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Development and Field Application of Density Management Diagrams and Size-Density Surface Models Developed for the Boreal Mixedwood Stands of Ontario

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ABSTRACT

This instructional booklet describes the construction and interpretation of the density management diagram (DMD) and the size-density surface model. These two models assist forest managers to better understand mixedwood stand development, and provide an aid for the planning of thinning prescriptions in boreal Ontario.

The DMD is an age independent, average stand mortality model that predicts the structural development of fully stocked natural stands. This model has been used previously for mixed-species stands, although it is better known for even-aged, single-species stands where the maximum plant size-density relationship is based on the $-3/2$ power rule (or law) of self-thinning.

This concept has been expanded in the surface model to enable multispecies stand development and interspecific competition to be followed. The surface model illustrates the relationship between plant size and density for all possible combinations of two dominant tree species. Examples are provided to assist the user in interpreting the models in black spruce (*Picea mariana* [Mill.] B.S.P.)-jack pine (*Pinus banksiana* Lamb.) stands.

The models will assist forest managers in facilitating management and habitat maintenance planning strategies. The utility of the surface is discussed in relation to stand development, and examples are provided to illustrate the effect of silvicultural treatments on stand structure.

RÉSUMÉ

L'auteur présente deux modèles destinés à aider les gestionnaires forestiers à mieux comprendre le développement des peuplements mixtes et à planifier les éclaircies dans la région boréale de l'Ontario : le diagramme de gestion de la densité et le modèle de surface taille-densité.

Le diagramme de gestion de la densité est un modèle de la mortalité moyenne des peuplements qui sert à prévoir le développement structurel des peuplements naturels de densité adéquate. Ce modèle a déjà été utilisé pour les peuplements mixtes quoiqu'il est mieux connu

pour les peuplements monospécifiques équiennes où le rapport maximal taille-densité des plantes répond à la règle (ou loi) d'autoéclaircie (dite de la puissance $-3/2$). Ce concept a été élargi dans le modèle de surface pour permettre de suivre le développement des peuplements plurispécifiques et la compétition interspécifique. Ce modèle montre le rapport entre la taille et la densité des plantes pour toutes les combinaisons possibles de deux essences dominantes. Des exemples sont fournis pour aider l'utilisateur à interpréter les modèles dans les peuplements d'épinettes noires et de pins gris.

Ces modèles aideront les gestionnaires forestiers en facilitant les stratégies de planification de la gestion et du maintien des habitats. L'utilité de la surface est discutée en fonction du développement des peuplements, et des exemples sont présentés pour montrer l'effet des traitements sylvicoles sur la structure des peuplements.

TABLE OF CONTENTS

INTRODUCTION	1
METHODS	
Database	1
Species	1
Stand Types	
Density management diagram stand types	1
Surface model stand types	2
DMD MODEL CONSTRUCTION	
Theory	2
Construction	2
SURFACE MODEL CONSTRUCTION	
Theory	4
Construction	4
INTERPRETING THE MODELS	
Example 1: A thinning prescription to modify the species composition within a stand	6
Example 2: Prediction of the development of stand structure in a multispecies stand	9
CONCLUSIONS	9
ACKNOWLEDGMENTS	9
LITERATURE CITED	11

DEVELOPMENT AND FIELD APPLICATION OF DENSITY MANAGEMENT DIAGRAMS AND SIZE-DENSITY SURFACE MODELS DEVELOPED FOR THE BOREAL MIXEDWOOD STANDS OF ONTARIO

INTRODUCTION

Two models that would assist forest managers to better understand mixedwood stand development, and to provide an aid in planning thinning prescriptions are the density management diagram (DMD) and the size-density surface model. This instructional booklet describes their construction and interpretation.

The DMD is an age independent, average stand mortality model that predicts the structural development of fully stocked natural stands. This model has been used previously for mixed-species stands, although it is better known for even-aged, single-species stands where the maximum plant size-density relationship is based on the $-3/2$ power rule (or law) of self-thinning. This concept has been expanded in the surface model to enable multispecies stand development and interspecific competition to be followed. The surface model illustrates the relationship between plant size and density for all possible combinations of two dominant tree species within a stand.

METHODS

Database

Five data sources were used to construct a representative mixedwood database for boreal Ontario. Data for four of the sources came from permanent sample plots containing remeasurement data. These are commonly known as the American Can (James River-Marathon Ltd.), Boise-Cascade (now known as Stone-Consolidated Corporation), Kimberly-Clark (of Canada Ltd.), and Spruce Falls (Power and Paper Company Ltd.) data sets. The Ontario Ministry of Natural Resources (OMNR) provided access to data from temporary sample plots located in the Geraldton region of northwestern Ontario.

As all five data sets varied in structure, a different method of assembly was required for each. All stems with a diameter equal to or greater than 2.54 cm were used. Where required, height values were estimated using a modified Chapman-Richard's function and total stem volume values were estimated using the standard volume equations of Honer et al. (1983). All analyses were undertaken using SAS¹ software. The main characteristics of each data set are summarized in Table 1.

Species

The main species considered in this study were balsam fir (*Abies balsamea* [L.] Mill.), black spruce (*Picea mariana* [Mill.] B.S.P.), jack pine (*Pinus banksiana* Lamb.), and trembling aspen (*Populus tremuloides* Michx.). Additional species included the softwoods: cedar (*Thuja occidentalis* L.), larch (*Larix laricina* [Du Roi] K. Koch), and white spruce (*Picea glauca* [Moench] Voss), and the hardwoods: balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyifera* Marsh). Hereafter, balsam fir, black spruce, jack pine, and trembling aspen will be referred to as fir, spruce, pine, and aspen, respectively.

Stand Types

Density management diagram stand types

Stand density management diagrams were developed for six mixedwood stand types. These were further divided into pine-spruce and pine-aspen-spruce, and three stand structures for each stand type were used. Structures, based on three different species combinations (per stand type), were expressed as a percentage of the basal area that each species contributed to the stand. The three pine-spruce

Table 1. Data set characteristics for five data sources.

Plot type	American Can	Boise-Cascade	Kimberly-Clark	MNR-Geraldton	Spruce Falls
	Permanent	Permanent	Permanent	Temporary	Permanent
Number of plots	185	1 255	118	416	85
Number of measurements	2-6	1-3	2-10	1	1-12
Density (stems ha ⁻¹)	482-11 009	<100-1 470	<100-2 543	<100-22 456	418-23 762

¹Statistical Analysis Systems (SAS) Institute Inc., Cary, NC. 27513.

structures were 25:75, 50:50, and 75:25. The three aspen-pine-spruce structures were 20:20:60, 30:30:40, and 60:20:20. To ensure that sufficient data were present for each stand type an allowable range of ± 5 percent was set for basal area values for all stand types. For example, the 25:75 pine-spruce stand structure represented a range of basal areas from 20 to 30 percent pine and from 70 to 80 percent spruce. For any one stand the sum of the basal area values typically fell between 90–100 percent of the total, with lesser species making up the difference.

Surface model stand types

Four mixed-species stand types were used. Three of these were dominated by two species and the fourth was comprised of a multispecies mixture. The species mixtures were fir-spruce, pine-spruce, aspen-spruce, and pooled hardwood and pooled softwood species. Additional stand types were considered, for example fir-aspen and aspen-white spruce, but these provided insufficient data for development of a model.

DMD MODEL CONSTRUCTION

Theory

The DMD is a powerful age and (mostly) site independent, natural mortality model. Ample empirical evidence exists to support a general relationship between plant size and density for fully stocked stands undergoing intraspecific, density-dependent mortality (White 1981). Although this model has been used primarily for even-aged, single-species stands, it has been extended to enable an investigation of mixed-species stands.

Binkley (1984) used the DMD model to examine Douglas-fir (*Pseudotsuga menziesii* [Marb.] Franco)-red alder (*Alnus rubra* Bong) stands in the northwestern United States and British Columbia. In addition, Sterba and Monserud (1993) produced a model for several species combinations using data sets from northern Idaho and northwestern Montana. In this case, the number of species within the stands ranged from two to eight. Another example of the multispecies DMD approach, using species-averaged parameters, was published by Kohyama (1992). The simulated tree density-mean tree size trajectories given for three warm temperate species in a multispecies stand were similar to those reported for even-aged monocultures. Furthermore, the upper boundary of the size-density trajectories did not change when recruitment from seedlings was taken into account. In a simulation of a multispecies system they showed the same density-size dynamics in terms of total yield as did a species-averaged system, but not in terms of each species cohort.

The DMD is based on the plant size-to-density relationship. The best expression that relates these variables is the following equation:

$$v = K\rho^\alpha \quad [1]$$

where: v = mean plant size;
 α , K = constants; and
 ρ = stand density.

Using log transformed axes and assuming the theoretical slope of -1.5, the equation can be rewritten as:

$$\ln(v) = K - 1.5 \times \ln(\rho) \quad [2]$$

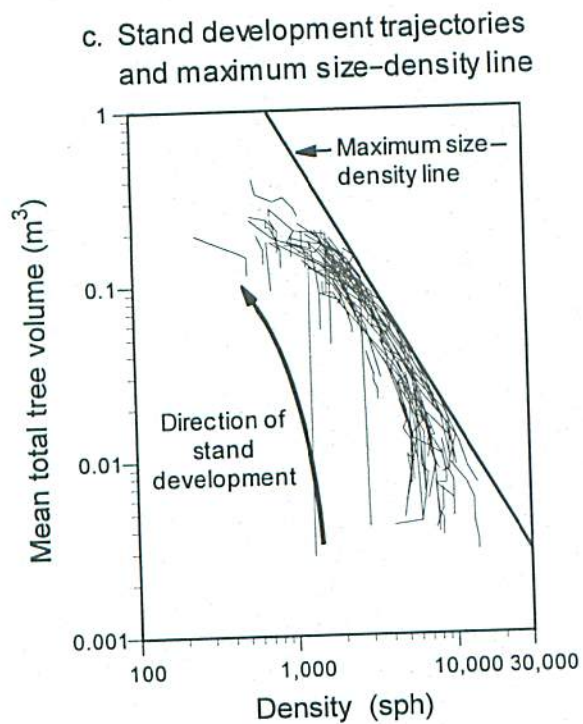
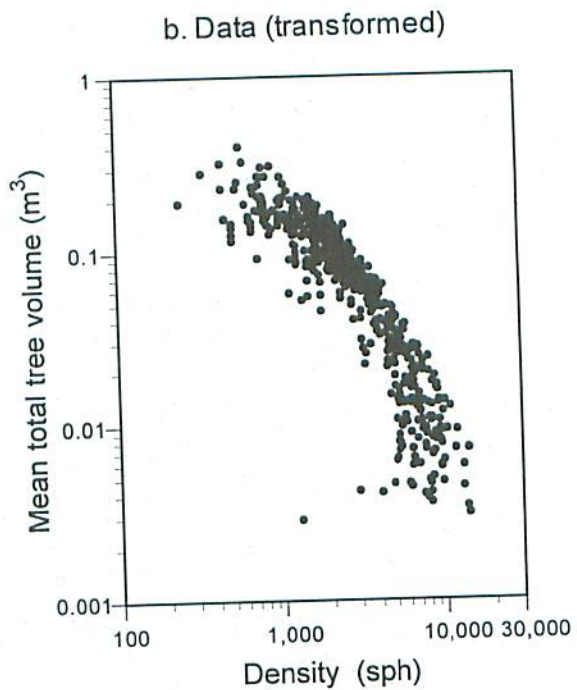
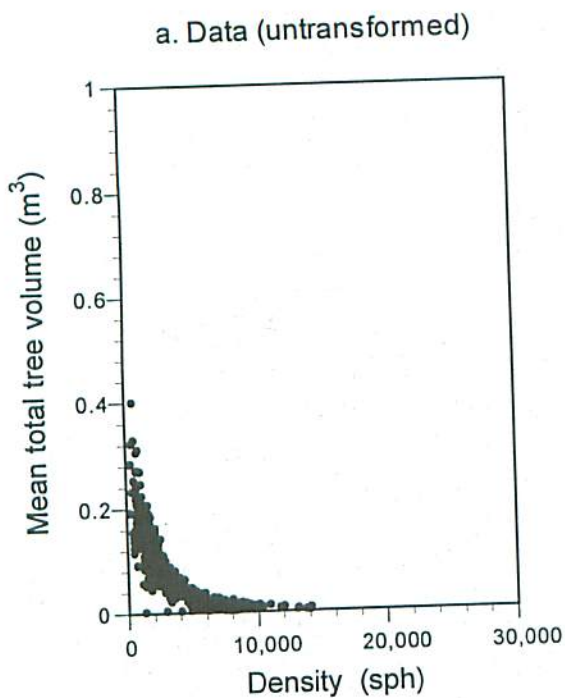
where: \ln = natural logarithm; and
 K = y intercept.

This equation relates the reciprocal changes in density to size and is commonly known as the -3/2 power rule (or law) of self-thinning. However, the opinion of White (1981), and others who support the rule, is that the equation represents only a very general relationship. For those that use the DMD model and accept that it is an average, stand-level model where local variations are to be expected, it is regarded as one of the most useful tools available to the forester for making decisions about stand density (Puettmann et al. 1993).

Construction

Data were first plotted in a scattergram using the DMD format, i.e., plant size variable (mean total tree volume) on the dependent axis (y-axis) and stand density on the independent axis (x-axis), as shown in Figure 1a. The negatively correlated relationship between plant size and density becomes apparent after the axes are transformed using natural logarithms (Fig. 1b). By joining the baseline and subsequent remeasurement data for each stand to create separate stand development trajectories, the self-thinning nature of stand development becomes apparent (Fig. 1c).

To fit the maximum size-density line a subset of the data was used. Density data were logarithmically transformed and sorted into density classes of 0.1 stems per hectare. Within each density class the maximum total stem volume was determined with species-independent values. Equation 2 was then calibrated using the reduced data set. The model therefore defines the maximum upper boundary for any combination of plant size and density. This model, known as the "biological" maximum size-density line, was assigned a relative density (r.d.) of 1.00 (Fig. 1d). Three additional and parallel lines were then fitted: the mortality initiation (r.d. = 0.55), the maximum stand production initiation (r.d. = 0.40), and the crown closure lines (r.d. = 0.15). The relative density values were taken



d. Basic concepts of the density management diagram

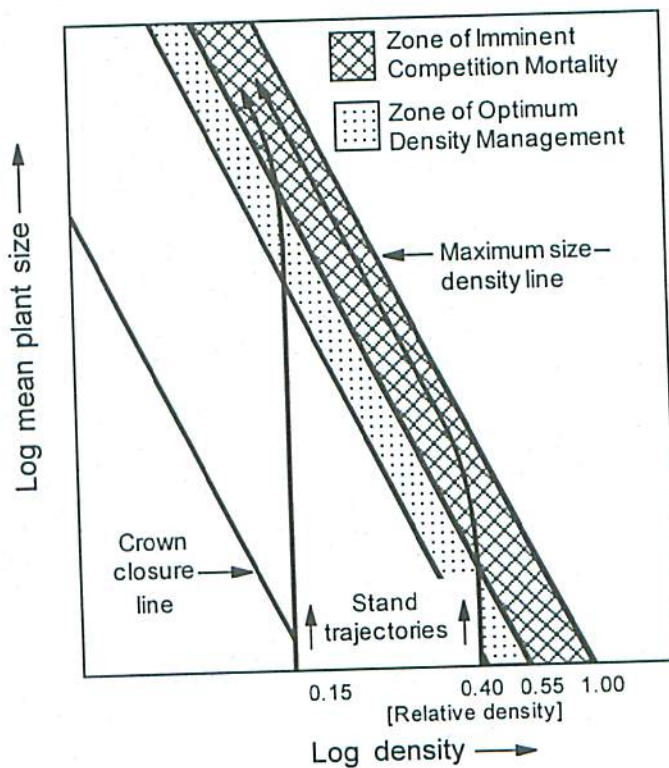


Figure 1. Calibration of the density management diagram using data from pure stands of black spruce. Shown are untransformed data (a); transformed data (b); stand trajectories and the fitted 'biological' maximum size-density line (c); and the basic concepts of the density management diagram (d).

from Langsaeter (1941) and were not determined empirically here. The zone between the maximum size–density and mortality initiation lines is known as the Zone of Imminent Competition Mortality (ZICM). The zone between the mortality initiation and maximum stand production initiation lines is known as the Zone of Optimum Density Management (ZODM).

SURFACE MODEL CONSTRUCTION

Theory

Size–density surface models have appeared sporadically in the literature over the last decade. McFadden and Oliver (1988) provided an example of a generic model for single forest tree species by relating stand age, density, and mean plant size. A rigorous mathematical treatment for models of this type was provided by Burrows (1991). Watkinson (1985) employed a different format to model two herbaceous species and used the surface model to relate density and size using densities for both species as independent axes and plant size as the dependent variable.

Age is not required to fit the surface model, and in mixed-species stands it can be difficult to determine. The surface models discussed in this paper relate density, tree size, and species composition. This format is an extension of the DMD model, and was first reported by Puettmann et al. (1992). These authors examined mortality in pure and mixed stands of Douglas-fir and red alder. The species composition variable defined by one of the independent axes is somewhat unusual. This axis comprises two juxtaposed linear axes that represent the varying proportions of two species within a stand, with each axis having an opposite trajectory to the other. The scale represents the percentage (0–100) that each species contributes to the total stand basal area. The surface models reported here differ from the Puettmann et al. (1992) format in that the plant size variable is mean total tree volume and not quadratic mean diameter.

Construction

For each stand type three separate data sets characterized the full range of stand conditions:

1. Species A - pure stand
2. Species B - pure stand
3. Species A, B - mixed stand

Table 2 summarizes the data for pure and mixed stands of black spruce and jack pine.

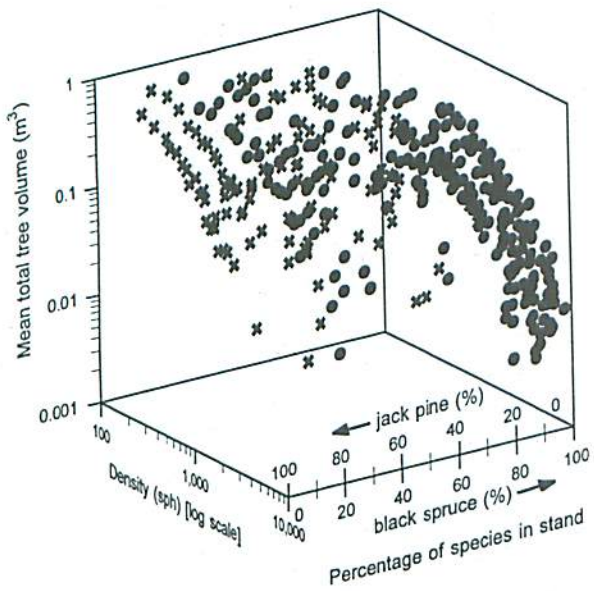
For pure stands, a lower limit of 80 percent was set as the minimum basal area contribution of the dominant species to the total basal area for the stand. In addition, many of the stands in this study had a minor proportion of other species present (<20 percent of the total), but they were not considered to have a significant influence on stand development. For mixed stands, both species had to be present and their basal areas when combined were required to constitute more than 80 percent of the total plot basal area. The contribution of each species ranged from 20 to 80 percent of the total. These data sets, when combined, covered the full range of potential stand conditions that could exist in that particular stand type, and were based as a percentage of the basal area that each species contributed to the total stand basal area.

The data from the three data sets were then combined and a density–species composition matrix was created based on density class (100 stems per hectare intervals) and species composition (5 percent basal area intervals). Within each cell of the matrix the species-independent maximum total stem volume was determined. A scattergram of this reduced data set for pine–spruce stands is shown in Figure 2a. The size–density surface model was then fitted using a distance weighted least squares algorithm (Fig. 2b) and the direction of stand development is shown in Figure 2c. Each patch of the surface required a weighted quadratic multiple regression on all the points. This method produces a locally weighted three-dimensional surface using an algorithm after McLain (1974). Unlike linear or low order polynomial smoothing, however, the surface is allowed to flex locally to better fit the data. The amount of flex of the surface is controlled by a tension parameter that is related inversely to the number of data observations.

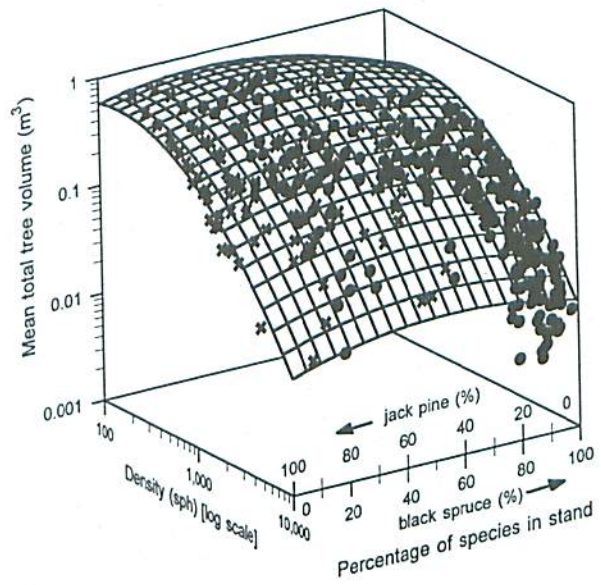
The maximum size–density line of the DMD is equivalent to the slope of the size–density surface model. The surface therefore represents the maximum size–density relationship only. The relationship between the DMD and the surface model is shown in Figure 3.

Table 2. Data for pure and mixed stands of black spruce and jack pine.

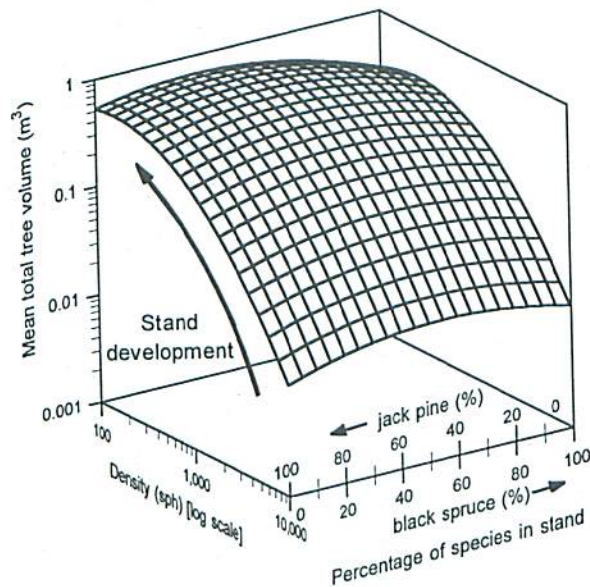
	Black spruce	Mixed	Jack pine
Number of stands	84	451	592
Number of measurements	584	1 936	1 273
Density (stems ha ⁻¹)	247–9 909	103–7 057	103–9 612
Basal area (percentage of total)	81–100	20–79	81–100



a. Model calibration data for black spruce and jack pine



b. Fitting the surface model



c. Fitted surface model

Figure 2. Procedure for preparing data and model fitting for the size–density surface model. The model was fitted to combined pure and mixed stands of black spruce and jack pine. The maximum total tree volume data for spruce (*) and pine (x) are plotted by density and species composition classes (a). The surface model is then fitted (b), and the surface model, minus the data, is shown in (c). The arrow indicates the direction of stand development.

INTERPRETING THE MODELS

Example 1. A thinning prescription to modify the species composition within a stand

Pukkala et al. (1994) reported in a Finnish study that yields from mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* [L.] Karst.) could be higher than from pure stands of either species. This favorable result was due to good management practices based on an

understanding of stand dynamics. In this case, pine was actively encouraged at the beginning of the rotation and the proportion of spruce was gradually increased as the stand developed. The yield of timber from the entire rotation was shown to be greater than from comparable sites where either of the species was dominant. These authors did point out, however, that such a result was typically achievable on sites where neither species was clearly superior over the other. The theoretical basis for such a result probably lies in niche theory.

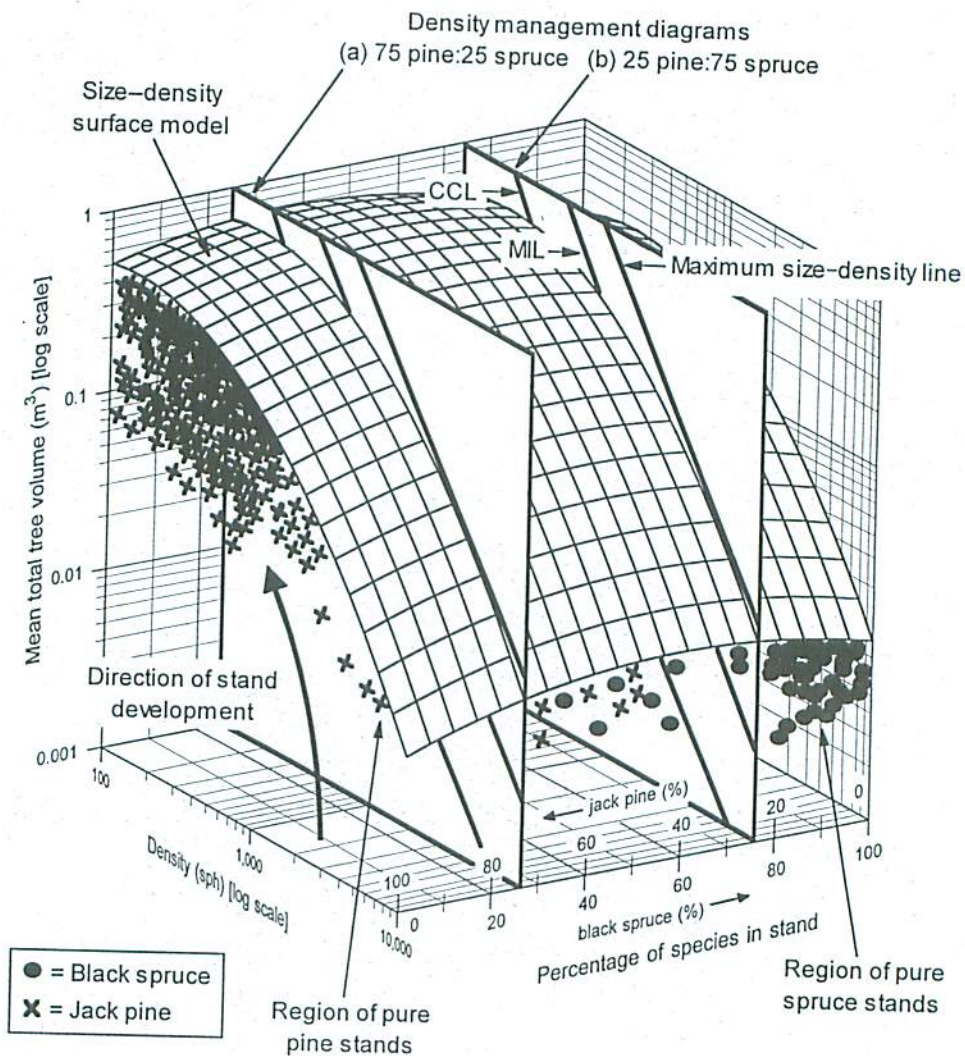


Figure 3. Relationship between the density management diagram (DMD) and the size-density surface model. Both models depict density-dependent mortality in combined pure and mixed-species stands of black spruce and jack pine. The DMDs are for 75:25 and 25:75 pine-spruce stands (ratios are percentages of total stand basal area). The maximum size-density line, the mortality initiation line (MIL), and crown closure line (CCL) of the DMD are located. The surface model represents the maximum tree size-density relationship for all possible combinations of pine and spruce. The locations of pure pine and pure spruce stands are identified. Mixed pine-spruce stands lie between the two pure stand types.

Kelty (1992) suggested a potential productivity advantage if two or more species are present at the same site, as they must use resources differently if they are to coexist. If this is indeed the case then resources are used more completely and yields can be expected to be greater than if the site was dominated by a single species. Given the findings from the Finnish study it would be desirable to know if a similar outcome could be achieved in one or more mixedwood stand types in Ontario.

The following hypothetical example is offered using a pine-spruce stand, perhaps the simplest case to illustrate the utility of the surface as once pine and spruce have become established the relative basal areas of both species remain somewhat constant throughout the development of the stand (V. Smith, pers. comm).

Two potential stand development scenarios have been plotted on the pine-spruce DMD (Fig. 4). Consider a stand

in which there is a 75:25 pine-spruce mixture (Fig. 4a). One potential trajectory of stand development is shown by the ABCF pathway. However, it has been decided that the stand structure found in a mature 25:75 pine-spruce stand is a more desirable habitat type. The forester is then requested to produce a plan that illustrates the potential stand structures for the starting and final stand conditions. In addition, a management scenario that would encourage the development of the desired structure is also required. The forester decides to thin the 75:25 pine-spruce stand by removing 50 percent of the pine (by basal area). The residual stand would then have a 25:75 pine-spruce stand structure.

The desired stand structure (25:75 pine-spruce) is shown in Figure 4b, and the target habitat zone (E) is identified. Note in the mature 25:75 pine-spruce stand that pine is the larger sized tree, although it represents only 25 percent of the basal area of the stand. The stand development pathway

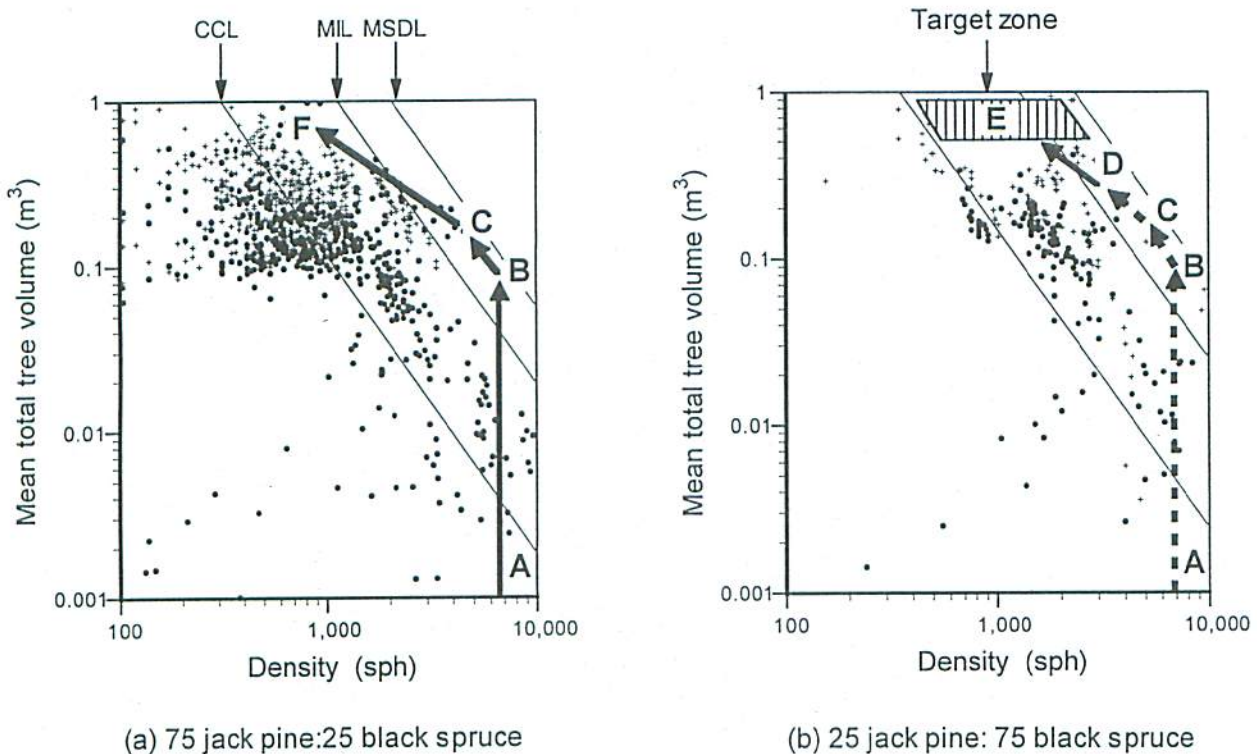


Figure 4. Density management diagrams for black spruce-jack pine stands with basal area ratios of 75:25 [pine:spruce, Fig. 4(a)] and 25:75 [pine:spruce, Fig. 4(b)]. Shown are data for spruce (•) and pine (+). Three parallel models are shown: MSDL (maximum size-density line), MIL (mortality initiation line), and CCL (crown closure line). Figure 4(a) shows the trajectory of stand development from stand establishment (A), to the beginning of density-dependent mortality (B), to the stage when a thinning is undertaken (C). If there is no thinning then the stand will grow to (F). Figure 4(b) shows the path of the entire trajectory from stand establishment to the target zone (shaded zone, E). CD represents a thinning. The solid lines indicate that the trajectory remains within a stand type, and the dashed lines indicate the trajectory within the 75:25 pine-spruce stand type (cf. trajectories in Fig. 5).

illustrating this management scenario is shown by the ABCDE pathway (Fig. 4b). The ABC pathway is the same as in Figure 4a, and the thinning treatment is shown by CD. Following the thinning the stand will likely develop naturally along the DE pathway.

The same pathway is also shown on the surface model (Fig. 5). The juvenile stage of stand development (A) is not represented on the surface. It can be assumed that there is no competition for resources until the stand reaches (B), when competition-induced mortality commences.

As time progresses less competitive and usually smaller sized individuals succumb, and mean tree size increases while density decreases. If there was no silvicultural intervention the path of stand development would most likely follow the ABCF trajectory, i.e., basal area proportions remain relatively the same throughout the development of the stand.

In addition to plotting potential trajectories of stand development, maximum stand volume and basal area estimates can be calculated for each stage of stand

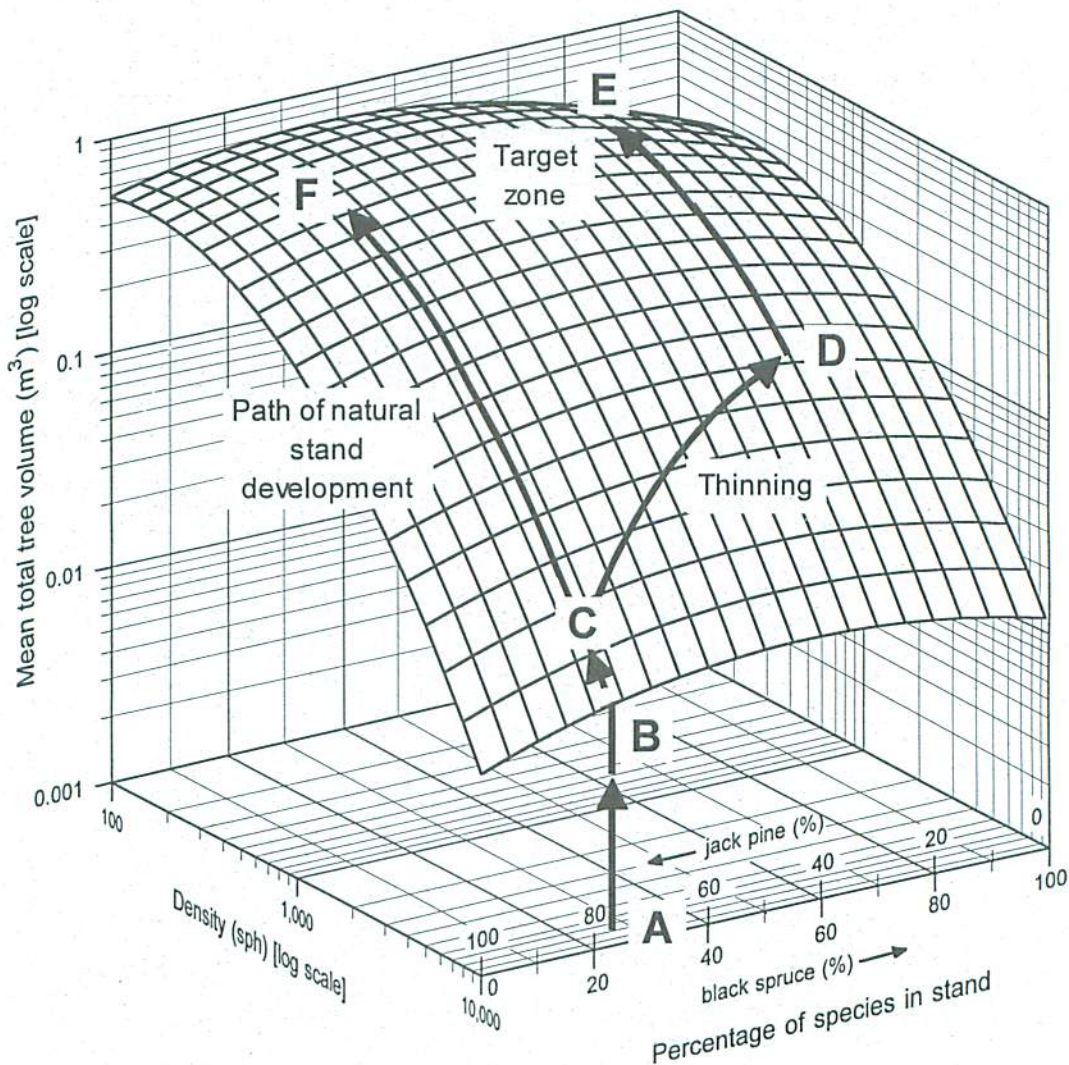


Figure 5. Size-density surface model for a black spruce-jack pine stand type. Following establishment (A) with a 75:25 pine:spruce mixture (ratios are percentages of total stand basal area), the stand commences density-dependent mortality (B), and following a period of growth two options are considered at (C). Scenario 1: leave the stand unattended, thereby allowing it to develop along the ABCF pathway. Scenario 2: undertake a thinning whereby half of the pine is removed (CD). The stand now reflects a 25:75 pine:spruce species mixture and develops toward a predetermined target zone (DE) (cf. trajectories in Fig. 4).

development. Furthermore, if a series of up to nine DMD's are included in the development of a management plan, for example 10:90, 20:80...90:10 (values are basal area percentages by stand), then stand structure information could also be determined.

Example 2. Prediction of the development of stand structure in a multispecies stand

The pine-spruce stand type is a good starting point to introduce the concept of the size-density surface model and to illustrate the trajectories of stand development. This is due to the relative species stability within this stand type; therefore trajectories can be plotted with some degree of confidence. However, for other mixedwood stand types in boreal Ontario the ability to plot trajectories, or predict stand development, is more complicated. This is due to the successional changes that many stand types undergo during their development. For example, consider the three trajectories plotted on the surface model of Figure 6.

Aspen is a common boreal species found in Ontario's mixedwood forests. Typically, aspen dominates the early stages of stand growth and then gives way to one or more softwood species during the successional development of the stand. Figure 6 is a generic surface model for Species X and Species Y. For comparative purposes the ABCD trajectory is similar to the one that would be expected in a pine-spruce stand type, as is the thinning treatment (CE) that is applied for the ABCEF pathway. Now consider that the site favors the development of aspen and either pine or spruce. Aspen grows quickly, establishes itself as the early dominant species, and suppresses the early growth of pine and spruce. As the aspen eventually dies out, thereby releasing the other two species, its dominance in the stand decreases. Then, either pine or spruce and then spruce become the dominant species as the stand matures. This being the case, the ABG pathway is the likely path of stand development; with Species X in this case being aspen, and Species Y being pine and/or spruce.

These simplified examples illustrate the utility of the density dependent mortality models presented here, but field testing is required. It is likely that the size-density surface model will be used in conjunction with the DMD. Other models may also be included at the discretion of forest and wildlife habitat managers; for example, use of an appropriate stand growth model so that volumes can be estimated with some degree of confidence. Forest and wildlife habitat managers will then have a powerful set of tools that will allow them to work toward developing successful management strategies for the boreal mixedwoods of northern Ontario.

CONCLUSIONS

The maximum size-density relationships reported here for mixedwood stands were developed by combining data for pure and mixed stands. The DMD shows the potential development of stand structure to the maximum size-density line. The surface model illustrates the maximum size-density relationship between the species and represents the full range of potential species distributions within a stand. Furthermore, the surface model acknowledges the fact that the proportion of the species in mixed-species populations changes throughout development of the stand.

The size-density surface model differs from the size-density line of the DMD in interpretation. The size-density trajectory for pure-species stands not only yields the maximum size-density trajectory or maximum size-density line, but also predicts the development of the stand toward this maximum. In mixed-species populations, however, the size-density relationship alone cannot predict the development below and along the self-thinning surface. For both pure- and mixed-species stands the development and dynamics of individual stands may vary with populations and environmental conditions, even though the initial species proportions may be similar.

The construction and interpretation of the size-density models of stand development require some effort on the part of the intended user before their utility can be appreciated. The DMD predicts the development of the stand from establishment, whereas only the maximum size-density relationship can be interpreted from the size-density surface. Both model types are average stand level models, and as a consequence discrepancies for individual stands are to be expected.

The potential utility of the size-density surface and DMD models was shown and examples were provided to demonstrate their usefulness for forest and wildlife habitat managers.

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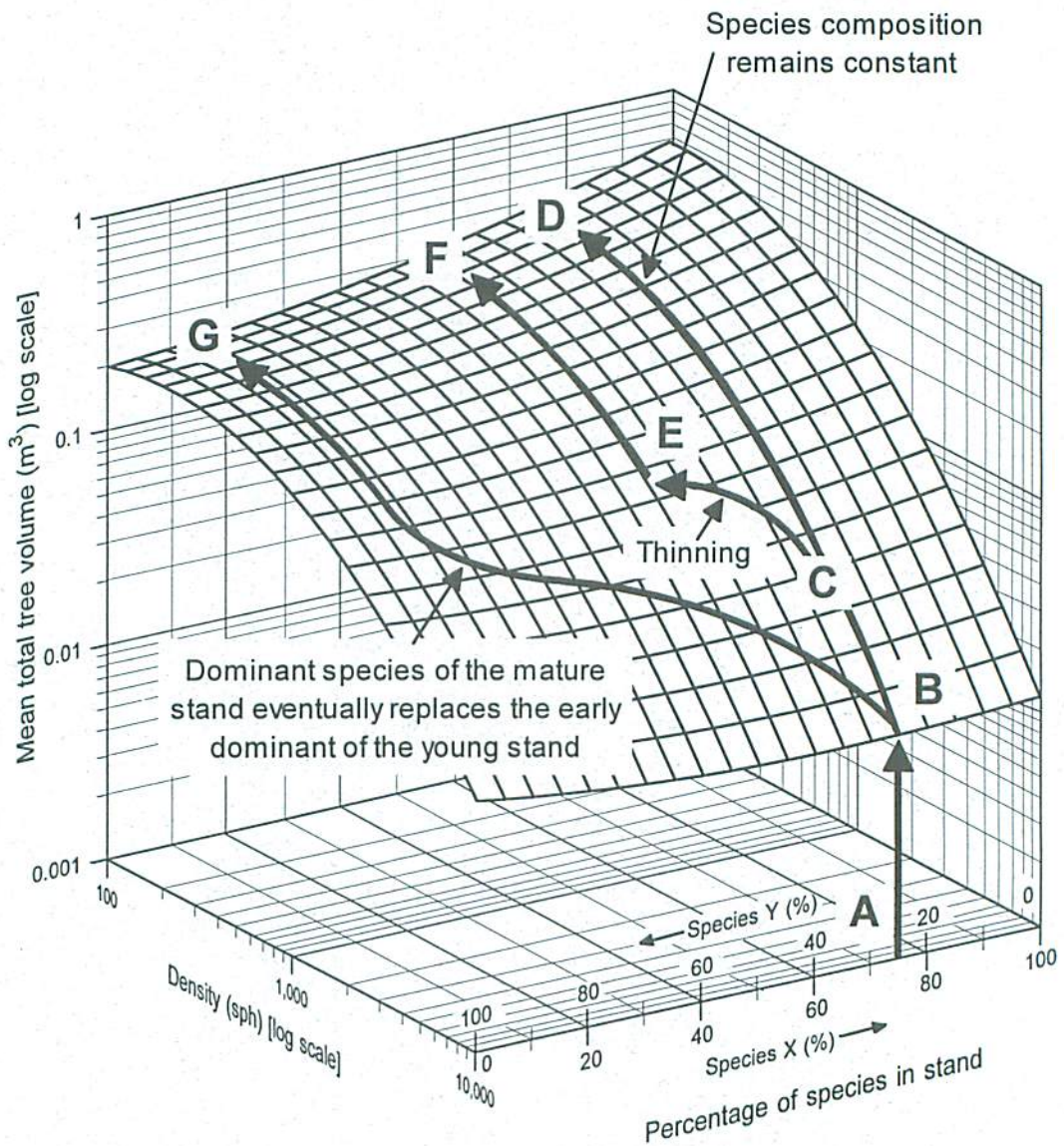


Figure 6. Potential stand development scenarios using a generic size–density surface model. The stand is dominated by two species, X and Y. Three stand development scenarios are shown. The stand established (A) with a 75 X:25 Y species mixture (ratios are percentages of total stand basal area). Density-dependent mortality commences (B) as competition for resources between individuals increases. Scenario 1: the stand contains codominant species and the relative basal areas remain constant throughout the life of the stand, as found in the black spruce and jack pine stand type. The stand develops along the ABCD pathway. Scenario 2: a thinning is undertaken at C to reduce the content of Species X and increase the proportion of Species Y from 75X:25Y to 55X:45Y. The stand would then develop along the ABCE pathway, for example removing pine to encourage spruce. Scenario 3: Species X is the early successional dominant that eventually becomes replaced by Species Y as the stand develops toward maturity. The stand would then develop along the ABG pathway, for example trembling aspen replaced by black spruce in an aspen–spruce stand type.

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LITERATURE CITED

- Binkley, D. 1984. Importance of size–density relationships in mixed stands of Douglas-fir and red alder. *For. Ecol. Manage.* 9:81–85.
- Burrows, F.M. 1991. Biomass production, structural deformation, self-thinning and thinning mechanisms in monocultures. *Phil. Trans. Roy. Soc. Lond. Series B.* 333:119–145.
- Honer, T.G.; Ker, M.F.; Alemdag, I.S. 1983. Metric timber tables for the commercial tree species of central and eastern Canada. Environment Canada, Can. For. Serv., Maritimes Forest Research Centre, Fredericton, NB. Inf. Rep. M-X-140. 139 p.
- Kelty, M.J. 1992. Comparative productivity of monocultures and mixed-species stands. p. 125–141 in M.J. Kelty, B.C. Larson and C.D. Oliver, eds. *The Ecology and Silviculture of Mixed-species Forests: A Festschrift for David M. Smith.* Kluwer Academic Publishers, Dordrecht, the Netherlands. 287 p.
- Kohyama, T. 1992. Density–size dynamics of trees simulated by a one-sided competition multi-species model of rain forest stands. *Ann. Bot.* 70:451–460.
- Langsaeter, A. 1941. Om tynning I enaldret gran-og furuskog. *Medel. f. d. Norske Skogforsoksvesen* 8:131–216.
- McFadden, G.; Oliver, C.D. 1988. Three-dimensional forest growth model relating tree size, tree number, and stand age: Relation to previous models and to self-thinning. *For. Sci.* 343:662–676.
- McLain, D.H. 1974. Drawing contours from arbitrary data points. *Comput. J.* 17:318–324.
- Puettmann, K.J.; DeBell, D.S.; Hibbs, D.E. 1993. Density management diagram for red alder. Oregon State University, Forest Research Laboratory, Corvallis, OR. Research Contribution 2. 6 p.
- Puettmann, K.J.; Hibbs, D.E.; Hann, D.W. 1992. The dynamics of mixed stands of *Alnus rubra* and *Pseudotsuga menziesii*: Extension of size–density analysis to species mixture. *J. Ecol.* 80:449–458.
- Pukkala, T.; Vettenranta, J.; Kolström T.; Miina, J. 1994. Productivity of mixed stands of *Pinus sylvestris* and *Picea abies*. *Scand. J. For. Res.* 9:143–153.
- Sterba, H.; Monserud, R.A. 1993. The maximum density concept applied to uneven-aged mixed-species stands. *For. Sci.* 393:432–452.
- Watkinson, A.R. 1985. Plant responses to crowding. p. 272–289 in J. White, ed. *Studies on Plant Demography: A Festschrift for John L. Harper.* Academic Press, London, England.
- White, J. 1981. The allometric interpretation of the self-thinning rule. *J. Theor. Biol.* 89:475–500.