Some Recent Japanese Theories of Yield-Density Relationships and Their Application to Monterey Pine Plantations

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ABSTRACT. Stand growth is viewed in terms of a simple biological model which will allow the forester to relate density and yield at any stage of stand development. Empirically determined size-density relationships of forest stands, and theoretical derivations of these relationships, have been developed by Japanese scientists and are reviewed here. These include the 3/2 power law for self-thinning to identify the maximum average tree size-density relationship of a species; the reciprocal yield law for defining yield as a function of density at any stage of stand development; and the relationship between stand height and the reciprocal yield coefficients. The regions of random and competition related mortality are identified and separated. An application of these density dependent yield functions is given for *Pinus radiata* D. Don plantations. FOREST SCI. 23:517–534.

ADDITIONAL KEY WORDS. Stand density, yield forecasting, competition mortality, *Pinus radiata*.

STUDIES OF INTRASPECIFIC COMPETITION by Japanese scientists have led to several interesting theories from which yield-density relationships of forest stands can be modeled concisely. Beyond a cursory perspective of how these models relate to some of the more common approaches to yield modeling, this report does not discuss the large body of North American literature dealing with competition measures, indices, or models.

Historically, yield table construction has been oriented toward the prediction of future stand conditions since these are important to the estimation of crop values. In an attempt at simplification, early yield tables employed the concept of normal stocking. Normal stocking is the mean stocking level of a large number of undisturbed stands. However, the growth of stands with abnormal stocking could not be predicted by these tables without the use of rather tentative adjustment techniques.

More recently, notably since the advent of the computer, complex regression models have been generated to predict growth and yield for many combinations of age, site, and stocking. These have bypassed the normality concept, and as a result are more complicated than the earlier models. The many variables that affect growth interact in ways that are only approximated by the variable transformation search that precedes the final model. The resulting prediction models are usually acceptable within the range of variables examined.

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Consideration is also being given to mathematical models founded on logical propositions concerning the biology of growth. Mathematical growth models can be used in the formation and refinement of causal relationships applicable to any generalized growth theory. Pienaar (1965) expected "such theory could form the basis for the truly scientific management of forests and plantations, in providing a sound and obective basis for decision theory." Forest managers need such a tool to choose rationally among the spectra of management regimes or treatment options. They must have techniques to extrapolate short-term experimental results through rotation age, and this will require the development of models which have more general applicability.

Some well conceived biological models of intraspecific competition are found in the Japanese literature. Shinozaki and Kira (1956), Turnbull (1963), Pienaar (1965), Willey and Heath (1969), and White and Harper (1970) introduced these Japanese concepts into the English language literature; and limited applications to managed softwood forests are discussed by Tadaki (1963, 1964), Ando (1968) and Aiba (1975a), although no comprehensive explanation or substantive use for these models has been found. These models merit further investigation because of the biological validity, indicated by their applicability to diverse species, and, from a mathematical viewpoint, their extreme simplicity. The value of a parsimonious model is expounded on by George Box (1976): ". . . the scientist . . . should seek an economical description of natural phenomena." This is not meant to discredit the large number of approaches to stand modeling that rely upon complex models, but rather, it is a recognition of the need for an additional model where the interrelationships between the important stand parameters of density, mortality, and yield can be easily displayed.

Unthinned Monterey pine (*Pinus radiata* D. Don) plantation data are used to demonstrate the utility of this theory as a framework for understanding the basic yield-density relationships of a species. Further, these data are used to demonstrate the accuracy of these general models.

MAXIMUM SIZE-DENSITY RELATIONSHIPS

An analysis of competition-induced mortality by Yoda and others (1963) led to a development known as the 3/2 power law of self-thinning, which describes a maximum size-density relationship applicable to stands of any age or site. Yoda and others used radishes (*Raphanus sativus* L.), soybeans (*Glycine max* (L.) Merr.), sesame (*Sesamum inducum*) and buckwheat (*Fagopyrum sagittatum*), sudan grass (*Sorghum sudanense*), and maize (*Zea mays* L.) at various densities (stems per unit area) to observe self-thinning. He and his co-workers observed that for low initial planting densities there was no mortality, but as initial density increased the density of surviving plants at a fixed time after sowing approached a fixed maximum. They suggested that in pure even-aged stands there is a maximum population density dependent on the plants' stage of development. Furthermore, as time increases, these upper limits tend to converge on a fixed density level. Since average plant size was greater for buckwheat than sesame at the same density in self-thinning situations, tolerance to overcrowding must vary by species. Fertilizer application increased growth rates but did not change maximum density for a given average plant weight.

In a series of experiments to identify mean plant weight-density relationships at maximum stocking, Yoda and others (1963) also established plots in pure stands of *Plantago asiatica*, *Erigeron canadensis*, *Ambrosia artemisiifolia elatior*, *Amaranthus retroflexus*, *Chenopodium album centrorubrum*, and other weed species. They found that "in spite of differences in age, stage of growth, locality and micro-habitat

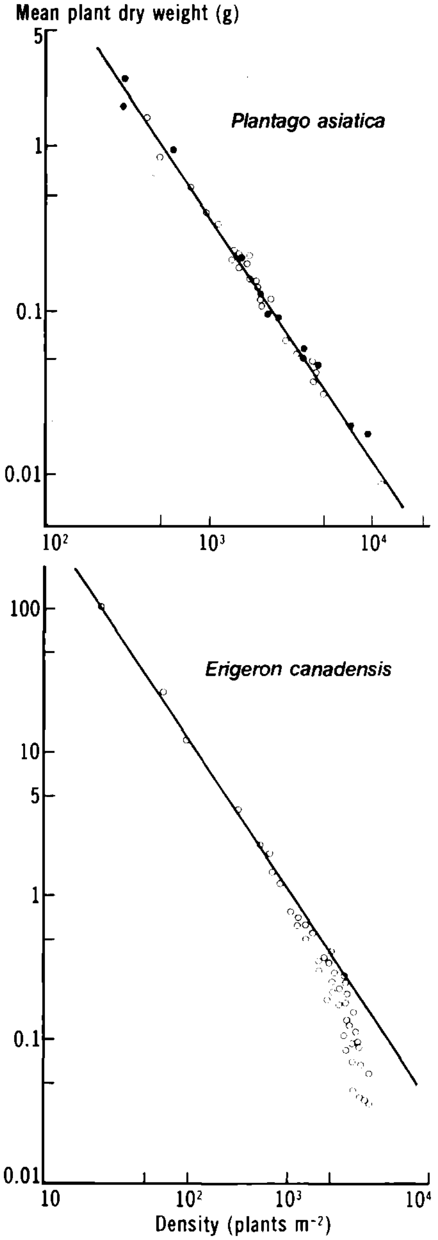

FIGURE 1. The relationship between the logarithms of density and mean plant weight in overcrowded plots of *Plantago asiatica* and *Erigeron canadensis* (Yoda and others 1963).

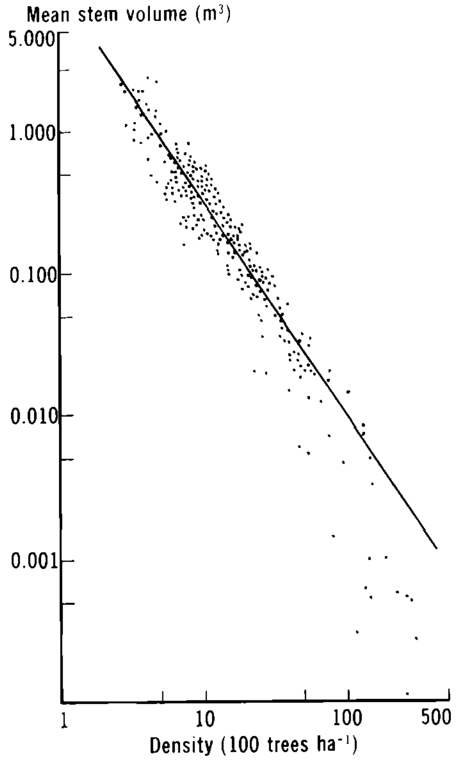

FIGURE 2. The relationship between the logarithms of mean stem volume and density in pure natural stands of *Pinus densiflora* in Honsyû, Japan (Yoda and others 1963).

conditions, a single line represents the plant size-density relation throughout the stands (for each species in self-thinning situations)."

In every instance the slope of the line was close to –1.5 (Fig. 1) when the logarithms of mean plant weight were plotted against logarithms of density. This observation has become the basis for the 3/2 power law of self-thinning.

This relationship between the maximum plant size and density was derived by Yoda and others. The term maximum plant size refers to the maximum attainable value of the average plant size for a given stand condition and not to the maximum size of the individual trees within the stand. Two simple assumptions about a plant's space requirements were made. First, plants of the same species have a particular shape independent of their size or stage of development. This is the expected outcome of identical growth rates for differing plant parts. Constant differential growth rates for different plant parts have been shown for many species and the resulting relationship identified as the allometric principle (Huxley 1932). Second, self-thinning must occur when the site is fully occupied by the species.

For fully occupied sites at any stage of development Yoda and others (1963) stated the relationship between average ground area occupied by a plant (S) and the current density in terms of plants per unit area (ρ),

$$S \propto (1/\rho) \tag{1}$$

The relationship between ground area (S) and mean plant weight (w) was achieved by the use of a dimensional analysis. The basic dimension (L) refers to the linear measurement of some unspecified plant part.

$$S \propto L^2 \quad \text{(area is a quadratic function of a linear dimension)} \tag{2}$$

and

$$w \propto L^3 \quad \text{(weight is a cubic function of a linear dimension)} \tag{3}$$

therefore:

$$S \propto L^2 \propto (L^3)^{2/3} \propto (w)^{2/3} \tag{4}$$

Substituting equation (1) for S

$$1/\rho \propto (w)^{2/3} \tag{5}$$

then

$$w \propto (\rho)^{-3/2} \tag{6}$$

or

$$w = C\,(\rho)^{-3/2} \tag{7}$$

$$\ln(w) = \ln(C) - 3/2 \ln(\rho) \tag{8}$$

The power constant in the maximum size-density relationship (equation 6) would be an indeterminant constant if the allometric principle had been used instead of the restrictive assumption of constant tree shape. The –3/2 coefficient is, however, verified empirically for tree species. Yoda and others graphed the average aboveground dry weight per tree against density for overcrowded stands of *Abies sachalinensis* and *Betula* spp. and found a straight line relationship with a slope of approximately –3/2. This line is subsequently referred to as the maximum size-density relationship.

American forestry literature contains mention of similar relationships between mean tree diameter at breast height (DBH) and density. The effective similarity between the competition density law of the maximum size-density relationship and Reineke's maximum stand density curves can be demonstrated through the weight-DBH relationship given by Ogawa and others (1961):

$$w \propto \mathrm{DBH}^{2.5} \tag{9}$$

Thus the 3/2 power law can be rewritten in terms of DBH as:

$$\ln(\rho) = \ln(C) - 1.67 \ln(\mathrm{DBH}) \tag{10}$$

The 2.5 exponent in the weight-DBH relationship was derived from trees within a stand, but we expect the exponent relating mean weight to DBH between stands to be slightly less. Reineke (1933) estimated the slope of the logarithmic relationship for maximum numbers of trees per unit area and average DBH as –1.605 for 12 of 14 tree species evaluated. MacKinney and Chaiken (1935) estimated the slope for loblolly pine as –1.707. McArdle and others (1961) tabulated normal densities as functions of mean DBH for Douglas-fir, and their values closely approximated a log-log relationship with a slope of –1.54. Bailey (1972) estimated the constant in Reineke's stand density index model as –1.58 for *Pinus radiata* in New Zealand. Satoo (1962) and Curtis (1971) showed these power relationships are interpretable as an expression of the allometric relationship between crown area and DBH. As such, the slope of the maximum size-density relationship might be expected to vary between species.

Since volume and weight are approximately proportional, the 3/2 power law (equation 8) should apply to volume as well as weight and this has been shown for *Pinus densiflora* (Fig. 2).

Beyond the simple geometric relationships used to explain this law, the real causes lie in physiological processes which are genetically controlled. The environment can and does affect growth rate, but apparently does not alter maximum plant weight for a given plant density—a phenomenon independent of age. Westoby's (1977) reformulation of the 3/2 power law has leaf area proportional to density to the –3/2 power. By using leaf area instead of ground area, the resulting formulation is not subject to variance of leaf area for a given mean plant weight. Westoby shows that his reformulated power law eliminates much of the variance in White and Harper's (1970) data for *Helianthus annus*. This formulation of the power law will not be discussed further since leaf area is difficult to measure in forest stands, and since the small improvement in fit with *Helianthus annus* data was due to the wide variation in leaf area over a range of light regimes, which is unlikely to be imposed upon forest stands.

YIELD-DENSITY RELATIONSHIPS

The basic relationships between yield and density for any stage of stand development have been mathematically described with varying degrees of complexity and success. Holliday (1960) described them in terms relating to two morphological groups: vegetative and reproductive. Since the reproductive component of forests is a small part of the total yield, it will not be considered further. Vegetative yield, however, refers to total dry matter production on an area basis, and is most successfully described by the asymptotic relationship between final yield and density.

Willey and Heath (1969) reviewed five types of yield-density equations—polynomial, exponential, Mitscherlich, geometric, and reciprocal—which relate mean yield per plant and density for a particular stage of stand development. They concluded that reciprocal equations ". . . offer the best possibilities of being able to describe yield-density relationships accurately and meaningfully." The family of equations they discussed included:

(i) Shinozaki and Kira (1956): $1/w = a + b\rho$ (11)

(ii) de Wit (1960): $1/w = (1/PQ) + (1/P) \cdot \rho$ (12)

(iii) Bleasdale and Nelder (1960): $1/w^{\theta} = a + b\rho^{\theta}$ (13)

(iv) Bleasdale and Nelder (1960): $1/w^{\theta} = a + b\rho^{\phi}$ (14)

(v) Bleasdale and Thompson (1966): $1/w^{\theta} = a + b\rho$ (15)

(vi) Farazdaghi and Harris (1968): $1/w = a + b\rho^{\gamma}$ (16)

where

w = mean plant weight

ρ = density in plants per unit area.

The coefficients for these equations (a, b, P, Q, ϕ, θ, γ) are dependent upon the stage of stand development; for particular values of the coefficients, the equations all reduce to the simple form of equation 11.

Derivation of these equations from biological principles differs between equations. Several, including the equation by Shinozaki and Kira (1956), start with a logistic growth equation which defines plant weight as a function of age. This logistic growth equation does not refer to population trends as the original usage of the term "logistic growth" implied.

A derivation of this logistic growth equation for an individual plant develops from the assumption that the rate of change of mean weight (w) with respect to time (t) is proportional to that fraction of final weight (W) not yet achieved:

$$dw/dt \propto [1 - (w/W)] \tag{17}$$

For different individuals, each at the same relative stage of development:

$$dw/dt \propto w \tag{18}$$

Combining equations (17) and (18):

$$dw/dt \propto w\,[1 - (w/W)] \tag{19}$$

or

$$(1/w)(dw/dt) = \lambda\,[1 - (w/W)] \tag{20}$$

Integrated over time:

$$w = W/(1 + Ke^{-\lambda t}) \tag{21}$$

This is a common form of the logistic growth equation.

This form of logistic equation models growth independently of density, and is applicable in the period following germination when no inhibitory effects of density exist. When growth equations other than logistic are adopted, "this assumption (of non-competition) is to be replaced by some other complicated conditions in which the growth coefficient correspondent to λ usually depends on ρ" (Shinozaki and Kira 1956).

Shinozaki and Kira went on to develop their reciprocal yield equation which included the law of constant final yield formulated by Hozumi and others (1956). The law of constant final yield states that final (as time approaches infinity) yield per unit area (Y) is constant and independent of density. Thus:

$$W = Y/\rho \tag{22}$$

Initial or precompetition plant size (w_0) is independent of density, and the logistic growth equation estimates initial plant weight as:

$$w_0 = W/(1 + K) \tag{23}$$

Equations (22) and (23) were combined:

$$w_0 = (Y/\rho)/(1 + K) \tag{24}$$

$$K = [Y/(w_0\rho)] - 1 \tag{25}$$

With K defined, the logistic growth equation becomes:

$$1/w = (1/W)\cdot(1 + Ke^{-\lambda t}) \tag{26}$$

Defining A and B at a particular age:

$$A = (1 - e^{-\lambda t})/Y \tag{27}$$

$$B = e^{-\lambda t}/w_0 \tag{28}$$

and rewriting equation 26, with W replaced through equation 22, K replaced through equation 25, and incorporating the definitions of A and B, the reciprocal yield law of the competition-density effect was defined:

$$1/w = A\rho + B \tag{29}$$

Equation 29 can be stated on a unit area basis by defining the current yield (y) as the product of mean weight and density:

$$y = \rho/(A\rho + B) \tag{30}$$

Equation 29 is referenced in Japanese literature as the reciprocal law of the competition-density effect and the yield form (equation 30) is referenced as the reciprocal equation of the yield-density effect. Either equation enables yields being achieved by different planting densities to be compared at any point in time. These relationships have been demonstrated by Shinozaki and Kira (1961) with data for soybean (Fig. 3).

For a given age, equation 29 defines a line that relates mean weight to density (Fig. 3); subsequently as age increases, yield becomes density independent (Fig. 3). A similar relationship (Fig. 4) showing volume per hectare as a function of density was developed by Ando (1968) from data for *Pinus densiflora.* Although the two heaviest densities show substantial mortality, the basic reciprocal relationship is easily discernible.

The A and B coefficients of the reciprocal yield law are constant for any stage of stand development, which was originally described by stand age. Ando (1962) utilized the established concept of mean stand height as a scale of biological time and, for groups of stands with a common mean height, related the A and B coefficients to that height. Using *Cryptomeria japonica* (planted in Japan and Formosa), *Pinus densiflora,* and *Larix leptotepis,* he plotted the A and B coefficients against mean stand height on log-log paper to produce a straight line represented by the relationships:

$$A = aH^{-b} \tag{31}$$

$$B = a'H^{-b'} \tag{32}$$

The coefficients (a, b, a', b') vary with the species.

Further, Hatiya and Ando (1962) offered a derivation of these equation forms to predict the A and B coefficients as functions of mean stand height.

THE MAXIMUM SIZE-DENSITY RELATIONSHIP AND THE RECIPROCAL EQUATION

The density-effect relationship given by the reciprocal yield equation describes mean plant weight as a function of density before substantial mortality occurs. The 3/2 power law estimates maximum mean plant weight as a function of density in stands where substantial mortality is occurring maintaining this maximum condition. This relationship is independent of initial stocking and the stage of stand development. A transitional period exists between the stand being described by the reciprocal

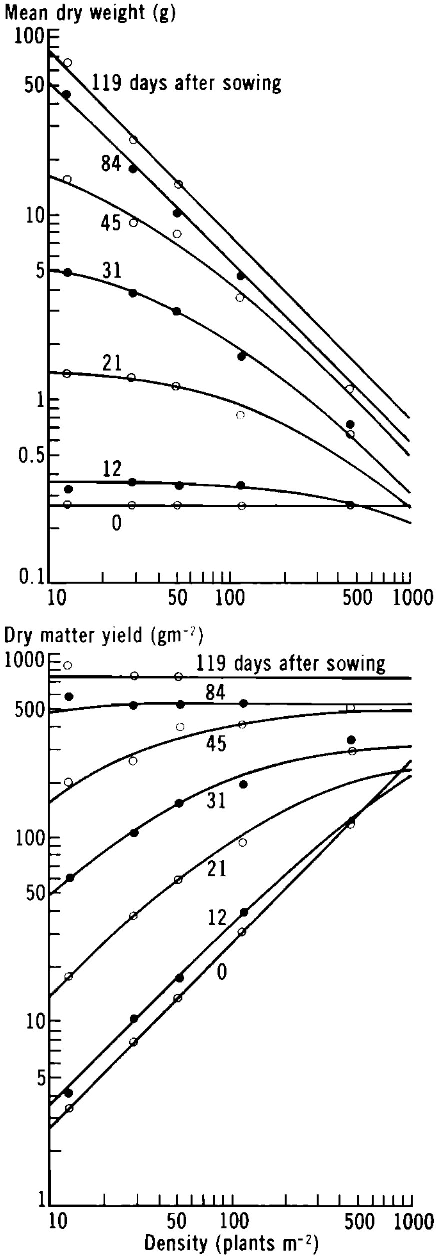

Figure 3. The relationship between the logarithms of mean plant weight, dry matter yield and density for periods of growth following sowing of soybean (*Glycine max* (L.) Merr) (Shinozaki and Kira 1961).

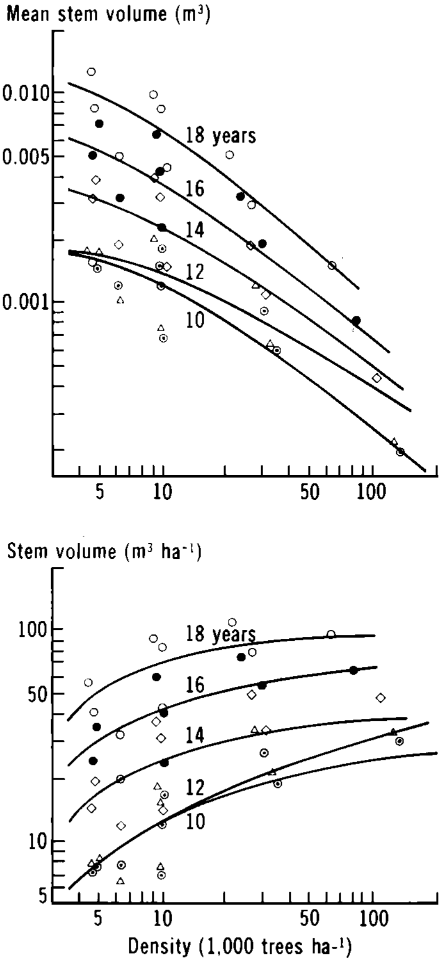

Figure 4. The relationship between the logarithms of mean stem volume, stem volume per hectare and density for *Pinus densiflora* var. *lime* (Ando 1968).

yield law and when it follows the 3/2 power law. This transitional period requires additional equations to resolve the apparent conflict of two different estimates for mean plant weight at the onset of self-thinning.

The conflict between the two laws is presented for buckwheat (*Fagopyrum sagittatum*) in Figure 5. Here the reciprocal law is represented by a family of solid lines,

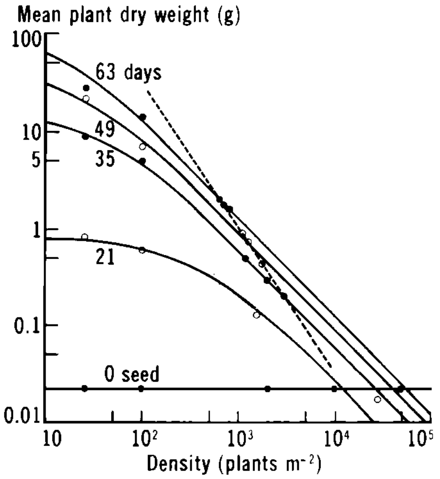

FIGURE 5. A characterization of the reciprocal yield law (solid lines) and the 3/2 power law (dashed line) for the mean plant dry weight of variable density populations of buckwheat (*Fagopyrum sagittatum*) as they develop in time (Yoda and others 1963).

and the 3/2 power law by a broken line. Each of six density regimes is represented by five points. The less dense plots do not decrease in density over time, as do the plots with high initial densities. Sufficient mortality occurs so that the points fall either close to or below the broken line which represents the 3/2 power law. Thus, the reciprocal yield law is applied to all stands, even though competition-induced mortality is occurring.

Initially, a plantation develops virtually free of intraspecific competition during which time mortality percent is independent of density. The occurrence of competition-related mortality is limited to stands meeting certain size-density criteria which are defined for *Pinus radiata* later in the discussion.

FOREST MANAGEMENT APPLICATIONS

Yield tables developed by Tadaki (1963, 1964) for *Cryptomeria japonica* allow future yields to be estimated for managed stands under various thinning regimes. Included are the full stocking line of the 3/2 power law, reciprocal curves relating mean volume to density for selected mean heights, and natural thinning curves relating density to mean volume. These latter curves are of the form:

$$1/\rho = Av + B \qquad (33)$$

Coefficients are chosen to cause the $\rho - v$ trend to become tangent to the full stocking line, but the mortality data used to justify these trends are very limited. Sample thinning regimes were constructed on the assumption that thinnings from below do not alter the relationships expressed by the reciprocal equation. Thinnings were simulated when stand densities reached 30, 50, and 70 percent of the full density for their mean volumes. Mortality after thinning was assumed to correspond with the natural thinning curves for stands with the same mean volume and density. The results were not, however, subjected to validation with real data, and Tadaki (1963) concluded that "this method must be further discussed and improved in the future."

Ando (1968) constructed yield tables and density control diagrams, which related height, diameter, volume and density to each other, for *Cryptomeria japonica*, *Chamaecyparis obtusa*, *Pinus densiflora*, and *Larix leptolepis*. These included thinning regimes based on maintaining a fixed percentage of the full stocking yield for a given height. The *A* and *B* coefficients of the reciprocal equation (equation 29) were expressed as functions of height. Separate control diagrams were recommended for different districts, but average diagrams were presented for each species. No solid statistical justification is given for using the individual district diagrams rather than the average diagram.

Aiba (1975b) devised a similar density control diagram for *Cryptomeria japonica* plantations which can be used to construct thinning regimes and also to estimate the future yields of stands for density-volume combinations outside the scope of the reciprocal yield law. While stands with lower densities due to either heavy thinning or high natural mortality were not used by Aiba in the construction of the reciprocal curves, the resulting equations can project the growth of these stands.

AN APPLICATION OF JAPANESE THEORIES TO *Pinus radiata* PLANTATIONS

The Japanese theories concerning yield-density relationships, which were discussed earlier, are applied to permanent sample plot data from unthinned New Zealand plantations of *Pinus radiata*[1] in order to give a comprehensive example of their use and to test the adequacy of the equations. The same data had previously been analyzed and reported by Bailey (1972) and used by Clutter and Allison (1974). Measurement of most of the 54 plots used was begun in 1925 at age 6 and repeated at ages 7, 16, 19, and 23 with annual measurement from age 23 to 39 or 40. A major infestation by the wood wasp *Sirex noctilio* Fabr. began in 1946. At each measurement, diameters at breast height (DBH) were tallied and sufficient heights taken to calculate mean stand height (H) and predominant mean height (H_D). The latter is the mean of the heights of 40 trees, each the tallest on its 1/40th of an acre (0.010 ha).

Calculation of plot volumes was based on the work of Lewis (1954) and Beekhuis (1966). Lewis developed a stand volume/basal area ratio as a function of height which was mathematically described by Beekhuis as a stand volume equation estimating volume (V) to basal area (BA) as a function of top height (or site height). That this relationship might prove to be largely unaffected by density was suggested by Beekhuis and verified by Fenton and others (1968). Top height closely approximates predominant mean height and "for most purposes (they) may be considered synonymous" (Beekhuis 1966). Beekhuis' volume equation can be expressed in metric units with a substitution of H_D for H as:

$$V/\mathrm{BA} = 0.9144 + 0.3\,H_D \qquad (34)$$

Figure 6 shows all of the data in terms of mean tree volume and density expressed as trees per hectare, with lines representing the history of selected single plots and the shaded area representing the general range and trends for all data. The maximum size-density relationship for this data is shown by the heavy line with a slope of –3/2 positioned immediately above the scatter of plot data (Fig. 6) and is described by:

$$\ln(v) = 10.08 - 3/2 \ln(\rho) \qquad (35)$$

There is an obvious indication that the plots were developing rapidly toward some upper limit but fell away from it soon after the onset of the *Sirex* attack. High mortality continued for approximately 16 years and then subsided, allowing the plots to once again approach this maximum size-density relationship. An independent approximation of the maximum size-density relationship is provided by data from *P. radiata* plantation spacing trials of the New Zealand Forest Service at Tarawera[2] (Fig. 7). In the average size-density trends for four spacings ranging

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[1] Data provided by A. W. Grayburn, New Zealand Forest Products Limited.

[2] Data was provided by Ryde James, of the Forest Research Institute, New Zealand Forest Service.

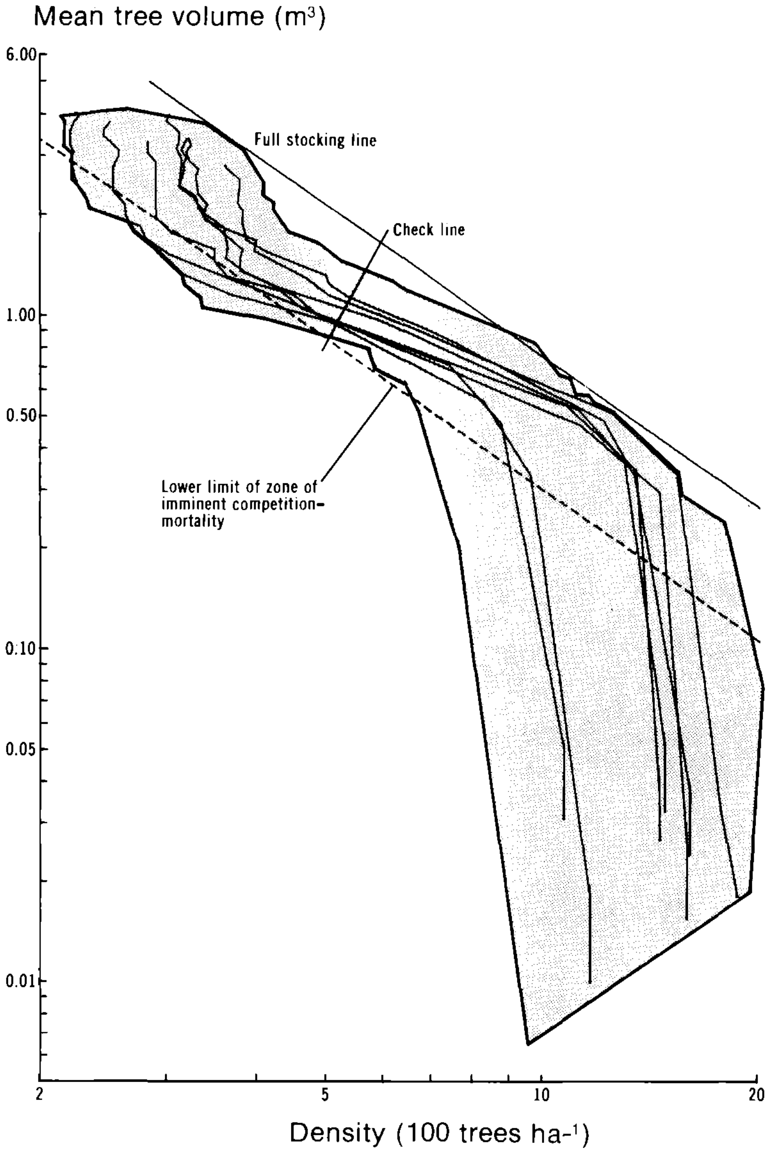

FIGURE 6. *Pinus radiata* plot data with the upper stocking line and the lower limit of the zone of imminent competition-mortality indicated.

from 1328 to 5312 stems per hectare, the upper line is not meaningfully different from that constructed from the plots in our original data which were generally at lower densities. The Tarawera plots with high initial densities are reaching the full stocking condition, whereas plots with lower initial densities are experiencing a small amount of competition-induced mortality but have yet to reach a maximum size-density condition.

We define a zone of imminent competition-mortality as the region above the lower line in Figure 6 where density can substantially affect mortality. The lower limit is described by:

$$\ln(v) = 9.16 - 3/2 \ln(\rho) \qquad (36)$$

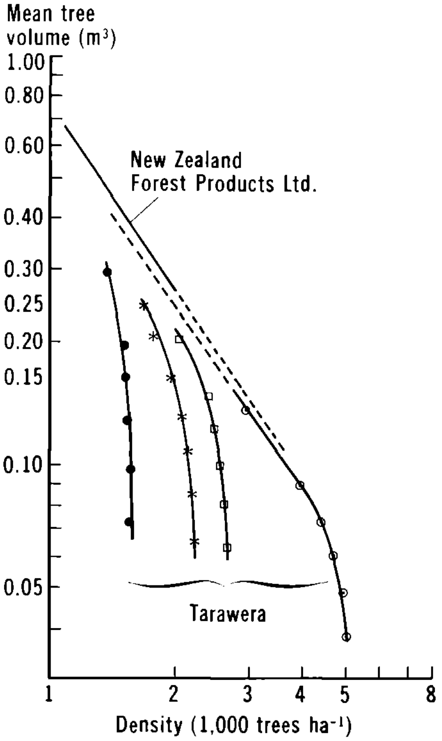

FIGURE 7. The maximum size-density relationship for *Pinus radiata* established from N. Z. Forest Products Ltd. data and stand development patterns at Tarawera at four spacings.

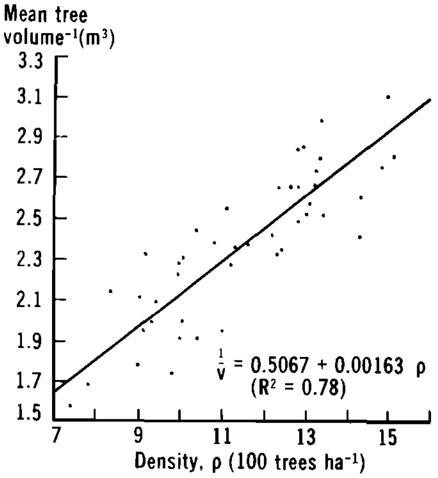

FIGURE 8. The reciprocal yield equation at a predominant mean height of 25 meters.

The lower bound of the zone of imminent competition-mortality was drawn parallel to the upper stocking line and immediately below the onset of significant mortality for most of the plots. Within this zone mortality may be related to competition, whereas below it mortality is independent of density. Competition-related mortality may be due to any causal agent (Spurr 1962). The position of the lower boundary is not exactly known. Three of the plots in Figure 6 had yearly mortality exceeding 5 percent before reaching the defined lower bound of the zone of imminent competition-mortality. Whether this is related to density cannot be determined.

Next, the competition-density relationship expressed by the reciprocal yield equation (29) was fitted to the data and the coefficients related to mean height (equa-

TABLE 1. A *and* B *coefficients of the reciprocal yield equation for selected heights.*

H_D (m)	Number of data points	R^2	$A \times 1000$	B
15	15	0.31	2.90	3.86
20	11			
25	47	.78	1.63	.51
30	47	.81	1.24	.41
35	54	.64	1.03	.33
40	54	.45	.85	.22
45	48	.56	.77	.12

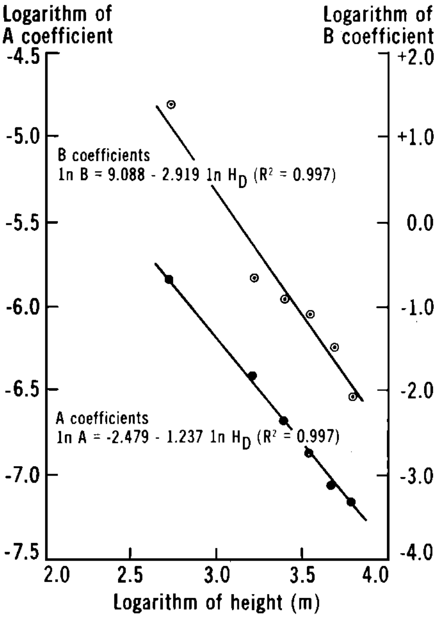

FIGURE 9. The A and B coefficients of the reciprocal yield equation at selected heights for *Pinus radiata*.

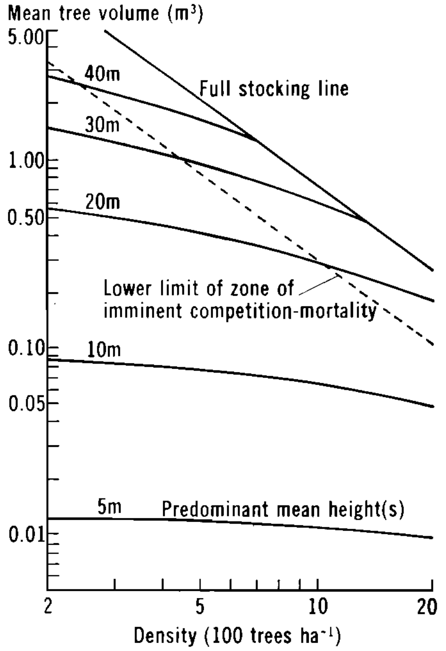

FIGURE 10. A graphical representation of the *Pinus radiata* growth model with mean tree volume expressed as a function of the logarithms of density and predominant mean height.

tions 31 and 32). Since estimates of mean tree volume and density at particular ages or heights were needed, the data sets for each plot had to be interpolated. Second degree polynomial splines were fitted to height, density, and volume data for each plot. Their intercepts with the desired age or height line were then calculated. By restricting interpolation to periods of not over 4 years, the number of data points was reduced and errors minimized. For each set of points obtained by this method the reciprocal of mean volume ($1/v$) was regressed against density (ρ). An example is shown in Figure 8 where each point represents a stand with a mean height of 25 meters. Similar regressions were performed for several heights and ages, and the constant height relationships were found to be consistently better than the constant age relationships, as suggested by Ando (1962). Reciprocal equation regressions were developed for heights from 15 m through 45 m (Table 1). Below 15 m, slopes of the regressions were not significantly different from zero at the 95 percent confidence level; the 20 m height class was omitted due to insufficient sample points; and, for the 25 m height class, longer interpolation periods were allowed in order to increase the number of data points. Figure 9 shows the log-log relationships of A and B against predominant mean height. These relationships are equivalent to:

$$A = 0.08383\, H_D^{-1.2368} \qquad (37)$$

$$B = 8849\, H_D^{-2.9186} \qquad (38)$$

The coefficients of these equations are of the same order of magnitude as reported by Ando (1962) for other conifer species. The resulting competition-density relationships are presented in Figure 10.

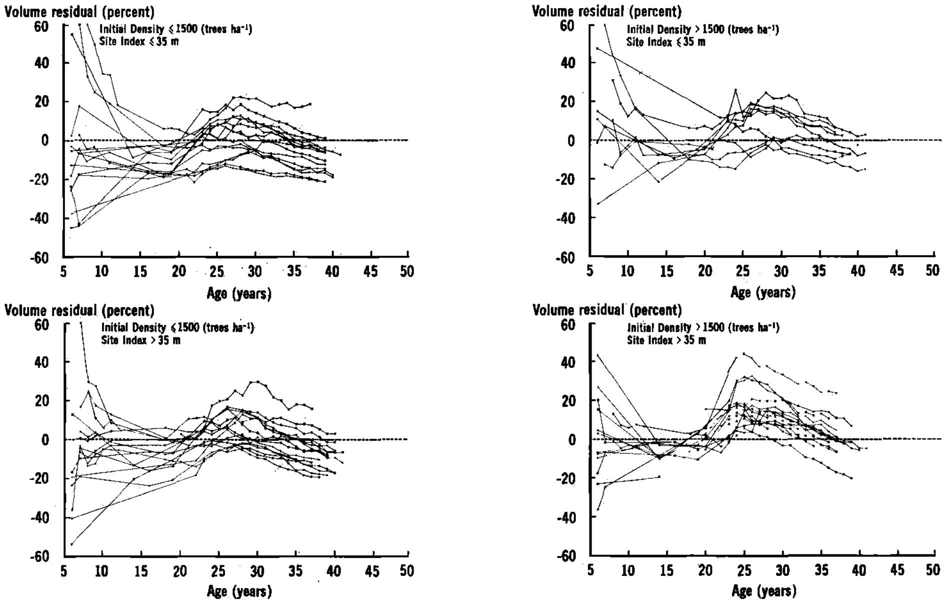

FIGURE 11. Volume residuals (percent) for mean tree volume estimated from predominant mean height and current density for four combinations of initial density and site index. Site indices are based on age 25.

There has been concern that the upper stocking line can vary with initial planting density, and it has been suggested that low initial densities may lead to high upper stocking lines.[3] To examine this concern, we regressed density at the check line shown in Figure 6 against plot variables that included initial density, aspect, elevation, and several soil characteristics. The check line had been drawn perpendicular ($\ln v = 33.136 + 5.9296 \ln \rho$) to the volume/density trends in a region where these trends were essentially parallel to one another on the assumption that differences in maximum stocking would be evident there.

No regression line could be generated at the 95 percent confidence level, even though there was a positive correlation between density at the check line and initial density; the correlation could explain only 5 percent of the variation in the former value. This demonstrated weakness of the correlation is more important than whether high initial density causes a slightly higher or lower upper stocking line.

Residuals from estimated mean tree volumes—predicted from predominant mean height and current density—for 53 plots were portioned into 4 subsets according to site and initial density (Fig. 11). Then for each plot percent error in the estimation of mean tree volume was computed for different points in time. Positive residuals correspond to overestimates. Though the estimation errors appear to be large, it should be recognized that:

(i) at young ages there is almost no correlation between mean volume and density, so the scatter at age 6 is purely random variation and is to be expected.

(ii) although only four coefficients (equations 37, 38) were used, the magnitude of the volume estimates is approximately correct over a range of mean tree volumes from 0.005 to 5.0 m^3.

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[3] Mitchell, Kenneth J., in Forest Ecology Workshop presentation, Durham, N. C., December 1975.

TABLE 2. Predicted yields for initial densities of 800 and 1500 trees per hectare at site indices 34.1 and 39.7 meters.

SITE INDEX 34.1 m at base age 25
(80 feet at age 20)

Initial density 800					Initial density 1500				
Age	DBH (cm)	H_D (m)	V (m^3/ha)	ρ (trees/ha)	Age	DBH (cm)	H_D (m)	V (m^3/ha)	ρ (trees/ha)
6	9.9	6.4	17	800	6	9.3	6.4	29	1500
12	22.2	16.8	180	780	12	18.8	16.8	241	1463
18	28.4	25.7	415	761	18	25.5	25.7	464	1056
24	34.2	33.0	608	614	24	34.2	33.0	608	614
30	41.6	39.1	730	426	30	41.6	39.1	730	426
36	48.0	44.3	833	325	36	48.0	44.3	833	325
42	53.5	48.7	924	264	42	53.5	48.7	924	264

SITE INDEX 39.7 m at base age 25
(95 feet at age 20)

6	13.4	8.8	40	800	6	12.2	8.8	63	1500
12	25.4	21.0	286	780	12	20.9	21.0	361	1463
18	31.5	30.8	564	712	18	31.5	30.8	564	712
24	40.9	38.5	719	438	24	40.9	38.5	719	438
30	48.7	44.9	846	316	30	48.7	44.9	846	316
36	55.3	50.2	954	249	36	55.3	50.2	954	249
42	61.0	54.7	1047	207	42	61.0	54.7	1047	207

Two obvious biases are an underestimate of growth beyond age 30 for most of the plots and underestimates of final yield on the plots with low initial densities. The difference in residuals between plots with high and low initial densities shows a bias which is to be expected in the reciprocal yield law (equation 29), because its derivation assumes density is constant over time.

However, substantial changes in density occur in the zone of imminent competition-mortality. For two stands at similar stages of development (same dominant height), with one subject to competition mortality, but the other at a lower density and therefore not manifesting such mortality, certain differences can be expected. The trees of the denser stand will be growing at slower rates, as described by the reciprocal equation of the competition density effect, and if mortality occurs so that the stands arrive at the same density level, the remaining trees will have smaller mean volumes than the trees in the originally less dense stand. The reciprocal yield law, which does not take mortality into account, would not recognize this and would estimate equal mean tree volumes for the two stands. Ando (1968) assumed that any thinning from below, either natural or artificial, would change density and mean tree size in such a way as not to invalidate the reciprocal equation. However, Aiba (1975a) in examining data from plantations immediately after thinning concluded that the reciprocal equation could not adequately account for the effects of thinning. The same conclusion can be drawn for naturally thinned stands after examining the biases in Figure 11. The reciprocal equation should be modified to incorporate the effect of different past densities on current mean tree volume.

Sample yield tables are presented in Table 2; they incorporate the maximum size-density relationship (equation 35), the reciprocal yield coefficient relationships (equations 37 and 38), and site curves from Bailey and Clutter (1974). No density dependent errors were discernible in the site curves. Mortality was assumed to be

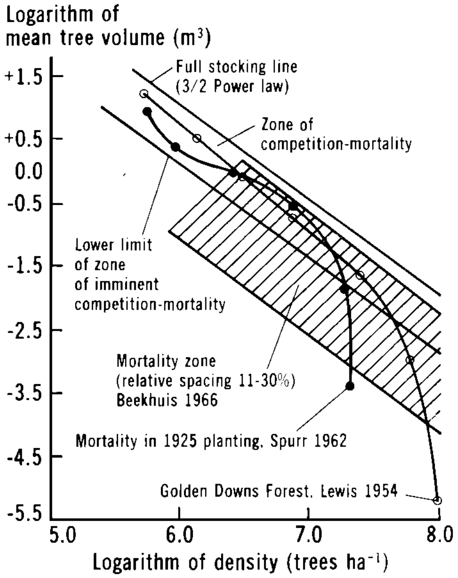

FIGURE 12. A comparison of estimated density dependent mortality trends for *Pinus radiata.*

0.42 percent per year until the plots reached the middle of the zone of imminent competition-mortality. Stand parameter estimates in this multiple-density yield table are of the same order of magnitude as the mean results presented by Lewis (1954) and Spurr (1962).

THE MODEL'S UTILITY

The early yield table for unthinned *Pinus radiata* by Lewis (1954) relied on a graphical description of the gross trends in permanent plots; whereas Spurr (1962) went one step further and characterized the relationship between growth rate and mortality. Spurr observed "that trees destined to die in a given year invariably declined in annual basal area increment over at least the 12 years prior to their death. . . . When their annual basal area increment dropped below 0.02 sq. ft. (18.6 cm^2), trees on the average had eight years to live regardless of the actual cause of death." This recognition that competition eventually leads to certain mortality is also found in the maximum size-density relationship. A further advantage of the maximum size-density relationship is that it reflects the species potential, whereas with Spurr's (1962) empirical approach, the temporary reduction in density due to *Sirex* has become embodied in a yield table which continues to underestimate net yields even though *Sirex* is under control.

Beekhuis (1966) recognized that mortality due to *Sirex* was abnormal and should not be incorporated in future yield projections. However, his relative spacing method of estimating maximum density for a given mean stand height could not be verified since ". . . none of the plots . . . have yet reached the stage at which they maintain a constant maximum density . . ." (Beekhuis 1966). Bailey (1972) and Clutter and Allison (1974) developed relationships for survival percent as functions of age. Other flexible mathematical models were used to describe many stand parameters, but little attempt was made to describe stand condition that might exist if planting densities had been greatly different or if the *Sirex* outbreak had not occurred. Our zone of imminent competition-mortality is compared with a similar zone defined by Beekhuis (1966), and local yield tables by Lewis (1954) and Spurr (1962) in Figure 12.

The model which we have presented is not the best possible characterization of the test data set, but it is a biologically derived model which can aid in the understanding of the interaction between the stand parameters of age, height, density, and mean volume.

RECOMMENDATIONS

Plantation development can be viewed in terms of the fundamental concepts of competition and self-thinning presented here. The reciprocal equation, the full stocking line and the zone of imminent competition-mortality, or refinements of these relationships, can be used in identifying the density-related growth and mortality characteristics of a species. Experimentation can be directed towards the early determination of the coefficients for these models; for example, high density stands can be planted to quickly determine the full stocking line. The use of these simple models will aid in the prediction of yield for situations that are rapidly changing through the application of genetics and refined silvicultural practice.

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