Linkages between silviculture and ecology: an analysis of density management diagrams

Steven B. Jack [a,*], James N. Long [b]

[a] Department of Forest Science, Texas A &M University, College Station, TX 77843-2135, USA
[b] Department of Forest Resources, Utah State University, Utah, USA

Abstract

Density management diagrams (DMDs) are used to quickly examine alternative density management regimes. DMDs are based upon several ecological concepts, and thus demonstrate links between quantitative silviculture and ecology. We group the important ecological concepts incorporated into DMDs into three broad categories: (1) the generality of allometric relationships; (2) the nature of size-density relationships; and (3) the ability of relative density indices to characterize stand development. We review the evidence for each of these categories as they are applied in DMDs. There is strong evidence for the application of allometric relationships to predict stand yield and for the ability of relative density indices to characterize elements of stand development. Some ambiguity exists concerning the application of size-density relationships. Specifically, there is some evidence indicating that maximum size-density relationships may vary with genetics, management practices, and environmental conditions. In general, we conclude that DMDs rest on a strong conceptual foundation.

Keywords: DMD; Size-density; Self-thinning; Relative density

1. Introduction

Silviculturists design and implement strategies to achieve desired future stand conditions which may represent a wide range of stand structures and species compositions. These strategies require accurate predictions about future stand development, including stand structure and the competitive effects at tree and stand levels.

Predictions of stand development depend largely on ecological concepts. Quantitative silviculture applies principles, concepts and models from population ecology, production ecology and biometrics to assess and make predictions relating to various aspects of stand development. It also relates how density influences stand structure, canopy dynamics and production efficiency.

A tool used increasingly in quantitative silviculture is the density management diagram (Fig. 1), a deceptively simple tool which is useful in the design, display and evaluation of alternative density management regimes. These diagrams incorporate basic as-

* Corresponding author. Tel: (409) 845-5077; fax: (409) 845-6049; e-mail: s-jack@tamu.edu.

sumptions concerning the density-dependent behavior of populations, including self-thinning and reactions to competition (Drew and Flewelling, 1979). These basic assumptions, some of which are more widely accepted than others, are based on important links between quantitative silviculture and tree population dynamics.

In this paper, we illustrate the use of density management diagrams and evaluate fundamental assumptions which underlie their construction and which form several important linkages with population ecology, production ecology and biometrics. These basic concepts and assumptions can be grouped into three general categories:

1. The generality of basic allometric relations;
2. The nature of maximum size-density relations; and
3. The indexing of relative density.

We examine the validity of each of these categories and evaluate their suitability for use in density management.

2. Density management diagrams: components and use

Density management diagrams (DMDs), which have also been referred to as stand 'density control diagrams' and 'yield-density diagrams', are graphical representations of simple stand average models. Formats vary considerably (examples of the most common formats are shown in Fig. 1), but most include mean or average size of some tree measure (e.g. volume (Fig. 1a) or diameter (Fig. 1b)) and stand density on the major, logarithmic axes; they also include additional sets of lines corresponding to: (1) an index of stocking or relative density (several relative density indices are defined in Table 1); (2) stand volume or mean diameter (depending on which of the two is displayed on a major axis); (3) site or top height. We distinguish between DMDs and many other commonly used stocking charts and nomograms (e.g. Gingrich, 1967); a key difference is that DMDs include site or top height which, together
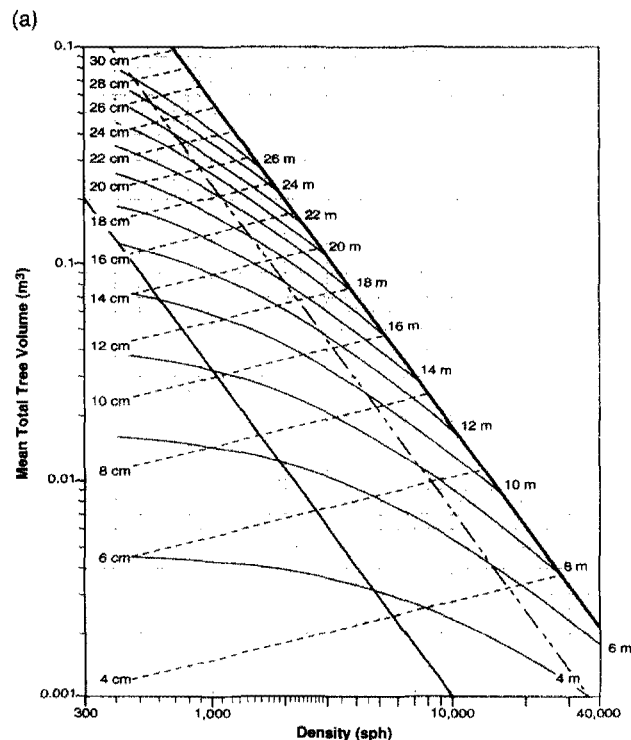
(a)

Fig. 1. Examples of density management diagrams for: (a) jack pine (after Archibald and Bowling, 1995, used with permission of authors); (b) teak (Kumar et al., 1995); and (c) deciduous broad-leaved forest (Kikuzawa, 1982). The different formats result from the use of different relative density indices and the tree size measures defining the axes.
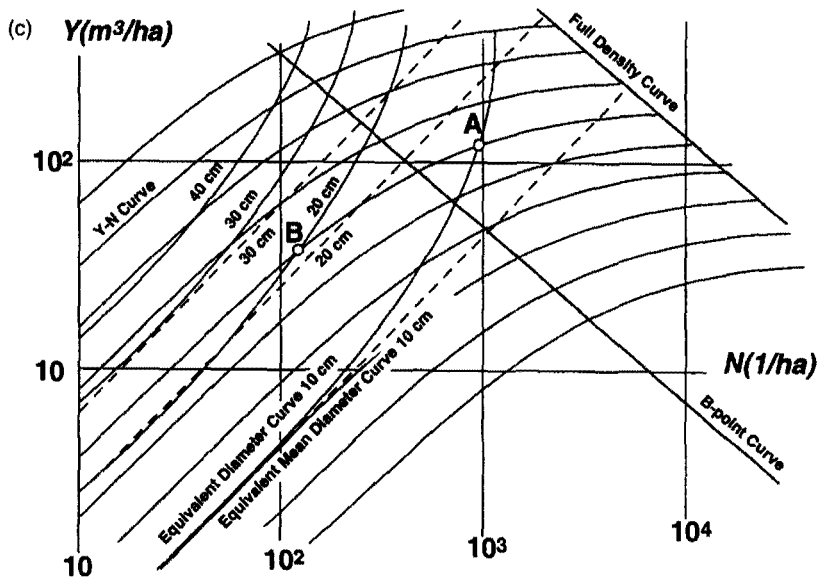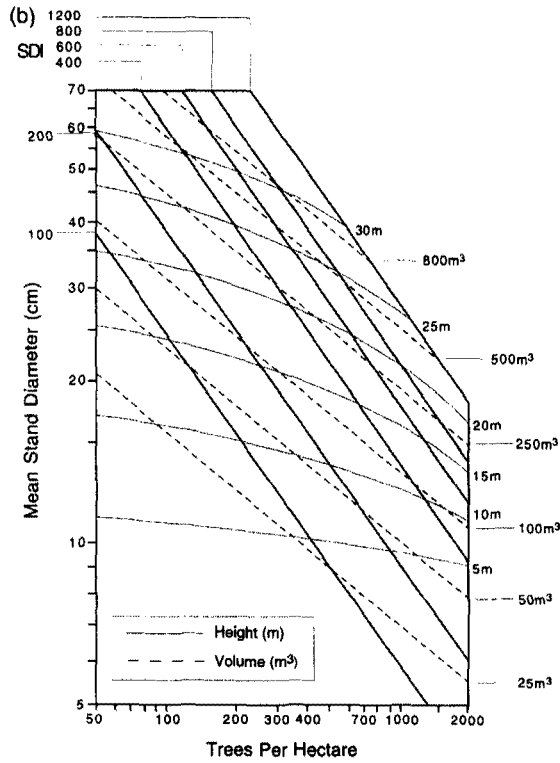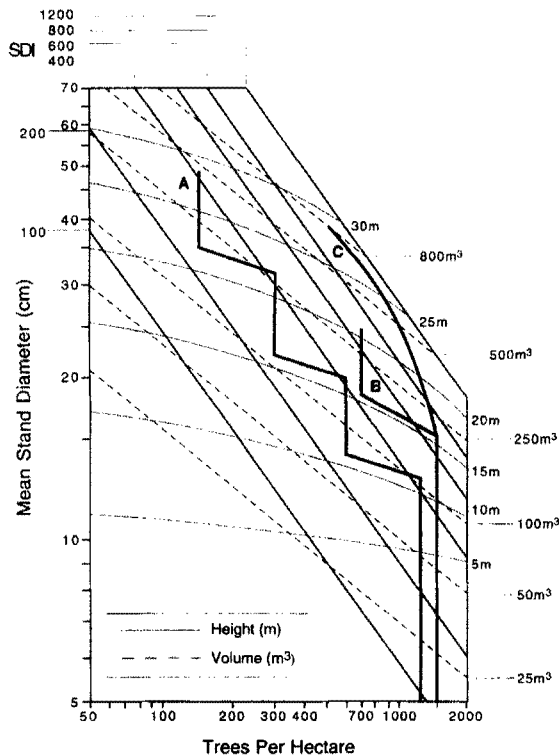
Fig. 1 (continued).

Fig. 2. Two representative density management regimes (A: 'log', B: 'pole') and an unthinned control (C) for teak (after Kumar et al., 1995). The 'log' regime utilizes a series of commercial thinnings to produce log and pole-sized trees, while the 'pole' regime uses one early commercial thinning to quickly produce pole-sized trees. The 'control' regime represents the natural self-thinning trajectory for a stand with no density manipulation. Yield data for the regimes are provided in Table 2.

with appropriate site index curves, allow estimates of growth rates. Density management diagrams have been constructed for many species, including most of

the commercially important Japanese tree species (Ando, 1968), and for the following North American tree species: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Drew and Flewelling, 1979; Long et al., 1988); lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) (Flewelling and Drew, 1985; Mc-Carter and Long, 1986); jack pine (*Pinus banksiana* Lamb.) (Archibald and Bowling, 1995); red alder (*Alnus rubra* Bong.) (Hibbs, 1987); red pine (*Pinus resinosa* Ait.) (Smith and Brand, 1989); western redcedar (*Thuja plicata* Donn ex E. Don) (Smith, 1989); slash pine (*Pinus elliottii* Engelm.) (Dean and Jokela, 1992); black spruce (*Picea mariana* (Mill.) B.S.P.) (Newton and Weetman, 1993); loblolly pine (*Pinus taeda* L.) (Dean and Baldwin, 1993; Williams, 1993); and Cooper pine (*Pinus cooperi*) (Chiapetta, 1990).

Though at first glance DMDs may appear complicated and unwieldy, these diagrams make it possible to quickly design and evaluate the consequences of alternative density management regimes. Fig. 2 illustrates two alternative regimes for a teak (*Tectona grandis* L.f.) stand (Kumar et al., 1995), as well as a natural self-thinning trajectory. The regimes and their 'trajectories' in the diagram are determined by their different objectives: the 'pole' regime produces a large number of teak poles in a fairly short rotation using a single thinning operation (horizontal movement along the trajectory), while the 'log' regime provides a combination of poles and large logs through a series of commercial thinnings. The self-thinning alternative represents a typical development pattern for an unthinned regime. Further details regarding these particular regimes can be found in Kumar et al. (1995).

Table 1
Examples of commonly used relative density indices incorporating various mean size parameters

$SDI = TPH \, (Dq/25)^{1.6}$	Reineke's (1933) Stand Density Index (*SDI*), using quadratic mean diameter (*Dq*) and trees per hectare (*TPH*). Sometimes presented as a ratio (%*SDI*) of the observed *SDI* to the maximum *SDI* for the species.
$RD = 0.00007854 * TPH * Dq^{1.5}$	Curtis' (1982) Relative Density (*RD*). Very similar to *SDI*.
$\%HT = (10000/TPH)^{0.5}/HT$	Spacing of Wilson (1946) as a percent of height (%*HT*).
$p_r = TPH/TPH_{max}$ (where $TPH_{max} = a^* \, v^{-0.67}$ with a = species-specific coefficient)	Drew and Flewelling's (1979) Relative Density (p_r), is the ratio of actual stand density to the maximum stand density (*TPH_{max}*) attainable with a given mean stem volume (v).

Table 2
Comparison of two density management regimes and an unthinned control (after Kumar et al., 1995)

	Age (years)	Ht (m)	TPH		Dq (cm)		Removed	
			Before	After	Before	After	TPH	Vol. (m³ ha⁻¹)
Pole production regime								
CT	29	15.5	1600	700	15	18.2	900	140
EOR	45	21	700	–	25	–	700	340
Total yield = 480 m³ ha⁻¹								
MAI = 10.7 m³ ha⁻¹ a⁻¹								
Log production regime								
CT	17	11	1200	600	13	14	600	30
CT	30	16	600	300	20	22	300	50
CT	49	22	300	240	31	35	60	85
EOR	74	29	140	–	50	–	140	450
Total yield = 615 m³ ha⁻¹								
MAI = 8.3 m³ ha⁻¹ a⁻¹								
Unthinned regime								
EOR	74	29	550	–	40	–	550	800
Total yield = 800 m³ ha⁻¹								
MAI = 10.8 m³ ha⁻¹ a⁻¹								

Ht: site top height; TPH: trees per hectare; Dq: quadratic mean diameter; CT: commercial thinning; EOR: end of rotation; MAI: mean annual increment.

The ability to estimate volume and top height make it possible to construct simple yield tables for each regime (Table 2). Stand top height depends on
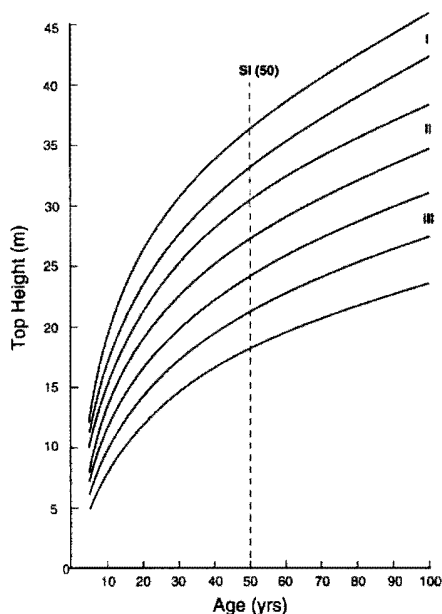

Fig. 3. Site index curves for Indian teak (after Drechsel and Zech, 1994).

site quality, yet is generally independent of stand density; it is this independence that is the basis for using site index as a measure of site quality (Tesch, 1980). Thus, given appropriate site index equations or curves (Fig. 3), site height estimated from the DMD can be used to estimate stand age. This makes it possible to determine the time required to reach particular stand structures, developmental stages, or yields, and to develop simple yield tables.

This information can be coupled with assumptions about biological and economic constraints. For example, bark beetle attacks are more likely in stands with certain combinations of diameter and stand density (Cochran, 1992; Anhold et al., in review), or harvest might be impractical below specific thresholds of volume and tree size (Long, 1985; McCarter and Long, 1986). A DMD rapidly identifies alternatives incompatible with management objectives and eliminates them from further consideration.

3. Basic assumptions

The regimes represented in Fig. 2 illustrate the basic constructs and assumptions involved in the

construction and use of density management diagrams (Drew and Flewelling, 1979). For example, the unthinned alternative assumes that self-thinning is predictable and conservative (Smith and Hann, 1984; Tang et al., 1994); more specifically, the lines corresponding to the maximum size-density relationship and to the on-set of self-thinning are assumed to be correct for all sites. Further, it is assumed that the various allometric relations are approximately correct for unthinned stands, independent of site quality, and that changes following artificial thinning are either short-lived or silviculturally unimportant. Finally, it is assumed that relative density, derived from mean tree size and number, effectively indexes important functions and processes such as competition and site occupancy. For example, maximum individual tree growth occurs at relative densities below some threshold representing the onset of competition, and maximum net stand growth occurs at relative densities ranging from the lower limit of full site occupancy to the beginning of self-thinning (Drew and Flewelling, 1979; McCarter and Long, 1986). These principles and concepts are central to many aspects of stand development, and are examined in more detail below.

3.1. Species-specific allometric relationships provide reasonable stand-average predictions of stand structure and yield

Allometric relationships are the cornerstone of much of forest mensuration and yield prediction, where the difficulty of measuring many meaningful characteristics of forest stands increases the reliance on surrogate measures. For centuries foresters have established relationships between average tree size and density (number of stems per unit area). Higher absolute densities are associated with smaller average size (measured as diameter at breast height, crown width, crown projection area, or leaf area per tree) due to increased competition for physical space or available resources such as light, nutrients and water (e.g. Reineke, 1933; Stiell, 1966; Hamilton, 1969; Assmann, 1970; Curtis, 1970; Dean and Long, 1992).

Allometric relationships are also useful predictors of stand yield. For example, 'Eichorn's Law' (Assmann, 1970; Falkenhagen, 1980) predicts standing volume or volume production, reportedly independent of site quality, using average height, and has been the basis of many yield tables. Assmann (1970) concludes that while Eichorn's Law holds fairly well for predicting yield, it is dependent on site class (quality). Falkenhagen (1980) reformulated Eichorn's Law using diameter at breast height (DBH), which is easier to measure than height, and found that the relationship is accurate for stands with similar productivity potential and stand history. Japanese scientists used DBH to predict total biomass or volume in forest stands (e.g., Ogawa et al., 1961; Tadaki, 1966; also, work cited in White, 1981, and Satoo and Madgwick, 1982). Osawa and Allen (1993) note, however, that the population mean allometry, not allometric relationships derived for individual trees, is important for predicting population yield. While the individual tree and stand average allometric relationships are often similar, they may diverge in some situations. Similar relationships occur in other plant populations, e.g., the competition-density effect and yield-density relations (Shinozaki and Kira, 1961; Yoda et al., 1963; review by Westoby, 1984) for herbaceous plants, where plant populations of the same age but with different densities differ in average size (usually average plant mass) and total yields. Thus it appears that simple allometric relationships can provide reasonable predictions of stand yield.

Allometric relationships appear to be largely independent of site quality (Assmann, 1970; Drew and Flewelling, 1977; Long and Smith, 1990; Osawa and Allen, 1993). Site quality does not appear to affect the relationship between average size and density, but it does affect the growth, i.e. the better the site quality, the sooner growth to a given average size occurs. Miller (1981) applied this concept in his model for the effect of fertilization on forest stand development: fertilization increases yield by temporarily accelerating stand development. This effect has been confirmed in slash pine where fertilization had relatively little effect on dimensional relationships (Jack et al., 1988; Jokela et al., 1989; Colbert et al., 1990). Similarly, Dean and Jokela (1992) found that soil groups differing in productive capacities in the Southeastern coastal plain did not affect slash pine growth and allometric relationships.

There are indications, however, that allometries differ between genetic families, especially at young

ages (Lee, 1989). Even so, stand yields later in the rotation are often similar, depending somewhat on whether the yield under consideration is total or merchantable volume. Cameron (1988) tested the allometric yield predictions incorporated in the density management diagram of Drew and Flewelling (1979) for Douglas-fir on plantation data from British Columbia, and found that allometric relationships may also vary between geographic regions.

There is also the so-called 'memory problem' (Drew and Flewelling, 1979; Long, 1985; Cameron, 1988) associated with changes in structure; i.e. a stand which was heavily thinned will not have the same average size (e.g. mean DBH) or the same allometries as a comparable stand of the same density that was not thinned. The density management diagrams assume such structural differences are either short-lived or of limited silvicultural importance (Drew and Flewelling, 1979). This limitation is a trade-off between using the relatively simple, stand average DMD approach and more complicated methods.

There is ample evidence that simple allometric relationships can provide reasonably accurate stand average predictions of yield. Factors such as family differences at young ages, the 'memory problem,' and variation over broad geographic areas should be considered before applying DMDs, but we do not think these limitations invalidate use of the technique within a species.

3.2. There is a predictable, species-specific maximum for combinations of average size and density

This postulate has strong implications for the processes of stand development and self-thinning. The existence of a boundary on combinations of average size and density implies that average size increases only to some limit, beyond which there is a decline in the number of individuals (Fig. 4). The universality of species-specific boundaries is also a central point in the debate regarding the validity and generality of the ' −3/2 self-thinning law' first proposed by Yoda et al. (1963) (see Weller, 1987, 1990; Zeide, 1987, 1991; Osawa and Sugita, 1989; Lonsdale, 1990 for recent contributions to the debate).

Much of the debate over the self-thinning law concerns whether it applies to individual stand trajec-
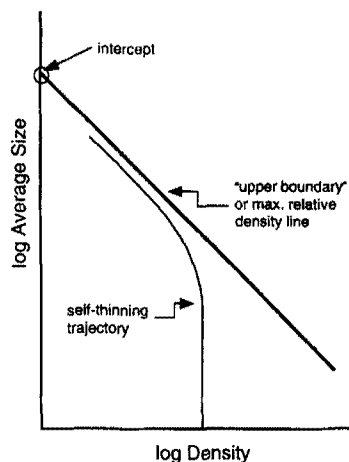

Fig. 4. Schematic representation of important concepts related to self-thinning. The self-thinning trajectory represents a typical development pattern for an individual even-aged stand which undergoes density-dependent mortality through time.

tories during stand development, or to the upper boundary, or to both. The original −3/2 relationship (Yoda et al., 1963) focused on the maximum boundary condition, but subsequent discussions dealt with the trajectory aspect, especially in the English-language literature (Weller, 1990). The boundary or maximum size-density relationship is of primary importance in the construction and use of DMDs. Thinning regimes are usually imposed in managed stands to 'capture' potential mortality (Drew and Flewelling, 1979), thus they are not typically allowed to follow natural self-thinning trajectories. For density management, the boundary determines the appropriate combinations of size and density to meet particular objectives, and is the topic of this paper. In considering the maximum boundary line, we examine assumptions regarding the constancy of the slope, lack of curvature, the value of the intercept term, and the combined effect of the slope and intercept on the boundary.

3.2.1. The slope of the maximum size-density boundary is universal, i.e. it is independent of species and site quality

The line representing the relationship between maximum mean size and absolute density is usually straight when plotted on log-log axes (Fig. 4) (White, 1981; Weller, 1987). The slope of the line changes with the measure of size, e.g. for average weight or

volume the slope is -1.5, for total weight or volume the slope is -0.5, for quadratic mean diameter the slope is -0.625. Nonetheless, the slope is assumed to be independent of site quality and species.

Though based upon a substantial body of empirical evidence, this assumption has been subject to considerable debate in the recent ecological literature. Many researchers find there is more variation in the 'universal' slope than was previously believed (Zeide, 1985; Zeide, 1987; Weller, 1987; Verwijst, 1989; Lonsdale, 1990; Hynynen, 1993), particularly when considering a range of species (Zeide, 1985, 1987; Weller, 1987) rather than the slope within a species. Variation in the slope between species was noted in the earliest papers dealing with size-density relationships (e.g. Reineke, 1933; Yoda et al., 1963), but these deviations were often viewed as being close to the 'expected' slope and were cited as additional supporting evidence in the quest to find a universal rule for plant ecology (see review in Weller, 1987). These deviations are now thought to indicate significant and useful information about differences in species biology (Zeide, 1985). Currently, many believe the slope varies between species, but not within a species.

Thus, DMDs should allow for variation in the slope of the size-density relationship between species and not assume a universal, fixed value. This variation between species can be easily incorporated in DMDs if the slope for a particular species can be determined. There is much less variation in slopes within a species; for example, the slope of the maximum size-density boundary line for any species does not appear to vary with site quality. Within species variation in slope, if found, would greatly limit the utility of DMDs, perhaps to site-specific uses.

3.2.2. The upper boundary of size and density combinations has no curvature

Some researchers, particularly Zeide (1987) and Zeide (1985), believe the maximum size-density boundary is better represented as a curve in log-log space. This may depend on whether the trajectories of individual stands or a maximum boundary condition for a species is being represented (Fig. 4). Zeide (1987) and Zeide (1995) focus on the continued reduction in full canopy closure in individual stands (i.e. the trajectory aspect) throughout stand develop-

ment (Long and Smith, 1992). Zeide (1991) maintains that the absolute upper boundary for a species could be a straight line in log-log space. The absolute boundary proposed, however, is only a conceptual construct and can never be actually measured, and any empirically determined boundary will probably be curvilinear (Zeide, 1991).

Two other factors are related to the shape of the maximum boundary. First, it is often assumed that the trajectory for a stand is asymptotic to the presumed upper boundary (Smith and Hann, 1984), and that an asymptotic function accurately models stand trajectories (Smith and Hann, 1984; Puettmann et al., 1993). Second, older self-thinning stands often tend to 'fall away' from the upper boundary, and the trajectory slope decreases (White and Harper, 1970). This is often attributed to the inability of the old, large trees surviving self-thinning to fully recapture the available resources following the death of other large trees (White and Harper, 1970). This interpretation is similar to Zeide's contention that canopy closure decreases during stand development (Zeide, 1987; Zeide, 1995). These cases concern trajectories of individual stands, though, rather than a species' absolute size-density maximum.

Even if a curve more accurately represents maximum combinations of average size and density DMDs could be constructed on this basis, although curved boundaries might make such diagrams more difficult to construct and use. There is no compelling evidence to assume that a curved boundary is necessary, however. Where abundant data are available, the boundary is well represented by a straight line when plotted using log-log axes.

3.2.3. The intercept, or level, of the boundary line is constant for a given species, e.g. it is independent of site quality

Though the slope of the boundary relationship in log-log space may be independent of species (for the same average size measure), the y-intercept (Fig. 4) for the line, which determines the level of the boundary, varies widely between species. Norberg (1988) suggests that the intercept of the boundary is affected by both the 'packing density', or plant biomass per volume, and by the ratio of plant height to width. The first of these is strongly correlated with relative shade tolerance, while the second is related to gross

plant or crown shape (Norberg, 1988). Crown shape also affects the intercept value for tree species (Harper, 1977). In general, shade-tolerant species have a greater intercept than intolerant species, and conifers have higher intercepts than hardwood species (White and Harper, 1970; Harper, 1977). A greater intercept means that, for equivalent average size, more individuals of a shade-tolerant or coniferous species will survive (Harper, 1977).

Within a species, however, the intercept is assumed to be constant and thus independent of site quality, i.e. a population on a high quality site will reach the boundary more quickly than the same density of trees on a lower quality site, even though both achieve the same boundary. This constancy is fundamental to the general utility of density management diagrams, and allows the use of site index curves to determine the time required to reach particular stand structural characteristics.

Some evidence appears to show that the intercept varies with site quality in some specific instances (Strub and Bredenkamp, 1985; Barreto, 1989; Hynynen, 1993). Most evidence, however, indicates the intercept is independent of site quality; e.g., the Drew and Flewelling (1979) study for Douglas-fir stands and a study by Dean, Long and Smith (unpublished data) which examined combinations of average tree volume and density for lodgepole pine in three different site index classes (Fig. 5). Similarly, Smith and Hann (1984) found soil types did not affect either the intercept or slope parameters of red alder in Oregon.

Intraspecific variation in the intercept term of the boundary line has been found in two specific situations: artificial manipulation of light and nutrient availabilities, and major differences in climate. For example, artificial shading (Hiroi and Monsi, 1966; Aikman and Watkinson, 1980) and severe nutrient deficiencies (Hutchings and Budd, 1981a; Lonsdale and Watkinson, 1982; Morris and Myerscough, 1991) reduce the intercept or level of the boundary. DeBell et al. (1989) and Harms et al. (1994) found that the stockability (which is similar to a maximum size-density relationship) of loblolly pine varies considerably between South Carolina and Hawaii. Harms et al. (1994) attribute this variation to the dissimilar climatic regimes of the two areas. For example, Vose et al. (1994) suggest that differences in temperature
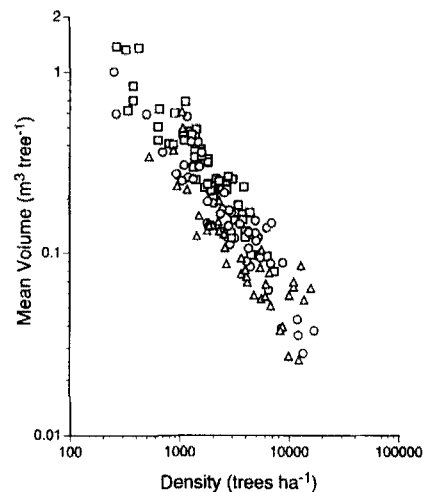

Fig. 5. Mean volume and density of lodgepole pine stands. Site indices range from 11 to 31 m (base age 100 years). Site indices are grouped into site classes of high (squares), medium (circles) and low (triangles).

result in substantially higher leaf area index for stands of loblolly pine in Hawaii than in its natural range.

Genetic differences may also influence the intercept of the maximum size-density relationship, though reports are not consistent (e.g. Nance et al., 1987 and references therein; Schmidtling, 1988; Buford, 1989). Family differences in the intercept are not significant after accounting for confounding factors such as genotype-environment interactions, differences in early growth patterns, crown position differences, and altered site index due to cultural treatments (Lee, 1989; Buford and Burkhart, 1987). The lack of strong evidence to suggest that different intercept terms are required, however, may be due to the lack of rigorous testing of such relationships rather than to overwhelming evidence showing no effect.

Given the ambiguity of the published information regarding maxima for combinations of size and density, the information reviewed above does not fully support the concept of a single, species-specific boundary. Thus, further study of this relationship is warranted.

3.2.4. Boundary line determination

Much depends on how the boundary condition is determined. The simplest method assumes a fixed

slope and relies on visual placement of the line in the appropriate position (e.g. Drew and Flewelling, 1979; McCarter and Long, 1986). Others have employed various regression procedures, using either linear least squares (e.g. White and Harper, 1970; Bazzaz and Harper, 1976; Lonsdale, 1990), principle components (e.g. Mohler et al., 1978; Weller, 1987), or reduced major axis (e.g. Zeide, 1987) analyses on a subset of the data which is representative of the uppermost, or most crowded, stands. Other statistical methods have been used to determine boundary conditions (e.g. Blackburn et al., 1992), but are seldom used in plant ecology. As Zeide (1991) notes, each of these methods assumes the available data represent the maximum combinations of size and density. It is not possible to test the validity of this assumption, but clearly the more data available, the stronger the support for this assumption.

One statistical consideration is that the intercept and slope of the boundary line (in log-log space) both affect the upper boundary at a particular density. Some of the difficulty in finding a constant, universal slope for self-thinning plant populations may reflect the interactions involved in simultaneously fitting the two parameters, and how these interactions affect the placement of the maximum size-density boundary (Jack and Long, 1991a).

3.3. Relative density can be effectively characterized with a simple function relating mean size and absolute density

A fundamental concept of quantitative silviculture is that site occupancy is related to the size and number of trees on a unit area, and that a given degree of site occupancy can result from either many small trees or a fewer number of large trees (Baker, 1950). Therefore, relative density is typically expressed as a function of mean size and absolute density (Table 1). Not surprisingly, all of these expressions of relative density are highly correlated (Daniel et al., 1979; Curtis, 1982; West, 1982; Marshall et al., 1992).

The ecological importance and silvicultural utility of relative density indices rest on the proposition that stands with the same relative density, regardless of differences in age, site quality or mean size and density, share many fundamental population-level attributes (Reineke, 1933; Curtis, 1970; Drew and Flewelling, 1979), including self-thinning, canopy closure, mean live crown ratio, and growth-growing stock relations. All of these factors may affect the evaluation of alternative regimes using DMDs.

3.3.1. Zone of imminent competition mortality

An alternative to a species' average self-thinning line (e.g., the 'full density curve' represented in Fig. 1c) is to predict the on-set of density-related mortality. Drew and Flewelling (1977) suggest that self-thinning occurs over a fairly wide range of relative densities. The upper bound of this 'zone of imminent competition mortality' is the species-specific maximum size-density relation (i.e. maximum relative density) and the lower bound represents the relative density beyond which self-thinning is likely. Based on repeated measurements in stands of radiata pine and Douglas-fir, Drew and Flewelling (1979) hypothesize this threshold of self-thinning corresponds to densities of approximately 55% of the species maximum density for a given mean volume. Mortality can occur at relative densities below this threshold, but the probability of mortality at these lower levels would not change by reducing stand density. Drew and Flewelling (1979) concede the difficulty of testing this lower bound, but argue it is consistent with available empirical evidence.

Self-thinning stands appear to move progressively towards a size-density asymptote and mortality may be continuous from very early in stand development, e.g. following crown closure. Analytical models have been developed to characterize the size-density trajectory (Hozumi, 1977; Smith and Hann, 1984; Flewelling and Drew, 1985; Hara, 1985; Smith and Brand, 1989; Smith, 1989; Tang et al., 1994) which smooth stand-to-stand variability as well as episodic variability in mortality (DeBell and Franklin, 1987). Self-thinning in a stand, particularly in small plots, may be unpredictable on time scales shorter than decades. Focusing on the death of individual trees or short-term mortality will obscure even strong trends in the size-density relations of self-thinning populations (Drew and Flewelling, 1977). It may be more realistic to define a relative density along the stand development trajectory where there is some specified probability of mortality, e.g. 15% (Smith and Hann, 1984); this approach results in a lower threshold

relative density for stands with high initial densities than those with low initial densities.

3.3.2. Canopy closure

Crown closure is commonly assumed to represent the threshold of strong competitive interaction and stand development. Prior to crown closure tree growth is essentially independent of stand density; following crown closure, self-pruning and crown class differentiation accelerate, and the plastic response of tree growth to stand density is expressed (Long and Smith, 1984).

Crown closure, as a function of mean size and density, is typically estimated as the point at which adjacent crowns first touch, assuming either square or triangular spacing. In several studies, the crown closure line in DMDs was close to a constant relative density, e.g., 15 to 25%, depending on the relative density index (Drew and Flewelling, 1979; McCarter and Long, 1986). In western redcedar the crown closure line was steeper than a constant relative density line; i.e. the relative density at which crown closure occurs is inversely proportional to initial stand density (Smith, 1989). This may be due to the development of crown shyness as mean tree size increases (Putz et al., 1984): as trees increase in size, the swaying and physical interaction abrades branch tips of adjacent trees and reduces the ratio of crown width to stem diameter (Long and Smith, 1992; Osawa and Allen, 1993).

3.3.3. Live crown ratio

Self-pruning involves the death of branches at the base of a tree's crown. Self-pruning and the resultant lifting of the live crown accelerates following crown closure (Beekhuis, 1965; Assmann, 1970; Marshall et al., 1992). While the average depth of live crowns continues to increase in crowded populations, the ratio of live crown length to total tree height progressively declines with increasing relative density (Fig. 6). Average live crown ratio may predict thinning response; as a general rule-of-thumb, live crown ratios in conifer stands should not be allowed to decline below about 40% in order to maintain the trees' capacity for timely response to thinning (Daniel et al., 1979).
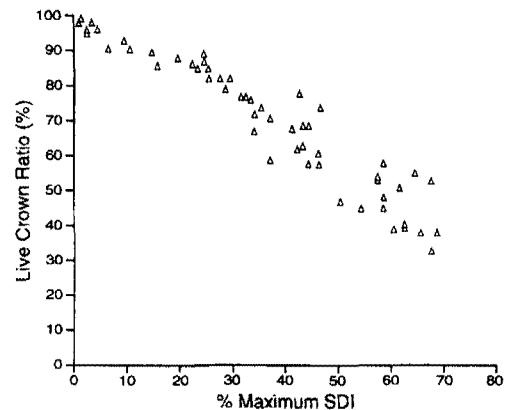

Fig. 6. Relationship between average live crown ratio (crown length to total height) and relative density for stands of lodgepole pine, ponderosa pine and Douglas-fir. Stand ages range from less than 15 to over 100 years; site indices range from 11 to 43 m (at 50 years base age) (after Long, 1985).

3.3.4. Growth-growing stock relations

Stand growth is clearly a function of relative density since a high-density stand can produce substantially more total volume than a low-density stand. More specifically, below some threshold of relative density (e.g. corresponding to crown closure or the onset of competitive interaction) stand growth increases linearly with relative density as the number of open-grown trees increases. Above this threshold, however, growth increases at a decreasing rate due to increasing between-tree competition. It is often assumed that above some threshold relative density (corresponding to 'full site occupancy') the countervailing influences of increasing tree number and decreasing individual tree growth results in perfect density compensation such that stand gross growth is independent of relative density (Langsaeter, 1941; Mar:Møller, 1947; Braathe, 1957).

Smith (1986) characterizes growth-growing stock relations with three alternatives which differ only at high relative densities. One model assumes growth continues to increase up to the maximum relative density; the second assumes that growth eventually peaks and then declines with increasing relative density; and the third assumes that growth eventually reaches a plateau, i.e. perfect density compensation with increasing relative density. These models all depend on how 'growth' is characterized. As relative

density increases beyond the onset of self-thinning, gross growth may be stable or continue to increase, but net growth will decline. Similarly, above some threshold relative density, growth will decline if it is based only on those trees greater than some minimum size (Kilpatrick et al., 1981). Reukema and Bruce (1977) suggest that this peak in growth occurs at a constant relative density, regardless of the specified minimum tree size.

Generally, total gross growth appears to increase with relative density up to the threshold representing the onset of competition, followed by an asymptotic increase in growth up to the maximum relative density (e.g. Fig. 7, after Day and Rudolph, 1972), a pattern which corresponds to the first model of Smith (1986). Results of many spacing and thinning trials seem to support this model (e.g. Mar:Møller, 1947; Braathe, 1957; Kilpatrick et al., 1981; Curtis. 1992; Dean and Jokela, 1992; Jack and Long, 1992; Marshall et al., 1992). Long (1985) suggests that the linear phase extends to about 25% of maximum SDI and contends 'little' growth potential would be lost if relative density was above a threshold of about 35% of maximum SDI (Fig. 8, after Long, 1985). Marshall et al. (1992) suggest that relative densities above 40% of maximum SDI may be appropriate to achieve 'near-maximum' stand growth.

Growth-growing stock relations are almost certainly a function of the amount and distribution of stand leaf area. The increase in leaf area index (LAI) with relative density is a striking example of an emergent property (sensu Salt, 1979) in stand development (Mar:Møller, 1947; Marks and Bormann, 1972; Mohler et al., 1978). Size-density relations in

Fig. 8. Generalized relationship between stand growth and relative density (after Long, 1985).

self-thinning populations may be a consequence of allometry and the redistribution of maximum leaf area among fewer individuals (Long and Smith, 1984; Osawa and Allen, 1993). Experimental manipulation of LAI, with reduced light or clipping of leaves, affects self-thinning behavior in herbaceous populations (Westoby and Braun, 1980; Hutchings and Budd, 1981b; Dean and Long, 1985).

For some species, LAI appears to be essentially independent of relative density above some threshold level, e.g. red pine (Smith and Brand, 1989) and lodgepole pine (Jack and Long, 1991b). No such plateau was observed for subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), but LAI was still strongly related to relative density (Jack and Long, 1991b). The distribution of leaf area among trees, however, is not independent of relative density (Jarvis, 1975; Long and Smith, 1984; Jack and Long, 1991b). The distribution of foliage among a few large trees or many small trees affects foliar efficiency, i.e. stem production per unit leaf area (Smith and Long, 1989, 1992; Long and Smith, 1990; Roberts et al., 1993), and thus is important for stand production.

The form of the growth-relative density relation appears to be very general, but actual growth also depends on species, site quality and age. Interestingly, however, both current and mean annual increment may culminate at constant relative densities (Reukema and Bruce, 1977; Smith, 1989).
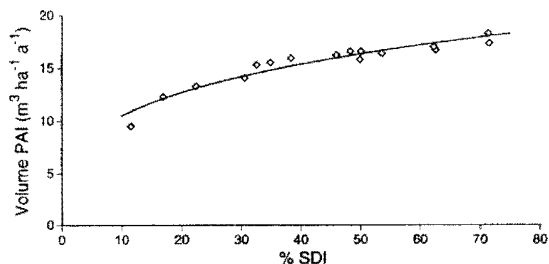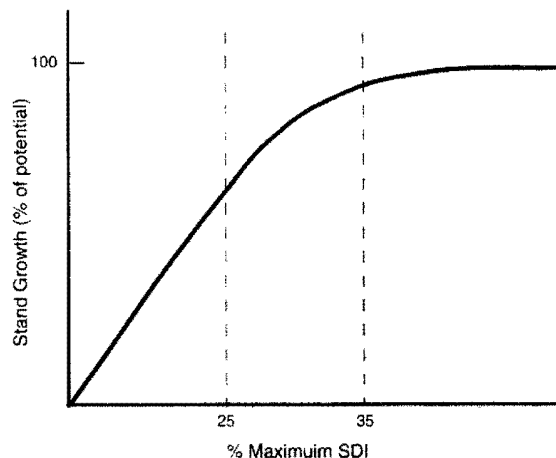

Fig. 7. Periodic annual volume increment (Volume PAI) as a function of relative density (percentage of species-maximum SDI) for stands of red pine. Results are from Day and Rudolph (1972).

4. Summary and conclusions

Density management diagrams integrate relationships between density, stand structure, canopy dynamics and production efficiency, and link quantitative silviculture to population ecology, production ecology and biometrics. DMDs are simple stand average models in graphical form that are especially useful in the rapid design and evaluation of alternative density management regimes. Despite their great practical value DMDs have not been developed for many important tree species, and most are limited to single-species (see Kikuzawa, 1982 as an exception) and essentially even-aged stands.

There is considerable evidence supporting the accuracy of allometric equations in yield prediction and the use of relative density as an index of important stand characteristics. There is less certainty regarding the concept of a single species-wide limit for combinations of average size and density. Allometric equations have a long history in plant ecology (Niklas, 1994), and the utility of such equations for yield predictions in DMDs is well-established in the forestry literature. There is also considerable support for the use of relative density in predicting relationships such as self-thinning, canopy structure and growth-growing stock relations, a finding which is consistent with the basic premise of quantitative silviculture that a given degree of site occupancy can result from many small trees or fewer large trees.

There is less evidence to indicate that there is a constant maximum size-density relation for a particular species. It is exceedingly important to determine the degree to which observed intraspecific-variation in maximum size-density relations is silviculturally important. DMDs supposedly apply over a wide range of conditions such as site quality, and determining when models should be refit to reflect local data warrants additional study. Similarly, more should be learned about possible influences of genetic and genetic-site interactions on size-density relations, and whether these influences are silviculturally important (e.g. Perala et al., 1995).

Overall, we believe our review indicates that density management diagrams are a useful tool with a sound conceptual base. As with any tool, users should recognize their limitations and intended use: DMDs are useful for the rapid analysis of many alternative density management regimes and are not intended to be detailed growth and yield models. Once one or two alternatives are identified, other tools can provide more detailed yield analyses.

References

Aikman, D.P. and A.R., Watkinson, 1980. A model for growth and self-thinning in even-aged monocultures of plants. Ann. Bot., 45: 419-427.

Ando, T., 1968. Ecological studies on the stand density control in even-aged stands. Bull. Gov. For. Exp. Stn. Tokyo, 210: 1-153.

Anhold, J.A., M.J. Jenkins and J.N. Long. in review. Management of lodgepole pine stand density to reduce susceptibility to mountain pine beetle attack. West. J. Appl. For.

Archibald, D.J. and C., Bowling, 1995. Jack pine density management diagram for boreal Ontario. OMNR, Northeast and Northwest Science and Technology. TN-005 (NWST TN-31), 21 pp.

Assmann, E., 1970. The Principles of Forest Yield Study. Pergamon, Oxford, 506 pp.

Baker, F.S., 1950. The Principles of Silviculture. McGraw-Hill, New York, 414 pp.

Barreto, L.S., 1989. The '3/2 power law': a comment on the specific constancy of K. Ecol. Model., 45: 237-245.

Bazzaz, F.A. and Harper, J.L., 1976. Relationship between plant weight and numbers in mixed populations of *Sinapsis alba* (L.) Rabenh. and *Lepidium sativum* L. J. Appl. Ecol., 13: 211-216.

Beekhuis, J., 1965. Crown depth of radiata pine in relation to stand density and height. New Zealand J. For., 10: 43-61.

Blackburn, T.M., Lawton, J.H. and Perry, J.N., 1992. A method of estimating the slope of upper bounds of plots of body size and abundance in natural animal assemblages. Oikos, 65: 107-112.

Braathe, P., 1957. Thinnings in even-aged stands: a summary of European literature. Fac. of Forestry, Univ. of New Brunswick, Fredericton, NB, 92 pp.

Buford, M.A., 1989. Mean stem size and total volume development of various loblolly pine seed sources planted at one location. Can. J. For. Res., 19: 396-400.

Buford, M.A. and Burkhart, H.E., 1987. Genetic improvement

effects on growth and yield of loblolly pine plantations. For. Sci., 33: 704-724.

Cameron, I.R., 1988. An evaluation of the density management diagram for coastal Douglas-fir. Econ. And Reg. Development Agreement, B.C. Ministry of Forests and Lands, 17 pp.

Chiapetta, S.R., 1990. Stand density management and stem quality in *Pinus cooperi*. MS Thesis, Colorado State University, Fort Collins, CO, 29 pp.

Cochran, P.H., 1992. Stocking levels and underlying assumptions for uneven-aged ponderosa pine stands. USDA For. Serv. Res. Note PNW-RN-509, 10 pp.

Colbert, S.R., Jokela, E.J. and Neary, D.G., 1990. Effects of annual fertilization and sustained weed control on dry matter partitioning, leaf area, and growth efficiency of juvenile loblolly and slash pine. For. Sci., 36: 995-1014.

Curtis, R.O., 1970. Stand density measures: an interpretation. For. Sci., 16: 403-414.

Curtis, R.O., 1982. A simple index of stand density for Douglas-fir. For. Sci., 28: 92-94.

Curtis, R.O., 1992. Levels-of-growing-stock cooperative study in Douglas-fir: Report No. 11 — Stampede Creek: a 20-year progress report. USDA For. Serv. Res. Pap. PNW-RP-442, 47 pp.

Daniel, T.W., Helms, J.A. and Baker, F.S., 1979. Principles of Silviculture, 2nd edn. McGraw-Hill Co., NY, 500 pp.

Day, M.W. and Rudolph, V.J., 1972. Thinning plantation red pine. Mich. Agri. Expt. Sta. Res. Pap. No. 151, 11 pp.

Dean, T.J. and Baldwin, Jr., V.C., 1993. Using a density-management diagram to develop thinning schedules for loblolly pine plantations. USDA For. Serv. Res. Pap. SO-275, 7 pp.

Dean, T.J. and Jokela, E.J., 1992. A density-management diagram for slash pine plantations in the Lower Coastal Plain. South. J. Appl. For., 16: 178-185.

Dean, T.J. and Long, J.N., 1985. Response of self-thinning to artificially reduced levels of leaf area in monocultures of *Trifolium pratense*. Ann. Bot., 55: 361-366.

Dean, T.J. and Long, J.N., 1992. Influence of leaf area and canopy structure on size-density relations in even-aged lodgepole pine stands. For. Ecol. Manage., 49: 109-117.

DeBell, D.S. and Franklin, J.F., 1987. Old-growth Douglas-fir and western hemlock: a 36-year record of growth and mortality. West. J. Appl. For., 2: 111-114.

DeBell, D.S., Harms, W.R. and Whitesell, C.D., 1989. Stockability: a major factor in productivity differences between *Pinus taeda* plantations in Hawaii and the Southeastern United States. For. Sci., 35: 708-719.

Drechsel, P. and Zech, W., 1994. DRIS evaluation of teak (*Tectona grandis* L.f.) mineral nutrition and effects of nutrition and site quality on teak growth in West Africa. For. Ecol. Manage., 70: 121-133.

Drew, T.J. and Flewelling, J.W., 1977. Some recent Japanese theories of yield density relationships and their application to Monterey pine plantations. For. Sci., 23: 517-534.

Drew, T.J. and Flewelling, J.W., 1979. Stand density management: an alternative approach and its application to Douglas-fir plantations. For. Sci., 25: 518-532.

Falkenhagen, E.R., 1980. The law of Eichorn: use, extension and applicability in South Africa. South African J. For., 114: 7-12.

Flewelling, J.W. and Drew, T.J., 1985. A stand density management diagram for lodgepole pine. In: D.M. Baumgartner, R.G. Krebill, J.T. Arnott and G.F. Weetman (Editors). Lodgepole Pine: The Species and its Management. Symp. Proc., Spokane, WA. Coop. Ext., Washington State Univ., pp. 239-244.

Gingrich, S.F., 1967. Measuring and evaluating stocking and stand density in upland hardwood forest in the Central States. For. Sci., 13: 38-53.

Hamilton, G.J., 1969. The dependence of volume increment of individual trees on dominance, crown dimensions, and competition. Forestry, 42: 133-144.

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

Harms, W.R., DeBell, D.S. and Whitesell, C.D., 1994. Stand and tree characteristics and stockability in *Pinus taeda* plantations in Hawaii and South Carolina. Can. J. For. Res., 24: 511-521.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, NY, 892 pp.

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

Hiroi, T. and Monsi, M., 1966. Dry matter economy of *Helianthus annuus* communities grown at varying densities and light intensities. J. Fac. Sci. Univ. Tokyo, 9: 241-285.

Hozumi, K., 1977. Ecological and mathematical considerations on self-thinning in even-aged pure stands. I. Mean plant weight-density trajectory during the course of self-thinning. Bot. Mag., 90: 165-179.

Hutchings, M.J. and Budd, C.S.J., 1981a. Plant competition and its course through time. BioSci., 31: 640-645.

Hutchings, M.J. and Budd, C.S.J., 1981b. Plant self-thinning and leaf area dynamics in experimental and natural monocultures. Oikos, 36: 319-325.

Hynynen, J., 1993. Self-thinning models for even-aged stands of *Pinus sylvestris, Picea abies*, and *Betula penula*. Scand. J. For. Res., 8: 326-336.

Jack, S.B. and Long, J.N., 1991a. Analysis of stand density effects on canopy structure: a conceptual approach. TREES: Structure and Function, 5: 44-49.

Jack, S.B. and Long, J.N., 1991b. Response of leaf area index to density for two contrasting tree species. Can. J. For. Res., 21: 1760-1764.

Jack, S.B. and Long, J.N., 1992. Forest production and the organization of foliage within crowns and canopies. For. Ecol. Manage., 49: 233-245.

Jack, S.B., Stone, E.L. and Swindel, B.F., 1988. Stem form changes in unthinned slash and loblolly pine stands following midrotation fertilization. South. J. Appl. For., 12: 90-97.

Jokela, E.J., Harding, R.B. and Nowak, C.A., 1989. Long-term effects of fertilization on stem form, growth relations, and yield estimates of slash pine. For. Sci., 35: 832-842.

Jarvis, P.G., 1975. Water transfer in plants. In: D.A. de Vries and N.K. van Alfen (Editors). Heat and mass transfer in the environment of vegetation. Scripta Book, Washington, D.C., pp. 369-394.

Kikuzawa, K., 1982. Yield-density diagram for natural deciduous broad-leaved forest stands. For. Ecol. Manage., 4: 341-358.

Kilpatrick, D.J., Sanderson, J.M. and Savill, P.S., 1981. The influence of five respacing treatments on the growth of Sitka spruce. Forestry, 54: 17-29.

Kumar, B.M., Long, J.N. and Kumar, P., 1995. A density management diagram for teak plantations of Kerala in peninsular India. For. Ecol. Manage., 74: 125-131.

Langsaeter, A., 1941. Om tynning i enaldret gran-og furuskog Medd. f Det norske Skogforsoksvesen, 8: 131-216.

Lee, J.T., 1989. Basal Area Growth Response to Competition Among Improved Families of Loblolly Pine (*Pinus taeda* L.) in a 20-year-old Row Plot Progeny Trial. M.S. Thesis, Texas A&M University, College Station, TX, 41 pp.

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

Long, J.N., McCarter, J.B. and Jack, S.B., 1988. A modified density management diagram for coastal Douglas-fir. West. J. Appl. For., 3: 88-89.

Long, J.N. and Smith, F.W., 1984. Relation between size and density in developing stands: a description and possible mechanism. For. Ecol. Manage., 7: 191-206.

Long, J.N. and Smith, F.W., 1990. Determinants of stemwood production in *Pinus contorta* var. *latifolia* forests: the influence of site quality and stand structure. J. Appl. Ecol., 27: 847-856.

Long, J.N. and Smith, F.W., 1992. Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and crown dynamics. For. Ecol. Manage., 53: 53-64.

Lonsdale, W.M., 1990. The self-thinning rule: dead or alive? Ecology, 71: 1373-1388.

Lonsdale, W.M. and Watkinson, A.R., 1982. Light and self-thinning. New Phytol., 90: 431-445.

Marks, P.L. and Bormann, F.H., 1972. Revegetation following forest cutting: mechanisms for return to steady-state nutrient cycling. Science, 176: 914-915.

Mar: Møller, C., 1947. The effect of thinning, age, and site on foliage, increment, and loss of dry matters. J. For., 45: 393-404.

Marshall, D.D., Bell, J.F. and Tappeiner, J.C., 1992. Levels-of-growing-stock cooperative study in Douglas-fir: Report No. 10 — The Hoskins Study, 1963-83. USDA For. Serv. Res. Pap. PNW-RP-448, 65 pp.

McCarter, J.B. and Long, J.N., 1986. Density management of lodgepole pine. West. J. Appl. For., 1: 6-11.

Miller, H.G., 1981. Forest fertilization: some guiding concepts. Forestry, 54: 157-167.

Mohler, C.L., Marks, P.L. and Sprugel, D.G., 1978. Stand structure and allometry of trees during self-thinning of pure stands. J. Ecol., 66: 599-614.

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

Nance, W.L., McCutchan, B.G., Talbert, C.B., Buford, M.A., Foster, G.S. and Sprinz, P.T., 1987. Experimental approaches for evaluating genetic effects on stand growth and yield. In: D.L. Rockwood (Editor). Statistical Considerations in Genetic Testing of Forest Trees. Proceedings of the 1986 Workshop of Southern Regional Information Exchange Group 40, 25–26 June 1986, Gainesville, FL, pp. 22-39.

Newton, P.F. and Weetman, G.F., 1993. Stand density management diagrams and their development and utility in black spruce management. For. Chron., 69: 421-430.

Niklas, K.J., 1994. Plant Allometry and the Scaling of Form and Process. The University of Chicago Press, Chicago, IL, 395 pp.

Norberg, R.A., 1988. Theory of growth geometry of plants and self-thinning of plant populations: geometric similarity, elastic similarity, and different growth modes of plant parts. Am. Nat., 131: 220-256.

Ogawa, H., Yoda, K. and Kira, T., 1961. A preliminary survey on the vegetation of Thailand. Nature and Life in S.E. Asia, 1: 1-157.

Osawa, A. and Allen, R.B., 1993. Allometric theory explains self-thinning relationships of mountain beech and red pine. Ecology, 74: 1020-1032.

Osawa, A. and Sugita, S., 1989. The self-thinning rule: another interpretation of Weller's results. Ecology, 70: 279-283.

Perala, D.A., Leary, R.A. and Cieszewski, C.J., 1995. Stockability, growth, and yield of the circumboreal aspens (*Populus tremuloides* Michx., *P. tremula* L.). USDA Forest Service Res. Pap. NC-321, 24 pp.

Puettmann, K.J., Hann, D.W. and Hibbs, D.E., 1993. Evaluation of the size-density relationships for pure red alder and Douglas-fir stands. For. Sci., 39: 7-27.

Putz, F.E., Parker, G.G. and Archibald, R.M., 1984. Mechanical abrasion and intercrown spacing. Am. Midl. Nat., 112: 24-28.

Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agr. Res., 46: 627-638.

Reukema, D.L. and Bruce, D., 1977. Effects of thinning on yield of Douglas-fir: concepts and some estimates obtained by simulation. USDA For. Serv. Gen. Tech. Rep. PNW-58, 36 pp.

Roberts, S.D., Long, J.N. and Smith, F.W., 1993. Canopy stratification and leaf area efficiency: a conceptualization. For. Ecol. Manage., 60: 143-156.

Salt, G.W., 1979. A comment of the use of the term emergent properties. Am. Nat., 113: 145-148.

Satoo, T. and Madgwick, H.A.I., 1982. Forest Biomass. Martinus Nijhoff/Dr. W. Junk Publishers, The Hague, 152 pp.

Schmidtling, R.C., 1988. Racial variation in self-thinning trajectories in loblolly pine. In: A.R. Ek, S.R. Shifley and T.E. Burk (Editors). Forest Growth Modelling and Prediction. USDA For. Serv. Gen. Tech. Rep. NC-120, pp. 611-618.

Shinozaki, K. and Kira, T., 1961. Interspecific competition among higher plants. X. The C-D rule, its theory and practical uses. J. Biol. Osaka City Univ., 12: 69-82.

Smith, D.M., 1986. The Practice of Silviculture, 8th edn. John Wiley and Sons, NY, 527 pp.

Smith, F.W. and Long, J.N., 1989. The influence of canopy structure on stemwood production and growth efficiency of *Pinus contorta* var. *latifolia*. J. Appl. Ecol., 26: 681-691.

Smith, F.W. and Long, J.N., 1992. Determinants of stemwood production in coniferous forests: a comparison of *Pinus contorta* var. *latifolia* and *Abies lasiocarpa*. In: M.G.R. Cannell,

D.C. Malcolm and P.A. Robertson (Editors). The Ecology of Mixed-Species Stands of Trees. Special Publ. Series of the British Ecological Society, Number 11. Blackwell Sci. Publ., Edinburgh, pp. 87-98.

Smith, N.J., 1989. A stand-density control diagram for western redcedar, *Thuja plicata*. For. Ecol. Manage., 27: 235-244.

Smith, N.J. and Brand, D.G., 1989. Compatible growth models and stand density diagrams. In: A.R. Ek, S.R. Shifley and T.E. Burk (Editors). Forest Growth Modelling and Prediction. USDA For. Serv. Gen. Tech. Rep. NC-120. pp. 636-643.

Smith, N.J. and Hann, D.W., 1984. A new analytical model based on the $-3/2$ power rule of self-thinning. Can. J. For. Res., 14: 605-609.

Stiell, W.M., 1966. Red pine crown development in relation to spacing. Dept. For., Can. For. Res. Branch Pub. No. 1145, 44 pp.

Strub, M.R. and Bredenkamp, B.V., 1985. Carrying capacity and thinning response of *Pinus taeda* in the CCT experiments. South African For. J., 133: 6-11.

Tadaki, Y., 1966. Some discussions on the leaf biomass of forest stands and trees. Bull. Gov. For. Exp. Stn. Tokyo, 184: 135-161.

Tang, S., Meng, C.H., Meng, F.R. and Wang, Y.H., 1994. A growth and self-thinning model for pure even-age stands: theory and applications. For. Ecol. Manage., 70: 67-73.

Tesch, S.D., 1980. The evolution of forest yield determination and site classification. For. Ecol. Manage., 3: 169-182.

Verwijst, T., 1989. Self-thinning in even-aged natural stands of *Betula pubescens*. Oikos, 56: 264-268.

Vose, J.M., Dougherty, P.M., Long, J.N., Smith, F.W., Gholz, H.L. and Curran, P.J., 1994. Factors influencing the amount and distribution of leaf area of pine stands. Ecol. Bull. (Copenhagen), 43: 102-114.

Weller, D.E., 1987. A reevaluation of the $-3/2$ power rule of plant self-thinning. Ecol. Monogr., 57: 23-43.

Weller, D.E., 1990. Will the real self-thinning rule please stand up? — A reply to Osawa and Sugita. Ecology, 71: 2004-2007.

West, P.W., 1982. Comparison of stand density measures in even-aged regrowth eucalypt forest of southern Tasmania. Can. J. For. Res., 13: 22-31.

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

Westoby, M. and Braun, L., 1980. The effect of clipping on self-thinning in *Trifolium pratense*. Aust. J. Ecol., 5: 407-409.

White, J., 1981. The allometric interpretation of the self-thinning rule. J. Theor. Biol., 89: 475-500.

White, J. and Harper, J.L., 1970. Correlated changes in plant size and number in plant populations. J. Ecol., 58: 467-485.

Williams, R.A., 1993. Stand density management diagram for loblolly pine plantations in north Louisiana. South. J. Appl. For., 18: 40-45.

Wilson, F.G., 1946. Numerical expression of stocking in terms of height. J. For., 44: 756-761.

Yoda, K., Kira, T., Ogawa, H. and K. Hozumi, 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. (Intraspecific competition among higher plants. XI.) J. Biol. Osaka City Univ., 14: 107-129.

Zeide, B., 1985. How much space does a seedling need? For. Ecol. Manage., 11: 225-229.

Zeide, B., 1987. Analysis of the $3/2$ power law of self-thinning. For. Sci., 33: 517-537.

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

Zeide, B., 1995. A relationship between size of trees and their number. For. Ecol. Manage., 72: 265-272.