solutions used here were linear over the interval $3.0 \leq \log N \leq 3.7$, so regression of $\log B$ against $\log N$ was applied to data within this interval to estimate the slope, $\hat{\beta}$, and intercept, $\hat{\alpha} = \log K$, of a self-thinning line for each simulation. The intercept of each regression line at $\log N = 3.35$, $\hat{\alpha}_{3.35}$, was also calculated to provide a measure of thinning line position near the center of range of data. Coefficients of determination were so high (all $r^2 > 0.97$) that the regression estimates of $\hat{\beta}$ and $\hat{\alpha}$ were identical to those from principal component analysis. PCA is preferable to regression when the two methods give different results (Chapter 4). The time required for the density of individuals to fall from the initial value of 10,000 to 1000 was recorded as a measure of the average rate of self-thinning.

Because the model is complex, a controlled procedure was used to identify model parameters that affect the self-thinning trajectory. In each of six simulation experiments, a parameter was varied across 5-15 simulations and the resulting group of self-thinning trajectories was compared to a control group of ten trajectories generated by the reference parameter set. This control group was analyzed to estimate the ranges of variation in $\hat{\beta}$, $\hat{\alpha}$, and $\hat{\alpha}_{3.35}$ strictly due to stochastic model factors. Values of $\hat{\beta}$, $\hat{\alpha}$, or $\hat{\alpha}_{3.35}$ well outside these ranges in an experimental

simulation indicated that the parameter being studied did alter the self-thinning line beyond the normal limits of stochastic variation and therefore has a role in positioning the self-thinning line. The seven parameters that have entries in the "Range of Variation" column of Table 3.2 were investigated in these simulation experiments, but one experiment considered parameters b and q together. For each experimental group, $\log B$ - $\log N$ plots were used to visually compare the variation among thinning trajectories to the variation among the control trajectories. The mean, range, and coefficient of variation (CV) of $\hat{\beta}$, $\hat{\alpha}$, and $\hat{\alpha}_{3.35}$ were also tabulated for each simulation experiment and compared to the same statistics for the control group. For five of the experiments, Spearman correlation coefficients, r_s , (Sokal and Rohlf 1981) between the experimental parameter and $\hat{\beta}$, $\hat{\alpha}$, and $\hat{\alpha}_{3.35}$ were calculated and tested for statistical significance to determine if these thinning line descriptors varied systematically with the experimental parameter. Although this application of statistical tests to simulation results may initially seem contrived, it is appropriate for a model with stochastic factors. Chance variations among a small number of stochastic simulations can produce meaningless correlations in the same manner as in real data. When high correlations were found, further analysis was done to estimate the precise relationship between the slope or intercept and the model parameter.

Table 3.2. Simulation Model Parameters and Their Reference Values.

| Symbol | Meaning | Units | Reference Value | Range of Variation |
|--------------------|--|--------------------------|--------------------|------------------------------|
| p | Allometric power relating ZOI radius to weight | | 0.333 | 0.27-0.49 |
| d | Density of biomass in occupied space | g/m ³ | 6200 | 631-39810 |
| | Competition algorithm | | 1 | 1-6 |
| g ₁ | Maximum assimilation rate per unit of ground area covered | g/m ² /time | 25 | 10-50 |
| b | Constant relation metabolic rate to weight | (g/m ²)(1/q) | 0.00147 | 1.47x10 ⁻¹⁰ -147* |
| q | Power relating metabolic rate to weight | | 2 | 0.5-3.5* |
| A _{plot} | Plot area | m ² | 0.02 | 0.000632-0.0632** |
| τ | Height to radius ratio for VOI's of plants of weight \bar{w}_0 | | 1 | |
| RGR _{min} | Minimum survivable relative growth rate | | 0 | |
| Δt | Time step | time | 0.1 | |
| (Δt) _m | Time interval over which RGR's are averaged | time | 0.1 | |
| n ₀ | Initial number of plants | | 200 | |
| \bar{w}_0 | Initial average weight | g | 0.0001 | |
| s \bar{w}_0 | Standard deviation of initial weight | g | 5x10 ⁻⁵ | |

*b and q were varied together in a single set of simulations (see text).

**A_{plot} was varied to give initial plant densities from 3160 to 316,000 plants/m².

Results

The simulation model mimics several behaviors of real plant populations (Figure 3.1). Initially uncrowded populations trace a nearly vertical path in the log B-log N plane, but eventually bend toward and move along a negatively sloped self-thinning line. Model populations show other behaviors of real plant monocultures, including nearly logistic increase in biomass (Hutchings and Budd 1981a), approximately exponential mortality during self-thinning (Yoda et al. 1963, Harper 1977), and the development of skewed size distributions from initially symmetric distributions (White and Harper 1970, Hutchings and Budd 1981a).

Information on individual simulations is presented in Table 3.3, including the experimental parameter value (if any) and the three thinning line descriptors $\hat{\beta}$, $\hat{\alpha}$, and $\hat{\alpha}_{3.35}$. All the thinning line regressions were based on at least eight points, but most used between 20 and 70. Coefficients of determination, r^2 , were uniformly high ($r^2 \geq 0.97$), confirming that trajectories were well described by a straight line over the range $3.0 \leq \log N \leq 3.7$. The thinning line descriptors are further summarized in Table 3.4, where means, ranges, and coefficients of variation are given for each of six experimental or control groups, along with Spearman correlations with the experimental parameter (if any). Table 3.3 also gives the time required for the density to fall from 10,000 to 1000. Systematic changes in these times within the simulation experiments show that all parameters affected the

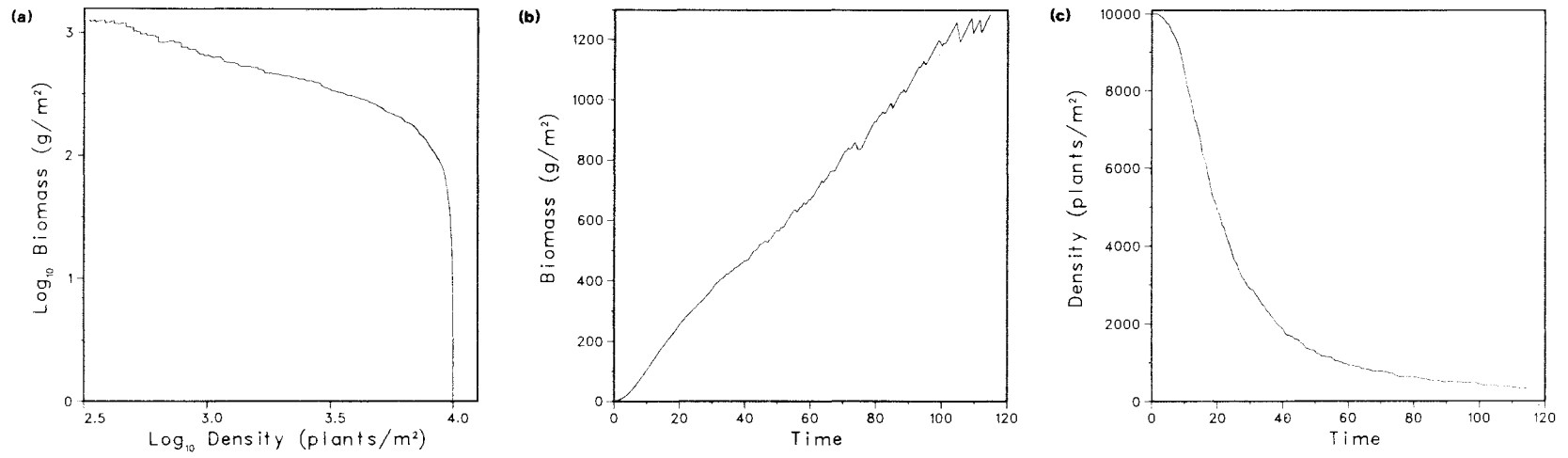


Figure 3.1. Typical dynamic behavior of the simulation model. (a) is a log B-log N self-thinning plot, (b) shows the logistic increase in total population biomass, and (c) shows approximately exponential mortality commencing with the onset of thinning around time 20. The reference parameters (Table 3.2) were used.

Table 3.3. Self-thinning Lines for the Simulation Experiments.

| Parameter Varied | Parameter Value | Time to $\log N = 3^*$ | Estimated Thinning Line | | |
|--|-----------------|------------------------|-------------------------|--------------------------|--|
| | | | Slope $\hat{\beta}$ | Intercept $\hat{\alpha}$ | Intercept at $\log N = 3.35$ $\hat{\alpha}_{3.35}$ |
| None (Figure 3.2) | | 70 | -0.69 | 4.94 | 2.64 |
| | | 55 | -0.55 | 4.48 | 2.63 |
| | | 54 | -0.55 | 4.46 | 2.63 |
| | | 67 | -0.65 | 4.83 | 2.67 |
| | | 59 | -0.62 | 4.73 | 2.66 |
| | | 58 | -0.59 | 4.62 | 2.65 |
| | | 59 | -0.72 | 5.05 | 2.62 |
| | | 59 | -0.64 | 4.79 | 2.65 |
| | | 58 | -0.54 | 4.45 | 2.64 |
| | | 60 | -0.67 | 4.90 | 2.66 |
| p (Figure 3.3) | 0.27 | 426 | -0.98 | 6.69 | 3.41 |
| | 0.29 | 203 | -0.91 | 6.23 | 3.17 |
| | 0.31 | 106 | -0.69 | 5.22 | 2.91 |
| | 0.33 | 65 | -0.70 | 5.02 | 2.66 |
| | 0.33333 | 57 | -0.61 | 4.68 | 2.64 |
| | 0.35 | 41 | -0.57 | 4.42 | 2.50 |
| | 0.37 | 27 | -0.42 | 3.71 | 2.30 |
| | 0.39 | 19 | -0.35 | 3.36 | 2.18 |
| | 0.41 | 14 | -0.28 | 2.97 | 2.02 |
| | 0.43 | 11 | -0.24 | 2.70 | 1.89 |
| | 0.45 | 8 | -0.22 | 2.54 | 1.80 |
| 0.47 | 7 | -0.09 | 2.00 | 1.68 | |
| 0.49 | 6 | -0.11 | 1.97 | 1.58 | |
| d (Figure 3.4) | 631 | 6 | -0.45 | 3.17 | 1.65 |
| | 1000 | 9 | -0.55 | 3.66 | 1.83 |
| | 1585 | 15 | -0.56 | 3.90 | 2.03 |
| | 2512 | 22 | -0.60 | 4.25 | 2.26 |
| | 3981 | 36 | -0.60 | 4.47 | 2.45 |
| | 6310 | 60 | -0.61 | 4.70 | 2.65 |
| | 10000 | 90 | -0.63 | 4.93 | 2.83 |
| | 15850 | 158 | -0.63 | 5.16 | 3.06 |
| | 25120 | 251 | -0.55 | 5.11 | 3.27 |
| | 39810 | 378 | -0.59 | 5.44 | 3.45 |
| Competition algorithm (Figure 3.5) | 1 | 59 | -0.68 | 4.93 | 2.64 |
| | 2 | 36 | -0.70 | 4.76 | 2.43 |
| | 3 | 65 | -0.64 | 4.60 | 2.47 |
| | 4 | 84 | -0.57 | 4.65 | 2.73 |
| | 5 | >100 | -0.62 | 4.89 | 2.82 |
| | 6 | 44 | -0.74 | 4.99 | 2.52 |
| g ₁ (Figure 3.6a) | 10 | >100 | -0.54 | 4.43 | 2.63 |
| | 15 | >100 | -0.71 | 5.03 | 2.65 |
| | 20 | 71 | -0.64 | 4.79 | 2.64 |
| | 25 | 55 | -0.59 | 4.60 | 2.62 |
| | 30 | 52 | -0.64 | 4.80 | 2.65 |
| | 35 | 37 | -0.63 | 4.76 | 2.63 |
| | 40 | 38 | -0.59 | 4.62 | 2.65 |
| | 45 | 36 | -0.71 | 5.06 | 2.68 |
| | 50 | 30 | -0.64 | 4.79 | 2.65 |
| q (Figure 3.6b) | 0.5 | 58 | -0.62 | 4.71 | 2.64 |
| | 1.0 | 64 | -0.64 | 4.80 | 2.64 |
| | 1.5 | 59 | -0.64 | 4.78 | 2.65 |
| | 2.0 | 57 | -0.58 | 4.59 | 2.64 |
| | 2.5 | 61 | -0.67 | 4.88 | 2.62 |
| | 3.0 | 73 | -0.68 | 4.92 | 2.65 |
| | 3.5 | 57 | | | |

*The time required for plant density to drop from its initial value of $\log N = 4.0$ to $\log N = 3.0$.

Table 3.4. Thinning Line Statistics for the Simulation Experiments.

| Figure | Parameter Varied | Slope $\hat{\beta}$ | | | Intercept $\hat{\alpha}$ | | | Intercept at log N = 3.35 $\hat{\alpha}_{3.35}$ | | | | | |
|--------|-----------------------|---------------------|-------|------|--------------------------|------|-------|---|-------------------------|------|-------|------|-------------------------|
| | | Mean | Range | CV | r_s^a | Mean | Range | CV | r_s^a | Mean | Range | CV | r_s^a |
| 3.2 | none | -0.62 | 0.18 | 10.2 | | 4.72 | 0.59 | 4.5 | | 2.64 | 0.05 | 0.6 | |
| 3.3 | p | -0.48 | 0.89 | 61.2 | 0.99* (<0.0001) | 3.96 | 4.72 | 39.2 | -1.00* (<0.0001) | 2.37 | 1.83 | 24.4 | -1.00* (<0.0001) |
| 3.4 | d | -0.58 | 0.17 | 9.2 | -0.49 (0.15) | 4.48 | 2.28 | 16.3 | 0.99* (<0.0001) | 2.55 | 1.80 | 24.0 | -1.00* (<0.0001) |
| 3.5 | Competition algorithm | -0.66 | 0.16 | 8.9 | | 4.80 | 0.38 | 3.3 | | 2.60 | 0.39 | 5.9 | |
| 3.6a | g ₁ | -0.63 | 0.17 | 8.9 | -0.20 (0.61) | 4.76 | 0.63 | 4.2 | 0.25 (0.52) | 2.64 | 0.06 | 0.6 | 0.40 (0.28) |
| 3.6b | q | -0.64 | 0.10 | 5.7 | -0.60 (0.21) | 4.78 | 0.34 | 2.5 | 0.60 (0.21) | 2.64 | 0.03 | 0.4 | 0.26 (0.62) |

^aSpearman correlation of the thinning line descriptor with the model parameter. The significance level of the correlation is given in parentheses.

*Significant at the 95% confidence level ($P \leq 0.05$).

rate of self-thinning, except q , which had no effect, and initial density, which was not amenable to this analysis. The log B-log N plot of the control group simulations (Figure 3.2) shows that there are variations in the self-thinning trajectory that can only be attributed to persistent effects of the stochastic initial conditions. However, the slopes of the self-thinning lines are quite similar and the lines are all positioned within a narrow vertical band.

Only the allometric power, p , altered the self-thinning slope. This effect is demonstrated visually by comparing the experimental thinning diagram (Figure 3.3a) to Figure 3.2 and quantitatively by the high Spearman correlation between p and $\hat{\beta}$ ($r_s = 0.99$, $P < 0.0001$). The relationship between $\hat{\beta}$ and $1/p$ is linear (Figure 3.3b), and the regression equation $\hat{\beta} = -0.555(1/p) + 1.05$ ($r^2 = 0.98$, $P < 0.0001$, 95% CI for slope = $[-0.604, -0.506]$, 95% CI for intercept = $[0.91, 1.18]$) was very close to the ideal linear relationship $\hat{\beta} = -0.50(1/p) + 1.00$ developed in Chapter 2. The parameter p also altered the self-thinning intercept, $\hat{\alpha}$, ($r_s = -1.00$, $P < 0.0001$), which was also linearly related to $(1/p)$ (Figure 3.3c), again as predicted in Chapter 2. The regression equation was $\hat{\alpha} = 2.97(1/p) - 4.18$ ($r^2 = 0.99$, $P < 0.0001$, 95% CI for slope = $[2.80, 3.13]$, 95% CI for intercept = $[-4.65, -3.72]$).

The parameter d , the density of biomass in occupied space, affected the position of the self-thinning line (Figure 3.4a), as measured by the thinning intercept $\hat{\alpha}$ ($r_s = 0.99$, $P < 0.0001$).

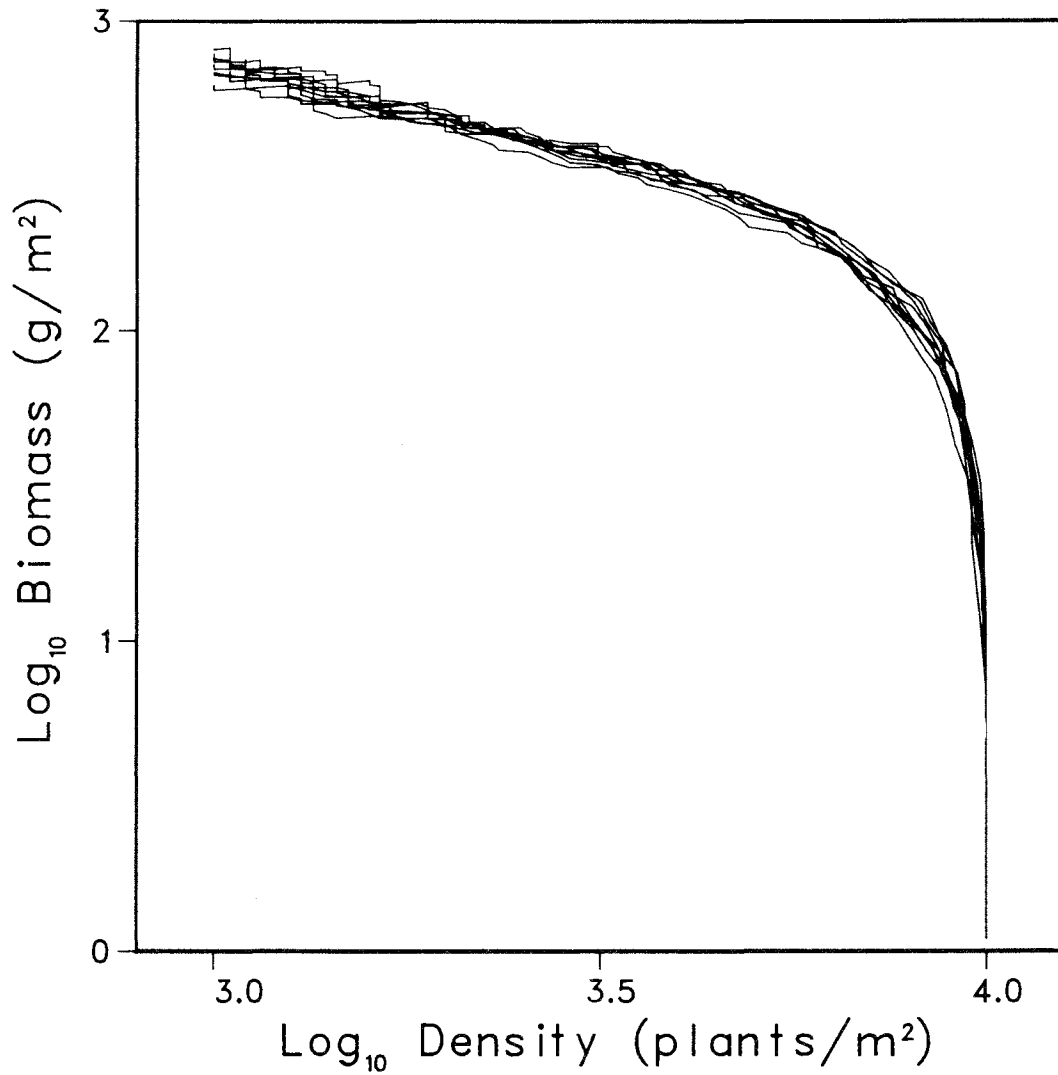


Figure 3.2. Variations in the self-thinning trajectory due to stochastic factors in the simulation model. The ten runs all used the reference parameter set (Table 3.2) and differed only in the initial plant locations and weights.

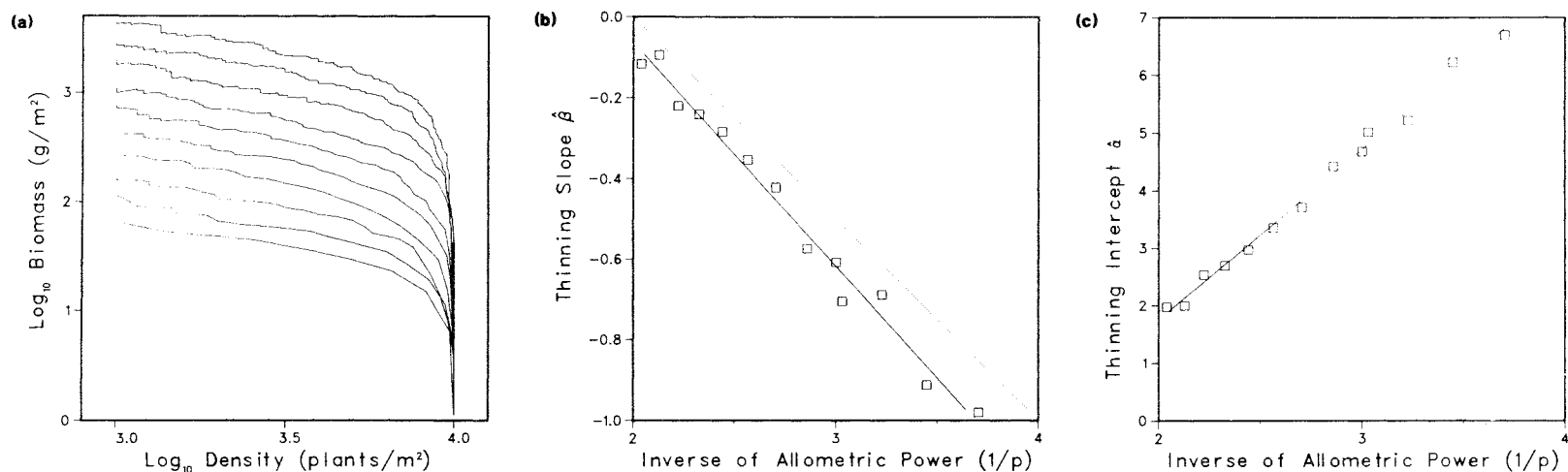


Figure 3.3. Effect of the allometric power, p , on the self-thinning line. (a) shows 13 simulations with p values between 0.27 (highest curve) and 0.49 (lowest curve). In (b), the fitted thinning slopes, $\hat{\beta}$, (Table 3.4) are plotted against $(1/p)$. The solid regression line is $\hat{\beta} = -0.555(1/p) + 1.05$ ($r^2 = 0.98$, $P < 0.0001$, 95% CI for slope = $[-0.604, -0.506]$, 95% CI for intercept = $[0.91, 1.18]$). The dotted line is $\beta = -0.5(1/p) + 1$ (Chapter 2). (c) plots the thinning intercept, $\hat{\alpha}$, against $(1/p)$ and the regression line $\hat{\alpha} = 2.97(1/p) - 4.18$ ($r^2 = 0.99$, $P < 0.0001$, 95% CI for slope = $[2.80, 3.13]$, 95% CI for intercept = $[-4.65, -3.72]$).

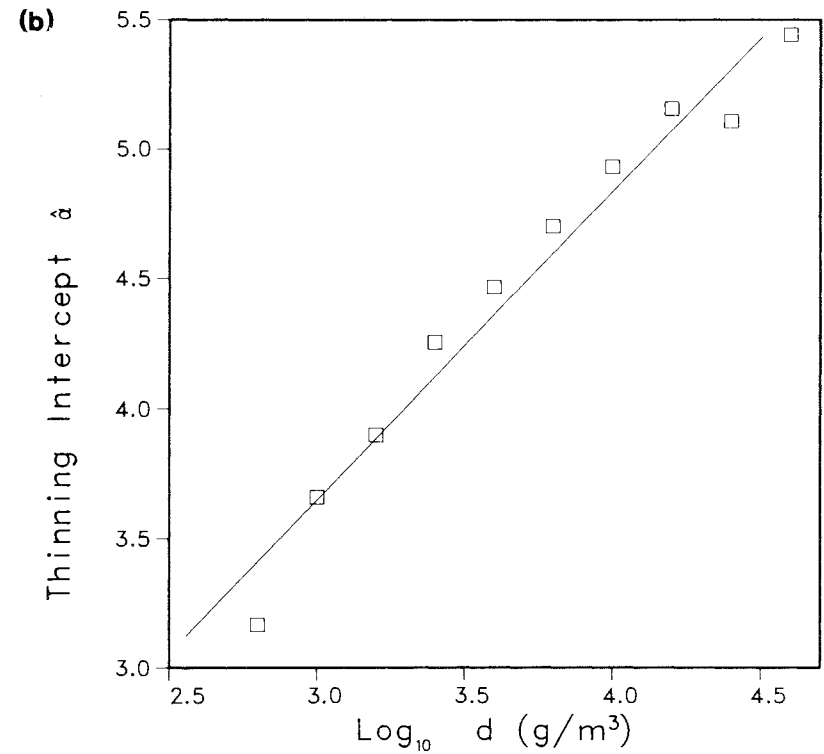
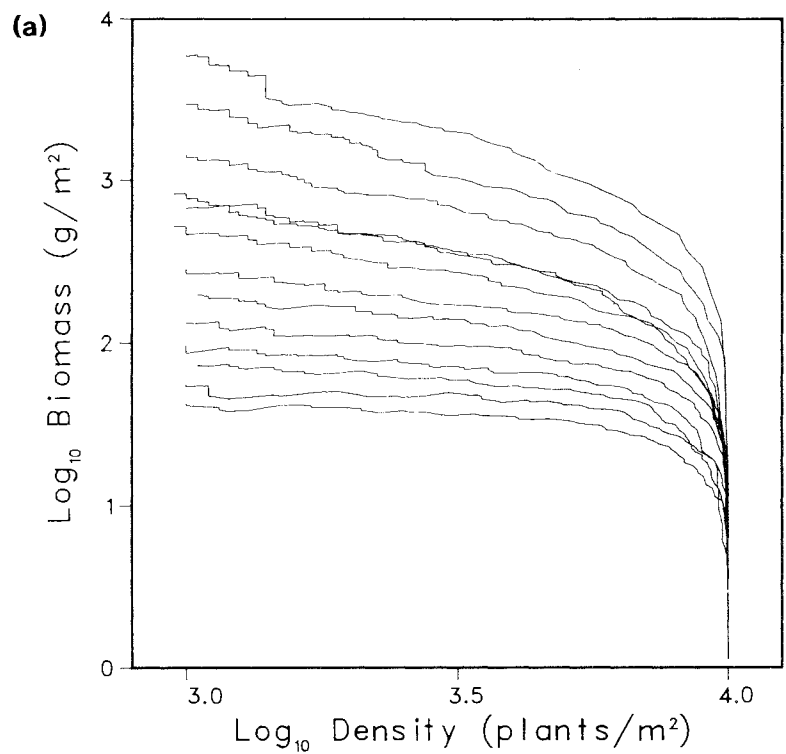


Figure 3.4. Effect of the density of biomass in occupied space, d , on the self-thinning line. (a) shows trajectories for ten values of d between 631 (lowest curve) and 39810 (highest curve), while (b) plots the fitted thinning intercept, $\hat{\alpha}$, (Table 3.4) against $\log d$. The regression line is $\alpha = 1.19 \log d + 0.09$ ($r^2 = 0.97$, $P < 0.0001$).

The relationship between $\hat{\alpha}$ and $\log d$ is apparently linear (Figure 3.4b), as predicted in Chapter 2. The regression equation is $\hat{\alpha} = 1.186 \log d + 0.0891$ ($r^2 = 0.97$, $P < 0.0001$). Thinning slope was not affected by d , as shown by the low correlation between d and $\hat{\beta}$ ($r_s = -0.49$, $P = 0.15$) and by the fact the range and CV of $\hat{\beta}$ in the experimental group (0.17 and 9.2%, respectively) were not greater than the corresponding values for the control group (0.18 and 10.2%).

The thinning lines are more widely spread among the six simulations using the different competition algorithms (Figure 3.5) than among control group simulations, indicating that thinning line position is affected by this algorithm. Spearman correlations could not be calculated for this simulation experiment because the competition algorithm is a nominal variable that can not be ranked, but further support does come from a comparison of the ranges of variation of $\hat{\alpha}_{3.35}$. This range is eight times larger among the experimental simulations than in the control group, and the CV is almost ten times larger. A similar comparison of $\hat{\alpha}$ values seems to contradict this conclusion; however, when the interpretations $\hat{\alpha}_{3.35}$ and $\hat{\alpha}$ differ, $\hat{\alpha}_{3.35}$ is the more reliable measure of thinning line position because it lies in the middle of the range of the data while $\hat{\alpha}$ is an extrapolation of the regression lines well outside the data (Sokal and Rohlf 1981). A lack of effect of the competition algorithm on thinning slope is indicated by the similar means and ranges for $\hat{\beta}$ in the control and experimental groups.

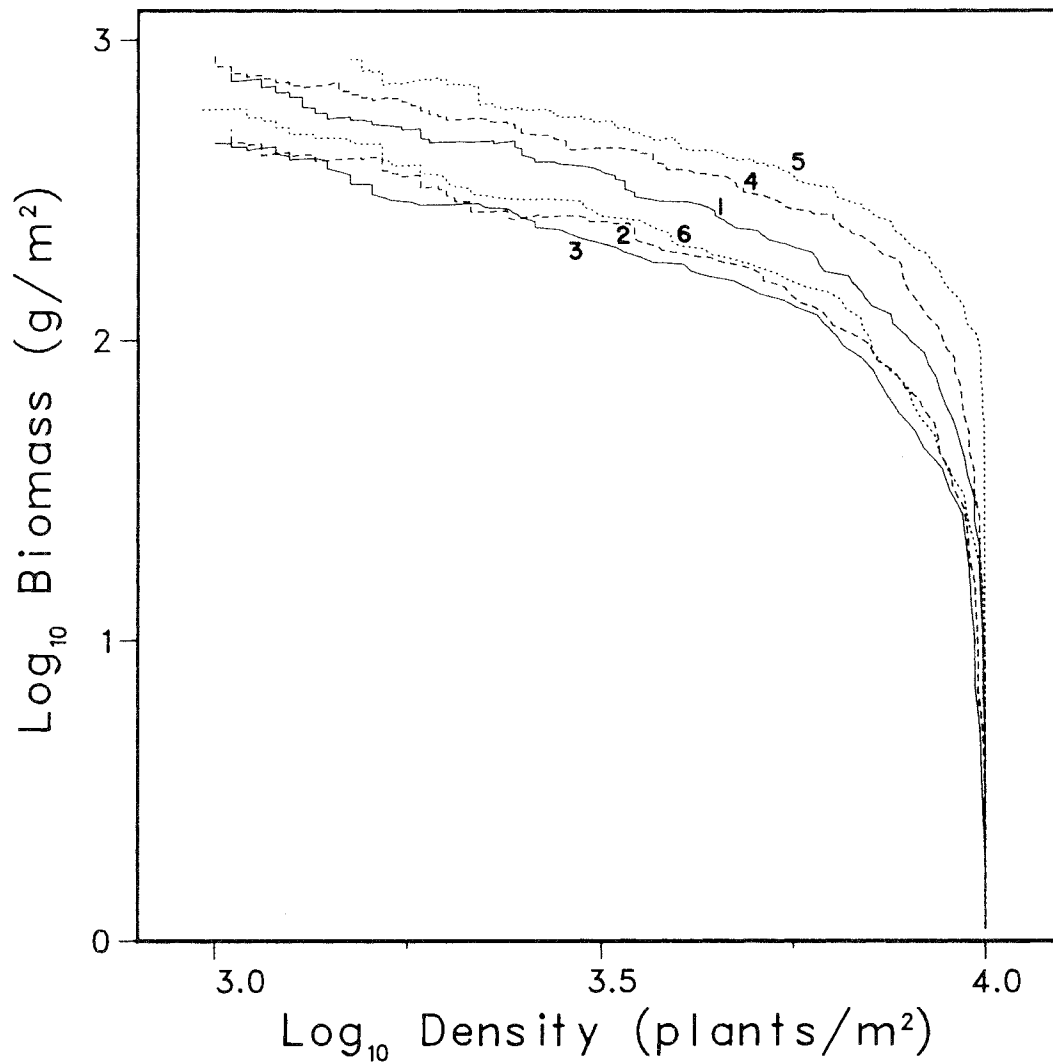


Figure 3.5. Effect of the competition algorithm on the self-thinning line. Curves for six simulations are marked with competition algorithm identification numbers (Table 3.1).

The assimilation rate, g_1 , had no effect on the self-thinning trajectory, as indicated by similarity of Figure 3.6a to Figure 3.2, the near equality of the ranges and CVs of the thinning line descriptors to the same statistics for the control group, and the low Spearman correlations of g_1 with the thinning line descriptors.

Metabolic cost parameters b and q were likewise unimportant in positioning the self-thinning line (Figure 3.6b). In this simulation experiment, the power q relating maintenance cost to weight was varied from 0.5 to 3.5. Simultaneously, the parameter b was adjusted so that the initial maintenance cost (second term of equation 3.1) for a plant of weight \bar{w}_0 (10^{-4} g) was constant across the seven simulations. However, as growth increased average weight above \bar{w}_0 , differences in maintenance cost due to differences in q became important. Interpretation of this simulation experiment is complicated by the two trajectories that are decreasing in both biomass and density by the end of the simulation. The explanation is that maintenance costs affect the maximum possible size for a model plant, which can be calculated by setting equation 3.6 equal to zero and solving for w_{\max} to obtain

$$w_{\max} = [g_1 c_1 / b]^{1/(q-2p)} . \quad (3.10)$$

The differences in q across the simulations led to differences in w_{\max} and this limitation became important in two simulations; however, all the simulations followed a common path through the log B-log N plane until the two populations became limited by

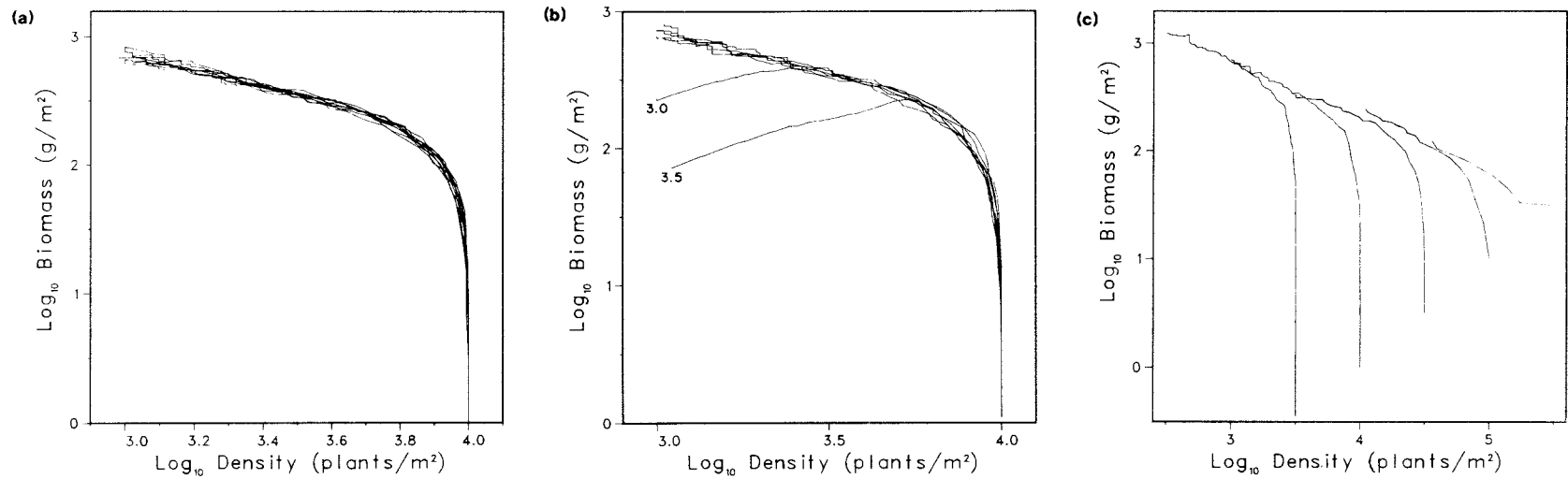


Figure 3.6. Simulations for three parameters that did not affect the self-thinning line. In (a) parameter g_1 was varied from 10 to 50 $\text{g}/\text{m}^2/\text{time unit}$ across ten simulations. (b) was generated by using six values of parameter q between 0.5 and 3.0. Two curves are marked with the associated values of q (Table 3.4). (c) shows thinning trajectories for five simulations started at initial densities of 3160, 10000, 31600, 100000, and 316000 plants/m^2 .

w_{\max} and diverged sharply from the common path. Before fitting the thinning line in the $q = 3.0$ simulation, data points with $\log N$ values below 3.4 were eliminated. No thinning line was fitted to the $q = 3.5$ simulation since the maximum weight limitation took effect before the linear portion of the thinning trajectory was established. The visually evident lack of effect of q on the thinning line estimates is further supported by the failure of $\hat{\beta}$, $\hat{\alpha}$, and $\hat{\alpha}_{3.35}$ to exceed the limits established in the control group and by the low Spearman correlations between q and the thinning line descriptors.

Variations in initial density also had no effect on the position of the self-thinning line (Figure 3.6c). The five different initial densities were created by placing 200 plants on different sized plots. This was the only way to vary initial density over a large range because model limitations precluded direct manipulations of the initial number of plants. The maximum initial number was 600 and simulations were stopped when less than 20 plants remained because the thinning trajectory made undesirably sharp jumps at low population sizes. Although the resulting trajectories start from different points in the plane, all converge on the same thinning line, at least within the limits of the stochastic variation seen in Figure 3.2. A more quantitative analysis was not possible because there was no common range of linear behavior over which to fit self-thinning lines, so this simulation experiment is not included in Tables 3.3 and 3.4.

Discussion

This analysis has identified only one parameter, the power p relating area occupied to individual weight, that affected the slope of the model self-thinning line. Three parameters affected thinning line position: p ; the density of biomass in occupied space, d ; and the competition algorithm. These results agree with the simpler model of Chapter 2 and together suggest that the regularities of self-thinning can be explained by the shape-dependent occupation of space. The linearity and slope of the self-thinning line are determined by the power relationship relating space occupied to plant size, and the thinning intercept is related to at least two additional factors. The implications of these results have already been discussed in Chapter 2. The possibility that the conclusions of Chapter 2 were biased due to an over-simplified, spatially homogenous model can now be discarded because the detailed representation of individual size, location, and competitive interactions in the simulation model led to the same results. Although spatially averaged models are not useful for many applications in plant ecology (Schaffer and Leigh 1976), they are appropriate tools for investigating self-thinning because of the unusual degree of spatial uniformity that is present in even-aged monospecific stands.

Model parameters representing resource availability and utilization efficiency (maximum assimilation rate g_1) and

metabolic costs (q and b) affected only the rate of self-thinning, not the slope or position of the thinning line. Initial density also did not affect the thinning line. However, the model did not allow the parameters of individual shape and density, p and d , to vary in response to these important environmental factors. Real plants can respond to environmental limitations by varying their shapes (Hutchings 1975, Harper 1977) and canopy densities (Lonsdale and Watkinson 1983a), and density stress can cause permanent alterations in plant geometry (Peet and Christensen 1980). The exact responses would vary among species. Environmental factors could, then, induce changes in the self-thinning line, not because the factors are key determinants of the thinning line, rather because they affect the thinning line indirectly by altering the growth parameters of the plants.

The important effects of the competition algorithm on the rate of self-thinning and the position of the thinning line are significant new results of this analysis. The competition algorithm is related to the allowable overlap between plants (Chapter 2) and to the degree of asymmetry in competitive interactions, so measures of these factors should be related to the self-thinning line. This prediction is tested in Chapters 5 and 6, where the relationships of shade tolerance with thinning slope and intercept are considered.

The persistent effect of the stochastic initial conditions seen in Figure 3.2 is also interesting. Since all parameters were held constant, these differences could only be attributed to random variations in the initial weight distributions and initial plant

locations. This result suggests that even if all other sources of variation could be eliminated from thinning experiments, observed self-thinning lines could still differ in position because of these stochastic factors.

Some results of this analysis are relevant to other theories about the causes of the self-thinning rule. The unimportance of metabolic parameters b and q in positioning the self-thinning line argues against the hypothesis that the self-thinning rule derives from a $2/3$ power relationship between metabolic costs and plant weight (Jones 1982), and against an important role in fixing the self-thinning slope for the fraction of assimilate devoted to maintenance (Pickard 1983). The simulations of Figure 3.5 indirectly address another theory that the $-3/2$ exponent of the \bar{w} - N relationship is maintained during thinning by mutual adjustment of plant allometry and stand structure (the distribution of individual sizes--Mohler et al. 1978). Figure 3.7 shows how the frequency distributions of individual plant weight change with time for the four simulations generated by competition algorithms 1, 2, 3, and 5. These time plots of the first four moments of the weight distribution (average, coefficient of variation, skewness, and kurtosis) show that the four competition algorithms lead to widely different dynamics of stand structure. If the mutual adjustment hypothesis is correct, thinning slopes should also be different since stand structure varies without any possibility of compensatory adjustments in plant allometry (parameter p was $1/3$ for all four

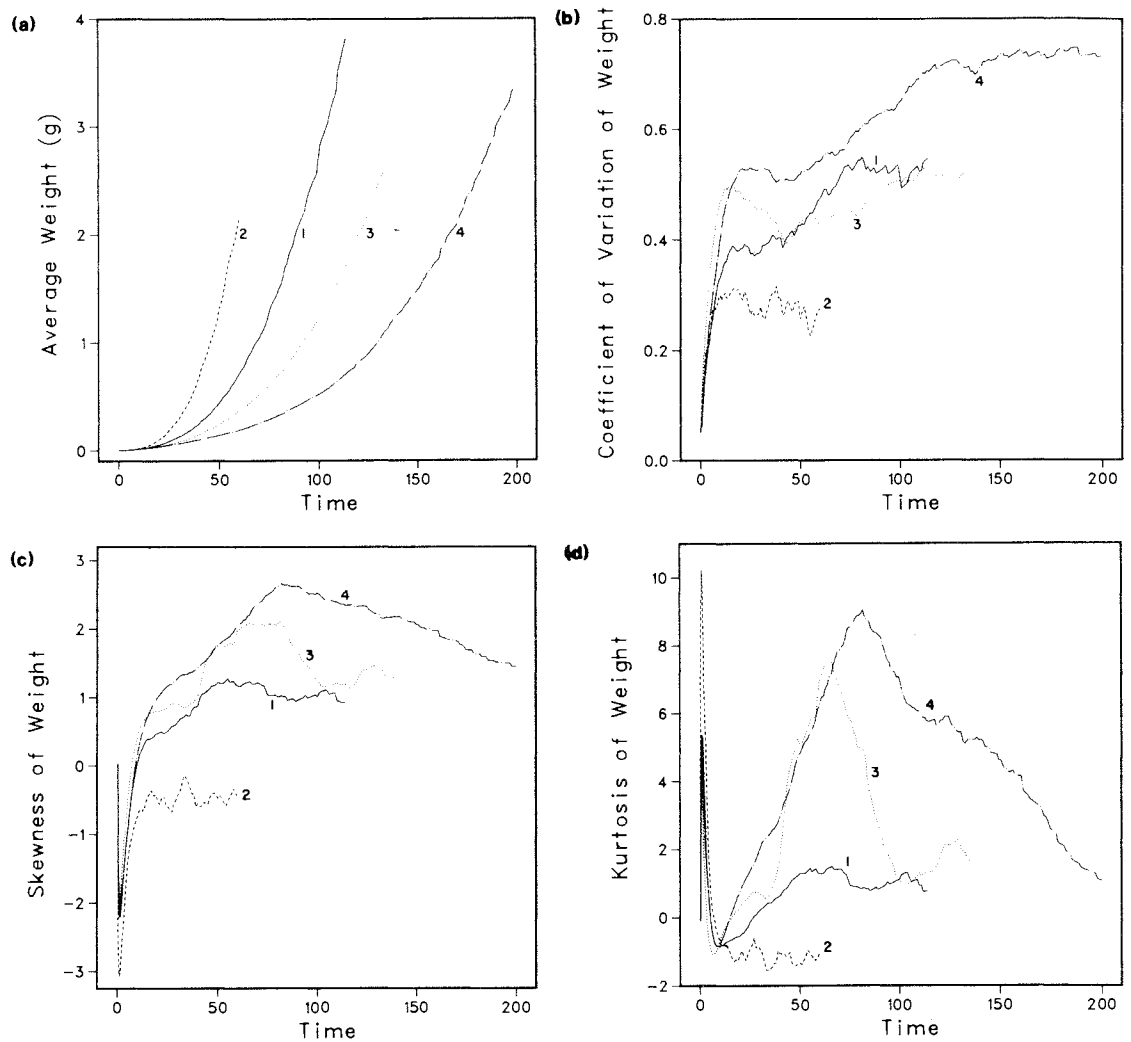


Figure 3.7. Dynamics of the weight distributions in four simulations with different competition algorithms. Algorithm numbers (Table 3.1) were 1 (solid line), 2 (dashed line), 3 (dotted line), and 4 (chain-dotted line). The mean, coefficient of variation, skewness, and kurtosis of each of the weight distributions are shown in (a) through (d). Methods of calculation are given in Sokal and Rohlf (1981).

simulations). However, if plant allometry sets the thinning slope, the simulations should give the same thinning slope despite the differences in competitive regime and size distribution dynamics. Since thinning slope did not vary among the four simulations, the allometric hypothesis is supported and the mutual adjustment hypothesis is not.

CHAPTER 4

SOME PROBLEMS IN TESTING THE SELF-THINNING RULE

Introduction

Many self-thinning lines with slopes near $\gamma = -3/2$ have now been reported, and their sheer number is considered strong evidence for the self-thinning rule, or even a self-thinning law (see references in Hutchings 1983). However, an analysis of size-density data is not simply a matter of regressing $\log \bar{w}$ against $\log N$ and so demonstrating the self-thinning rule. Some important analytical difficulties must be fully discussed before the large body of evidence is embraced as convincing proof for the rule. The principal problem areas are (1) the data selected to test the hypothesis, (2) the points used to estimate a thinning line, (3) the curve fitting methods used, (4) the choice between the $\log \bar{w}$ - $\log N$ or $\log B$ - $\log N$ formulations of the rule, and (5) the conclusions drawn from the results. Recommendations for resolving some difficulties are presented here, and the implications for acceptance of the self-thinning rule are discussed.

Selecting Test Data

Many data sets have been reported to exhibit a linear relationship between $\log \bar{w}$ and $\log N$ with a slope near $\gamma = -3/2$, but it is usually easy to find evidence for a hypothesis, regardless of whether or not it is generally true. Therefore, the mere

existence of such evidence does not verify the hypothesis. Rigorous verification instead comes from failure of the opposite endeavor, to find evidence that contradicts or falsifies the hypothesis (Popper 1963). The emphasis on compiling corroborative evidence for the thinning rule has diverted attention from data that do not conform. Violations of the rule have been discussed only for shoot populations of clonal perennials (Hutchings 1979) and for thinning under very low illumination (Westoby and Howell 1982, Lonsdale and Watkinson 1982), but there are other violations besides these special cases, such as thinning slopes of $\hat{\gamma} = -2.59$ and -4.5 for tropical trees Shorea robusta and Tectona grandis (O'Neill and DeAngelis 1981), $\hat{\gamma} = -1.2$ the temperate tree Abies balsamea (Sprugel 1984), and $\hat{\gamma} = -3.2$ for seedling populations of the woodland herb Allium ursinum (Ernst 1979).

Information contradicting the self-thinning rule has been missed even in the very sources from which supporting evidence has been drawn. For example, data for one stand of Pinus strobus (Spurr et al. 1957) have been repeatedly cited in self-thinning studies (Hozumi 1977, 1980, Hara 1984), and a self-thinning slope of $\hat{\gamma} = -1.7$ has been fit (White 1980). However, the report of Spurr et al. also presented data for a second stand which gives a thinning slope of $\hat{\gamma} = -2.11$ (Table A.2). This second, unreported stand contradicts the self-thinning rule in two ways: the thinning slope is quite different from the predicted value, and both the slope and intercept change from stand to stand. A second example refers to a yield table for Pinus ponderosa (Meyer 1938) reported to give a

thinning line of $\log \bar{w} = -1.33 \log N + 4.06$ (White 1980). However, the $\log B$ - $\log N$ thinning plot for the complete yield table (Figure 4.1a) shows that 13 thinning lines could be fit since information is given for 13 values of site index, a general measure of site including soil composition, fertility, slope, aspect, and climate (Bruce and Schumacher 1950). The existence of the twelve unreported thinning lines contradicts two tenets of the self-thinning rule: the thinning line is not independent of site quality and the thinning intercepts are not species constants. The data from some yield tables even give different thinning slopes for different site indexes, as shown in Figure 4.1b for Sequoia sempervirens (Lindquist and Palley 1963).

Editing Data Sets

A second major problem in testing the self-thinning rule arises because the thinning line is an asymptotic constraint approached only as stands become sufficiently crowded. To estimate the slope and position of a thinning line using linear statistics, data points from populations that are not limited by the hypothesized linear constraint must be eliminated. These would include points from young populations that have not yet reached the thinning line, older stands understocked because of poor establishment or density-independent mortality, and senescent stands. Failure to eliminate such points will bias the thinning line estimates (Mohler et al. 1978), but when the data are confounded by biological variability and measurement errors, recognition and elimination of

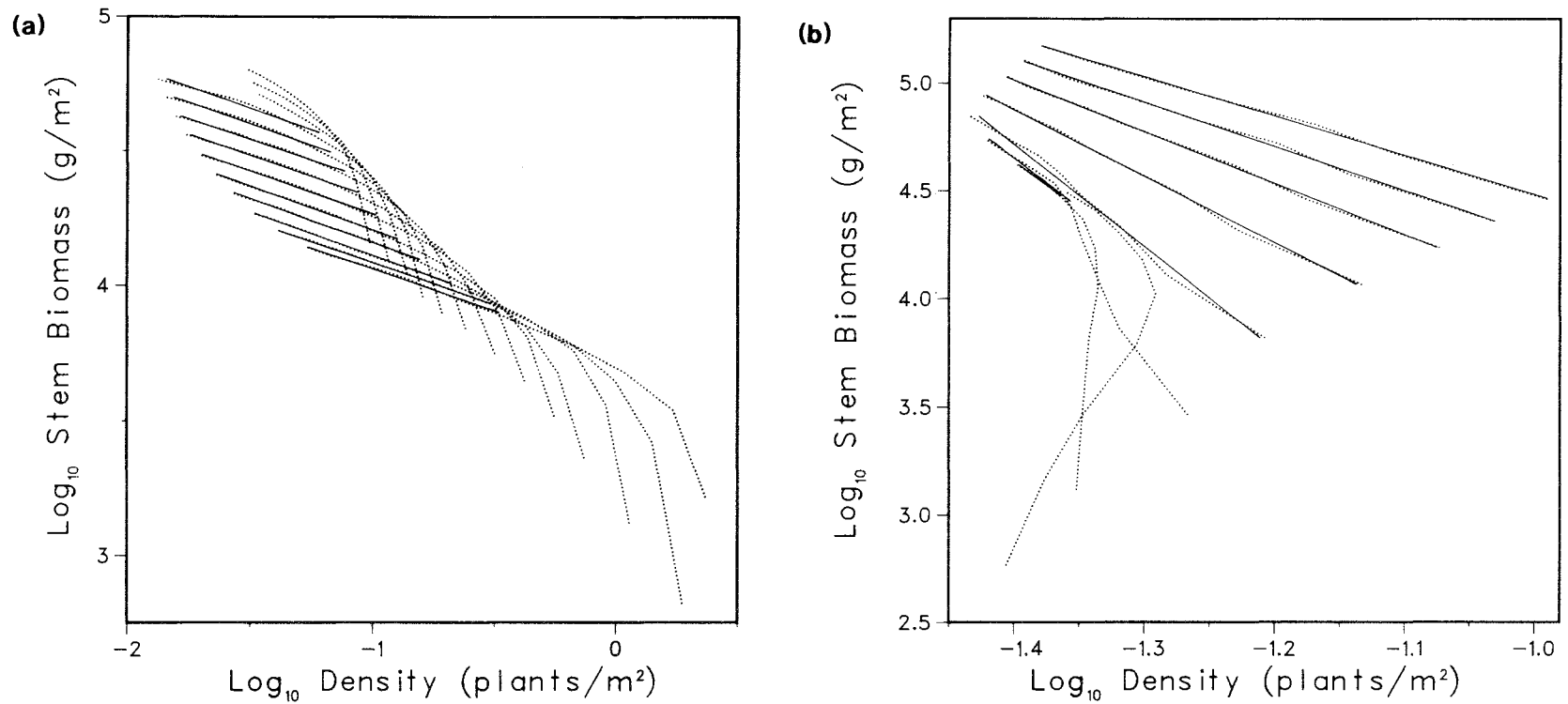


Figure 4.1. Two forestry yield tables showing variation in thinning line parameters with site index. Dotted lines connect data points and solid lines are PCA thinning lines. (a) shows data for *Pinus ponderosa* (Meyer 1938). Thinning slopes, $\hat{\beta}$, for ten site indexes were near -0.31 (between -0.307 and -0.326), but intercepts ranged from 3.75 to 4.18. (b) shows data for *Sequoia sempervirens* (Lindquist and Palley 1963). Thinning slopes for six site indexes ranged from -4.15 to -1.81 while intercepts ranged from -1.93 to 2.67. Tables B.1 and B.2 give additional information.

spurious points is difficult. Since there is no a priori estimate of the thinning line position, decisions to eliminate data points must be made a posteriori (Westoby and Howell 1982). This is true even if detailed field notes (Mohler et al. 1978) or mortality curves (Hutchings and Budd 1981a) are available to aid the process. With such a posteriori manipulations, no thinning analysis can be done in a strictly objective way. Figure 4.2 presents three data sets that illustrate these problems. Each plot shows how the slope, intercept, r^2 , significance level, and confidence interval all change with the points used to fit the thinning line (Table 4.1). The results are very sensitive to certain points, yet there is no objective way to decide whether or not to include those points.

The sensitivity of thinning line parameters to the choice of data points also has important statistical implications. The uncertainties about including or excluding some points should be counted in forming confidence intervals and performing tests of significance. However, existing statistical methods do not take such uncertainties into account, so estimated r^2 values are too high and confidence intervals are too narrow.

Some data sets show more than one region of linear behavior and so present the analyst with still another subjective decision: Which linear region is relevant to the self-thinning rule? Figure 4.3 presents a yield table for Populus deltoides (Williamson 1913) that illustrates this problem. White (1980) fit the thinning line $\log \bar{w} = -1.8 \log N + 3.08$ through the data for ages 7 to 15, while

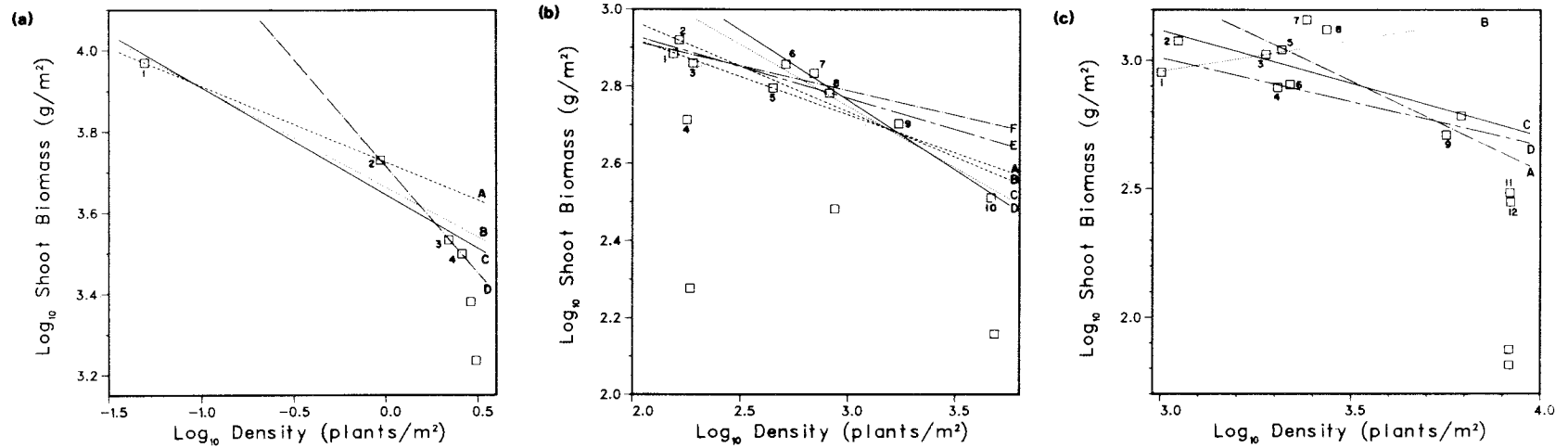


Figure 4.2. Three examples of the sensitivity of self-thinning line parameters to the points chosen for analysis. In each plot, several thinning lines (capital letters) are fitted to different combinations of points (numbers) as indicated in Table 4.1. Data in (a), (b), and (c) are for *Populus tremuloides* (Pollard 1971, 1972), *Triticum* sp. (Puckridge and Donald 1967, White and Harper 1970), and *Tagetes patula* (Ford 1975).

Table 4.1. Three Examples of the Sensitivity of the Fitted Self-thinning Line to the Points Chosen for Analysis.

| Figure ^a | Line ^b | Points Included ^c | r ² | pd | PCA Thinning Line ^e | | |
|---------------------|-------------------|------------------------------|----------------|--------|--------------------------------|----------------|-----------|
| | | | | | Slope | | Intercept |
| | | | | | β | 95% CI | |
| 4.5a | A | 1-2 | 1.00 | | -0.19 | | 3.73 |
| | B | 1-3 | 0.94 | 0.16 | -0.25 | | 3.66 |
| | C | 1-4 | 0.94* | 0.030 | -0.26 | [-0.48, -0.07] | 3.65 |
| | D | 2-4 | 0.99* | 0.010 | -0.53 | [-0.64, -0.42] | 3.72 |
| 4.5b | A | 1-10 | 0.63* | 0.0061 | -0.20 | [-0.33, -0.08] | 3.32 |
| | B | 1-3,5-10 | 0.86* | 0.0003 | -0.24 | [-0.32, -0.15] | 3.43 |
| | C | 5-10 | 0.91* | 0.0030 | -0.31 | [-0.46, -0.18] | 3.70 |
| | D | 6-10 | 0.98* | 0.0008 | -0.36 | [-0.45, -0.28] | 3.84 |
| | E | 1-3,5-9 | 0.80* | 0.0027 | -0.16 | [-0.25, -0.08] | 3.26 |
| | F | 1-3,5-8 | 0.66* | 0.027 | -0.13 | [-0.24, -0.02] | 3.17 |
| 4.5c | A | 1-10 | 0.34 | 0.075 | -0.41 | | 4.36 |
| | B | 1-8 | 0.06 | 0.54 | +0.24 | | 2.22 |
| | C | 3-10 | 0.48 | 0.056 | -0.70 | | 5.38 |
| | D | 4,6,9,10 | 0.84 | 0.079 | -0.35 | | 4.03 |

^aSpecies names and references are given in the legend of Figure 4.2.

^bThese letters label the fitted lines in Figure 4.2.

^cThe numbers of data points in Figure 4.2 used to fit the thinning line.

^dThe statistical significance of the log B-log N correlation.

^eThe method of fitting the thinning line by principal component analysis is discussed in Chapter 5.

*Significant at the 95% confidence level ($P \leq 0.05$).

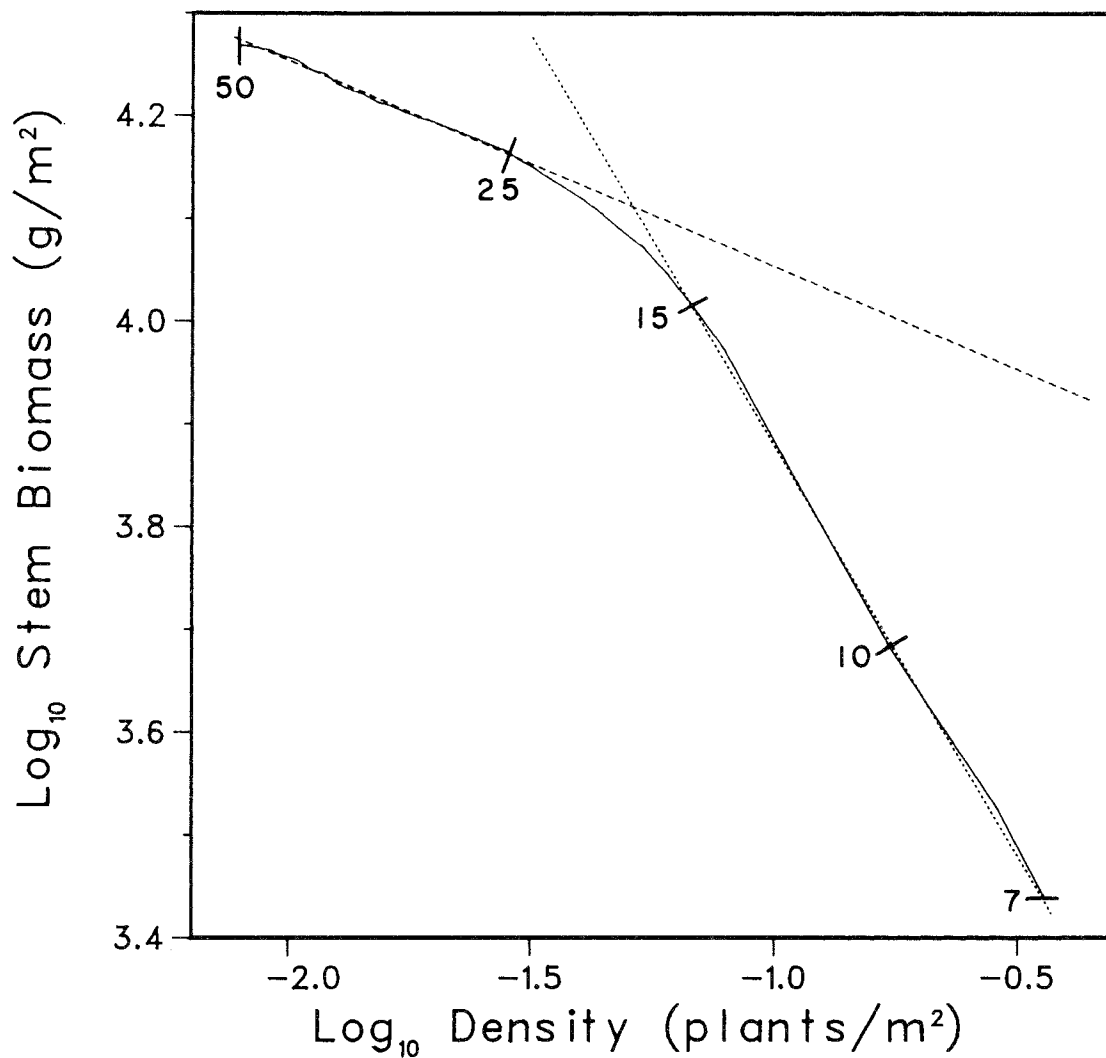


Figure 4.3. Example of a data set with two regions of linear behavior. White (1980) fit the dotted line $\log \bar{w} = -1.80 \log N + 3.08$ to yield table data (solid line) for juvenile stands (7-15 years old) of *Populus deltoides* (Williamson 1913). Older stands follow the dashed line $\log B = -0.20 \log N + 3.85$ fit to 25-50 year old stands (Table B.2)

the present study has fit a line of shallower slope, $\log B = -0.20 \log N + 3.85$, to the data for ages 25 through 50. The line fit by White may be more typical of the steep ascent of juvenile populations through the $\log B$ - $\log N$ plane, while the second line may represent the self-thinning behavior of more mature stands.

Fitting the Self-thinning Line

Most self-thinning lines have been estimated by linear regression of $\log \bar{w}$ against $\log N$, but regression is inappropriate for thinning data because $\log N$ is not a good independent variable, that is, it is neither measured without error nor controlled by the experimenter. Although principal component analysis (PCA--Mohler et al. 1978) and geometric mean regression (GMR--Gorham 1979) have been proposed as more appropriate fitting methods, the true self-thinning line is actually not estimable. In general, the slope, $\hat{\beta}_{yx}$, of a linear bivariate relationship for Y in terms of X is given by the linear structural relationship (Madansky 1959, Moran 1971, Jolicoeur 1975),

$$\hat{\beta}_{yx} = \frac{s_{yy} - \lambda s_{xx} + \left[(s_{yy} - \lambda s_{xx})^2 + 4 \lambda s_{xy}^2 \right]^{1/2}}{2 s_{xy}}, \quad (4.1)$$

where s_{xx} , s_{yy} , and s_{xy} are sums of squares and cross products corrected for the mean and λ is the ratio of the error variance in Y to the error variance in X . These error variances are the

residuals around the true linear relationship between Y and X, not the total sample variances. Particular values of λ give the standard methods as special cases of this general equation: $\lambda = \infty$ (no error in X) gives $\hat{\beta}_{yx} = s_{xy}/s_{xx}$, the regression of Y against X; $\lambda = 0$ (no error in Y) gives $\hat{\beta}_{yx} = s_{yy}/s_{xy}$, as obtained from regressing X against Y; $\lambda = 1$ (equal marginal variances of X and Y) gives the PCA solution; and $\lambda = s_{yy}/s_{xx}$ (marginal variances in the same ratio as the total sample variances) gives the GMR solution, $\hat{\beta}_{yx} = \text{sign}(s_{xy}) s_{yy}/s_{xx}$. If the relationship between X and Y is strongly linear (high r^2), then all solutions are similar, but as the association becomes less strict (lower r^2), the discrepancies among the solutions increase and results become more sensitive to λ . Figure 4.4 shows these four particular solutions for a typical thinning data set (Mohler et al. 1978). Although this data set showed a very significant log B-log N relationship ($r^2 = 0.40$, $P < 0.0001$), the four solutions ranged from $\hat{\beta} = -0.34$ to -0.87 , and the regression of log B against log N gave -0.34 while PCA gave -0.41 .

Two sources of variation are reflected by λ : measurement errors, which can be estimated by replication, and natural biological variability, which can not be estimated (Ricker 1973, 1975). Since λ can not be known, the true solution of equation 4.1 is unestimable (Ricker 1975, Sprent and Dolby 1980) and the slope of the self-thinning line must be based on some assumed value of λ . For most self-thinning data, there is no basis to

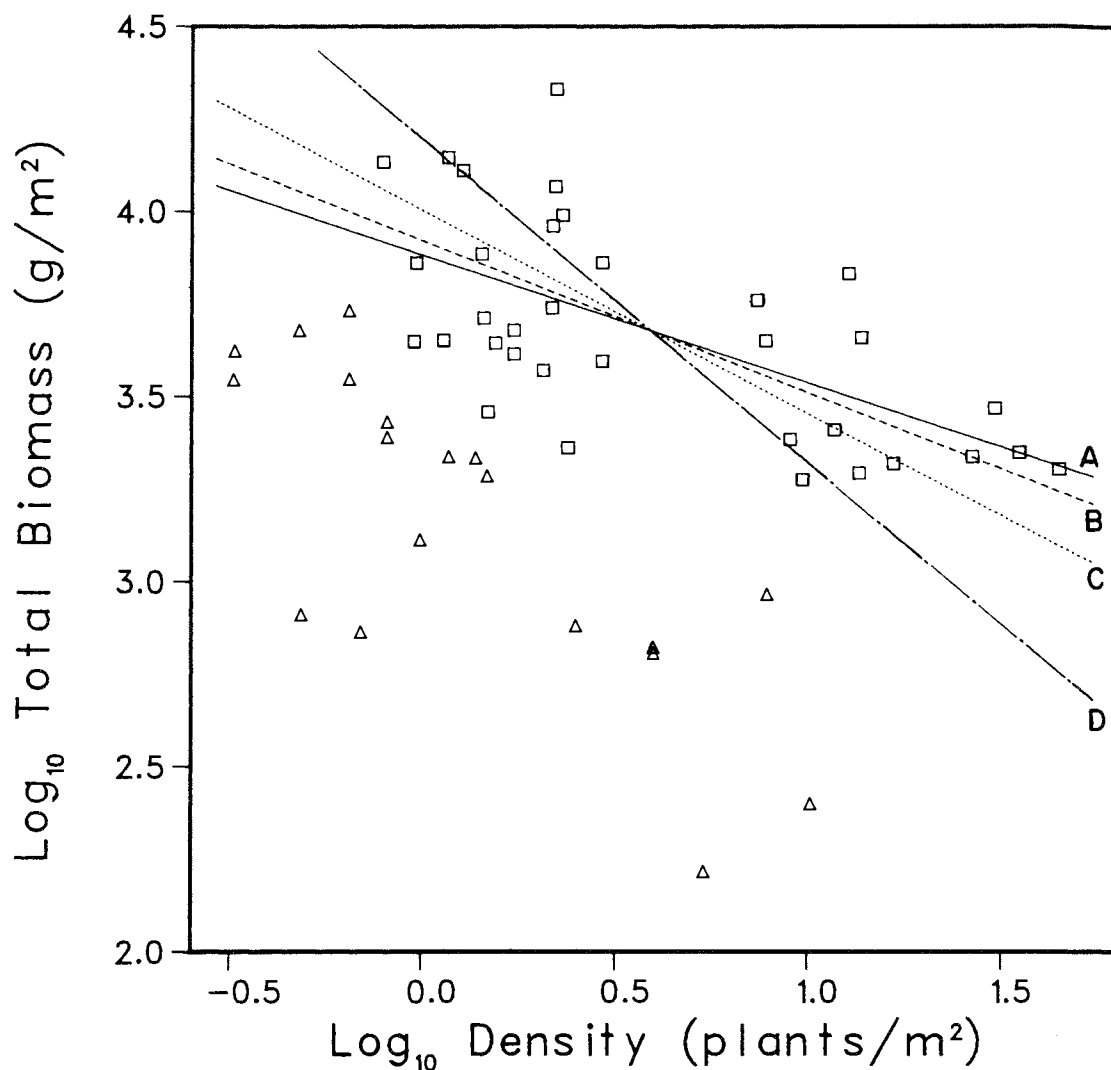


Figure 4.4. Thinning lines fit to one data set by four methods. The data are for *Prunus pensylvanica* (Mohler et al. 1978). Lines were fit to the 34 square points by regression of log B on log N, regression of log N on log B, geometric mean regression, and principal components analysis (lines A, D, C, and B, respectively). Equations for the four lines were, respectively, $\log B = -0.34 \log N + 3.88$, $\log B = -0.87 \log N + 4.19$, $\log B = -0.55 \log N + 4.00$, and $\log B = -0.41 \log N + 3.92$, while confidence intervals for the slopes were $[-0.50, -0.19]$, $[-1.58, -0.60]$, $[-0.72, -0.42]$, and $[-0.61, -0.23]$. For all four lines, $r^2 = 0.40$ and $P < 0.0001$.

assume the marginal variation of $\log N$ is less than that of $\log B$ (or vice versa), so the most reasonable assumption is that the two marginal variances are approximately equal, giving $\lambda = 1$ and leading to the PCA solution of equation 4.1. Regression analysis implicitly assumes that one of the variables is error free and λ takes one of the extreme possible values $\lambda = 0$ and $\lambda = \infty$ (Moran 1971). Since this extreme assumption is clearly untrue for self-thinning data, many reported thinning lines estimated by regression analysis are potentially in error.

The use of PCA has created yet another statistical problem: many studies now report the percentage of variance explained (%EV) by the first principal component (PC) rather than the correlation coefficient, r , or r^2 . Unlike r^2 , which ranges from 0 to 1, %EV ranges from 0.5 to 1 because the first PC always explains at least 50% of the total variation, even if the two variables are completely uncorrelated. Therefore, %EV values are always higher than r^2 values. This has been misinterpreted by some authors as an indication that PCA is more reliable than regression. Actually, the exact method of fitting a straight line (Y-X regression, X-Y regression, PCA, or GMR) is irrelevant to the calculation and interpretation of correlations or coefficients of determination since these measure the strength of linear association rather than the position of any particular line in the plane. The reported measure of association should always be r or r^2 , regardless of the fitting method used (Sprent and Dolby 1980).

Choosing the Best Mathematical Representation

The recommended use of PCA focuses attention on another question: Should the thinning rule be tested by relating $\log \bar{w}$ to $\log N$ or by relating $\log B$ to $\log N$? The two choices are mathematically equivalent (Chapter 1), and when the regression of $\log B$ against $\log N$ is compared to the regression of $\log \bar{w}$ on $\log N$ for a set of data, the slopes differ by exactly one ($\beta = \gamma + 1$) and the confidence intervals have identical widths. However, neither of these conditions holds when $\log \bar{w}$ - $\log N$ PCA is compared to $\log B$ - $\log N$ PCA, so one CI may include the predicted slope of the self-thinning rule while the other CI does not. Although mathematically equivalent, the $\log \bar{w}$ - $\log N$ and $\log B$ - $\log N$ formulations of self-thinning rule are not statistically equivalent when appropriate curve fitting methods are used, so an explicit decision is required: Which formulation is more appropriate for testing the self-thinning rule?

The $\log B$ - $\log N$ formulation is the correct choice because the $\log \bar{w}$ - $\log N$ alternative suffers from two major limitations. Changes in average weight can be misleading because average weight increases when small individuals die, even if the survivors do not actually gain weight (Westoby and Brown 1980). Average size increases through two processes--growth of living plants and elimination of small plants--so that the average size of the stand increases more rapidly than the sizes of individuals composing it (Bruce and

Schumacher 1950). Attempts to relate $\log \bar{w}$ to $\log N$ are actually correlating some combination of growth and mortality with mortality, so the results are difficult to interpret. However, total stand biomass only increases through growth, so a correlation of $\log B$ with $\log N$ directly addresses the growth-mortality relationship and focuses attention on the extent to which mortality permits a more than compensatory increase in the size of the survivors.

The second shortcoming of the $\log \bar{w}$ - $\log N$ analysis is more serious and damaging to the case for the self-thinning rule: the analysis is statistically invalid, gives biased results, and leads to unjustified conclusions. To understand why, consider the methods used to measure plant biomass. Stand biomass is often measured directly by harvesting all the plants in a stand and weighing them as a single group. Even when each individual is weighed (or individual weights estimated from a relationship between weight and some plant dimension) stand biomass is still estimated directly as the sum of the individual weights. Average weight is then derived from the original stand measurements by dividing the biomass by the density. In general, there are "serious drawbacks" in analyzing such derived ratios (Sokal and Rohlf 1981), but these problems are particularly acute when the ratio is correlated with one of the variables from which it was derived. Such an analysis gives correlations that have been variously called "spurious" (Pearson 1897, as cited in Snedecor and Cochran 1956), "artificial" (Riggs 1963), and "forced" (Gold 1977).

A high correlation between $\log \bar{w}$ and $\log N$ is both unsurprising and meaningless because $\log N$ is used to calculate $\log \bar{w}$. This is most easily seen when the original measurements of $\log B$ and $\log N$ are unrelated so that the sample correlation coefficient is low and not statistically significant. After deriving average weight from $\log \bar{w} = \log B - \log N$, $\log \bar{w}$ is a function of $\log N$ even though $\log B$ was not. The variance of $\log \bar{w}$ is $\text{Var}(\log B) + \text{Var}(\log N) - 2 \text{Cov}(\log B, \log N)$ (Snedecor and Cochran 1956), which reduces to $\text{Var}(\log B) + \text{Var}(\log N)$ because the covariance of unrelated variables is zero. Thus, the variance of $\log \bar{w}$ is higher than the variance of $\log B$, and all of the additional variation is directly attributable to $\log N$. Since $\log N$ explains more of the variance in $\log \bar{w}$ than in $\log B$, the correlation between $\log \bar{w}$ and $\log N$ is higher and more significant than the correlation between $\log B$ and $\log N$. Although mathematically real, this higher correlation does not represent an increase in the information content of the data, but is a "wonderful tool for misleading the unwary" (Gold 1977).

The deceptive effects of this data transformation are also present in simple plots of the data. This is important because self-thinning data must be edited to remove extraneous points before fitting a thinning line. Since plots of the data are essential tools for recognizing such points, a data transformation that creates artificial linear trends in the plot will obviously disrupt the editing procedure. In the most extreme case, the distorted $\log \bar{w}$ - $\log N$ plot may suggest a linear relationship when none was present in the original $\log B$ - $\log N$ data. More subtle errors arise

when a real log B-log N correlation exists, but points that are not associated with the constraint of the thinning line are mistakenly included in fitting the thinning line.

A few examples will illustrate how the deceptive effects of the data transformation pervade the existing evidence for the self-thinning rule. In the first example, the log \bar{w} -log N plot (Figure 4.5a) for a study of Trifolium pratense (Black 1960) shows a linear trend and high correlation ($r^2 = 0.76$) between log \bar{w} and log N among nine data points purported to form a thinning line that agrees with the self-thinning rule (White and Harper 1970). However, the untransformed log B-log N plot (Figure 4.5b) shows the true situation: there is no significant negative correlation between log B and log N for the nine points, and time trajectories of stands cut steeply across the proposed thinning line rather than approaching it asymptotically.

Figure 4.6 illustrates a less extreme case where a linear trend is present, but the log \bar{w} -log N plot gives a distorted impression of which points lie along the constraining line. The log B-log N plot of the data (Chenopodium album, Yoda et al. 1963) shows an apparent linear constraint which could be estimated by fitting a line through the 13 square data points in Figure 4.6b. The remaining 14 points are distant from the constraint and should be removed before curve fitting, but this is hidden in the distorted log \bar{w} -log N plot (Figure 4.6a), where the artificial linearization causes the extraneous data points to fall in line with the others. Fitting a thinning line through all 27 data points by PCA of log \bar{w} against

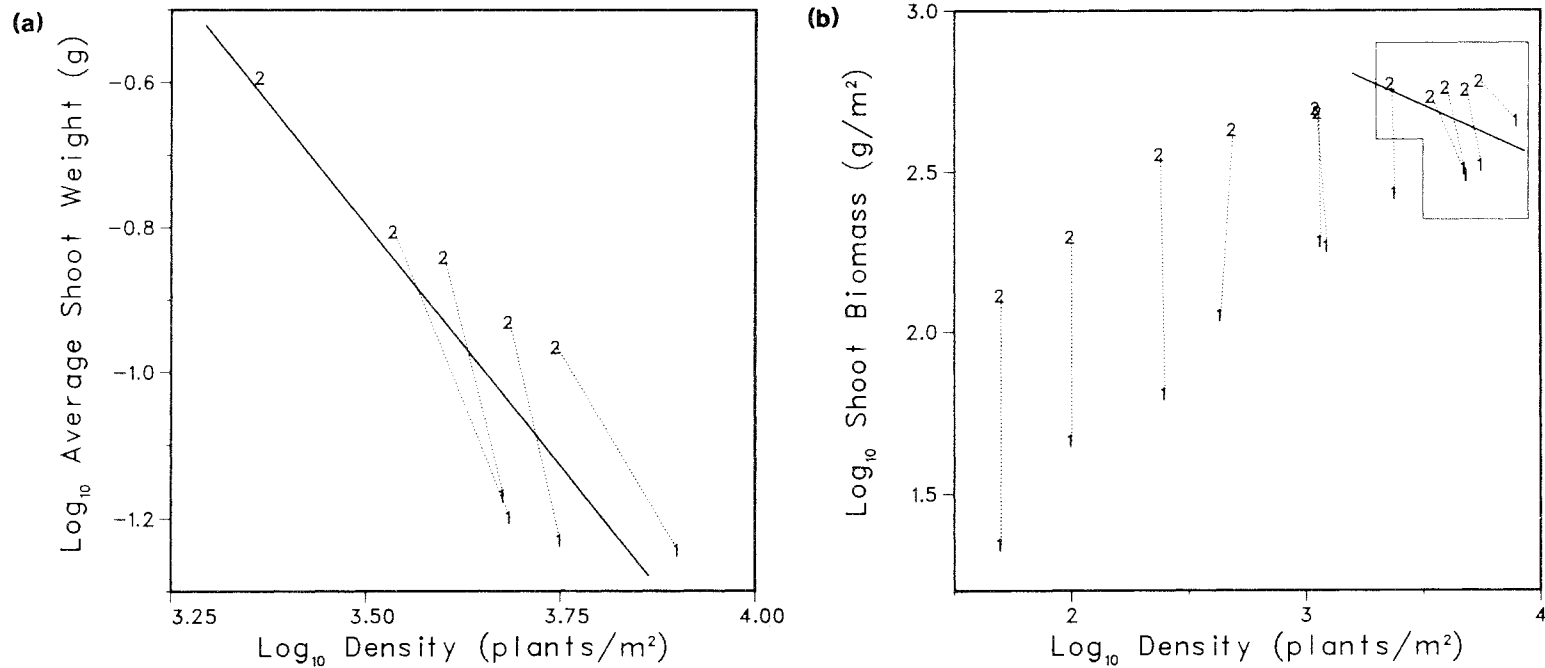


Figure 4.5. Example of a spurious reported self-thinning line. (a) White and Harper (1970) fit the solid regression line $\log \bar{w} = -1.33 \log N + 3.86$ ($n = 9$, $r^2 = 0.76$, $P = 0.003$) to data for Trifolium pratense (Black 1960). In (b) the nine points are in the box and other points omitted by White and Harper are also shown. The original measurements of $\log B$ and $\log N$ for the nine points are uncorrelated ($r^2 = 0.13$, $P = .33$). Time trajectories for different initial densities (dotted lines) cut through the proposed thinning line and do not approach it.

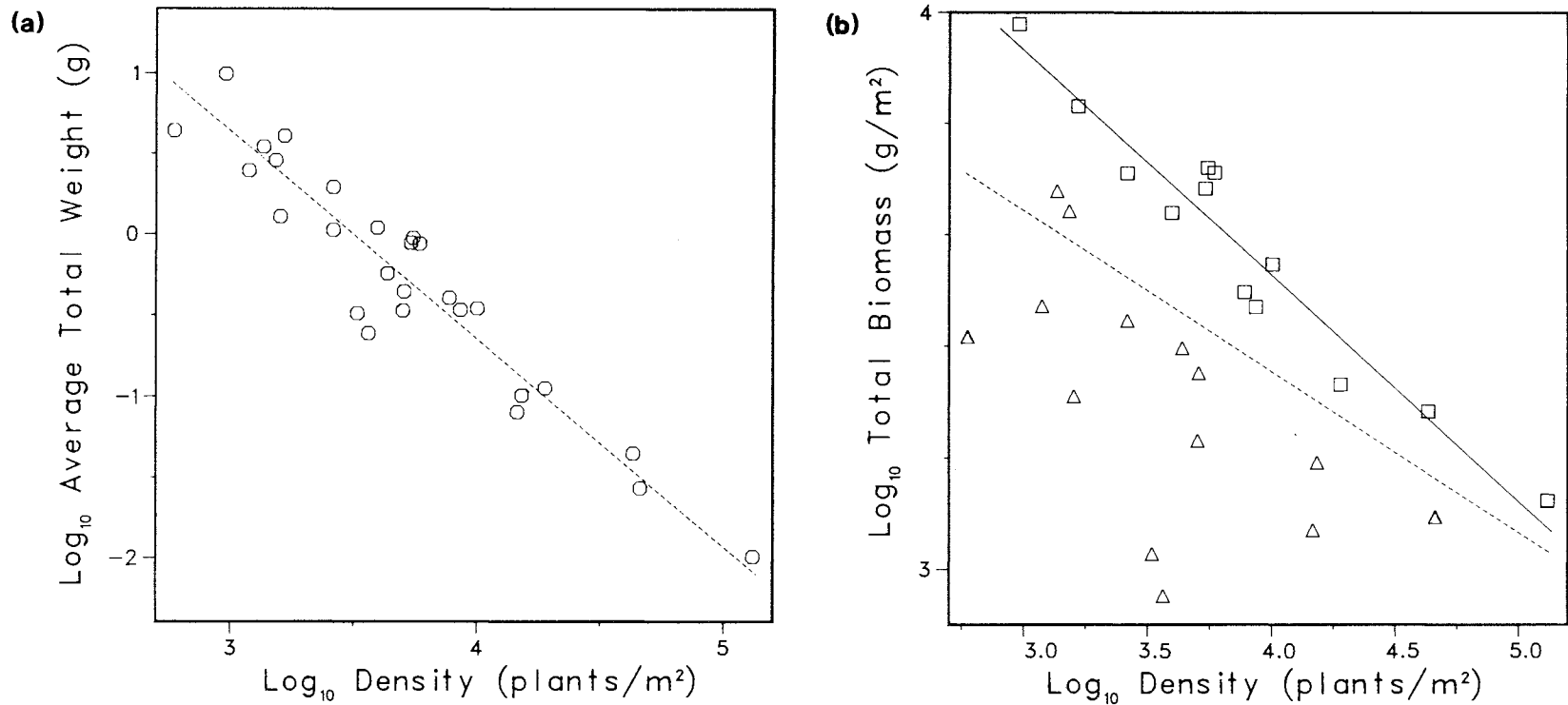


Figure 4.6. Example of potential bias in data editing in the $\log \bar{w}$ - $\log N$ plane. Data are for *Chenopodium album* (Yoda et al. 1963). In the $\log \bar{w}$ - $\log N$ plot (a) all 27 data points follow a common linear trend, represented by the dotted line. The equation of this line, estimated from PCA of $\log B$ and $\log N$, is $\log B = -1.33 \log N + 3.94$ ($r^2 = 0.90$, $P < 0.0001$, 95% CI for $\hat{\beta} = [-1.53, -1.16]$). When the artificial enhancement of linearity is removed on examination of the $\log B$ - $\log N$ plot of (b), an apparent linear constraint is still evident; however, many data points fall relatively far from the constraining line (triangles). A new (solid) PCA line through the 13 points closer to the border of the constrained region has the equation $\log B = -0.41 \log N + 5.15$ ($r^2 = 0.93$, $P < 0.0001$, 95% CI for $\hat{\beta} = [-0.48, -0.33]$), and the inadequacy of the dotted line is revealed.

log N gives $\log \bar{w} = -1.33 \log N + 3.94$ ($r^2 = 0.90$, $P < 0.0001$, 95% CI for slope = $[-1.53, -1.16]$), while the 13 points actually near the constraint in the log B-log N plot give $\log B = -0.41 \log N + 5.15$ ($r^2 = 0.93$, $P < 0.0001$, 95% CI for slope = $[-0.48, -0.33]$). The distorted log \bar{w} -log N plot changes the selection of relevant points, the estimated thinning line, and its comparison to the self-thinning rule.

The transformation can artificially straighten data that are actually curved in the log B-log N plane. The straight lines in the log \bar{w} -log N plane of Figure 4.7a seem to be a reasonable fits to the data (Fagopyrum esculentum--Furnas 1981), but the log B-log N plot (Figure 4.7b) reveals the true curvature of the data and the inadequacy of the straight line model. This curve straightening deception is important in editing data sets with juvenile or senescent stands, which often curve gradually toward or away from the thinning line.

A final example shows how the log \bar{w} -log N plot can lead to questionable conclusions about the effects of an experimental treatment on self-thinning. To evaluate the effects of a fertilizer treatment on self-thinning behavior, five plots of Erigeron canadensis received different fertilizer applications in a ratio of 5:4:3:2:1 before seeds were planted (Yoda et al. 1963). The conclusion that the thinning trajectory was insensitive to soil fertility seems justified in the log \bar{w} -log N plot (Figure 4.8a), where the five treatments seem to approach the same thinning line despite the large differences in fertility. However, the

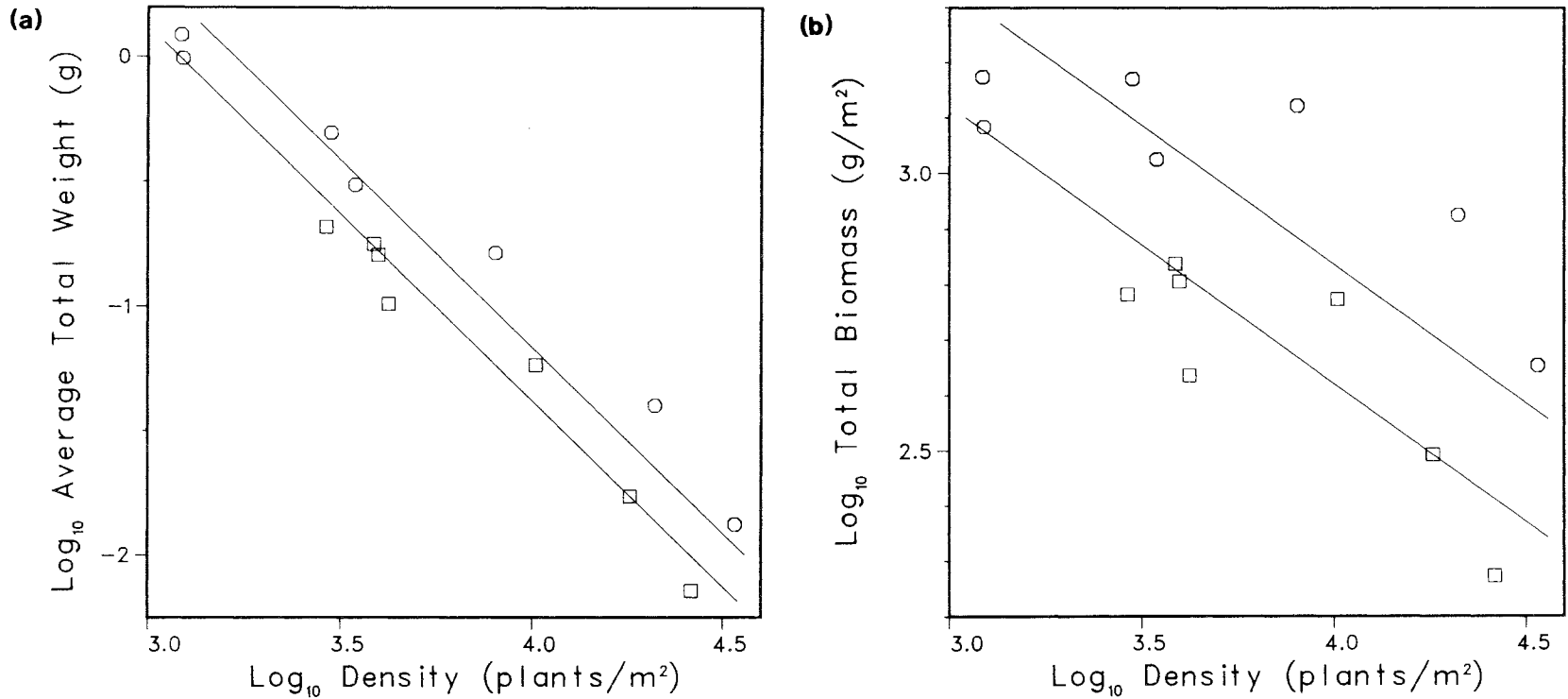


Figure 4.7. Example of deceptive straightening of curves in the $\log \bar{w}$ - $\log N$ plane. Data are from an experiment with *Fagopyrum esculentum* where the circle population received five times as much fertilizer as the square population (Furnas 1981). Both trajectories appear reasonably linear in the $\log \bar{w}$ - $\log N$ plot (a), and the two lines $\log \bar{w} = -1.50 \log N + 4.837$ and $\log \bar{w} = -1.50 \log N + 4.622$ reported by Furnas seem to fit the data well. The $\log B$ - $\log N$ plot (b) reveals the the inadequacy of the straight line model for these data.

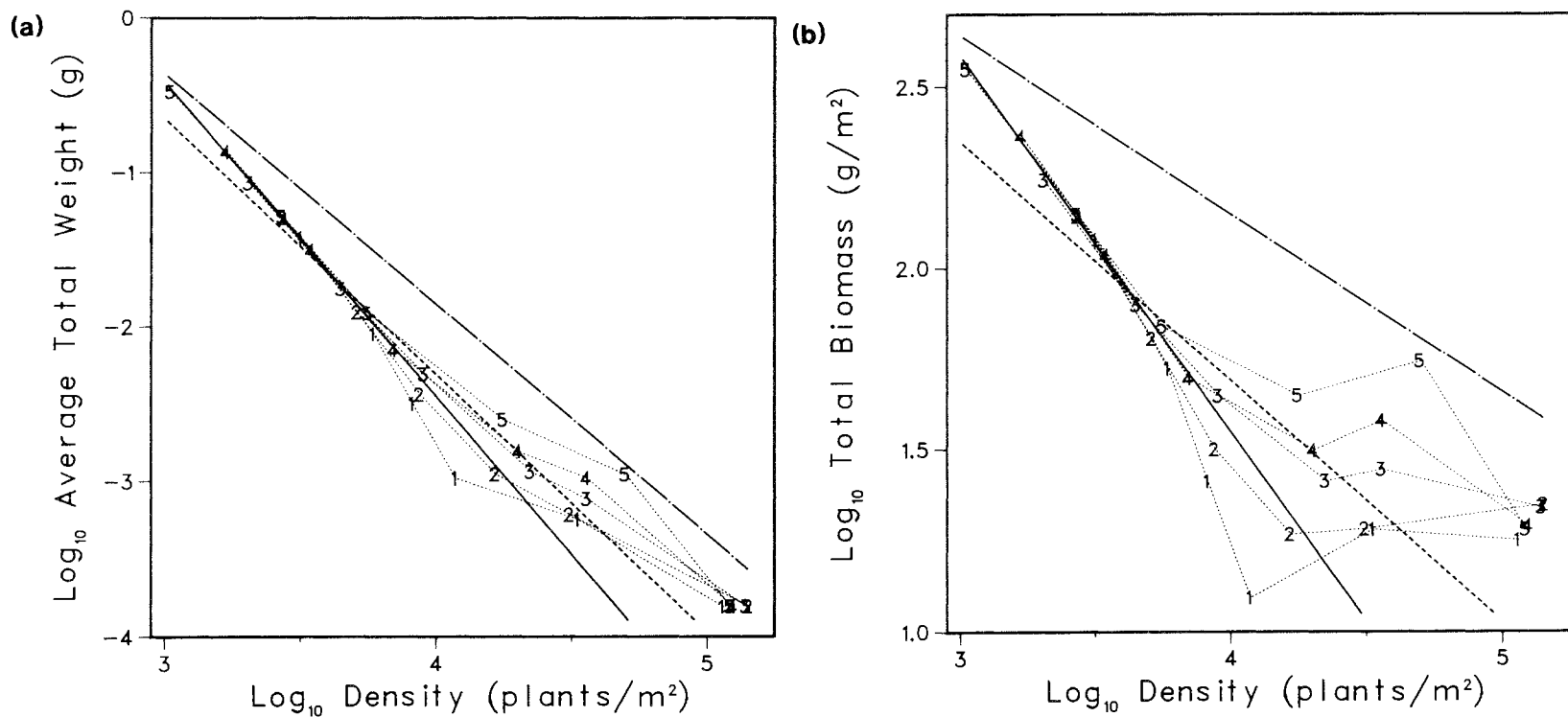


Figure 4.8. Potential misinterpretation of experimental results due to deceptive effects of the $\log \bar{w}$ - $\log N$ plot. Numbers marking data points (*Erigeron canadensis*--Yoda et al. 1963) indicate the relative amount of fertilizer applied before planting. Yoda et al. concluded that the overall trend of the data show a slope of -1.5 (chain-dot line) in the $\log \bar{w}$ - $\log N$ plot (a). White (1980) reported the dotted regression line $\log \bar{w} = -1.66 \log N + 4.31$ ($r^2 = 0.93$, $P < 0.0001$, 95% CI for slope = [-1.86, -1.47]). In (b) the present study fit the PCA line (solid line) $\log B = -1.04 \log N + 5.70$ ($r^2 = 0.99$, $P < 0.0001$, 95% CI for slope = [1.12, -0.96]).

log B-log N (Figure 4.8b) plot suggests a very different interpretation. The populations do respond to fertility differences and initially follow very different trajectories, but the differences gradually disappear and are gone around the fourth harvest, about 4.5 months after planting. It seems reasonable that over this long interval, leaching and plant uptake removed fertilizer from the soil, all five treatments approached a background fertility level, and only then did the treatments converge on a common trajectory.

The log B-log N plot also suggests a thinning line that is very different from the expected value of $\beta = -1/2$. This plot reveals a fact that is obscured in the log \bar{w} -log N plot: all five plots lost biomass between harvests two and three, which is not surprising because these harvests were made during the winter. Because winter conditions apparently interfered with growth, early harvests should not be included in estimating a thinning line. PCA analysis of harvests four through six gives $\log B = -1.04 \log N + 5.70$ ($r^2 = 0.99$, $P < 0.0001$, 95% CI for slope = $[-1.12, -0.96]$). This slope is not close to the hypothesized value of $\beta = -1/2$ and is statistically different from $-1/2$ ($P < 0.0001$).

Testing Agreement with the Self-thinning Rule

Evaluation of the self-thinning rule has been hindered by the lack of an objective definition of how close to the predicted value a thinning slope must be to agree quantitatively with the rule. White (1980) reported that many thinning slopes fall between

$\hat{\gamma} = -1.8$ and $\hat{\gamma} = -1.3$ and presented all these values as examples of the same quantitative rule. However, this arbitrary range has no objective basis and its limits represent very different predictions about population growth. A population following a thinning trajectory of slope $\gamma = -1.3$ over a 100-fold decrease in density will increase its biomass about fourfold, while a population following a trajectory of slope $\gamma = -1.8$ will increase its biomass about 40-fold over the same 100-fold density decrease. Although the two populations show qualitatively similar behavior in following a linear trajectory in the log size-log density plane, they show a tenfold difference in biomass response to the same degree of density decrease and thus would not seem to obey the same quantitative rule. Over a 1000-fold density decrease, one population shows an eightfold biomass increase, while the other thinning population shows a 250-fold biomass increase and the discrepancy between the two thinning regimes increases exponentially as larger amounts of density decrease are considered.

A statistical test of the hypothesis that an observed thinning slope is equal to the predicted value provides a more objective test of agreement with the self-thinning rule. The confidence interval for the slope of a fitted thinning line can be compared to the predicted value. If the CI includes the predicted value, then the data can not be said to contradict the rule and the slope is close to the idealized value within the limits of resolution of the data. If the CI does not contain the predicted slope, then the data are in quantitative disagreement with the self-thinning rule.

This statistical test of agreement with the self-thinning rule should be accompanied by tests of relevant alternative hypotheses. Only data sets that can discriminate among alternatives can provide convincing support for the self-thinning rule. Two alternative hypotheses are particularly relevant: the null hypotheses that no competitive effect was observed, and the hypothesis that a carrying capacity keeps stand biomass below a fixed level. If the null hypothesis is true, there will be no significant relationship between $\log B$ and $\log N$ or a positive relationship. If a biomass is fixed at a constant level, there will again be no significant relationship between $\log B$ and $\log N$. Only data sets that have a statistically significant negative correlation between $\log B$ and $\log N$ can clearly reject these alternatives. Data sets that do not reject the null hypothesis do not support the self-thinning rule or any other hypothesis about the course of plant competition. Such data do not even demonstrate the presence of competition.

Unfortunately, the interpretation of hypothesis tests is confounded by the uncertainties of data editing. The analysis can not account for these uncertainties, so the confidence interval of the fitted thinning slope is too narrow and the probability of making a Type I statistical error (rejecting a true null hypothesis) is increased by some unknown amount. A test with the 95% confidence interval actually gives less than 95% confidence.

Discussion

The problems with the evidence for the self-thinning rule can be grouped into three categories of solvability: (1) omissions that can be rectified by analyzing and interpreting a greater breadth of information, (2) problems that can be fixed by using the best available statistical methods, and (3) unsolvable problems. The inattention to potentially contradictory information can be remedied by analyzing new data and by integrating existing contradictory examples into the body of data used to test the rule and delimit ranges of variation for thinning line parameters.

There are three areas where improvement of analytical methods is possible: the analysis should relate $\log B$ to $\log N$ because the alternative of relating $\log \bar{w}$ to $\log N$ is statistically invalid; PCA should be used rather than regression, which relies on unrealistic assumptions about the error structure of the data; and statistical tests of hypothesis should be used to interpret the results. The importance of making these improvements can be partially evaluated by quantifying the prevalence of less desirable methods. Table A.5 lists the methods used to estimate 76 reported self-thinning lines for experimental and field data (EFD) and Table B.4 gives similar information for 16 thinning lines for forestry yield table data (FYD). All of the FYD and 69 (91%) of EFD thinning lines were estimated by relating $\log \bar{w}$ to $\log N$. For this large majority of studies, the points selected for analysis may not be the best choices, the correlations are inflated, spurious relationships may

have been created and interpreted, and the interpretation of the effects of experimental treatments and environmental factors may be biased. Few studies have included explicit statistical tests of the hypotheses that the estimated thinning slope is zero or equal to the value predicted by the thinning rule. Even if they had, the results of the tests would be meaningless because of the spurious component of the relationship between $\log \bar{w}$ and $\log N$ present in all studies that used the $\log \bar{w}$ - $\log N$ analysis.

The majority of studies have not used the best curve fitting methods. All of the FYD thinning lines were fit by regression, while 37 (49%) of the EFD thinning lines were regressions and only 15 (20%) used the more appropriate technique of PCA. Nineteen (25%) were graphical analyses that used no statistics, four (5%) assumed axiomatically that the thinning slope was $\gamma = -3/2$, and one (1%) one did not specify the statistical method.

The third category of unsolvable problems includes the need to edit data before fitting the self-thinning line. Editing of data before addressing some hypothesis should be suspect because it reduces the objectivity of the analysis and affects the confidence levels of statistical tests, but no alternative procedure for thinning analysis has been developed. However, these deleterious effects of editing are seriously compounded when the original data are transformed to average weights before editing, which can lead to false linear trends and disguise the need to remove certain points from consideration. These effects can be avoided by analyzing data in $\log B$ - $\log N$ form.

The prevalence of some correctable problems in analysis and interpretation of self-thinning data suggests that a major reanalysis of the evidence is required. Such an analysis is presented in Chapter 5.

NEW TESTS OF THE SELF-THINNING RULE

Introduction

This chapter presents some new analyses of the support for the self-thinning rule and the extent of variation among self-thinning lines. This is the first effort to critically and comprehensively review the full spectrum of available evidence, and it reveals patterns that are not apparent when the evidence is judged on a piece-by-piece basis. No analysis can be perfect because the data must be edited before fitting the thinning line, resulting in some loss of objectivity and distortion of significance tests (Chapter 4). However, the analysis can be done as rigorously and consistently as possible by: (1) eliminating a priori biases, (2) using $\log B$ - $\log N$ data to avoid compounding the problems of editing with the artificial linearity and spurious correlation of $\log \bar{w}$ - $\log N$ plots, (3) using the best method for estimating the self-thinning line (principal component analysis of $\log B$ and $\log N$), and (4) using statistical tests to objectively interpret the results.

This analysis considers 488 self-thinning lines, 137 from experimental and field data and 351 from forestry yield tables. This is the largest sample of thinning lines considered in any single study and includes many data sets not previously analyzed in a self-thinning context. The new data are important in guarding

against any a priori bias toward the self-thinning rule. Five different analyses address the constancy of observed thinning lines and their agreement with the self-thinning rule: (1) Statistical hypothesis tests are used to test for significant relationships between $\log B$ and $\log N$ and for quantitative agreement with the self-thinning rule. (2) The frequency distributions of thinning slope and intercepts are prepared to provide a complete description of the observed variations. (3) Plant groups are compared to determine if thinning line parameters vary among groups or if a single thinning rule applies to all plants. (4) The constancy of thinning line parameters with respect to a functional measure of plant performance is tested by checking for significant correlations of thinning slope and intercept with shade tolerance. (5) Finally, when several thinning lines were estimated for a particular species, the results are compared to determine if thinning slope and intercept are species constants.

Methods

Data were collected from two classes of studies:

(1) experimental and field studies (EFD) and forestry yield tables (FYD). Thirty-nine sources of EFD and 51 sources of FYD were examined (Tables A.1 and B.1). Many of these sources reported more than one study or yield table, so 95 studies were represented in the EFD and the FYD contained 77 yield tables. Some of these contained information for several thinning lines, so that a total of 488 thinning lines were fit, 137 for EFD and 351 for FYD. To ensure

comparability among studies, stand biomass values were converted to common units of g/m^2 while plant densities were converted to individuals/ m^2 . For forestry data, stand yields in volumes of wood were converted to weights per unit of forest area (g/m^2) by multiplying by the wood density of the species (Table B.1).

Fifty-six different species were represented in monospecific studies in the EFD, along with seven different two-species combinations, three multi-species mixtures, and two studies of monogeneric populations of unspecified species. The FYD considered 32 different single-species forests, two types of two-species forests, four multi-species forest types, and seven monogeneric forests of unspecified species. Some of the single-species forest types were examined in both the EFD and FYD. When these duplications are accounted for, a total of 78 different monospecific population types were considered. The multi-species stands were included because the thinning rule has been proposed to also apply for two species stands (White and Harper 1970, Bazazz and Harper 1976, Malmberg and Smith 1980) and multi-species stands (White 1980, Westoby and Howell 1981).

Some of the EFD studies presented data only in graphical form. In an initial attempt to acquire these data, requests for listings were sent to the authors of 12 studies and two data sets were successfully completed. The remaining graphical data sets were reconstructed from graphs by measuring the horizontal and vertical positions of each data point and axis tic mark to the nearest 0.05 mm with a micrometer. Regressions relating labeled axis values

to the micrometer measurements were used to recover the actual data values. Coefficients of determination for these regressions were uniformly high ($r^2 \geq 0.98$), indicating that the graphs were of good quality and that this method was adequate for recovering the data. For individual numbers published in both written and graphical form, the reconstructed values were within 5% of the true values. Slopes, intercepts, and r^2 values estimated from reconstructed data were within 2% of the published values when reanalyzed with the points and fitting methods used by the authors, again suggesting good recovery of the original information. Reconstructed data has also been used in other studies of self-thinning (White and Harper 1970, White 1980, Lonsdale and Watkinson 1983a). Forty-two of the 95 EFD studies required some reconstruction from graphical data. These are indicated by the inclusion of figure numbers in the reference column of Table A.1. No reconstruction was necessary for the FYD.

Many sources gave data for stands grown under different conditions of light, fertilization, site quality, initial density, and other factors that may affect the thinning line. Data from the different conditions could be used to estimate separate thinning lines or pooled to estimate a single line. To simplify the present analysis and preserve comparability with the original reports, the EFD were reanalyzed with the same grouping used by the original authors, except where those authors later decided that the separate thinning lines were not different. Table A.1 gives the conditions that subdivided some studies into several thinning trajectories.

Thinning lines were fitted separately for different site indexes in the FYD, except where the source clearly indicated that the same relationships were used to develop the tables for different site indexes.

Log B-log N plots were examined to select points for fitting thinning lines. In many cases, the selection of points used by the original authors was not changed. However, log B-log N plots of some data sets revealed that points included in the original log \bar{w} -log N analysis were not closely associated with the thinning line and these points were removed in this analysis. Point selections were never altered when the sources gave justification for particular choices or validated their choices with field notes or mortality curves (Mohler et al. 1978, Hutchings and Budd 1981b). A complete count of the number of data sets for which the point selections were changed here is not possible because many studies did not report how many data points or which ones were used. Of 63 previously cited thinning trajectories (Table A.5), 33 indicated which points were used. Twenty-four of these were analyzed here with no changes and the point selections of the remaining 9 were altered. These studies can be identified by comparing the sample size columns of Tables A.2 and A.5.

Each edited data set was analyzed for the strength and position of linear trend. The strength was measured by calculating the Pearson correlation coefficient (Sprent and Dolby 1980), and a straight line was fit by principal component analysis (PCA)

(Jolicoeur 1973, 1975). Thinning intercepts, $\hat{\alpha}$, were calculated from $\hat{\beta}$ and the mean values of $\log B$ and $\log N$ using

$$\hat{\alpha} = \overline{\log B} - \hat{\beta} \overline{\log N} , \quad (5.1)$$

where $\overline{\log B}$ is the average value of $\log B$ and $\overline{\log N}$ is the average of $\log N$.

The statistical significance of each correlation in the EFD was examined by testing the null hypothesis that $\log B$ and $\log N$ were uncorrelated, and 95% confidence intervals for the PCA slopes (Jolicoeur and Heusner 1971) were used to test agreement with the value of $\beta = -1/2$ predicted by the self-thinning rule. With low correlation or few data, the PCA confidence limits can be imaginary, but this is correctly interpreted as the absence of a significant relationship (Jolicoeur 1973). The 95% confidence limits for the intercept were calculated by applying equation 5.1 to the confidence limits of $\hat{\beta}$.

None of these statistical tests were applied to the FYD, because yield tables are the predictions of curve fitting procedures. The biological variability and measurement errors inherent in the original forestry data are absent in a yield table, so statistical inferences drawn from a single thinning line would be invalid and the high r^2 values (Table B.2) provide only a crude index of low variability around the fitted line. However, a large sample of FYD thinning lines can be examined to look at the statistical distributions and ranges of variation of thinning line parameters, but in all the following analyses, the EFD and FYD are

considered separately because of the different levels of statistical testing that were possible in the two groups.

Univariate statistics were computed to describe the frequency distributions of $\hat{\beta}$ and $\hat{\alpha}$. In the EFD, 55 data sets gave biomass measurements based on aboveground parts only while 20 also included roots. ANOVA and nonparametric Kruskal-Wallis tests (Sokal and Rohlf 1981) were used to compare $\hat{\beta}$ and $\hat{\alpha}$ between the two groups and determine if their statistical distributions should be examined separately.

The thinning lines were then divided into broad plant groups. Six categories were used for the EFD: herbaceous monocots, herbaceous dicots, temperate angiosperm trees, temperate gymnosperm trees, Australian trees (genus Eucalyptus), and tropical angiosperm trees (Table A.1). The FYD were divided into three categories: temperate gymnosperms, temperate angiosperms, and Eucalypts (Table B.1). ANOVA and Kruskal-Wallis tests were done to determine if $\hat{\beta}$ and $\hat{\alpha}$ differed significantly among the groups. Spearman rank correlations were also calculated for the FYD to relate $\hat{\beta}$ and $\hat{\alpha}$ to shade tolerance, a common forestry measure summarizing the ability of a species to regenerate in the presence of competition (Baker 1949, Harlow et al. 1978). These correlations were tested to determine if thinning line parameters varied significantly with shade tolerance. Finally, tables were prepared for all species examined in more than one study. For the EFD, the 95% confidence intervals of the thinning line parameters were compared to test for significant differences among the estimates.

Results

Detailed information for each thinning line, including the number of points, experimental conditions, correlation, thinning slope and intercept, confidence intervals, etc. are given in Tables A.2 and A.3 for the EFD and Table B.2 for the FYD.

Sixty-three of the thinning lines were cited in previous studies as demonstrations of the self-thinning rule (Table A.5), but did not provide strong support for the rule when tested statistically. Nineteen (30%) did not show any significant correlation between $\log B$ and $\log N$ at the 95% confidence level. The remaining 44 (70%) were significant, but the slopes of 20 (32%) were statistically different from the thinning rule prediction $\beta = -1/2$, with 7 (11%) greater than and 13 (21%) less than $-1/2$. Only 24 (38%) of the slopes were both statistically significant and not different from the predicted value. Thirty-one additional thinning lines from data not previously analyzed in a self-thinning study also showed a significant $\log B$ - $\log N$ correlation. When combined with the 44 from the previously cited group, this gave a total of 75 significant thinning lines. Of these 75, 34 (45%) were not statistically different from $-1/2$. The remaining 41 (55%) were different, with 14 (19%) greater than and 27 (36%) less than $-1/2$.

Univariate statistics for the slopes and intercepts of these 75 thinning lines are presented for two groups: data sets with biomass measurements of aboveground parts only and data sets with biomass measurements that included roots (Table 5.1). ANOVA

Table 5.1. Statistical Distributions of Thinning Line Slope and Intercept.

| Statistic | Field and Experimental Data ^a | | | | | | Forestry Yield Table Data | |
|-------------|--|----------------|---------------|----------------|---------------|----------------|---------------------------|----------------|
| | Shoot Biomass | | Total Biomass | | All Data Sets | | Bole Biomass | |
| | $\hat{\beta}$ | $\hat{\alpha}$ | $\hat{\beta}$ | $\hat{\alpha}$ | $\hat{\beta}$ | $\hat{\alpha}$ | $\hat{\beta}$ | $\hat{\alpha}$ |
| n | 55 | 55 | 20 | 20 | 75 | 75 | 351 | 351 |
| Mean | -0.863 | 4.08 | -0.804 | 4.48 | -0.847 | 4.18 | -0.876 | 3.45 |
| Std. dev. | 0.701 | 1.12 | 0.862 | 1.62 | 0.742 | 1.27 | 1.024 | 1.04 |
| CV(%) | 81 | 27 | 107 | 36 | 88 | 30 | 117 | 30 |
| Std. err. | 0.095 | 0.15 | 0.193 | 0.36 | 0.086 | 0.15 | 0.055 | 0.06 |
| Skewness | -2.57 | 0.33 | -2.59 | 1.89 | -2.51 | 1.25 | -4.36 | -4.30 |
| Kurtosis | 7.14 | 2.03 | 7.21 | 6.86 | 6.59 | 5.64 | 21.04 | 23.45 |
| Range | 3.662 | 6.27 | 3.56 | 8.53 | 3.66 | 8.65 | 8.014 | 8.60 |
| Percentiles | | | | | | | | |
| 0 (Min.) | -3.808 | 1.28 | -3.760 | 1.40 | -3.808 | 1.28 | -8.132 | -4.18 |
| 1 | * | * | * | * | * | * | -6.641 | -2.53 |
| 5 | -2.838 | 1.64 | -3.687 | 1.48 | -2.838 | 1.65 | -2.411 | -1.90 |
| 10 | -1.589 | 2.94 | -2.207 | 3.15 | -1.589 | 3.07 | -1.268 | 2.74 |
| 25 | -0.986 | 3.65 | -0.951 | 3.89 | -0.986 | 3.70 | -0.848 | 3.33 |
| 50 (Median) | -0.649 | 3.84 | -0.468 | 4.13 | -0.622 | 3.97 | -0.618 | 3.68 |
| 75 | -0.503 | 4.63 | -0.332 | 4.91 | -0.465 | 4.63 | -0.480 | 3.95 |
| 90 | -0.316 | 5.37 | -0.226 | 6.31 | -0.299 | 5.58 | -0.370 | 4.12 |
| 95 | -0.249 | 6.53 | -0.205 | 9.75 | -0.220 | 6.53 | -0.318 | 4.27 |
| 99 | * | * | * | * | * | * | -0.222 | 4.39 |
| 100 (Max.) | -0.146 | 7.54 | -0.204 | 9.93 | -0.146 | 9.93 | -0.119 | 4.42 |

^aThe three categories under this heading are based on the method of biomass measurement. "Shoot Biomass" includes thinning trajectories from biomass measurements of aboveground parts only. "Total Biomass" trajectories are based on biomass measurements that include aboveground and belowground parts. "All Data Sets" gives statistics for both of these groups combined.

*Indicates that the 1st (or 99th) percentile value is identical to the minimum (or maximum) due to small sample size.

detected no significant differences between the two group means for both $\hat{\beta}$ ($F_{1,73} = 0.09$, $P = 0.76$) and for $\hat{\alpha}$ ($F_{1,73} = 1.44$, $P = 0.23$). Lack of significance was also obtained in the Kruskal-Wallis tests for $\hat{\beta}$ ($H_2 = 3.02$, $P = 0.08$) and $\hat{\alpha}$ ($H_2 = 1.90$, $P = 0.16$), so the two groups were pooled and their composite statistical distribution is also given. Table 5.1 also includes analogous statistics for the 351 thinning lines fitted to data sets in the FYD. Figure 5.1 gives histograms for $\hat{\beta}$ and $\hat{\alpha}$. The distributions were also compared to the accepted ranges of variation $-0.8 \leq \hat{\beta} \leq -0.3$ and $3.5 \leq \hat{\alpha} \leq 4.4$ (White 1980). For the EFD, 24 (32%) of the values of $\hat{\beta}$ were outside this range, with 22 (29%) less than -0.8 and 2 (3%) greater than -0.3 . Thirty-four (46%) $\hat{\alpha}$ values were more extreme, with 14 (19%) less than 3.5 and 20 (27%) greater than 4.5. Among the FYD, 105 (30%) $\hat{\beta}$ values were more extreme, with 102 (29%) less than -0.8 and 3 (1%) greater than -0.3 . Of the FYD $\hat{\alpha}$ values, 124 (36%) were more extreme with 122 (35%) less than 3.5 and 2 (1%) greater than 4.4.

Comparisons among broad plant groups showed that thinning parameters are not constant across the entire plant kingdom. ANOVA and Kruskal-Wallis tests detected significant differences in both $\hat{\beta}$ and $\hat{\alpha}$ among the six groups in the EFD and among the three groups of the FYD (Table 5.2). Because the Eucalypt group of the FYD was so extreme, two-way comparisons between the angiosperm and gymnosperm groups were also done. The differences in $\hat{\beta}$ between these two more similar groups were also statistically significant. For $\hat{\alpha}$, the ANOVA detected no significant differences between the

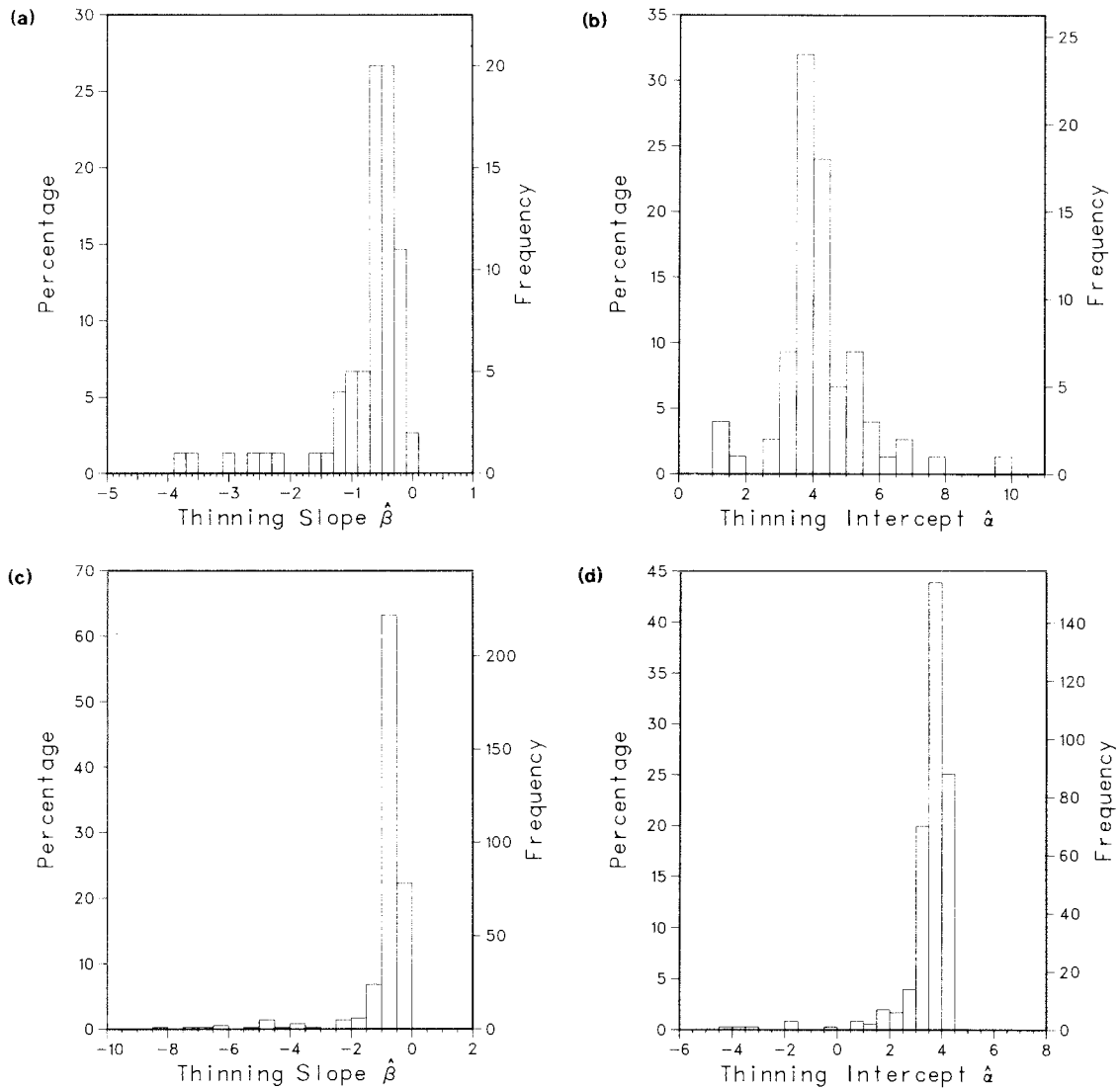


Figure 5.1. Histograms for the slopes and intercepts of fitted thinning lines. (a) and (b) show the distributions of slope and intercept, respectively, for log B-log N thinning lines in the experimental and field data. (c) and (d) show the same distributions for thinning lines in the forestry yield table data.

Table 5.2. Comparisons of Thinning Line Slope and Intercept Among Plant Groups.

| Group | n | Slope $\hat{\beta}$ | | Intercept $\hat{\alpha}$ | |
|---|-----|---------------------|--------|--------------------------|--------|
| | | Mean | Median | Mean | Median |
| <u>Experimental and Field Data</u> | | | | | |
| Herbaceous monocots | 8 | -0.44 | -0.39 | 4.45 | 4.24 |
| Herbaceous dicots | 25 | -0.74 | -0.65 | 5.17 | 5.09 |
| Temperate angiosperm trees | 15 | -0.65 | -0.53 | 3.78 | 3.72 |
| Temperate gymnosperm trees | 19 | -0.87 | -0.65 | 3.79 | 3.88 |
| <u>Eucalyptus</u> trees | 4 | -1.26 | -1.03 | 2.87 | 3.07 |
| <u>Tropical</u> angiosperm trees | 4 | -2.56 | -2.55 | 2.20 | 2.21 |
| All of the above | 75 | -0.85 | -0.62 | 4.18 | 3.97 |
| Tests for Significant Differences Among Six Groups | | | | | |
| ANOVA | | $F(5,69) = 7.68$ | | $P < 0.0001^*$ | |
| | | $F(5,69) = 10.9$ | | $P < 0.0001^*$ | |
| Kruskal-Wallis | | $H(5) = 17.9$ | | $P = 0.0031^*$ | |
| | | $H(5) = 41.1$ | | $P < 0.0001^*$ | |
| <u>Forestry Yield Table Data</u> | | | | | |
| Temperate angiosperm trees | 58 | -0.60 | -0.63 | 3.50 | 3.56 |
| Temperate gymnosperm trees | 281 | -0.80 | -0.61 | 3.54 | 3.72 |
| <u>Eucalyptus</u> trees | 12 | -3.90 | -4.39 | 1.09 | 1.79 |
| All temperate trees | 339 | -0.77 | -0.61 | 3.53 | 3.68 |
| All of the above | 351 | -0.88 | -0.62 | 3.45 | 3.68 |
| Tests for Differences Between Gymnosperms and Angiosperms | | | | | |
| ANOVA | | $F(1,337) = 4.85$ | | $P = 0.028^*$ | |
| | | $F(1,337) = 0.13$ | | $P = 0.8$ | |
| Kruskal-Wallis | | $H(1) = 3.77$ | | $P = 0.052$ | |
| | | $H(1) = 8.30$ | | $P = 0.004^*$ | |
| Tests for Differences Among Three Groups | | | | | |
| ANOVA | | $F(2,348) = 79.9$ | | $P < 0.0001^*$ | |
| | | $F(2,348) = 38.9$ | | $P < 0.0001^*$ | |
| Kruskal-Wallis | | $H(2) = 14.9$ | | $P = 0.0006^*$ | |
| | | $H(2) = 11.9$ | | $P = 0.0027^*$ | |

*Significant at the 95% confidence level ($P \leq 0.05$)

two groups while the Kruskal-Wallis analysis did. This indicates that the mean values of $\hat{\alpha}$ are similar, but one of the groups has a disproportionate number of extreme values of $\hat{\alpha}$ (in this case, the gymnosperm group has more high values), causing the rank based Kruskal-Wallis test to detect a difference.

Thinning slope and intercept were both correlated with shade tolerance in the FYD. The correlation analysis was done separately for the angiosperms and gymnosperms because of the observed differences in $\hat{\beta}$ and $\hat{\alpha}$ between these two groups. The Eucalypt group was not analyzed because shade tolerances were not available. For the 46 angiosperm thinning trajectories analyzed, $\hat{\beta}$ was significantly correlated with shade tolerance but thinning intercept was not (Table 5.3). Both $\hat{\beta}$ and $\hat{\alpha}$ were significantly correlated with tolerance in the gymnosperms; however, the sign of the correlation of $\hat{\beta}$ with shade tolerance was opposite to that observed for the angiosperms, further justifying the separate analyses of the two groups.

Thinning line parameters were not constant for species considered in more than one study. Both $\hat{\beta}$ and $\hat{\alpha}$ show considerable variation within species in the EFD (Table 5.4). In some cases, parameter estimates for a given species are quite different, but the confidence intervals for the estimates are so large that the differences are not statistically significant. In other cases, the differences are statistically significant, as indicated by non-overlap of the 95% confidence intervals. Eight (20%) of the 40 possible pairwise within-species comparisons of $\hat{\beta}$

Table 5.3. Spearman Correlations of Shade Tolerance with Thinning Line Slope and Intercept in the Forestry Yield Data.

| Thinning Parameter | Means for Shade Tolerance Groups ^a | | | | | Spearman Correlation | |
|------------------------------|---|----------------|----------------|----------------|----------------|-------------------------|---------|
| | 1 | 2 | 3 | 4 | 5 | r_s | p^b |
| <u>Temperate Angiosperms</u> | | | | | | | |
| Slope $\hat{\beta}$ | -0.391 (10) | -0.547 (18) | -0.685 (18) | | | -0.52* (46) | 0.0002 |
| Intercept $\hat{\alpha}$ | 3.632 (10) | 3.437 (18) | 3.517 (18) | | | -0.19 (46) | 0.22 |
| <u>Temperate Gymnosperms</u> | | | | | | | |
| Slope $\hat{\beta}$ | -0.916 (32) | -0.748 (78) | -0.642 (47) | -1.149 (69) | -0.459 (41) | 0.35* (267) | <0.0001 |
| Intercept $\hat{\alpha}$ | 3.123 (32) | 3.438 (78) | 3.732 (47) | 3.280 (69) | 4.172 (41) | 0.57* (267) | <0.0001 |

^aSample sizes are given in parentheses.

^bStatistical significance level.

*Significant at the 95% confidence level ($P \leq 0.05$).

Table 5.4. Thinning Line Slopes and Intercepts of Species for which Several Thinning Lines Were Fit from Experimental or Field Data.

| Id. Code ^b | Condition ^c | r ² | Thinning Line Parameters ^a | | | | | |
|----------------------------|------------------------|----------------|---------------------------------------|-------------------|--------------------|----------------|----------------|--------------------|
| | | | Slope | | | Intercept | | |
| | | | $\hat{\beta}$ | 95% CI | Diff. ^d | $\hat{\alpha}$ | 95% CI | Diff. ^d |
| <u>Abies sachalinensis</u> | | | | | | | | |
| A | 19A | 0.841 | -0.649 | [-0.776, -0.535]* | C | 4.16 | [4.15, 4.17] | C |
| B | 24T | 0.839 | -0.465 | [-0.965, -0.104] | C | 4.39 | [4.07, 4.83] | C |
| C | 119A | 0.971 | -2.786 | [-5.645, -1.772]* | AB | 1.71 | [-0.49, 2.49] | AB |
| <u>Beta vulgaris</u> | | | | | | | | |
| A | 33T | 0.592 | -1.335 | [-3.355, -0.648]* | | 6.38 | [4.54, 11.80] | |
| B | 34T | 0.645 | -2.304 | [-5.478, -1.348]* | CDEF | 9.93 | [7.08, 19.38] | CDEF |
| C | 43A 18% L.I. | 0.957 | -0.662 | [-0.839, -0.509]* | B | 4.79 | [4.17, 5.50] | B |
| D | 43A 25% L.I. | 0.916 | -0.692 | [-0.973, -0.470] | B | 5.12 | [4.22, 6.25] | B |
| E | 43A 37% L.I. | 0.940 | -0.668 | [-0.886, -0.486] | B | 5.09 | [4.39, 5.94] | B |
| F | 43A 55% L.I. | 0.934 | -0.649 | [-0.838, -0.487] | B | 5.22 | [4.59, 5.95] | B |
| G | 43A 100% L.I. | 0.698 | -0.648 | [-1.415, -0.197] | | 5.30 | [3.55, 8.27] | |

Table 5.4. (continued)

| Id. Code ^b | Condition ^c | r ² | Thinning Line Parameters ^a | | | | | |
|----------------------------|------------------------|----------------|---------------------------------------|-------------------|--------------------|----------------|---------------|--------------------|
| | | | Slope | | | Intercept | | |
| | | | $\hat{\beta}$ | 95% CI | Diff. ^d | $\hat{\alpha}$ | 95% CI | Diff. ^d |
| <u>Erigeron canadensis</u> | | | | | | | | |
| A 15T | | 0.930 | -0.621 | [-0.688, -0.558]* | B | 4.36 | [4.19, 4.55] | B |
| B 21T | | 0.987 | -1.038 | [-1.121, -0.962]* | A | 5.70 | [5.43, 6.00] | A |
| <u>Eucalyptus regnans</u> | | | | | | | | |
| A 98A | S.I. 28.9 | 0.971 | -2.478 | [-5.012, -1.559]* | | 1.39 | [-1.63, 2.48] | |
| B 98A | S.I. 33.5 | 0.964 | -1.066 | [-2.132, -0.549]* | | 3.44 | [2.31, 3.99] | |
| <u>Lolium perenne</u> | | | | | | | | |
| A 38A | 100% L.I. | 0.549 | -0.324 | [-0.674, -0.034] | | 3.79 | [2.88, 4.89] | |
| B 91A | 100% L.I. | 0.908 | -0.427 | [-0.543, -0.319] | | 4.80 | [4.37, 5.27] | |
| C 91T | 100% L.I. | 0.854 | -0.245 | [-0.330, -0.163]* | | 4.20 | [3.87, 4.54] | |
| D 92A | 23% L.I. | 0.776 | -0.544 | [-1.509, -0.011] | | 4.33 | [2.28, 8.06] | |
| E 92A | 44% L.I. | 0.786 | -0.503 | [-1.273, -0.027] | | 4.28 | [2.48, 7.20] | |

Table 5.4. (continued)

| Id. Code ^b | Condition ^c | r ² | Thinning Line Parameters ^a | | | | | |
|--------------------------|------------------------|----------------|---------------------------------------|-------------------|--------------------|----------------|---------------|--------------------|
| | | | Slope | | | Intercept | | |
| | | | $\hat{\beta}$ | 95% CI | Diff. ^d | $\hat{\alpha}$ | 95% CI | Diff. ^d |
| <u>Picea abies</u> | | | | | | | | |
| A 137A | | 0.983 | -0.422 | [-0.462, -0.383]* | | 3.90 | [3.88, 3.92] | |
| B 137T | | 0.982 | -0.433 | [-0.476, -0.392]* | | 3.97 | [3.95, 3.99] | |
| <u>Pinus strobus</u> | | | | | | | | |
| A 8A | Lot 2B | 0.986 | -0.724 | [-0.830, -0.628]* | B | 3.78 | [3.74, 3.83] | BC |
| B 8A | Lot 2C | 0.987 | -1.116 | [-1.278, -0.976]* | A | 3.34 | [3.22, 3.43] | A |
| C 93A | | 0.955 | -0.954 | [-1.189, -0.764]* | | 3.44 | [3.25, 3.60] | A |
| <u>Pinus taeda</u> | | | | | | | | |
| A 82A | | 0.468 | -0.305 | [-0.499, -0.130]* | B | 4.21 | [4.11, 4.30] | B |
| B 102A | | 0.939 | -0.670 | [-0.837, -0.526]* | A | 3.42 | [3.23, 3.59] | A |

Table 5.4. (continued)

| Id. Code ^b | Condition ^c | r ² | Thinning Line Parameters ^a | | | | | |
|-------------------------------|------------------------|----------------|---------------------------------------|-----------------|--------------------|----------------|--------|--------------------|
| | | | Slope | | | Intercept | | |
| | | | $\hat{\beta}$ | 95% CI | Diff. ^d | $\hat{\alpha}$ | 95% CI | Diff. ^d |
| <u>Trifolium subterraneum</u> | | | | | | | | |
| A 10A | Full light | 0.836 | -0.473 | [-0.660,-0.310] | | | 4.60 | [3.97, 5.33] |
| B 35A | | 0.716 | -0.622 | [-0.928,-0.382] | | | 5.17 | [4.33, 6.23] |

^aOnly species for which more than one statistically significant thinning line ($P \leq 0.05$) were fit are included (see Table A.2 for actual significance levels).

^bTable A.1 associates the numeric part of each Id. code with a particular species and study. The letter indicates the type of biomass measurements made: A = aboveground parts only, T = aboveground and belowground parts both included.

^cSee Table A.1 and the references given there for more information on condition.

^dThe letters in this column identify table entries (see letters at left of table) for the same species that are significantly different from the current estimate of $\hat{\beta}$ or $\hat{\alpha}$. Statistical disagreement (at $P \leq 0.05$) between estimates is indicated by non-overlap of confidence intervals.

*Indicates slopes that are significantly different ($P \leq 0.05$) from the value $\beta = -1/2$ predicted by the self-thinning rule.

were significant, as were 9 (23%) of the 40 possible comparisons of $\hat{\alpha}$. Since the confidence level is 95%, 2 of 40 comparisons should be different by chance alone, but both analysis gave a least 4 times this number. For the FYD, individual thinning line estimates (Table B.2) were not retabulated because so many thinning trajectories (264) were involved and because 95% confidence intervals could not be calculated. Instead, the sample sizes, means, standard deviations, coefficients of variation, minima, maxima, and ranges are given for $\hat{\beta}$ and $\hat{\alpha}$ for each species (Table 5.5). Although significance tests were not possible, the large observed ranges again indicate that $\hat{\beta}$ and $\hat{\alpha}$ are not species constants.

Discussion

The predictions of the self-thinning rule have been tested here through five different analyses: (1) statistical tests of the hypothesis that the slope of the self-thinning line is $\beta = -1/2$, (2) examination of the frequency distributions and ranges of variation of thinning line slope and intercept, $\hat{\alpha}$, (3) tests for variation in $\hat{\beta}$ and $\hat{\alpha}$ among plant groups, (4) tests for correlations of $\hat{\beta}$ and $\hat{\alpha}$ with shade tolerance, and (5) examination of the variation in $\hat{\alpha}$ and $\hat{\beta}$ for particular species. Although many data sets do show the predicted region of linear association between $\log B$ and $\log N$, all five analyses indicate that the slope of this relationship does not take the same value $\beta = -1/2$ across the entire plant kingdom. Therefore, the evidence

Table 5.5. Statistics for Thinning Line Slope and Intercept of Species for which Several Thinning Lines Were Fit from Forestry Yield Data.

| Species ^a | Number of ^b | | Thinning Slope $\hat{\beta}$ | | | | | | Thinning Intercept $\hat{\alpha}$ | | | | | |
|--|------------------------|-------------|------------------------------|-----------------|-----------------|-------|-------|-------|-----------------------------------|-----------------|-----------------|-------|------|-------|
| | Yield Tables | Thin. Lines | Mean | SD ^c | CV ^d | Min. | Max. | Range | Mean | SD ^c | CV ^d | Min. | Max. | Range |
| <u>Species Considered in More Than One Yield Table</u> | | | | | | | | | | | | | | |
| <u>Alnus rubra</u> | 3 | 8 | -0.41 | 0.19 | 46 | -0.65 | -0.12 | 0.53 | 3.46 | 0.42 | 12 | 2.69 | 4.08 | 1.39 |
| <u>Picea glauca</u> | 2 | 9 | -0.75 | 0.30 | 39 | -1.28 | -0.52 | 0.76 | 3.59 | 0.31 | 9 | 3.01 | 3.83 | 0.82 |
| <u>Pinus banksiana</u> | 3 | 10 | -0.79 | 0.39 | 50 | -1.73 | -0.24 | 1.49 | 3.06 | 0.27 | 9 | 2.51 | 3.51 | 1.00 |
| <u>Pinus echinata</u> | 4 | 20 | -0.72 | 0.23 | 32 | -0.97 | -0.40 | 0.56 | 3.53 | 0.35 | 10 | 3.14 | 4.05 | 0.91 |
| <u>Pinus elliotii</u> | 2 | 11 | -0.56 | 0.16 | 28 | -0.83 | -0.38 | 0.45 | 3.62 | 0.34 | 9 | 3.22 | 3.99 | 0.77 |
| <u>Pinus palustris</u> | 2 | 14 | -1.04 | 0.22 | 21 | -1.28 | -0.80 | 0.48 | 3.01 | 0.49 | 16 | 2.20 | 3.52 | 1.32 |
| <u>Pinus ponderosa</u> | 3 | 27 | -0.72 | 0.66 | 92 | -2.44 | -0.31 | 2.13 | 3.36 | 0.90 | 27 | 1.08 | 4.18 | 3.10 |
| <u>Pinus resinosa</u> | 2 | 8 | -1.07 | 0.48 | 45 | -1.97 | -0.63 | 1.34 | 3.46 | 0.47 | 14 | 2.73 | 4.21 | 1.48 |
| <u>Pinus strobus</u> | 3 | 12 | -0.74 | 0.18 | 25 | -1.07 | -0.53 | 0.54 | 3.68 | 0.15 | 4 | 3.43 | 3.88 | 0.45 |
| <u>Pinus taeda</u> | 3 | 17 | -0.69 | 0.20 | 28 | -0.90 | -0.25 | 0.65 | 3.48 | 0.34 | 10 | 3.05 | 4.10 | 1.05 |
| <u>Pseudotsuga menziesii</u> | 3 | 20 | -0.60 | 0.15 | 25 | -0.71 | -0.26 | 0.45 | 3.80 | 0.22 | 6 | 3.59 | 4.26 | 0.67 |
| <u>Sequoia sempervirens</u> | 2 | 10 | -2.68 | 1.45 | 54 | -4.75 | -1.22 | 3.53 | 1.20 | 2.24 | 186 | -1.93 | 3.44 | 5.37 |
| <u>Tsuga neterophylla</u> | 4 | 37 | -0.44 | 0.08 | 18 | -0.61 | -0.36 | 0.25 | 4.21 | 0.14 | 3 | 3.93 | 4.42 | 0.48 |

Table 5.5. (continued)

| Species ^a | Number of ^b | | Thinning Slope $\hat{\beta}$ | | | | | | Thinning Intercept $\hat{\alpha}$ | | | | | |
|--|------------------------|----------------|------------------------------|-----------------|-----------------|-------|-------|-------|-----------------------------------|-----------------|-----------------|-------|-------|-------|
| | Yield Tables | Thin. Lines | Mean | SD ^c | CV ^d | Min. | Max. | Range | Mean | SD ^c | CV ^d | Min. | Max. | Range |
| <u>Species Considered in More Than One Yield Table</u> | | | | | | | | | | | | | | |
| <u>Abies balsamea</u> | 1 | 4 | -0.59 | 0.00 | 1 | -0.60 | -0.59 | 0.01 | 3.80 | 0.02 | 1 | 3.77 | 3.81 | 0.05 |
| <u>Abies concolor</u> | 1 | 7 | -0.57 | 0.01 | 2 | -0.59 | -0.56 | 0.03 | 3.84 | 0.13 | 4 | 3.67 | 3.98 | 0.31 |
| <u>Castanea dentata</u> | 1 | 3 | -0.65 | 0.01 | 2 | -0.66 | -0.64 | 0.02 | 3.62 | 0.06 | 2 | 3.56 | 3.67 | 0.11 |
| <u>Chamaecyparis thyoides</u> | 1 | 6 | -0.53 | 0.01 | 2 | -0.54 | -0.51 | 0.03 | 3.80 | 0.14 | 4 | 3.53 | 3.89 | 0.36 |
| <u>Eucalyptus globus</u> | 1 | 4 | -5.80 | 1.86 | 32 | -8.13 | -3.80 | 4.33 | 1.06 | 0.98 | 93 | -0.21 | 2.06 | 2.27 |
| <u>Eucalyptus microtheca</u> | 1 | 3 | -6.84 | 0.39 | 6 | -7.22 | -6.44 | 0.78 | -3.67 | 0.51 | 14 | -4.18 | -3.17 | 1.01 |
| <u>Eucalyptus sieberi</u> | 1 | 3 | -0.62 | 0.07 | 12 | -0.69 | -0.55 | 0.15 | 4.12 | 0.03 | 1 | 4.09 | 4.14 | 0.06 |
| <u>Liriodendron tulipifera</u> | 1 | 3 | -1.15 | 0.12 | 10 | -1.24 | -1.02 | 0.23 | 2.69 | 0.18 | 7 | 2.53 | 2.88 | 0.35 |
| <u>Liquidambar styraciflua</u> | 1 | 6 | -0.39 | 0.03 | 8 | -0.42 | -0.33 | 0.09 | 3.87 | 0.11 | 3 | 3.74 | 4.03 | 0.30 |
| <u>Picea mariana</u> | 1 | 3 | -0.83 | 0.04 | 5 | -0.85 | -0.78 | 0.07 | 3.72 | 0.01 | 0 | 3.72 | 3.72 | 0.01 |
| <u>Picea rubrens</u> | 1 | 5 | -0.54 | 0.00 | 1 | -0.55 | -0.54 | 0.01 | 3.86 | 0.10 | 3 | 3.72 | 3.97 | 0.25 |
| <u>Pinus monticola</u> | 1 | 4 | -0.79 | 0.02 | 2 | -0.80 | -0.77 | 0.04 | 3.88 | 0.11 | 3 | 3.75 | 4.01 | 0.25 |
| <u>Populus tremuloides</u> | 1 | 4 | -0.33 | 0.07 | 23 | -0.43 | -0.27 | 0.16 | 3.62 | 0.12 | 3 | 3.46 | 3.74 | 0.28 |
| <u>Thuja occidentalis</u> | 1 | 6 | -0.35 | 0.04 | 11 | -0.41 | -0.30 | 0.11 | 3.58 | 0.08 | 2 | 3.46 | 3.67 | 0.21 |

^aOnly results from monospecific yield tables are included (Tables B.1 and B.2).

^bGives the number of yield tables for the species and the total number of thinning lines fit.

^cStandard deviation.

^dCoefficient of variation expressed as a percentage.

does not support the hypothesis that all plants obey the same quantitative self-thinning rule. These analyses also confirm predictions about the variations in thinning parameters from previous studies and from the models presented here.

The statistical tests of the 63 thinning lines reported to demonstrate the self-thinning rule show that this body of evidence does not strongly support the rule. Many of the reported high correlations between $\log W$ and $\log N$ proved spurious when the $\log B$ - $\log N$ data were reanalyzed, and 30% of the thinning lines did not even show a significant relationship between biomass and density. There could be two basic explanations for this result: the data are too variable or too few to detect the existence of a true relationship between $\log B$ and $\log N$, or there really is no relationship, as when stand biomass is maintained at a carrying capacity. Either way, the data do not support the self-thinning rule. Seventy percent of the thinning lines did show the predicted significant linear relationship between $\log B$ and $\log N$, but 32% of the thinning slopes were significantly different from $\beta = -1/2$ and disagreed quantitatively with the thinning rule. Deviations of the thinning slope from the predicted value are particularly important because β is the exponent of a power relationship, $B = K N^\beta$ so small differences in β represent large differences in the predictions of the equation (Chapter 4). Only 38% of the thinning slopes were both significantly different from 0 and not significantly different from $\beta = -1/2$. Because of the inherent ambiguities of statistical testing, these represent two

possibilities: a true relationship of slope $\beta = -1/2$ is present, or some different true slope is present but the data are so variable as to obscure this difference. In fact, many data sets were too variable to be useful in resolving alternative hypothesis about the slope of the thinning line. Strictly speaking, the most that can be claimed is that these 38% of the thinning lines do represent statistically significant relationships between $\log B$ and $\log N$ and the slopes are close to $\beta = -1/2$ within the resolution of the data.

In short, 30% of the data sets did not demonstrate any relationship between biomass and density while another 32% disagreed quantitatively with the $-1/2$ slope predicted by the thinning rule. This gives 62% of the data sets that were either useless for testing the rule or in quantitative disagreement with it, and only 38% that potentially support for the rule.

These tests must be interpreted with an important caveat: the true confidence level of each test is less than the nominal 95% because the necessary step of editing the data to fit the thinning line increases the probability of a Type I statistical error (rejection of a true null hypothesis) by some unknown amount. Some additional percentage of the thinning lines actually showed no correlation between $\log B$ and $\log N$, while some slopes that tested as significantly different from $\beta = -1/2$ are actually different at some lower confidence level. At present, all we can do is acknowledge and decry this limitation and argue that the analysis is still the most objective that is currently possible. Since the

other four analyses also show that thinning slopes vary widely from $\beta = -1/2$, confidence in the test results seems justified.

The frequency distributions of thinning slope and intercept show greater variations in these parameters than suggested by the often cited ranges $-0.8 \leq \hat{\beta} \leq -0.3$ and $3.5 \leq \hat{\alpha} \leq 4.4$ proposed by White (1980). Both distributions have single modes near their accepted values of $\beta = -1/2$ and $\alpha = 4$, but more extreme values are also present. The tendencies for $\hat{\beta}$ to be near $-1/2$ and for $\hat{\alpha}$ to be near 4 reflect the fact that values near the mode of a distribution are more frequently observed than extreme values. The commonness of modal values does not indicate that a limited range is rigidly imposed by a biological law. Seventy percent of the 426 $\hat{\beta}$ values in the combined EFD and FYD were within White's range, as were 42% of the $\hat{\alpha}$ values, so these ranges do include a large percentage of the observations, but not all. The greater variation observed here has a simple explanation, White's ranges were based on 36 data sets collected precisely because their thinning slopes were close to $\beta = -1/2$, but attempts were made here to avoid prejudicing the analysis with this criterion.

The observed departures of the thinning slope from $\beta = -1/2$ for trees in both the EFD and FYD support Sprugel's (1984) speculation that a thinning slope of $\gamma = -3/2$ ($\beta = -1/2$) is the exception rather than the rule for woody plants. Since herbaceous species also showed such departures, Sprugel's prediction applies for all plants. White (1981) has suggested that thinning slopes steeper than $\gamma = -2$ ($\beta = -1$) are prima facie evidence of

significant departure from the classic thinning rule. Seventeen (23%) of the EFD and 45 (13%) of the FYD slopes meet this criterion.

Additional evidence of variation in thinning line parameters was found in the existence of statistically significant differences in thinning line parameters among plant groups, and in the observation of significant correlations between thinning line parameters and shade tolerance (as predicted by Westoby and Howell 1981, Lonsdale and Watkinson 1983a). These results argue against a single, quantitative thinning rule for all plants (as claimed by White 1981, Hutchings 1983). Thinning line slope and intercept were not even constant among thinning lines for a particular species, so these parameters are not species constants (as suggested by Mohler et al. 1978, Hozumi 1980, White 1981, Hutchings 1983). This result complements evidence that thinning slope and intercept can vary within a single yield table when data from different site indexes are compared (Chapter 4). This has also been reported by Hara (1984), and Furnas (1981) has shown experimentally that the position of a thinning line can respond to changes in nutrient availability. Unfortunately, the biological interpretation of α is confounded because thinning slopes are variable. The constants of power equations have direct biological interpretations only if the powers of the relationships are identical (White and Gould 1965).

The existence of variation in thinning slope and intercept supports the the models of Chapters 2 and 3, which predicted that the slope of the thinning line depends on how the shape of the space occupied by a plant changes with growth, while the intercept is

additionally affected by the density of biomass in occupied space and the way interacting plants partition areas of overlap. If these models are correct, then thinning slope should vary among species because different species have different shapes and densities of biomass per unit of space (Mohler et al. 1978, Furnas 1981, Lonsdale and Watkinson 1983a). Thinning parameters should also vary within a species because plants change shape and canopy density in response to growing conditions (Harper 1977). Between-species and within-species variations are both present in the data analyzed here, just as predicted. The observed correlations of thinning line parameters with shade tolerance also confirm the importance of differences in allowable overlap between plants in positioning the thinning line.

SELF-THINNING AND PLANT ALLOMETRY

Introduction

The documentation of significant variation among the slopes of self-thinning lines (Chapter 5) verifies one major prediction of the mathematical model (Chapter 2), but the true test of the model comes in determining if the variations in self-thinning slope can be related to differences in plant allometry. Here three questions are addressed that provide such tests: (1) Are thinning slope and intercept correlated with available measures of plant allometry? (2) Do differences in thinning slope among plant groups (Chapter 5) reflect corresponding differences in plant allometry? (3) Do the correlations of thinning slope with shade tolerance (Chapter 5) reflect corresponding correlations between shade tolerance and plant allometries? The results and conclusions are related to those of previous studies to explain why allometric models have been discounted (Westoby 1976, Mohler et al. 1978, White 1981).

Expected Relationships between Thinning Slope and Plant Allometry

The model predicts that the slope of the self-thinning line in the log B-log N plane is $\beta = -1/[2p] + 1$ (or equivalently $\gamma = -1/[2p]$ in the log \bar{w} -log N plane), where p is the allometric power relating the radius of the zone of influence (ZOI) to weight according to the power equation $R \propto w^p$ (Chapter 2). This

prediction is referred to here as the allometric hypothesis. Hypothetically, it could be tested by measuring both $\hat{\beta}$ and $\hat{\rho}$ for several populations and testing statistically to determine if $\hat{\beta}$ and $\hat{\rho}$ follow the expected relationship. However, the actual measurement of ZOIs is problematic. It is difficult to define precisely where the ZOI of an individual ends, especially in highly competitive situations where the zones may be tightly packed and overlapping to varying degrees. Even when the ZOI is defined as the canopy area (White 1981), the actual measurement is still difficult and less accurate than other common measurements, such as height or bole diameter at breast height (DBH). Consequently, few data are available for relating the ZOI to weight and no published data were found where both $\hat{\rho}$ and $\hat{\beta}$ could be estimated simultaneously.

Plant ecologists and foresters routinely measure some parameters of plant shape, such as height, DBH, or bole basal area (BSLA), that can be used to fit allometric equations. Thinning slope can be related to these other measures of plant allometry. For example, the allometric equation $\bar{h} \propto \bar{w}^{\phi_{hw}}$ could be fit to average height and average weight measurements of the same stands used to estimate a self-thinning slope. Values of $\hat{\phi}_{hw}$ for several species could then be correlated with $\hat{\beta}$ to test if the two parameters are significantly related.

Geometric models can be further analyzed to suggest a functional form for the β - ϕ_{hw} relationship. Assume that plant height, the density of biomass in occupied space, and the ZOI radius all vary with plant weight according to allometric power functions

$h \propto w^{\phi_{hw}}$, $d \propto w^{\phi_{dw}}$, and $R \propto w^p$. If the volume of space occupied by a plant (VOI) is approximately cylindrical, then the volume is $v = \pi R^2 h$ and plant weight is $w = v d = \pi R^2 h d$. Since $w \propto R^2 h d$ and R , h , and d are allometrically related to weight, the two sets of equations can be combined to give $w \propto w^{2p} w^{\phi_{hw}} w^{\phi_{dw}}$ and the allometric powers are constrained by

$$2p + \phi_{hw} + \phi_{dw} = 1 \quad . \quad (6.1)$$

The predicted relationship $\beta = -1/(2p) + 1$ can be solved for p to give

$$p_{\text{est}} = \frac{1}{2(1 - \beta)} \quad , \quad (6.2)$$

where the symbol p_{est} emphasizes that p is not directly measured but derived by mathematical transformation of measured $\hat{\beta}$ values. Combining equations 6.1 and 6.2 gives a relationship between p_{est} , ϕ_{hw} , and ϕ_{dw} that should obtain if the allometric hypothesis is true

$$p_{\text{est}} = \frac{1}{2} [1 - (\phi_{hw} + \phi_{dw})] \quad . \quad (6.3)$$

This relationship is useful because of its linear form, simple geometric derivation, and clear representation of the compromises inherent in plant growth: allocation of more resources to height growth (higher ϕ_{hw}) or to packing more biomass in space already occupied (higher ϕ_{dw}) leaves fewer resources for expanding the

ZOI radially (lower p). Less radial expansion in turn means less conflict with neighbors, less self-thinning, and a steeper (more negatively sloped) thinning line.

To focus on the compromises between height growth and radial growth, assume that d is fairly constant ($\phi_{dw} = 0$). Equation 6.3 simplifies to

$$p_{est} = -\frac{1}{2} \phi_{hw} + \frac{1}{2}, \quad (6.4)$$

which defines a triangular region in the $p_{est}-\phi_{hw}$ plane that is bounded by the two axes $p_{est} = 0$ and $\phi_{hw} = 0$ and by the line $p_{est} = -0.5 \phi_{hw} + 0.5$. Empirical measurements of p_{est} and $\hat{\phi}_{hw}$ would lie around this line, except that ϕ_{dw} is not generally zero because the density of biomass in occupied space does vary with plant size (Lonsdale and Watkinson 1983a). Since measurements of d through time are not generally available for estimating $\hat{\phi}_{dw}$, equation 6.3 can not be used and variation in ϕ_{dw} will contribute to the errors in the simpler model of equation 6.4. Ignoring ϕ_{dw} and fitting a linear relationship between p and $\hat{\phi}_{hw}$ will produce a line in the $p_{est}-\phi_{hw}$ plane below equation 6.4; however, a negative correlation between p_{est} and $\hat{\phi}_{hw}$ will still support the allometric hypothesis, particularly if the functional form of the relationship approximates equation 6.4.

Other measurements besides height are commonly available for trees and can be used to fit allometric relationships to weight ($\overline{DBH} \propto \bar{w}^{\phi_{Dw}}$ or $\overline{BSLA} \propto \bar{w}^{\phi_{Bw}}$) that can be related to β . However,

DBH and BSLA are measures of the tree bole, not the VOI, so the expected relationship of ϕ_{Dw} or ϕ_{Bw} can not be simply derived from the geometry of the VOI. Also, mechanical considerations require that bole diameter increase to support any increase in tree weight, whether the growth is upward, radial, or simply an increase in the density of biomass in the VOI. Hence the DBH-weight or BSLA-weight allometries should not be sensitive measures of change in the VOI shape and should not necessarily correlate strongly with p_{est} .

DBH and height data can be combined to fit another allometric relation $\bar{h} \propto \overline{DBH}^{\phi_{hD}}$. Although interpretation of ϕ_{hD} is again confounded because DBH is not a measure of the VOI, h is a VOI dimension so some expectations for the p_{est} - ϕ_{hD} relationship can be deduced geometrically. If the VOI expands only radially ($p = 0.5$ and $\phi_{hw} = 0$ in equation 6.4), then ϕ_{hD} will be zero since height is constant. If the VOI expands both radially and upward ($p < 0.5$ and $\phi_{hw} > 0$), then DBH will increase to support the additional weight and ϕ_{hD} will be positive. Thus, a line representing the relationship in a p - ϕ_{hD} plot would pass through the point $(\phi_{hD}, p) = (0, 0.5)$ and would be negatively sloped. An observed negative correlation between p_{est} and $\hat{\phi}_{hD}$ would, then, support the allometric hypothesis. Furthermore, BSLA is simply related to DBH by $BSLA \propto DBH^2$, so the above logic also applies for the relationship between p_{est} and ϕ_{hB} . Although the functional form of the relationship of p_{est} to ϕ_{hD} or ϕ_{hB} is not geometrically obvious, it is reasonable to use a linear model unless this assumption proves inappropriate.

Methods

Information to test the allometric hypothesis was available in the sources of experimental and field data (EFD) and forestry yield table data (FYD) analyzed in Chapter 5 since average stand height, DBH, or BSLA were often reported along with stand biomass and density. All height and DBH measurements were converted to common units of m, while basal areas were converted to m^2 and divided by the density of individuals to give average basal area per tree. Many studies did not measure one or more of these dimensions, so fewer data were available for estimating allometric relationships. Of the 75 data sets in the EFD that showed significant relationships between $\log B$ and $\log N$ (Chapter 5), 31 had accompanying measurements of stand height, 8 reported DBH, and 29 reported BSLA. Of the 351 EFD thinning lines, 325 had height measurements, 334 had DBH, and 318 had BSLA.

Dimensional measurements from the same stands used to estimate $\hat{\beta}$ were log transformed and analyzed with principal component analysis (PCA, Chapter 5) to fit allometric equations relating $\log \bar{h}$, $\log \overline{DBH}$, and $\log \overline{BSLA}$ to $\log \bar{w}$; $\log \bar{h}$ to $\log \overline{DBH}$; and $\log \bar{h}$ to $\log \overline{BSLA}$. For each proposed allometric relationship in the EFD, the null hypothesis that the two variables were uncorrelated was tested and only relationships significant at the 95% confidence level were retained for further analysis. Similar statistical tests for the FYD were not possible (see Chapter 5) so the EFD and FYD were again analyzed separately.

Values of $\hat{\beta}$ (Chapter 5) were transformed to p_{est} values and correlated with the five allometric powers using both Spearman and Pearson correlation calculations. The correlation coefficients were tested and when a significant relationship was found, linear regression was used to estimate an equation for the relationship. Principal component analysis was not used because the objective was to predict p_{est} from an independent allometric parameter rather than to estimate a functional relationship between two variables. With this objective, regression is the appropriate technique despite errors in the independent variable (Ricker 1973, Sokal and Rohlf 1982).

Univariate descriptive statistics and histograms were calculated for each allometric parameter, and ANOVA and Kruskal-Wallis tests of differences among plant groups were performed. Spearman correlations of shade tolerance with each allometric power for the temperate angiosperm and temperate gymnosperm groups of the FYD were also calculated. Additional information on the groups and methods is given in Chapter 5.

Results

Table A.3 presents allometric powers fitted to data sets in the EFD. The PCA slope and intercept of each allometric equation are given, along with the correlation and statistical significance of the relationship. For the five allometric powers, $\hat{\phi}_{hw}$, $\hat{\phi}_{Dw}$, $\hat{\phi}_{Bw}$, $\hat{\phi}_{hD}$, and $\hat{\phi}_{hB}$, there were 23, 8, 23, 6, and 19, respectively, statistically significant relationships. Table B.3

gives the results of allometric regressions for the forestry yield data. Values of p_{est} calculated from fitted thinning slopes (Chapter 5) are included in Tables A.2 and B.2. Tables 6.1 and 6.2 give univariate statistics for p_{est} and the five allometric powers in the EFD and FYD, while Figures 6.1 and 6.2 present the corresponding histograms.

Two of the correlations between the transformed thinning slope and the allometric powers of the EFD were statistically significant ($P < 0.05$ --Table 6.3, Figure 6.3). Values of $\hat{\phi}_{hw}$ were negatively correlated with p_{est} ($r = -0.55$, $P < 0.0026$) and 30% of the observed variation in p_{est} was explained by the regression $p_{est} = -0.710 \hat{\phi}_{hw} + 0.501$. This equation does not differ significantly in either slope or intercept from the predicted equation $p = -0.5 \phi_{hw} + 0.5$. The failure of $\hat{\phi}_{Dw}$ and $\hat{\phi}_{hD}$ to correlate significantly with p_{est} is inconclusive because of the small sample sizes ($n \leq 8$). The allometric power $\hat{\phi}_{Bw}$ also showed no significant correlation with p_{est} , despite a larger sample size, but BSLA was not expected to be a good indicator of thinning slope. The allometry $\hat{\phi}_{hB}$ showed a statistically significant correlation with p_{est} ($r = -0.44$, $P = 0.032$) and the regression explained 19% of the variation in p_{est} .

All five correlations between p_{est} and the allometric powers in the FYD were significant ($P < 0.0001$, Table 6.3), but the high confidence levels were partly due to the large sample sizes ($n > 309$). The coefficients of determination give a more realistic assessment of the ability of these allometric parameters

Table 6.1. Statistical Distributions of Allometric Powers for Experimental and Field Data.

| Statistic | Allometric Parameter | | | | | |
|-------------|----------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| | p_{est} | $\hat{\Phi}_{hw}$ | $\hat{\Phi}_{Dw}$ | $\hat{\Phi}_{Bw}$ | $\hat{\Phi}_{hD}$ | $\hat{\Phi}_{hB}$ |
| n | 75 | 28 | 7 | 28 | 6 | 24 |
| Mean | 0.298 | 0.317 | 0.341 | 0.795 | 1.070 | 0.401 |
| Std. dev. | 0.075 | 0.068 | 0.038 | 0.108 | 0.134 | 0.118 |
| CV (%) | 25 | 21 | 11 | 14 | 13 | 29 |
| Std. err. | 0.009 | 0.013 | 0.015 | 0.020 | 0.055 | 0.024 |
| Skewness | -0.75 | -0.31 | -0.53 | -0.15 | -0.57 | 0.07 |
| Kurtosis | 0.444 | -0.52 | 0.66 | 0.23 | -0.44 | -1.13 |
| Range | 0.332 | 0.262 | 0.118 | 0.503 | 0.355 | 0.386 |
| Percentiles | | | | | | |
| 0 (Min.) | 0.104 | 0.184 | 0.274 | 0.542 | 0.860 | 0.229 |
| 1 | * | * | * | * | * | * |
| 5 | 0.130 | 0.189 | * | 0.589 | * | 0.229 |
| 10 | 0.194 | 0.202 | * | 0.651 | * | 0.241 |
| 25 | 0.252 | 0.269 | 0.321 | 0.704 | 0.959 | 0.273 |
| 50 (Median) | 0.308 | 0.321 | 0.347 | 0.827 | 1.078 | 0.399 |
| 75 | 0.341 | 0.377 | 0.374 | 0.866 | 1.202 | 0.490 |
| 90 | 0.385 | 0.398 | * | 0.893 | * | 0.573 |
| 95 | 0.410 | 0.425 | * | 1.003 | * | 0.608 |
| 99 | * | * | * | * | * | * |
| 100 (Max.) | 0.436 | 0.446 | 0.392 | 1.045 | 1.215 | 0.615 |

*Indicates percentiles that are identical to the minimum (or maximum) values due to small sample size.

Table 6.2. Statistical Distributions of Allometric Powers for Forestry Yield Table Data.

| Statistic | Allometric Parameter | | | | | |
|-------------|----------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| | Pest | $\hat{\Phi}_{hw}$ | $\hat{\Phi}_{Dw}$ | $\hat{\Phi}_{Bw}$ | $\hat{\Phi}_{hD}$ | $\hat{\Phi}_{hB}$ |
| n | 351 | 325 | 334 | 318 | 323 | 309 |
| Mean | 0.298 | 0.274 | 0.368 | 0.747 | 0.770 | 0.387 |
| Std. dev. | 0.067 | 0.059 | 0.057 | 0.108 | 0.230 | 0.130 |
| C.V. (%) | 22 | 22 | 16 | 14 | 30 | 34 |
| Std. err. | 0.004 | 0.003 | 0.003 | 0.006 | 0.013 | 0.007 |
| Skewness | -1.46 | 0.352 | 0.626 | 1.19 | 1.12 | 1.77 |
| Kurtosis | 2.91 | 0.666 | 11.4 | 18.8 | 1.99 | 5.74 |
| Range | 0.392 | 0.399 | 0.644 | 1.341 | 1.435 | 0.927 |
| Percentiles | | | | | | |
| 0 (min.) | 0.054 | 0.118 | 0.165 | 0.330 | 0.327 | 0.131 |
| 1 | 0.065 | 0.137 | 0.202 | 0.338 | 0.353 | 0.163 |
| 5 | 0.147 | 0.183 | 0.259 | 0.584 | 0.473 | 0.232 |
| 10 | 0.220 | 0.209 | 0.303 | 0.655 | 0.545 | 0.274 |
| 25 | 0.271 | 0.234 | 0.340 | 0.697 | 0.595 | 0.294 |
| 50 (Median) | 0.309 | 0.271 | 0.375 | 0.750 | 0.733 | 0.362 |
| 75 | 0.338 | 0.310 | 0.402 | 0.810 | 0.873 | 0.438 |
| 90 | 0.365 | 0.357 | 0.424 | 0.855 | 1.072 | 0.535 |
| 95 | 0.379 | 0.371 | 0.432 | 0.868 | 1.225 | 0.617 |
| 99 | 0.409 | 0.426 | 0.484 | 0.940 | 1.570 | 0.958 |
| 100 (Max.) | 0.447 | 0.517 | 0.810 | 1.670 | 1.762 | 1.058 |

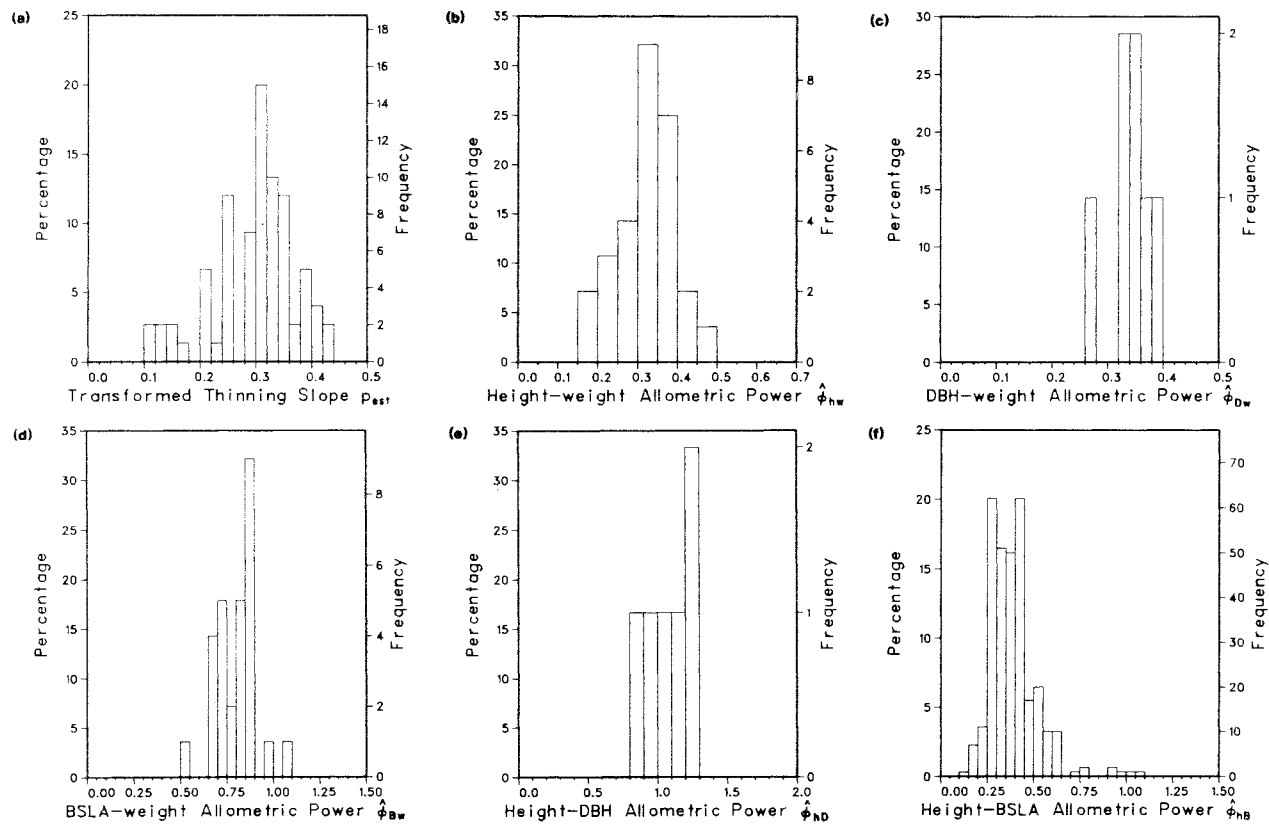


Figure 6.1. Histograms of allometric powers of the experimental and field data. (a) through (f) show, respectively, the statistical distributions of the transformed thinning slope, p_{ests} , and the allometric powers $\hat{\phi}_{hw}$, $\hat{\phi}_{Dw}$, $\hat{\phi}_{Bw}$, $\hat{\phi}_{hD}$, and $\hat{\phi}_{hB}$.

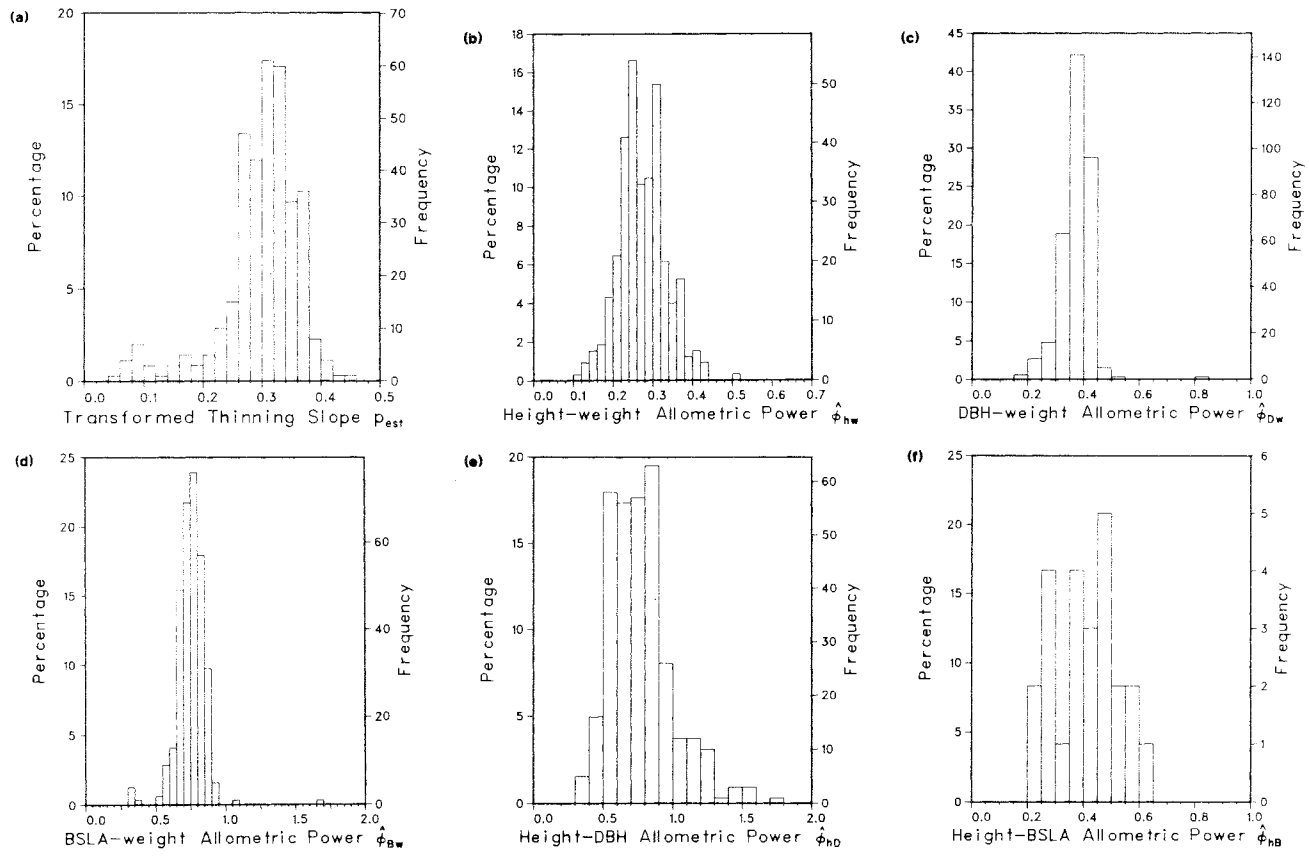


Figure 6.2. Histograms of allometric powers of the forestry yield table data. (a) through (f) show, respectively, the statistical distributions of the transformed thinning slope, p_{est} , and the allometric powers $\hat{\phi}_{hw}$, $\hat{\phi}_{dw}$, $\hat{\phi}_{bw}$, $\hat{\phi}_{hd}$, and $\hat{\phi}_{hb}$.

Table 6.3. Correlations and Regressions Relating Transformed Thinning Slope to Allometric Powers.

| Allometric Power | n | Spearman Correlation | | Pearson Correlation | | Linear Regression Equation | | | | |
|------------------------------------|-----|----------------------|----------|---------------------|----------|----------------------------|---------------|----------------|----------------|---------------|
| | | r_s | P | r | P | Slope | | | Intercept | |
| | | | | | | r^2 | $\hat{\beta}$ | 95% CI | $\hat{\alpha}$ | 95% CI |
| <u>Experimental and Field Data</u> | | | | | | | | | | |
| $\hat{\Phi}_{hw}$ | 28 | -0.51 | 0.0056* | -0.55 | 0.0026* | 0.30 | -0.71 | [-1.14, -0.26] | 0.50 | [0.36, 0.64] |
| $\hat{\Phi}_{Uw}$ | 7 | -0.57 | 0.18 | -0.63 | 0.13 | 0.40 | -0.84 | [-2.02, 0.34] | 0.53 | [0.13, 0.94] |
| $\hat{\Phi}_{Bw}$ | 28 | 0.20 | 0.30 | 0.14 | 0.49 | 0.02 | 0.11 | [-0.21, 0.44] | 0.19 | [-0.08, 0.45] |
| $\hat{\Phi}_{nD}$ | 6 | -0.14 | 0.79 | 0.15 | 0.78 | 0.02 | 0.06 | [-0.45, 0.56] | 0.18 | [-0.36, 0.72] |
| $\hat{\Phi}_{nB}$ | 24 | -0.46 | 0.024* | -0.44 | 0.032* | 0.19 | -0.35 | [-0.67, -0.03] | 0.41 | [0.28, 0.55] |
| <u>Forestry Yield Table Data</u> | | | | | | | | | | |
| $\hat{\Phi}_{nw}$ | 325 | -0.44 | <0.0001* | -0.46 | <0.0001* | 0.21 | -0.54 | [-0.65, -0.43] | 0.45 | [0.41, 0.48] |
| $\hat{\Phi}_{Uw}$ | 334 | 0.47 | <0.0001* | 0.48 | <0.0001* | 0.23 | 0.58 | [0.47, 0.69] | 0.09 | [0.04, 0.13] |
| $\hat{\Phi}_{Bw}$ | 318 | 0.55 | <0.0001* | 0.59 | <0.0001* | 0.35 | 0.36 | [0.30, 0.41] | 0.03 | [-0.01, 0.07] |
| $\hat{\Phi}_{nD}$ | 323 | -0.57 | <0.0001* | -0.67 | <0.0001* | 0.45 | -0.20 | [-0.23, -0.18] | 0.45 | [0.43, 0.47] |
| $\hat{\Phi}_{nB}$ | 309 | -0.56 | <0.0001* | -0.71 | <0.0001* | 0.50 | -0.36 | [-0.40, -0.32] | 0.44 | [0.42, 0.45] |

*Significant at the 95% confidence level ($P \leq 0.05$).

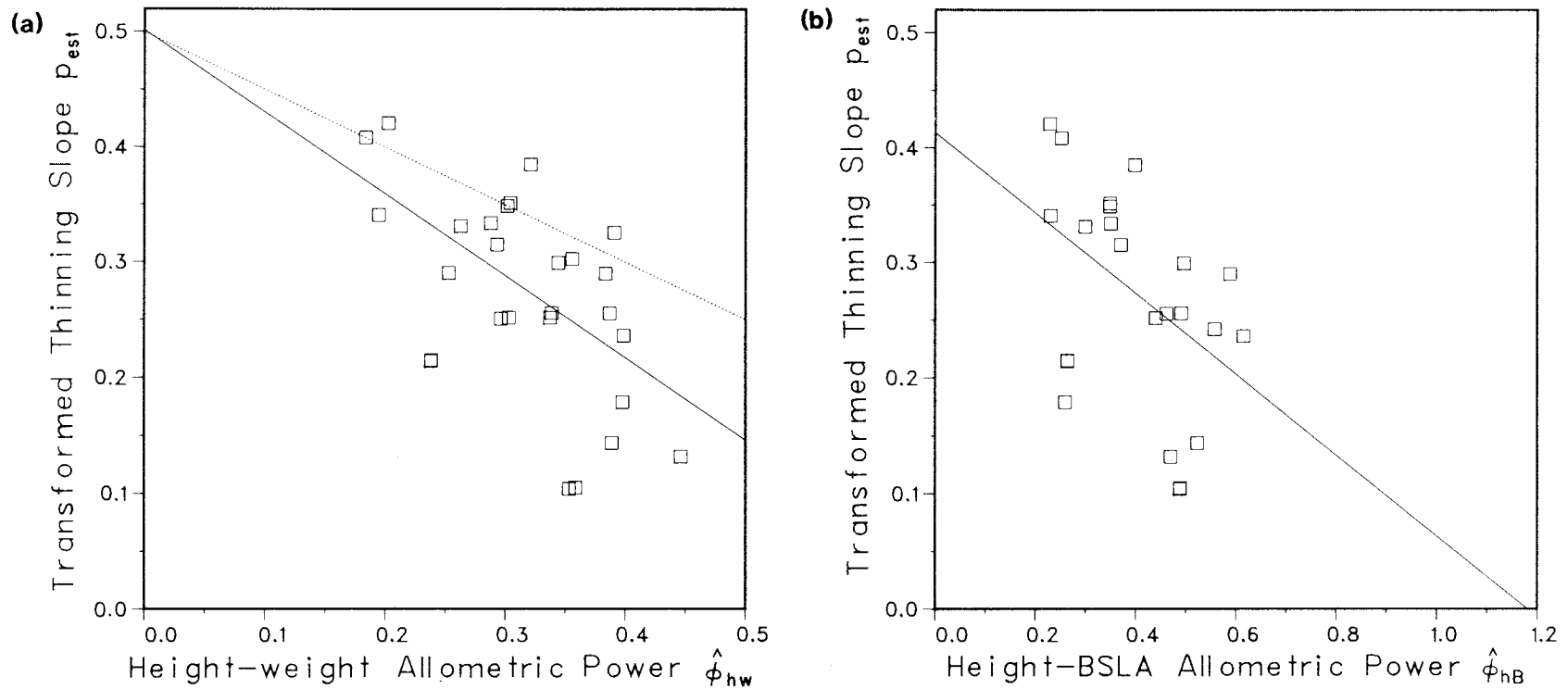


Figure 6.3. Observed relationships between transformed thinning slope and allometric powers in the experimental and field data. (a) shows p_{est} , plotted against the $\hat{\phi}_{hw}$, the average height-average weight allometric power. The solid line is the regression $p_{est} = -0.71 \hat{\phi}_{hw} + 0.50$, which is not significantly different (Table 6.3) from the predicted relationship $p = -0.5 \hat{\phi}_{hw} + 0.50$ (dotted line). (b) shows p_{est} plotted against $\hat{\phi}_{hB}$, the average height-average BSLA allometry. The solid regression line is $p_{est} = -0.35 \hat{\phi}_{hB} + 0.41$.

to predict p_{est} : 21% to 50% of the variance in p_{est} was explained. Even $\hat{\phi}_{Dw}$ and $\hat{\phi}_{Bw}$, which were not expected to relate well with p_{est} , were actually significantly correlated to p_{est} and explained 23% and 35%, respectively, of its variance. The relationship of p_{est} to $\hat{\phi}_{hw}$ explained 21% of the variance in p_{est} , and the regression line $p_{est} = -0.54 \hat{\phi}_{hw} + 0.445$ was close to the expected equation $p = -0.5 \hat{\phi}_{hw} + 0.5$ and did not differ significantly in slope from this line. The regression intercept of -0.445 was significantly less than expected, but the difference was small: the regression intercept was 11% below the expected 0.5. The position of the observed relationship below the expected one in the p_{est} - $\hat{\phi}_{hw}$ plane is partly due to the invalid but necessary assumption that $\phi_{dw} = 0$. Figure 6.4 shows the relationships of p_{est} with $\hat{\phi}_{hw}$, $\hat{\phi}_{hD}$, and $\hat{\phi}_{hB}$.

Small group sizes hindered the comparisons among the six groups of the EFD (herbaceous monocots, herbaceous dicots, temperate angiosperm trees, temperate gymnosperm trees, Eucalypts, and tropical angiosperm trees--see Table 6.4). Height was the most commonly measured plant dimension, yet only 28 of the 75 data sets that showed a significant log B-log N relationship also had height data and showed a significant log \bar{h} -log \bar{w} relationship. Group sizes were as low as one or two observations, so the absence of differences in $\hat{\phi}_{hw}$ among the six groups is inconclusive. A significant difference among the four tree groups was observed for $\hat{\phi}_{hB}$, and the mean values of $\hat{\beta}$ and $\hat{\phi}_{hB}$ for three groups were ranked in accordance with the allometric hypothesis: more

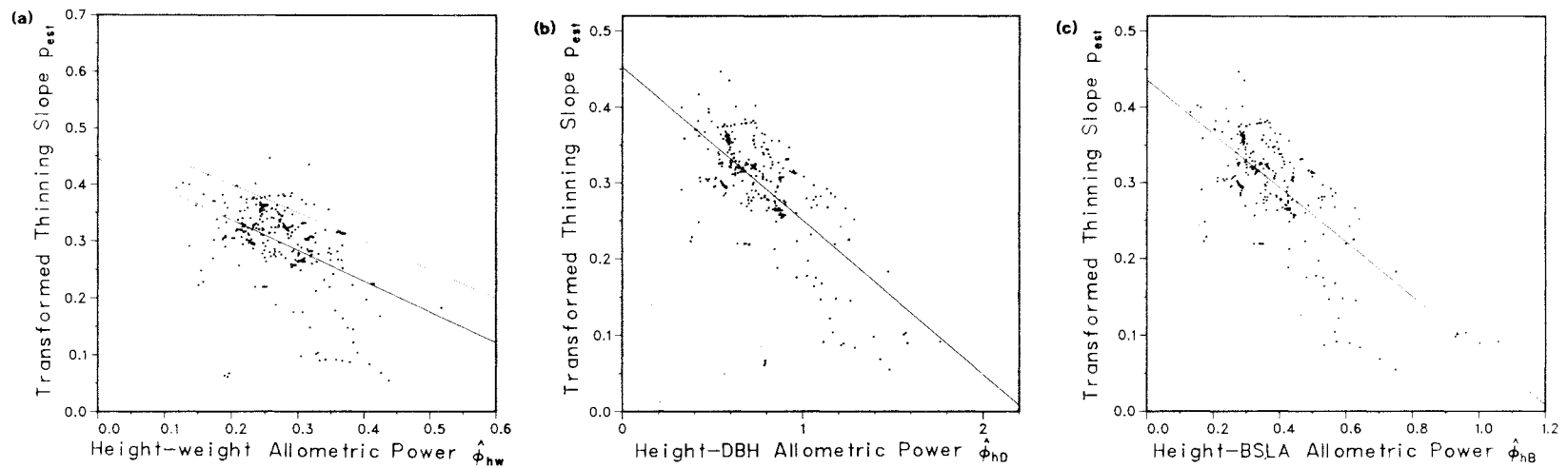


Figure 6.4. Observed relationships between transformed thinning slope and allometric powers in the forestry yield table data. (a) shows the transformed thinning slope, p_{est} , plotted against $\hat{\phi}_{hw}$, the average height-average weight allometry. The solid line is the regression $p_{est} = -0.54 \hat{\phi}_{hw} + 0.45$ while the dotted line is the predicted relationship $p = -0.5 \hat{\phi}_{hw} + 0.50$. (b) shows p_{est} plotted against $\hat{\phi}_{hD}$, the average height-average DBH allometry. The regression line is $p_{est} = -0.20 \hat{\phi}_{hD} + 0.45$. (c) shows p_{est} plotted against $\hat{\phi}_{hB}$, the average height-average BSLA allometry, and the regression line is $p_{est} = -0.36 \hat{\phi}_{hB} + 0.44$. Table 6.3 gives further statistical information.

Table 6.4. Tests for Differences in Allometric Powers Among Groups in the Experimental and Field Data.

| Allometric Power | Group Means ^a | | | | | | Tests for Differences Among Groups | | | |
|-------------------|--------------------------|---------------|------------------|------------------|--------------|-----------------|------------------------------------|-----------------------------|--------------------------------------|-----------------------------|
| | Herbs | | Trees | | | | All Groups ^b | | Temperate Trees Angio. vs. Gymno. | |
| | Mono-cots. | Di-cots. | Temperate Angio. | Temperate Gymno. | Eucal. | Tropical Angio. | ANOVA ^c | Kruskal-Wallis ^d | ANOVA ^c | Kruskal-Wallis ^d |
| $\hat{\beta}$ | -0.44 (8) | -0.74 (25) | -0.65 (15) | -0.87 (19) | -1.26 (4) | -2.56 (4) | 7.68(5,69) P<0.0001* | 17.9(5) P=0.0031* | 0.90(1,32) P=0.35 | 0.37(1) P=0.54 |
| $\hat{\alpha}$ | 4.45 (8) | 5.17 (25) | 3.78 (15) | 3.79 (19) | 2.87 (4) | 2.20 (4) | 10.9(5,69) P<0.0001* | 41.1(5) P<0.0001* | 0.00(1,32) P=0.97 | 1.43(1) P=0.23 |
| ρ_{est} | 0.36 (8) | 0.30 (25) | 0.32 (15) | 0.30 (19) | 0.24 (4) | 0.16 (4) | 5.77(5,69) P=0.0002* | 17.9(5) P=0.0031* | 0.57(1,32) P=0.46 | 0.37(1) P=0.54 |
| $\hat{\phi}_{hw}$ | 0.30 (1) | 0.33 (2) | 0.27 (9) | 0.35 (10) | 0.36 (2) | 0.30 (4) | 1.88(5,22) P=0.14 | 7.13(5) P=0.21 | 7.51(1,17) P=0.014* | 5.61(1) P=0.018* |
| $\hat{\phi}_{Dw}$ | | | 0.27 (1) | 0.33 (3) | 0.37 (3) | | 10.62(2,4) P=0.025* | 4.00(2) P=0.14 | 13.7(1,2) P=0.066 | 1.80(1) P=0.18 |
| $\hat{\phi}_{Bw}$ | | | 0.82 (8) | 0.79 (12) | 0.76 (4) | 0.81 (4) | 0.25(3,24) P=0.86 | 1.44(3) P=0.70 | 0.32(1,18) P=0.58 | 0.38(1) P=0.54 |

Table 6.4. (continued)

| Allo- metric Power | Group Means ^a | | | | | | Tests for Differences Among Groups | | | |
|--------------------------|--------------------------|--------------|---------------------|---------------------|-------------|--------------------|------------------------------------|---------------------------------|--------------------------------------|---------------------------------|
| | Herbs | | Trees | | | | All Groups ^b | | Temperate Trees Angio. vs. Gymno. | |
| | Mono- cots. | Di- cots. | Temperate Angio. | Temperate Gymno. | Eucal. | Tropical Angio. | ANOVA ^c | Kruskal- Wallis ^d | ANOVA ^c | Kruskal- Wallis ^d |
| $\hat{\phi}_{hD}$ | | | | 1.14 (3) | 1.01 (3) | | 1.56(1,4) P=0.28 | 1.19(1) P=0.28 | | |
| $\hat{\phi}_{hB}$ | | | 0.28 (7) | 0.46 (10) | 0.51 (3) | 0.38 (4) | 7.35(3,20) P=0.0017* | 12.0(3) P=0.0076* | 20.4(1,15) P=0.0004* | 9.17(1) P=0.0025* |

^aGroup sizes are given in parentheses.

^bTests for differences among all groups for which data were available.

^cF ratios for the ANOVAs are given, along with the degrees of freedom (in parentheses). P values are the statistical significance levels.

^dThe H statistic from the Kruskal-Wallis test is given, along with the degrees of freedom (in parentheses) used to estimate the statistical significance level, P, by the χ^2 approximation.

*Indicates significance at the 95% confidence level ($P \leq 0.05$).

negative thinning slopes corresponded to larger values of $\hat{\phi}_{hB}$. The fourth group, tropical angiosperm trees, was anomalous. It had the most negative mean $\hat{\beta}$, which should have been accompanied by the largest mean value of $\hat{\phi}_{hB}$, but the actual value of $\hat{\phi}_{hB}$ was the second lowest of the four groups. Sample sizes are again so small ($n \leq 4$ for two groups) so the results are not conclusive and detailed speculation on this anomaly is unwarranted.

A more conclusive analysis is possible for two tree groups, temperate angiosperms and temperate gymnosperms, that had larger group sizes ($n \geq 7$) for $\hat{\beta}$, $\hat{\phi}_{hw}$, and $\hat{\phi}_{hB}$. The difference in $\hat{\beta}$ between the two groups was not statistically significant; however, the gymnosperms seemed to have steeper self-thinning slopes (mean $\hat{\beta} = -0.87$) than did the angiosperms (mean $\hat{\beta} = -0.61$). If the allometric hypothesis is correct, this trend should be accompanied by a greater emphasis in height growth relative to radial growth in the gymnosperms than in the angiosperms. Such trends were present and statistically significant. For the gymnosperms, $\hat{\phi}_{hw}$ (mean $\hat{\phi}_{hw} = 0.35$) was significantly greater than for the angiosperms (mean $\hat{\phi}_{hw} = 0.27$). In addition, $\hat{\phi}_{hB}$ for the gymnosperms (mean $\hat{\phi}_{hB} = 0.46$) significantly exceeded the angiosperm value (mean $\hat{\phi}_{hB} = 0.28$).

The larger number of thinning trajectories and the more complete availability of dimensional data in the FYD permitted a more conclusive analysis of among-group differences (Table 6.5). The three groups of trees were temperate angiosperms, temperate gymnosperms, and Eucalypts, with mean $\hat{\beta}$ values of -0.60, -0.80,

Table 6.5. Tests for Differences in Allometric Powers Among Groups in the Forestry Yield Table Data.

| Allometric Power | Group Means ^a | | | Tests for Differences Among Groups | | | |
|-------------------|--------------------------|----------------|---------------|------------------------------------|-----------------------------|-----------------------------|-----------------------------|
| | | | | All Three Groups | | Angiosperms vs. Gymnosperms | |
| | Angio. | Gymno. | Eucal. | ANOVA ^b | Kruskal-Wallis ^c | ANOVA ^b | Kruskal-Wallis ^c |
| $\hat{\beta}$ | -0.60 (58) | -0.80 (281) | -3.90 (12) | 79.9(348) P<0.0001 | 14.9 P=0.0006 | 4.85(337) P=0.028 | 3.77 P=0.052 |
| $\hat{\alpha}$ | 3.50 (58) | 3.54 (281) | 1.09 (12) | 38.9(348) P<0.0001 | 11.9 P=0.0027 | 0.13(337) P=0.8 | 8.30 P=0.004 |
| ρ_{est} | 0.32 (58) | 0.30 (281) | 0.17 (12) | 29.1(348) P<0.0001 | 14.9 P=0.0006 | 7.28(337) P=0.0073 | 3.77 P=0.052 |
| $\hat{\phi}_{hw}$ | 0.22 (47) | 0.28 (260) | 0.30 (9) | 23.8(322) P<0.0001 | 36.3 P<0.0001 | 49.9(314) P<0.0001 | 36.9 P<0.0001 |
| $\hat{\phi}_{Dw}$ | 0.40 (53) | 0.36 (269) | 0.33 (12) | 11.4(331) P<0.0001 | 20.3 P<0.0001 | 18.3(307) P<0.0001 | 18.1 P<0.0001 |
| $\hat{\phi}_{Bw}$ | 0.85 (44) | 0.73 (265) | 0.73 (9) | 25.3(315) P<0.0001 | 44.6 P<0.0001 | 50.2(320) P<0.0001 | 44.8 P<0.0001 |
| $\hat{\phi}_{hD}$ | 0.56 (45) | 0.80 (269) | 0.98 (9) | 28.1(320) P<0.0001 | 51.4 P<0.0001 | 49.9(312) P<0.0001 | 49.9 P<0.0001 |
| $\hat{\phi}_{hB}$ | 0.27 (38) | 0.40 (265) | 0.53 (6) | 42.9(306) P<0.0001 | 21.8 P<0.0001 | 36.2(301) P<0.0001 | 41.4 P<0.0001 |

^aGroup sizes are given in parentheses.

^bF ratios for ANOVA are given, along with the denominator degrees of freedom (in parentheses). The three and two-group tests have, respectively, two and one degree(s) of freedom in the numerator of the F ratio. P values are the statistical significance levels.

^cThe H statistic from the Kruskal-Wallis test is given. Two and one degrees(s) of freedom, respectively, were used in the three-group and two-group tests to estimate statistical significance levels, P, by the χ^2 approximation.

and -3.90, respectively. These means were significantly different, both when all three groups were considered and when only the temperate angiosperms and temperate gymnosperms are compared (Chapter 5). The allometric hypothesis predicts that the allometric powers should be ranked in the same order: angiosperms with the lowest rate of height growth relative to radial growth, gymnosperms intermediate, and Eucalypts highest. This prediction is verified for all three of the allometric measures, $\hat{\Phi}_{hw}$, $\hat{\Phi}_{hD}$, and $\hat{\Phi}_{hB}$. The groups show the expected rankings and the differences among groups are statistically significant.

The observed correlations of shade tolerance with β in the FYD (Chapter 5) were accompanied by corresponding correlations of tolerance with the allometric powers (Table 6.6). For the gymnosperms, a significant positive correlation of β with tolerance was accompanied by negative correlations of shade tolerance with $\hat{\Phi}_{hw}$, $\hat{\Phi}_{hD}$, and $\hat{\Phi}_{hB}$, so shallower thinning slopes were associated with less emphasis on height growth relative to radial growth as predicted by the allometric hypothesis. The angiosperms showed very different behavior: thinning slope was negatively correlated with tolerance. This result is still consistent with the allometric hypothesis because the negative correlation between shade tolerance and β is accompanied by positive correlations of tolerance with $\hat{\Phi}_{hw}$, $\hat{\Phi}_{hD}$, and $\hat{\Phi}_{hB}$. However, the positive correlations of tolerance with $\hat{\Phi}_{hD}$ and $\hat{\Phi}_{hB}$ are not statistically significant, while the correlation between tolerance and the $\hat{\Phi}_{hw}$ allometry is of

Table 6.6. Spearman Correlations of Shade Tolerance with Allometric Powers in the Forestry Yield Table Data.

| Parameter | Means for Shade Tolerance Groups ^a | | | | | Spearman Correlation | |
|------------------------------|---|----------------|----------------|---|---|----------------------|----------------|
| | 1 | 2 | 3 | 4 | 5 | r _s | p ^b |
| <u>Temperate Angiosperms</u> | | | | | | | |
| $\hat{\beta}$ | -0.391 (10) | -0.547 (18) | -0.685 (18) | | | -0.52* (46) | 0.0002 |
| $\hat{\alpha}$ | 3.632 (10) | 3.437 (18) | 3.517 (18) | | | -0.19 (46) | 0.22 |
| Pest | 0.364 (10) | 0.335 (18) | 0.299 (18) | | | -0.52* (46) | 0.0002 |
| $\hat{\phi}_{hw}$ | 0.191 (7) | 0.220 (18) | 0.231 (16) | | | 0.29 (41) | 0.070 |
| $\hat{\phi}_{Dw}$ | 0.350 (10) | 0.416 (16) | 0.404 (18) | | | 0.19 (44) | 0.21 |
| $\hat{\phi}_{Bw}$ | 0.835 (9) | 0.906 (12) | 0.811 (16) | | | -0.18 (37) | 0.28 |
| $\hat{\phi}_{hD}$ | 0.502 (7) | 0.551 (16) | 0.577 (16) | | | 0.20 (39) | 0.22 |
| $\hat{\phi}_{hB}$ | 0.241 (6) | 0.249 (12) | 0.289 (16) | | | 0.25 (34) | 0.14 |
| Wood Density | 430. (10) | 522. (18) | 722. (18) | | | 0.92* (46) | <0.0001 |

Table 6.6. (continued)

| Parameter | Means for Shade Tolerance Groups ^a | | | | | Spearman Correlation | |
|------------------------------|---|----------------|----------------|----------------|----------------|----------------------|---------|
| | 1 | 2 | 3 | 4 | 5 | r_s | p^b |
| <u>Temperate Gymnosperms</u> | | | | | | | |
| $\hat{\beta}$ | -0.916 (32) | -0.748 (78) | -0.642 (47) | -1.149 (69) | -0.459 (41) | 0.35* (267) | <0.0001 |
| $\hat{\alpha}$ | 3.123 (32) | 3.438 (78) | 3.732 (47) | 3.280 (69) | 4.172 (41) | 0.57* (267) | <0.0001 |
| ρ_{est} | 0.266 (32) | 0.300 (78) | 0.308 (47) | 0.279 (69) | 0.344 (41) | 0.35* (267) | <0.0001 |
| $\hat{\phi}_{hw}$ | 0.299 (32) | 0.285 (78) | 0.274 (47) | 0.301 (69) | 0.247 (41) | -0.24* (267) | <0.0001 |
| $\hat{\phi}_{Dw}$ | 0.348 (32) | 0.345 (78) | 0.378 (47) | 0.354 (69) | 0.411 (41) | 0.46* (267) | <0.0001 |
| $\hat{\phi}_{Bw}$ | 0.721 (32) | 0.702 (78) | 0.758 (46) | 0.699 (68) | 0.821 (41) | 0.40* (265) | <0.0001 |
| $\hat{\phi}_{hD}$ | 0.865 (32) | 0.834 (78) | 0.745 (47) | 0.885 (69) | 0.603 (41) | -0.36* (267) | <0.0001 |
| $\hat{\phi}_{hB}$ | 0.420 (32) | 0.410 (78) | 0.370 (46) | 0.457 (68) | 0.301 (41) | -0.31* (265) | <0.0001 |
| Wood Density | 564. (32) | 553. (78) | 500. (47) | 415. (69) | 511. (41) | -0.42* (267) | <0.0001 |

^aSample sizes are given in parentheses.

^bStatistical significance level.

*Significant at the 95% confidence level ($P < 0.05$).

borderline significance ($P = 0.07$). These low confidence levels probably reflect the small sample sizes available for the angiosperms. The 46 angiosperm thinning trajectories considered in this analysis were drawn from only 15 different yield tables. The tables for mixed hardwood forests that contributed many estimates of $\hat{\beta}$ could not be used because average shade tolerances could not be assigned to these diverse communities.

Discussion

These results strongly support the allometric hypothesis. Logical deductions from the basic hypothesis $\beta = -1/(2p) + 1$ predicted that the height-weight, height-DBH, and height-BSLA allometric powers would be negatively correlated with the transformed thinning slope. This prediction was repeatedly verified by significant observed correlations of p_{est} with all three allometric powers of the FYD and with $\hat{\phi}_{hw}$ and $\hat{\phi}_{hB}$ in the EFD. Only in the single case of $\hat{\phi}_{hD}$ in the EFD were the results inconclusive because of the small sample size ($n = 6$). An equation was also predicted for the expected relationship between p_{est} and ϕ_{hw} ($p_{est} = -0.5 \phi_{hw} + 0.5$) and the observed relationships in the EFD and FYD were both close to this prediction.

The allometric hypothesis is further supported by the association of differences in thinning slope among groups with corresponding differences in plant allometry, as expected if allometric factors determine β . This correspondence was also observed when the correlation of shade tolerance with $\hat{\beta}$ was

compared to the correlations of tolerance with the allometric powers. The results of these two analyses were not as statistically significant as the results of direct correlation of p_{est} with the allometric parameters because these two analyses are less powerful and group sizes were small. Nevertheless, several significant trends were documented that did verify the predictions of the allometric hypothesis.

The results also address some questions posed in previous studies. Lonsdale and Watkinson (1983a) questioned whether plants growing at densities high enough to thin actually have different shapes. The variation documented in the univariate distributions of the allometric powers, the significant differences in these powers among groups, and the significant correlations of these powers with shade tolerance indicate that there are important variations in the shapes of plants undergoing self-thinning. Miyanishi et al. (1979) and Perry (1984) posed another important question: Are observed variations in the thinning slope due to experimental errors or biological reality? In fact, variations in self-thinning slope are systematically related to variations in plant allometry, so the deviations from the idealized value $\beta = -1/2$ are real, not simply errors in observing a biological constant.

There are several reasons why this study has found strong evidence for the allometric hypothesis while previous studies (Westoby 1976, Mohler et al. 1978, White 1981) did not. A major problem was the accepted belief that all thinning slopes are near the value predicted by the self-thinning rule, so that the goal was

to show how the diverse allometries of real plants are resolved to give the same thinning slope. Allometric models that failed to do this were judged to be in contradiction of empirical evidence (White 1981). New information on the true variability among thinning slopes (Chapters 4 and 5) leads naturally to a new emphasis: Can the observed variation be attributed to variation in plant allometry? The present results indicate that it can. Previous studies have also been hindered by small sample sizes. One of the major studies (Mohler et al. 1978) considered only two species for which both allometric data and self-thinning lines were available. The present results show so much variation around a relationship between thinning slope and an allometric parameter (Figures 6.3 and 6.4) that a sample of two points would be useless in detecting the trend. More data were available here because theoretical models were carefully analyzed to predict the relationship between thinning slope and allometries involving frequently measured plant dimensions, such as the height, DBH, and BSLA. Previous studies (Mohler et al. 1978, White 1981) have tried to predict thinning slope directly from some allometry involving crown area, which is more difficult to measure and less frequently reported than height or DBH.

Another factor in the present success is the method of fitting allometric powers. Typically two variables, such as height and weight, are measured for a sample of individuals and the allometric equation is fit to these data, so the allometry describes a relationship among individual plants. In contrast, the thinning

line is a relationship based on aggregate measurements of density and biomass for whole populations rather than for individuals. Here allometric powers were fit to aggregate stand variables, such as average height and average weight, so the results are more commensurate with thinning slope than allometric powers derived at the individual plant level. These whole-stand allometric powers also directly address the time-dynamics of shape change with stand growth, while allometries measured from a sample of individual plants focus more on the static size structure within a single sample. A dynamic emphasis is more relevant because self-thinning is a dynamic, whole-stand process. The whole-stand approach also permits allometric powers to be fit to the same stands of plants used to estimate $\hat{\beta}$. Other studies (Mohler et al. 1978, White 1981) have compared thinning slopes to allometric data from a small subsample of individuals or from completely different sources. This introduces confounding variations because allometric relationships vary significantly with site, time, and other factors (Hutchings 1975). Thinning slopes are also not species constants (Chapters 4 and 5).

Previous studies of self-thinning and allometry also had other problems. Westoby (1976) tested the allometric derivation of the self-thinning rule by measuring the thinning slope of prostrate cultivars of Trifolium subterraneum. He predicted that the plants would grow only radially and give log w-log N thinning slopes near -1, but the observed thinning slope was near the more typical value $\gamma = -3/2$. This was interpreted as a falsification of the

allometric theory. However, the experiment and conclusion have been questioned by White (1981), who does not accept the assumption that height remains constant for this species. The high variability around the relationships observed here demonstrates the futility of testing the allometric hypothesis with a single observation. The most detailed previous review of allometry and self-thinning (White 1981) also has some inconsistencies. This analysis predicted the range of variation in thinning slopes from two tree allometries, the weight-DBH allometry and the crown area-DBH allometry. While the effects of variation in the crown area-DBH allometry on thinning slope were carefully considered, the relationship between weight and DBH was fixed at $w \propto \text{DBH}^{2.5}$, despite evidence in the same report that the allometric power actually ranges from 1.8 to 3.3. In view of this omission, the derived ranges for thinning slopes are suspect, as are the conclusions drawn from these ranges.

There are, then, many reasons why this study found significant relationships between plant allometry and self-thinning slope while previous studies did not. However, the successes of this study were less than hoped. Several statistically significant relationships between thinning slope and allometric powers were found, but the most predictive explained only 50% of the variation among thinning slopes. There are at least five major sources of variation that reduced the explanatory power of the regressions: errors in estimating the thinning slope, errors introduced by the invalid assumption that the density of biomass in occupied space does not vary with size, differences in measurement methods among studies,

differences in the criteria for counting individuals, and errors from using independent variables that are only indirectly related to p , the allometry hypothesized to actually determine β .

The potentially serious errors from a posteriori manipulations required in estimating β have already been discussed (Chapter 4), as have the errors from incorrectly assuming that $\phi_{hd} = 0$. Differences in measurement methods also reduced explanatory power. For example, the regression model predicting p_{est} from $\hat{\phi}_{hw}$ for the FYD is derived from studies that variously defined stand height as the height of the tallest tree, the average of dominant trees only, the average of dominant and codominant trees, or the average of all trees. Other variations come from different criteria for deciding which individuals should be counted. In forest surveys, individuals below a certain DBH are commonly ignored, and this threshold varies with species, stand size, and the purpose of the study. Studies also differ in including certain plant parts in biomass measurements. Ecologists tend to include small twigs, roots, and leaves, while foresters tend to ignore these parts and report only the economically important volume of harvestable wood. These wood volumes vary further with the method of harvesting and the uses being considered (lumber, pulp, poles, etc.).

The indirect method of testing the allometric hypothesis also reduces the explanatory power of statistical models. The allometric powers ϕ_{hw} , ϕ_{hd} , and ϕ_{hb} are only indirectly related to the power p that is hypothesized to determine the thinning slope, and these indirect relationships are confounded by structural and

mechanical constraints on plant form. When the uncertainties due to measurement errors, differences in defining measurements, and the use of indirect allometric measures are all combined, the relatively low coefficients of determination observed in relating thinning slope to allometric powers are no longer surprising. Rather, the ability to simply detect the statistically significant correlations between thinning slope and allometric measures is a major positive result.

The statistical models demonstrate the importance of allometric factors in determining the thinning slope, but the significant proportion of unexplained variance admits the possibility that other factors may also affect β , such as the physiological parameters considered in some recent models (Pickard 1983, Perry 1984).

Some of the present results are also of interest beyond the context of the self-thinning rule. For example, one analysis of the FYD indicated opposite syndromes of adaptation to shading in the gymnosperm and angiosperm trees of the northern temperate forests. Among the gymnosperms, more tolerant trees exhibit shallower thinning slopes, greater height growth relative to radial growth, and wood that is less dense. On the other hand, the angiosperms show steeper thinning slopes with increasing shade tolerance (suggesting less height growth relative to radial growth) and greater wood density. Further analysis of this dichotomy in the adaptive responses to shading between the two groups of trees may yield insight into the origin and evolution of the two taxa and may contribute to general theories of tree strategies and forest dynamics.

THE OVERALL SIZE-DENSITY RELATIONSHIP

Introduction

This chapter considers the overall relationship between size and density among stands of different species and evaluates its relevance to the self-thinning rule. This relationship has been observed by plotting $\log \bar{w}$ against $\log N$ for stands of species ranging from herbs to trees (Gorham 1979), and by plotting self-thinning lines for many species on a single $\log \bar{w}$ - $\log N$ plot (White 1980). In both cases, the data are grouped around the line $\log \bar{w} = -3/2 \log N + 4$. This trend is referred to here as the overall relationship to distinguish it from the self-thinning lines of individual populations.

The existence of the overall relationship has been interpreted as strong evidence for the self-thinning rule. It has been claimed to show that: (1) The model for intraspecific thinning of Yoda et al. (1963) also applies to interspecific weight-density relationships (Gorham 1979). (2) The same self-thinning law applies to all plants (Hutchings and Budd 1981a, Hutchings 1983). (3) The slope and position of the thinning line are insensitive to plant geometry (Furnas 1981, Hutchings and Budd 1981a). (4) The empirical generality of the self-thinning rule is beyond question (White 1981). The causes of the overall relationship are examined here to determine if the existence of the relationship actually supports such interpretations.

Models of the Overall Size-density RelationshipHeuristic Model

The overall relationship between size and density can be deduced from basic principles using a heuristic model for fully-stocked stands of different plant species. Assume that all the plants in a given stand are the same size and shape and that each plant occupies a cylindrical volume of space called its volume of influence (VOI). Plant weight and the volume and dimensions of this cylinder are related by

$$w = v d = (\pi R^2 h) d \quad , \quad (7.1)$$

where w is plant weight (in g), v is the size of the VOI (in m^3), d is the density of plant material in the VOI (in g/m^3), and R and h are the radius and height, respectively, (in m) of the VOI. The ground area occupied by each plant is πR^2 and if all ground area is covered the density of plants per m^2 is simply

$$N = 1 / (\pi R^2) \quad . \quad (7.2)$$

The shape of the plants in a stand can be represented by the height to VOI radius ratio, $\tau = h/R$. Since $h = \tau R$, equation 7.1 can be rewritten as

$$w = (\pi R^3 \tau) d \quad , \quad (7.3)$$

which can be combined with equation 7.2 to give

$$w = [\tau d / \sqrt{\pi}] N^{-3/2} , \quad (7.4)$$

for a particular stand.

If plants in all stands had exactly the same values of τ and d , then the overall relationship among all stands would reduce to $\bar{w} = K N^{-3/2}$ where $K = \tau d / \sqrt{\pi}$. Actually, τ and d will vary among stands. Gorham's (1979) data can be used to estimate a range for τ . Assume that VOIs are cylindrical and that the base area, \bar{a} , of a VOI is $1/N$, then substitute and solve $\bar{a} = \pi \bar{R}^2$ to obtain $\bar{R} = (\pi N)^{-1/2}$. The estimated \bar{R} values can then be divided into the reported average heights to yield τ , which ranges from 2 to 12 for Gorham's 65 stands. Measurements of biomass per unit of canopy volume can provide estimates of d , the density of biomass in occupied space. For trees, the measurements range from 600 to 40000 g/m^3 , with most falling between 4000 and 13000 g/m^3 (White 1980). Lonsdale and Watkinson (1983a) reported values between 1500 and 5200 g/m^3 for three herbaceous species. Combining the ranges for τ and d with the log-transformed version of equation 7.4,

$$\log \bar{w} = -3/2 \log N + \log(\tau d / \sqrt{\pi}) , \quad (7.5)$$

yields equations for the minimum and maximum average weights possible at any plant density. The minimum values of 2 and 600 for τ and d , respectively, give $\log \bar{w} = -3/2 \log N + 2.83$, while the respective maximum values of 12 and 40000 give the parallel line $\log \bar{w} = -3/2 \log N + 5.43$. These two lines define a region of the $\log \bar{w}$ - $\log N$ plane enclosing all fully-stocked stands of identically

sized plants. Gorham's (1979) line, $\log \bar{w} = -1.49 \log N + 3.99$, is parallel to the boundary lines in the approximate center of the enclosed region. The principal axis line through a random sample of points distributed uniformly between the model boundary lines would have a slope of $-3/2$ and would be near Gorham's line.

Improved Model

The assumption that all plants in each stand are the same size and shape is clearly invalid, so this section analyzes a more complex model which represents each stand as a population with a lognormal distribution of individual weights. Within each stand, base area is represented by a simple power function of weight. Lognormal weight distributions have been repeatedly observed in plant stands (Koyama and Kira 1956, Obeid et al. 1967, White and Harper 1970, Hutchings and Budd 1981a). Power functions relating plant dimensions to weight have been validated and applied by both ecologists (Whittaker and Woodwell 1968, Hutchings 1975) and foresters (Bruce and Schumacher 1950). The weight distribution of a stand is specified by the lognormal distribution parameters ζ and σ , and the mean weight is

$$\bar{w} = e^{(\zeta + 0.5\sigma^2)} \quad (7.6)$$

(Johnson and Kotz 1970). The area occupied by an individual is obtained by assuming that all plants fill a cylindrical VOI to a density of $d \text{ g/m}^3$, and that the height to radius ratio of a plant

of average weight is τ . Solving $\bar{w} = \pi \bar{R}^3 \tau d$ for \bar{R} then gives the base radius of a plant of average weight

$$\bar{R}_{\bar{w}} = \left[\frac{\bar{w}}{\pi \tau d} \right]^{(1/3)}, \quad (7.7)$$

and the base area of the plant of average weight is simply $\pi \bar{R}^2$.

Across an entire stand, R is related to w by

$$R = c w^p, \quad (7.8)$$

where c and p are constants, so that base area a is

$$a = \pi c^2 w^{2p}. \quad (7.9)$$

Equations 7.7 and 7.9 can now be combined to fix the value of c at $c = \sqrt{a} / (\sqrt{\pi} \bar{w}^p)$ and yield a general formula for the base area of any plant

$$a = \pi \left[\frac{1}{\bar{w}^p} \left(\frac{\bar{w}}{\pi \tau d} \right)^{1/3} \right]^2 w^{2p}, \quad (7.10)$$

which simplifies to $a = c_1 w^{2p}$, where $c_1 = \pi c^2$. Since

$\ln w$ is normally distributed with mean ζ and standard deviation

σ (Johnson and Kotz 1970) and c_1 and p are constants,

$\ln a = \ln (c_1 w^{2p}) = \ln c_1 + 2p \ln w$ is normally distributed

with mean $\ln c_1 + 2p \zeta$ and standard deviation $2p \sigma$. The

expected value of a is

$$\bar{a} = e^{[\ln c_1 + 2p\zeta + 0.5 (2p\sigma)^2]}, \quad (7.11)$$

which simplifies to

$$\bar{a} = c_1 e^{2p (\zeta + p\sigma^2)} . \quad (7.12)$$

Assuming $N = 1 / \bar{a}$, equation 7.12 gives

$$N = 1 / [c_1 e^{2p (\zeta + p\sigma^2)}] , \quad (7.13)$$

the plant density for a stand at 100% cover specified by parameters ζ , σ , d , and p .

The overall $\log \bar{w}$ - $\log N$ relationship for this model was estimated by using Monte Carlo techniques to select parameters for 500 plant stands, then calculating the resulting densities (equation 7.13) and fitting a relationship between $\log \bar{w}$ and $\log N$. Parameters ζ and σ were actually derived from two parameters with more direct biological interpretations: the average weight \bar{w} and ρ , which measures the range of weights within a population. Individual weights in a crowded plant population commonly span about two orders of magnitude (White 1980). This information was applied to the distribution of $\ln w$ by assuming that the ninety-ninth percentile weight is approximately ρ times the first percentile value, where ρ ranged from 10 to 1000 to allow for deviations from the reported value of 100. Since $\ln w$ is normally distributed, the ninety-ninth percentile value is 4.652 standard deviations above the first percentile value and $e^{4.652\sigma} = \rho$. With this information, ζ and σ can be calculated sequentially from $\sigma = \rho/4.652$ and $\zeta = \ln \bar{w} - 0.5 \sigma^2$.

Values of the input parameters $\log \tau$, ρ , $\log d$, $\log \bar{w}$, and $\log \rho$ were chosen from uniform random distributions on the intervals given in Table 7.1. Statistics for the 500 derived values of ζ , σ , \bar{R} , \bar{h} , \bar{a} , N , and B are given in Table 7.2, along with values of a constant κ calculated from $\kappa = B \sqrt{N}$. Since \bar{w} was chosen a priori and random parameter variations were imposed in deriving N , \bar{w} is a truly independent variable and the correct method for estimating an overall linear relationship between $\log \bar{w}$ and $\log N$ is regression of $\log N$ against $\log \bar{w}$. The regression line was $\log N = -0.654 \log \bar{w} + 2.799$ ($r^2 = 0.96$, $P < 0.0001$, 95% CI for slope = $[-0.67, -0.64]$), which can be rearranged to give $\log \bar{w} = -1.53 \log N + 4.28$ (95% CI for slope = $[-1.56, -1.49]$), or equivalently, $\log B = -0.53 \log N + 4.28$ (95% CI for slope = $[-0.56, -0.49]$). Figure 7.1 shows the 500 hypothetical plant stands and this fitted relationship after transformation to $\log B$ - $\log N$ form to facilitate comparison with real plant data.

Discussion

The models show that the linear overall relationship between \log size and \log density results from the simple geometry of packing three-dimensional objects onto a two-dimensional surface. The slope of $-3/2$ in the $\log \bar{w}$ - $\log N$ plane follows directly from assuming a cylindrical shape for the VOI. The volume of any cylinder is a cubic function of the base radius while the base area is a function of the same radius squared, so that the ratio of these two powers is $3/2$. This result is robust to changes in the basic cylindrical

Table 7.1. Parameter Ranges for Monte Carlo Analysis of the Improved Model.

| Parameter | Parameter limits ^a | | Antilog limits ^b | |
|----------------|-------------------------------|---------|-----------------------------|---------|
| | Minimum | Maximum | Minimum | Maximum |
| $\log \bar{w}$ | -2.00 | 7.00 | 0.01 | 107 |
| $\log \tau$ | 0.30 | 1.08 | 2 | 12 |
| p | 0.05 | 0.45 | | |
| $\log d$ | 2.78 | 4.60 | 600 | 40000 |
| $\log x$ | 1.00 | 3.00 | 10 | 1000 |

^aParameter values for 500 plant stands were chosen from uniform random distributions on the indicated intervals.

^bThese columns give the antilogs of the limits of parameters for which uniform random distributions of the log values were used.

Table 7.2. Ranges of Variation of Variables Derived in the Monte Carlo Analysis of the Improved Model.

| Variable ^a | Mean | St. Dev. | Percentiles | | | | |
|-----------------------|--------|----------|-------------|----------|--------------|--------|-------------|
| | | | Min. 0 | 5 | Median 50 | 95 | Max. 100 |
| ζ | 4.94 | 6.07 | -5.48 | -4.25 | 4.80 | 14.5 | 15.9 |
| σ | 1.00 | 0.28 | 0.496 | 0.551 | 1.01 | 1.43 | 1.48 |
| \bar{R} | 0.657 | 1.21 | 0.00238 | 0.00557 | 0.126 | 3.08 | 8.99 |
| $\log \bar{R}$ | -0.889 | 0.881 | -2.62 | -2.25 | -0.90 | 0.49 | 0.95 |
| \bar{h} | 3.57 | 6.68 | 0.0105 | 0.0278 | 0.598 | 18.1 | 42.0 |
| $\log \bar{h}$ | -0.185 | 0.891 | -1.98 | -1.56 | -0.22 | 1.26 | 1.62 |
| \bar{a} | 6.38 | 24.0 | 0.0000188 | 0.000112 | 0.0598 | 33.6 | 258.7 |
| $\log \bar{a}$ | -1.24 | 1.76 | -4.73 | -3.94 | -1.22 | 1.53 | 2.41 |
| N | 1680 | 5632 | 0.00387 | 0.0298 | 16.7 | 8893 | 53270 |
| $\log N$ | 1.24 | 1.76 | -2.41 | -1.53 | 1.22 | 3.95 | 4.73 |
| B | 31110 | 72750 | 34.1 | 117 | 3927 | 142500 | 727600 |
| $\log B$ | 3.62 | 0.98 | 1.53 | 2.07 | 3.59 | 5.15 | 5.86 |
| κ | 35350 | 44340 | 1042 | 2150 | 18590 | 127100 | 294400 |
| $\log \kappa$ | 4.24 | 0.55 | 3.02 | 3.33 | 4.27 | 5.10 | 5.47 |

^aStatistics are calculated for 500 plant stands with input parameters chosen randomly from the ranges in Table 7.1.

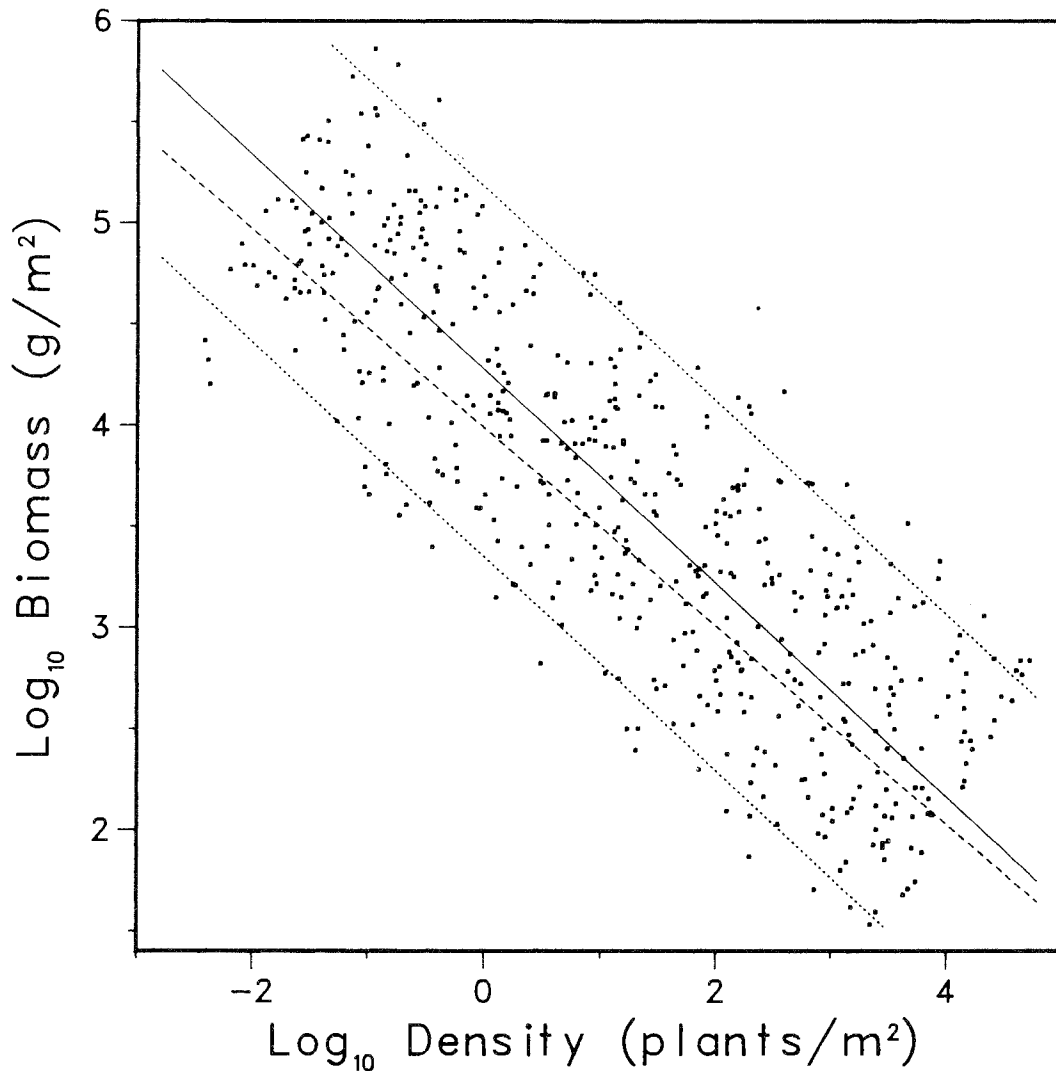


Figure 7.1. Monte Carlo analysis of the improved model for the overall size-density relationship. The data points represent 500 hypothetical plant stands characterized by parameter values chosen from uniform random distributions (Table 7.1). The solid line is the overall relationship $\log B = -0.53 \log N + 4.28$ ($r^2 = 0.96$, $P < 0.0001$, 95% CI for slope = $[-0.56, -0.49]$) fit by regressing $\log N$ against $\log \bar{w}$ and transforming the resulting equation into an expression for $\log B$ as a function of $\log N$. The dotted lines with intercepts of 3.33 and 5.10 are parallel to this line and enclose 90% of the data points. The dashed line is the relationship $\log B = -0.49 + 3.99$ fitted to data from 65 stands of 29 plant species by Gorham (1979).

model, since other geometric solids that might represent real VOIs (cones, pyramids, spheroids, rectangular solids, hexagonal solids, and any general prismatoids) show the same power relationships of volume and base area to a linear dimension of the base. The variation around the overall trend is related to the ranges of possible values for plant shape and the density of biomass in occupied space. The more complex model yields similar predictions, thus demonstrating that the heuristic results are not artifacts of assuming that all plants in a given stand are the same size and shape. Both models can be used to understand why the overall relationship obtains and both show that the origin of this relationship is different from the allometric factors that determine the slopes of single species thinning lines (Chapter 6).

The multi-species plots of Gorham (1979) and White (1980) address a fundamentally different question from an analysis of the self-thinning lines of individual populations. The former address the overall relationship determined by simple geometry while the latter addresses the time dynamics of space occupation by a single growing population. Because different phenomena are being examined, the existence of the overall relationship does not provide evidence for or against the self-thinning rule. It certainly does not show that self-thinning lines are insensitive to plant geometry. Instead, geometric differences are reflected by variations around the overall relationship.

This interpretation would still admit the hypothesis that the self-thinning trajectories of individual stands all approximate the

line $\log \bar{w} = -3/2 \log N + 4$ and so coincide with the overall relationship despite the differences in causality. This might seem justified on examining plots like that of White (1980) (Figure 7.2a), where thinning lines from many species seem to lie along a single line. However, in addressing real data, the $\log \bar{w}$ - $\log N$ diagram gives a distorted view in which the appearance of linearity and high correlation is artificially enhanced while variations among the data are hidden (Chapter 4). When the thinning lines are examined in an unbiased $\log B$ - $\log N$ diagram (Figure 7.2b) an overall relationship with a slope of $-1/2$ is present, but individual self-thinning lines vary widely in both slope and position around that trend. The same type of distortion is evident in Gorham's analysis. The $\log \bar{w}$ - $\log N$ plot (Figure 7.3a) shows the fitted line $\log \bar{w} = -1.49 \log N + 3.99$ and dotted lines enclosing 75% of the 65 stands examined (as in Gorham 1979). This plot appears to admit little potential variation from the overall trend and seems to justify the conclusion self-thinning lines must fall in a narrow band paralleling the overall relationship. However, the $\log B$ - $\log N$ plot of the same data (Figure 7.3b) with the dotted lines enclosing 90% of the observed stands shows that individual self-thinning lines can vary widely in slope and position from the overall trend yet still fall within the 90% limits. Thus, the overall relationship is consistent with different thinning slopes and intercepts for particular populations. In fact, the hypothesis that all self-thinning lines closely approximate $\log B = -1/2 \log N + 4$ has already been disproven (Chapter 5).

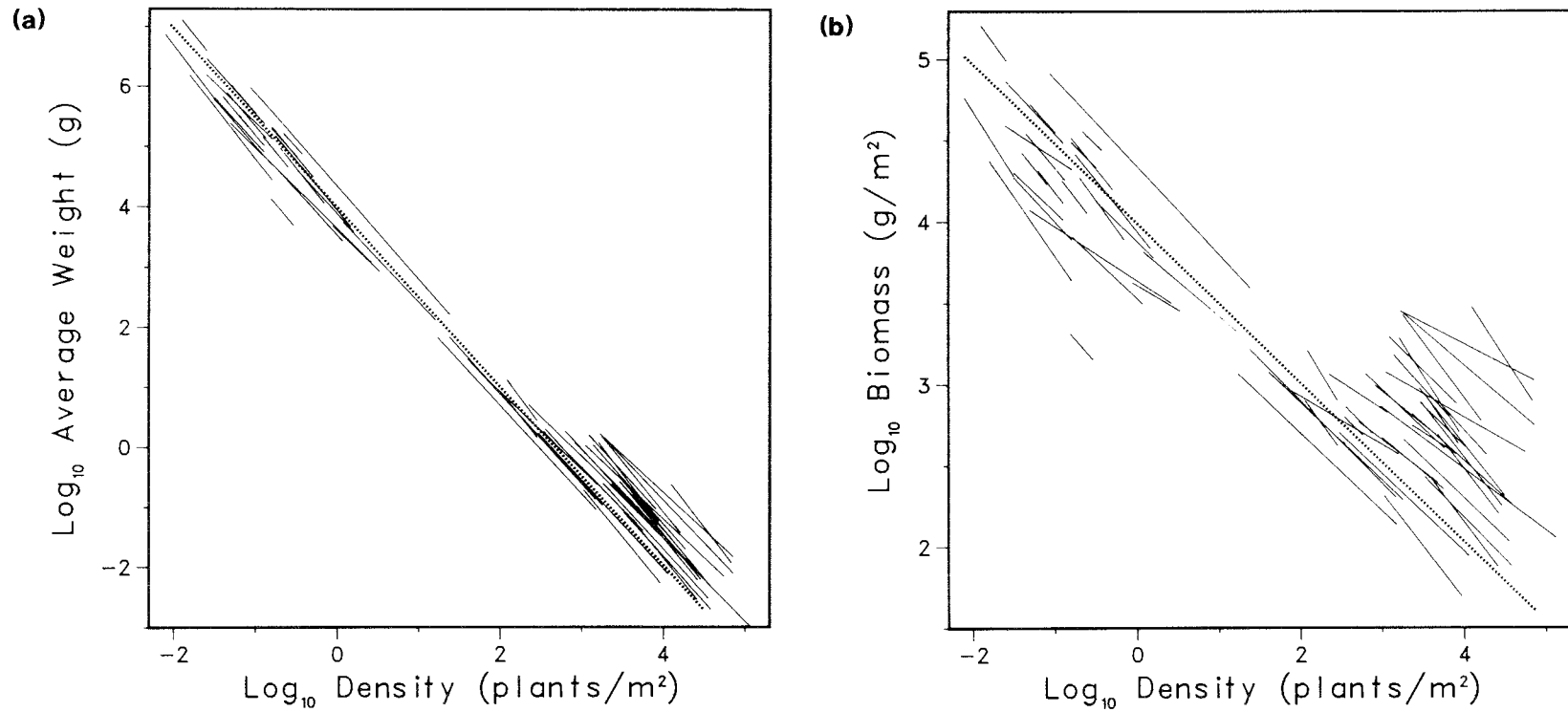


Figure 7.2. Previous analysis of the overall size-density relationship among thinning lines. (a) shows 65 previously cited self-thinning lines drawn by applying a reported thinning slope and intercepts (Table A.5) over the range of $\log N$ values covered by the thinning line (Table A.3). A similar plot of 31 thinning lines was constructed by White (1980). The dotted line is the overall relationship $\log \bar{w} = -1.49 \log N + 3.99$ (Gorham 1979). (b) shows the same 65 self-thinning lines and Gorham's line replotted in the $\log B$ - $\log N$ plane.

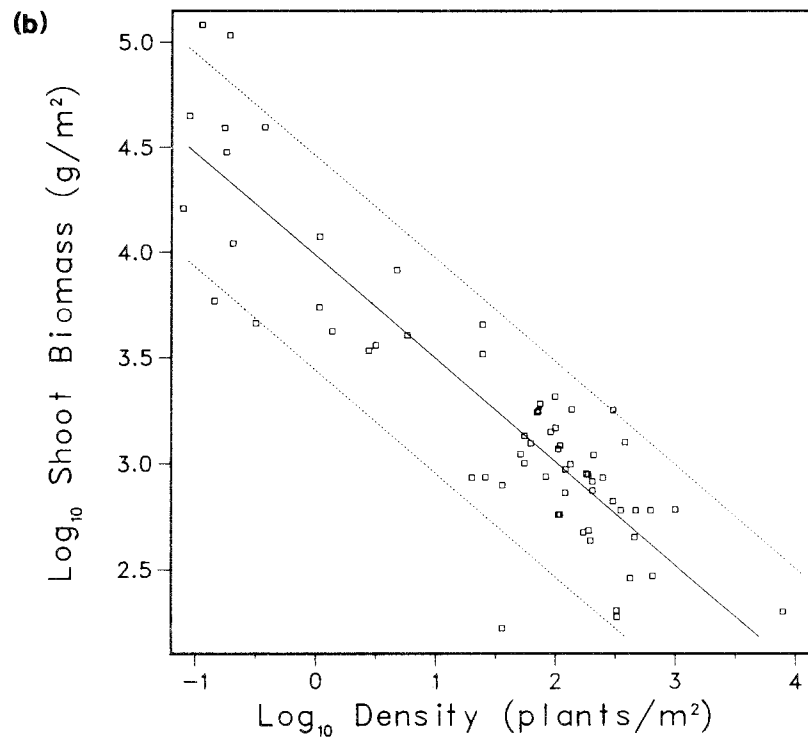
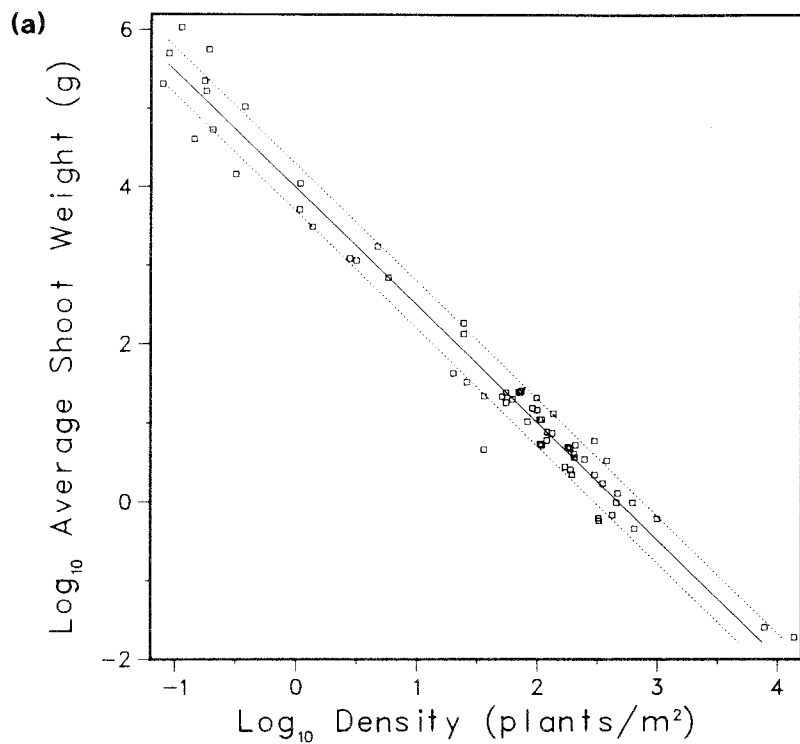


Figure 7.3. Gorham's analysis of the overall size-density relationship among stands of different species. (a) shows data for 65 fully-stocked stands of species as analyzed by Gorham (1979). The solid line is $\log \bar{w} = -1.49 \log N + 3.99$ and the dotted lines enclose 75% of the observations. In (b) the same data and fitted line are shown in a log B-log N plot, along with dotted lines enclosing 90% of the plant stands.

Further verification of the models for the overall relationship can be obtained by comparing the predicted limits of variation around the relationship to the observed limits. This can be done by calculating a value κ for a sample of real plant stands using

$$\kappa = B \sqrt{N} \quad , \quad (7.14)$$

which can be interpreted as the intercept at $\log N = 0$ of the line $\log B = -1/2 \log N + \log \kappa$ passing through the point $(\log N, \log B)$. $\log \kappa$ is in some ways similar to $\log K$, the intercept of a self-thinning line. Both κ and K are constants of power equations and both are related to plant shape and the density of biomass in occupied space. However, the two constants are associated with fundamentally different phenomena. K relates to the time-dynamic self-thinning line determined by the particular allometry of a given stand while κ relates to the overall relationship between size and density among all plant stands. Different symbols are used here to preserve this important distinction. Values of κ were calculated here for the 1033 individual stands used to construct 75 self-thinning lines from experimental and field data (EFD) and the 3330 stands used to estimate 351 self-thinning lines for forestry yield table data (FYD). Chapter 5 details the data sources and self-thinning analyses.

Table 7.3 presents summary statistics for calculated values of κ and $\log \kappa$ for both the EFD and the FYD while Figure 7.4 gives histograms for the distributions of $\log \kappa$. The range of $\log \kappa$

Table 7.3. Statistical Distributions of κ and $\log \kappa$.

| Statistic | Experimental and Field Data ^a | | | | | | Forestry Yield Table data | |
|-------------|--|---------------|---------------|---------------|---------------|---------------|---------------------------|---------------|
| | Shoot biomass | | Total biomass | | All data sets | | Bole Biomass | |
| | κ | $\log \kappa$ | κ | $\log \kappa$ | κ | $\log \kappa$ | κ | $\log \kappa$ |
| n | 700 | | 333 | | 1033 | | 3330 | |
| Mean | 21830 | 4.01 | 32600 | 4.14 | 25300 | 4.05 | 7746 | 3.82 |
| Std. dev. | 43350 | 0.47 | 70440 | 0.46 | 53800 | 0.47 | 4196 | 0.27 |
| CV (%) | 199 | 12 | 216 | 11 | 213 | 12 | 54 | 7 |
| Std. err. | 1638 | 0.02 | 3860 | 0.03 | 1674 | 0.01 | 72.7 | 0.005 |
| Skewness | 5.00 | 0.78 | 3.92 | 1.37 | 4.73 | 0.93 | 0.87 | -0.77 |
| Kurtosis | 30.1 | 1.13 | 15.8 | 1.79 | 25.1 | 1.40 | 1.60 | 0.80 |
| Range | 385300 | 3.49 | 479900 | 2.58 | 481000 | 3.58 | 30110 | 2.00 |
| Percentiles | | | | | | | | |
| 0 (Min.) | 125 | 2.10 | 1257 | 3.10 | 125 | 2.10 | 308 | 2.49 |
| 1 | 1010 | 3.00 | 3049 | 3.48 | 1671 | 3.22 | 1045 | 3.02 |
| 5 | 2815 | 3.45 | 4160 | 3.62 | 3074 | 3.49 | 2203 | 3.34 |
| 10 | 3461 | 3.54 | 4593 | 3.66 | 3992 | 3.60 | 2798 | 3.45 |
| 25 | 5115 | 3.71 | 7013 | 3.85 | 5437 | 3.74 | 4312 | 3.63 |
| 50 (Median) | 7690 | 3.89 | 11030 | 4.04 | 8508 | 3.93 | 7325 | 3.86 |
| 75 | 17010 | 4.23 | 18290 | 4.26 | 17310 | 4.24 | 10460 | 4.02 |
| 90 | 52560 | 4.72 | 55890 | 4.75 | 52830 | 4.72 | 13460 | 4.13 |
| 95 | 82470 | 4.92 | 194500 | 5.29 | 91810 | 4.96 | 14820 | 4.17 |
| 99 | 280100 | 5.45 | 394200 | 5.60 | 305700 | 5.49 | 18320 | 4.26 |
| 100 (Max.) | 385500 | 5.59 | 481200 | 5.68 | 481200 | 5.68 | 30420 | 4.48 |

^aThe three categories under this heading are based on the method of biomass measurement. "Shoot Biomass" includes thinning trajectories from biomass measurements of aboveground parts only. "Total Biomass" trajectories are based on biomass measurements that include aboveground and belowground parts. "All Data Sets" gives statistics for both of these groups combined.

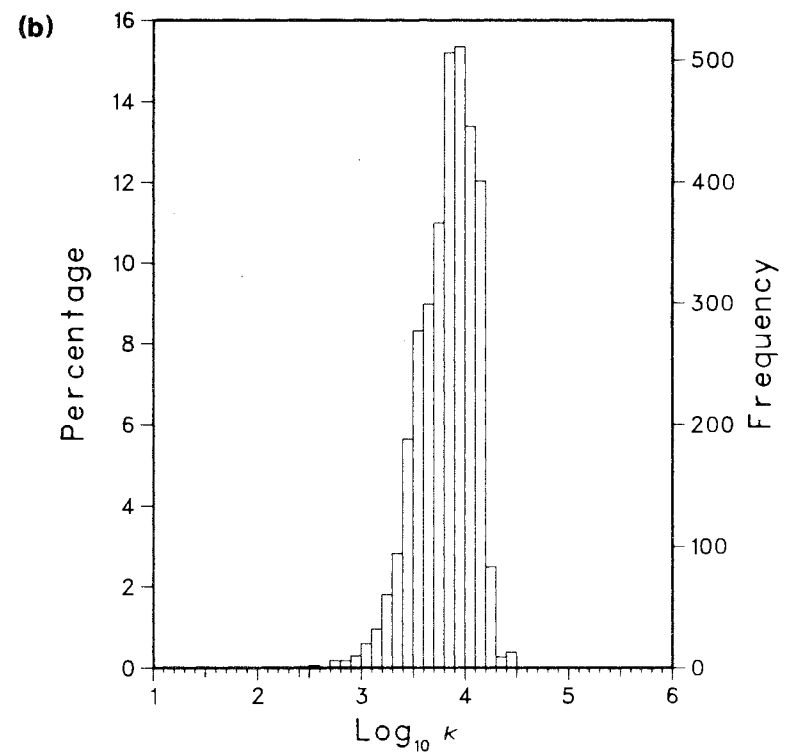
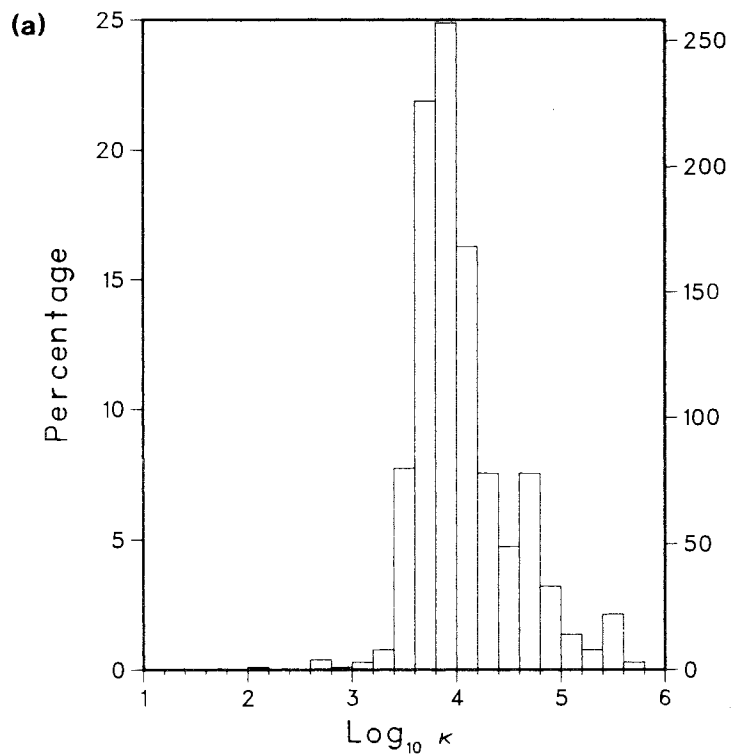


Figure 7.4. Histograms of $\log \kappa$. (a) shows the distribution of $\log \kappa$ values for the 1033 data points of the experimental and field data, while (b) gives the distribution of $\log \kappa$ for the 3330 data points of the forestry yield table data.

predicted by the heuristic model is $2.83 \leq \log \kappa \leq 5.43$ when the parameter ranges $600 \leq d \leq 40000$ and $2 \leq \tau \leq 12$ were used. Considering the extreme simplicity of the model and the crudity of the estimated parameter ranges, the agreement between the predicted range and the range observed for the EFD ($2.10 \leq \log \kappa \leq 5.68$) is remarkable. Agreement is likewise good with the predicted range $3.01 \leq \log \kappa \leq 5.47$ of the more complex model. Values of $\log \kappa$ for the FYD are consistently lower than the model predictions because many tree parts were not included in the wood volumes from which stand biomasses were estimated. The close agreement of predicted and observed κ ranges, despite the crude model parameter estimates, supports the adequacy of the model as a representation of the overall relationship. The fact that simple models produce the overall relationship with very minimal information suggests that this relationship is, indeed, a symptom of a very simple geometric phenomenon and not an area of profound biological interest. Equation 7.4 can be transformed to $\log B = -1/2 \log N + \log(\tau d / \sqrt{\pi})$ and combined with equation 7.12 to give $\log \kappa = \log(\tau d / \sqrt{\pi})$ and $\kappa = \tau d / \sqrt{\pi}$. According to this equation, κ can be interpreted as an composite measure of shape and density factors. The median values of $\log \kappa$ near 4 observed in both the EFD and FYD corresponds to a value of 5600 g/m^3 for the product τd .

The self-thinning rule has also been judged important in defining an ultimate thinning line which even constrains populations, such as clonal perennial herbs, that do not obey the self-thinning rule (Hutchings 1979). Theories have been proposed to

explain the different patterns of biomass-density dynamics of clonal herbs (Hutchings and Barkham 1976, Hutchings 1979, Pitelka 1984), but all assume that plant populations are eventually constrained to lie below a line of slope $-3/2$ in the $\log \bar{w}$ - $\log N$ plane. Hutchings (1979) proposed the line $\log \bar{w} = -3/2 \log N + 4.3$ while White (as cited in Pitelka 1984) has suggested that few plant populations exceed the size-density combinations defined by $\log \bar{w} = -3/2 \log N + 5$. White (1981) stated that the constraint imposed by this ultimate thinning line demonstrates the importance of the self-thinning rule, even for species whose stand dynamics do not necessarily trace a line of slope $-3/2$ in the $\log \bar{w}$ - $\log N$ plane.

The ultimate thinning line is explained by the simple models, which predict that all stands must lie below the line defined by extreme values of certain model parameters. In the heuristic model, stand biomass can be increased by raising plant height so that taller, more massive columns of biomass rest on the same piece of ground. Alternatively, more biomass can be packed into each cubic meter of biological volume by increasing d . Structural requirements and genetic limitations must ultimately constrain how tall and thin plants can become and still remain upright in the face of gravity, wind, and rain. Energetic constraints must limit the density of biomass per unit of ground area. No photoautotroph can pack more grams of living biomass onto a given surface than can be maintained by the conversion of the radiant energy falling on that surface. Also, natural selection would not favor plants that waste energy maintaining biomass beyond the amount that would give adequate

structural support, maximal capture of resources, and maximum reproduction.

The adequacy of the simple models for explaining the ultimate thinning line is supported by the good agreement between observed maximal values of $\log \kappa$ and the maximal values predicted from crude guesses about the maximum values of τ and d . The ninety-ninth percentile for $\log \kappa$ in the EFD is approximately 5.0, supporting the assertion that most stands fall below the line $\log \bar{w} = -3/2 \log N + 5.0$ (White, as cited in Pitelka 1984). However, the slope of this line is a consequence of simple geometry while its intercept is determined by energetic and structural constraints. A thorough exploration and quantitative evaluation of the general constraints on structure and biomass accumulation across the entire plant kingdom would be of great biological interest (and very difficult), but the existence of the ultimate thinning line of slope $-3/2$ is unsurprising. The term "ultimate thinning line" is also a misnomer. The constraint is not related to self-thinning dynamics and should hold regardless of how growth and mortality proceed in a given stand. In fact, a stand can approach this line by decreasing in average weight or actually increasing the density of individuals per unit area (Pitelka 1984), rather than by a mortality process as implied by the term "thinning."

The overall relationship between size and density among stands of plants with different thinning behaviors also has significance for efforts to construct single species thinning lines. Since it is often difficult to obtain successive measurements of a given stand

through time, thinning lines have been commonly estimated from single measurements of stands of different ages. If the stands are grown under equivalent conditions and actually follow the same thinning trajectory, this method will give good results. However, if the stands are following different thinning lines, possibly due to genetic variations in plant geometry or differences in illumination or site fertility, then the thinning analysis will tend to reveal the overall relationship rather than the particular thinning trajectory of any of the stands. For example, Mohler et al. (1978) presented thinning data for Prunus pensylvanica and reported a thinning slope of -1.46 from fitting $\log \bar{w}$ against $\log N$ by principal component analysis. However, their data were collected from four sites in New Hampshire that were up to 100 km apart (Marks 1974). Elevations at these sites ranged from 340 to 570 m on north, south, and southeast facing slopes. At some sites, Prunus pensylvanica shared dominance with an important codominant Populus tremuloides. It seems likely that the large differences in slope, aspect, and other factors among sites many kilometers apart might mean that the stands would in fact follow different thinning trajectories. The analysis of Mohler et al. (1978) which gave a slope near $-3/2$ may then have revealed the overall relationship among stands following different thinning trajectories rather than the particular time trajectory of one of the stands.

CONCLUSION

This study has examined the self-thinning rule from both theoretical and empirical perspectives and made major advances in explaining observed size-density relationships. These include: (1) developing and analyzing explanatory models to produce testable hypothesis about underlying causes, (2) considering some important but largely unrecognized difficulties in testing the self-thinning rule and suggesting remedies for some problems, (3) completing a major analysis of self-thinning data to quantify the extent of variation in thinning line slope and intercept, (4) relating this variation to variations in plant allometry to verify that allometric factors are important in positioning the thinning line, and (5) developing models to explain the overall size-density relationship and evaluate its relevance to the self-thinning rule. The results of this study provide a basic explanatory theory for the rule and clarify its scientific importance.

Several hypotheses about the cause of the self-thinning rule were derived from two mathematical models: a spatially averaged two-equation model and a simulation model that details individual sizes, locations, and competitive interactions. These hypotheses included: (1) Self-thinning lines are linear because plant dimensions and plant size are related by power functions. (2) The slope of the thinning line is determined by the allometry between the area occupied by an individual and its weight (the allometric

hypothesis). (3) The intercept of the thinning line is complexly related to plant allometry, the density of biomass in occupied space, and the partitioning of contested areas among competing individuals. Although the allometric hypothesis is not new (Westoby 1976, Miyanishi et al. 1979), the present models fill a major gap by deriving the hypothesis from time dynamic models rather than from ad hoc geometric arguments. The dynamic models can explain aspects of the thinning rule that simple geometric arguments can not, such as the dual nature of the thinning line as a time trajectory and a constraint separating feasible biomass-density combinations from impossible ones (Hozumi 1977, White 1981) and the change in thinning slope under low illumination (Westoby 1977). The models developed here emphasize a simple biological interpretation rather than an exact mathematical solution and relate the slope and intercept of the thinning line to meaningful ecological parameters rather than to arbitrary constants; therefore, the models are heuristically useful and yield hypotheses that can be tested with measurable biological data.

Chapter 4 considered the difficulties of testing the self-thinning rule and charted an optimal course for this task. Many potentially serious problems, such as the need for a posteriori data editing, do not presently have a good solution. Such problems have been previously discussed (Mohler et al. 1978, Hutchings and Budd 1981b), but their gravity has not been fully appreciated. These limitations have been explored here so that their implications for the acceptance of the rule can be evaluated. Other aspects of

the analysis do have an optimal solution and much of the data supporting the self-thinning rule has not been analyzed in the best possible way. The problems include inattention to contradictory data, an invalid data transformation, inappropriate fitting techniques, and lack of hypotheses testing. In view of these problems, the results and interpretations of many studies are questionable.

Chapter 5 presented the most exhaustive analysis of the self-thinning rule to date. Biomass and density data from previous self-thinning studies were reanalyzed to ensure that the selections of data, curve-fitting methods, and statistical interpretations were the most appropriate, and additional data not previously analyzed in a self-thinning context were included to broaden the body of test data. The data from previous studies did not provide strong support for the self-thinning rule. Many data sets that were claimed to corroborate the rule did not show any significant relationship between size and density, or gave a thinning slope different from the thinning rule prediction. The present analysis is also the most complete description of the variation in thinning slope and intercept, which are more variable than currently accepted. This greater variability was evidenced by by variations beyond currently accepted limits, by statistically significant differences in thinning slope and intercept among plant groups, and by significant correlations of slope and intercept with shade tolerance for forest trees.

The most important result of this study was the observation that variations in thinning slope are correlated with variations in plant allometry (Chapter 6). Such correlations were found in directly relating thinning slopes to allometric powers and in comparing among-group differences in thinning slope to among-group differences in allometric powers. This result supports the allometric hypothesis and verifies that the self-thinning rule is at least partly explainable by simple allometric arguments, despite previous failures to validate geometric models (Westoby 1976, Mohler et al. 1978, White 1981).

Finally, the slope of the overall size-density relationship among stands of different species was shown to be a trivial consequence of the geometry of packing objects onto a surface and of the limitation of the plant shape and the density of biomass in occupied space to biologically reasonable values. As such, the overall relationship represents a phenomenon different from the individual self-thinning line and does not provide evidence for or against the self-thinning rule.

The models suggest some additional analyses of self-thinning lines and tests of the hypotheses considered here. Some controlled experiments measuring thinning slope and several plant dimensions for species of differing allometric properties would be appropriate for verifying the evidence for the allometric hypothesis. It would also be instructive to gather data on plant allometry, density of biomass in occupied space, and the extent of overlap between

neighbors for several experimental populations to determine if these factors can explain the differences among thinning intercepts.

The results of this study have important implications for the scientific importance of the self-thinning rule. This rule does not qualify as an ecological law. The accepted constancy of the proposed law $\bar{w} = K N^{-3/2}$ (equivalently $B = K N^{-1/2}$) is based on a body of data, analysis, and interpretation that is flawed in many ways. The slopes and intercepts of thinning lines are actually quite variable and can be explained by simple geometric models. The variability in the thinning slope is particularly important because β is actually an exponent in the power equation $B = K N^\beta$ so small differences in β represent major differences in the predicted course of growth and mortality. Since the slopes of thinning lines do not take the same constant value, they do not provide evidence of the operation of a single quantitative law. Sprugel (1984) has also recently suggested that the $\log \bar{w}$ - $\log N$ thinning slope of $-3/2$ for trees is actually the exception rather than the rule. The recommendation of Pickard (1983) seems appropriate: It would now be profitable to proceed beyond the self-thinning rule to the analysis of deeper questions.

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APPENDIXES

APPENDIX A
EXPERIMENTAL AND FIELD DATA

Table A.1. Sources of Experimental and Field Data

| Id. Code ^a | Species | Group ^b | Study Type ^c | Data Type ^d | Conditions ^e | Reference ^f |
|-----------------------|--|--------------------|-------------------------|------------------------|-----------------------------|---|
| 1 | <u>Prunus pensylvanica</u> | TTmA | N | A | | Marks 1974, Tabs. 2,3 |
| 5 | <u>Populus tremuloides</u> | TTmA | N | A | | Pollard 1971, Tab. 1 |
| 7 | <u>Triticum</u> ^g | HM | F | TD | | Pollard 1972, Tab. 2 Puckridge and Donald 1967, Fig. 1, Tab. 2; White and Harper 1970, Fig. 5 |
| 8 | <u>Pinus strobus</u> | TTmG | P | T | Plot | Spurr et al. 1957, Tabs. 1,2 |
| 10 | <u>Trifolium subterraneum</u> | HD | E | T | | Westoby and Howell 1982, Tab. 1 |
| 14 | <u>Liquidambar styraciflua</u> | TTmA | N | T | | Tepper and Bamford 1960, Tab. 1 |
| 15 | <u>Erigeron canadensis</u> | HD | N | N | | Yoda et al. 1963, Fig. 14 |
| 16 | <u>Plantago asiatica</u> | HD | N | N | | Yoda et al. 1963, Fig. 13 |
| 17 | <u>Amaranthus retroflexus</u> | HD | N | N | | Yoda et al. 1963, Fig. 16 |
| 18 | <u>Ambrosia artemisiifolia</u> | HD | N | N | | Yoda et al. 1963, Fig. 15 |
| 19 | <u>Abies sachalinensis</u> | TTmG | N | N | | Yoda et al. 1963, Fig. 22 |
| 20 | <u>Chenopodium album</u> | HD | N | N | | Yoda et al. 1963, Fig. 17 |
| 21 | <u>Erigeron canadensis</u> | HD | F | T | | Yoda et al. 1963, Tabs. 2,3 |
| 22 | <u>Prunus pensylvanica</u> | TTmA | N | A | | Mohler et al. 1978 |
| 23 | <u>Abies balsamea</u> | TTmG | N | A | | Mohler et al. 1978 |
| 24 | <u>Abies sachalinensis</u> | TTmG | N | N | | Hozumi and Shinozaki 1970, Tab. 2A |
| 26 | <u>Betula</u> ^g | TTmA | N | N | | Yoda et al. 1963, Fig. 23 |
| 27 | <u>Trifolium praetense</u> | HD | E | T | | Westoby and Brown 1980, Fig. 2 |
| 28 | <u>Trifolium praetense</u> | HD | E | T | Illumination | Hutchings and Budd 1981b, Fig. 4 |
| 29 | <u>Fagopyrum esculentum</u> | HD | F | TD | | Yoda et al. 1963, Fig. 21 |
| 30 | <u>Trifolium praetense</u> | HD | F | TD | | Black 1960, Fig. 1, Tabs. 1-3 |
| 31 | <u>Medicago sativa</u> | HD | F | TD | | Black 1960, Fig. 1, Tabs. 1-3 |
| 32 | <u>Fagopyrum esculentum</u> | HD | E | TD | Fertility | Furnas 1981, Fig. 4.1 |
| 33 | <u>Beta vulgaris</u> | HD | E | TD | | Furnas 1981, Fig. 4.2 |
| 34 | <u>Beta vulgaris</u> | HD | E | T | | Furnas 1981, Fig. 4.5 |
| 35 | <u>Trifolium subterraneum</u> | HD | E | T | | Westoby 1976, Fig. 1 |
| 36 | <u>Ceanothus megacarpus</u> | S | N | A | | Schlesinger and Gill 1978, Fig. 3, Tab. 1 |
| 38 | <u>Lolium perenne</u> | HM | E | TD | Illumination | Kays and Harper 1974, Fig. 4 |
| 39 | <u>Betula</u> ^g | TTmA | N | N | Site | Hozumi and Shinozaki 1970, Tab. 2B,2C |
| 40 | <u>Tagetes patula</u> | HD | E | TD | | Ford 1975, Fig. 12 |
| 41 | <u>Quercus robur</u> | TTmA | N | A | | Barkham 1978, Tab. 5 |
| 43 | <u>Beta vulgaris</u> | HD | E | T | Illumination | Westoby and Howell 1981, Fig. 1 |
| 44 | <u>Helianthus annuus</u> | HD | F | TD | Experiment; Illumination | Hiroi and Monsi 1966, Figs. 1,5,6, Tab. 2 |
| 45 | <u>Picea mariana</u> | TTmG | N | A | | Hatcher 1963, Tab. 11 |
| 48 | <u>Corylus avellana</u> | TTmA | C | A | | Jeffers 1956, Tabs. 16-18 |
| 49 | <u>Fagopyrum esculentum</u> | HD | E | TD | | Furnas 1981, Fig. 4.6 |
| 50 | <u>Brassica juncea</u> | HD | F | TD | Illumination | Furnas 1981, Fig. 4.10 |
| 51 | <u>Sinapis alba</u> and <u>Leontodon sativum</u> | HD | E | T | | Bazzaz and Harper 1976, Fig. 1 |
| 52 | <u>Cryptomeria japonica</u> | TTmG | F | T | | Tadaki and Shidei 1959, Tabs. 1-3 |
| 53 | <u>Brassica napus</u> and <u>Raphanus sativus</u> | HD | E | T | | White and Harper 1970, Fig. 2 |

Table A.1. (continued)

| Id. Code ^a | Species | Group ^b | Study Type ^c | Data Type ^d | Conditions ^e | Reference ^f |
|-----------------------|---|--------------------|-------------------------|------------------------|-------------------------|--|
| 54 | <u>Larix occidentalis</u> and <u>Pinus monticola</u> | TTmG | N | T | | Foiles 1956, Tabs. 1,2 |
| 55 | <u>Trifolium praetense</u> | HD | E | T | | Malmberg and Smith 1982, Fig. 4 |
| 56 | <u>Medicago sativa</u> | HD | E | T | | Malmberg and Smith 1982, Fig. 4 |
| 57 | <u>Medicago sativa</u> and <u>Trifolium pratense</u> | HD | E | T | | Malmberg and Smith 1982, Fig. 3 |
| 58 | <u>Beta vulgaris</u> and <u>Brassica juncea</u> | HD | F | T | | Furnas 1981, Figs. 4.8,4.9 |
| 80 | <u>Taxodium distichum</u> | TTmG | N | N | | Schlesinger 1978, Fig. 3C |
| 81 | <u>Abies veitchii</u> and <u>Abies mariesii</u> | TTmG | N | A | | Oshima et al. 1958, Tab. 2, Fig. 4 |
| 82 | <u>Pinus taeda</u> | TTmG | N | AD | | Peet and Christensen 1980, Fig. 3; Christensen and Peet 1982, Fig. 15.2 |
| 84 | <u>Pinus densiflora</u> | TTmG | N | N | | Yoda et al. 1963, Fig. 24 |
| 86 | <u>Festuca pratensis</u> | HM | E | T | | Lonsdale and Watkinson 1983a, Figs. 1,2C |
| 87 | <u>Agrostemma githago</u> | HD | E | T | | Lonsdale and Watkinson 1983a, Figs. 1,2C |
| 88 | <u>Chicorium endivium</u> | HD | E | T | | Lonsdale and Watkinson 1983a, Figs. 1,2C |
| 89 | <u>Capsella bursa-pastoris</u> | HD | E | T | Grazing level | Dirzo and Harper 1980, Fig. 3 |
| 90 | <u>Poa annua</u> | HM | E | T | Grazing level | Dirzo and Harper 1980, Fig. 3 |
| 91 | <u>Lolium perenne</u> | HM | E | TD | Illumination | Lonsdale and Watkinson 1982, Fig. 1 |
| 92 | <u>Lolium perenne</u> | HM | E | T | Illumination | Lonsdale and Watkinson 1982, Fig. 5 |
| 93 | <u>Pinus strobus</u> | TTmG | P | T | | Beck 1978, Tab. 2; Wahlenberg 1955, Fig. 2 |
| 95 | <u>Eucalyptus obliqua</u> | TE | P | T | | Hillis and Brown 1978, Tab. 10.17 |
| 96 | <u>Eucalyptus pilularis</u> | TE | N | T | | Hillis and Brown 1978, Tab. 10.21 |
| 97 | <u>Eucalyptus regnans</u> | TE | N | T | | Hillis and Brown 1978, Tab. 10.24 |
| 98 | <u>Eucalyptus regnans</u> | TE | P | T | Site Index | Hillis and Brown 1978, Tab. 10.26 |
| 99 | <u>Eucalyptus deglupta</u> | TE | P | T | | Hillis and Brown 1978, Tab. 10.34 |
| 101 | <u>Eucalyptus grandis</u> | TE | P | A | | Cannell 1982, Page 11 |
| 102 | <u>Pinus taeda</u> | TTmG | N | A | | Cannell 1982, Page 320 |
| 103 | <u>Fagus sylvatica</u> | TTmA | N | A | | Cannell 1982, Page 31 |
| 104 | <u>Fagus sylvatica</u> | TTmA | N | A | | Cannell 1982, Page 58 |
| 105 | <u>Fagus sylvatica</u> | TTmA | N | A | | Cannell 1982, Page 72 |
| 106 | <u>Acer spicatum</u> | TTmA | N | A | | Cannell 1982, Page 33 |
| 109 | Mixed hardwoods (E. Canada) | TTmA | N | A | | Cannell 1982, Page 34 |
| 110 | <u>Pinus banksiana</u> | TTmG | N | A | | Cannell 1982, Page 44 |
| 111 | <u>Shorea robusta</u> | TTrA | P | A | | Cannell 1982, Page 79 |
| 112 | <u>Cyclobalanopsis</u> <u>myrsinaefolia</u> | TTmA | C | A | | Cannell 1982, Page 108 |
| 113 | <u>Tectona grandis</u> | TTrA | P | A | | Cannell 1982, Page 83 |
| 114 | <u>Abies veitchii</u> | TTmG | N | A | | Cannell 1982, Page 129 |
| 115 | <u>Camellia japonica</u> | TTmA | N | D | | Cannell 1982, Page 99 |
| 116 | <u>Eucalyptus obliqua</u> | TE | N | A | | Cannell 1982, Page 14 |
| 117 | <u>Abies firma</u> and <u>Tsuga sieboldii</u> | TTmG | N | A | | Cannell 1982, Page 124 |

Table A.1. (continued)

| Id. Code ^a | Species | Group ^b | Study Type ^c | Data Type ^d | Conditions ^e | Reference ^f |
|-----------------------|--|--------------------|-------------------------|------------------------|-------------------------|------------------------|
| 118 | <u>Eucalyptus tereticornis</u> | TE | P | A | | Cannell 1982, Page 78 |
| 119 | <u>Abies sachalinensis</u> | TTmG | P | A | | Cannell 1982, Page 126 |
| 120 | <u>Cryptomeria japonica</u> | TTmG | P | A | | Cannell 1982, Page 151 |
| 121 | <u>Betula</u> ^g | TTmA | N | A | | Cannell 1982, Page 238 |
| 122 | <u>Cryptomeria japonica</u> | TTmG | P | A | | Cannell 1982, Page 146 |
| 123 | <u>Castanea sativa</u> | TTmA | C | A | | Cannell 1982, Page 239 |
| 124 | <u>Abies</u> ^g | TTmG | N | A | | Cannell 1982, Page 133 |
| 125 | <u>Pinus sylvestris</u> | TTmG | P | A | | Cannell 1982, Page 243 |
| 126 | <u>Quercus pubescens</u> | TTmA | N | A | | Cannell 1982, Page 68 |
| 128 | <u>Pinus pumila</u> | TTmG | N | A | | Cannell 1982, Page 176 |
| 130 | <u>Pinus nigra</u> | TTmG | P | A | | Cannell 1982, Page 243 |
| 131 | <u>Alnus rubra</u> | TTmA | N | A | | Cannell 1982, Page 252 |
| 132 | <u>Cryptomeria japonica</u> | TTmG | P | A | | Cannell 1982, Page 146 |
| 133 | <u>Populus deltoides</u> | TTmA | N | A | | Cannell 1982, Page 266 |
| 135 | <u>Pinus banksiana</u> and mixed hardwoods | TTmG | N | A | | Cannell 1982, Page 300 |
| 136 | <u>Picea abies</u> | TTmG | P | A | | Cannell 1982, Page 73 |
| 137 | <u>Picea abies</u> | TTmG | N | A | | Cannell 1982, Page 361 |
| 138 | <u>Alnus incana</u> and <u>Salix</u> ^g | TTmA | N | A | | Cannell 1982, Page 251 |

^aAn arbitrary number assigned to facilitate cross-referencing among data tables.

^bOne of seven categories. HM = herbaceous monocots; HD = herbaceous dicots; S = shrubs; TTmA = trees, temperate angiosperms; TTmG = trees, temperate gymnosperms; TTrA = trees, tropical angiosperms; and TE = trees of genus Eucalyptus.

^cLevel of experimental control. N = natural field populations, P = tree plantations, C = coppiced trees, F = outdoor experiments, and E = greenhouse or light chamber experiments.

^dIndicates how observations of stands at different densities and biomasses were generated. T = repeated measurements of a single population (time series), A = observations of populations of different ages (age series), D = observations of populations started at different initial densities (density series), N = not specified.

^eNatural conditions or experimental treatments that may have affected thinning line slope or position, so that separate thinning lines were fitted to subsets of the data points from a single source. "Plot" and "site" both refer to different physical locations at which plant populations were observed. "Illumination" means that different populations received to different intensities of light. "Grazing level" and "fertility" likewise indicate that different populations were subjected to different levels of the indicated stress or resource. "Experiment" refers to different experiments that were considered separately in the reference. "Site index" is a measure of site quality used by foresters, here the height in meters of the largest trees when the stand is 20 years old. See the references given for further details.

^fTabular data were taken from the indicated table numbers. Figure numbers refer to graphs from which data were reconstructed.

^gGeneric name only indicates that the specific name was not given in the reference, or that more than one species from the genus were present.

Table A.2. Self-thinning Lines Fit to Experimental and Field Data

| Id. Code ^a | Condition ^b | No. of Points ^c | | r^2 | p^d | PCA Self-thinning Line ^e | | | | n_{est}^g |
|-----------------------|------------------------|----------------------------|-----|-------|----------|-------------------------------------|---------------------|----------------|---------------|-------------|
| | | n_T | n | | | Slope | | Intercept | | |
| | | | | | | $\hat{\beta}$ | 95% CI ^f | $\hat{\alpha}$ | 95% CI | |
| 1A | | 4 | 3 | 0.983 | 0.0829 | -0.429 | | 3.77 | | 0.350 |
| 1T | | 4 | 3 | 0.980 | 0.0911 | -0.424 | | 3.84 | | 0.351 |
| 5A | | 7 | 4 | 0.941 | 0.0300* | -0.264 | [-0.484, -0.065]* | 3.65 | [3.61, 3.67] | 0.396 |
| 7A | | 33 | 5 | 0.985 | 0.0008* | -0.362 | [-0.448, -0.280]* | 3.85 | [3.60, 4.11] | 0.367 |
| 8A | Lot 28 | 9 | 7 | 0.986 | <0.0001* | -0.724 | [-0.830, -0.628]* | 3.78 | [3.73, 3.83] | 0.290 |
| 8A | Lot 2C | 8 | 7 | 0.937 | <0.0001* | -1.116 | [-1.278, -0.976]* | 3.34 | [3.22, 3.43] | 0.236 |
| 10A | Full light | 10 | 10 | 0.836 | 0.0002* | -0.473 | [-0.660, -0.310] | 4.60 | [3.97, 5.33] | 0.339 |
| 14A | | 6 | 4 | 0.971 | 0.0145* | -0.667 | [-1.117, -0.348] | 3.71 | [3.37, 3.96] | 0.300 |
| 15T | | 47 | 31 | 0.930 | <0.0001* | -0.621 | [-0.688, -0.558]* | 4.36 | [4.19, 4.55] | 0.308 |
| 16T | | 38 | 38 | 0.926 | <0.0001* | -0.472 | [-0.518, -0.428] | 3.98 | [3.83, 4.13] | 0.340 |
| 17T | | 21 | 17 | 0.898 | <0.0001* | -0.588 | [-0.703, -0.483] | 4.06 | [3.80, 4.35] | 0.315 |
| 18T | | 51 | 43 | 0.886 | <0.0001* | -0.539 | [-0.601, -0.479] | 3.80 | [3.66, 3.96] | 0.325 |
| 19A | | 28 | 26 | 0.841 | <0.0001* | -0.649 | [-0.776, -0.535]* | 4.16 | [4.15, 4.17] | 0.303 |
| 20T | | 27 | 13 | 0.929 | <0.0001* | -0.405 | [-0.482, -0.332]* | 5.15 | [4.87, 5.45] | 0.356 |
| 21T | | 30 | 13 | 0.987 | <0.0001* | -1.038 | [-1.121, -0.962]* | 5.70 | [5.43, 6.00] | 0.245 |
| 22T | | 53 | 34 | 0.395 | <0.0001* | -0.410 | [-0.611, -0.234] | 3.92 | [3.82, 4.04] | 0.355 |
| 23T | | 29 | 23 | 0.654 | <0.0001* | -0.204 | [-0.273, -0.138]* | 3.88 | [3.88, 3.89] | 0.415 |
| 24T | | 9 | 5 | 0.839 | 0.0290* | -0.465 | [-0.965, -0.104] | 4.39 | [4.07, 4.83] | 0.341 |
| 26A | | 46 | 27 | 0.656 | <0.0001* | -1.033 | [-1.406, -0.760]* | 3.83 | [3.73, 3.89] | 0.246 |
| 27A | | 5 | 2 | 1.000 | | -0.313 | | 4.33 | | 0.381 |
| 28A | Low L.I. | 10 | 7 | 0.394 | 0.1310 | -0.851 | | 4.62 | | 0.270 |
| 28A | Med. L.I. | 14 | 8 | 0.137 | 0.3666 | -1.192 | | 6.53 | | 0.228 |
| 28A | High L.I. | 14 | 7 | 0.861 | 0.0026* | -0.627 | [-0.978, -0.360] | 4.78 | [3.95, 5.86] | 0.307 |
| 29T | | 25 | 9 | 0.954 | <0.0001* | -0.690 | [-0.836, -0.561]* | 5.08 | [4.68, 5.55] | 0.296 |
| 30A | | 22 | 9 | 0.137 | 0.3266 | -0.608 | | 4.89 | | 0.311 |
| 31A | | 22 | 11 | 0.180 | 0.1938 | -0.434 | | 3.95 | | 0.349 |
| 32T | 20% N.C. | 7 | 5 | 0.003 | 0.9289 | -0.024 | | 2.86 | | 0.488 |
| 32T | 100% N.C. | 7 | 5 | 0.024 | 0.8027 | -0.029 | [-0.430, 0.362] | 3.21 | [1.88, 4.59] | 0.485 |
| 33T | | 10 | 10 | 0.592 | 0.0092* | -1.335 | [-3.355, -0.648]* | 6.38 | [4.54, 11.80] | 0.214 |
| 34T | | 10 | 10 | 0.645 | 0.0052* | -2.304 | [-5.478, -1.348]* | 9.93 | [7.08, 19.38] | 0.151 |
| 35A | | 22 | 13 | 0.716 | 0.0003* | -0.622 | [-0.928, -0.382] | 5.17 | [4.33, 6.23] | 0.308 |
| 36A | | 11 | 10 | 0.226 | 0.1653 | -0.188 | [-0.514, 0.105] | 3.64 | [3.49, 3.80] | 0.421 |
| 38A | 30% L.I. | 20 | 7 | 0.054 | 0.6144 | 0.055 | [-0.227, 0.347] | 1.98 | [1.03, 2.89] | 0.529 |
| 38A | 70% L.I. | 20 | 8 | 0.422 | 0.0814 | -0.452 | [-1.429, 0.112] | 4.16 | [2.36, 7.28] | 0.344 |
| 39A | 100% L.I. | 20 | 8 | 0.549 | 0.0354* | -0.324 | [-0.674, -0.034] | 3.79 | [2.88, 4.89] | 0.378 |
| 39A | Kitami | 6 | 5 | 0.752 | 0.0569 | -0.429 | [-1.118, 0.030] | 4.85 | [4.52, 5.07] | 0.350 |
| 39A | Shirogane | 7 | 7 | 0.043 | 0.6554 | 0.051 | [-0.247, 0.359] | 4.69 | [4.59, 4.80] | 0.527 |
| 40A | | 14 | 10 | 0.343 | 0.0750 | -0.414 | [-1.146, 0.069] | 4.36 | [2.74, 6.82] | 0.354 |
| 41A | | 5 | 5 | 0.930 | 0.0081* | -0.618 | [-1.005, -0.331] | 3.84 | [3.43, 4.15] | 0.309 |
| 43A | 18% L.I. | 10 | 7 | 0.957 | 0.0001* | -0.662 | [-0.839, -0.509]* | 4.79 | [4.17, 5.50] | 0.301 |
| 43A | 25% L.I. | 10 | 7 | 0.916 | 0.0007* | -0.692 | [-0.973, -0.470] | 5.12 | [4.22, 6.25] | 0.296 |
| 43A | 37% L.I. | 10 | 7 | 0.940 | 0.0003* | -0.668 | [-0.886, -0.485] | 5.09 | [4.39, 5.94] | 0.300 |

Table A.2. (continued)

| Id. Code ^a | Condition ^b | No. of Points ^c | | r ² | p ^d | PCA Self-thinning Line ^e | | | | p _{est} ^q |
|-----------------------|------------------------|----------------------------|-----|----------------|----------------|-------------------------------------|---------------------|----------------|----------------|-------------------------------|
| | | n _T | n | | | Slope | | Intercept | | |
| | | | | | | $\hat{\beta}$ | 95% CI ^f | $\hat{\alpha}$ | 95% CI | |
| 43A | 55% L.I. | 11 | 8 | 0.934 | <0.0001* | -0.649 | [-0.838, -0.487] | 5.22 | [4.59, 5.95] | 0.303 |
| 43A | 100% L.I. | 9 | 7 | 0.698 | 0.0192* | -0.648 | [-1.415, -0.197] | 5.30 | [3.55, 8.27] | 0.303 |
| 44A | Ex. 2-60% L.I. | 27 | 4 | 0.838 | 0.0844 | -0.868 | | 4.69 | | 0.268 |
| 44A | Ex. 2-100% L.I. | 27 | 4 | 0.790 | 0.1168 | -0.926 | | 5.14 | | 0.260 |
| 44T | Ex. 1-23% L.I. | 29 | 10 | 0.157 | 0.2576 | -0.106 | [-0.318, 0.098] | 2.57 | [2.14, 3.02] | 0.452 |
| 44T | Ex. 1-60% L.I. | 32 | 8 | 0.834 | 0.0015* | -0.313 | [-0.460, -0.176]* | 3.60 | [3.28, 3.95] | 0.381 |
| 44T | Ex. 1-100% L.I. | 32 | 6 | 0.364 | 0.2048 | -0.147 | [-0.453, 0.133] | 3.42 | [2.69, 4.21] | 0.436 |
| 44T | Ex. 2-60% L.I. | 27 | 4 | 0.842 | 0.0826 | -0.867 | | 4.71 | | 0.268 |
| 44T | Ex. 2-100% L.I. | 27 | 4 | 0.764 | 0.1259 | -0.968 | | 5.25 | | 0.254 |
| 45A | | 32 | 25 | 0.391 | 0.0008* | -0.475 | [-0.775, -0.232] | 3.77 | [3.66, 3.86] | 0.339 |
| 48A | | 7 | 7 | 0.589 | 0.0439* | -0.721 | [-2.545, -0.052] | 3.72 | [3.53, 4.25] | 0.291 |
| 49T | | 12 | 10 | 0.089 | 0.4031 | -0.075 | [-0.283, 0.126] | 3.03 | [2.37, 3.72] | 0.465 |
| 50T | 15% L.I. | 12 | 12 | 0.391 | 0.0296 | 0.284 | [0.037, 0.568] | 0.97 | [0.19, 1.65] | 0.698 |
| 50T | 100% L.I. | 22 | 22 | 0.021 | 0.5217 | 0.038 | [-0.085, 0.162] | 2.27 | [1.91, 2.62] | 0.520 |
| 51A | | 30 | 24 | 0.131 | 0.0819 | -0.304 | [-0.741, 0.048] | 3.64 | [2.45, 5.13] | 0.383 |
| 52A | | 9 | 3 | 0.829 | 0.2711 | -1.594 | | 6.52 | | 0.193 |
| 53T | | 36 | 29 | 0.547 | <0.0001* | -0.391 | [-0.541, -0.255] | 4.31 | [3.87, 4.80] | 0.359 |
| 54A | | 4 | 4 | 0.978 | 0.0113* | -1.454 | [-2.504, -0.924]* | 3.35 | [2.63, 3.71] | 0.204 |
| 55A | | 17 | 11 | 0.333 | 0.0633 | -1.879 | [-0.596, 18.075] | 9.69 | [-66.11, 4.81] | 0.174 |
| 56A | | 17 | 11 | 0.766 | 0.0004* | -0.780 | [-1.186, -0.488] | 5.76 | [4.65, 7.32] | 0.281 |
| 57A | | 21 | 13 | 0.559 | 0.0033* | -1.017 | [-2.011, -0.519]* | 6.58 | [4.70, 10.32] | 0.248 |
| 58T | | 32 | 23 | 0.030 | 0.4304 | -0.088 | [-0.334, 0.147] | 2.50 | [1.98, 3.14] | 0.460 |
| 80A | | 18 | 5 | 0.876 | 0.0192* | -0.725 | [-1.506, -0.277] | 4.23 | [3.70, 4.54] | 0.290 |
| 81A | | 7 | 4 | 0.886 | 0.0588 | -0.615 | [-2.769, 0.123] | 4.06 | [3.87, 4.64] | 0.310 |
| 82A | | 42 | 17 | 0.468 | 0.0025* | -0.305 | [-0.499, -0.130]* | 4.21 | [4.11, 4.30] | 0.383 |
| 84A | | 286 | 243 | 0.248 | <0.0001* | -0.529 | [-0.653, -0.417] | 3.73 | [3.61, 3.84] | 0.327 |
| 86A | | 18 | 15 | 0.582 | 0.0009* | -0.985 | [-1.721, -0.562]* | 7.54 | [5.67, 10.80] | 0.252 |
| 87A | | 15 | 12 | 0.934 | <0.0001* | -0.651 | [-0.781, -0.535]* | 5.49 | [5.05, 5.98] | 0.303 |
| 88A | | 18 | 15 | 0.864 | <0.0001* | -0.993 | [-1.265, -0.779]* | 6.52 | [5.75, 7.50] | 0.251 |
| 89A | Grazed | 5 | 3 | 0.995 | 0.0447* | -0.612 | [-1.592, -0.089] | 4.14 | [2.09, 7.99] | 0.310 |
| 89A | Ungrazed | 5 | 5 | 0.948 | 0.0051* | -0.618 | [-0.932, -0.372] | 4.28 | [3.36, 5.45] | 0.309 |
| 90A | Grazed | 5 | 2 | 1.000 | | -0.870 | | 5.67 | | 0.267 |
| 90A | Ungrazed | 5 | 2 | 1.000 | | -0.479 | | 4.36 | | 0.338 |
| 91A | 17% L.I. | 25 | 13 | 0.464 | 0.0104* | -0.146 | [-0.252, -0.042]* | 2.81 | [2.43, 3.20] | 0.436 |
| 91A | 100% L.I. | 25 | 10 | 0.908 | <0.0001* | -0.427 | [-0.543, -0.319] | 4.80 | [4.36, 5.27] | 0.350 |
| 91T | 17% L.I. | 20 | 13 | 0.293 | 0.0559 | -0.097 | [-0.199, 0.003] | 2.66 | [2.30, 3.04] | 0.456 |
| 91T | 100% L.I. | 20 | 10 | 0.854 | 0.0001* | -0.245 | [-0.330, -0.163]* | 4.20 | [3.87, 4.54] | 0.402 |
| 92A | 17% L.I. | 5 | 5 | 0.760 | 0.0539 | -0.189 | [-0.398, 0.006] | 2.69 | [1.96, 3.48] | 0.421 |
| 92A | 23% L.I. | 5 | 5 | 0.776 | 0.0483* | -0.544 | [-1.509, -0.011] | 4.33 | [2.28, 8.06] | 0.324 |
| 92A | 44% L.I. | 5 | 5 | 0.786 | 0.0450* | -0.503 | [-1.273, -0.027] | 4.28 | [2.48, 7.20] | 0.333 |
| 92A | 100% L.I. | 7 | 5 | 0.712 | 0.0725 | -0.474 | [-1.589, 0.124] | 4.38 | [2.08, 8.67] | 0.339 |
| 93A | | 8 | 8 | 0.955 | <0.0001* | -0.954 | [-1.189, -0.764]* | 3.44 | [3.25, 3.60] | 0.256 |

Table A.2. (continued)

| Id. Code ^a | Condition ^b | No. of Points ^c | | r ² | p ^d | PCA Self-thinning Line ^e | | | | p _{est} ^g |
|-----------------------|------------------------|----------------------------|----|----------------|----------------|-------------------------------------|---------------------|----------------|----------------|-------------------------------|
| | | n _T | n | | | Slope | | Intercept | | |
| | | | | | | $\hat{\beta}$ | 95% CI ^f | $\hat{\alpha}$ | 95% CI | |
| 95A | | 3 | 2 | 1.000 | | -0.757 | | 4.04 | | 0.285 |
| 96A | | 28 | 4 | 0.892 | 0.0554 | -1.262 | | 3.02 | | 0.221 |
| 97A | | 4 | 2 | 1.000 | | -0.841 | | 3.79 | | 0.272 |
| 98A | S.I. 22.8 | 4 | 2 | 1.000 | | -3.005 | | 1.55 | | 0.125 |
| 98A | S.I. 28.9 | 4 | 4 | 0.971 | 0.0146* | -2.478 | [-5.012, -1.559]* | 1.39 | [-1.63, 2.48] | 0.144 |
| 98A | S.I. 33.5 | 4 | 4 | 0.964 | 0.0183* | -1.066 | [-2.132, -0.549]* | 3.44 | [2.31, 3.99] | 0.242 |
| 99A | | 10 | 7 | 0.664 | 0.0255* | -0.986 | [-3.077, -0.309] | 2.70 | [-0.84, 3.84] | 0.252 |
| 101A | | 8 | 8 | 0.040 | 0.6340 | -29.542 | [-4.882, 7.398] | -27.20 | [-1.16, 11.80] | 0.016 |
| 102A | | 10 | 9 | 0.939 | <0.0001* | -0.670 | [-0.837, -0.526]* | 3.42 | [3.23, 3.59] | 0.299 |
| 103A | | 3 | 3 | 0.901 | 0.2038 | -0.958 | | 3.77 | | 0.255 |
| 103T | | 3 | 3 | 0.949 | 0.1450 | -0.782 | | 3.97 | | 0.281 |
| 104A | | 6 | 6 | 0.945 | 0.0011* | -0.467 | [-0.636, -0.318] | 3.72 | [3.51, 3.91] | 0.341 |
| 105A | | 3 | 3 | 0.861 | 0.2431 | -0.218 | | 4.07 | | 0.411 |
| 105T | | 3 | 3 | 0.847 | 0.2560 | -0.204 | | 4.14 | | 0.415 |
| 106A | | 8 | 8 | 0.770 | 0.0042* | -0.534 | [-0.889, -0.261] | 3.46 | [3.43, 3.49] | 0.326 |
| 109A | | 11 | 4 | 0.013 | 0.8861 | 0.060 | | 3.48 | | 0.532 |
| 110A | | 12 | 8 | 0.280 | 0.1777 | 0.187 | [-0.125, 0.539] | 4.04 | [3.72, 4.40] | 0.615 |
| 110T | | 4 | 3 | 0.780 | 0.3108 | 0.548 | | 4.28 | | 1.106 |
| 111A | | 12 | 10 | 0.848 | 0.0002* | -3.808 | [-5.766, -2.810]* | 1.28 | [-0.18, 2.02] | 0.104 |
| 111T | | 12 | 10 | 0.842 | 0.0002* | -3.760 | [-5.766, -2.755]* | 1.40 | [-0.09, 2.14] | 0.105 |
| 112A | | 3 | 3 | 0.998 | 0.0270* | -1.301 | [-2.495, -0.746]* | 4.38 | [4.26, 4.64] | 0.217 |
| 113A | | 6 | 5 | 0.887 | 0.0167* | -1.326 | [-3.173, -0.660]* | 3.02 | [1.09, 3.72] | 0.215 |
| 113T | | 6 | 5 | 0.878 | 0.0189* | -1.335 | [-3.430, -0.639]* | 3.10 | [0.91, 3.83] | 0.214 |
| 114A | | 9 | 9 | 0.890 | 0.0001* | -0.299 | [-0.396, -0.206]* | 4.07 | [4.05, 4.10] | 0.385 |
| 114T | | 9 | 9 | 0.887 | 0.0001* | -0.299 | [-0.397, -0.205]* | 4.16 | [4.13, 4.19] | 0.385 |
| 115A | | 4 | 4 | 0.893 | 0.0552 | -0.587 | [-2.050, 0.055] | 4.04 | [3.64, 4.22] | 0.315 |
| 116A | | 4 | 3 | 1.000 | 0.0074* | -0.513 | [-0.591, -0.439] | 3.94 | [3.85, 4.02] | 0.330 |
| 117A | | 7 | 3 | 0.953 | 0.1384 | -0.089 | [-0.361, 0.171] | 4.47 | [4.16, 4.77] | 0.459 |
| 118A | | 5 | 3 | 0.681 | 0.3819 | -1.421 | | 2.83 | | 0.207 |
| 118T | | 5 | 3 | 0.650 | 0.4029 | -1.389 | | 2.91 | | 0.209 |
| 119A | | 5 | 4 | 0.971 | 0.0144* | -2.786 | [-5.645, -1.772]* | 1.71 | [-0.49, 2.49] | 0.132 |
| 120A | | 7 | 7 | 0.238 | 0.2665 | -0.109 | [-0.352, 0.122] | 4.01 | [3.93, 4.10] | 0.451 |
| 120T | | 7 | 7 | 0.339 | 0.1699 | -0.133 | [-0.364, 0.084] | 4.09 | [4.01, 4.16] | 0.441 |
| 121A | | 9 | 8 | 0.575 | 0.0292* | -0.509 | [-1.149, -0.087] | 3.58 | [3.09, 3.90] | 0.331 |
| 121T | | 4 | 3 | 0.624 | 0.4200 | -0.509 | | 3.70 | | 0.331 |
| 122A | | 5 | 5 | 0.772 | 0.0499* | -0.956 | [-20.004, -0.005] | 3.84 | [0.56, 4.01] | 0.256 |
| 123A | | 4 | 4 | 0.975 | 0.0125* | -1.790 | [-3.279, -1.133]* | 3.72 | [3.41, 4.42] | 0.179 |
| 124A | | 7 | 4 | 0.052 | 0.7711 | -0.031 | [-0.547, 0.468] | 4.14 | [4.03, 4.26] | 0.485 |
| 125A | | 3 | 3 | 0.949 | 0.1450 | -0.380 | | 3.70 | | 0.362 |
| 126A | | 6 | 5 | 0.988 | 0.0005* | -0.586 | [-0.709, -0.474] | 3.67 | [3.62, 3.71] | 0.315 |
| 128A | | 4 | 4 | 0.466 | 0.3174 | -0.192 | | 4.30 | | 0.419 |
| 130A | | 3 | 3 | 0.785 | 0.3066 | -0.876 | | 3.31 | | 0.267 |

Table A.2. (continued)

| Id. Code ^a | Condition ^b | No. of Points ^c | | r^2 | p^d | PCA Self-thinning Line ^e | | | | |
|-----------------------|------------------------|----------------------------|-----|-------|----------|-------------------------------------|---------------------|----------------|---------------|-------------|
| | | n_T | n | | | Slope | | Intercept | | p_{est}^g |
| | | | | | | $\hat{\beta}$ | 95% CI ^f | $\hat{\alpha}$ | 95% CI | |
| 131A | | 6 | 6 | 0.956 | 0.0007* | -0.498 | [-0.657, -0.356] | 3.70 | [3.59, 3.81] | 0.334 |
| 131T | | 4 | 4 | 0.953 | 0.0236* | -0.224 | [-0.384, -0.075]* | 4.11 | [3.93, 4.28] | 0.408 |
| 132A | | 8 | 8 | 0.206 | 0.2580 | -0.294 | | 3.86 | | 0.386 |
| 133A | | 8 | 8 | 0.566 | 0.0312* | -0.188 | [-0.362, -0.024]* | 3.73 | [3.63, 3.82] | 0.421 |
| 135A | | 5 | 5 | 0.854 | 0.0248* | -3.047 | [-11.936, -1.628]* | 4.63 | [3.54, 11.44] | 0.124 |
| 136A | | 3 | 3 | 0.714 | 0.3593 | -0.284 | | 4.00 | | 0.389 |
| 136T | | 3 | 3 | 0.763 | 0.3240 | -0.331 | | 4.05 | | 0.376 |
| 137A | | 17 | 12 | 0.983 | <0.0001* | -0.422 | [-0.462, -0.383]* | 3.90 | [3.88, 3.92] | 0.352 |
| 137T | | 17 | 12 | 0.982 | <0.0001* | -0.433 | [-0.476, -0.392]* | 3.97 | [3.95, 3.99] | 0.349 |
| 138A | | 3 | 3 | 0.798 | 0.2969 | -0.550 | | 3.42 | | 0.323 |
| 138T | | 3 | 3 | 0.783 | 0.3082 | -0.544 | | 3.61 | | 0.324 |

^aTable A.1 associates the numeric part of each Id. code with a particular species and study. The letter indicates the type of biomass measurements made: A = aboveground parts only, T = aboveground and belowground parts both included.

^bSee Table A.1 and the references given there for further information on condition.

^c n_T is the total number of log B-log N points reported for each code and condition. n is the number of points remaining after removing points not relevant to the thinning line. This is the number of points used to fit the PCA relationship between log B and log N.

^dThe statistical significance of the correlation between log B and log N. * indicates significance at the 95% confidence level ($P \leq 0.05$).

^eThinning lines were fitted to log B-log N data using principal component analysis (PCA). Formulas for this analysis and for computing 95% confidence limits are given in Jolicœur and Heusner (1971).

^f* indicates thinning slopes that are statistically different at the 95% confidence level from the thinning rule prediction of $\beta = -1/2$.

^gTransformed values of the log B-log N thinning slope, $\hat{\beta}$, calculated from $p_{est} = 0.5 / (1 - \hat{\beta})$ (Chapter 6).

Table A.3. Ranges of Log B and Log N Used to Fit Self-thinning Lines to Experimental and Field Data.

| Id. Code ^a | Condition ^b | n | Log N ^c | | | Log B ^c | | |
|-----------------------|------------------------|----|--------------------|-------|-------|--------------------|------|------|
| | | | Min. | Max. | Mean | Min. | Max. | Mean |
| 1A | | 3 | 0.08 | 1.20 | 0.61 | 3.27 | 3.76 | 3.51 |
| 1T | | 3 | 0.08 | 1.20 | 0.61 | 3.34 | 3.83 | 3.58 |
| 5A | | 4 | -1.31 | 0.41 | -0.14 | 3.50 | 3.97 | 3.68 |
| 7A | | 5 | 2.71 | 3.67 | 3.07 | 2.51 | 2.86 | 2.74 |
| 8A | Lot 2B | 7 | -0.70 | -0.16 | -0.46 | 3.89 | 4.29 | 4.12 |
| 8A | Lot 2C | 7 | -0.87 | -0.43 | -0.69 | 3.83 | 4.33 | 4.10 |
| 10A | Full light | 10 | 3.05 | 4.74 | 3.87 | 2.36 | 3.17 | 2.77 |
| 14A | | 4 | -0.91 | -0.61 | -0.77 | 4.12 | 4.31 | 4.23 |
| 15T | | 31 | 1.38 | 3.16 | 2.78 | 2.33 | 3.41 | 2.64 |
| 16T | | 38 | 2.47 | 4.05 | 3.29 | 2.01 | 2.88 | 2.43 |
| 17T | | 17 | 1.61 | 3.25 | 2.49 | 2.17 | 3.18 | 2.60 |
| 18T | | 43 | 1.24 | 3.17 | 2.43 | 2.09 | 3.11 | 2.49 |
| 19A | | 26 | -1.06 | 1.38 | 0.07 | 3.51 | 5.08 | 4.11 |
| 20T | | 13 | 2.98 | 5.12 | 3.87 | 3.12 | 3.98 | 3.58 |
| 21T | | 13 | 3.03 | 3.96 | 3.55 | 1.65 | 2.55 | 2.01 |
| 22T | | 34 | -0.10 | 1.65 | 0.59 | 3.28 | 4.33 | 3.68 |
| 23T | | 23 | -0.81 | 1.12 | 0.08 | 3.49 | 4.06 | 3.87 |
| 24T | | 5 | 0.50 | 1.39 | 0.88 | 3.79 | 4.18 | 3.98 |
| 26A | | 27 | -0.75 | 0.16 | -0.24 | 3.66 | 4.62 | 4.07 |
| 27A | | 2 | 2.83 | 3.12 | 2.98 | 3.35 | 3.44 | 3.40 |
| 28A | Low L.I. | 7 | 3.21 | 3.44 | 3.31 | 1.70 | 1.90 | 1.81 |
| 28A | Med. L.I. | 8 | 3.08 | 3.22 | 3.16 | 2.69 | 2.83 | 2.76 |
| 28A | High L.I. | 7 | 2.96 | 3.22 | 3.09 | 2.74 | 2.92 | 2.84 |
| 29T | | 9 | 2.80 | 3.75 | 3.16 | 2.44 | 3.10 | 2.90 |
| 30A | | 9 | 3.37 | 3.90 | 3.66 | 2.49 | 2.78 | 2.66 |
| 31A | | 11 | 3.00 | 3.74 | 3.46 | 2.28 | 2.62 | 2.46 |
| 32T | 20% N.C. | 5 | 3.46 | 4.01 | 3.66 | 2.64 | 2.84 | 2.77 |
| 32T | 100% N.C. | 5 | 3.09 | 3.90 | 3.42 | 3.03 | 3.17 | 3.12 |
| 33T | | 10 | 2.54 | 2.87 | 2.68 | 2.56 | 2.96 | 2.80 |
| 34T | | 10 | 2.77 | 3.27 | 2.98 | 2.64 | 3.58 | 3.07 |
| 35A | | 13 | 3.14 | 3.80 | 3.46 | 2.78 | 3.21 | 3.01 |
| 36A | | 10 | 0.00 | 0.88 | 0.49 | 3.41 | 3.77 | 3.54 |
| 38A | 30% L.I. | 7 | 2.80 | 3.91 | 3.24 | 1.99 | 2.26 | 2.16 |
| 38A | 70% L.I. | 8 | 2.67 | 3.88 | 3.19 | 2.43 | 3.07 | 2.72 |
| 38A | 100% L.I. | 8 | 2.50 | 3.82 | 3.13 | 2.53 | 3.07 | 2.78 |
| 39A | Kitami | 5 | -0.86 | -0.06 | -0.48 | 4.82 | 5.24 | 5.06 |
| 39A | Shirogane | 7 | -0.84 | 0.08 | -0.34 | 4.56 | 4.79 | 4.67 |
| 40A | | 10 | 3.00 | 3.79 | 3.37 | 2.71 | 3.16 | 2.97 |
| 41A | | 5 | -1.25 | -0.87 | -1.07 | 4.38 | 4.61 | 4.50 |
| 43A | 18% L.I. | 7 | 3.61 | 4.41 | 4.03 | 1.82 | 2.44 | 2.12 |
| 43A | 25% L.I. | 7 | 3.68 | 4.42 | 4.03 | 2.02 | 2.65 | 2.33 |
| 43A | 37% L.I. | 7 | 3.47 | 4.46 | 3.88 | 2.16 | 2.80 | 2.50 |

Table A.3. (continued)

| Id. Code ^a | Condition ^b | n | Log N ^c | | | Log B ^c | | |
|--------------------------|------------------------|-----|--------------------|-------|-------|--------------------|------|------|
| | | | Min. | Max. | Mean | Min. | Max. | Mean |
| 43A | 55% L.I. | 8 | 3.46 | 4.49 | 3.88 | 2.30 | 2.99 | 2.70 |
| 43A | 100% L.I. | 7 | 3.68 | 4.27 | 3.88 | 2.62 | 3.04 | 2.78 |
| 44A | Ex. 2-60% L.I. | 4 | 2.05 | 2.45 | 2.17 | 2.59 | 2.95 | 2.80 |
| 44A | Ex. 2-100% L.I. | 4 | 2.09 | 2.45 | 2.23 | 2.91 | 3.29 | 3.08 |
| 44T | Ex. 1-23% L.I. | 10 | 1.76 | 2.92 | 2.11 | 2.07 | 2.45 | 2.35 |
| 44T | Ex. 1-60% L.I. | 8 | 1.88 | 3.19 | 2.35 | 2.62 | 3.07 | 2.87 |
| 44T | Ex. 1-100% L.I. | 6 | 2.35 | 3.06 | 2.59 | 2.96 | 3.16 | 3.04 |
| 44T | Ex. 2-60% L.I. | 4 | 2.05 | 2.45 | 2.17 | 2.61 | 2.97 | 2.82 |
| 44T | Ex. 2-100% L.I. | 4 | 2.09 | 2.45 | 2.23 | 2.93 | 3.32 | 3.10 |
| 45A | | 25 | -0.78 | 0.06 | -0.38 | 3.62 | 4.24 | 3.95 |
| 48A | | 7 | -0.05 | 0.52 | 0.29 | 3.27 | 3.76 | 3.51 |
| 49T | | 10 | 2.95 | 3.62 | 3.29 | 2.70 | 2.85 | 2.79 |
| 50T | 15% L.I. | 12 | 2.17 | 3.34 | 2.76 | 1.46 | 2.05 | 1.76 |
| 50T | 100% L.I. | 22 | 2.03 | 4.00 | 2.91 | 2.08 | 2.56 | 2.38 |
| 51A | | 24 | 2.86 | 3.76 | 3.41 | 2.35 | 2.93 | 2.61 |
| 52A | | 3 | 1.83 | 1.93 | 1.88 | 3.45 | 3.58 | 3.53 |
| 53T | | 29 | 2.92 | 3.64 | 3.28 | 2.84 | 3.23 | 3.03 |
| 54A | | 4 | -0.81 | -0.58 | -0.69 | 4.17 | 4.52 | 4.35 |
| 55A | | 11 | 3.66 | 3.92 | 3.80 | 2.40 | 2.82 | 2.55 |
| 56A | | 11 | 3.64 | 3.95 | 3.82 | 2.68 | 2.96 | 2.78 |
| 57A | | 13 | 3.51 | 3.92 | 3.77 | 2.55 | 2.94 | 2.74 |
| 58T | | 23 | 2.14 | 3.41 | 2.60 | 1.98 | 2.63 | 2.27 |
| 80A | | 5 | -0.78 | -0.51 | -0.68 | 4.62 | 4.83 | 4.73 |
| 81A | | 4 | -0.32 | 0.88 | 0.27 | 3.58 | 4.26 | 3.90 |
| 82A | | 17 | -0.85 | -0.05 | -0.53 | 4.23 | 4.51 | 4.37 |
| 84A | | 243 | -1.57 | -0.26 | -0.98 | 3.74 | 4.78 | 4.25 |
| 86A | | 15 | 4.09 | 4.83 | 4.43 | 2.85 | 3.54 | 3.18 |
| 87A | | 12 | 3.25 | 4.20 | 3.77 | 2.75 | 3.45 | 3.04 |
| 88A | | 15 | 3.21 | 3.94 | 3.60 | 2.57 | 3.26 | 2.94 |
| 89A | Grazed | 3 | 3.77 | 4.10 | 3.93 | 1.63 | 1.83 | 1.74 |
| 89A | Ungrazed | 5 | 3.55 | 4.00 | 3.73 | 1.81 | 2.09 | 1.97 |
| 90A | Grazed | 2 | 3.77 | 3.94 | 3.85 | 2.24 | 2.39 | 2.31 |
| 90A | Ungrazed | 2 | 3.68 | 3.94 | 3.81 | 2.48 | 2.60 | 2.54 |
| 91A | 17% L.I. | 13 | 2.91 | 4.53 | 3.66 | 2.13 | 2.50 | 2.27 |
| 91A | 100% L.I. | 10 | 3.23 | 4.85 | 4.06 | 2.74 | 3.45 | 3.07 |
| 91T | 17% L.I. | 13 | 2.91 | 4.53 | 3.66 | 2.15 | 2.50 | 2.31 |
| 91T | 100% L.I. | 10 | 3.23 | 4.85 | 4.06 | 3.04 | 3.46 | 3.20 |
| 92A | 17% L.I. | 5 | 3.18 | 4.56 | 3.76 | 1.86 | 2.10 | 1.99 |
| 92A | 23% L.I. | 5 | 3.52 | 4.58 | 3.86 | 1.92 | 2.57 | 2.23 |
| 92A | 44% L.I. | 5 | 3.27 | 4.55 | 3.78 | 1.92 | 2.69 | 2.38 |
| 92A | 100% L.I. | 5 | 3.37 | 4.57 | 3.85 | 2.13 | 2.78 | 2.56 |
| 93A | | 8 | -1.14 | -0.57 | -0.82 | 3.96 | 4.56 | 4.22 |
| 95A | | 2 | -0.16 | 0.16 | 0.00 | 3.92 | 4.16 | 4.04 |

Table A.3. (continued)

| Id. Code ^a | Condition ^b | n | Log N ^c | | | Log B ^c | | |
|--------------------------|------------------------|----|--------------------|-------|-------|--------------------|------|------|
| | | | Min. | Max. | Mean | Min. | Max. | Mean |
| 96A | | 4 | -1.19 | -1.04 | -1.11 | 4.32 | 4.49 | 4.42 |
| 97A | | 2 | -1.18 | -1.04 | -1.11 | 4.66 | 4.78 | 4.72 |
| 98A | S.I. 22.8 | 2 | -1.02 | -0.98 | -1.00 | 4.50 | 4.61 | 4.55 |
| 98A | S.I. 28.9 | 4 | -1.31 | -0.97 | -1.19 | 3.82 | 4.65 | 4.33 |
| 98A | S.I. 33.5 | 4 | -1.25 | -0.82 | -1.07 | 4.32 | 4.74 | 4.58 |
| 99A | | 7 | -1.80 | -1.46 | -1.69 | 4.22 | 4.54 | 4.36 |
| 101A | | 8 | -1.12 | -0.91 | -1.06 | 3.35 | 4.60 | 3.99 |
| 102A | | 9 | -1.52 | -0.85 | -1.17 | 3.98 | 4.40 | 4.21 |
| 103A | | 3 | -0.92 | -0.59 | -0.74 | 4.30 | 4.63 | 4.48 |
| 103T | | 3 | -0.92 | -0.59 | -0.74 | 4.41 | 4.67 | 4.54 |
| 104A | | 6 | -1.81 | -0.84 | -1.28 | 4.11 | 4.51 | 4.32 |
| 105A | | 3 | -1.61 | -0.44 | -0.99 | 4.20 | 4.44 | 4.28 |
| 105T | | 3 | -1.61 | -0.44 | -0.99 | 4.26 | 4.49 | 4.34 |
| 106A | | 8 | -0.17 | 0.52 | 0.10 | 3.14 | 3.62 | 3.40 |
| 109A | | 4 | -0.31 | 0.23 | -0.11 | 3.35 | 3.60 | 3.47 |
| 110A | | 8 | -1.46 | -0.42 | -1.01 | 3.64 | 4.02 | 3.85 |
| 110T | | 3 | -0.76 | -0.42 | -0.57 | 3.85 | 4.04 | 3.97 |
| 111A | | 10 | -0.95 | -0.50 | -0.74 | 3.26 | 4.75 | 4.10 |
| 111T | | 10 | -0.95 | -0.50 | -0.74 | 3.35 | 4.82 | 4.19 |
| 112A | | 3 | 0.08 | 0.35 | 0.22 | 3.92 | 4.27 | 4.10 |
| 113A | | 5 | -1.26 | -0.71 | -1.05 | 4.07 | 4.80 | 4.41 |
| 113T | | 5 | -1.26 | -0.71 | -1.05 | 4.16 | 4.88 | 4.50 |
| 114A | | 9 | -0.92 | 3.00 | 0.29 | 3.26 | 4.44 | 3.98 |
| 114T | | 9 | -0.92 | 3.00 | 0.29 | 3.35 | 4.52 | 4.07 |
| 115A | | 4 | -0.37 | -0.05 | -0.28 | 4.08 | 4.28 | 4.21 |
| 116A | | 3 | -1.25 | -1.06 | -1.16 | 4.48 | 4.58 | 4.54 |
| 117A | | 3 | -1.45 | -0.91 | -1.14 | 4.55 | 4.60 | 4.58 |
| 118A | | 3 | -1.08 | -0.78 | -0.91 | 3.89 | 4.27 | 4.12 |
| 118T | | 3 | -1.08 | -0.78 | -0.91 | 3.94 | 4.31 | 4.17 |
| 119A | | 4 | -0.93 | -0.56 | -0.77 | 3.29 | 4.34 | 3.85 |
| 120A | | 7 | -0.72 | 0.61 | -0.35 | 3.91 | 4.17 | 4.05 |
| 120T | | 7 | -0.72 | 0.61 | -0.35 | 4.01 | 4.26 | 4.14 |
| 121A | | 8 | -1.13 | -0.30 | -0.77 | 3.81 | 4.24 | 3.97 |
| 121T | | 3 | -1.06 | -0.30 | -0.74 | 3.91 | 4.34 | 4.08 |
| 122A | | 5 | -0.44 | 0.00 | -0.17 | 3.77 | 4.18 | 4.01 |
| 123A | | 4 | 0.15 | 0.88 | 0.47 | 2.20 | 3.55 | 2.88 |
| 124A | | 4 | -0.38 | 0.98 | 0.23 | 4.08 | 4.24 | 4.14 |
| 125A | | 3 | -1.09 | -0.28 | -0.68 | 3.79 | 4.09 | 3.96 |
| 126A | | 5 | -0.91 | -0.20 | -0.40 | 3.78 | 4.20 | 3.90 |
| 128A | | 4 | 0.90 | 1.94 | 1.50 | 3.88 | 4.17 | 4.02 |
| 130A | | 3 | -0.95 | -0.28 | -0.56 | 3.46 | 4.07 | 3.80 |
| 131A | | 6 | -1.44 | 0.35 | -0.72 | 3.49 | 4.32 | 4.06 |
| 131T | | 4 | -1.44 | -0.73 | -1.12 | 4.26 | 4.42 | 4.36 |

Table A.3. (continued)

| Id. Code ^a | Condition ^b | n | Log N ^c | | | Log B ^c | | |
|--------------------------|------------------------|----|--------------------|-------|-------|--------------------|------|------|
| | | | Min. | Max. | Mean | Min. | Max. | Mean |
| 132A | | 8 | -0.92 | 0.00 | -0.35 | 3.76 | 4.18 | 3.96 |
| 133A | | 8 | -1.02 | 0.24 | -0.56 | 3.62 | 3.93 | 3.83 |
| 135A | | 5 | 0.60 | 0.99 | 0.77 | 1.60 | 2.90 | 2.29 |
| 136A | | 3 | -1.52 | -0.83 | -1.19 | 4.21 | 4.42 | 4.34 |
| 136T | | 3 | -1.52 | -0.83 | -1.19 | 4.29 | 4.52 | 4.44 |
| 137A | | 12 | -1.07 | 0.14 | -0.50 | 3.85 | 4.34 | 4.11 |
| 137T | | 12 | -1.07 | 0.14 | -0.50 | 3.93 | 4.42 | 4.19 |
| 138A | | 3 | -0.34 | 0.70 | 0.07 | 3.03 | 3.65 | 3.38 |
| 138T | | 3 | -0.34 | 0.70 | 0.07 | 3.22 | 3.84 | 3.57 |

^aTable A.1 associates the numeric part of each Id. code with a particular species and study. The letter indicates the type of biomass measurements made: A = aboveground parts only, T = aboveground and belowground parts both included.

^bSee Table A.1 and the references given there for more information on condition.

^cThe mean, minimum, and maximum are given for log B and log N over the n data points used to fit the thinning line for each code and condition.

Table A.4. Fitted Allometric Relationships for Experimental and Field Data.

| Id. Code ^a | Condition ^b | Allometric Relationship Fit by PCA ^c | | | | |
|--|------------------------|---|----------------|----------------|----------------|----------------|
| | | n | r ² | p ^d | $\hat{\phi}_1$ | $\hat{\phi}_0$ |
| height-weight allometry: $\log \bar{h} = \hat{\phi}_1 \log \bar{w} + \hat{\phi}_0$ ($\hat{\phi}_1 = \hat{\phi}_{hw}$) ^e | | | | | | |
| 1A | | 3 | 0.997 | 0.0367* | 0.282 | -0.091 |
| 1T | | 3 | 0.996 | 0.0390* | 0.283 | -0.113 |
| 8A | Lot 2B | 7 | 0.997 | <0.0001* | 0.384 | -0.610 |
| 8A | Lot 2C | 7 | 0.998 | <0.0001* | 0.399 | -0.725 |
| 44A | Ex. 2-60% L.I. | 4 | 0.977 | 0.0115* | 0.368 | -0.202 |
| 44A | Ex. 2-100% L.I. | 4 | 0.921 | 0.0404* | 0.471 | -0.394 |
| 44T | Ex. 2-60% L.I. | 4 | 0.975 | 0.0126* | 0.368 | -0.209 |
| 44T | Ex. 2-100% L.I. | 4 | 0.919 | 0.0416* | 0.463 | -0.397 |
| 48A | | 7 | 0.735 | 0.0137* | 0.253 | -0.086 |
| 81A | | 4 | 0.998 | 0.0011* | 0.348 | -0.587 |
| 86A | | 15 | 0.831 | <0.0001* | 0.303 | 0.016 |
| 87A | | 12 | 0.973 | <0.0001* | 0.356 | -0.167 |
| 88A | | 15 | 0.899 | <0.0001* | 0.296 | -0.212 |
| 93A | | 8 | 0.951 | <0.0001* | 0.339 | -0.418 |
| 98A | S.I. 28.9 | 3 | 1.000 | 0.0064* | 0.389 | -0.747 |
| 98A | S.I. 33.5 | 3 | 0.993 | 0.0540 | 0.366 | -0.576 |
| 99A | | 7 | 0.994 | <0.0001* | 0.337 | -0.441 |
| 102A | | 9 | 0.928 | <0.0001* | 0.344 | -0.544 |
| 103A | | 3 | 0.980 | 0.0892 | 0.328 | -0.453 |
| 103T | | 3 | 0.993 | 0.0533 | 0.359 | -0.640 |
| 104A | | 6 | 0.991 | <0.0001* | 0.195 | 0.191 |
| 105A | | 3 | 0.959 | 0.1292 | 0.167 | 0.424 |
| 105T | | 3 | 0.959 | 0.1292 | 0.169 | 0.404 |
| 106A | | 8 | 0.977 | <0.0001* | 0.391 | -0.712 |
| 110A | | 8 | 0.953 | <0.0001* | 0.334 | -0.429 |
| 110T | | 3 | 0.320 | 0.6170 | 0.251 | -0.062 |
| 111A | | 10 | 0.931 | <0.0001* | 0.353 | -0.619 |
| 111T | | 10 | 0.935 | <0.0001* | 0.358 | -0.676 |
| 112A | | 3 | 0.967 | 0.1154 | 0.279 | -0.295 |
| 113A | | 5 | 0.938 | 0.0067* | 0.239 | -0.125 |
| 113T | | 5 | 0.939 | 0.0065* | 0.238 | -0.144 |
| 114A | | 9 | 0.974 | <0.0001* | 0.321 | -0.512 |
| 114T | | 9 | 0.974 | <0.0001* | 0.321 | -0.541 |
| 115A | | 4 | 0.983 | 0.0085* | 0.163 | 0.253 |
| 116A | | 3 | 0.891 | 0.2137 | 0.188 | 0.366 |
| 119A | | 4 | 0.997 | 0.0013* | 0.446 | -1.131 |
| 120A | | 7 | 0.954 | 0.0002* | 0.297 | -0.361 |
| 120T | | 7 | 0.954 | 0.0002* | 0.291 | -0.361 |
| 121A | | 8 | 0.970 | <0.0001* | 0.263 | -0.118 |
| 121T | | 3 | 1.000 | 0.0022* | 0.243 | -0.066 |
| 122A | | 5 | 0.958 | 0.0038* | 0.387 | -0.725 |

Table A.4. (continued)

| Id. Code ^a | Condition ^b | Allometric Relationship Fit by PCA ^c | | | | |
|--|------------------------|---|----------------|----------|----------------|----------------|
| | | n | r ² | pd | $\hat{\Phi}_1$ | $\hat{\Phi}_0$ |
| height-weight allometry: $\log \bar{h} = \hat{\Phi}_1 \log \bar{w} + \hat{\Phi}_0$ ($\hat{\Phi}_1 = \hat{\Phi}_{hw}$) ^e | | | | | | |
| 123A | | 4 | 0.974 | 0.0131* | 0.398 | -0.471 |
| 124A | | 4 | 0.984 | 0.0082* | 0.371 | -0.718 |
| 125A | | 3 | 0.966 | 0.1189 | 0.436 | -1.013 |
| 126A | | 5 | 0.774 | 0.0492* | 0.293 | -0.554 |
| 128A | | 4 | 0.992 | 0.0038* | 0.382 | -1.130 |
| 130A | | 3 | 0.979 | 0.0930 | 0.365 | -0.682 |
| 131A | | 6 | 0.978 | 0.0002* | 0.288 | -0.154 |
| 131T | | 4 | 0.982 | 0.0093* | 0.184 | 0.390 |
| 132A | | 8 | 0.938 | <0.0001* | 0.322 | -0.473 |
| 133A | | 8 | 0.962 | <0.0001* | 0.203 | 0.337 |
| 136A | | 3 | 0.991 | 0.0621 | 0.282 | -0.179 |
| 136T | | 3 | 0.991 | 0.0613 | 0.272 | -0.154 |
| 137A | | 12 | 0.985 | <0.0001* | 0.304 | -0.278 |
| 137T | | 12 | 0.985 | <0.0001* | 0.302 | -0.291 |
| 138A | | 3 | 1.000 | 0.0043* | 0.228 | -0.054 |
| 138T | | 3 | 1.000 | 0.0006* | 0.229 | -0.100 |
| $\overline{\text{DBH}}$ -weight allometry: $\log \overline{\text{DBH}} = \hat{\Phi}_1 \log \bar{w} + \hat{\Phi}_0$ ($\hat{\Phi}_1 = \hat{\Phi}_{Dw}$) ^e | | | | | | |
| 8A | Lot 2B | 7 | 0.999 | <0.0001* | 0.321 | -2.334 |
| 8A | Lot 2C | 7 | 0.997 | <0.0001* | 0.328 | -2.348 |
| 14A | | 4 | 0.995 | 0.0025* | 0.274 | -2.113 |
| 54A | | 2 | 1.000 | | 0.278 | -2.034 |
| 81A | | 4 | 1.000 | 0.0002* | 0.395 | -2.662 |
| 93A | | 8 | 0.994 | <0.0001* | 0.347 | -2.482 |
| 95A | | 2 | 1.000 | | 0.169 | -1.754 |
| 96A | | 4 | 0.993 | 0.0037* | 0.310 | -2.099 |
| 97A | | 2 | 1.000 | | 0.317 | -2.364 |
| 98A | S.I. 22.8 | 2 | 1.000 | | 0.422 | -2.946 |
| 98A | S.I. 28.9 | 4 | 1.000 | 0.0002* | 0.374 | -2.687 |
| 98A | S.I. 33.5 | 4 | 0.996 | 0.0020* | 0.347 | -2.556 |
| 99A | | 7 | 0.993 | <0.0001* | 0.392 | -2.816 |
| $\overline{\text{BSLA}}$ -weight allometry: $\log \overline{\text{BSLA}} = \hat{\Phi}_1 \log \bar{w} + \hat{\Phi}_0$ ($\hat{\Phi}_1 = \hat{\Phi}_{Bw}$) ^e | | | | | | |
| 8A | Lot 2B | 7 | 0.998 | <0.0001* | 0.651 | -4.817 |
| 8A | Lot 2C | 7 | 0.999 | <0.0001* | 0.648 | -4.759 |
| 14A | | 4 | 0.999 | 0.0006* | 0.542 | -4.303 |
| 45A | | 25 | 0.963 | <0.0001* | 0.826 | -5.701 |
| 52A | | 3 | 0.997 | 0.0344* | 0.774 | -5.259 |
| 54A | | 4 | 0.997 | 0.0014* | 0.664 | -5.030 |
| 93A | | 8 | 0.992 | <0.0001* | 0.698 | -5.089 |

Table A.4. (continued)

| Id. Code ^a | Condition ^b | Allometric Relationship Fit by PCA ^c | | | | |
|--|------------------------|---|----------------|----------|----------------|----------------|
| | | n | r ² | pd | $\hat{\Phi}_1$ | $\hat{\Phi}_0$ |
| BSLA-weight allometry: $\log \overline{BSLA} = \hat{\Phi}_1 \log \bar{w} + \hat{\Phi}_0$ ($\hat{\Phi}_1 = \hat{\Phi}_{BW}$) ^e | | | | | | |
| 95A | | 2 | 1.000 | | 0.765 | -5.467 |
| 96A | | 4 | 0.997 | 0.0016* | 0.719 | -5.174 |
| 97A | | 2 | 1.000 | | 0.633 | -4.820 |
| 98A | S.I. 22.8 | 2 | 1.000 | | 0.839 | -5.971 |
| 98A | S.I. 28.9 | 4 | 1.000 | 0.0002* | 0.746 | -5.466 |
| 98A | S.I. 33.5 | 4 | 0.996 | 0.0018* | 0.692 | -5.204 |
| 99A | | 7 | 0.999 | <0.0001* | 0.766 | -5.630 |
| 101A | | 8 | 0.949 | <0.0001* | 0.650 | -5.040 |
| 102A | | 9 | 0.994 | <0.0001* | 0.697 | -5.091 |
| 103A | | 3 | 0.978 | 0.0950 | 0.666 | -5.106 |
| 103T | | 3 | 0.991 | 0.0590 | 0.728 | -5.478 |
| 104A | | 6 | 1.000 | <0.0001* | 0.844 | -6.071 |
| 105A | | 3 | 1.000 | 0.0021* | 0.806 | -5.813 |
| 105T | | 3 | 1.000 | 0.0021* | 0.815 | -5.907 |
| 109A | | 4 | 0.994 | 0.0031* | 1.231 | -7.368 |
| 110A | | 8 | 1.000 | <0.0001* | 0.850 | -5.856 |
| 110T | | 3 | 0.992 | 0.0584 | 0.819 | -5.763 |
| 111A | | 10 | 0.988 | <0.0001* | 0.720 | -5.314 |
| 111T | | 10 | 0.989 | <0.0001* | 0.730 | -5.425 |
| 112A | | 3 | 0.997 | 0.0328* | 1.045 | -6.865 |
| 113A | | 5 | 0.992 | 0.0003* | 0.887 | -6.143 |
| 113T | | 5 | 0.991 | 0.0003* | 0.886 | -6.212 |
| 114A | | 7 | 0.997 | <0.0001* | 0.864 | -5.891 |
| 114T | | 7 | 0.998 | <0.0001* | 0.858 | -5.942 |
| 115A | | 4 | 0.995 | 0.0026* | 0.845 | -6.045 |
| 116A | | 3 | 1.000 | 0.0067* | 0.849 | -5.883 |
| 117A | | 3 | 0.999 | 0.0204* | 0.891 | -6.190 |
| 118A | | 3 | 0.954 | 0.1379 | 1.030 | -6.746 |
| 118T | | 3 | 0.960 | 0.1283 | 1.051 | -6.904 |
| 119A | | 4 | 0.997 | 0.0017* | 0.951 | -6.357 |
| 121A | | 8 | 0.961 | <0.0001* | 0.866 | -6.033 |
| 121T | | 3 | 0.955 | 0.1358 | 0.878 | -6.201 |
| 122A | | 5 | 1.000 | <0.0001* | 0.841 | -5.836 |
| 123A | | 3 | 0.992 | 0.0564 | 1.223 | -6.684 |
| 124A | | 4 | 0.966 | 0.0172* | 1.567 | -8.768 |
| 126A | | 5 | 0.995 | 0.0002* | 0.809 | -5.670 |
| 131A | | 6 | 0.994 | <0.0001* | 0.827 | -5.789 |
| 131T | | 4 | 0.989 | 0.0053* | 0.734 | -5.360 |
| 132A | | 8 | 0.993 | <0.0001* | 0.871 | -5.940 |
| 133A | | 8 | 0.989 | <0.0001* | 0.874 | -5.961 |
| 136A | | 3 | 1.000 | 0.0012* | 0.822 | -5.762 |
| 136T | | 3 | 1.000 | 0.0004* | 0.794 | -5.688 |

Table A.4. (continued)

| Id. Code ^a | Condition ^b | Allometric Relationship Fit by PCA ^c | | | | |
|---|------------------------|---|----------------|----------|----------------|----------------|
| | | n | r ² | pd | $\hat{\phi}_1$ | $\hat{\phi}_0$ |
| BSLA-weight allometry: $\log \overline{\text{BSLA}} = \hat{\phi}_1 \log \bar{w} + \hat{\phi}_0$ ($\hat{\phi}_1 = \hat{\phi}_{\text{Bw}}$) ^e | | | | | | |
| 137A | | 12 | 0.998 | <0.0001* | 0.872 | -6.062 |
| 137T | | 12 | 0.998 | <0.0001* | 0.865 | -6.099 |
| 138A | | 3 | 1.000 | 0.0084* | 0.766 | -5.295 |
| 138T | | 3 | 1.000 | 0.0121* | 0.769 | -5.450 |
| height-DBH allometry: $\log \bar{h} = \hat{\phi}_1 \log \overline{\text{DBH}} + \hat{\phi}_0$ ($\hat{\phi}_1 = \hat{\phi}_{\text{hD}}$) ^e | | | | | | |
| 8A | Lot 2B | 7 | 0.993 | <0.0001* | 1.198 | 2.225 |
| 8A | Lot 2C | 7 | 0.991 | <0.0001* | 1.215 | 2.205 |
| 81A | | 4 | 0.997 | 0.0016* | 0.883 | 2.205 |
| 93A | | 8 | 0.976 | <0.0001* | 0.993 | 2.060 |
| 98A | S.I. 28.9 | 3 | 0.999 | 0.0201* | 1.041 | 2.107 |
| 98A | S.I. 33.5 | 3 | 0.995 | 0.0455* | 1.114 | 2.219 |
| 99A | | 7 | 0.999 | <0.0001* | 0.860 | 2.039 |
| height-BSLA allometry: $\log \bar{h} = \hat{\phi}_1 \log \overline{\text{BSLA}} + \hat{\phi}_0$ ($\hat{\phi}_1 = \hat{\phi}_{\text{hB}}$) ^e | | | | | | |
| 8A | Lot 2B | 7 | 0.991 | <0.0001* | 0.588 | 2.225 |
| 8A | Lot 2C | 7 | 0.993 | <0.0001* | 0.615 | 2.205 |
| 93A | | 8 | 0.978 | <0.0001* | 0.491 | 2.060 |
| 98A | S.I. 28.9 | 3 | 0.999 | 0.0206* | 0.523 | 2.107 |
| 98A | S.I. 33.5 | 3 | 0.994 | 0.0490* | 0.557 | 2.219 |
| 99A | | 7 | 0.990 | <0.0001* | 0.440 | 2.039 |
| 102A | | 9 | 0.921 | <0.0001* | 0.496 | 1.974 |
| 103A | | 3 | 1.000 | 0.0057* | 0.494 | 2.065 |
| 103T | | 3 | 1.000 | 0.0057* | 0.494 | 2.065 |
| 104A | | 6 | 0.987 | <0.0001* | 0.230 | 1.592 |
| 105A | | 3 | 0.961 | 0.1271 | 0.207 | 1.627 |
| 105T | | 3 | 0.961 | 0.1271 | 0.207 | 1.627 |
| 110A | | 8 | 0.956 | <0.0001* | 0.394 | 1.874 |
| 110T | | 3 | 0.408 | 0.5586 | 0.355 | 1.802 |
| 111A | | 10 | 0.905 | <0.0001* | 0.488 | 1.982 |
| 111T | | 10 | 0.905 | <0.0001* | 0.488 | 1.982 |
| 112A | | 3 | 0.947 | 0.1483 | 0.264 | 1.530 |
| 113A | | 5 | 0.901 | 0.0137* | 0.264 | 1.521 |
| 113T | | 5 | 0.901 | 0.0137* | 0.264 | 1.521 |
| 114A | | 7 | 0.941 | 0.0003* | 0.399 | 1.740 |
| 114T | | 7 | 0.941 | 0.0003* | 0.399 | 1.740 |
| 115A | | 4 | 0.967 | 0.0167* | 0.192 | 1.417 |
| 116A | | 3 | 0.898 | 0.2070 | 0.223 | 1.672 |
| 117A | | 3 | 0.000 | 1.0000 | 0.000 | 1.415 |
| 119A | | 4 | 0.999 | 0.0007* | 0.470 | 1.854 |

Table A.4. (continued)

| Id. Code ^a | Condition ^b | Allometric Relationship Fit by PCA ^c | | | | |
|---|------------------------|---|----------------|----------|----------------|----------------|
| | | n | r ² | pd | $\hat{\phi}_1$ | $\hat{\phi}_0$ |
| height-BSLA allometry: $\log \bar{h} = \hat{\phi}_1 \log \overline{\text{BSLA}} + \hat{\phi}_0$ ($\hat{\phi}_1 = \hat{\phi}_{hB}$) ^e | | | | | | |
| 121A | | 8 | 0.941 | <0.0001* | 0.299 | 1.707 |
| 121T | | 3 | 0.954 | 0.1380 | 0.271 | 1.639 |
| 122A | | 5 | 0.960 | 0.0034* | 0.462 | 1.964 |
| 123A | | 3 | 0.997 | 0.0347* | 0.260 | 1.505 |
| 124A | | 4 | 0.990 | 0.0052* | 0.239 | 1.365 |
| 126A | | 5 | 0.803 | 0.0396* | 0.371 | 1.521 |
| 131A | | 6 | 0.993 | <0.0001* | 0.351 | 1.866 |
| 131T | | 4 | 0.998 | 0.0012* | 0.252 | 1.735 |
| 132A | | 8 | 0.922 | 0.0002* | 0.368 | 1.718 |
| 133A | | 8 | 0.933 | <0.0001* | 0.229 | 1.714 |
| 136A | | 3 | 0.991 | 0.0609 | 0.343 | 1.795 |
| 136T | | 3 | 0.991 | 0.0609 | 0.343 | 1.795 |
| 137A | | 12 | 0.986 | <0.0001* | 0.349 | 1.837 |
| 137T | | 12 | 0.986 | <0.0001* | 0.349 | 1.837 |
| 138A | | 3 | 1.000 | 0.0127* | 0.297 | 1.521 |
| 138T | | 3 | 1.000 | 0.0127* | 0.297 | 1.521 |

^aTable A.1 associates the numeric part of each Id. code with a particular species and study. The letter indicates the type of biomass measurements made: A = aboveground parts only, T = aboveground and belowground parts both included.

^bSee Table A.1 and the references given there for more information on condition.

^cThe general allometric relation is $\log Y = \hat{\phi}_1 \log X + \hat{\phi}_0$, where Y is $\log \bar{h}$, $\log \overline{\text{DBH}}$, or $\log \overline{\text{BSLA}}$ and X is $\log \bar{w}$, $\log \overline{\text{DBH}}$, or $\log \overline{\text{BSLA}}$. (DBH and BSLA here refer to the diameter and breast height and basal area at breast height, respectively, of the boles of individual trees). Y and X are paired as indicated in the sub-headings within the table. The number of data points and coefficient of determination (r^2) are given for each allometric relationship. The slope and intercept ($\hat{\phi}_1$ and $\hat{\phi}_0$, respectively) are fit using principal component analysis (Jolicoeur and Heusner 1971).

^dThe statistical significance of the correlation between the two measurements $\log Y$ and $\log X$, where Y and X are as explained in footnote c.

^eThe mathematical symbols $\hat{\phi}_{hw}$, $\hat{\phi}_{Dw}$, $\hat{\phi}_{Bw}$, $\hat{\phi}_{hD}$, and $\hat{\phi}_{hB}$ are used in Chapter 6 to represent the five allometric powers in this table.

Table A.5. Self-thinning Lines from Experimental and Field Data Cited by Previous Authors as Support for the Self-thinning Rule.

| Id. Code ^a | Condition ^b | Dep. Var. ^c | Fitting Method ^d | No. of Points ^e | | r ² or %EV ^f | Thinning Line Equation | | | | Reference ⁱ |
|-----------------------|------------------------|------------------------|-----------------------------|----------------------------|----|------------------------------------|------------------------|---------------------------|----------------|-----------------|--------------------------------------|
| | | | | n _T | n | | Slope | | Intercept | | |
| | | | | | | | $\hat{\beta}_9$ | 95% CI or SE ^h | $\hat{\alpha}$ | SE ^h | |
| 1T | | W | Reg | | | | -0.43 | | 3.85 | | White 1980 |
| 5A | | W | Reg | | | | -0.33 | | 3.64 | | White 1980 |
| 7A | | W | Reg | | 10 | | -0.39 | | 3.83 | | White 1980 |
| 8A | Lot 2B | W | Reg | | | | -0.70 | | 3.78 | | White 1980 |
| 10A | Full light | B | Reg | 10 | 6 | | -0.29 | 0.21 | 3.96 | 0.75 | Westoby and Howell 1982 |
| 14A | | W | Reg | | | | -0.66 | | 3.65 | | White 1980 |
| 15T | | W | Gra | | 47 | | | | | | Yoda et al. 1963 |
| + | | W | Reg | | | | -0.51 | | 3.92 | | White 1980 |
| 16T | | W | Gra | | 38 | | | | | | Yoda et al. 1963 |
| + | | W | Reg | | | | -0.48 | | 3.89 | | White 1980 |
| 17T | | W | Gra | | 21 | | | | | | Yoda et al. 1963 |
| + | | W | Reg | | | | -0.48 | | 3.85 | | White 1980 |
| 18T | | W | Gra | | 51 | | | | | | Yoda et al. 1963 |
| + | | W | Reg | | | | -0.48 | | 3.66 | | White 1980 |
| 19A | | W | Gra | | 29 | | | | | | Yoda et al. 1963 |
| + | | W | Reg | | | | -0.54 | | 4.34 | | White 1980 |
| 20T | | W | Gra | | 27 | | | | | | Yoda et al. 1963 |
| + | | W | Reg | | | | -0.38 | | 4.00 | | White 1980 |
| 21T | | W | Gra | | 30 | | | | | | Yoda et al. 1963 |
| + | | W | Reg | | 30 | 25 | | | 4.31 | | White and Harper 1970; White 1980 |
| 22T | | W | PCA | 53 | 34 | 0.98* | -0.46 | | | | Mohler et al. 1978 |
| 23T | | W | PCA | 29 | 23 | 0.98 | -0.22 | | | | Mohler et al. 1978 |
| 26A | | W | Gra | | 46 | | -0.50 | | | | Yoda et al. 1963 |
| + | | W | Reg | | | | -0.63 | | 3.94 | | White 1980 |
| 27T | | B | Gra | | 20 | | | | | | Westoby 1980 |
| 28A | Low L.I. | W | PCA | 10 | 7 | 0.95* | -0.74 | | | | Hutchings and Budd 1981b |
| 28A | Medium L.I. | W | PCA | 14 | 8 | 0.95* | -0.91 | | | | Hutchings and Budd 1981b |
| 28A | High L.I. | W | PCA | 14 | 7 | >0.99* | -0.62 | | | | Hutchings and Budd 1981b |
| 29T | | W | Gra | | 25 | | | | | | Yoda et al. 1963 |
| + | | W | Reg | | | | -0.48 | | 4.41 | | White 1980 |
| 30A | | W | Reg | | 9 | 0.76 | -0.33 | | 3.86 | | White and Harper 1970; White 1980 |
| 31A | | W | Reg | | 11 | 0.89 | -0.42 | | 3.93 | | White and Harper 1970; White 1980 |
| 32T | 20% N.C. | W | Ax | | 7 | | | | 4.62 | 0.04 | Furnas 1981 |
| 32T | 100% N.C. | W | Ax | | 7 | | | | 4.84 | 0.05 | Furnas 1981 |
| 33T | Restricted | W | Ax | | 5 | | | | 4.07 | 0.04 | Furnas 1981 |
| + | Control | W | Ax | | 5 | | | | 4.14 | 0.04 | Furnas 1981 |
| 35A | | W | Reg | 22 | 13 | | -0.56 | [-0.79,-0.33] | 4.95 | | Westoby 1976 |
| 38A | 70% L.I. | W | Gra | | 20 | | | | | | Kays and Harper 1974 |
| 38A | 100% L.I. | W | Gra | | 20 | | | | | | Kays and Harper 1974 |
| 40A | | W | | | 8 | | | | | | Ford 1975 |
| 41A | | W | Gra | | 5 | | | | | | Barkham 1978 |
| 43A | 18% L.I. | B | Reg | 10 | 7 | 0.95 | -0.67 | 0.18 | | | Westoby and Howell 1981 |
| 43A | 25% L.I. | B | Reg | 10 | 7 | 0.92 | -0.66 | 0.07 | | | Westoby and Howell 1981 |
| 43A | 37% L.I. | B | Reg | 10 | 7 | 0.94 | -0.65 | 0.08 | | | Westoby and Howell 1981 |
| 43A | 55% L.I. | B | Reg | 11 | 8 | 0.93 | -0.64 | 0.09 | | | Westoby and Howell 1981 |
| 43A | 100% L.I. | B | Reg | 9 | 7 | 0.67 | -0.56 | 0.07 | | | Westoby and Howell 1981 |
| 44T | Ex. 1-60% L.I. | W | Reg | | 8 | 0.96 | -0.30 | | 3.53 | | White and Harper 1970 |
| 44T | Ex. 1-100% L.I. | W | Reg | | 9 | 0.97 | -0.33 | | 3.94 | | White and Harper 1970 |
| 44T | Ex. 2-60% L.I. | W | Reg | | 6 | 0.98 | -0.70 | | 4.34 | | White and Harper 1970 |
| + | | W | PCA | | | >0.99* | -0.79 | [-1.19,-0.65] | 4.51 | | Lonsdale and Watkinson 1983a |
| 44T | Ex. 2-100% L.I. | W | Reg | | 5 | 0.97 | -0.84 | | 4.96 | | White and Harper 1970 |
| + | | W | PCA | | | >0.99* | -0.89 | [-1.29,-0.45] | 5.06 | | Lonsdale and Watkinson 1983a |
| 45A | | W | Reg | | | | -0.48 | | 3.53 | | White 1980 |

Table A.5. (continued)

| Id. Code ^a | Condition ^b | Dep. Var. ^c | Fitting Method ^d | No. of Points ^e | | r ² or %EV ^f | Thinning Line Equation | | Reference ^g | |
|-----------------------|------------------------|------------------------|-----------------------------|----------------------------|----|------------------------------------|------------------------|---------------------------|------------------------|---|
| | | | | n _T | n | | Slope | Intercept | | |
| | | | | | | | $\hat{\beta}_9$ | 95% CI or SE ^h | $\hat{\alpha}$ | SE ^h |
| 48A | | W | Reg | | | | -0.30 | | 3.61 | White 1980 |
| 51A | Low fertility | W | Reg | 15 | | | -0.44 | 0.35 | | Bazzaz and Harper 1976 |
| | & High fertility | W | Reg | 15 | | | -0.64 | 0.19 | | Bazzaz and Harper 1976 |
| 52A | | W | Gra | 9 | | | | | | Tadaki and Shidei 1959 |
| 53T | | W | Reg | 36 | | 0.87 | -0.41 | | 4.19 | White and Harper 1970; White 1980 |
| 54A | | W | Gra | 4 | | | | | | Tadaki and Shidei 1959 |
| 55A | | W | Reg | 17 | | | | | | MalMBERG and Smith 1982 |
| 56A | | W | Reg | 34 | | | | | | MalMBERG and Smith 1982 |
| 57A | | W | Reg | 21 | | 0.87 | -0.75 | | 5.58 | MalMBERG and Smith 1982 |
| 82A | | W | Gra | | | | | | | Peet and Christensen 1980; Christensen and Peet 1982 |
| 84A | | W | Gra | | | | | | | Yoda et al. 1963 |
| 86A | | W | PCA | 18 | 15 | >0.99* | -0.78 | [-1.11,-0.52] | 6.67 | Lonsdale and Watkinson 1983a |
| 87A | | W | PCA | 15 | 12 | >0.99* | -0.68 | [-0.82,-0.56] | 5.64 | Lonsdale and Watkinson 1983a |
| 88A | | W | PCA | 18 | 15 | >0.99* | -0.79 | [-1.08,-0.55] | 5.82 | Lonsdale and Watkinson 1983a |
| 89A | Grazed | W | Reg | 5 | 3 | | -0.60 | | | Dirzo and Harper 1980 |
| 89A | Ungrazed | W | Reg | 5 | 5 | 0.96 | -0.80 | | | Dirzo and Harper 1980 |
| 90A | Grazed | W | Gra | 5 | | | | | | Dirzo and Harper 1980 |
| 90A | Ungrazed | W | Gra | 5 | | | | | | Dirzo and Harper 1980 |
| 91A | 100% L.I. | W | PCA | 25 | | >0.99* | -0.43 | [-0.51,-0.35] | 4.84 | Lonsdale and Watkinson 1982 |
| 91T | 100% L.I. | W | PCA | 25 | | >0.99* | -0.26 | [-0.33,-0.19] | 4.29 | Lonsdale and Watkinson 1982 |
| 92A | 23% L.I. | W | PCA | 5 | 5 | >0.99* | -0.52 | [-0.74,-0.30] | 4.26 | Lonsdale and Watkinson 1982 |
| 92A | 44% L.I. | W | PCA | 5 | 5 | >0.99* | -0.49 | [-0.71,-0.27] | 4.26 | Lonsdale and Watkinson 1982 |
| 92A | 100% L.I. | W | PCA | 5 | 5 | >0.99* | -0.46 | [-0.73,-0.19] | 4.37 | Lonsdale and Watkinson 1982 |

^aTable A.1 associates the numeric part of each Id. code with a particular species and study. The letter indicates the type of biomass measurements made: A = aboveground parts only, T = aboveground and belowground parts both included. "+" indicates that the line is a duplicate analysis of the previous code and condition by different author. "&" indicates a treatment or condition analyzed separately in the reference above, but combined with the preceding condition in the reanalysis of this report (Table A.2).

^bSee Table A.1 and the references given there for further information on condition.

^c"W" indicates that the data were analyzed with log \bar{w} -log N plots or by fitting log \bar{w} against log N, while "B" indicates that log B-log N plots or fitting was used.

^dMethod of estimating the thinning line. "Gra" indicates graphical analysis only with no statistics, "Reg" indicates regression analysis, and "PCA" indicates principal component analysis. "Ax" indicates a method used by Furnas (1981), who assumed a priori that thinning slopes were -1.5 in the log \bar{w} -log N plane, then used statistics to estimate the intercept under this axiom. Blanks indicate that the method of fitting was not specified.

^en_T is the total number of size-density points reported for each code and condition. n is the number of points remaining after removing points not relevant to the thinning line. This is the number of points used to fit the relationship between size and density. Blanks indicate that sample sizes were not given in the reference.

^fThis column contains coefficients of determination if the reference analyzed the data by correlation or regression. If the analysis was done by PCA, the number here is the percentage of the combined variance of the two variables explained by the first principal component (%EV).

^gMost thinning slopes were originally given for data in log \bar{w} -log N form. Such slopes were converted here to log B-log N form by adding 1 (Chapter 1). This facilitates comparison with the analyses in Table A.2.

^hSingle numbers in the column are standard errors. Paired numbers in brackets are 95% confidence limits.

ⁱThese are references for the self-thinning analysis only. References to the actual data are in Table A.1

*Percent variance explained (see footnote f).

APPENDIX B
FORESTRY YIELD TABLE DATA

Table B.1. Sources of Forestry Yield Table Data.

| Id. Code ^a | Species | Group ^b | Shade Tolerance ^c | Wood Density (kg/m ³) ^d | Conditions ^e | Reference ^f |
|-----------------------|---|--------------------|------------------------------|--|-------------------------|---|
| 201 | <u>Pinus ponderosa</u> | G | 2 | 472 | S.I.(ft) 100 | Meyer 1938, Tabs. 3-6 |
| 202 | <u>Alnus rubra</u> | A | 2 | 480 | S.I.(ft) 50 | Smith 1968, Tab. 3 |
| 203 | <u>Abies concolor</u> | G | 4 | 360 | S.I.(ft) 50 | Schumacher 1926, Tab. 1 |
| 204 | <u>Castanea dentata</u> | A | 3 | 737 | S.I.(ft) 50 | Frothingham 1912, Tabs. 17-19 |
| 205 | <u>Castanea dentata</u> and <u>Quercus</u> ^g | A | 3 | 737 | S.I.(ft) 50 | Frothingham 1912, Tabs. 20-22 |
| 206 | <u>Quercus</u> ^g | A | 3 | 737 | S.I.(ft) 50 | Frothingham 1912, Tabs. 23-25 |
| 207 | <u>Carya</u> ^g | A | 2 | 657 | S.I.(ft) 50 | Boisen and Newlin 1910, Tab. 14 |
| 208 | <u>Pinus monticola</u> | G | 3 | 432 | S.I.(ft) 50 | Haig 1932, Tab. 1 |
| 209 | <u>Populus tremuloides</u> | A | 1 | 400 | S.Q. (Ranks) | Baker 1925, Tabs. 14-17 |
| 210 | <u>Populus deltoides</u> | A | 1 | 384 | S.I.(ft) 50 | Williamson 1913, Tab. 3 |
| 211 | <u>Chamaecyparis thyoides</u> | G | 4 | 368 | S.I.(ft) 50 | Korstian 1931, Tabs. 22,25 |
| 212 | <u>Picea sitchensis</u> and <u>Tsuga heterophylla</u> | G | 4 | 472 | S.I.(ft) 100 | Meyer 1937, Tabs. 1-5 |
| 213 | <u>Picea rubrens</u> | G | 4 | 448 | S.I.(ft) 50 | Meyer 1929, Tabs. 2-6 |
| 214 | <u>Pinus</u> ^g | G | | 513 | S.Q. (Ranks) | Khil'mi 1957, Tabs. 13,14 |
| 215 | <u>Picea</u> ^g | G | | 416 | S.Q. (Ranks) | Khil'mi 1957, Tabs. 18,45 |
| 216 | <u>Quercus</u> ^g | A | | 737 | S.Q. (Ranks) | Khil'mi 1957, Tabs. 23,50 |
| 217 | <u>Pinus strobus</u> | G | 3 | 400 | S.Q. (Ranks) | Marty 1965, Tab. 1 |
| 218 | <u>Pinus strobus</u> | G | 3 | 400 | S.Q. (Ranks) | Marty 1965, Tab. 2 |
| 220 | <u>Pinus strobus</u> | G | 3 | 400 | S.Q. (Ranks) | Marty 1965, Tab. 4 |
| 221 | <u>Pseudotsuga menziesii</u> | G | 3 | 513 | S.I.(ft) 100 | McArdle 1930, Tab. 12 |
| 222 | <u>Pinus resinosa</u> | G | 2 | 529 | Spacing (Ranks) | Stiell and Berry 1973, Tabs. 4-8 |
| 223 | <u>Pinus</u> ^g | G | | 513 | S.Q. (Ranks) | Tseplyaev 1961, Tab. 47 |
| 224 | <u>Cedrus</u> ^g | G | | 448 | S.Q. (Ranks) | Tseplyaev 1961, Tab. 81 |
| 225 | <u>Populus</u> ^g | A | | 400 | S.Q. (Ranks) | Tseplyaev 1961, Tab. 134 |
| 227 | <u>Pinus ponderosa</u> | G | 2 | 472 | S.I.(ft) 100 | Behre 1928, Tabs. 2-6 |
| 228 | <u>Thuja occidentalis</u> | G | 4 | 304 | S.I.(ft) 160 | Gevorkiantz and Duerr 1939, Tabs. 18-24 |
| 229 | <u>Pinus taeda</u> | G | 2 | 609 | S.I.(ft) 50 | Schumacher and Coile 1960, Tab. 1 |
| 230 | <u>Pinus elliotii</u> | G | 3 | 609 | S.I.(ft) 50 | Schumacher and Coile 1960, Tab. 2 |
| 231 | <u>Pinus palustris</u> | G | 1 | 609 | S.I.(ft) 50 | Schumacher and Coile 1960, Tab. 3 |
| 232 | <u>Pinus echinata</u> | G | 2 | 609 | S.I.(ft) 50 | Schumacher and Coile 1960, Tab. 4 |
| 233 | <u>Pinus serotina</u> | G | 2 | 609 | S.I.(ft) 50 | Schumacher and Coile 1960, Tab. 5 |
| 234 | <u>Pinus taeda</u> | G | 2 | 609 | S.I.(ft) 50 | Ashe 1915, Tabs. 19,35,42 |
| 235 | <u>Pinus palustris</u> | G | 1 | 609 | S.I.(ft) 50 | Wahienberg 1946, Tabs. 4b,6c,7a,7,b |
| 236 | <u>Quercus</u> ^g (Upland oaks) | A | 3 | 737 | S.I.(ft) 50 | Schnurr 1937, Tab. 2 |
| 237 | <u>Picea glauca</u> | G | 4 | 400 | Spacing (Ranks) | Stiell 1976, Tabs. 10-13 |
| 238 | <u>Abies balsamea</u> | G | 5 | 416 | S.I.(ft) 65 | Meyer 1929, Tabs. 35-49 |
| 239 | <u>Picea glauca</u> | G | 4 | 400 | S.I.(ft) 65 | Meyer 1929, Tabs. 29-33 |
| 241 | <u>Picea</u> ^g and <u>Abies</u> ^g | G | 4 | 416 | S.I.(ft) 50 | Bakuzis and Hansen 1965, Tabs. 89,91,93,95,97 |
| 242 | <u>Alnus rubra</u> | A | 2 | 480 | S.I.(ft) 50 | Smith 1968, Tab. 5 |
| 243 | <u>Alnus rubra</u> | A | 2 | 480 | Crown width | Smith 1968, Tab. 6 |
| 244 | <u>Southern mixed hardwoods</u> | A | | 641 | S.I.(ft) 50 | Frothingham 1931, Tab. 8 |
| 245 | <u>Northern mixed hardwoods</u> | A | | 641 | S.Q. (Ranks) | Gevorkiantz and Duerr 1937, Tab. 3 |
| 246 | <u>Populus</u> ^g (Aspen) | A | 1 | 464 | S.I.(ft) 50 | Kittredge and Gevorkiantz 1929, Tab. 1 |
| 247 | <u>Eucalyptus globus</u> | E | | 889 | S.Q. (Ranks) | Jacobs 1979, Tab. A3.5 |
| 248 | <u>Eucalyptus microtheca</u> | E | | 801 | S.Q. (Ranks) | Jacobs 1979, Tab. A3.13 |
| 249 | <u>Liriodendron tulipifera</u> | A | 2 | 448 | S.I.(ft) 50 | McCarthy 1933, Tab. 17 |
| 250 | <u>Fraxinus</u> ^g | A | 3 | 641 | S.Q. (Ranks) | Strettt 1915, Tab. 15 |
| 251 | <u>Pseudotsuga menziesii</u> | G | 3 | 513 | none | McArdle et al. 1949, Tab. 25 |

Table B.1. (continued)

| Id. Code ^a | Species | Group ^b | Shade Tolerance ^c | Wood Density (kg/m ³) ^d | Conditions ^e | Reference ^f |
|-----------------------|--|--------------------|------------------------------|--|-------------------------|--|
| 252 | <u>Sequoia sempervirens</u> | G | 4 | 416 | S.I.(ft) 100 | Lindquist and Palley 1963, Tabs. 1,2,4-6 |
| 253 | <u>Pinus echinata</u> | G | 2 | 609 | S.I.(ft) 50 | Mattoon 1915, Tab. 14 |
| 254 | <u>Pinus echinata</u> | G | 2 | 609 | S.I.(ft) 50 | Mattoon 1915, Tab. 16 |
| 255 | <u>Picea sitchensis</u> | G | 4 | 424 | S.I.(ft) 50 | Cary 1922, Tabs. 6-9 |
| 256 | <u>Pinus banksiana</u> | G | 1 | 464 | S.I.(ft) 50 | Eyre 1944, Tab. 8 |
| 257 | <u>Pinus banksiana</u> | G | 1 | 464 | S.I.(ft) 50 | Bella 1968, Tabs. 2-6 |
| 258 | <u>Pinus resinosa</u> | G | 2 | 529 | S.I.(ft) 50 | Eyre and Zehngraft 1948, Tab. 10 |
| 259 | <u>Tsuga heterophylla</u> | G | 5 | 521 | S.I.(ft) 100 | Barnes 1962, Tabs. 3,5,7,9,12 |
| 260 | <u>Tsuga heterophylla</u> | G | 5 | 521 | S.I.(ft) 100 | Barnes 1962, Tabs. 4,6,8,10,13 |
| 261 | <u>Tsuga heterophylla</u> | G | 5 | 521 | S.I.(ft) 100 | Barnes 1962, Tabs. 4,6,8,10,14 |
| 262 | <u>Picea sitchensis and Tsuga heterophylla</u> | G | 4 | 472 | S.I.(ft) 100 | Taylor 1934, Tabs. 4-8 |
| 263 | <u>Picea mariana</u> | G | 4 | 529 | S.I.(ft) 50 | Fox and Kruse 1939, Tab. 2 |
| 264 | <u>Pinus banksiana</u> | G | 1 | 464 | S.I.(ft) 50 | Boudoux 1978, Tabs. 3,4 |
| 265 | <u>Fraxinus americana</u> | A | 3 | 657 | S.I.(ft) 50 | Patton 1922, page 37 |
| 266 | <u>Pseudotsuga menziesii</u> | G | 3 | 512 | S.I.(ft) 50 | Schumacher 1930, Tabs. 2-5,7 |
| 267 | Northern mixed hardwoods | A | | 641 | S.I.(ft) 50 | Forbes 1961, Tab. 14 |
| 268 | Northern mixed hardwoods | A | | 641 | S.I.(ft) 50 | Vermont Ag. Expt. Sta. 1914, Tab. 8 |
| 269 | <u>Quercus</u> ^g (Red oaks) | A | 3 | 737 | S.I.(ft) 50 | Patton 1922, page 37 |
| 270 | <u>Pinus taeda</u> | G | 2 | 609 | S.I.(ft) 50 | USDA 1929, Tabs. 33-38 |
| 271 | <u>Pinus palustris</u> | G | 1 | 609 | S.I.(ft) 50 | USDA 1929, Tabs. 68-70 |
| 272 | <u>Pinus ponderosa</u> | G | 2 | 472 | S.I.(ft) 100 | Show 1925, Tab. 2 |
| 273 | <u>Pinus echinata</u> | G | 2 | 609 | S.I.(ft) 50 | USDA 1929, Tabs. 98-102 |
| 274 | <u>Pinus elliotii</u> | G | 3 | 609 | S.I.(ft) 50 | USDA 1929, Tabs. 130-134 |
| 276 | <u>Sequoia sempervirens</u> | G | 4 | 416 | S.I.(ft) 50 | Bruce 1923, Tabs. 1-3 |
| 277 | <u>Liquidamber styraciflua</u> | A | 2 | 593 | S.I.(ft) 50 | Winters and Osborne 1935, Tabs. 4-8 |
| 278 | <u>Tsuga heterophylla</u> | G | 5 | 520 | S.I.(ft) 100 | Barnes 1962, Tab. 27 |
| 279 | <u>Eucalyptus delegatensis</u> | E | | 617 | S.I.(m) 50 | Hillis and Brown 1978, Tab. 10.1 |
| 280 | <u>Eucalyptus regnans</u> | E | | 689 | S.I.(m) 50 | Hillis and Brown 1978, Tab. 10.22 |
| 281 | <u>Eucalyptus sieberi</u> | E | | 840 | S.I.(m) 50 | Hillis and Brown 1978, Tab. 10.27 |

^aAn arbitrary number assigned to facilitate cross-referencing among tables.

^bOne of three categories. A = temperate angiosperms, E = trees of genus Eucalyptus, G = temperate gymnosperms.

^cFrom references above or Baker (1949).

^dFrom references above or Peattie (1950, 1953). Used to convert stand volumes (m³ of wood per m² of ground area) to stand biomasses (grams of wood per m²).

^eDifferences in growing site or cultural practice that may affect thinning line. S.I. = height of trees (in either feet or meters, as indicated) when the stand is at the specified age (in years). This measure, called 'site index', is a widely used indicator of the quality of a site for tree growth. S.Q. = Site quality measured by ranks rather than by site index. Lower numbers are of lower quality. Spacing = ranked initial densities in tree plantations, with lower numbers indicating higher initial densities. Crown width = a ranked measure of canopy openness. Lower numbers indicate a more open canopy. See references for further details.

^fData are taken from the indicated tables in the reference.

^gGeneric name only indicates that the specific name was not given or that more than one species from the genus were present.

Table B.2. Self-thinning Lines Fit to Forestry Yield Table Data.

| Id. Code ^a | Cond. ^b | No. of Points ^c | | r ^d | PCA Thinning Line ^e | | | Log N ^f | | | Log B ^f | | |
|-----------------------|--------------------|----------------------------|----|----------------|--------------------------------|----------------|-------|--------------------|-------|-------|--------------------|------|------|
| | | n _T | n | | $\hat{\beta}$ | $\hat{\alpha}$ | Pest | Min. | Max. | Mean | Min. | Max. | Mean |
| 201 | 40 | 18 | 13 | -0.998 | -0.308 | 3.75 | 0.382 | -1.27 | -0.49 | -0.97 | 3.90 | 4.14 | 4.05 |
| 201 | 50 | 19 | 14 | -0.997 | -0.310 | 3.77 | 0.382 | -1.38 | -0.52 | -1.07 | 3.93 | 4.21 | 4.11 |
| 201 | 60 | 19 | 14 | -1.000 | -0.324 | 3.79 | 0.378 | -1.49 | -0.69 | -1.18 | 4.01 | 4.27 | 4.17 |
| 201 | 70 | 19 | 14 | -0.999 | -0.326 | 3.83 | 0.377 | -1.57 | -0.81 | -1.27 | 4.09 | 4.34 | 4.25 |
| 201 | 80 | 19 | 14 | -0.999 | -0.321 | 3.89 | 0.378 | -1.64 | -0.91 | -1.35 | 4.17 | 4.41 | 4.32 |
| 201 | 90 | 19 | 14 | -0.998 | -0.318 | 3.95 | 0.379 | -1.71 | -0.99 | -1.42 | 4.25 | 4.49 | 4.40 |
| 201 | 100 | 19 | 14 | -0.997 | -0.314 | 4.01 | 0.380 | -1.76 | -1.06 | -1.47 | 4.33 | 4.56 | 4.47 |
| 201 | 110 | 19 | 14 | -0.997 | -0.307 | 4.08 | 0.383 | -1.80 | -1.12 | -1.52 | 4.41 | 4.63 | 4.55 |
| 201 | 120 | 19 | 14 | -0.993 | -0.318 | 4.12 | 0.379 | -1.84 | -1.17 | -1.56 | 4.48 | 4.70 | 4.62 |
| 201 | 130 | 19 | 14 | -0.988 | -0.318 | 4.18 | 0.379 | -1.87 | -1.22 | -1.59 | 4.55 | 4.77 | 4.69 |
| 201 | 140 | 9 | 4 | -0.999 | -0.498 | 3.98 | 0.334 | -1.46 | -1.26 | -1.37 | 4.61 | 4.71 | 4.66 |
| 201 | 150 | 9 | 4 | -0.998 | -0.479 | 4.04 | 0.338 | -1.49 | -1.30 | -1.40 | 4.66 | 4.75 | 4.71 |
| 201 | 160 | 9 | 4 | -0.998 | -0.524 | 4.01 | 0.328 | -1.52 | -1.33 | -1.43 | 4.71 | 4.81 | 4.76 |
| 202 | 80 | 11 | 9 | -0.999 | -0.653 | 3.30 | 0.303 | -1.38 | -0.76 | -1.15 | 3.79 | 4.19 | 4.05 |
| 202 | 96 | 11 | 9 | -0.998 | -0.470 | 3.59 | 0.340 | -1.46 | -0.86 | -1.24 | 3.98 | 4.27 | 4.17 |
| 202 | 112 | 11 | 9 | -0.999 | -0.484 | 3.62 | 0.337 | -1.54 | -0.94 | -1.31 | 4.07 | 4.37 | 4.25 |
| 203 | 30 | 11 | 8 | -1.000 | -0.563 | 3.67 | 0.320 | -0.83 | -0.59 | -0.73 | 4.00 | 4.14 | 4.08 |
| 203 | 40 | 11 | 8 | -0.998 | -0.575 | 3.69 | 0.317 | -0.96 | -0.73 | -0.87 | 4.10 | 4.24 | 4.19 |
| 203 | 50 | 11 | 8 | -1.000 | -0.585 | 3.77 | 0.315 | -1.05 | -0.83 | -0.96 | 4.25 | 4.39 | 4.33 |
| 203 | 60 | 11 | 8 | -1.000 | -0.564 | 3.89 | 0.320 | -1.14 | -0.91 | -1.05 | 4.40 | 4.54 | 4.48 |
| 203 | 70 | 11 | 8 | -0.999 | -0.558 | 3.95 | 0.321 | -1.23 | -0.99 | -1.13 | 4.51 | 4.64 | 4.59 |
| 203 | 80 | 11 | 8 | -0.999 | -0.570 | 3.98 | 0.318 | -1.31 | -1.07 | -1.21 | 4.58 | 4.72 | 4.67 |
| 203 | 90 | 11 | 8 | -0.999 | -0.580 | 3.96 | 0.316 | -1.38 | -1.15 | -1.29 | 4.63 | 4.77 | 4.71 |
| 204 | 62 | 13 | 7 | -0.997 | -0.640 | 3.56 | 0.305 | -1.14 | -0.91 | -1.04 | 4.13 | 4.29 | 4.22 |
| 204 | 71 | 13 | 8 | -0.998 | -0.638 | 3.64 | 0.305 | -1.23 | -0.92 | -1.09 | 4.22 | 4.42 | 4.33 |
| 204 | 80 | 13 | 8 | -0.998 | -0.657 | 3.67 | 0.302 | -1.31 | -1.01 | -1.17 | 4.32 | 4.52 | 4.43 |
| 205 | 58 | 13 | 8 | -0.997 | -0.766 | 3.44 | 0.283 | -1.02 | -0.76 | -0.90 | 4.02 | 4.21 | 4.13 |
| 205 | 68 | 13 | 8 | -0.997 | -0.691 | 3.56 | 0.296 | -1.15 | -0.88 | -1.03 | 4.16 | 4.35 | 4.27 |
| 205 | 80 | 13 | 8 | -0.999 | -0.630 | 3.67 | 0.307 | -1.24 | -0.95 | -1.11 | 4.27 | 4.45 | 4.37 |
| 206 | 52 | 13 | 9 | -0.996 | -0.807 | 3.31 | 0.277 | -1.07 | -0.72 | -0.92 | 3.89 | 4.16 | 4.05 |
| 206 | 64 | 13 | 9 | -0.996 | -0.747 | 3.41 | 0.286 | -1.20 | -0.85 | -1.04 | 4.03 | 4.29 | 4.19 |
| 206 | 75 | 13 | 9 | -0.998 | -0.698 | 3.50 | 0.294 | -1.28 | -0.93 | -1.14 | 4.15 | 4.39 | 4.29 |
| 207 | 49 | 11 | 11 | -0.992 | -0.787 | 2.94 | 0.280 | -1.79 | -0.76 | -1.36 | 3.57 | 4.42 | 4.01 |
| 208 | 40 | 8 | 6 | -0.997 | -0.795 | 4.01 | 0.279 | -0.66 | -0.13 | -0.49 | 4.11 | 4.55 | 4.39 |
| 208 | 50 | 8 | 6 | -0.997 | -0.803 | 3.94 | 0.277 | -0.84 | -0.31 | -0.66 | 4.18 | 4.63 | 4.47 |
| 208 | 60 | 8 | 6 | -0.998 | -0.796 | 3.83 | 0.278 | -1.07 | -0.53 | -0.89 | 4.25 | 4.69 | 4.54 |
| 208 | 70 | 8 | 6 | -0.997 | -0.766 | 3.75 | 0.283 | -1.27 | -0.73 | -1.10 | 4.31 | 4.75 | 4.59 |
| 209 | 1 | 7 | 4 | -0.976 | -0.318 | 3.46 | 0.379 | -1.46 | -0.97 | -1.20 | 3.76 | 3.92 | 3.85 |
| 209 | 2 | 9 | 6 | -0.937 | -0.282 | 3.63 | 0.390 | -1.61 | -0.89 | -1.20 | 3.85 | 4.05 | 3.97 |
| 209 | 3 | 11 | 7 | -0.947 | -0.270 | 3.74 | 0.394 | -1.57 | -0.92 | -1.21 | 3.96 | 4.14 | 4.07 |
| 209 | 4 | 13 | 8 | -0.985 | -0.433 | 3.66 | 0.349 | -1.33 | -0.95 | -1.16 | 4.05 | 4.23 | 4.16 |
| 210 | 136 | 44 | 28 | -0.998 | -0.199 | 3.85 | 0.417 | -2.10 | -1.49 | -1.83 | 4.15 | 4.27 | 4.22 |
| 211 | 20 | 17 | 14 | -0.998 | -0.537 | 3.53 | 0.325 | -0.42 | 0.26 | -0.17 | 3.38 | 3.74 | 3.62 |
| 211 | 30 | 17 | 14 | -0.997 | -0.529 | 3.76 | 0.327 | -0.53 | 0.16 | -0.27 | 3.67 | 4.02 | 3.90 |

Table B.2. (continued)

| Id. Code ^a | Cond. ^b | No. of Points ^c | | r^d | PCA Thinning Line ^e | | | Log N ^f | | | Log B ^f | | |
|-----------------------|--------------------|----------------------------|-----|--------|--------------------------------|----------------|-----------|--------------------|-------|-------|--------------------|------|------|
| | | n_T | n | | $\hat{\beta}$ | $\hat{\alpha}$ | D_{est} | Min. | Max. | Mean | Min. | Max. | Mean |
| 211 | 40 | 17 | 14 | -0.999 | -0.510 | 3.86 | 0.331 | -0.65 | 0.05 | -0.40 | 3.83 | 4.19 | 4.07 |
| 211 | 50 | 17 | 14 | -0.999 | -0.535 | 3.89 | 0.326 | -0.81 | -0.14 | -0.56 | 3.96 | 4.32 | 4.19 |
| 211 | 60 | 17 | 14 | -0.998 | -0.534 | 3.88 | 0.326 | -1.02 | -0.34 | -0.76 | 4.05 | 4.42 | 4.29 |
| 211 | 70 | 17 | 14 | -0.998 | -0.535 | 3.84 | 0.326 | -1.25 | -0.56 | -0.99 | 4.13 | 4.49 | 4.37 |
| 212 | 60 | 18 | 14 | -0.994 | -0.509 | 3.95 | 0.331 | -1.06 | -0.50 | -0.83 | 4.18 | 4.48 | 4.37 |
| 212 | 80 | 19 | 15 | -0.993 | -0.551 | 3.97 | 0.322 | -1.19 | -0.55 | -0.93 | 4.24 | 4.61 | 4.49 |
| 212 | 100 | 19 | 15 | -0.993 | -0.542 | 4.03 | 0.324 | -1.34 | -0.68 | -1.08 | 4.37 | 4.74 | 4.61 |
| 212 | 120 | 19 | 15 | -0.994 | -0.554 | 4.05 | 0.322 | -1.50 | -0.84 | -1.24 | 4.49 | 4.86 | 4.73 |
| 212 | 140 | 19 | 15 | -0.992 | -0.572 | 4.03 | 0.318 | -1.65 | -1.03 | -1.41 | 4.59 | 4.96 | 4.84 |
| 212 | 160 | 19 | 15 | -0.991 | -0.556 | 4.06 | 0.321 | -1.80 | -1.17 | -1.55 | 4.67 | 5.04 | 4.92 |
| 212 | 180 | 19 | 15 | -0.992 | -0.586 | 3.99 | 0.315 | -1.92 | -1.31 | -1.68 | 4.72 | 5.10 | 4.97 |
| 212 | 200 | 19 | 15 | -0.993 | -0.565 | 3.99 | 0.319 | -2.06 | -1.43 | -1.81 | 4.77 | 5.14 | 5.01 |
| 213 | 30 | 10 | 6 | -0.998 | -0.545 | 3.72 | 0.324 | -0.38 | -0.11 | -0.29 | 3.78 | 3.93 | 3.88 |
| 213 | 40 | 10 | 6 | -0.996 | -0.536 | 3.83 | 0.325 | -0.65 | -0.39 | -0.57 | 4.04 | 4.18 | 4.13 |
| 213 | 50 | 10 | 6 | -0.998 | -0.542 | 3.88 | 0.324 | -0.81 | -0.54 | -0.73 | 4.18 | 4.32 | 4.27 |
| 213 | 60 | 10 | 6 | -0.997 | -0.538 | 3.93 | 0.325 | -0.91 | -0.64 | -0.82 | 4.28 | 4.42 | 4.37 |
| 213 | 70 | 10 | 6 | -0.997 | -0.540 | 3.97 | 0.325 | -0.98 | -0.71 | -0.90 | 4.36 | 4.50 | 4.45 |
| 214 | 1 | 11 | 6 | -0.998 | -0.636 | 3.79 | 0.306 | -0.96 | -0.64 | -0.82 | 4.19 | 4.39 | 4.31 |
| 214 | 2 | 13 | 9 | -0.997 | -0.638 | 3.79 | 0.305 | -1.20 | -0.73 | -1.01 | 4.25 | 4.55 | 4.44 |
| 214 | 3 | 13 | 9 | -0.997 | -0.622 | 3.83 | 0.308 | -1.33 | -0.87 | -1.15 | 4.36 | 4.65 | 4.54 |
| 214 | 4 | 13 | 9 | -0.998 | -0.625 | 3.85 | 0.308 | -1.40 | -0.97 | -1.23 | 4.45 | 4.73 | 4.62 |
| 214 | 5 | 13 | 9 | -0.999 | -0.606 | 3.91 | 0.311 | -1.45 | -1.03 | -1.29 | 4.53 | 4.79 | 4.69 |
| 214 | 6 | 13 | 9 | -0.999 | -0.608 | 3.95 | 0.311 | -1.50 | -1.09 | -1.34 | 4.60 | 4.86 | 4.77 |
| 215 | 1 | 9 | 9 | -0.999 | -0.994 | 3.65 | 0.251 | -0.75 | 0.11 | -0.46 | 3.53 | 4.37 | 4.10 |
| 215 | 2 | 10 | 10 | -0.998 | -0.964 | 3.66 | 0.255 | -0.91 | 0.23 | -0.51 | 3.40 | 4.50 | 4.15 |
| 215 | 3 | 11 | 11 | -0.995 | -0.971 | 3.65 | 0.254 | -1.04 | 0.45 | -0.55 | 3.12 | 4.61 | 4.18 |
| 215 | 4 | 11 | 11 | -0.996 | -0.939 | 3.68 | 0.258 | -1.15 | 0.27 | -0.68 | 3.36 | 4.72 | 4.32 |
| 215 | 5 | 11 | 11 | -0.997 | -0.905 | 3.74 | 0.262 | -1.22 | 0.07 | -0.79 | 3.62 | 4.81 | 4.45 |
| 215 | 6 | 11 | 11 | -0.998 | -0.904 | 3.76 | 0.263 | -1.28 | -0.08 | -0.90 | 3.79 | 4.90 | 4.58 |
| 216 | 1 | 11 | 11 | -1.000 | -0.729 | 3.65 | 0.289 | -1.48 | 0.04 | -0.96 | 3.61 | 4.72 | 4.35 |
| 216 | 2 | 11 | 11 | -0.999 | -0.739 | 3.66 | 0.288 | -1.59 | -0.17 | -1.10 | 3.76 | 4.81 | 4.47 |
| 216 | 3 | 11 | 11 | -0.998 | -0.747 | 3.66 | 0.286 | -1.68 | -0.32 | -1.21 | 3.87 | 4.89 | 4.56 |
| 217 | 54 | 10 | 6 | -0.997 | -0.562 | 3.77 | 0.320 | -1.27 | -0.72 | -1.03 | 4.16 | 4.47 | 4.34 |
| 217 | 64 | 10 | 6 | -0.997 | -0.544 | 3.82 | 0.324 | -1.35 | -0.88 | -1.14 | 4.29 | 4.55 | 4.44 |
| 217 | 75 | 10 | 6 | -0.996 | -0.528 | 3.87 | 0.327 | -1.42 | -1.00 | -1.23 | 4.39 | 4.61 | 4.53 |
| 218 | 50 | 10 | 10 | -0.997 | -0.776 | 3.58 | 0.281 | -1.09 | -0.16 | -0.79 | 3.69 | 4.40 | 4.19 |
| 218 | 60 | 10 | 10 | -0.999 | -0.803 | 3.59 | 0.277 | -1.19 | -0.27 | -0.90 | 3.80 | 4.53 | 4.32 |
| 218 | 70 | 10 | 10 | -0.998 | -0.788 | 3.65 | 0.280 | -1.26 | -0.35 | -0.97 | 3.91 | 4.62 | 4.41 |
| 220 | 40 | 9 | 6 | -0.995 | -1.065 | 3.43 | 0.242 | -0.60 | -0.31 | -0.47 | 3.74 | 4.07 | 3.93 |
| 220 | 50 | 9 | 6 | -0.992 | -0.985 | 3.50 | 0.252 | -0.72 | -0.40 | -0.57 | 3.88 | 4.20 | 4.07 |
| 220 | 60 | 9 | 6 | -0.991 | -0.879 | 3.59 | 0.266 | -0.85 | -0.49 | -0.68 | 4.00 | 4.32 | 4.19 |
| 220 | 70 | 9 | 6 | -0.987 | -0.746 | 3.69 | 0.286 | -0.99 | -0.56 | -0.78 | 4.09 | 4.41 | 4.28 |
| 220 | 80 | 9 | 6 | -0.984 | -0.623 | 3.79 | 0.308 | -1.15 | -0.64 | -0.90 | 4.16 | 4.48 | 4.35 |
| 220 | 90 | 9 | 6 | -0.979 | -0.528 | 3.88 | 0.327 | -1.30 | -0.71 | -1.00 | 4.22 | 4.54 | 4.41 |

Table B.2. (continued)

| Id. Code ^a | Cond. ^b | No. of Points ^c | | r^d | PCA Thinning Line ^e | | | Log N ^f | | | Log B ^f | | |
|-----------------------|--------------------|----------------------------|-----|--------|--------------------------------|----------------|-----------|--------------------|-------|-------|--------------------|------|------|
| | | n_T | n | | $\hat{\beta}$ | $\hat{\alpha}$ | P_{est} | Min. | Max. | Mean | Min. | Max. | Mean |
| 221 | 80 | 15 | 13 | -0.996 | -0.629 | 3.64 | 0.307 | -1.21 | -0.42 | -0.94 | 3.88 | 4.38 | 4.23 |
| 221 | 90 | 15 | 13 | -0.995 | -0.655 | 3.66 | 0.302 | -1.25 | -0.50 | -1.00 | 3.96 | 4.46 | 4.31 |
| 221 | 100 | 15 | 13 | -0.996 | -0.667 | 3.68 | 0.300 | -1.31 | -0.57 | -1.05 | 4.03 | 4.53 | 4.38 |
| 221 | 110 | 15 | 13 | -0.995 | -0.684 | 3.69 | 0.297 | -1.36 | -0.64 | -1.11 | 4.10 | 4.60 | 4.45 |
| 221 | 120 | 15 | 13 | -0.994 | -0.683 | 3.72 | 0.297 | -1.43 | -0.71 | -1.17 | 4.17 | 4.67 | 4.52 |
| 221 | 130 | 15 | 13 | -0.993 | -0.695 | 3.72 | 0.295 | -1.48 | -0.77 | -1.23 | 4.23 | 4.73 | 4.58 |
| 221 | 140 | 15 | 13 | -0.992 | -0.693 | 3.73 | 0.295 | -1.54 | -0.84 | -1.29 | 4.27 | 4.77 | 4.62 |
| 221 | 150 | 15 | 13 | -0.992 | -0.697 | 3.73 | 0.295 | -1.60 | -0.90 | -1.35 | 4.31 | 4.81 | 4.66 |
| 221 | 160 | 15 | 13 | -0.990 | -0.696 | 3.72 | 0.295 | -1.65 | -0.96 | -1.40 | 4.34 | 4.84 | 4.69 |
| 221 | 170 | 15 | 13 | -0.990 | -0.694 | 3.71 | 0.295 | -1.72 | -1.02 | -1.46 | 4.37 | 4.87 | 4.72 |
| 221 | 180 | 15 | 13 | -0.992 | -0.696 | 3.68 | 0.295 | -1.78 | -1.08 | -1.53 | 4.39 | 4.89 | 4.74 |
| 221 | 190 | 15 | 13 | -0.991 | -0.700 | 3.64 | 0.294 | -1.85 | -1.16 | -1.60 | 4.41 | 4.91 | 4.76 |
| 221 | 200 | 15 | 13 | -0.992 | -0.705 | 3.60 | 0.293 | -1.93 | -1.23 | -1.67 | 4.43 | 4.93 | 4.78 |
| 221 | 210 | 15 | 13 | -0.991 | -0.691 | 3.59 | 0.296 | -2.01 | -1.30 | -1.75 | 4.45 | 4.95 | 4.80 |
| 222 | 1 | 35 | 8 | -0.997 | -0.631 | 4.21 | 0.307 | -0.66 | -0.44 | -0.52 | 4.48 | 4.62 | 4.54 |
| 222 | 2 | 35 | 8 | -0.997 | -0.880 | 3.98 | 0.266 | -0.72 | -0.54 | -0.61 | 4.45 | 4.61 | 4.51 |
| 222 | 3 | 35 | 8 | -0.996 | -1.242 | 3.62 | 0.223 | -0.78 | -0.64 | -0.69 | 4.42 | 4.59 | 4.49 |
| 222 | 4 | 35 | 5 | -0.999 | -1.535 | 3.27 | 0.197 | -0.85 | -0.77 | -0.80 | 4.44 | 4.57 | 4.50 |
| 222 | 5 | 35 | 5 | -0.995 | -1.975 | 2.73 | 0.168 | -0.92 | -0.86 | -0.88 | 4.42 | 4.55 | 4.47 |
| 223 | 1 | 15 | 13 | -0.999 | -0.338 | 4.02 | 0.374 | -1.59 | -0.84 | -1.35 | 4.30 | 4.55 | 4.48 |
| 224 | 3 | 17 | 14 | -0.995 | -0.504 | 3.91 | 0.333 | -1.36 | -0.61 | -1.14 | 4.23 | 4.60 | 4.49 |
| 225 | 1 | 6 | 6 | -0.998 | -0.687 | 3.40 | 0.296 | -1.32 | -0.56 | -1.02 | 3.78 | 4.31 | 4.09 |
| 227 | 40 | 16 | 13 | -0.994 | -0.511 | 2.99 | 0.331 | -1.41 | -0.79 | -1.17 | 3.41 | 3.73 | 3.59 |
| 227 | 50 | 16 | 13 | -0.995 | -0.508 | 3.26 | 0.331 | -1.46 | -0.83 | -1.22 | 3.70 | 4.02 | 3.88 |
| 227 | 60 | 16 | 13 | -0.995 | -0.508 | 3.41 | 0.332 | -1.51 | -0.88 | -1.27 | 3.88 | 4.20 | 4.06 |
| 227 | 70 | 16 | 13 | -0.995 | -0.509 | 3.50 | 0.331 | -1.57 | -0.94 | -1.33 | 4.00 | 4.32 | 4.18 |
| 227 | 80 | 16 | 13 | -0.994 | -0.509 | 3.55 | 0.331 | -1.63 | -1.01 | -1.39 | 4.07 | 4.39 | 4.26 |
| 227 | 90 | 16 | 13 | -0.994 | -0.509 | 3.57 | 0.331 | -1.70 | -1.07 | -1.46 | 4.13 | 4.45 | 4.31 |
| 227 | 100 | 16 | 13 | -0.993 | -0.508 | 3.60 | 0.332 | -1.77 | -1.14 | -1.53 | 4.20 | 4.52 | 4.38 |
| 227 | 110 | 16 | 13 | -0.994 | -0.509 | 3.64 | 0.331 | -1.84 | -1.21 | -1.60 | 4.27 | 4.59 | 4.45 |
| 227 | 120 | 16 | 13 | -0.977 | -0.509 | 3.67 | 0.331 | -1.91 | -1.28 | -1.68 | 4.35 | 4.67 | 4.53 |
| 228 | 25 | 14 | 11 | -0.998 | -0.407 | 3.46 | 0.355 | -0.55 | 0.06 | -0.34 | 3.42 | 3.68 | 3.59 |
| 228 | 35 | 14 | 11 | -0.998 | -0.372 | 3.52 | 0.364 | -0.75 | -0.11 | -0.53 | 3.56 | 3.80 | 3.72 |
| 228 | 45 | 15 | 12 | -0.997 | -0.368 | 3.56 | 0.366 | -0.93 | -0.10 | -0.65 | 3.58 | 3.89 | 3.80 |
| 228 | 55 | 15 | 12 | -0.998 | -0.340 | 3.60 | 0.373 | -1.07 | -0.24 | -0.79 | 3.67 | 3.96 | 3.87 |
| 228 | 65 | 15 | 12 | -0.998 | -0.319 | 3.64 | 0.379 | -1.21 | -0.37 | -0.93 | 3.75 | 4.02 | 3.94 |
| 228 | 75 | 15 | 12 | -0.998 | -0.301 | 3.67 | 0.384 | -1.34 | -0.49 | -1.05 | 3.81 | 4.06 | 3.98 |
| 229 | 60 | 7 | 7 | -0.999 | -0.892 | 3.05 | 0.264 | -1.23 | -0.80 | -1.09 | 3.76 | 4.14 | 4.02 |
| 229 | 70 | 7 | 7 | -0.999 | -0.898 | 3.05 | 0.263 | -1.33 | -0.91 | -1.19 | 3.86 | 4.24 | 4.12 |
| 229 | 80 | 7 | 7 | -0.997 | -0.895 | 3.07 | 0.264 | -1.41 | -0.99 | -1.27 | 3.94 | 4.32 | 4.21 |
| 229 | 90 | 7 | 7 | -0.997 | -0.887 | 3.11 | 0.265 | -1.48 | -1.05 | -1.34 | 4.03 | 4.41 | 4.30 |
| 229 | 100 | 7 | 7 | -0.995 | -0.888 | 3.13 | 0.265 | -1.55 | -1.12 | -1.40 | 4.11 | 4.49 | 4.38 |
| 229 | 110 | 7 | 7 | -0.992 | -0.884 | 3.17 | 0.265 | -1.60 | -1.17 | -1.45 | 4.18 | 4.56 | 4.45 |
| 229 | 120 | 7 | 7 | -0.988 | -0.880 | 3.21 | 0.266 | -1.64 | -1.21 | -1.49 | 4.26 | 4.63 | 4.53 |

Table B.2. (continued)

| Id. Code ^a | Cond. ^b | No. of Points ^c | | r^d | PCA Thinning Line ^e | | | Log N ^f | | | Log B ^f | | |
|--------------------------|--------------------|-------------------------------|-----|--------|--------------------------------|----------------|-------|--------------------|-------|-------|--------------------|------|------|
| | | n_T | n | | $\hat{\beta}$ | $\hat{\alpha}$ | Pest | Min. | Max. | Mean | Min. | Max. | Mean |
| 230 | 50 | 7 | 7 | -0.999 | -0.565 | 3.36 | 0.320 | -1.09 | -0.49 | -0.90 | 3.64 | 3.98 | 3.87 |
| 230 | 60 | 7 | 7 | -0.998 | -0.602 | 3.36 | 0.312 | -1.20 | -0.67 | -1.03 | 3.76 | 4.09 | 3.98 |
| 230 | 70 | 7 | 7 | -0.999 | -0.640 | 3.35 | 0.305 | -1.30 | -0.81 | -1.14 | 3.88 | 4.19 | 4.08 |
| 230 | 80 | 7 | 7 | -0.998 | -0.680 | 3.34 | 0.298 | -1.37 | -0.93 | -1.23 | 3.98 | 4.29 | 4.18 |
| 230 | 90 | 7 | 7 | -0.998 | -0.751 | 3.29 | 0.286 | -1.43 | -1.04 | -1.31 | 4.08 | 4.38 | 4.28 |
| 230 | 100 | 7 | 7 | -0.997 | -0.833 | 3.22 | 0.273 | -1.48 | -1.13 | -1.37 | 4.17 | 4.47 | 4.37 |
| 231 | 50 | 7 | 5 | -1.000 | -1.278 | 2.20 | 0.219 | -1.36 | -1.19 | -1.29 | 3.72 | 3.93 | 3.85 |
| 231 | 60 | 7 | 5 | -1.000 | -1.283 | 2.34 | 0.219 | -1.37 | -1.19 | -1.30 | 3.87 | 4.09 | 4.00 |
| 231 | 70 | 7 | 5 | -1.000 | -1.274 | 2.48 | 0.220 | -1.37 | -1.20 | -1.30 | 4.01 | 4.23 | 4.14 |
| 231 | 80 | 7 | 5 | -1.000 | -1.274 | 2.59 | 0.220 | -1.38 | -1.21 | -1.31 | 4.12 | 4.34 | 4.25 |
| 231 | 90 | 7 | 5 | -1.000 | -1.278 | 2.68 | 0.220 | -1.38 | -1.21 | -1.31 | 4.22 | 4.44 | 4.35 |
| 231 | 100 | 7 | 5 | -1.000 | -1.281 | 2.76 | 0.219 | -1.39 | -1.22 | -1.32 | 4.32 | 4.54 | 4.45 |
| 232 | 40 | 7 | 7 | -1.000 | -0.937 | 3.18 | 0.258 | -0.88 | -0.37 | -0.68 | 3.52 | 4.00 | 3.82 |
| 232 | 50 | 7 | 7 | -1.000 | -0.937 | 3.18 | 0.258 | -1.05 | -0.54 | -0.85 | 3.68 | 4.16 | 3.98 |
| 232 | 60 | 7 | 7 | -1.000 | -0.927 | 3.19 | 0.260 | -1.19 | -0.68 | -0.99 | 3.81 | 4.29 | 4.11 |
| 232 | 70 | 7 | 7 | -1.000 | -0.939 | 3.18 | 0.258 | -1.30 | -0.80 | -1.11 | 3.92 | 4.40 | 4.22 |
| 232 | 80 | 7 | 7 | -1.000 | -0.944 | 3.17 | 0.257 | -1.41 | -0.90 | -1.21 | 4.02 | 4.50 | 4.31 |
| 232 | 90 | 7 | 7 | -1.000 | -0.968 | 3.14 | 0.254 | -1.50 | -1.00 | -1.30 | 4.09 | 4.58 | 4.39 |
| 232 | 100 | 7 | 7 | -1.000 | -0.961 | 3.15 | 0.255 | -1.57 | -1.07 | -1.38 | 4.17 | 4.66 | 4.47 |
| 233 | 50 | 7 | 7 | -1.000 | -0.569 | 3.32 | 0.319 | -1.02 | -0.45 | -0.84 | 3.58 | 3.90 | 3.79 |
| 233 | 60 | 7 | 7 | -0.999 | -0.615 | 3.33 | 0.310 | -1.10 | -0.55 | -0.93 | 3.67 | 4.01 | 3.90 |
| 233 | 70 | 7 | 7 | -0.999 | -0.664 | 3.33 | 0.301 | -1.17 | -0.63 | -1.00 | 3.76 | 4.11 | 4.00 |
| 233 | 80 | 7 | 7 | -0.999 | -0.723 | 3.32 | 0.290 | -1.22 | -0.70 | -1.05 | 3.83 | 4.21 | 4.08 |
| 233 | 90 | 7 | 7 | -0.998 | -0.802 | 3.29 | 0.278 | -1.25 | -0.75 | -1.10 | 3.90 | 4.30 | 4.17 |
| 233 | 100 | 7 | 7 | -0.996 | -0.898 | 3.23 | 0.263 | -1.27 | -0.80 | -1.13 | 3.97 | 4.39 | 4.25 |
| 234 | 70 | 6 | 5 | -0.989 | -0.441 | 3.68 | 0.347 | -1.43 | -1.05 | -1.28 | 4.14 | 4.31 | 4.25 |
| 234 | 84 | 9 | 7 | -0.963 | -0.246 | 4.10 | 0.401 | -1.54 | -1.07 | -1.36 | 4.37 | 4.48 | 4.43 |
| 234 | 99 | 9 | 7 | -0.962 | -0.449 | 3.91 | 0.345 | -1.57 | -1.17 | -1.41 | 4.44 | 4.60 | 4.54 |
| 235 | 40 | 18 | 18 | -0.995 | -0.888 | 2.97 | 0.265 | -1.14 | -0.28 | -0.85 | 3.17 | 3.94 | 3.72 |
| 235 | 50 | 18 | 18 | -0.999 | -0.804 | 3.26 | 0.277 | -1.17 | -0.31 | -0.89 | 3.50 | 4.19 | 3.97 |
| 235 | 60 | 18 | 18 | -0.999 | -0.813 | 3.41 | 0.276 | -1.21 | -0.35 | -0.93 | 3.69 | 4.37 | 4.16 |
| 235 | 70 | 18 | 18 | -0.999 | -0.829 | 3.49 | 0.273 | -1.25 | -0.40 | -0.97 | 3.81 | 4.51 | 4.29 |
| 235 | 80 | 18 | 18 | -0.999 | -0.854 | 3.52 | 0.270 | -1.31 | -0.45 | -1.02 | 3.87 | 4.61 | 4.39 |
| 235 | 90 | 18 | 18 | -0.998 | -0.882 | 3.51 | 0.266 | -1.36 | -0.51 | -1.08 | 3.93 | 4.69 | 4.46 |
| 235 | 100 | 18 | 18 | -0.998 | -0.897 | 3.50 | 0.264 | -1.42 | -0.57 | -1.14 | 3.97 | 4.75 | 4.52 |
| 235 | 110 | 18 | 18 | -0.997 | -0.881 | 3.50 | 0.266 | -1.49 | -0.62 | -1.20 | 4.02 | 4.78 | 4.56 |
| 236 | 40 | 10 | 9 | -0.996 | -0.772 | 3.29 | 0.282 | -0.99 | -0.09 | -0.70 | 3.40 | 4.09 | 3.84 |
| 236 | 50 | 10 | 9 | -0.996 | -0.781 | 3.32 | 0.281 | -1.10 | -0.21 | -0.81 | 3.52 | 4.21 | 3.96 |
| 236 | 60 | 10 | 9 | -0.996 | -0.780 | 3.34 | 0.281 | -1.21 | -0.32 | -0.93 | 3.62 | 4.31 | 4.06 |
| 236 | 70 | 10 | 9 | -0.996 | -0.779 | 3.34 | 0.281 | -1.32 | -0.43 | -1.04 | 3.70 | 4.39 | 4.14 |
| 236 | 80 | 10 | 10 | -0.997 | -0.833 | 3.26 | 0.273 | -1.44 | -0.22 | -1.06 | 3.40 | 4.46 | 4.13 |
| 237 | 1 | 28 | 12 | -0.988 | -0.620 | 3.83 | 0.309 | -0.81 | -0.40 | -0.55 | 4.07 | 4.31 | 4.17 |
| 237 | 2 | 28 | 8 | -0.996 | -0.702 | 3.70 | 0.294 | -0.86 | -0.61 | -0.70 | 4.12 | 4.30 | 4.19 |
| 237 | 3 | 28 | 8 | -0.994 | -0.922 | 3.45 | 0.260 | -0.91 | -0.70 | -0.77 | 4.09 | 4.28 | 4.17 |

Table B.2. (continued)

| Id. Code ^a | Cond. ^b | No. of Points ^c | | r^d | PCA Thinning Line ^e | | | Log N ^f | | | Log B ^f | | |
|--------------------------|--------------------|-------------------------------|-----|--------|--------------------------------|----------------|-------|--------------------|-------|-------|--------------------|------|------|
| | | n_T | n | | $\hat{\beta}$ | $\hat{\alpha}$ | Dist | Min. | Max. | Mean | Min. | Max. | Mean |
| 237 | 4 | 28 | 8 | -0.995 | -1.158 | 3.18 | 0.232 | -0.95 | -0.77 | -0.84 | 4.07 | 4.27 | 4.15 |
| 237 | 5 | 28 | 5 | -0.999 | -1.280 | 3.01 | 0.219 | -0.97 | -0.86 | -0.91 | 4.11 | 4.26 | 4.18 |
| 238 | 40 | 8 | 5 | -0.997 | -0.598 | 3.77 | 0.313 | -0.54 | -0.27 | -0.44 | 3.93 | 4.10 | 4.03 |
| 238 | 50 | 8 | 5 | -0.998 | -0.591 | 3.80 | 0.314 | -0.71 | -0.43 | -0.61 | 4.06 | 4.22 | 4.16 |
| 238 | 60 | 8 | 5 | -0.998 | -0.588 | 3.81 | 0.315 | -0.86 | -0.58 | -0.76 | 4.16 | 4.32 | 4.26 |
| 238 | 70 | 8 | 5 | -0.998 | -0.589 | 3.81 | 0.315 | -1.01 | -0.73 | -0.90 | 4.24 | 4.40 | 4.34 |
| 239 | 40 | 8 | 5 | -0.999 | -0.524 | 3.72 | 0.328 | -0.71 | -0.35 | -0.58 | 3.90 | 4.10 | 4.02 |
| 239 | 50 | 8 | 5 | -0.999 | -0.524 | 3.78 | 0.328 | -0.82 | -0.45 | -0.69 | 4.02 | 4.22 | 4.14 |
| 239 | 60 | 8 | 5 | -0.998 | -0.521 | 3.82 | 0.329 | -0.94 | -0.57 | -0.80 | 4.11 | 4.31 | 4.23 |
| 239 | 70 | 8 | 5 | -0.998 | -0.524 | 3.82 | 0.328 | -1.07 | -0.71 | -0.94 | 4.19 | 4.39 | 4.31 |
| 241 | 20 | 6 | 5 | -0.990 | -4.100 | 2.03 | 0.098 | -0.25 | -0.20 | -0.23 | 2.84 | 3.08 | 2.99 |
| 241 | 30 | 6 | 5 | -0.997 | -4.571 | 1.86 | 0.090 | -0.40 | -0.35 | -0.38 | 3.47 | 3.69 | 3.61 |
| 241 | 40 | 6 | 5 | -0.984 | -3.830 | 1.92 | 0.104 | -0.51 | -0.45 | -0.49 | 3.66 | 3.89 | 3.80 |
| 241 | 50 | 6 | 5 | -0.991 | -3.935 | 1.50 | 0.101 | -0.62 | -0.57 | -0.60 | 3.73 | 3.96 | 3.87 |
| 241 | 60 | 6 | 5 | -0.984 | -4.467 | 0.68 | 0.091 | -0.74 | -0.69 | -0.72 | 3.77 | 4.00 | 3.91 |
| 242 | 56 | 6 | 3 | -0.963 | -0.393 | 3.23 | 0.359 | -1.33 | -1.29 | -1.31 | 3.74 | 3.75 | 3.74 |
| 242 | 73 | 7 | 4 | -0.964 | -0.148 | 3.78 | 0.435 | -1.34 | -1.24 | -1.28 | 3.97 | 3.98 | 3.97 |
| 242 | 90 | 8 | 4 | -0.951 | -0.119 | 4.08 | 0.447 | -1.38 | -1.22 | -1.30 | 4.22 | 4.24 | 4.23 |
| 243 | 1 | 12 | 7 | -0.998 | -0.551 | 2.69 | 0.322 | -2.33 | -1.89 | -2.13 | 3.73 | 3.96 | 3.86 |
| 243 | 2 | 7 | 5 | -0.969 | -0.480 | 3.38 | 0.338 | -1.69 | -1.20 | -1.46 | 3.96 | 4.17 | 4.08 |
| 244 | 70 | 6 | 3 | -1.000 | -1.352 | 2.58 | 0.213 | -1.31 | -1.25 | -1.28 | 4.27 | 4.35 | 4.31 |
| 244 | 86 | 6 | 4 | -1.000 | -0.898 | 3.24 | 0.263 | -1.38 | -1.25 | -1.32 | 4.36 | 4.48 | 4.42 |
| 244 | 102 | 6 | 5 | -0.996 | -0.753 | 3.49 | 0.285 | -1.44 | -1.23 | -1.34 | 4.41 | 4.57 | 4.51 |
| 245 | 1 | 12 | 5 | -0.995 | -0.568 | 3.28 | 0.319 | -1.63 | -1.45 | -1.54 | 4.10 | 4.20 | 4.15 |
| 245 | 2 | 11 | 5 | -0.991 | -0.437 | 3.54 | 0.348 | -1.73 | -1.53 | -1.63 | 4.21 | 4.29 | 4.25 |
| 245 | 3 | 9 | 4 | -0.998 | -0.446 | 3.55 | 0.346 | -1.79 | -1.63 | -1.72 | 4.28 | 4.35 | 4.32 |
| 246 | 30 | 4 | 4 | -0.997 | -0.874 | 3.08 | 0.267 | -0.56 | 0.01 | -0.29 | 3.07 | 3.56 | 3.34 |
| 246 | 50 | 6 | 4 | -0.984 | -0.470 | 3.51 | 0.340 | -1.01 | -0.49 | -0.75 | 3.72 | 3.96 | 3.86 |
| 246 | 60 | 7 | 4 | -0.998 | -0.352 | 3.74 | 0.370 | -1.24 | -0.80 | -1.04 | 4.02 | 4.17 | 4.11 |
| 246 | 70 | 7 | 4 | -0.992 | -0.348 | 3.81 | 0.371 | -1.35 | -0.91 | -1.15 | 4.12 | 4.27 | 4.21 |
| 246 | 80 | 7 | 4 | -0.997 | -0.361 | 3.83 | 0.367 | -1.44 | -1.01 | -1.24 | 4.19 | 4.34 | 4.28 |
| 247 | 1 | 7 | 4 | -0.990 | -3.804 | 2.06 | 0.104 | -0.57 | -0.55 | -0.56 | 4.13 | 4.22 | 4.18 |
| 247 | 2 | 7 | 4 | -0.988 | -4.973 | 1.53 | 0.084 | -0.58 | -0.56 | -0.57 | 4.31 | 4.43 | 4.38 |
| 247 | 3 | 7 | 4 | -0.994 | -6.286 | 0.85 | 0.069 | -0.60 | -0.58 | -0.59 | 4.47 | 4.61 | 4.55 |
| 247 | 4 | 7 | 4 | -0.991 | -8.132 | -0.21 | 0.055 | -0.62 | -0.59 | -0.60 | 4.60 | 4.79 | 4.70 |
| 248 | 1 | 9 | 5 | -0.996 | -6.444 | -3.17 | 0.067 | -1.07 | -0.95 | -1.02 | 2.98 | 3.69 | 3.40 |
| 248 | 2 | 10 | 6 | -0.999 | -6.855 | -3.66 | 0.064 | -1.12 | -0.97 | -1.06 | 3.02 | 4.01 | 3.59 |
| 248 | 3 | 11 | 7 | -0.992 | -7.224 | -4.18 | 0.061 | -1.16 | -0.98 | -1.09 | 2.98 | 4.22 | 3.72 |
| 249 | 100 | 9 | 3 | -0.995 | -1.243 | 2.53 | 0.223 | -1.36 | -1.27 | -1.31 | 4.11 | 4.22 | 4.17 |
| 249 | 110 | 9 | 3 | -0.998 | -1.188 | 2.64 | 0.229 | -1.39 | -1.30 | -1.34 | 4.18 | 4.29 | 4.24 |
| 249 | 120 | 9 | 3 | -0.999 | -1.015 | 2.88 | 0.248 | -1.44 | -1.33 | -1.38 | 4.23 | 4.34 | 4.29 |
| 250 | 2 | 13 | 4 | -0.993 | -0.659 | 3.69 | 0.301 | -1.18 | -1.09 | -1.13 | 4.41 | 4.47 | 4.44 |
| 250 | 3 | 13 | 8 | -0.993 | -0.549 | 3.82 | 0.323 | -1.39 | -1.10 | -1.26 | 4.42 | 4.59 | 4.51 |
| 251 | 1 | 27 | 27 | -0.999 | -0.645 | 3.74 | 0.304 | -1.77 | -0.42 | -1.30 | 3.99 | 4.87 | 4.58 |

Table B.2. (continued)

| Id. Code ^a | Cond. ^b | No. of Points ^c | | r^d | PCA Thinning Line ^e | | | Log N ^f | | | Log B ^f | | |
|--------------------------|--------------------|-------------------------------|-----|--------|--------------------------------|----------------|-----------|--------------------|-------|-------|--------------------|------|------|
| | | n_T | n | | $\hat{\beta}$ | $\hat{\alpha}$ | p_{est} | Min. | Max. | Mean | Min. | Max. | Mean |
| 252 | 120 | 9 | 3 | -0.993 | -4.466 | -1.62 | 0.091 | -1.40 | -1.36 | -1.38 | 4.47 | 4.62 | 4.55 |
| 252 | 140 | 9 | 5 | -0.987 | -4.593 | -1.78 | 0.089 | -1.42 | -1.36 | -1.39 | 4.43 | 4.74 | 4.60 |
| 252 | 160 | 9 | 9 | -0.996 | -4.748 | -1.93 | 0.087 | -1.43 | -1.21 | -1.35 | 3.82 | 4.84 | 4.48 |
| 252 | 180 | 9 | 9 | -0.999 | -3.084 | 0.56 | 0.122 | -1.43 | -1.13 | -1.32 | 4.07 | 4.94 | 4.63 |
| 252 | 200 | 9 | 9 | -0.999 | -2.392 | 1.66 | 0.147 | -1.41 | -1.07 | -1.29 | 4.24 | 5.03 | 4.75 |
| 252 | 220 | 9 | 9 | -0.999 | -2.043 | 2.25 | 0.164 | -1.39 | -1.03 | -1.27 | 4.36 | 5.11 | 4.84 |
| 252 | 240 | 9 | 9 | -0.999 | -1.814 | 2.67 | 0.178 | -1.38 | -0.99 | -1.24 | 4.46 | 5.17 | 4.92 |
| 253 | 47 | 14 | 10 | -0.999 | -0.858 | 3.35 | 0.269 | -1.18 | -0.59 | -0.93 | 3.85 | 4.35 | 4.14 |
| 253 | 57 | 15 | 13 | -0.998 | -0.727 | 3.49 | 0.290 | -1.42 | -0.39 | -1.00 | 3.77 | 4.48 | 4.22 |
| 253 | 66 | 15 | 14 | -0.996 | -0.618 | 3.60 | 0.309 | -1.65 | -0.36 | -1.15 | 3.82 | 4.59 | 4.31 |
| 254 | 50 | 12 | 12 | -1.000 | -0.947 | 3.24 | 0.257 | -1.25 | -0.57 | -1.00 | 3.77 | 4.42 | 4.18 |
| 254 | 61 | 13 | 9 | -0.999 | -0.691 | 3.64 | 0.296 | -1.34 | -1.00 | -1.19 | 4.32 | 4.56 | 4.46 |
| 254 | 70 | 13 | 11 | -0.992 | -0.809 | 3.51 | 0.276 | -1.44 | -1.03 | -1.28 | 4.32 | 4.66 | 4.55 |
| 255 | 87 | 14 | 7 | -0.983 | -0.547 | 4.39 | 0.323 | -1.76 | -1.26 | -1.54 | 5.06 | 5.33 | 5.23 |
| 256 | 40 | 7 | 4 | -0.997 | -0.868 | 2.91 | 0.268 | -0.90 | -0.51 | -0.72 | 3.35 | 3.68 | 3.54 |
| 256 | 53 | 7 | 4 | -0.995 | -0.773 | 3.03 | 0.282 | -1.08 | -0.67 | -0.89 | 3.53 | 3.85 | 3.72 |
| 256 | 66 | 7 | 4 | -0.992 | -0.683 | 3.14 | 0.297 | -1.20 | -0.78 | -1.01 | 3.66 | 3.94 | 3.83 |
| 257 | 45 | 13 | 13 | -1.000 | -0.541 | 3.07 | 0.324 | -1.28 | -0.10 | -0.95 | 3.13 | 3.76 | 3.58 |
| 257 | 49 | 13 | 11 | -0.999 | -0.655 | 3.00 | 0.302 | -1.20 | -0.55 | -0.97 | 3.37 | 3.79 | 3.64 |
| 257 | 53 | 13 | 11 | -1.000 | -0.874 | 3.04 | 0.267 | -1.08 | -0.62 | -0.91 | 3.59 | 3.99 | 3.84 |
| 257 | 54 | 13 | 11 | -0.999 | -1.011 | 2.98 | 0.249 | -1.03 | -0.55 | -0.85 | 3.55 | 4.03 | 3.84 |
| 257 | 57 | 13 | 10 | -1.000 | -1.731 | 2.51 | 0.183 | -0.91 | -0.74 | -0.84 | 3.79 | 4.09 | 3.97 |
| 258 | 40 | 9 | 6 | -0.991 | -0.733 | 3.26 | 0.289 | -1.19 | -0.87 | -1.09 | 3.89 | 4.12 | 4.06 |
| 258 | 52 | 10 | 6 | -0.998 | -0.824 | 3.19 | 0.274 | -1.35 | -1.04 | -1.24 | 4.05 | 4.31 | 4.22 |
| 258 | 60 | 10 | 6 | -0.997 | -0.711 | 3.40 | 0.292 | -1.48 | -1.17 | -1.37 | 4.23 | 4.45 | 4.37 |
| 259 | 100 | 17 | 14 | -0.994 | -0.466 | 4.05 | 0.341 | -1.59 | -0.80 | -1.27 | 4.40 | 4.78 | 4.65 |
| 259 | 110 | 17 | 13 | -0.998 | -0.425 | 4.14 | 0.351 | -1.64 | -0.98 | -1.36 | 4.54 | 4.83 | 4.71 |
| 259 | 120 | 17 | 13 | -0.996 | -0.407 | 4.19 | 0.355 | -1.69 | -1.03 | -1.40 | 4.59 | 4.86 | 4.76 |
| 259 | 130 | 17 | 13 | -0.997 | -0.396 | 4.23 | 0.358 | -1.72 | -1.08 | -1.44 | 4.64 | 4.90 | 4.80 |
| 259 | 140 | 17 | 13 | -0.999 | -0.390 | 4.25 | 0.360 | -1.75 | -1.11 | -1.47 | 4.68 | 4.93 | 4.83 |
| 259 | 150 | 17 | 13 | -0.999 | -0.378 | 4.29 | 0.363 | -1.79 | -1.14 | -1.51 | 4.71 | 4.97 | 4.86 |
| 259 | 160 | 17 | 13 | -0.999 | -0.379 | 4.31 | 0.363 | -1.81 | -1.16 | -1.53 | 4.74 | 4.99 | 4.89 |
| 259 | 170 | 17 | 13 | -0.998 | -0.383 | 4.32 | 0.362 | -1.83 | -1.18 | -1.55 | 4.77 | 5.02 | 4.92 |
| 259 | 180 | 17 | 13 | -0.999 | -0.376 | 4.35 | 0.363 | -1.84 | -1.20 | -1.57 | 4.80 | 5.05 | 4.94 |
| 259 | 190 | 17 | 13 | -0.999 | -0.377 | 4.37 | 0.363 | -1.86 | -1.22 | -1.59 | 4.82 | 5.07 | 4.97 |
| 259 | 200 | 17 | 13 | -0.999 | -0.377 | 4.39 | 0.363 | -1.87 | -1.24 | -1.60 | 4.85 | 5.10 | 4.99 |
| 259 | 210 | 17 | 13 | -1.000 | -0.375 | 4.40 | 0.364 | -1.89 | -1.25 | -1.62 | 4.87 | 5.11 | 5.01 |
| 260 | 60 | 14 | 7 | -0.999 | -0.563 | 4.00 | 0.320 | -0.85 | -0.59 | -0.72 | 4.33 | 4.48 | 4.41 |
| 260 | 70 | 14 | 9 | -0.999 | -0.563 | 4.03 | 0.320 | -0.96 | -0.59 | -0.79 | 4.36 | 4.57 | 4.47 |
| 260 | 80 | 15 | 9 | -0.997 | -0.555 | 4.04 | 0.322 | -1.08 | -0.73 | -0.91 | 4.44 | 4.64 | 4.55 |
| 260 | 90 | 15 | 9 | -0.998 | -0.513 | 4.11 | 0.331 | -1.18 | -0.79 | -0.99 | 4.51 | 4.71 | 4.62 |
| 260 | 100 | 15 | 9 | -0.998 | -0.480 | 4.15 | 0.338 | -1.26 | -0.88 | -1.08 | 4.57 | 4.75 | 4.67 |
| 260 | 110 | 15 | 9 | -0.995 | -0.455 | 4.20 | 0.344 | -1.34 | -0.95 | -1.15 | 4.63 | 4.80 | 4.73 |
| 260 | 120 | 15 | 9 | -0.997 | -0.411 | 4.26 | 0.354 | -1.41 | -1.03 | -1.23 | 4.68 | 4.84 | 4.77 |

Table B.2. (continued)

| Id. Code ^a | Cond. ^b | No. of Points ^c | | r^d | PCA Thinning Line ^e | | | Log N ^f | | | Log B ^f | | |
|--------------------------|--------------------|-------------------------------|-----|--------|--------------------------------|----------------|-------|--------------------|-------|-------|--------------------|------|------|
| | | n_T | n | | $\hat{\beta}$ | $\hat{\alpha}$ | Pest | Min. | Max. | Mean | Min. | Max. | Mean |
| 260 | 130 | 15 | 9 | -0.998 | -0.402 | 4.29 | 0.357 | -1.46 | -1.07 | -1.27 | 4.72 | 4.88 | 4.80 |
| 260 | 140 | 15 | 9 | -0.999 | -0.382 | 4.33 | 0.362 | -1.51 | -1.13 | -1.33 | 4.76 | 4.90 | 4.84 |
| 260 | 150 | 15 | 9 | -0.999 | -0.377 | 4.35 | 0.363 | -1.55 | -1.15 | -1.36 | 4.78 | 4.93 | 4.86 |
| 260 | 160 | 15 | 9 | -0.999 | -0.370 | 4.37 | 0.365 | -1.57 | -1.18 | -1.39 | 4.81 | 4.96 | 4.89 |
| 260 | 170 | 15 | 9 | -0.994 | -0.383 | 4.37 | 0.362 | -1.59 | -1.25 | -1.42 | 4.83 | 4.98 | 4.91 |
| 260 | 180 | 15 | 9 | -1.000 | -0.358 | 4.42 | 0.368 | -1.62 | -1.23 | -1.43 | 4.85 | 5.00 | 4.93 |
| 261 | 60 | 14 | 8 | -0.999 | -0.612 | 3.93 | 0.310 | -0.85 | -0.53 | -0.70 | 4.26 | 4.46 | 4.36 |
| 261 | 70 | 14 | 8 | -0.999 | -0.597 | 3.97 | 0.313 | -0.96 | -0.65 | -0.82 | 4.35 | 4.55 | 4.45 |
| 261 | 80 | 15 | 9 | -0.997 | -0.608 | 3.97 | 0.311 | -1.08 | -0.73 | -0.91 | 4.40 | 4.62 | 4.52 |
| 261 | 90 | 15 | 9 | -0.999 | -0.543 | 4.05 | 0.324 | -1.18 | -0.79 | -0.99 | 4.47 | 4.68 | 4.59 |
| 261 | 100 | 15 | 9 | -0.997 | -0.528 | 4.08 | 0.327 | -1.26 | -0.88 | -1.08 | 4.53 | 4.74 | 4.65 |
| 261 | 110 | 15 | 9 | -0.997 | -0.499 | 4.12 | 0.333 | -1.34 | -0.95 | -1.15 | 4.59 | 4.78 | 4.70 |
| 261 | 120 | 15 | 9 | -0.997 | -0.476 | 4.16 | 0.339 | -1.41 | -1.03 | -1.23 | 4.64 | 4.83 | 4.74 |
| 261 | 130 | 15 | 9 | -0.997 | -0.440 | 4.22 | 0.347 | -1.46 | -1.07 | -1.27 | 4.68 | 4.86 | 4.78 |
| 261 | 140 | 15 | 9 | -0.995 | -0.423 | 4.25 | 0.351 | -1.51 | -1.13 | -1.33 | 4.72 | 4.89 | 4.82 |
| 261 | 150 | 15 | 9 | -0.998 | -0.414 | 4.28 | 0.354 | -1.55 | -1.15 | -1.36 | 4.75 | 4.92 | 4.84 |
| 261 | 160 | 15 | 9 | -0.999 | -0.410 | 4.30 | 0.355 | -1.57 | -1.18 | -1.39 | 4.78 | 4.94 | 4.87 |
| 262 | 70 | 13 | 13 | -0.998 | -0.584 | 4.02 | 0.316 | -0.85 | 0.34 | -0.43 | 3.80 | 4.49 | 4.27 |
| 262 | 80 | 13 | 13 | -0.998 | -0.580 | 4.01 | 0.316 | -0.98 | 0.23 | -0.56 | 3.86 | 4.56 | 4.34 |
| 262 | 90 | 13 | 13 | -0.997 | -0.595 | 3.99 | 0.314 | -1.09 | 0.07 | -0.68 | 3.92 | 4.62 | 4.39 |
| 262 | 100 | 13 | 13 | -0.997 | -0.595 | 3.99 | 0.313 | -1.21 | -0.04 | -0.79 | 3.98 | 4.68 | 4.46 |
| 262 | 110 | 13 | 13 | -0.998 | -0.598 | 3.98 | 0.313 | -1.31 | -0.14 | -0.89 | 4.04 | 4.74 | 4.52 |
| 262 | 120 | 13 | 13 | -0.998 | -0.598 | 3.98 | 0.313 | -1.38 | -0.23 | -0.98 | 4.10 | 4.80 | 4.57 |
| 262 | 130 | 13 | 13 | -0.998 | -0.600 | 3.99 | 0.313 | -1.46 | -0.32 | -1.07 | 4.15 | 4.85 | 4.63 |
| 262 | 140 | 13 | 13 | -0.998 | -0.599 | 3.99 | 0.313 | -1.55 | -0.39 | -1.15 | 4.20 | 4.90 | 4.67 |
| 262 | 150 | 13 | 13 | -0.998 | -0.587 | 4.00 | 0.315 | -1.63 | -0.47 | -1.23 | 4.25 | 4.94 | 4.72 |
| 263 | 26 | 9 | 4 | -0.968 | -0.848 | 3.72 | 0.271 | -0.40 | -0.31 | -0.36 | 3.98 | 4.05 | 4.02 |
| 263 | 33 | 11 | 7 | -0.998 | -0.850 | 3.72 | 0.270 | -0.60 | -0.32 | -0.48 | 3.98 | 4.22 | 4.12 |
| 263 | 39 | 11 | 9 | -0.996 | -0.776 | 3.72 | 0.281 | -0.77 | -0.32 | -0.59 | 3.96 | 4.30 | 4.18 |
| 264 | 40 | 9 | 4 | -0.936 | -0.243 | 3.51 | 0.402 | -0.94 | -0.56 | -0.72 | 3.63 | 3.73 | 3.68 |
| 264 | 50 | 11 | 7 | -0.938 | -0.551 | 3.41 | 0.322 | -0.94 | -0.60 | -0.76 | 3.71 | 3.90 | 3.83 |
| 265 | 77 | 6 | 4 | -0.979 | -0.250 | 4.06 | 0.400 | -1.38 | -0.90 | -1.15 | 4.28 | 4.39 | 4.35 |
| 266 | 60 | 12 | 8 | -0.995 | -0.256 | 4.16 | 0.398 | -1.31 | -0.96 | -1.16 | 4.40 | 4.49 | 4.45 |
| 266 | 80 | 14 | 11 | -0.989 | -0.336 | 4.14 | 0.374 | -1.55 | -0.93 | -1.29 | 4.44 | 4.65 | 4.58 |
| 266 | 100 | 14 | 11 | -0.993 | -0.334 | 4.22 | 0.375 | -1.73 | -1.13 | -1.48 | 4.58 | 4.79 | 4.71 |
| 266 | 120 | 14 | 12 | -0.993 | -0.331 | 4.26 | 0.376 | -1.87 | -1.16 | -1.58 | 4.62 | 4.87 | 4.78 |
| 266 | 140 | 8 | 8 | -0.964 | -0.566 | 3.93 | 0.319 | -1.68 | -1.01 | -1.37 | 4.44 | 4.84 | 4.71 |
| 267 | 42 | 12 | 8 | -0.987 | -0.719 | 3.62 | 0.291 | -0.96 | -0.63 | -0.79 | 4.06 | 4.29 | 4.19 |
| 268 | 54 | 12 | 7 | -0.996 | -0.381 | 3.71 | 0.362 | -1.02 | -0.65 | -0.86 | 3.95 | 4.10 | 4.04 |
| 269 | 75 | 6 | 6 | -0.994 | -0.654 | 3.43 | 0.302 | -1.57 | -0.42 | -1.09 | 3.68 | 4.42 | 4.15 |
| 270 | 60 | 14 | 14 | -0.994 | -0.597 | 3.68 | 0.313 | -1.17 | -0.22 | -0.85 | 3.79 | 4.34 | 4.19 |
| 270 | 70 | 14 | 14 | -0.994 | -0.626 | 3.64 | 0.308 | -1.30 | -0.34 | -0.98 | 3.83 | 4.43 | 4.26 |
| 270 | 80 | 14 | 14 | -0.994 | -0.627 | 3.65 | 0.307 | -1.40 | -0.45 | -1.08 | 3.91 | 4.50 | 4.33 |
| 270 | 90 | 14 | 14 | -0.991 | -0.625 | 3.67 | 0.308 | -1.48 | -0.52 | -1.16 | 3.97 | 4.56 | 4.40 |

Table B.2. (continued)

| Id. Code ^a | Cond. ^b | No. of Points ^c | | r^d | PCA Thinning Line ^e | | | Log N ^f | | | Log B ^f | | |
|--------------------------|--------------------|-------------------------------|-----|--------|--------------------------------|----------------|-----------|--------------------|-------|-------|--------------------|------|------|
| | | n_T | n | | $\hat{\beta}$ | $\hat{\alpha}$ | P_{est} | Min. | Max. | Mean | Min. | Max. | Mean |
| 270 | 100 | 14 | 14 | -0.990 | -0.641 | 3.68 | 0.305 | -1.55 | -0.59 | -1.22 | 4.02 | 4.63 | 4.46 |
| 270 | 110 | 14 | 14 | -0.991 | -0.656 | 3.69 | 0.302 | -1.59 | -0.64 | -1.26 | 4.08 | 4.73 | 4.52 |
| 270 | 120 | 14 | 14 | -0.991 | -0.646 | 3.73 | 0.304 | -1.63 | -0.68 | -1.31 | 4.13 | 4.74 | 4.58 |
| 271 | 40 | 18 | 18 | -0.995 | -0.888 | 2.97 | 0.265 | -1.14 | -0.28 | -0.85 | 3.17 | 3.94 | 3.72 |
| 271 | 50 | 18 | 18 | -0.999 | -0.804 | 3.26 | 0.277 | -1.17 | -0.31 | -0.89 | 3.50 | 4.19 | 3.97 |
| 271 | 60 | 18 | 18 | -0.999 | -0.813 | 3.41 | 0.276 | -1.21 | -0.35 | -0.93 | 3.69 | 4.37 | 4.16 |
| 271 | 70 | 18 | 18 | -0.999 | -0.829 | 3.49 | 0.273 | -1.25 | -0.40 | -0.97 | 3.81 | 4.51 | 4.29 |
| 271 | 80 | 18 | 18 | -0.999 | -0.854 | 3.52 | 0.270 | -1.31 | -0.45 | -1.02 | 3.87 | 4.61 | 4.39 |
| 271 | 90 | 18 | 18 | -0.998 | -0.882 | 3.51 | 0.266 | -1.36 | -0.51 | -1.08 | 3.93 | 4.69 | 4.46 |
| 271 | 100 | 18 | 18 | -0.998 | -0.897 | 3.50 | 0.264 | -1.42 | -0.57 | -1.14 | 3.97 | 4.75 | 4.52 |
| 271 | 110 | 18 | 18 | -0.997 | -0.881 | 3.50 | 0.266 | -1.49 | -0.62 | -1.20 | 4.02 | 4.78 | 4.56 |
| 272 | 50 | 8 | 6 | -0.998 | -1.656 | 2.12 | 0.188 | -1.25 | -1.08 | -1.18 | 3.90 | 4.18 | 4.07 |
| 272 | 60 | 9 | 7 | -0.956 | -1.855 | 1.89 | 0.175 | -1.36 | -1.14 | -1.25 | 3.94 | 4.35 | 4.21 |
| 272 | 71 | 9 | 7 | -0.984 | -2.373 | 1.18 | 0.148 | -1.41 | -1.25 | -1.34 | 4.11 | 4.50 | 4.37 |
| 272 | 81 | 10 | 8 | -0.997 | -2.439 | 1.08 | 0.145 | -1.44 | -1.26 | -1.38 | 4.15 | 4.61 | 4.45 |
| 272 | 103 | 10 | 10 | -0.999 | -1.848 | 1.93 | 0.176 | -1.49 | -1.06 | -1.37 | 3.88 | 4.69 | 4.46 |
| 273 | 40 | 18 | 15 | -0.995 | -0.404 | 3.85 | 0.356 | -0.97 | -0.06 | -0.67 | 3.87 | 4.22 | 4.12 |
| 273 | 50 | 18 | 15 | -0.988 | -0.437 | 3.90 | 0.348 | -1.11 | -0.34 | -0.82 | 4.02 | 4.36 | 4.26 |
| 273 | 60 | 18 | 15 | -0.990 | -0.449 | 3.94 | 0.345 | -1.24 | -0.47 | -0.95 | 4.13 | 4.47 | 4.37 |
| 273 | 70 | 18 | 15 | -0.993 | -0.454 | 3.98 | 0.344 | -1.34 | -0.58 | -1.06 | 4.22 | 4.57 | 4.46 |
| 273 | 80 | 18 | 15 | -0.993 | -0.414 | 4.05 | 0.354 | -1.45 | -0.70 | -1.18 | 4.36 | 4.64 | 4.54 |
| 273 | 90 | 18 | 15 | -0.994 | -0.481 | 3.96 | 0.338 | -1.59 | -0.84 | -1.31 | 4.34 | 4.70 | 4.59 |
| 273 | 100 | 18 | 15 | -0.988 | -0.471 | 3.95 | 0.340 | -1.76 | -1.00 | -1.49 | 4.39 | 4.76 | 4.65 |
| 274 | 60 | 10 | 8 | -0.999 | -0.378 | 3.96 | 0.363 | -0.94 | -0.42 | -0.74 | 4.12 | 4.32 | 4.24 |
| 274 | 70 | 10 | 8 | -0.997 | -0.399 | 3.98 | 0.357 | -1.08 | -0.56 | -0.89 | 4.20 | 4.41 | 4.33 |
| 274 | 80 | 10 | 8 | -0.998 | -0.403 | 3.99 | 0.356 | -1.21 | -0.69 | -1.01 | 4.27 | 4.48 | 4.40 |
| 274 | 90 | 10 | 9 | -0.998 | -0.422 | 3.97 | 0.352 | -1.32 | -0.69 | -1.08 | 4.26 | 4.54 | 4.43 |
| 274 | 100 | 10 | 9 | -0.998 | -0.440 | 3.95 | 0.347 | -1.43 | -0.81 | -1.19 | 4.30 | 4.58 | 4.47 |
| 276 | 84 | 9 | 9 | -0.998 | -1.222 | 3.35 | 0.225 | -1.06 | -0.60 | -0.88 | 4.09 | 4.62 | 4.43 |
| 276 | 95 | 9 | 9 | -0.997 | -1.220 | 3.42 | 0.225 | -1.07 | -0.62 | -0.89 | 4.17 | 4.70 | 4.51 |
| 276 | 112 | 9 | 9 | -0.998 | -1.224 | 3.44 | 0.225 | -1.10 | -0.65 | -0.93 | 4.24 | 4.77 | 4.58 |
| 277 | 70 | 5 | 4 | -1.000 | -0.333 | 3.74 | 0.375 | -1.05 | -0.36 | -0.75 | 3.86 | 4.09 | 3.98 |
| 277 | 80 | 9 | 7 | -0.996 | -0.362 | 3.79 | 0.367 | -1.40 | -0.52 | -1.09 | 3.99 | 4.31 | 4.19 |
| 277 | 90 | 10 | 9 | -0.995 | -0.396 | 3.83 | 0.358 | -1.50 | -0.27 | -1.12 | 3.94 | 4.45 | 4.27 |
| 277 | 100 | 10 | 9 | -0.993 | -0.414 | 3.88 | 0.354 | -1.54 | -0.40 | -1.20 | 4.06 | 4.54 | 4.38 |
| 277 | 110 | 10 | 9 | -0.990 | -0.418 | 3.95 | 0.353 | -1.55 | -0.46 | -1.24 | 4.16 | 4.63 | 4.46 |
| 277 | 120 | 8 | 7 | -0.994 | -0.395 | 4.03 | 0.358 | -1.51 | -0.50 | -1.18 | 4.24 | 4.65 | 4.50 |
| 278 | 1 | 33 | 19 | -1.000 | -0.373 | 4.31 | 0.364 | -1.92 | -1.29 | -1.60 | 4.79 | 5.02 | 4.90 |
| 279 | 40 | 11 | 10 | -0.993 | -0.640 | 3.72 | 0.305 | -1.53 | -0.52 | -1.14 | 4.02 | 4.67 | 4.45 |
| 280 | 51 | 8 | 6 | -0.988 | -0.552 | 3.83 | 0.322 | -1.71 | -1.41 | -1.57 | 4.60 | 4.76 | 4.70 |
| 281 | 27 | 5 | 5 | -0.992 | -0.691 | 4.09 | 0.296 | -0.89 | -0.17 | -0.57 | 4.18 | 4.67 | 4.48 |
| 281 | 30 | 5 | 5 | -0.990 | -0.621 | 4.11 | 0.308 | -1.00 | -0.29 | -0.68 | 4.27 | 4.70 | 4.53 |
| 281 | 33 | 5 | 5 | -0.979 | -0.547 | 4.14 | 0.323 | -1.11 | -0.41 | -0.79 | 4.34 | 4.71 | 4.58 |

Table B.2. (continued)

| Id. Code ^a | Cond. ^b | No. of Points ^c | | r^d | PCA Thinning Line ^e | | | Log N ^f | | | Log B ^f | | |
|--------------------------|--------------------|-------------------------------|-----|--------|--------------------------------|----------------|-----------|--------------------|-------|-------|--------------------|------|------|
| | | n_T | n | | $\hat{\beta}$ | $\hat{\alpha}$ | p_{est} | Min. | Max. | Mean | Min. | Max. | Mean |
| 281 | 27 | 5 | 5 | -0.992 | -0.691 | 4.09 | 0.296 | -0.89 | -0.17 | -0.57 | 4.18 | 4.67 | 4.48 |
| 281 | 30 | 5 | 5 | -0.990 | -0.621 | 4.11 | 0.308 | -1.00 | -0.29 | -0.68 | 4.27 | 4.70 | 4.53 |
| 281 | 33 | 5 | 5 | -0.979 | -0.547 | 4.14 | 0.323 | -1.11 | -0.41 | -0.79 | 4.34 | 4.71 | 4.58 |

^aTable B.1 associates each Id. code with a particular yield table.

^bSee Table B.1 and the references given there for more information on condition.

^c n_T is the total number of log B-log N points given for each code and condition. n is the number of points remaining after removing points not relevant to the thinning line. This is the number of points used to fit the PCA relationship between log B and log N.

^dThese correlation coefficients have little statistical meaning because the natural variability present in real forest measurements has been removed from yield table predictions. These values are included only as a crude index of variation around the fitted line.

^e $\hat{\beta}$ and $\hat{\alpha}$ are, respectively, the slope and intercept of the fitted PCA thinning line. Formulas for principle components analysis are given in Jolicoeur and Heusner (1971). p_{est} is a transformation of the thinning slope calculated by $p_{est} = 0.5 / (1 - \hat{\beta})$. See discussion in Chapter 6.

^fThe mean, minimum, and maximum are given for log B and for log N over the n data points used to fit each thinning line.

Table B.3. Fitted Allometric Relationships for Forestry Yield Table Data.

| | | Allometric Relationships Fit by Principal Component Analysis ^C | | | | | | | | | | | | | | |
|-----------------------|--------------------|---|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|
| Id. Code ^a | Cond. ^b | $\log \bar{h} - \log \bar{w}$ | | | $\log \overline{DBH} - \log \bar{w}$ | | | $\log \overline{BSLA} - \log \bar{w}$ | | | $\log \bar{h} - \log \overline{DBH}$ | | | $\log \bar{h} - \log \overline{BSLA}$ | | |
| | | n | r | $\hat{\phi}_{HW}$ | n | r | $\hat{\phi}_{DW}$ | n | r | $\hat{\phi}_{BW}$ | n | r | $\hat{\phi}_{HD}$ | n | r | $\hat{\phi}_{HB}$ |
| 201 | 40 | 13 | 0.988 | 0.159 | 13 | 1.000 | 0.381 | 13 | 1.000 | 0.764 | 13 | 0.985 | 0.417 | 13 | 0.986 | 0.207 |
| 201 | 50 | 14 | 0.994 | 0.188 | 14 | 0.998 | 0.381 | 14 | 1.000 | 0.763 | 14 | 0.993 | 0.492 | 14 | 0.993 | 0.246 |
| 201 | 60 | 14 | 0.997 | 0.215 | 14 | 1.000 | 0.381 | 14 | 1.000 | 0.755 | 14 | 0.998 | 0.564 | 14 | 0.997 | 0.284 |
| 201 | 70 | 14 | 1.000 | 0.234 | 14 | 1.000 | 0.377 | 14 | 1.000 | 0.754 | 14 | 1.000 | 0.620 | 14 | 0.999 | 0.310 |
| 201 | 80 | 14 | 1.000 | 0.250 | 14 | 1.000 | 0.379 | 14 | 1.000 | 0.757 | 14 | 1.000 | 0.660 | 14 | 1.000 | 0.331 |
| 201 | 90 | 14 | 1.000 | 0.257 | 14 | 1.000 | 0.379 | 14 | 1.000 | 0.759 | 14 | 1.000 | 0.679 | 14 | 1.000 | 0.339 |
| 201 | 100 | 14 | 0.999 | 0.271 | 14 | 1.000 | 0.381 | 14 | 1.000 | 0.761 | 14 | 0.999 | 0.711 | 14 | 0.999 | 0.355 |
| 201 | 110 | 14 | 0.999 | 0.278 | 14 | 0.999 | 0.384 | 14 | 1.000 | 0.765 | 14 | 0.999 | 0.724 | 14 | 0.999 | 0.363 |
| 201 | 120 | 14 | 1.000 | 0.281 | 14 | 1.000 | 0.380 | 14 | 1.000 | 0.759 | 14 | 0.999 | 0.738 | 14 | 0.999 | 0.370 |
| 201 | 130 | 14 | 1.000 | 0.280 | 14 | 0.999 | 0.380 | 14 | 0.999 | 0.758 | 14 | 0.999 | 0.736 | 14 | 0.999 | 0.369 |
| 201 | 140 | 4 | 0.999 | 0.273 | 4 | 1.000 | 0.333 | 4 | 1.000 | 0.668 | 4 | 1.000 | 0.821 | 4 | 1.000 | 0.409 |
| 201 | 150 | 4 | 0.999 | 0.275 | 4 | 1.000 | 0.339 | 4 | 1.000 | 0.676 | 4 | 1.000 | 0.810 | 4 | 1.000 | 0.406 |
| 201 | 160 | 4 | 1.000 | 0.271 | 4 | 1.000 | 0.326 | 4 | 1.000 | 0.656 | 4 | 1.000 | 0.832 | 4 | 1.000 | 0.414 |
| 202 | 80 | 9 | 0.999 | 0.231 | 9 | 1.000 | 0.347 | | | | 9 | 0.998 | 0.665 | | | |
| 202 | 96 | 9 | 0.999 | 0.229 | 9 | 1.000 | 0.392 | | | | 9 | 0.999 | 0.584 | | | |
| 202 | 112 | 9 | 1.000 | 0.211 | 9 | 1.000 | 0.393 | | | | 9 | 0.999 | 0.537 | | | |
| 203 | 30 | 8 | 0.995 | 0.215 | 8 | 1.000 | 0.322 | 8 | 1.000 | 0.662 | 8 | 0.994 | 0.670 | 8 | 0.994 | 0.325 |
| 203 | 40 | 8 | 0.998 | 0.208 | 8 | 1.000 | 0.332 | 8 | 1.000 | 0.653 | 8 | 0.997 | 0.626 | 8 | 0.997 | 0.318 |
| 203 | 50 | 8 | 0.993 | 0.219 | 8 | 1.000 | 0.322 | 8 | 1.000 | 0.656 | 8 | 0.991 | 0.681 | 8 | 0.991 | 0.333 |
| 203 | 60 | 8 | 0.997 | 0.213 | 8 | 1.000 | 0.330 | 8 | 1.000 | 0.664 | 8 | 0.995 | 0.644 | 8 | 0.996 | 0.320 |
| 203 | 70 | 8 | 0.996 | 0.209 | 8 | 1.000 | 0.332 | 8 | 1.000 | 0.669 | 8 | 0.995 | 0.630 | 8 | 0.995 | 0.313 |
| 203 | 80 | 8 | 0.998 | 0.216 | 8 | 1.000 | 0.327 | 8 | 1.000 | 0.660 | 8 | 0.998 | 0.661 | 8 | 0.999 | 0.328 |
| 203 | 90 | 8 | 0.999 | 0.222 | 8 | 1.000 | 0.329 | 8 | 1.000 | 0.660 | 8 | 0.999 | 0.675 | 8 | 0.999 | 0.336 |
| 204 | 62 | 7 | 0.997 | 0.205 | 7 | 0.999 | 0.427 | 7 | 1.000 | 0.849 | 7 | 0.995 | 0.480 | 7 | 0.996 | 0.241 |
| 204 | 71 | 8 | 0.995 | 0.189 | 8 | 1.000 | 0.408 | 8 | 1.000 | 0.818 | 8 | 0.993 | 0.462 | 8 | 0.994 | 0.230 |
| 204 | 80 | 8 | 0.997 | 0.174 | 8 | 1.000 | 0.404 | 8 | 1.000 | 0.818 | 8 | 0.997 | 0.431 | 8 | 0.997 | 0.213 |
| 205 | 58 | 8 | 0.998 | 0.250 | 8 | 1.000 | 0.444 | 8 | 1.000 | 0.884 | 8 | 0.998 | 0.563 | 8 | 0.998 | 0.282 |
| 205 | 68 | 8 | 0.996 | 0.234 | 8 | 1.000 | 0.455 | 8 | 1.000 | 0.915 | 8 | 0.996 | 0.515 | 8 | 0.996 | 0.256 |
| 205 | 80 | 8 | 0.997 | 0.192 | 8 | 1.000 | 0.449 | 8 | 1.000 | 0.898 | 8 | 0.997 | 0.429 | 8 | 0.997 | 0.214 |
| 206 | 52 | 9 | 0.999 | 0.264 | 9 | 0.999 | 0.369 | 9 | 1.000 | 0.730 | 9 | 0.998 | 0.715 | 9 | 0.998 | 0.362 |
| 206 | 64 | 9 | 0.994 | 0.233 | 9 | 1.000 | 0.408 | 9 | 1.000 | 0.824 | 9 | 0.995 | 0.572 | 9 | 0.994 | 0.283 |
| 206 | 75 | 9 | 0.998 | 0.217 | 9 | 1.000 | 0.428 | 9 | 1.000 | 0.857 | 9 | 0.998 | 0.508 | 9 | 0.998 | 0.254 |
| 207 | 49 | 11 | 0.995 | 0.258 | 11 | 0.993 | 0.333 | | | | 11 | 0.982 | 0.770 | | | |
| 208 | 40 | 6 | 0.999 | 0.301 | 6 | 1.000 | 0.375 | 6 | 1.000 | 0.748 | 6 | 0.999 | 0.804 | 6 | 0.999 | 0.402 |
| 208 | 50 | 6 | 0.999 | 0.302 | 6 | 1.000 | 0.372 | 6 | 1.000 | 0.745 | 6 | 0.999 | 0.812 | 6 | 0.999 | 0.405 |
| 208 | 60 | 6 | 1.000 | 0.302 | 6 | 1.000 | 0.376 | 6 | 1.000 | 0.745 | 6 | 1.000 | 0.802 | 6 | 0.999 | 0.405 |
| 208 | 70 | 6 | 0.999 | 0.294 | 6 | 1.000 | 0.372 | 6 | 1.000 | 0.754 | 6 | 0.999 | 0.790 | 6 | 0.999 | 0.390 |
| 209 | 1 | | | | 4 | 0.997 | 0.166 | 4 | 0.999 | 0.837 | | | | | | |
| 209 | 2 | | | | 6 | 0.988 | 0.202 | 6 | 0.999 | 0.862 | | | | | | |
| 209 | 3 | 7 | 0.965 | 0.118 | 7 | 0.992 | 0.251 | 7 | 0.999 | 0.889 | 7 | 0.988 | 0.479 | 7 | 0.953 | 0.131 |
| 209 | 4 | | | | 8 | 0.998 | 0.433 | 8 | 0.999 | 0.844 | | | | | | |
| 210 | 136 | 28 | 0.998 | 0.166 | 28 | 0.998 | 0.392 | | | | 28 | 0.999 | 0.422 | | | |
| 211 | 20 | 14 | 1.000 | 0.217 | 14 | 0.999 | 0.406 | 14 | 1.000 | 0.780 | 14 | 1.000 | 0.535 | 14 | 1.000 | 0.278 |

Table B.3. (continued)

| Allometric Relationships Fit by Principal Component Analysis ^C | | | | | | | | | | | | | | | | |
|---|--------------------|-------------------------------|-------|-------------------|-------------------------|-------|-------------------|--------------------------|-------|-------------------|-------------------------|-------|-------------------|--------------------------|-------|-------------------|
| Id. Code ^a | Cond. ^b | log \bar{h} - log \bar{w} | | | log DBH - log \bar{w} | | | log BSLA - log \bar{w} | | | log \bar{h} - log DBH | | | log \bar{h} - log BSLA | | |
| | | n | r | $\hat{\phi}_{hw}$ | n | r | $\hat{\phi}_{Dw}$ | n | r | $\hat{\phi}_{Bw}$ | n | r | $\hat{\phi}_{h0}$ | n | r | $\hat{\phi}_{hB}$ |
| 211 | 30 | 14 | 0.999 | 0.220 | 14 | 0.999 | 0.399 | 14 | 1.000 | 0.790 | 14 | 0.999 | 0.553 | 14 | 1.000 | 0.279 |
| 211 | 40 | 14 | 1.000 | 0.217 | 14 | 1.000 | 0.402 | 14 | 1.000 | 0.800 | 14 | 1.000 | 0.538 | 14 | 1.000 | 0.271 |
| 211 | 50 | 14 | 1.000 | 0.219 | 14 | 1.000 | 0.397 | 14 | 1.000 | 0.792 | 14 | 1.000 | 0.552 | 14 | 1.000 | 0.277 |
| 211 | 60 | 14 | 1.000 | 0.218 | 14 | 1.000 | 0.400 | 14 | 1.000 | 0.792 | 14 | 1.000 | 0.545 | 14 | 1.000 | 0.276 |
| 211 | 70 | 14 | 1.000 | 0.217 | 14 | 1.000 | 0.400 | 14 | 1.000 | 0.793 | 14 | 1.000 | 0.544 | 14 | 1.000 | 0.274 |
| 212 | 60 | 14 | 0.999 | 0.278 | 14 | 1.000 | 0.397 | 14 | 1.000 | 0.790 | 14 | 0.999 | 0.701 | 14 | 0.999 | 0.352 |
| 212 | 80 | 15 | 1.000 | 0.282 | 15 | 0.999 | 0.387 | 15 | 1.000 | 0.777 | 15 | 0.999 | 0.728 | 15 | 0.999 | 0.363 |
| 212 | 100 | 15 | 1.000 | 0.279 | 15 | 1.000 | 0.391 | 15 | 1.000 | 0.781 | 15 | 0.999 | 0.714 | 15 | 0.999 | 0.357 |
| 212 | 120 | 15 | 1.000 | 0.282 | 15 | 1.000 | 0.390 | 15 | 1.000 | 0.778 | 15 | 0.999 | 0.722 | 15 | 0.999 | 0.362 |
| 212 | 140 | 15 | 1.000 | 0.286 | 15 | 1.000 | 0.386 | 15 | 1.000 | 0.773 | 15 | 0.999 | 0.742 | 15 | 0.999 | 0.371 |
| 212 | 160 | 15 | 1.000 | 0.283 | 15 | 1.000 | 0.389 | 15 | 1.000 | 0.778 | 15 | 0.999 | 0.729 | 15 | 0.999 | 0.364 |
| 212 | 180 | 15 | 1.000 | 0.292 | 15 | 1.000 | 0.384 | 15 | 1.000 | 0.768 | 15 | 0.999 | 0.760 | 15 | 0.999 | 0.380 |
| 212 | 200 | 15 | 1.000 | 0.284 | 15 | 1.000 | 0.387 | 15 | 1.000 | 0.774 | 15 | 0.999 | 0.735 | 15 | 0.999 | 0.367 |
| 213 | 30 | 6 | 0.997 | 0.260 | 6 | 0.999 | 0.404 | 6 | 1.000 | 0.795 | 6 | 0.993 | 0.644 | 6 | 0.997 | 0.328 |
| 213 | 40 | 6 | 0.994 | 0.291 | 6 | 1.000 | 0.396 | 6 | 1.000 | 0.799 | 6 | 0.994 | 0.738 | 6 | 0.994 | 0.365 |
| 213 | 50 | 6 | 0.996 | 0.288 | 6 | 0.999 | 0.394 | 6 | 1.000 | 0.796 | 6 | 0.996 | 0.731 | 6 | 0.996 | 0.362 |
| 213 | 60 | 6 | 0.999 | 0.278 | 6 | 1.000 | 0.400 | 6 | 1.000 | 0.800 | 6 | 0.998 | 0.697 | 6 | 0.999 | 0.348 |
| 213 | 70 | 6 | 1.000 | 0.271 | 6 | 1.000 | 0.396 | 6 | 1.000 | 0.797 | 6 | 1.000 | 0.685 | 6 | 1.000 | 0.340 |
| 214 | 1 | | | | | | | | | | | | | | | |
| 214 | 2 | | | | | | | | | | | | | | | |
| 214 | 3 | | | | | | | | | | | | | | | |
| 214 | 4 | | | | | | | | | | | | | | | |
| 214 | 5 | | | | | | | | | | | | | | | |
| 214 | 6 | | | | | | | | | | | | | | | |
| 215 | 1 | | | | | | | | | | | | | | | |
| 215 | 2 | | | | | | | | | | | | | | | |
| 215 | 3 | | | | | | | | | | | | | | | |
| 215 | 4 | | | | | | | | | | | | | | | |
| 215 | 5 | | | | | | | | | | | | | | | |
| 215 | 6 | | | | | | | | | | | | | | | |
| 216 | 1 | | | | | | | | | | | | | | | |
| 216 | 2 | | | | | | | | | | | | | | | |
| 216 | 3 | | | | | | | | | | | | | | | |
| 217 | 54 | 6 | 0.997 | 0.242 | 6 | 1.000 | 0.372 | 6 | 1.000 | 0.745 | 6 | 0.995 | 0.651 | 6 | 0.995 | 0.325 |
| 217 | 64 | 6 | 0.998 | 0.266 | 6 | 1.000 | 0.391 | 6 | 1.000 | 0.781 | 6 | 0.996 | 0.682 | 6 | 0.996 | 0.341 |
| 217 | 75 | 6 | 0.999 | 0.280 | 6 | 1.000 | 0.408 | 6 | 0.999 | 0.814 | 6 | 0.998 | 0.687 | 6 | 0.997 | 0.343 |
| 218 | 50 | 10 | 0.999 | 0.360 | 10 | 1.000 | 0.336 | 10 | 1.000 | 0.673 | 10 | 0.998 | 1.072 | 10 | 0.998 | 0.535 |
| 218 | 60 | 10 | 1.000 | 0.350 | 10 | 1.000 | 0.330 | 10 | 1.000 | 0.662 | 10 | 1.000 | 1.060 | 10 | 1.000 | 0.529 |
| 218 | 70 | 10 | 1.000 | 0.346 | 10 | 1.000 | 0.339 | 10 | 1.000 | 0.669 | 10 | 0.999 | 1.022 | 10 | 0.999 | 0.517 |
| 220 | 40 | 6 | 0.999 | 0.353 | 6 | 0.999 | 0.292 | 6 | 0.999 | 0.579 | 6 | 0.999 | 1.212 | 6 | 1.000 | 0.611 |
| 220 | 50 | 6 | 0.998 | 0.368 | 6 | 0.999 | 0.286 | 6 | 1.000 | 0.575 | 6 | 0.998 | 1.288 | 6 | 0.998 | 0.641 |
| 220 | 60 | 6 | 0.997 | 0.366 | 6 | 1.000 | 0.297 | 6 | 1.000 | 0.584 | 6 | 0.997 | 1.237 | 6 | 0.996 | 0.627 |
| 220 | 70 | 6 | 0.995 | 0.348 | 6 | 0.999 | 0.302 | 6 | 1.000 | 0.611 | 6 | 0.990 | 1.156 | 6 | 0.992 | 0.569 |

Table B.3. (continued)

| Allometric Relationships Fit by Principal Component Analysis ^C | | | | | | | | | | | | | | | | |
|---|--------------------|-------------------------------|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|
| Id. Code ^a | Cond. ^b | log \bar{h} - log \bar{w} | | | log \overline{DBH} - log \bar{w} | | | log \overline{BSLA} - log \bar{w} | | | log \bar{h} - log \overline{DBH} | | | log \bar{h} - log \overline{BSLA} | | |
| | | n | r | $\hat{\phi}_{hw}$ | n | r | $\hat{\phi}_{Dw}$ | n | r | $\hat{\phi}_{Bw}$ | n | r | $\hat{\phi}_{hD}$ | n | r | $\hat{\phi}_{hB}$ |
| 220 | 80 | 6 | 0.993 | 0.321 | 6 | 0.999 | 0.321 | 6 | 0.999 | 0.642 | 6 | 0.988 | 1.008 | 6 | 0.987 | 0.499 |
| 220 | 90 | 6 | 0.988 | 0.292 | 6 | 0.999 | 0.340 | 6 | 0.999 | 0.674 | 6 | 0.979 | 0.866 | 6 | 0.980 | 0.432 |
| 221 | 80 | 13 | 0.998 | 0.216 | 13 | 1.000 | 0.415 | 13 | 0.999 | 0.825 | 13 | 0.996 | 0.519 | 13 | 0.996 | 0.261 |
| 221 | 90 | 13 | 0.999 | 0.223 | 13 | 0.999 | 0.408 | 13 | 0.999 | 0.821 | 13 | 0.998 | 0.546 | 13 | 0.998 | 0.272 |
| 221 | 100 | 13 | 0.999 | 0.227 | 13 | 0.999 | 0.410 | 13 | 0.999 | 0.821 | 13 | 0.997 | 0.552 | 13 | 0.997 | 0.276 |
| 221 | 110 | 13 | 0.999 | 0.226 | 13 | 0.999 | 0.406 | 13 | 0.999 | 0.814 | 13 | 0.997 | 0.556 | 13 | 0.997 | 0.277 |
| 221 | 120 | 13 | 0.999 | 0.231 | 13 | 0.999 | 0.410 | 13 | 0.999 | 0.817 | 13 | 0.997 | 0.563 | 13 | 0.997 | 0.282 |
| 221 | 130 | 13 | 0.999 | 0.231 | 13 | 0.999 | 0.407 | 13 | 0.999 | 0.813 | 13 | 0.996 | 0.566 | 13 | 0.996 | 0.283 |
| 221 | 140 | 13 | 0.998 | 0.232 | 13 | 0.999 | 0.410 | 13 | 0.999 | 0.815 | 13 | 0.996 | 0.565 | 13 | 0.996 | 0.284 |
| 221 | 150 | 13 | 0.998 | 0.233 | 13 | 1.000 | 0.409 | 13 | 0.999 | 0.813 | 13 | 0.996 | 0.569 | 13 | 0.996 | 0.286 |
| 221 | 160 | 13 | 0.999 | 0.234 | 13 | 0.999 | 0.408 | 13 | 0.999 | 0.814 | 13 | 0.996 | 0.572 | 13 | 0.996 | 0.286 |
| 221 | 170 | 13 | 0.998 | 0.233 | 13 | 0.999 | 0.406 | 13 | 0.999 | 0.815 | 13 | 0.995 | 0.572 | 13 | 0.995 | 0.285 |
| 221 | 180 | 13 | 0.998 | 0.233 | 13 | 1.000 | 0.404 | 13 | 0.999 | 0.813 | 13 | 0.996 | 0.576 | 13 | 0.996 | 0.285 |
| 221 | 190 | 13 | 0.999 | 0.235 | 13 | 0.999 | 0.406 | 13 | 0.999 | 0.814 | 13 | 0.996 | 0.578 | 13 | 0.996 | 0.288 |
| 221 | 200 | 13 | 0.998 | 0.235 | 13 | 0.999 | 0.406 | 13 | 0.999 | 0.812 | 13 | 0.996 | 0.577 | 13 | 0.996 | 0.288 |
| 221 | 210 | 13 | 0.998 | 0.233 | 13 | 0.999 | 0.407 | 13 | 0.999 | 0.816 | 13 | 0.996 | 0.572 | 13 | 0.995 | 0.285 |
| 222 | 1 | 8 | 0.999 | 0.324 | 8 | 0.999 | 0.415 | 8 | 1.000 | 0.843 | 8 | 0.999 | 0.780 | 8 | 1.000 | 0.384 |
| 222 | 2 | 8 | 1.000 | 0.349 | 8 | 0.999 | 0.401 | 8 | 1.000 | 0.817 | 8 | 0.999 | 0.872 | 8 | 1.000 | 0.428 |
| 222 | 3 | 8 | 1.000 | 0.383 | 8 | 1.000 | 0.395 | 8 | 1.000 | 0.801 | 8 | 0.999 | 0.969 | 8 | 1.000 | 0.478 |
| 222 | 4 | 5 | 1.000 | 0.404 | 5 | 0.999 | 0.392 | 5 | 1.000 | 0.780 | 5 | 1.000 | 1.030 | 5 | 1.000 | 0.517 |
| 222 | 5 | 5 | 1.000 | 0.425 | 5 | 0.999 | 0.384 | 5 | 1.000 | 0.749 | 5 | 0.999 | 1.106 | 5 | 1.000 | 0.567 |
| 223 | 1 | 13 | 0.998 | 0.223 | 13 | 1.000 | 0.423 | | | | 13 | 0.998 | 0.527 | | | |
| 224 | 3 | 14 | 0.997 | 0.193 | 14 | 0.993 | 0.311 | | | | 14 | 0.994 | 0.618 | | | |
| 225 | 1 | 6 | 0.994 | 0.248 | 6 | 1.000 | 0.404 | | | | 6 | 0.993 | 0.616 | | | |
| 227 | 40 | 13 | 0.999 | 0.306 | 13 | 0.999 | 0.337 | 13 | 0.999 | 0.662 | 13 | 0.998 | 0.909 | 13 | 0.997 | 0.462 |
| 227 | 50 | 13 | 1.000 | 0.312 | 13 | 1.000 | 0.340 | 13 | 0.999 | 0.663 | 13 | 0.999 | 0.917 | 13 | 0.998 | 0.470 |
| 227 | 60 | 13 | 0.999 | 0.309 | 13 | 1.000 | 0.339 | 13 | 0.999 | 0.663 | 13 | 0.999 | 0.911 | 13 | 0.998 | 0.465 |
| 227 | 70 | 13 | 0.999 | 0.308 | 13 | 1.000 | 0.337 | 13 | 0.999 | 0.663 | 13 | 0.999 | 0.914 | 13 | 0.998 | 0.465 |
| 227 | 80 | 13 | 0.999 | 0.310 | 13 | 1.000 | 0.336 | 13 | 0.999 | 0.663 | 13 | 0.999 | 0.922 | 13 | 0.998 | 0.468 |
| 227 | 90 | 13 | 0.999 | 0.310 | 13 | 1.000 | 0.341 | 13 | 0.999 | 0.662 | 13 | 0.999 | 0.908 | 13 | 0.998 | 0.467 |
| 227 | 100 | 13 | 0.999 | 0.309 | 13 | 1.000 | 0.338 | 13 | 0.999 | 0.663 | 13 | 0.999 | 0.916 | 13 | 0.998 | 0.466 |
| 227 | 110 | 13 | 0.999 | 0.310 | 13 | 1.000 | 0.338 | 13 | 0.999 | 0.663 | 13 | 0.999 | 0.916 | 13 | 0.998 | 0.467 |
| 227 | 120 | 13 | 0.994 | 0.312 | 13 | 0.995 | 0.341 | 13 | 0.997 | 0.662 | 13 | 0.999 | 0.915 | 13 | 0.984 | 0.468 |
| 228 | 25 | 11 | 0.997 | 0.347 | 11 | 1.000 | 0.399 | 11 | 1.000 | 0.808 | 11 | 0.996 | 0.869 | 11 | 0.997 | 0.429 |
| 228 | 35 | 11 | 0.999 | 0.325 | 11 | 1.000 | 0.410 | 11 | 1.000 | 0.806 | 11 | 0.998 | 0.791 | 11 | 0.999 | 0.403 |
| 228 | 45 | 12 | 0.999 | 0.312 | 12 | 1.000 | 0.404 | 12 | 1.000 | 0.809 | 12 | 0.999 | 0.774 | 12 | 1.000 | 0.386 |
| 228 | 55 | 12 | 1.000 | 0.306 | 12 | 1.000 | 0.412 | 12 | 1.000 | 0.823 | 12 | 0.999 | 0.743 | 12 | 0.999 | 0.372 |
| 228 | 65 | 12 | 0.999 | 0.289 | 12 | 1.000 | 0.421 | 12 | 1.000 | 0.838 | 12 | 0.999 | 0.687 | 12 | 0.999 | 0.345 |
| 228 | 75 | 12 | 0.998 | 0.291 | 12 | 0.999 | 0.428 | 12 | 1.000 | 0.851 | 12 | 0.998 | 0.680 | 12 | 0.997 | 0.342 |
| 229 | 60 | 7 | 1.000 | 0.303 | 7 | 1.000 | 0.351 | 7 | 1.000 | 0.710 | 7 | 1.000 | 0.863 | 7 | 1.000 | 0.427 |
| 229 | 70 | 7 | 1.000 | 0.300 | 7 | 1.000 | 0.353 | 7 | 1.000 | 0.707 | 7 | 1.000 | 0.849 | 7 | 1.000 | 0.424 |
| 229 | 80 | 7 | 1.000 | 0.301 | 7 | 1.000 | 0.349 | 7 | 1.000 | 0.709 | 7 | 1.000 | 0.861 | 7 | 1.000 | 0.424 |
| 229 | 90 | 7 | 1.000 | 0.306 | 7 | 1.000 | 0.356 | 7 | 1.000 | 0.710 | 7 | 1.000 | 0.861 | 7 | 1.000 | 0.431 |

Table B.3. (continued)

| | | Allometric Relationships Fit by Principal Component Analysis ^c | | | | | | | | | | | | | | |
|-----------------------|--------------------|---|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|
| Id. Code ^a | Cond. ^b | log \bar{h} - log \bar{w} | | | log \overline{DBH} - log \bar{w} | | | log \overline{BSLA} - log \bar{w} | | | log \bar{h} - log \overline{DBH} | | | log \bar{h} - log \overline{BSLA} | | |
| | | n | r | $\hat{\phi}_{hw}$ | n | r | $\hat{\phi}_{Dw}$ | n | r | $\hat{\phi}_{Bw}$ | n | r | $\hat{\phi}_{hD}$ | n | r | $\hat{\phi}_{hB}$ |
| 229 | 100 | 7 | 1.000 | 0.301 | 7 | 1.000 | 0.358 | 7 | 1.000 | 0.707 | 7 | 1.000 | 0.841 | 7 | 1.000 | 0.426 |
| 229 | 110 | 7 | 1.000 | 0.304 | 7 | 1.000 | 0.353 | 7 | 1.000 | 0.708 | 7 | 1.000 | 0.860 | 7 | 1.000 | 0.429 |
| 229 | 120 | 7 | 1.000 | 0.306 | 7 | 1.000 | 0.361 | 7 | 1.000 | 0.710 | 7 | 0.999 | 0.848 | 7 | 1.000 | 0.431 |
| 230 | 50 | 7 | 1.000 | 0.297 | 7 | 1.000 | 0.360 | 7 | 1.000 | 0.727 | 7 | 1.000 | 0.823 | 7 | 1.000 | 0.408 |
| 230 | 60 | 7 | 1.000 | 0.285 | 7 | 1.000 | 0.366 | 7 | 1.000 | 0.733 | 7 | 1.000 | 0.778 | 7 | 1.000 | 0.389 |
| 230 | 70 | 7 | 1.000 | 0.286 | 7 | 1.000 | 0.368 | 7 | 1.000 | 0.745 | 7 | 1.000 | 0.778 | 7 | 1.000 | 0.384 |
| 230 | 80 | 7 | 1.000 | 0.272 | 7 | 1.000 | 0.376 | 7 | 1.000 | 0.763 | 7 | 1.000 | 0.724 | 7 | 1.000 | 0.357 |
| 230 | 90 | 7 | 1.000 | 0.265 | 7 | 1.000 | 0.384 | 7 | 1.000 | 0.773 | 7 | 1.000 | 0.691 | 7 | 1.000 | 0.343 |
| 230 | 100 | 7 | 1.000 | 0.260 | 7 | 1.000 | 0.394 | 7 | 1.000 | 0.784 | 7 | 1.000 | 0.659 | 7 | 1.000 | 0.331 |
| 231 | 50 | 5 | 0.999 | 0.236 | 5 | 1.000 | 0.369 | 5 | 1.000 | 0.728 | 5 | 0.999 | 0.639 | 5 | 1.000 | 0.324 |
| 231 | 60 | 5 | 0.999 | 0.253 | 5 | 1.000 | 0.358 | 5 | 1.000 | 0.720 | 5 | 1.000 | 0.706 | 5 | 0.999 | 0.351 |
| 231 | 70 | 5 | 0.999 | 0.249 | 5 | 1.000 | 0.366 | 5 | 1.000 | 0.728 | 5 | 0.999 | 0.678 | 5 | 0.999 | 0.342 |
| 231 | 80 | 5 | 0.999 | 0.247 | 5 | 1.000 | 0.361 | 5 | 1.000 | 0.729 | 5 | 0.999 | 0.685 | 5 | 0.999 | 0.340 |
| 231 | 90 | 5 | 1.000 | 0.253 | 5 | 1.000 | 0.360 | 5 | 1.000 | 0.726 | 5 | 0.999 | 0.702 | 5 | 1.000 | 0.348 |
| 231 | 100 | 5 | 1.000 | 0.249 | 5 | 1.000 | 0.355 | 5 | 1.000 | 0.724 | 5 | 1.000 | 0.702 | 5 | 1.000 | 0.345 |
| 232 | 40 | 7 | 1.000 | 0.293 | 7 | 1.000 | 0.337 | 7 | 1.000 | 0.661 | 7 | 1.000 | 0.870 | 7 | 1.000 | 0.443 |
| 232 | 50 | 7 | 1.000 | 0.296 | 7 | 1.000 | 0.337 | 7 | 1.000 | 0.666 | 7 | 1.000 | 0.877 | 7 | 1.000 | 0.445 |
| 232 | 60 | 7 | 1.000 | 0.290 | 7 | 1.000 | 0.330 | 7 | 1.000 | 0.666 | 7 | 1.000 | 0.879 | 7 | 1.000 | 0.436 |
| 232 | 70 | 7 | 1.000 | 0.295 | 7 | 1.000 | 0.331 | 7 | 1.000 | 0.664 | 7 | 1.000 | 0.893 | 7 | 1.000 | 0.445 |
| 232 | 80 | 7 | 1.000 | 0.297 | 7 | 1.000 | 0.328 | 7 | 1.000 | 0.661 | 7 | 1.000 | 0.906 | 7 | 1.000 | 0.449 |
| 232 | 90 | 7 | 1.000 | 0.290 | 7 | 1.000 | 0.329 | 7 | 1.000 | 0.655 | 7 | 1.000 | 0.883 | 7 | 1.000 | 0.443 |
| 232 | 100 | 7 | 1.000 | 0.292 | 7 | 1.000 | 0.327 | 7 | 1.000 | 0.656 | 7 | 1.000 | 0.892 | 7 | 1.000 | 0.444 |
| 233 | 50 | 7 | 0.999 | 0.247 | 7 | 1.000 | 0.346 | 7 | 1.000 | 0.701 | 7 | 0.999 | 0.714 | 7 | 1.000 | 0.352 |
| 233 | 60 | 7 | 1.000 | 0.249 | 7 | 1.000 | 0.349 | 7 | 1.000 | 0.697 | 7 | 1.000 | 0.712 | 7 | 1.000 | 0.356 |
| 233 | 70 | 7 | 1.000 | 0.255 | 7 | 1.000 | 0.351 | 7 | 1.000 | 0.703 | 7 | 1.000 | 0.727 | 7 | 1.000 | 0.363 |
| 233 | 80 | 7 | 1.000 | 0.251 | 7 | 1.000 | 0.350 | 7 | 1.000 | 0.703 | 7 | 1.000 | 0.718 | 7 | 1.000 | 0.357 |
| 233 | 90 | 7 | 1.000 | 0.247 | 7 | 1.000 | 0.353 | 7 | 1.000 | 0.699 | 7 | 1.000 | 0.698 | 7 | 1.000 | 0.353 |
| 233 | 100 | 7 | 1.000 | 0.252 | 7 | 1.000 | 0.353 | 7 | 1.000 | 0.702 | 7 | 1.000 | 0.715 | 7 | 1.000 | 0.360 |
| 234 | 70 | 5 | 0.999 | 0.292 | 5 | 0.996 | 0.315 | 5 | 0.999 | 0.768 | 5 | 0.995 | 0.925 | 5 | 0.999 | 0.380 |
| 234 | 84 | 7 | 0.990 | 0.236 | 7 | 1.000 | 0.377 | 5 | 0.999 | 0.916 | 7 | 0.985 | 0.629 | 5 | 0.998 | 0.288 |
| 234 | 99 | 7 | 0.989 | 0.192 | 7 | 0.999 | 0.403 | 5 | 0.996 | 0.765 | 7 | 0.984 | 0.475 | 5 | 0.996 | 0.277 |
| 235 | 40 | 18 | 0.997 | 0.305 | 18 | 0.998 | 0.366 | 18 | 0.999 | 0.735 | 18 | 0.997 | 0.835 | 18 | 0.998 | 0.416 |
| 235 | 50 | 18 | 0.991 | 0.331 | 18 | 0.999 | 0.382 | 18 | 0.998 | 0.761 | 18 | 0.996 | 0.872 | 18 | 0.997 | 0.437 |
| 235 | 60 | 18 | 0.994 | 0.321 | 18 | 0.998 | 0.382 | 18 | 0.999 | 0.756 | 18 | 0.998 | 0.843 | 18 | 0.998 | 0.426 |
| 235 | 70 | 18 | 0.994 | 0.320 | 18 | 0.998 | 0.379 | 18 | 0.999 | 0.751 | 18 | 0.998 | 0.847 | 18 | 0.998 | 0.427 |
| 235 | 80 | 18 | 0.994 | 0.310 | 18 | 0.999 | 0.365 | 18 | 0.999 | 0.739 | 18 | 0.997 | 0.853 | 18 | 0.997 | 0.421 |
| 235 | 90 | 18 | 0.994 | 0.309 | 18 | 0.998 | 0.358 | 18 | 0.999 | 0.725 | 18 | 0.997 | 0.865 | 18 | 0.997 | 0.426 |
| 235 | 100 | 18 | 0.995 | 0.308 | 18 | 0.999 | 0.353 | 18 | 0.999 | 0.721 | 18 | 0.997 | 0.873 | 18 | 0.998 | 0.427 |
| 235 | 110 | 18 | 0.994 | 0.306 | 18 | 0.999 | 0.354 | 18 | 0.999 | 0.723 | 18 | 0.997 | 0.868 | 18 | 0.996 | 0.425 |
| 236 | 40 | 9 | 0.994 | 0.319 | 9 | 1.000 | 0.380 | 9 | 1.000 | 0.749 | 9 | 0.993 | 0.844 | 9 | 0.993 | 0.426 |
| 236 | 50 | 9 | 0.995 | 0.292 | 9 | 1.000 | 0.371 | 9 | 1.000 | 0.745 | 9 | 0.993 | 0.788 | 9 | 0.993 | 0.391 |
| 236 | 60 | 9 | 0.997 | 0.272 | 9 | 1.000 | 0.375 | 9 | 1.000 | 0.747 | 9 | 0.997 | 0.725 | 9 | 0.996 | 0.364 |
| 236 | 70 | 9 | 0.997 | 0.266 | 9 | 1.000 | 0.379 | 9 | 1.000 | 0.747 | 9 | 0.997 | 0.702 | 9 | 0.996 | 0.355 |

Table 8.3. (continued)

| | | Allometric Relationships Fit by Principal Component Analysis ^c | | | | | | | | | | | | | | |
|-----------------------|--------------------|---|-------|-------------------|-------------------------|-------|-------------------|--------------------------|-------|-------------------|-------------------------|-------|-------------------|--------------------------|-------|-------------------|
| Id. Code ^a | Cond. ^b | log \bar{h} - log \bar{w} | | | log DBH - log \bar{w} | | | log BSLA - log \bar{w} | | | log \bar{h} - log DBH | | | log \bar{h} - log BSLA | | |
| | | n | r | $\hat{\phi}_{hw}$ | n | r | $\hat{\phi}_{Dw}$ | n | r | $\hat{\phi}_{Bw}$ | n | r | $\hat{\phi}_{hD}$ | n | r | $\hat{\phi}_{hB}$ |
| 236 | 80 | 10 | 0.998 | 0.267 | 10 | 1.000 | 0.381 | 10 | 1.000 | 0.757 | 10 | 0.998 | 0.701 | 10 | 0.998 | 0.352 |
| 237 | 1 | 12 | 0.999 | 0.290 | 12 | 1.000 | 0.373 | 12 | 1.000 | 0.752 | 12 | 0.999 | 0.778 | 12 | 1.000 | 0.386 |
| 237 | 2 | 8 | 1.000 | 0.300 | 8 | 0.999 | 0.349 | 8 | 1.000 | 0.706 | 8 | 0.999 | 0.859 | 8 | 1.000 | 0.425 |
| 237 | 3 | 8 | 1.000 | 0.322 | 8 | 1.000 | 0.333 | 8 | 0.999 | 0.672 | 8 | 1.000 | 0.965 | 8 | 1.000 | 0.479 |
| 237 | 4 | 8 | 1.000 | 0.340 | 8 | 0.999 | 0.325 | 8 | 0.999 | 0.638 | 8 | 0.999 | 1.046 | 8 | 1.000 | 0.532 |
| 237 | 5 | 5 | 1.000 | 0.348 | 5 | 0.999 | 0.295 | 5 | 0.999 | 0.579 | 5 | 0.999 | 1.179 | 5 | 0.999 | 0.600 |
| 238 | 40 | 5 | 0.998 | 0.257 | 5 | 0.999 | 0.399 | 5 | 1.000 | 0.779 | 5 | 0.995 | 0.642 | 5 | 0.998 | 0.32 ^a |
| 238 | 50 | 5 | 0.998 | 0.258 | 5 | 1.000 | 0.393 | 5 | 1.000 | 0.780 | 5 | 0.999 | 0.658 | 5 | 0.997 | 0.331 |
| 238 | 60 | 5 | 1.000 | 0.266 | 5 | 1.000 | 0.395 | 5 | 1.000 | 0.782 | 5 | 1.000 | 0.672 | 5 | 0.999 | 0.340 |
| 238 | 70 | 5 | 0.997 | 0.258 | 5 | 1.000 | 0.393 | 5 | 1.000 | 0.781 | 5 | 0.996 | 0.656 | 5 | 0.997 | 0.330 |
| 239 | 40 | 5 | 0.993 | 0.220 | 5 | 1.000 | 0.362 | 5 | 1.000 | 0.736 | 5 | 0.990 | 0.609 | 5 | 0.991 | 0.29 ^a |
| 239 | 50 | 5 | 0.999 | 0.221 | 5 | 1.000 | 0.368 | 5 | 1.000 | 0.739 | 5 | 0.999 | 0.600 | 5 | 0.999 | 0.299 |
| 239 | 60 | 5 | 0.998 | 0.235 | 5 | 0.999 | 0.374 | 5 | 1.000 | 0.738 | 5 | 0.996 | 0.629 | 5 | 0.997 | 0.318 |
| 239 | 70 | 5 | 0.996 | 0.241 | 5 | 1.000 | 0.372 | 5 | 1.000 | 0.737 | 5 | 0.995 | 0.648 | 5 | 0.994 | 0.327 |
| 241 | 20 | 5 | 0.986 | 0.305 | 5 | 0.984 | 0.221 | 5 | 0.992 | 0.330 | 5 | 0.960 | 1.393 | 5 | 0.980 | 0.929 |
| 241 | 30 | 5 | 0.999 | 0.333 | 5 | 0.994 | 0.210 | 5 | 0.998 | 0.332 | 5 | 0.993 | 1.582 | 5 | 0.998 | 1.002 |
| 241 | 40 | 5 | 0.993 | 0.331 | 5 | 0.992 | 0.210 | 5 | 0.994 | 0.344 | 5 | 0.993 | 1.573 | 5 | 0.976 | 0.961 |
| 241 | 50 | 5 | 0.997 | 0.327 | 5 | 0.997 | 0.210 | 5 | 0.997 | 0.350 | 5 | 0.999 | 1.560 | 5 | 0.989 | 0.934 |
| 241 | 60 | 5 | 0.998 | 0.358 | 5 | 0.994 | 0.203 | 5 | 0.991 | 0.337 | 5 | 0.994 | 1.762 | 5 | 0.983 | 1.058 |
| 242 | 56 | 3 | 1.000 | 0.285 | 3 | 0.980 | 0.810 | 3 | 0.986 | 1.670 | 3 | 0.981 | 0.345 | 3 | 0.987 | 0.169 |
| 242 | 73 | 4 | 0.967 | 0.317 | 4 | 0.995 | 0.545 | 4 | 0.996 | 1.093 | 4 | 0.987 | 0.593 | 4 | 0.985 | 0.294 |
| 242 | 90 | 4 | 0.999 | 0.258 | 4 | 0.999 | 0.473 | 4 | 1.000 | 0.931 | 4 | 0.999 | 0.546 | 4 | 0.999 | 0.277 |
| 243 | 1 | 7 | 0.998 | 0.225 | | | | | | | | | | | | |
| 243 | 2 | 5 | 0.988 | 0.179 | | | | | | | | | | | | |
| 244 | 70 | 3 | 0.999 | 0.328 | 3 | 0.998 | 0.388 | 3 | 0.999 | 0.763 | 3 | 1.000 | 0.845 | 3 | 1.000 | 0.430 |
| 244 | 86 | 4 | 0.999 | 0.329 | 4 | 1.000 | 0.411 | 4 | 1.000 | 0.837 | 4 | 0.999 | 0.801 | 4 | 1.000 | 0.393 |
| 244 | 102 | 5 | 0.999 | 0.315 | 5 | 0.999 | 0.417 | 5 | 0.999 | 0.844 | 5 | 1.000 | 0.754 | 5 | 1.000 | 0.373 |
| 245 | 1 | 5 | 0.999 | | 5 | 0.999 | 0.388 | 5 | 1.000 | 0.804 | | | | | | |
| 245 | 2 | 5 | 1.000 | | 5 | 1.000 | 0.454 | 5 | 1.000 | 0.893 | | | | | | |
| 245 | 3 | 4 | 0.995 | | 4 | 0.995 | 0.490 | 4 | 1.000 | 0.942 | | | | | | |
| 246 | 30 | 4 | 0.997 | 0.296 | 4 | 0.999 | 0.365 | 4 | 1.000 | 0.725 | 4 | 0.995 | 0.812 | 4 | 0.995 | 0.408 |
| 246 | 50 | 4 | 0.995 | 0.217 | 4 | 1.000 | 0.409 | 4 | 1.000 | 0.804 | 4 | 0.993 | 0.532 | 4 | 0.992 | 0.26 ^a |
| 246 | 60 | 4 | 0.999 | 0.176 | 4 | 1.000 | 0.427 | 4 | 1.000 | 0.855 | 4 | 0.999 | 0.412 | 4 | 0.999 | 0.206 |
| 246 | 70 | 4 | 0.998 | 0.173 | 4 | 1.000 | 0.431 | 4 | 1.000 | 0.855 | 4 | 0.998 | 0.402 | 4 | 0.998 | 0.203 |
| 246 | 80 | 4 | 0.998 | 0.191 | 4 | 1.000 | 0.419 | 4 | 1.000 | 0.841 | 4 | 0.998 | 0.455 | 4 | 0.997 | 0.227 |
| 247 | 1 | 4 | 1.000 | 0.390 | 4 | 0.995 | 0.333 | 4 | 1.000 | 0.689 | 4 | 0.994 | 1.167 | 4 | 1.000 | 0.566 |
| 247 | 2 | 4 | 1.000 | 0.408 | 4 | 0.999 | 0.316 | 4 | 1.000 | 0.635 | 4 | 1.000 | 1.290 | 4 | 0.999 | 0.643 |
| 247 | 3 | 4 | 1.000 | 0.426 | 4 | 0.999 | 0.298 | 4 | 1.000 | 0.607 | 4 | 0.999 | 1.430 | 4 | 1.000 | 0.702 |
| 247 | 4 | 4 | 1.000 | 0.438 | 4 | 1.000 | 0.295 | 4 | 1.000 | 0.584 | 4 | 1.000 | 1.483 | 4 | 1.000 | 0.750 |
| 248 | 1 | 5 | 0.999 | 0.197 | 5 | 0.995 | 0.248 | | | | 5 | 0.998 | 0.793 | | | |
| 248 | 2 | 6 | 0.996 | 0.191 | 6 | 0.999 | 0.241 | | | | 6 | 0.996 | 0.792 | | | |
| 248 | 3 | 7 | 0.996 | 0.195 | 7 | 0.998 | 0.248 | | | | 7 | 0.998 | 0.78 ^a | | | |
| 249 | 100 | 3 | 0.995 | 0.151 | 3 | 1.000 | 0.399 | 3 | 1.000 | 0.875 | 3 | 0.996 | 0.380 | 3 | 0.994 | 0.173 |

Table B.3. (continued)

| Allometric Relationships Fit by Principal Component Analysis ^C | | | | | | | | | | | | | | | | |
|---|--------------------|-------------------------------|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|
| Id. Code ^a | Cond. ^b | log \bar{h} - log \bar{w} | | | log \overline{DBH} - log \bar{w} | | | log \overline{BSLA} - log \bar{w} | | | log \bar{h} - log \overline{DBH} | | | log \bar{h} - log \overline{BSLA} | | |
| | | n | r | $\hat{\phi}_{hw}$ | n | r | $\hat{\phi}_{Dw}$ | n | r | $\hat{\phi}_{Bw}$ | n | r | $\hat{\phi}_{hD}$ | n | r | $\hat{\phi}_{hB}$ |
| 249 | 110 | 3 | 1.000 | 0.158 | 3 | 0.999 | 0.409 | 3 | 1.000 | 0.874 | 3 | 0.999 | 0.386 | 3 | 1.000 | 0.181 |
| 249 | 120 | 3 | 0.998 | 0.155 | 3 | 1.000 | 0.365 | 3 | 1.000 | 0.881 | 3 | 0.997 | 0.425 | 3 | 0.998 | 0.176 |
| 250 | 2 | | | | 4 | 0.999 | 0.442 | | | | | | | | | |
| 250 | 3 | | | | 8 | 0.999 | 0.332 | | | | | | | | | |
| 251 | 1 | 27 | 1.000 | 0.315 | 27 | 1.000 | 0.394 | | | | 27 | 0.999 | 0.800 | | | |
| 252 | 120 | 3 | 0.999 | 0.342 | 3 | 1.000 | 0.307 | 3 | 1.000 | 0.598 | 3 | 0.997 | 1.115 | 3 | 0.998 | 0.571 |
| 252 | 140 | 5 | 1.000 | 0.367 | 5 | 1.000 | 0.299 | 5 | 0.999 | 0.601 | 5 | 0.999 | 1.228 | 5 | 0.999 | 0.611 |
| 252 | 160 | 9 | 0.999 | 0.379 | 9 | 0.999 | 0.312 | 9 | 0.991 | 0.704 | 9 | 1.000 | 1.214 | 9 | 0.994 | 0.535 |
| 252 | 180 | 9 | 0.999 | 0.384 | 9 | 0.998 | 0.333 | 9 | 0.998 | 0.665 | 9 | 0.999 | 1.152 | 9 | 0.999 | 0.578 |
| 252 | 200 | 9 | 0.999 | 0.376 | 9 | 0.997 | 0.341 | 9 | 0.997 | 0.683 | 9 | 0.999 | 1.101 | 9 | 0.999 | 0.550 |
| 252 | 220 | 9 | 0.999 | 0.368 | 9 | 0.997 | 0.346 | 9 | 0.996 | 0.687 | 9 | 0.999 | 1.064 | 9 | 0.998 | 0.535 |
| 252 | 240 | 9 | 0.999 | 0.357 | 9 | 0.997 | 0.348 | 9 | 0.996 | 0.698 | 9 | 0.998 | 1.024 | 9 | 0.998 | 0.510 |
| 253 | 47 | 10 | 0.999 | 0.173 | 10 | 1.000 | 0.251 | 10 | 1.000 | 0.582 | 10 | 1.000 | 0.690 | 10 | 0.999 | 0.297 |
| 253 | 57 | 13 | 0.999 | 0.192 | 13 | 1.000 | 0.259 | 13 | 0.999 | 0.668 | 13 | 0.999 | 0.740 | 13 | 0.999 | 0.287 |
| 253 | 66 | 14 | 0.994 | 0.192 | 14 | 0.998 | 0.259 | 14 | 0.999 | 0.721 | 14 | 0.999 | 0.742 | 14 | 0.996 | 0.266 |
| 254 | 50 | 12 | 1.000 | 0.212 | 12 | 0.997 | 0.238 | 12 | 1.000 | 0.651 | 12 | 0.998 | 0.888 | 12 | 0.999 | 0.325 |
| 254 | 61 | 9 | 0.999 | 0.247 | 9 | 1.000 | 0.287 | 9 | 0.998 | 0.688 | 9 | 0.999 | 0.862 | 9 | 0.997 | 0.359 |
| 254 | 70 | 11 | 0.999 | 0.275 | 11 | 0.998 | 0.307 | 11 | 0.999 | 0.684 | 11 | 0.999 | 0.896 | 11 | 1.000 | 0.403 |
| 255 | 87 | 7 | 0.996 | 0.283 | 7 | 1.000 | 0.385 | | | | 7 | 0.996 | 0.738 | | | |
| 256 | 40 | 4 | 1.000 | 0.308 | 4 | 1.000 | 0.270 | 4 | 1.000 | 0.544 | 4 | 1.000 | 1.139 | 4 | 1.000 | 0.566 |
| 256 | 53 | 4 | 1.000 | 0.322 | 4 | 1.000 | 0.292 | 4 | 1.000 | 0.575 | 4 | 1.000 | 1.101 | 4 | 1.000 | 0.559 |
| 256 | 66 | 4 | 0.999 | 0.327 | 4 | 1.000 | 0.308 | 4 | 0.999 | 0.617 | 4 | 1.000 | 1.062 | 4 | 1.000 | 0.530 |
| 257 | 45 | 13 | 0.986 | 0.301 | 13 | 1.000 | 0.365 | 13 | 1.000 | 0.726 | 13 | 0.989 | 0.833 | 13 | 0.990 | 0.416 |
| 257 | 49 | 11 | 0.997 | 0.317 | 11 | 1.000 | 0.385 | 11 | 1.000 | 0.762 | 11 | 0.997 | 0.823 | 11 | 0.997 | 0.416 |
| 257 | 53 | 11 | 0.998 | 0.361 | 11 | 0.999 | 0.344 | 11 | 1.000 | 0.689 | 11 | 0.998 | 1.049 | 11 | 0.999 | 0.524 |
| 257 | 54 | 11 | 1.000 | 0.304 | 11 | 1.000 | 0.357 | 11 | 1.000 | 0.707 | 11 | 0.999 | 0.853 | 11 | 0.999 | 0.431 |
| 257 | 57 | 10 | 0.999 | 0.517 | 10 | 0.999 | 0.351 | 10 | 1.000 | 0.689 | 10 | 0.999 | 1.474 | 10 | 0.999 | 0.751 |
| 258 | 40 | 6 | 0.999 | 0.306 | 6 | 0.999 | 0.360 | 6 | 0.999 | 0.725 | 6 | 0.999 | 0.850 | 6 | 0.999 | 0.422 |
| 258 | 52 | 6 | 0.999 | 0.301 | 6 | 1.000 | 0.333 | 6 | 1.000 | 0.664 | 6 | 0.999 | 0.904 | 6 | 0.999 | 0.453 |
| 258 | 60 | 6 | 0.959 | 0.368 | 6 | 1.000 | 0.336 | 6 | 1.000 | 0.669 | 6 | 0.960 | 1.135 | 6 | 0.960 | 0.555 |
| 259 | 100 | 14 | 0.985 | 0.261 | 14 | 1.000 | 0.402 | 14 | 1.000 | 0.810 | 14 | 0.981 | 0.652 | 14 | 0.980 | 0.321 |
| 259 | 110 | 13 | 0.987 | 0.243 | 13 | 0.999 | 0.412 | 13 | 1.000 | 0.830 | 13 | 0.982 | 0.591 | 13 | 0.985 | 0.293 |
| 259 | 120 | 13 | 0.987 | 0.245 | 13 | 0.999 | 0.414 | 13 | 1.000 | 0.839 | 13 | 0.984 | 0.594 | 13 | 0.984 | 0.292 |
| 259 | 130 | 13 | 0.985 | 0.246 | 13 | 1.000 | 0.415 | 13 | 1.000 | 0.845 | 13 | 0.982 | 0.596 | 13 | 0.982 | 0.291 |
| 259 | 140 | 13 | 0.983 | 0.248 | 13 | 1.000 | 0.423 | 13 | 1.000 | 0.850 | 13 | 0.979 | 0.589 | 13 | 0.980 | 0.291 |
| 259 | 150 | 13 | 0.986 | 0.246 | 13 | 1.000 | 0.426 | 13 | 1.000 | 0.857 | 13 | 0.983 | 0.580 | 13 | 0.984 | 0.287 |
| 259 | 160 | 13 | 0.984 | 0.249 | 13 | 1.000 | 0.428 | 13 | 1.000 | 0.858 | 13 | 0.981 | 0.584 | 13 | 0.982 | 0.290 |
| 259 | 170 | 13 | 0.985 | 0.249 | 13 | 1.000 | 0.427 | 13 | 1.000 | 0.856 | 13 | 0.983 | 0.585 | 13 | 0.982 | 0.290 |
| 259 | 180 | 13 | 0.983 | 0.250 | 13 | 1.000 | 0.429 | 13 | 1.000 | 0.861 | 13 | 0.980 | 0.586 | 13 | 0.981 | 0.290 |
| 259 | 190 | 13 | 0.984 | 0.253 | 13 | 1.000 | 0.430 | 13 | 1.000 | 0.863 | 13 | 0.981 | 0.592 | 13 | 0.982 | 0.293 |
| 259 | 200 | 13 | 0.984 | 0.255 | 13 | 1.000 | 0.434 | 13 | 1.000 | 0.865 | 13 | 0.982 | 0.591 | 13 | 0.982 | 0.294 |
| 259 | 210 | 13 | 0.984 | 0.252 | 13 | 1.000 | 0.433 | 13 | 1.000 | 0.868 | 13 | 0.982 | 0.586 | 13 | 0.982 | 0.290 |
| 260 | 60 | 7 | 0.991 | 0.231 | 7 | 1.000 | 0.386 | 7 | 1.000 | 0.766 | 7 | 0.990 | 0.601 | 7 | 0.990 | 0.302 |

Table B.3. (continued)

| Allometric Relationships Fit by Principal Component Analysis ^C | | | | | | | | | | | | | | | | |
|---|--------------------|-------------------------------|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|
| Id. Code ^a | Cond. ^b | log \bar{h} - log \bar{w} | | | log \overline{DBH} - log \bar{w} | | | log \overline{BSLA} - log \bar{w} | | | log \bar{h} - log \overline{DBH} | | | log \bar{h} - log \overline{BSLA} | | |
| | | n | r | $\hat{\phi}_{HW}$ | n | r | $\hat{\phi}_{DW}$ | n | r | $\hat{\phi}_{BW}$ | n | r | $\hat{\phi}_{HD}$ | n | r | $\hat{\phi}_{HB}$ |
| 260 | 70 | 9 | 0.990 | 0.249 | 9 | 0.999 | 0.372 | 9 | 1.000 | 0.773 | 9 | 0.987 | 0.671 | 9 | 0.990 | 0.322 |
| 260 | 80 | 9 | 0.986 | 0.247 | 9 | 0.993 | 0.413 | 9 | 1.000 | 0.776 | 9 | 0.978 | 0.595 | 9 | 0.984 | 0.318 |
| 260 | 90 | 9 | 0.992 | 0.238 | 9 | 0.999 | 0.395 | 9 | 1.000 | 0.790 | 9 | 0.988 | 0.603 | 9 | 0.990 | 0.301 |
| 260 | 100 | 9 | 0.989 | 0.243 | 9 | 1.000 | 0.403 | 9 | 1.000 | 0.810 | 9 | 0.986 | 0.606 | 9 | 0.987 | 0.300 |
| 260 | 110 | 9 | 0.989 | 0.245 | 9 | 0.999 | 0.412 | 9 | 1.000 | 0.820 | 9 | 0.984 | 0.595 | 9 | 0.985 | 0.298 |
| 260 | 120 | 9 | 0.986 | 0.249 | 9 | 1.000 | 0.430 | 9 | 1.000 | 0.844 | 9 | 0.987 | 0.583 | 9 | 0.983 | 0.295 |
| 260 | 130 | 9 | 0.987 | 0.244 | 9 | 1.000 | 0.425 | 9 | 1.000 | 0.847 | 9 | 0.988 | 0.578 | 9 | 0.985 | 0.288 |
| 260 | 140 | 9 | 0.985 | 0.251 | 9 | 0.999 | 0.441 | 9 | 1.000 | 0.858 | 9 | 0.988 | 0.574 | 9 | 0.983 | 0.293 |
| 260 | 150 | 9 | 0.985 | 0.244 | 9 | 1.000 | 0.423 | 9 | 1.000 | 0.857 | 9 | 0.985 | 0.579 | 9 | 0.984 | 0.284 |
| 260 | 160 | 9 | 0.985 | 0.245 | 9 | 1.000 | 0.425 | 9 | 1.000 | 0.860 | 9 | 0.986 | 0.580 | 9 | 0.985 | 0.285 |
| 260 | 170 | 9 | 0.981 | 0.253 | 9 | 0.998 | 0.440 | 9 | 1.000 | 0.857 | 9 | 0.987 | 0.580 | 9 | 0.979 | 0.295 |
| 260 | 180 | 9 | 0.988 | 0.244 | 9 | 1.000 | 0.427 | 9 | 1.000 | 0.864 | 9 | 0.989 | 0.574 | 9 | 0.988 | 0.282 |
| 261 | 60 | 8 | 0.978 | 0.227 | 8 | 1.000 | 0.366 | 8 | 1.000 | 0.745 | 8 | 0.975 | 0.625 | 8 | 0.980 | 0.306 |
| 261 | 70 | 8 | 0.985 | 0.226 | 8 | 0.999 | 0.362 | 8 | 1.000 | 0.755 | 8 | 0.979 | 0.625 | 8 | 0.986 | 0.299 |
| 261 | 80 | 9 | 0.989 | 0.246 | 9 | 0.993 | 0.400 | 9 | 1.000 | 0.750 | 9 | 0.980 | 0.611 | 9 | 0.986 | 0.327 |
| 261 | 90 | 9 | 0.989 | 0.233 | 9 | 0.999 | 0.387 | 9 | 1.000 | 0.774 | 9 | 0.985 | 0.604 | 9 | 0.988 | 0.301 |
| 261 | 100 | 9 | 0.990 | 0.233 | 9 | 1.000 | 0.390 | 9 | 1.000 | 0.784 | 9 | 0.986 | 0.599 | 9 | 0.987 | 0.296 |
| 261 | 110 | 9 | 0.992 | 0.247 | 9 | 0.999 | 0.400 | 9 | 1.000 | 0.796 | 9 | 0.991 | 0.619 | 9 | 0.991 | 0.311 |
| 261 | 120 | 9 | 0.991 | 0.254 | 9 | 1.000 | 0.412 | 9 | 1.000 | 0.807 | 9 | 0.991 | 0.620 | 9 | 0.988 | 0.314 |
| 261 | 130 | 9 | 0.991 | 0.247 | 9 | 1.000 | 0.414 | 9 | 1.000 | 0.824 | 9 | 0.991 | 0.599 | 9 | 0.988 | 0.299 |
| 261 | 140 | 9 | 0.988 | 0.253 | 9 | 1.000 | 0.429 | 9 | 1.000 | 0.834 | 9 | 0.989 | 0.594 | 9 | 0.984 | 0.303 |
| 261 | 150 | 9 | 0.988 | 0.246 | 9 | 1.000 | 0.412 | 9 | 1.000 | 0.834 | 9 | 0.987 | 0.600 | 9 | 0.986 | 0.295 |
| 261 | 160 | 9 | 0.987 | 0.243 | 9 | 1.000 | 0.413 | 9 | 1.000 | 0.836 | 9 | 0.988 | 0.592 | 9 | 0.988 | 0.291 |
| 262 | 70 | 13 | 0.996 | 0.361 | 13 | 0.998 | 0.388 | 13 | 1.000 | 0.740 | 13 | 0.990 | 0.929 | 13 | 0.996 | 0.487 |
| 262 | 80 | 13 | 0.996 | 0.363 | 13 | 0.997 | 0.382 | 13 | 1.000 | 0.742 | 13 | 0.985 | 0.949 | 13 | 0.996 | 0.489 |
| 262 | 90 | 13 | 0.996 | 0.368 | 13 | 0.998 | 0.391 | 13 | 1.000 | 0.737 | 13 | 0.988 | 0.940 | 13 | 0.996 | 0.499 |
| 262 | 100 | 13 | 0.996 | 0.365 | 13 | 0.997 | 0.383 | 13 | 1.000 | 0.737 | 13 | 0.988 | 0.953 | 13 | 0.996 | 0.495 |
| 262 | 110 | 13 | 0.996 | 0.370 | 13 | 0.997 | 0.386 | 13 | 1.000 | 0.736 | 13 | 0.986 | 0.960 | 13 | 0.995 | 0.503 |
| 262 | 120 | 13 | 0.996 | 0.368 | 13 | 0.996 | 0.381 | 13 | 1.000 | 0.735 | 13 | 0.985 | 0.964 | 13 | 0.996 | 0.501 |
| 262 | 130 | 13 | 0.996 | 0.368 | 13 | 0.997 | 0.385 | 13 | 1.000 | 0.735 | 13 | 0.986 | 0.955 | 13 | 0.996 | 0.500 |
| 262 | 140 | 13 | 0.996 | 0.372 | 13 | 0.997 | 0.388 | 13 | 1.000 | 0.736 | 13 | 0.986 | 0.958 | 13 | 0.996 | 0.506 |
| 262 | 150 | 13 | 0.991 | 0.359 | 13 | 0.996 | 0.380 | 13 | 0.997 | 0.722 | 13 | 0.982 | 0.949 | 13 | 0.991 | 0.498 |
| 263 | 26 | 4 | 1.000 | 0.250 | 4 | 0.994 | 0.275 | 4 | 0.996 | 0.596 | 4 | 0.990 | 0.905 | 4 | 0.994 | 0.418 |
| 263 | 33 | 7 | 0.998 | 0.281 | 7 | 0.999 | 0.261 | 7 | 0.999 | 0.578 | 7 | 0.997 | 1.079 | 7 | 0.997 | 0.487 |
| 263 | 39 | 9 | 0.999 | 0.317 | 9 | 1.000 | 0.269 | 9 | 0.999 | 0.600 | 9 | 1.000 | 1.179 | 9 | 0.999 | 0.527 |
| 264 | 40 | 4 | 0.998 | 0.128 | 4 | 0.993 | 0.172 | 4 | 0.999 | 0.838 | 4 | 0.998 | 0.738 | 4 | 0.995 | 0.152 |
| 264 | 50 | 7 | 0.994 | 0.182 | 7 | 1.000 | 0.232 | 7 | 1.000 | 0.740 | 7 | 0.995 | 0.786 | 7 | 0.991 | 0.245 |
| 265 | 77 | 4 | 0.965 | 0.137 | 4 | 1.000 | 0.419 | 4 | 1.000 | 0.840 | 4 | 0.958 | 0.327 | 4 | 0.959 | 0.163 |
| 266 | 60 | 8 | 0.996 | 0.209 | 8 | 1.000 | 0.438 | 8 | 1.000 | 0.873 | 8 | 0.997 | 0.478 | 8 | 0.996 | 0.240 |
| 266 | 80 | 11 | 0.997 | 0.238 | 11 | 1.000 | 0.431 | 11 | 1.000 | 0.862 | 11 | 0.995 | 0.553 | 11 | 0.996 | 0.276 |
| 266 | 100 | 11 | 0.993 | 0.232 | 11 | 1.000 | 0.415 | 11 | 1.000 | 0.833 | 11 | 0.993 | 0.559 | 11 | 0.993 | 0.278 |
| 266 | 120 | 12 | 0.984 | 0.245 | 12 | 1.000 | 0.410 | 12 | 1.000 | 0.821 | 12 | 0.984 | 0.601 | 12 | 0.984 | 0.298 |
| 266 | 140 | 8 | 0.995 | 0.342 | 8 | 1.000 | 0.385 | 8 | 0.999 | 0.770 | 8 | 0.992 | 0.891 | 8 | 0.992 | 0.443 |

Table B.3. (continued)

| | | Allometric Relationships Fit by Principal Component Analysis ^C | | | | | | | | | | | | | | |
|-----------------------|--------------------|---|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|
| Id. Code ^a | Cond. ^b | log \bar{h} - log \bar{w} | | | log \overline{DBH} - log \bar{w} | | | log \overline{BSLA} - log \bar{w} | | | log \bar{h} - log \overline{DBH} | | | log \bar{h} - log \overline{BSLA} | | |
| | | n | r | $\hat{\phi}_{hw}$ | n | r | $\hat{\phi}_{Dw}$ | n | r | $\hat{\phi}_{Bw}$ | n | r | $\hat{\phi}_{hD}$ | n | r | $\hat{\phi}_{hB}$ |
| 267 | 42 | 8 | 0.987 | 0.138 | 8 | 0.999 | 0.418 | 8 | 1.000 | 0.830 | 8 | 0.982 | 0.329 | 8 | 0.983 | 0.165 |
| 268 | 54 | 7 | 0.993 | 0.147 | 7 | 0.999 | 0.346 | | | | 7 | 0.991 | 0.426 | | | |
| 269 | 75 | 6 | 0.982 | 0.187 | 6 | 0.998 | 0.395 | 6 | 0.998 | 0.791 | 6 | 0.969 | 0.472 | 6 | 0.969 | 0.234 |
| 270 | 60 | 14 | 0.991 | 0.327 | 14 | 1.000 | 0.377 | 14 | 1.000 | 0.742 | 14 | 0.989 | 0.873 | 14 | 0.991 | 0.441 |
| 270 | 70 | 14 | 0.994 | 0.318 | 14 | 1.000 | 0.366 | 14 | 1.000 | 0.725 | 14 | 0.993 | 0.872 | 14 | 0.993 | 0.439 |
| 270 | 80 | 14 | 0.991 | 0.320 | 14 | 0.999 | 0.365 | 14 | 1.000 | 0.723 | 14 | 0.993 | 0.881 | 14 | 0.991 | 0.443 |
| 270 | 90 | 14 | 0.991 | 0.321 | 14 | 1.000 | 0.362 | 14 | 1.000 | 0.726 | 14 | 0.991 | 0.893 | 14 | 0.990 | 0.442 |
| 270 | 100 | 14 | 0.993 | 0.315 | 14 | 1.000 | 0.364 | 14 | 1.000 | 0.716 | 14 | 0.993 | 0.870 | 14 | 0.990 | 0.439 |
| 270 | 110 | 14 | 0.990 | 0.313 | 14 | 0.999 | 0.359 | 14 | 1.000 | 0.709 | 14 | 0.991 | 0.877 | 14 | 0.989 | 0.441 |
| 270 | 120 | 14 | 0.991 | 0.311 | 14 | 1.000 | 0.357 | 14 | 1.000 | 0.714 | 14 | 0.991 | 0.877 | 14 | 0.989 | 0.436 |
| 271 | 40 | 18 | 0.997 | 0.305 | 18 | 0.998 | 0.366 | 18 | 0.999 | 0.735 | 18 | 0.997 | 0.835 | 18 | 0.998 | 0.416 |
| 271 | 50 | 18 | 0.991 | 0.331 | 18 | 0.999 | 0.382 | 18 | 0.998 | 0.761 | 18 | 0.996 | 0.872 | 18 | 0.997 | 0.437 |
| 271 | 60 | 18 | 0.994 | 0.321 | 18 | 0.998 | 0.382 | 18 | 0.999 | 0.756 | 18 | 0.998 | 0.843 | 18 | 0.998 | 0.426 |
| 271 | 70 | 18 | 0.994 | 0.320 | 18 | 0.998 | 0.379 | 18 | 0.999 | 0.751 | 18 | 0.998 | 0.847 | 18 | 0.998 | 0.427 |
| 271 | 80 | 18 | 0.994 | 0.310 | 18 | 0.999 | 0.365 | 18 | 0.999 | 0.739 | 18 | 0.997 | 0.853 | 18 | 0.997 | 0.421 |
| 271 | 90 | 18 | 0.994 | 0.309 | 18 | 0.998 | 0.358 | 18 | 0.999 | 0.725 | 18 | 0.997 | 0.865 | 18 | 0.997 | 0.426 |
| 271 | 100 | 18 | 0.994 | 0.311 | 18 | 0.999 | 0.353 | 18 | 0.999 | 0.723 | 18 | 0.997 | 0.884 | 18 | 0.997 | 0.431 |
| 271 | 110 | 18 | 0.994 | 0.306 | 18 | 0.999 | 0.354 | 18 | 0.999 | 0.723 | 18 | 0.997 | 0.868 | 18 | 0.996 | 0.425 |
| 272 | 50 | 6 | 0.989 | 0.267 | 6 | 0.999 | 0.312 | 6 | 0.999 | 0.623 | 6 | 0.981 | 0.859 | 6 | 0.981 | 0.426 |
| 272 | 60 | 7 | 0.997 | 0.308 | 7 | 0.994 | 0.287 | 7 | 0.994 | 0.573 | 7 | 0.983 | 1.071 | 7 | 0.983 | 0.532 |
| 272 | 71 | 7 | 0.998 | 0.319 | 7 | 0.997 | 0.269 | 7 | 0.997 | 0.537 | 7 | 0.992 | 1.186 | 7 | 0.992 | 0.591 |
| 272 | 81 | 8 | 0.998 | 0.384 | 8 | 0.998 | 0.303 | 8 | 0.998 | 0.609 | 8 | 0.998 | 1.267 | 8 | 0.998 | 0.630 |
| 272 | 103 | 10 | 0.989 | 0.294 | 10 | 0.997 | 0.306 | 10 | 0.997 | 0.613 | 10 | 0.997 | 0.967 | 10 | 0.997 | 0.482 |
| 273 | 40 | 15 | 0.998 | 0.267 | 15 | 0.996 | 0.321 | 15 | 1.000 | 0.716 | 15 | 0.996 | 0.829 | 15 | 0.996 | 0.372 |
| 273 | 50 | 15 | 0.999 | 0.272 | 15 | 0.999 | 0.350 | 15 | 0.999 | 0.701 | 15 | 0.997 | 0.774 | 15 | 0.997 | 0.387 |
| 273 | 60 | 15 | 0.999 | 0.278 | 15 | 0.999 | 0.347 | 15 | 0.999 | 0.695 | 15 | 0.997 | 0.800 | 15 | 0.996 | 0.398 |
| 273 | 70 | 15 | 0.998 | 0.276 | 15 | 0.999 | 0.341 | 15 | 0.999 | 0.693 | 15 | 0.995 | 0.809 | 15 | 0.995 | 0.397 |
| 273 | 80 | 15 | 0.998 | 0.280 | 15 | 0.999 | 0.356 | 15 | 0.999 | 0.713 | 15 | 0.998 | 0.786 | 15 | 0.999 | 0.393 |
| 273 | 90 | 15 | 0.999 | 0.272 | 15 | 0.998 | 0.346 | 15 | 1.000 | 0.680 | 15 | 0.997 | 0.785 | 15 | 0.998 | 0.400 |
| 273 | 100 | 15 | 0.999 | 0.264 | 15 | 0.998 | 0.338 | 15 | 0.999 | 0.685 | 15 | 0.997 | 0.781 | 15 | 0.996 | 0.385 |
| 274 | 60 | 8 | 0.999 | 0.269 | 8 | 1.000 | 0.368 | 8 | 1.000 | 0.763 | 8 | 0.999 | 0.731 | 8 | 1.000 | 0.352 |
| 274 | 70 | 8 | 0.999 | 0.261 | 8 | 1.000 | 0.359 | 8 | 1.000 | 0.750 | 8 | 0.999 | 0.728 | 8 | 0.999 | 0.348 |
| 274 | 80 | 8 | 0.999 | 0.260 | 8 | 1.000 | 0.358 | 8 | 1.000 | 0.749 | 8 | 0.999 | 0.727 | 8 | 1.000 | 0.348 |
| 274 | 90 | 9 | 0.998 | 0.270 | 9 | 0.999 | 0.369 | 9 | 1.000 | 0.750 | 9 | 1.000 | 0.733 | 9 | 0.998 | 0.360 |
| 274 | 100 | 9 | 0.998 | 0.273 | 9 | 0.998 | 0.370 | 9 | 1.000 | 0.741 | 9 | 1.000 | 0.738 | 9 | 0.998 | 0.368 |
| 276 | 84 | 9 | 0.996 | 0.411 | 9 | 0.998 | 0.329 | 9 | 0.999 | 0.660 | 9 | 0.991 | 1.255 | 9 | 0.991 | 0.622 |
| 276 | 95 | 9 | 0.997 | 0.415 | 9 | 0.998 | 0.330 | 9 | 0.999 | 0.662 | 9 | 0.993 | 1.260 | 9 | 0.993 | 0.625 |
| 276 | 112 | 9 | 0.997 | 0.415 | 9 | 0.998 | 0.331 | 9 | 0.998 | 0.662 | 9 | 0.992 | 1.256 | 9 | 0.992 | 0.625 |
| 277 | 70 | 4 | 0.999 | 0.233 | 4 | 1.000 | 0.402 | 4 | 1.000 | 0.777 | 4 | 0.999 | 0.581 | 4 | 0.999 | 0.301 |
| 277 | 80 | 7 | 1.000 | 0.223 | 7 | 0.999 | 0.366 | 7 | 1.000 | 0.761 | 7 | 0.999 | 0.609 | 7 | 1.000 | 0.293 |
| 277 | 90 | 9 | 0.999 | 0.224 | 9 | 0.999 | 0.359 | 9 | 1.000 | 0.756 | 9 | 1.000 | 0.625 | 9 | 0.999 | 0.297 |
| 277 | 100 | 9 | 0.998 | 0.220 | 9 | 0.997 | 0.358 | 9 | 0.999 | 0.749 | 9 | 1.000 | 0.613 | 9 | 0.995 | 0.293 |
| 277 | 110 | 9 | 0.996 | 0.213 | 9 | 0.997 | 0.362 | 9 | 0.999 | 0.748 | 9 | 1.000 | 0.591 | 9 | 0.992 | 0.284 |

Table B.3. (continued)

| | | Allometric Relationships Fit by Principal Component Analysis ^c | | | | | | | | | | | | | | |
|--------------------------|--------------------|---|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|--------------------------------------|-------|-------------------|---------------------------------------|-------|-------------------|
| Id. Code ^a | Cond. ^b | log \bar{h} - log \bar{w} | | | log \overline{DBH} - log \bar{w} | | | log \overline{BSLA} - log \bar{w} | | | log \bar{h} - log \overline{DBH} | | | log \bar{h} - log \overline{BSLA} | | |
| | | n | r | $\hat{\phi}_{hw}$ | n | r | $\hat{\phi}_{Dw}$ | n | r | $\hat{\phi}_{Bw}$ | n | r | $\hat{\phi}_{hD}$ | n | r | $\hat{\phi}_{hB}$ |
| 277 | 120 | 7 | 0.997 | 0.195 | 7 | 0.999 | 0.349 | 7 | 0.999 | 0.760 | 7 | 1.000 | 0.560 | 7 | 0.994 | 0.256 |
| 278 | 1 | 19 | 0.999 | 0.237 | 19 | 1.000 | 0.435 | 19 | 1.000 | 0.870 | 19 | 0.999 | 0.547 | 19 | 0.999 | 0.273 |
| 279 | 40 | 10 | 0.996 | 0.202 | 10 | 1.000 | 0.392 | 10 | 1.000 | 0.788 | 10 | 0.994 | 0.515 | 10 | 0.995 | 0.256 |
| 280 | 51 | 6 | 0.998 | 0.238 | 6 | 0.999 | 0.431 | 6 | 0.999 | 0.862 | 6 | 0.999 | 0.552 | 6 | 0.999 | 0.276 |
| 281 | 27 | | | | 5 | 1.000 | 0.393 | 5 | 1.000 | 0.786 | | | | | | |
| 281 | 30 | | | | 5 | 1.000 | 0.401 | 5 | 1.000 | 0.801 | | | | | | |
| 281 | 33 | | | | 5 | 1.000 | 0.402 | 5 | 1.000 | 0.807 | | | | | | |

^aTable B.1 associates each Id. code with a particular yield table.

^bSee Table B.1 and the references given there for further information on condition.

^cThe general formula for the allometric relation is $\log Y = \hat{\phi}_1 \log X + \hat{\phi}_0$, where Y is log \bar{h} , log \overline{DBH} , or log \overline{BSLA} and X is log \bar{w} , log \overline{DBH} , or log \overline{BSLA} . \overline{DBH} and \overline{BSLA} are, respectively, the diameter at breast height and the basal area at breast height of the boles of individual trees. Y and X are paired as indicated in the table heading. The number of data points, correlation (r), and slope for each relationship are given. The correlation values have little statistical meaning because most of the natural variability in the original forest data has been removed from the yield table predictions. They are included here only as a crude index of variation around the fitted line. Values of the intercept, $\hat{\phi}_0$, were calculated, but were not used in the analyses and are not given here. Formulas for principal component analysis are given in Jolicoeur and Heusner (1971).

Table B.4 Self-thinning Lines from Forestry Yield Table
Data Cited by Previous Authors in Support of the
Self-thinning Rule.

| Id. Code ^a | Condition ^b | No. of Points ^c | | Thinning ^d Line | | Reference ^f |
|--------------------------|------------------------|-------------------------------|-----|-------------------------------|----------------|------------------------|
| | | n_T | n | $\hat{\beta}^e$ | $\hat{\alpha}$ | |
| 201 | | | | -0.33 | 4.06 | White 1980 |
| 202,242,243 | | | | -0.54 | 3.46 | White 1980 |
| 203 | | | | -0.57 | 3.98 | White 1980 |
| 204 | | | | -0.63 | 3.54 | White 1980 |
| 206 | | | | -0.65 | 3.53 | White 1980 |
| 207 | 49 | | | -0.73 | 3.06 | White 1980 |
| 208 | | | | -0.63 | 4.01 | White 1980 |
| 209 | | | | -0.48 | 3.58 | White 1980 |
| 210 | 136 | | | -0.80 | 3.08 | White 1980 |
| 211 | | | | -0.49 | 3.88 | White 1980 |
| 212 | | | | -0.51 | 4.08 | White 1980 |
| 213 | | | | -0.57 | 3.85 | White 1980 |
| 216 | | | | -0.71 | 3.86 | White 1980 |
| 217 | 54,64,75 | 30 | 26 | -0.87 | | White 1981 |
| 221 | | | | -0.54 | 4.00 | White 1980 |
| 222 | part of 1 | 5 | 3 | -0.49 | | White 1981 |

^aTable B.1 associates each Id. code with a particular yield table. The presence of several codes in this column indicates that the reference did not specify which one of several yield tables from a single source was examined, making it impossible to determine which entry of Table B.1 compares directly to the reported thinning line.

^bSpecifies one of the conditions (site index, planting density, etc.) defined in Table B.1. Blanks indicate that the thinning reference did not state which condition or pooled combination of data from several conditions was analyzed. In these cases, it was not possible to determine which, if any, of the several thinning lines in Table B.2 from the same yield table is directly comparable with the one given above.

^c n_T is the total number of size-density data points given. n is the number of points remaining after removing points not relevant to the thinning line, so n is the number of points used to fit the thinning line. Blanks indicate that this information was not given in the thinning reference.

^dFit by regression of $\log \bar{w}$ against $\log N$, or of $\log \bar{v}$ against $\log N$ for codes 217 and 222 (where \bar{v} is mean stem volume per tree).

^eAll slopes were reported for $\log \bar{w}$ - $\log N$ thinning lines. The values above have been converted to $\log B$ - $\log N$ slopes by adding 1 (Chapter 1). This facilitates comparison with the analyses in Table B.2.

^fThese are references for the self-thinning analysis only. Original data sources are given in Table B.1.

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