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The dynamics of mixed stands of *Alnus rubra* and *Pseudotsuga menziesii*: extension of size–density analysis to species mixture

K.J. PUETTMANN*, D.E. HIBBS and D.W. HANN†

Department of Forest Science and †Department of Forest Resources, Oregon State University, Corvallis, OR 97331, USA

Summary

1. The monoculture self-thinning concept was expanded to polycultures by describing a self-thinning surface in a mixed-species size–density space. The size–density relationships of pure and mixed populations of *Alnus rubra* and *Pseudotsuga menziesii* in the Pacific Northwest, USA were investigated.

2. For polycultures of *A. rubra* and *P. menziesii*, the average size–density surface showed a near-planar region for stands consisting principally of *A. rubra*. Thus, *A. rubra* dominates stand dynamics in this region. At high proportions of *P. menziesii*, the surface showed a curvilinear increase towards the relative density level of pure *P. menziesii* stands. The curvilinear shape of the self-thinning surface cautions against using a single self-thinning line for mixed stands where the species proportion changes over time.

3. The complexity of the size–density relationship indicates the need for a more thorough exploration of the underlying population dynamics. The growth model allowed investigation of mixed-stand development by identifying stand density, relative dominance of one species, and species proportions as important factors driving stand development along the self-thinning surface.

4. Simulations of the growth model showed the need to investigate the development of younger populations, the spatial pattern of mixtures, and the effects of dominance of one species on population development.

Key-words: modelling, plant competition, plant population dynamics, self-thinning, $-3/2$ power law

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Introduction

The current interest in biodiversity has focused the attention of ecologists and land managers on the growth and development of mixed-species populations or polycultures. One of the most important components of population development is mortality. Mortality has been investigated by the self-thinning concept (Yoda *et al.* 1963) in a variety of even-aged, single-species populations, ranging from herbs to forest stands. This concept describes concomitant changes in plant size or mass and density (for review, see White 1980).

The self-thinning line represents the maximum average size for a given density and is expressed as

$$Y_i = a_1 + a_2 X_i \quad \text{eqn 1}$$

where Y_i is the log of the mean plant size, X_i the log of the current population density, a_1 the intercept of self-thinning line and a_2 the slope parameter of the self-thinning line.

Harper (1967) suggested expanding the self-thinning concept to mixed-species plant populations, but only a few experiments have addressed this possibility (for review, see White 1985). The first studies used two-species populations of herbaceous plants (White & Harper 1970; Bazzaz & Harper 1976). The investigators found that the common self-thinning line, calculated by combining the two species, had the same slope ($a_2 = -1.5$) as that expected for pure populations. In an experiment using *Trifolium pratense* and *Medicago sativa*, where the canopy did not develop distinct strata, Malmberg & Smith (1982) found the same mortality and growth

* Present address: Department of Forest Resources, University of Minnesota, St Paul, MN 55108, USA.

rate for both species. The self-thinning line had a slope of -1.5 , whether calculated for the combined species or for each individual species. If quadratic mean diameter (QMD) is used in tree populations instead of mass, then a different slope of the self-thinning line is expected (-0.623 instead of -1.5) (Reineke 1933; Long 1985). In a study of a multi-species stand in the Harvard Black Rock Forest (Cornwall, N. Y.), the self-thinning line for combined species had a slope of -0.67 (White 1985) using average QMD as size variable. In another study in the Harvard Forest (Petersham, Mass.) the slope was -0.54 (White 1985). Spurr & Barns (1980), also in the north-eastern United States, showed that the common self-thinning lines in mixed stands had values for intercept and slope similar to those for pure species stands.

Binkley (1984) assumed a slope of -1.5 for the average tree weight–density relationship and used the self-thinning line to compare pure stands of *Pseudotsuga menziesii* (Douglas fir) and mixed stands of *Alnus rubra* (red alder) and *P. menziesii* on sites with low and high fertility. On fertile sites, the self-thinning lines for mixed stands were lower than the line for pure *P. menziesii*, whereas on infertile sites the trend was reversed. Binkley attributed the effect of site quality to the interaction of nitrogen fixation and *A. rubra* competition. The results of Binkley's analysis have to be viewed with caution for several reasons. The assumption of a slope of -1.5 for all species may not be justified (Weller 1987; Barretto 1989). From the four stands Binkley used in his analysis, two were measured only once, which is not sufficient to establish a self-thinning line accurately (Stiell & Berry 1973; White 1980; Weller 1987). The third stand was grown from off-site seed sources, and the fourth stand included both thinned and unthinned plots with a substantial amount of other species present.

In the above studies, the exact proportions of the species in mixture have not been addressed. Instead, plant populations have been classified only as 'mixed'. This is a simplified view. Self-thinning in mixed stands should be viewed as a response surface over which species proportion can change, with the boundaries representing pure species and mixtures connecting the pure-species lines (Fig. 1). Both the slope and intercept of the self-thinning line of a mixture of these two species can vary with development of species proportion. Some authors do not provide information on species proportions (e.g. Binkley 1984). Others specify only the mixture at seeding time (e.g. Bazzaz & Harper 1976; Malmberg & Smith 1982). Although differential mortality for each species is acknowledged, the change in species proportion during self-thinning has been ignored.

In our analysis, we adopted the size–density relationship as defined by White (1981) and used

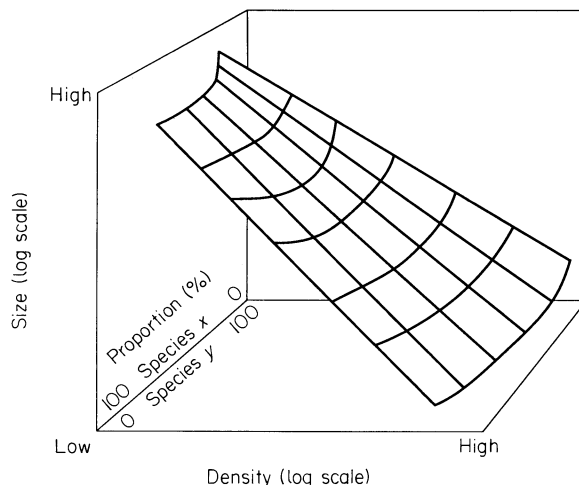


Fig. 1. The self-thinning lines for monocultures of species x and y are connected by the self-thinning line for species' mixtures. This results in expansion of the self-thinning lines to a self-thinning surface for pure- and mixed-species populations.

by Smith (1984) and Smith & Hann (1984, 1986). It is developed from log–log–transferred data and consists of a linear portion, the maximum size–density or self-thinning line (equation 1), and a curvilinear portion in which the trajectory approaches the maximum line asymptotically. The basic model form was adapted from Smith & Hann (1984):

$$Y_i = a_1 + a_2 \log(X_i) - a_1 a_4 \exp[a_3(X_1) - (X_i)], \text{ eqn 2}$$

where parameters are as in equation 1 and X_1 is the log initial population density, a_3 the intercept of the exponential function and a_4 an adjustment for relative density at the onset of mortality. Representing both parts of the trajectory in a single equation of this form has several advantages over the model for the self-thinning line (equation 1):

1. the problem of deciding which stands are in the linear stage of self-thinning (Weller 1987) is not pertinent and stands in all stages of self-thinning can be utilized;
2. the self-thinning line can be determined from a model such as that developed by Smith & Hann (1984) and is defined as the asymptote of the size–density trajectory;
3. the model can be expanded to include both pure and mixed-species populations;
4. the size–density trajectory also characterized the development of an average stand and can be expanded to a dynamic growth model.

An investigation into stand dynamics is a prerequisite to understanding development along the self-thinning surface of mixed-species populations. Population dynamics can then be integrated with the size–density relationship into a growth model. Smith & Hann (1986) developed two monospecies growth models based on the size–density relation-

ship for stands of *Alnus rubra* seedlings and *Pinus resinosa* (red pine) by incorporating a mortality equation. However, growth models for mixed-species populations require additional information about (i) population structure or relative dominance of one species and (ii) the species proportions in the mixture.

In this study, these factors are incorporated into a simple system to improve understanding of the size-density relationship and its underlying dynamics in mono- and polycultures using *Alnus rubra* Bong. (red alder) and *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) stands as an example. *A. rubra* and *P. menziesii* were chosen because of their widely overlapping distribution in the Pacific Northwest (Fowells 1965) and because interest in management of mixed *A. rubra*–*P. menziesii* stands has increased (Tarrant *et al.* 1983). On some sites they are severe competitors (Cole & Newton 1987; Shainsky 1988); on other sites *A. rubra* enhances *P. menziesii* growth due to its nitrogen-fixing ability (Tarrant 1961; Miller & Murray 1978). The main objective of our study was to extend the size–density concept to mixed-species populations and to investigate its underlying dynamics.

Methods

DATA

The data in this analysis are from permanent plots of pure stands of *A. rubra* and *P. menziesii* and mixed *A. rubra*–*P. menziesii* stands in north-western Oregon, western Washington, and south-western British Columbia (122–127°W, 45–52°N; Table 1, Fig. 2). Plots were established by private landowners and the US Forest Service to monitor stand growth and development, and the data are on file in the Forest Science Department, Oregon State University, Corvallis. All plots are in even-aged forests that were either planted or regenerated naturally after heavy disturbance, usually clear-cutting. The seed source of the natural regeneration was from residual trees or from trees in surrounding areas. The stands are in recovery phase after dis-

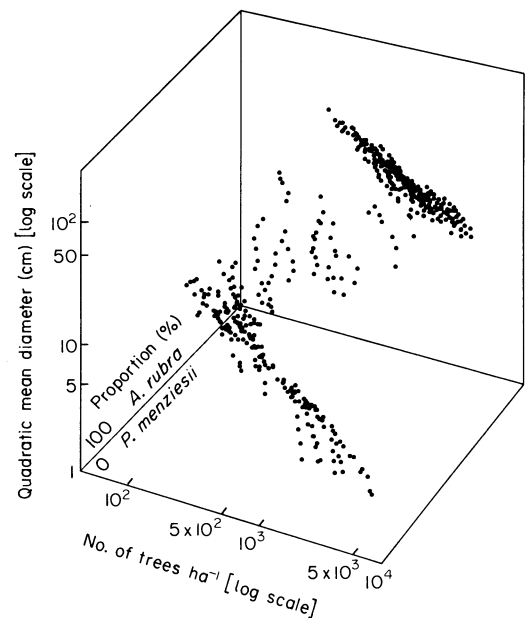


Fig. 2. Size–density measurements in pure and mixed populations of *Pseudotsuga menziesii* and *Alnus rubra*. A description of the data base is presented in Table 1.

turbance. Both *A. rubra* and *P. menziesii* are pioneer species and replacement towards more tolerant or climax species has not taken place.

In Table 1, and as a guide for model form development only, pure stands were defined as having 80% of basal area in one species, which is a common way of classifying pure and mixed stands in forest management (e.g. Worthington *et al.* 1960; King 1966). Actual species proportions were used for parameter estimation. Basal area proportion is a *better mixture indicator than tree number because it incorporates both size and number of trees*. Natural stands are rarely single- or two-species stands, and most stands had a minor proportion of other tree species present (<20% of basal area). These additional species are not considered to have a substantial influence on stand development and were therefore grouped together with the main species. Stands with >80% basal area in hardwoods were labelled pure *A. rubra*, and those with >80% conifers pure *P. menziesii*.

Table 1. Composition and measurement data (ranges in parentheses) for pure *Alnus rubra* stands, mixed *A. rubra*–*P. menziesii* and pure *Pseudotsuga menziesii* stands. Additional species present were grouped as *A. rubra* (hardwoods) or *P. menziesii* (softwoods)

	<i>A. rubra</i> *	Mixed	<i>P. menziesii</i> *
Number of stands	38	9	58
Number of measurements	221	47	276
Trees ha ⁻¹	2160 (330–11030)	980 (270–2450)	1520 (290–4160)
Quadratic mean diameter (cm)	18 (3–37)	23 (12–41)	25 (9–57)
Age at first measurement (years)	22 (1–65)	31 (21–47)	30 (6–43)
Measurement period (years)	16 (2–44)	21 (11–31)	15 (6–35)
Relative density	0.8 (0.3–1.2)	0.8 (0.4–1.2)	0.7 (0.1–1.2)

* Pure stands are defined as having 80–100% basal area of *A. rubra* or *P. menziesii*.

Other information necessary to characterize mixed stands includes relative density, stand structure expressed as relative size of a species, and site quality expressed as site index. Relative density was calculated as current density divided by the maximum density as determined from the size–density surface (Fig. 1). Because height information was not available for all stands, relative quadratic mean diameter (species QMD /stand QMD) was used as an indicator of stand structure or relative sociological position of a species within a stand.

Site index (SI) is based on the height–age relationship of the dominant trees and is therefore species specific. Because SI was not measured for the same species in all stands, a common SI variable was calculated from a data set of 10 stands that had information on *A. rubra* and *P. menziesii* site indices. The restricted conditions that allowed the coexistence of both species eliminated sites where they were not compatible. Therefore, the general relationship described by Harrington & Curtis (1986) was assumed in which good *A. rubra* sites are also good *P. menziesii* sites. In stands for which the *P. menziesii* site index was not known, it was converted from the *A. rubra* site index. The conversion equation was developed using first-, second- and third-order polynomials of *A. rubra* (SI_{Ar}) as potential independent variables. The *P. menziesii* SI (SI_{Pm}) was calculated from the equation

$$SI_{Pm} = -4.60 + 1.55 SI_{Ar}.$$

SIZE–DENSITY MODELS

The basic equation as developed by Smith & Hann (1984) (equation 2) is adjusted to allow populations to be analysed for which the initial density is not known:

$$Y_i = a_1 + a_2 X_i - [a_1(a_4 + I_1 a_5)] \exp[a_3(X_1 - X_i)], \quad \text{eqn 3}$$

where parameters are as in equation 2 and a_5 is a correction for proportion of initial density still alive at first measurement, I_1 is an indicator variable ($I_1 = 0$ if the initial density is known, elsewhere $I_1 = 1$) and i is the stand age.

To combine monoculture stands of two species in a single equation, equation 3 was modified using indicator variables (I_2) to accommodate the second species. The combined equation for either monocultures of both species was

$$Y_i = a_1 + I_2 b_1 + (a_2 + I_2 b_2) X_i - [(a_1 + I_2 b_1)(a_4 + I_1 a_5 + I_2 b_4)] \exp[(a_3 + I_2 b_3)(X_1 - X_i)], \quad \text{eqn 4}$$

where parameters are as in equation 3, and b parameters refer to species 2: b_1 is the intercept correction; b_2 the slope correction, b_3 the exponential curvature correction, b_4 a correction for proportion of initial density alive at first measurement and

relative density an onset of mortality and I_2 is a species indicator variable ($I_2 = 0$ for one species, elsewhere $I_2 = 1$).

To incorporate mixed stands, the indicator variable for the species (I_2) was replaced by a continuous variable representing species proportion (P). As a first step, P was incorporated untransformed, constituting a linear adjustment for species proportion. In the next step, P was raised to a power, c_j . This transformation allowed flexibility in determining the shape of the surface:

$$Y_i = a_1 + P^{c_1} b_1 + a_2 X_i + P^{c_2} b_2 X_i - [(a_1 + P^{c_1} b_1)(a_4 + I_1 a_5 + P^{c_4} b_4)] \exp[(a_3 + P^{c_3} b_3)(X_1 - X_i)], \quad \text{eqn 5}$$

where parameters are as in equation 5 and c_j is an exponent to the species proportion for the j^{th} parameter; $j = 1, 2, 3$ and 4.

MORTALITY AND PROPORTION SHIFT

To investigate the underlying dynamics of the size–density relationship in pure and mixed stands, we modelled mortality, the proportion of yearly mortality that is *P. menziesii*, and the shift in species proportion, all on an annual basis. The following attributes were used as independent variables in these three equations: stand density, relative density, species proportion, QMD , relative QMD , age and SI_{Pm} . Because the ratio of the trees dying to the number of trees alive at the beginning of a year is bounded by 0 and 1, a logistic equation was used. The proportion of yearly mortality that is *P. menziesii* was also modelled through a logistic equation as explained for stand mortality. Because the shift in species proportion can be negative, zero, or positive, a linear equation was used.

Annual shifts in proportion of basal area and mortality in *P. menziesii* were calculated only for stands that contained both *P. menziesii* and *A. rubra* ($n = 200$).

GROWTH MODEL

A growth simulator was derived from the equations predicting stand mortality, the proportion of annual mortality that is *P. menziesii*, the shifting species proportion, and the model for the size–density relationship. To utilize the size–density relationships as expressed in equation 5 for prediction of future stand development, the initial density before the onset of density-dependent mortality must be known. The equation for the size–density surface developed in equation 5 was solved for initial density. This allowed the calculation of the initial density from current stand conditions.

The accuracy of the simulation model were tested using three mixed stands from the data set with *P. menziesii* basal area components of 34%, 50% and 67%. A detailed description of these three

stands is presented in Table 2. Simulated stand values were obtained from the initial stand conditions projected for the periods over which these stands were measured. These values were then compared with the observed values for each stand.

FITTING METHOD

The non-linear and linear regressions were performed (SAS Institute 1987) with the Marquardt algorithm (Marquardt 1963) and the derivative-free DUD algorithm (Ralston & Jenrich 1978) used for non-linear fitting. To develop a biologically meaningful model, the parameter estimates were evaluated ($\alpha \leq 0.05$), and the variance inflation factors were expected to be < 10 . Non-significant estimates were screened and the difference in sums of squares from full and the reduced models were then tested.

In stands that did not show mortality, the annual mortality rate of 0 was replaced by $25/n$, where n is the sample size (Bartlett 1947) ($n = 438$ for stand mortality; $n = 200$ for *P. menziesii* mortality and species proportion). A weighted regression was applied to correct for the binomial distribution (Neter, Wassermann & Kutner 1983), with

$$w = np(1 - p),$$

where w is weight, n is sample size and p is proportion.

Results

SIZE-DENSITY MODELS

The initial step was to model the size-density trajectory for monocultures of *A. rubra* and *P. menziesii* in a single equation; equation 4 was fitted to the pure stands. The mean (\pm SE) parameters for equation 4 were estimated to be as follows

$$\begin{aligned} Y_i = & (7.33 \pm 0.18) - I_2(0.41 \pm 0.23) \\ & - [(0.61 \pm 0.02) - I_2(0.09 \pm 0.03)]X_i \\ & - \{[(7.33 \pm 0.18) - I_2(0.41 \pm 0.23)] \\ & \times [(0.08 \pm 0.01) - I_1(0.07 \pm 0.01)] \\ & + I_2(0.02 \pm 0.01)\} \\ & \exp\{[-3.48 \pm 1.14) - I_2(13.55 \pm 7.91)] \\ & \times (X_1 - X_i)\}. \end{aligned} \quad \text{eqn 6}$$

The model mean square error (MSE) was 0.0008. The species adjustment for the intercept (0.41) and the curvature of the size-density trajectory (13.55) as well as the adjustment for the proportion of the initial density present at the time of first measurement (0.02) were not significantly different from 0. Because the correction on the slope of the asymptote (0.09) was the only significant modifier parameter in eqn 6, the non-significant adjustment parameters were dropped from eqn 4 and the reduced model was fitted to the data of pure *A. rubra* and *P. menziesii* stands. The algorithm estimated the parameters to be

$$\begin{aligned} Y_i = & (7.21 \pm 0.13) - [(0.59 \pm 0.01) \\ & - I_2(0.03 \pm 0.003)]X_i \\ & - \{(7.21 \pm 0.13)[(0.10 \pm 0.01) \\ & - I_1(0.07 \pm 0.01)]\} \\ & \exp[(-2.63 \pm 0.97)(X_1 - X_i)]. \end{aligned} \quad \text{eqn 7}$$

The MSE for equation 7 was 0.00098 and all parameters in equation 7 were significant. In addition, an *F*-test implied that the equation with a correction on the slope of the asymptote was sufficient to represent the size-density relationships of pure *A. rubra* and *P. menziesii* stands.

To fit this model to the full data set containing data from pure and from mixed stands, the indicator variable for species was replaced by a continuous variable representing percent total basal area in *P. menziesii* (P_{Pm}). Assuming a linear connection between the pure stands using the parameter estimates from equation 7 as initial values yielded (MSE = 0.0009)

$$\begin{aligned} Y_i = & (7.12 \pm 0.11) - [(0.58 \pm 0.02) \\ & - P_{Pm}(0.03 \pm 0.004)]X_i \\ & - \{(7.12 \pm 0.11)[(0.09 \pm 0.01) \\ & - I_1(0.07 \pm 0.01)]\} \\ & \exp[(-2.62 \pm 0.79)(X_1 - X_i)]. \end{aligned} \quad \text{eqn 8}$$

Analysis of the residuals indicated a trend when plotted over proportion of basal area in *A. rubra*. Quadratic mean diameters for mixed stands with a high proportion of *A. rubra* were underestimated while those with a high proportion of *P. menziesii* were overestimated. Raising P_{Pm} to the power c yielded (MSE = 0.0009)

Table 2. Initial conditions for three stands used for comparisons of the growth model

	Stand 1	Stand 2	Stand 3
Proportion of basal area composed of <i>P. menziesii</i>	0.34	0.50	0.67
Stand age (years) at initial measurement	21	35	32
Duration of measurement period (years)	26	30	19
Stand density (trees ha ⁻¹)	913	1660	333
Stand quadratic mean diameter (cm)	21.0	12.0	26.9
Stand basal area (m ² ha ⁻¹)	31.56	18.85	19.03
Number of <i>P. menziesii</i> ha ⁻¹	297	1106	222
<i>P. menziesii</i> QMD (cm)	21.4	10.4	27.0

$$\begin{aligned}
 Y_1 = & (7.07 \pm 0.15) \\
 & - [(0.57 \pm 0.007) - P_{Pm}^{(3.09 \pm 1.20)} \\
 & (0.03 \pm 0.003)]X_i \\
 & - \{(7.07 \pm 0.15)[(0.10 \pm 0.003) \\
 & - I_1(0.08 \pm 0.006)]\} \\
 & \exp[(-2.57 \pm 0.07)(X_1 - X_i)]. \quad \text{eqn 9}
 \end{aligned}$$

The exponent (3.09) in equation 9 was significantly different from 0, but not from 1. However, the analysis of residuals indicated the trend over proportion of basal area was eliminated.

The behaviour of equation 9 is illustrated in Fig. 3, which shows the size-density surface covering stands with the full range of proportions of *A. rubra* and *P. menziesii*. The stands initiated at 10000 trees ha^{-1} [$X_1 = \log(10000)$] and gradually approached and developed along the self-thinning surface.

MORTALITY AND PROPORTION SHIFT

Using the logistic transformation, the equation for the annual stand mortality rate yielded

$$\begin{aligned}
 Y_t = & (-3.46 \pm 0.16) - (0.41 \pm 0.11)RQMD_t \\
 & + (0.00015 \pm 0.00002)N_t - (0.022 \pm 0.004)t_i \\
 & + (1.1 \pm 0.18)RD_t, \quad \text{eqn 10}
 \end{aligned}$$

in which $Y_t = \log[M_{s,t}/(1 - M_{s,t})]$, where $M_{s,t}$ is the proportion of trees dying, or $[(N_t - N_{t+1})/N_t]$, $RQMD_t$ is the relative *QMD* (*P. menziesii QMD*/stand *QMD*), N_t the number of trees ha^{-1} , RD_t the relative density (actual density/maximal density for given diameter and proportion) and t the total stand age; adjusted $R^2 = 0.54$, $MSE = 2.53$.

The proportion of the annual mortality that is

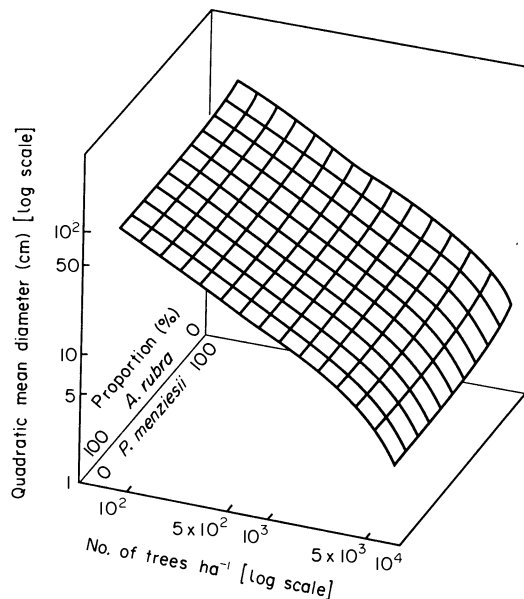


Fig. 3. Size-density surface for pure and mixed stands of *Pseudotsuga menziesii* and *Alnus rubra* that began at 10^4 trees ha^{-1} . The surface is a representation the size-density relationship of stands covering the full range of species proportions.

contributed from the *P. menziesii* components was modelled through

$$\begin{aligned}
 Z_t = & (-1.59 \pm 1.04) + (2.32 \pm 1.23)P_{Pm,t} \\
 & + (0.09 \pm 0.027)QMD_t + (0.0008 \pm 0.0003)N_t \\
 & - (0.073 \pm 0.024)SI_{Pm}, \quad \text{eqn 11}
 \end{aligned}$$

with parameters as in equation, and $Z_t = \log[PM_{Pm,t}/(1 - PM_{Pm,t})]$ is the proportion of trees dying that are *P. menziesii* and $P_{Pm,t}$ = proportion of basal area in *P. menziesii* (adjusted $R^2 = 0.49$, $MSE = 34$).

The equation for the annual change in basal area proportion was estimated to be

$$\begin{aligned}
 P_{Pm,t+1} - P_{Pm,t} = & (-0.004 \pm 0.0013) \\
 & + (0.00007 \pm 0.000026)t \\
 & + (0.0045 \pm 0.0009)RQMD_t \\
 & - (0.0016 \pm 0.0001)P_{Pm,t}, \quad \text{eqn 12}
 \end{aligned}$$

where variables are as in equations 10 and 11 (adjusted $R^2 = 0.14$, $MSE = 0.00001$).

GROWTH MODEL

Equations 10–12 were combined with the size-density surface (equation 9) to form a growth simulator which predicts development of pure and mixed *A. rubra*–*P. menziesii* stands. Three stands were selected for evaluation of the growth model. The results of the comparison of the predicted and observed stand development of the three stands are presented in Fig. 4.

Stand 1 started with 34% basal area of *P. menziesii*. The simulated proportion is very close to the actual stand proportions (Fig. 4e). The prediction for overall stand mortality was high, leading to overestimation of *QMD* (Fig. 4a,c), and is caused by overestimation *P. menziesii* mortality (Fig. 4d). No *P. menziesii* died between ages 21 and 26, but the simulation predicted high mortality for this period.

Stand 2 started with 50% basal area in *P. menziesii*. The shift in basal-area proportion was irregular, but the simulation seemed to reflect the long-term trends accurately for all components (Fig. 4f,i,h,j), except basal area (Fig. 4g).

The shift in basal-area proportion of stand 3 with 67% basal area in *P. menziesii* was very small and the simulated basal-area proportion represented the general trend (Fig. 4o). As with stand 1, the lack of *P. menziesii* mortality in the stand during the first measurement period (Fig. 4n) led to an underestimation of stand density (Fig. 4k). The resulting overestimation of *QMD* offset this effect (Fig. 4m), so that basal-area development was simulated very accurately (Fig. 4l).

Discussion

The size-density relationship for a mixed stand of two species was developed by combining the

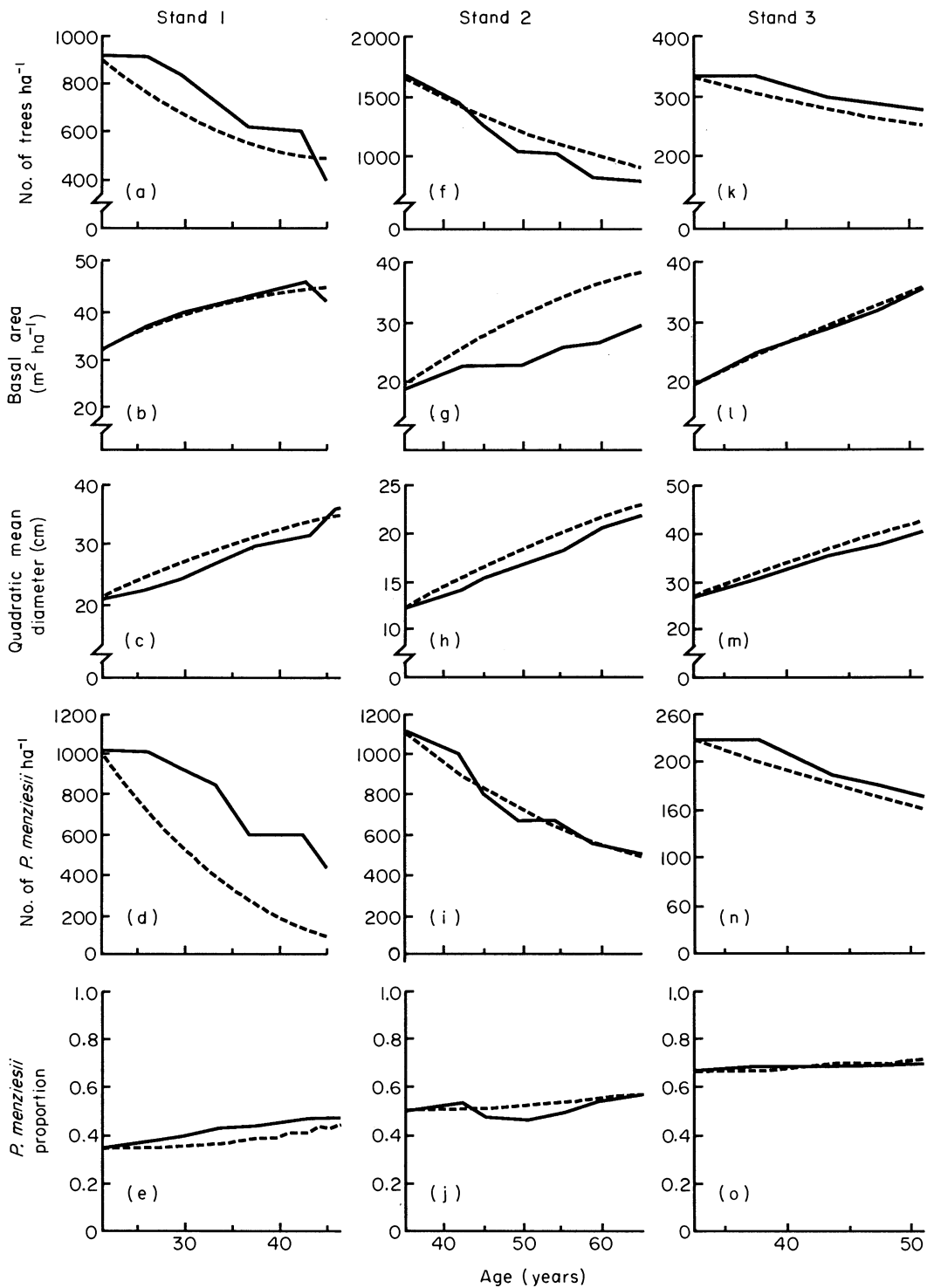


Fig. 4. Simulated (---) and actual (—) development of stand density, basal area, quadratic mean diameter, *Pseudotsuga menziesii* density, and *P. menziesii* proportion for stand 1 (a–e), stand 2 (f–j) and stand 3 (k–o). The initial composition of each stand is given in Table 2.

monoculture models into a single equation and then replacing the species indicator with a continuous variable representing species proportion. This approach utilizes the large database accumulated for monocultures, allows flexibility in determining the shape of the self-thinning surface, and is not limited to a two-species polyculture. Unlike earlier studies, the approach acknowledged the fact that the proportion of the species in mixed-species popu-

lations changes through stand development. The analytical model for polycultures can yield information about stable or planar regions of the self-thinning surface and regions where a minor shift in species proportion reflects strongly on the self-thinning properties of polycultures.

The size–density relationship for polycultures (equation 9 and Fig. 3) differs from the size–density trajectory for single-species stands in interpretation.

The size–density trajectory for monocultures not only yields the maximum size–density or self-thinning line, but also predicts development towards this maximum. In mixed populations, the size–density relationship alone cannot predict development below and along the self-thinning surface. Development and dynamics of individual stands may vary with population and environmental conditions, even though the initial species proportions are similar. Three possible self-thinning lines for a two-species mixture are presented in Fig. 5(a). The self-thinning lines for all three populations begin on the maximum self-thinning surface with 50% in each species. Self-thinning line 1 represents a stand in which species *x* dominates and mortality and growth patterns lead to its increased proportions. In trajectory 2 species proportions remain fairly stable. Trajectory 3 shows a dominant species *y*, the proportion of which is constantly increasing. In the case of *A. rubra* and *P. menziesii*, trajectory 1 would be followed on a good *A. rubra* (species *x*) site, such as that in the Cascade Head Study (Berntsen 1961). Trajectories 2 and 3 would be followed on sites where *P. menziesii* (species *y*) was dominant to various degrees.

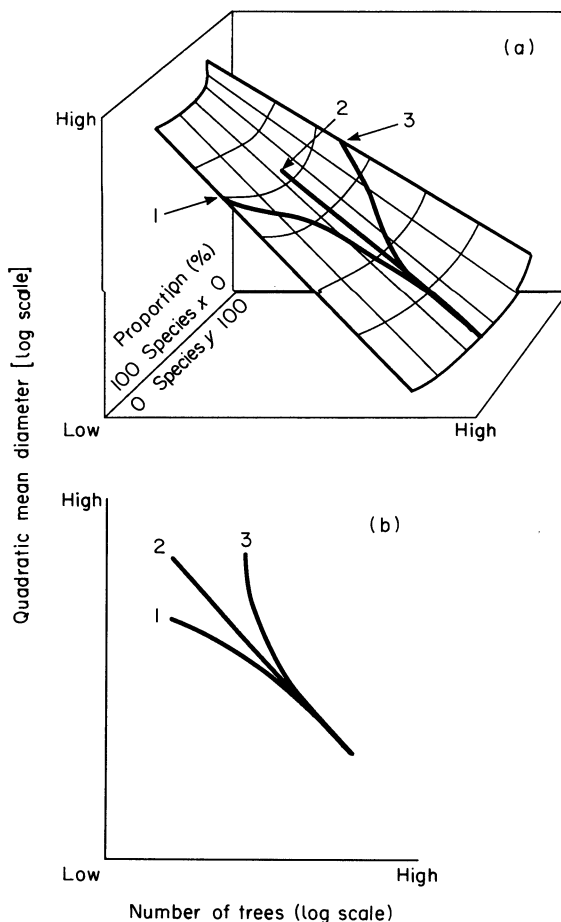


Fig. 5. (a) Conceptual self-thinning surface for a two-species mixture showing three possible self-thinning lines for developing stands. (b) Corresponding self-thinning lines projected into two dimensions.

The same size–density trajectories may also be analysed by the usual two-dimensional method (Fig. 5b). Although all stands are at the maximum density, only one of the three size–density trajectories reaches a linear portion (i.e. trajectory 2). For trajectory 1, slope decreases, whilst slope for trajectory 3 increases until a pure-species stand is reached. Consequently, self-thinning lines based on observations of individual stands (for examples see White 1985) only represent a single trajectory out of the numerous possibilities. Inferences based on studies of single stands are restricted to the specific stand and site conditions. A reliable estimate of a self-thinning model for mixed stands requires the analysis of the full spectrum of species proportion in mixed species stands.

Even if the self-thinning lines of pure species populations have the same slope but different intercepts, a change in species proportion will result in self-thinning lines for mixed species populations that are either non-linear or, if linear, they have a slope different from the pure-species value.

The self-thinning surface for *A. rubra* and *P. menziesii* stands was close to the *A. rubra* level for stands with low to medium proportions of *P. menziesii* (Fig. 3). In these ranges, it showed a stable, almost planar region. Mixed stands with <75% of basal area in *P. menziesii* had a maximum size for a given density close to that in pure *A. rubra* stands. This might indicate that stands with a lower to medium proportion of *A. rubra* can only exist when *A. rubra* is in a dominant position in the stand. In stands with >75% *P. menziesii*, this dominance is not assured and the self-thinning surface has a curvilinear increase towards the pure *P. menziesii* level (Fig. 3).

A model for both species, with a species adjustment only on the slope parameter, indicates that changing the slope while keeping other parameters constant was sufficient to represent the size–density relationship for *A. rubra* and *P. menziesii* in pure and mixed stands (Fig. 3). Even though the zero intercept for both *A. rubra* and *P. menziesii* is the same, within the density range that is biologically meaningful the maximum *QMD* of *P. menziesii* stands was higher than that of *A. rubra* stands (Fig. 3). The concave surface shape supports White's (1985) hypothesis that the self-thinning limits for mixed species populations do not exceed pure species limits.

The size–density surface as presented in equation 9 and Fig. 3 is the average size–density relationship for the stands represented by the data set. Individual stands lie above or below this surface due to erratic events, such as drought, frost, or pest problems (Hann & Wang 1990). Also, spatial pattern of tree distribution can lead to deviations from the maximum size–density relationship (Hamilton 1984).

The shift in species proportion occurred very slowly in the stands used in the analysis. All mixed stands showed that the proportion of *P. menziesii*

was increasing with the shift becoming faster as stands get older and as *P. menziesii* became dominant. This pattern might be influenced by the spatial pattern of the mixture. For example, in a clumped mixture, intra- and not interspecific competition has more influence on stand development and would stabilize basal-area proportions.

The analysis is limited by the availability of data representing all stages of development. From the slow increase of *P. menziesii*, it is obvious that other stages are not reflected in the data set. To broaden the scope beyond the data range the conceptual development of species proportions can be derived from the yield tables (Worthington *et al.* 1960; McArdle, Meyer & Bruce 1961). Due to its faster initial growth rate, *A. rubra* increases in basal area faster than does *P. menziesii*. In cases of complete dominance, *A. rubra* kills all the *P. menziesii*, resulting in a pure *A. rubra* stand. If some *P. menziesii* survive, they will overtop the *A. rubra* and *P. menziesii* basal area proportion increases (e.g. Berntsen 1961; Miller & Murray 1978). The model shows that this process is very slow during ages 20–60. However, it will eventually lead to a pure *P. menziesii* stand.

Using potted plants in a homogenous environment, both Bazzaz & Harper (1976) and Malmberg & Smith (1982) found mortality rates to be constant throughout the duration of their experiment. In the case of contrasting species, and thus a stratified canopy, the mortality rate was higher for the lower-stratum than for the upper-stratum species (Bazzaz & Harper 1976), whilst in the population with similar species and no distinct canopy strata the mortality rates were the same for both species (Malmberg & Smith 1982). In perennial plant populations, as investigated in this study, the environments are more diverse and constantly changing. Mortality patterns can therefore be very complex and vary over time, indicating that a more thorough investigation is needed. For *A. rubra* and *P. menziesii* stands, the equation predicting mortality rates indicated that mortality rates were determined largely by stand density. All else being equal, stand mortality rates decreased with age and with increased dominance of *P. menziesii*.

The complexity of stand development was shown in the analysis of stand dynamics and simulations using the growth model. Comparisons of the model predictions with the actual development of three stands brought out some of the strengths and weaknesses of the growth model (Fig. 4). Not all components of each stand were simulated with equal accuracy. The short-term erratic nature of mortality is especially problematic. The model predicts average stand development and consequently discrepancies for individual stands are to be expected. However, the general long-term dynamics of population development were well reflected.

The model indicated several areas of use. The first

concerns potential research on the development of populations before the onset of self-thinning. This is of special interest because initial growth and mortality can have substantial influence for population structure and development in late stages (Oliver & Larson 1990). Juvenile stands were not sufficiently represented in the data set, so the periods when one species (in this case *A. rubra*) has a potential growth advantage are not reflected well in the model. Measurements in mixed populations should be started at the time of establishment and followed closely through all stages to allow complete representation of population dynamics.

Another important question pointed out in the model is the effect of competitive interactions in relation to size difference and strata development. The growth model suggest that a stand with dominant *A. rubra* has higher overall mortality rates for both the entire stand and for *P. menziesii* than stands with dominant *P. menziesii*, implying that *A. rubra* is a more severe competitor of either species than is *P. menziesii* (see Shainsky 1988). This might change with time or environmental conditions. Detailed investigation of these effects is especially needed to evaluate manipulations of mixed populations, such as weed control (e.g. Newton, El Hassan & Zavitkowski 1968).

The effects of spatial pattern on development of mixed stands needs to be investigated. Hamilton (1984) and Schoonderwoerd & Mohren (1988) determined that spatial patterns influence growth and mortality patterns of pure-species populations. Local conditions, rather than average stand conditions, might be a better predictor of tree development. This phenomenon may be even more important in mixed-species stands because the species have different competitive abilities, which in turn determine development of the spatial patterns over time.

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