

Reevaluating the self-thinning boundary line for ponderosa pine (*Pinus ponderosa*) forests

Jianwei Zhang, William W. Oliver, and Robert F. Powers

Abstract: The self-thinning rule has been used extensively to predict population dynamics under intraspecific and interspecific competition. In forestry, it is an important silvicultural concept for maintaining stand health in the face of climate change and biotic stress, but uncertainty exists because traditional self-thinning limits were set subjectively without regard to site quality. We addressed this by analyzing ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) data from 109 research plots measured repeatedly and 59 inventory plots measured once across California. Self-thinning boundaries were fitted to the data with quantile regression and stochastic frontier function (SFF) techniques with and without site index (SI) as a covariate. The models from both methods fitted the data well with either research plots or all plots. Slopes for size-density trajectories were -0.45 with the 0.99 quantile and -0.47 for SFF. Maximum stand density indices (SDI) were 1250 trees per hectare (TPH) with the 0.99 quantile and 1050–1060 TPH with SFF. Mortality occurred when site occupancy from SFF reached 0.75, suggesting a zone of imminent mortality. Curvilinear trends in maximum SDI across SI for both methods indicate that self-thinning varies with site quality. Any management regimes that increase site quality and productivity will increase the self-thinning boundary.

Résumé : La loi de l'auto-éclaircie a été beaucoup utilisée pour prévoir la dynamique des populations soumises à une compétition intra et interspécifique. En foresterie, c'est un concept sylvicole important pour maintenir la santé des peuplements face aux changements climatiques et aux stress biotiques, mais des incertitudes subsistent parce que les limites traditionnelles de l'auto-éclaircie ont été fixées subjectivement sans égard à la qualité de station. Nous avons traité cette problématique en analysant des données sur le pin ponderosa (*Pinus ponderosa* Lawson & C. Lawson) récoltées dans 109 placettes de recherche mesurées de façon répétée et 59 placettes d'inventaire mesurées une seule fois à travers la Californie. Les limites de l'auto-éclaircie ont été ajustées aux données à l'aide de techniques de régression quantile et de fonction limite aléatoire (FLA) avec et sans l'ajout de l'indice de qualité de station (IQS) comme covariable. Les modèles obtenus avec chacune des deux méthodes se sont bien ajustés aux données provenant uniquement des placettes de recherche ou de l'ensemble des placettes. La pente des trajectoires entre la taille des arbres et la densité des peuplements était de $-0,45$ avec le quantile 0,99 et de $-0,47$ avec la FLA. La valeur maximale de l'indice de densité des peuplements (IDP) était de 1250 arbres à l'hectare avec le quantile 0,99 et de 1050 à 1060 arbres à l'hectare avec la FLA. La mortalité des arbres débutait lorsque l'occupation de la station atteignait 0,75 selon la FLA, ce qui indique une zone de mortalité imminente. Une tendance curvilinéaire entre l'IDP maximal et l'IQS dans le cas des deux méthodes indique que l'auto-éclaircie varie selon la qualité de station. Tout régime d'aménagement qui augmente la qualité et la productivité de la station va produire une augmentation de la limite de l'auto-éclaircie. [Traduit par la Rédaction]

Introduction

Competition among trees is an important factor determining stand dynamics in both natural forest and plantations. Stand density strongly relates to intensity of competition.

Foresters often manipulate stand density and structure to enhance stand function for the goals of managed lands (Pretzsch 2009). Ever since Reineke (1933) conceived stand density index (SDI) for characterizing self-thinning based on even-aged ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) stands in California, SDI has been used to determine how individual stands compare with a limit of stocking, beyond which the risk to mortality from natural causes is high. It has been extensively used in guiding forest management for ponderosa pine stand growth (Cochran and Barrett 1995; Oliver 1995, 1997; Long and Shaw 2005), resilience to insects (Oliver 1997; Fettig et al. 2007), wildlife habitat development (Moore and Deiter 1992), and fuel treatment (Zhang et al. 2010). Not only has it been developed for other forest species (Reineke 1933; Weller 1987; VanderSchaaf and Burkhardt 2007), but it has been applied to uneven-aged or mixed-species stands (Long and Daniel 1990; Solomon and Zhang 2002; Woodall et al. 2003, 2005). As Zeide (2005) stated, SDI “may not be a good

measure of density, but it is still the best we have” in forest management.

The self-thinning rule describes a universal relationship between size and density of organisms. Because the slope of the relationship in a logarithmic scale of size and density was found to be approximately $-3/2$ by Yoda et al. (1963), it is also called the $-3/2$ power rule or “Yoda’s law.” This significant ecological finding was simply a rediscovery of what had been described by Reineke (1933) for forest stands 30 years earlier. He called the self-thinning line the SDI line, and it was originally expressed as

$$(1) \quad \log N = k + \beta \log D$$

where N is the number of trees per acre and D is the quadratic mean diameter (QMD) at breast height in inches. Because k varied with species, Reineke (1933) proposed a reference point by using size–density combinations in terms of equivalence to the number of 10 in. (25.4 cm) stems per acre. With this alternative, the SDI can be directly calculated using eq. (2).

$$(2) \quad \text{SDI} = N(D/10)^{-\beta}$$

Received 5 April 2013. Accepted 22 July 2013.

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Table 1. Research plot information, elevation, stand history, and plot characteristics at the establishment year and at the latest measurement year for ponderosa pine across California, USA.

Location	No. of plots	Plot size (ha)	SI (m)	Elev. (m)	Stand history	Establishment year				Latest measurement		
						Year	TPH	QMD (cm)	Age (years)	Year	TPH	QMD (cm)
Adin Pass (AP)	1	0.40	21	1585	N	1957	300	15.2	61	2009	270	36.6
Challenge (CH)	20	0.08	28–41	810	P	1968	300–2990	*	*	2007	250–2496	15.2–40.9
Chester (CT)	18	0.04	25–31	1533	P	1987	1680	*	*	2010	1170–1680	13.6–22.0
Edson Creek (ER)	3	0.40	39–43	1190	N	1972	100–165	46.0–49.0	87	2005	96–120	67.8–72.6
Elliot Ranch (ER)	15	0.40	44–49	1183	P	1969	168–1370	17.8–25.4	20	2009	45–270	44.5–86.1
Feather Falls (FF)	18	0.04	40–44	1245	P	1988	1680	*	*	2008	1350–1680	16.6–24.7
Hog Lake (HL)	1	0.20	20	1494	N	1944	640	16.5	61	2009	480	35.1
Joseph Creek (JC)	3	0.40	19–25	1710	N	1974	460–700	19.1–24.1	62	2009	180–270	35.3–42.7
KC Reservoir (KC)	1	0.25	33	1219	P	1972	600	24.9	35	2009	400	46.0
Prattville (PR)	1	0.20	31	1433	P	1971	250	10.4	15	2009	250	42.4
Show Plantation (SP)	3	0.40	40–45	1189	P	1972	150–385	34.0–45.2	53	2005	126–222	51.8–65.5
Spaulding Butte (SB)	3	0.25	12–20	1417	P	1972	670–1310	10.7–14.2	52	2009	227–630	29.7–35.6
Sugar Hill (SH)	3	0.40	25–31	1646	P	1958	100–750	14.0–19.8	27	2009	106–740	32.3–58.4
Washington MT (WM)	1	0.40	19	1585	N	1963	300	19.1	42	2009	270	37.1
Whitmore (WH)	18	0.04	27–35	745	P	1986	1680	*	*	2007	1180–1680	10.1–18.7

Note: SI, site index at 100 years; N, natural stand; P, plantation; TPH, trees per hectare; QMD, quadratic mean diameter; *, indicates the plots that were established from seedlings.

Note that Reineke (1933) used -1.605 for β by pooling data over multiple species including 20 unmanaged and overstocked young natural ponderosa pine stands ranging from 6.6 to 21.0 cm QMD with plot size from 0.02 to 0.04 ha (M.W. Ritchie, personal communication (2012)). These plots were often adjacent to some large seed trees within mixed-conifer stands on the Stanislaus, Sierra, and Sequoia National Forests of the Sierra Nevada. By analyzing data for the ponderosa pine only, Oliver and Powers (1978) found as β of -1.77 to be a better fit. Neither publication provided any statistical inferences for the slopes. The maximum SDI boundary lines were visually hand-fitted by changing the intercept of the regression line. Trends for a given species were believed to be independent of site quality. Therefore, the concept was two-dimensional.

To easily compare stands in the prethinning stage, some users prefer to have the self-thinning boundary line with QMD as the dependent variable and density as the independent variable. Therefore, eq. (1) can be re-arranged as follows in metric units:

$$(3) \quad \log(\text{QMD}) = \beta_0 + \beta_1 \log(\text{TPH})$$

where QMD in centimetres and trees per hectare (TPH) are substituted for D and N in eq. (1) or (2). Although the slopes (β_1) may be constant (Hamilton et al. 1995), the intercept (β_0), which controls maximum SDI, differs considerably among species (Weller 1987; Oliver 1995; Woodall et al. 2005).

In the past, for an individual species within a particular geographic region, a common self-thinning boundary line was assumed (Reineke 1933; Yoda et al. 1963), regardless of site quality, because of a lack of rigorous testing. It has now been well-recognized that the self-thinning boundary lines vary with site productivity for a given species (DeBell et al. 1989; Bi 2001; Weiskittel et al. 2009). In general, a larger β_0 has been found in stands grown on the more productive land. The best way to capture these variations in a size-density trajectory for a species is to track stands with varied densities and a range of diameters until self-thinning occurs.

For example, Oliver (1995) examined the self-thinning rule using the revised slope of -1.77 from Reineke (1933) to hand-fit some plots and found that self-thinning started when SDI reached 568 TPH, “a zone of imminent mortality” and that significant mortality occurred when SDI reached 900 TPH, regardless of site quality. This value was well below the maximum SDI of 1236 TPH used in the USDA Forest Service’s Pacific Southwest Region in the

past or the varied numbers from 1000 to 2050 TPH used in other Forest Service Regions for the Forest Vegetation Simulator (Dixon 2002; Stage 1973). However, Oliver (1995) argued that an SDI of 900 TPH was the result of increased bark beetle (*Dendroctonus* spp.) activity during a contemporary drought. Conventional self-thinning rules only included intertree competition as a cause and did not account for episodic events like insect attack during periods of stress. Because bark beetles tend to target stressed trees (Fettig et al. 2007), separating beetle-caused mortality from stressed-caused mortality is difficult.

In this paper, we revisited the self-thinning rule by remeasuring plots used in Oliver’s (1995) paper across the region and by adding new data available to us in California. Our objectives were to (1) examine the intercepts and slopes of the self-thinning boundary lines using statistical inference from a much broader diameter range among stands with varying site qualities, (2) determine the maximum SDI for ponderosa pine in the region by reevaluating Oliver’s rule of self-thinning with presence of *Dendroctonus* spp. after 20 more years of stand development, and (3) determine if self-thinning is appreciably influenced by site quality.

Materials and methods

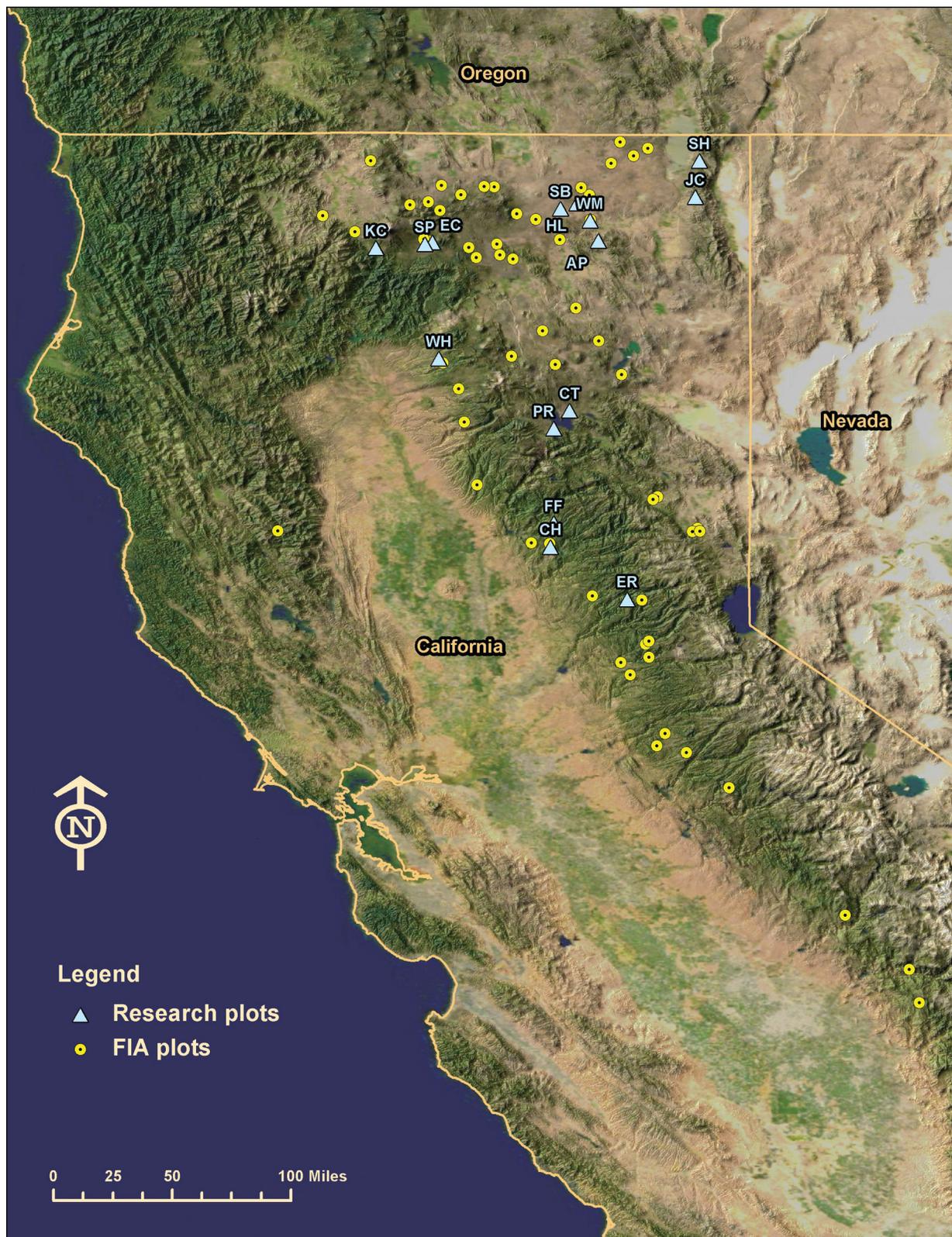
Data

Research plots

We located 109 permanent previously measured research plots of ponderosa pine established between 1944 and 1988 in California between latitudes 39.16°N and 41.83°N (Table 1 and Fig. 1). DBH, mortality, and condition of trees in all plots have been measured over multiple times since establishment. Previous measurements also included tree height and height of live crown either for all or for a 20% sample of trees in the plot. Inventories usually occurred every 5 years after plot establishment, yielding 688 observations in the database.

The plots were established in either natural even-aged pure stands or in monospecies plantations of ponderosa pine. Nine plots were in natural stands ranging in age from 42 to 87 years. The rest were from 1- (established from seedlings) to 53-year-old plantations. Site index (SI) of these plots ranges from 12 to 49 m at 100 years (Table 1), which is from Meyer’s table (Meyer 1938) based on the 75th percentile by plot height and total tree age (Ritchie et al. 2012). The SI estimate for each research plot was performed to eliminate the effect of spacing, fertilization, and vegetation control treatments on tree height in the original studies. We

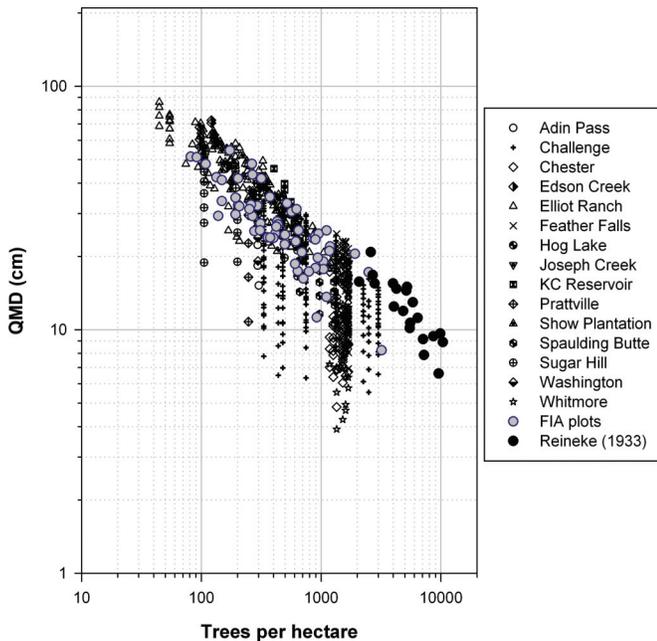
Fig. 1. Geographic locations of ponderosa pine plots used in the analysis. There are 109 research plots at 15 sites (abbreviations available in Table 1) and 59 plots from the US Forest Service Forest Inventory and Analysis (FIA) database across California, USA.



selected plots for this study based on the following criteria: (1) plot size must be at least 0.12 ha; if not, (2) plots must be contiguous within an experiment with ≥ 1 ha in total; (3) a plot must be buffered by trees for at least 10 m from a road; (4) self-thinning oc-

curred at the site as indicated by tree mortality; and (5) we eliminated thinned plots for nondensity studies but did include intensive management research plots receiving such treatments as initial spacing, vegetation control, and fertilization.

Fig. 2. Size–density plot in log–log scale for ponderosa pine based on 109 research plots, 59 plots from the US Forest Service Forest Inventory and Analysis database and 19 plots used by Reineke (1933), which were estimated from his figure, across California, USA.



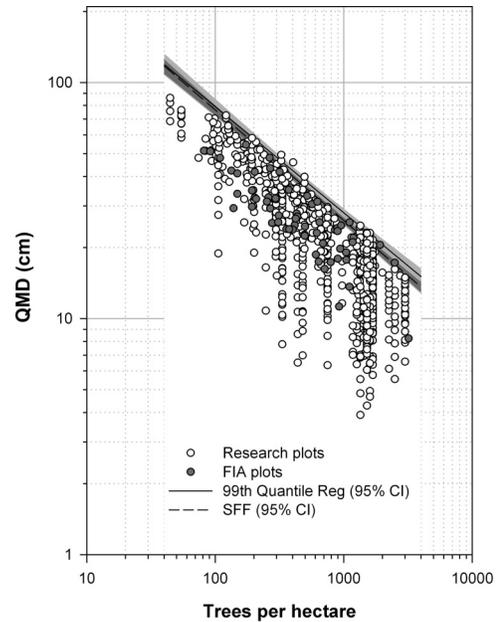
FIA plots

We also included data from ponderosa pine plots in California measured by the USDA Forest Service Forest Inventory and Analysis (FIADB; www.fs.fed.us/pnw/fia/publications/data/data.shtml) program. Each field inventory plot was a cluster of four circular macroplots with an 18.0 m radius for trees with DBH ≥ 61.0 cm. With the same center at each macroplot, a subplot with a 7.3 m radius was used for trees with DBH < 61 cm and ≥ 12.7 cm. Trees smaller than 12.7 cm were measured on microplots with a 2.1 m radius within each subplot (Woudenberg et al. 2010). The four subplots were arranged with one in the center of the cluster and the other three located 36.6 m away at azimuths of 120° , 240° , and 360° . In general, trees in the plot are uneven-aged. There were 1161 plots that were measured only once from 2001 to 2007. We only selected plots in which (1) ponderosa pine was the dominant species comprising at least 80% of stand basal area and (2) each set of macroplot, subplot, and microplot had to include at least 10 trees after excluding trees with heights shorter than 1.37 m. These constraints yielded 59 plots from the FIA database with latitudes between 36.69°N and 41.95°N (Fig. 1). Because the age of site trees was measured at breast height, we estimated the total age by adding the years for a seedling to reach 1.37 m. We estimated the years using 1.37 divided by mean annual height growth at the later years. Then, the SI was estimated from Meyer's table (Meyer 1938) based on total age and ranged from 16 to 49 m at 100 years in these plots.

Statistical analysis

The self-thinning boundary line (or maximum SDI line) was historically established with two techniques. First, a line was visually drawn along the upper boundary of data points plotted in a logarithmic scale of tree size and density (Reineke 1933; Yoda et al. 1963). Second, an ordinary least-squares regression was applied for all or arbitrarily selected observations to find the slope of the line that then was moved to the upper boundary of data. Although the least-squares regression technique is more objective, it requires data that meet various assumptions justifying the use of regression for purposes of prediction, such as normality and ho-

Fig. 3. The maximum stand density index (SDI) (or self-thinning) line and 95% confidence intervals obtained using 0.99 quantile regression (QR) or stochastic frontier function (SFF) analysis for all plots. Both research plots only and all plots provided identical parameter estimates for QR (Table 2) and similar parameter estimates for SFF (Table 3).



mogeneity of variance, which are often violated by data collected in uneven-aged stands on multiple sites and (or) at different years. In addition, this “average” maximum size–density line was not a “biological” self-thinning line per se (see Zhang et al. (2005)). Recently, researchers have used other techniques to fit the two parameters with major axis analysis or principle component analysis (Bi and Turvey 1997), production frontiers (Bi 2004; Zhang et al. 2005), and quantile regression (Zhang et al. 2005). Although each has its advantages and disadvantages in fitting the self-thinning line, these new methods eliminate many of the concerns over the historical approaches.

In this study, we used the quantile regression (QR) developed by Koenker and Bassett (1978) and stochastic frontier functions (SFFs) developed by Aigner et al. (1977) to model the relationship between QMD as a dependent variable and TPH as an independent variable (model (4.1)). Because site quality was reported to affect the site occupancy and perhaps the density–size relationship (Bi et al. 2000), we included plot-level SI as a covariate in model (4.2).

$$(4.1) \quad \log(\text{QMD}) = \beta_0 + \beta_1 \log(\text{TPH}) + \varepsilon$$

$$(4.2) \quad \log(\text{QMD}) = \beta_0 + \beta_1 \log(\text{TPH}) + \beta_2 \log(\text{SI}) + \varepsilon$$

where QMD, TPH, and SI were defined as before, β_i ($i = 0, 1, 2$) are regression coefficients, and ε is residual error for the model.

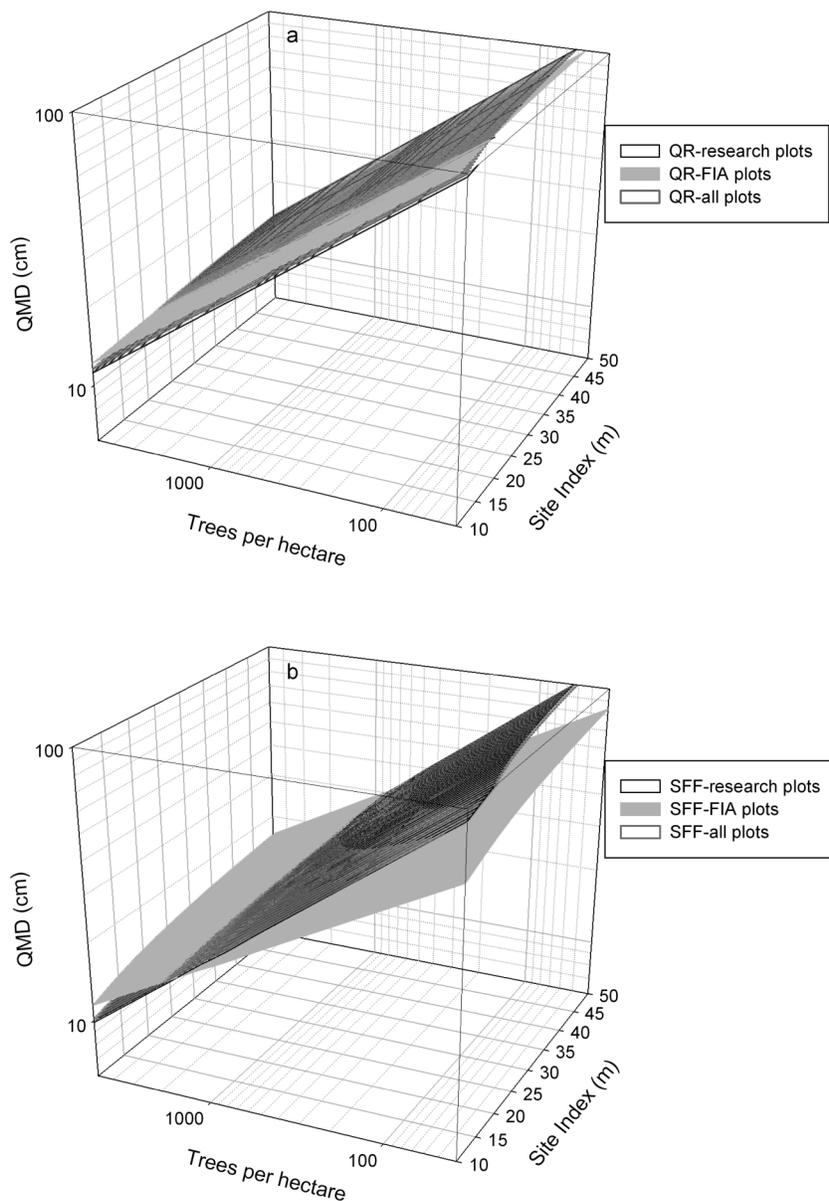
The QR estimates QMD rates of change as a function of TPH for all quantiles [0, 1], rather than just on changes in mean. QR is especially useful where the extremes are important, such as the upper quantile of diameter growth at given stand densities. This is critical for determining tree mortality with the SAS QUANTREG procedure (SAS Institute Inc. 2010) in this study. Furthermore, it offers considerable model robustness because it makes no distributional assumption about the error term in the model, making it more useful for heterogeneous data in many fields of ecology. It has been used to model self-thinning annual plants (Cade and Guo 2000) and forest stands (Zhang et al. 2005), and to estimate rates of

Table 2. Quantile regression coefficients and SEs (in parentheses), probability for testing $\beta_i = 0$, number of observations, objective function, Wald statistics, and probability of model fitting with a 99% quantile for model (4.1) without the site index term and model (4.2).

Model fit	Data set	$\beta_0 (\pm SE)$	P	$\beta_1 (\pm SE)$	P	$\beta_2 (\pm SE)$	P	n	Objective function	Wald	P	Max. SDI
Model (4.1)	Research plots only	2.797 (0.072)	<0.001	-0.450 (0.026)	<0.001			688	1.659	292.3	<0.001	1250
	FIA plots only	2.721 (0.546)	<0.001	-0.429 (0.178)	0.019			59	0.096	5.8	0.016	1162
	All plots	2.797 (0.065)	<0.001	-0.450 (0.023)	<0.001			747	1.769	389.8	<0.001	1250
Model (4.2)	Research plots only	2.571 (0.126)	<0.001	-0.449 (0.028)	<0.001	0.138 (0.063)	<0.029	688	1.602	265.0	<0.001	
	FIA plots only	2.670 (1.392)	0.060	-0.444 (0.280)	0.118	0.059 (0.779)	0.939	59	0.094	2.5	0.112	
	All plots	2.596 (0.118)	<0.001	-0.446 (0.024)	<0.001	0.119 (0.055)	<0.032	747	1.713	342.6	<0.001	

Note: Maximum stand density index (SDI) was estimated using a quadratic mean diameter (QMD) of 25.4 cm with these new parameterized equations for model (4.1) only.

Fig. 4. Self-thinning surfaces estimated from the full model (eq. (4.2)) with either the 99% quantile regression (QR) or the stochastic frontier function (SFF) using data from research plots, FIA plots, and all plots in California, USA.



change for functions along or near the upper boundary of the conditional distribution of response in ecology (Cade and Noon 2003). Because we were seeking the self-thinning boundary line, the highest quantile that showed the 95% confidence intervals in the SAS output was chosen.

The SFF was developed in econometrically modeling maximum and minimum production (Aigner et al. 1977) and has been successfully used to derive self-thinning lines in forestry (Bi et al. 2000; Bi 2004; Zhang et al. 2005). It not only estimates parameter standard errors and allows the incorporation of other independent

variables, but also outputs the site occupancy for each plot (Bi et al. 2000; Bi 2001). In the SFF regression, the error term ε in model (4) becomes a compound random variable $\nu - v$, where ν is a two-sided random variable assumed to be independent and identically distributed, $\nu \sim N(0, \sigma_\nu^2)$, and v is a non-negative random variable associated with technical inefficiency, assumed to be a half normal $v \sim N(0, \sigma_v^2)$ with $0 \leq v \leq \infty$. The term $0 \leq e^{-v} \leq 1$ becomes technical efficiency, i.e., the site occupancy. When $e^{-v} = 1$, the site is fully occupied; the system has reached the maximum growth at the present density, and any further growth must be with mortality in the stand. We used SAS QLM procedure (SAS Institute Inc. 2010) to fit SFF with maximum log-likelihood and site occupancy for each observation was estimated following Battese and Coelli (1988) and Bi (2001). The approximate confidence limits for the self-thinning line were estimated using bootstrapping techniques.

Before the analysis, we plotted QMD and TPH in a log-log scale (Fig. 2) to obtain the general relationship between both variables. We ran QR and SFF for models (4.1) and (4.2) using data from research plots only (109 plots and 688 observations) measured multiple times, FIA plots only (59 plots) measured once, and both (168 plots).

Results

Plot characteristics

Results indicated that all 15 research sites, although not all plots, experienced some rates of mortality based on the number of trees in the establishment year and the latest measurement year, suggesting that self-thinning had occurred (Table 1). At least one plot at each site exceeded SDI 494 TPH (200 trees·acre⁻¹) based on Oliver's slope (-1.77). The SDI value is close to 568 TPH (230 trees·acre⁻¹), defined as a threshold for a zone of imminent bark beetle mortality. Only 11 plots showed an SDI lower than 494 and mainly in plots established between 1986 and 1988.

Across 109 research plots, QMD ranged from 10.1 to 86.1 cm in the latest measurements and densities varied between 45 and 2496 TPH (Table 1 and Fig. 2). The range of QMD was much broader than the data used by Reineke (1933), with a QMD of 4–20 cm from which a self-thinning slope was determined (Fig. 2).

Over 59 FIA plots, the QMD ranged from 8.2 to 54.5 cm and plot densities spanned 82 and 3193 TPH (Fig. 2). Using Oliver's slope (-1.77), SDI ranged from 180 to 1311 TPH; 36 of 59 plots showed and SDI lower than 494 TPH. Mortality was recorded in 31 of 59 plots.

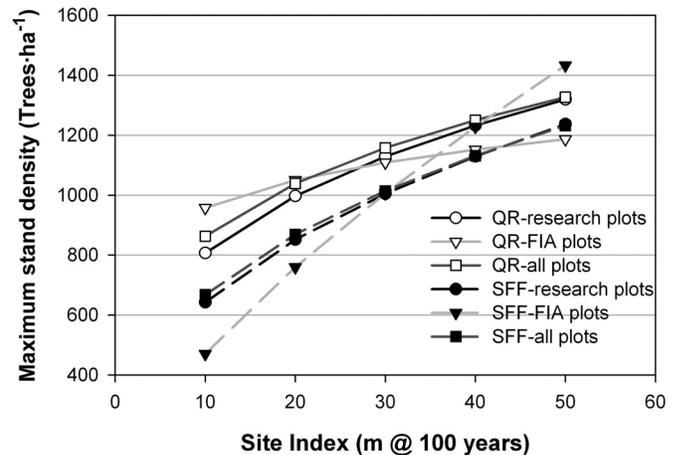
Quantile regression fit

We found that the 99th quantile line covered most stand observations (model (4.1)) (Supplementary data; Fig. 3).¹ Statistical tests from the model showed no evidence that either β_0 or β_1 was zero (Table 2). Variation of both parameter estimates was much higher when the model included FIA plots only because of the lower numbers of plots. Fitting parameter estimates were similar with either research plots only or all plots. We regarded the line fitted from all plots as our self-thinning boundary line with an intercept of 2.797 and a slope of -0.450, yielding the maximum SDI to be 1250 TPH for a QMD of 25.4 cm (Table 2).

If site quality measured by SI was considered (Table 2), we found that all terms (β_i) were nonsignificant for FIA plots ($P > 0.11$). In addition, the self-thinning plane estimated from FIA plots differed significantly from other planes based on research plots or all plots (Fig. 4). In fact, when we used data from either research plots or all plots, all terms (β_i) were highly significant ($P < 0.001$). The self-thinning equations were derived for research plots (eq. (5)) and for all plots (eq. (6)).

$$(5) \quad \log(\text{QMD}) = 2.571 - 0.449 \log(\text{TPH}) + 0.138 \log(\text{SI})$$

Fig. 5. Maximum stand density at a quadratic mean diameter (QMD) of 25.4 cm for different site indices estimated by the full model (eq. (4.2)) with either the 99% quantile regression (QR) or the stochastic frontier function (SFF) using data from research plots, FIA plots, and all plots in California, USA.



$$(6) \quad \log(\text{QMD}) = 2.596 - 0.446 \log(\text{TPH}) + 0.119 \log(\text{SI})$$

Because the self-thinning planes tended to overlap each other between models (Fig. 4a), we consider eq. (6) as our preferred self-thinning surface from quantile regression fit. Accordingly, the maximum SDI for a QMD of 25.4 cm would be 860 TPH at an SI of 10 m and 1330 TPH at an SI of 50 m (Fig. 5).

Stochastic frontier function

Similar trends were also found for parameter estimates with SFF analyses (Table 3). Using research plots only or all plots yielded a similar result without considering site quality (Supplementary data).¹ Figure 3 showed a self-thinning boundary line and its 95% confidence limits using all plots. Parameter estimates showed larger variation (SE) using FIA plots only than those using research plots only or all plots (Table 3). Both fits provided a similar maximum SDI of 1050 or 1060 TPH at a QMD of 25.4 cm.

The full-model (eq. (4.2)) fits suggest that the self-thinning boundary lines varied with SIs (Table 3). Therefore, the self-thinning trend should have been a plane (Fig. 4b). A positive coefficient (β_2) for SI indicated that, at a higher productive site, whether from higher soil fertility, favorable climate, or favorable silvicultural treatments, a stand could grow greater diameters (or biomass) for a given stand density without self-thinning mortality. The maximum SDI indexed to a QMD of 25.4 cm was lower than with the 0.99 quantile with 670 TPH at an SI of 10 m and 1230 TPH at an SI of 50 m (Fig. 5).

All research plots had reached 80% of site occupancy during their stand development (Fig. 6). Most showed the highest site occupancy in the final measurement. The FIA plots were close to or over 70% by the time the plots were measured. Mortality occurred when site occupancy reached 75%; heavy mortality occurred beyond 95% on research plots.

Discussion

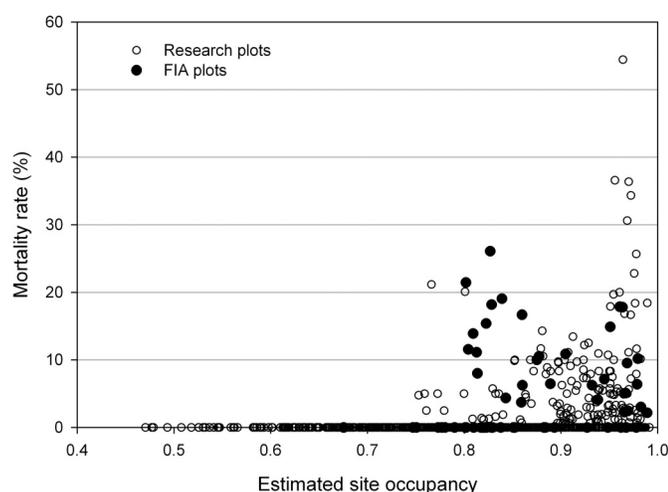
Our main purpose was to reevaluate size-density relationships for even-aged ponderosa pine and to statistically fit the self-thinning boundary lines (maximum SDI lines). Results showed that both QR and SFF fitted data well with both a full (eq. (4.2)) and reduced model (eq. (4.1)), if either research plots or all plots were

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2013-0133>.

Table 3. Regression coefficients and SEs (in parentheses), probability for testing $\beta_1 = 0$, number of observations and error terms of the stochastic frontier function (SFF) for model (4.1) without a site index term and model (4.2).

Model fit	Data set	β_0 (\pm SE)	P	β_1 (\pm SE)	P	β_2 (\pm SE)	P	n	σ	σ_v	σ_{ϵ}	AIC	Max. SDI
Model (4.1)	Research plots only	2.837 (0.027)	<0.001	-0.474 (0.010)	<0.001			688	0.255	0.030	0.253	-757.5	1050
	FIA plots only	2.470 (0.089)	<0.001	-0.370 (0.037)	0.001			59	0.113	0.074	0.086	-108.9	760
	All plots	2.820 (0.025)	<0.001	-0.468 (0.009)	<0.001			747	0.250	0.030	0.248	-849.8	1060
Model (4.2)	Research plots only	2.514 (0.055)	<0.001	-0.462 (0.010)	<0.001	0.188 (0.030)	<0.001	688	0.250	0.028	0.249	-790.4	
	FIA plots only	2.068 (0.168)	<0.001	-0.335 (0.032)	<0.001	0.232 (0.085)	0.006	59	0.132	0.048	0.123	-112.9	
	All plots	2.517 (0.052)	<0.001	-0.455 (0.009)	<0.001	0.173 (0.027)	<0.001	747	0.246	0.027	0.244	-883.9	

Note: Maximum stand density index (SDI) was estimated using a quadratic mean diameter (QMD) of 25.4 cm with these new parameterized equations for model (4.1) only. AIC, Akaike's information criterion.

Fig. 6. Relationship between mortality rate and site occupancy estimated from the full model (eq. (4.2)) with the stochastic frontier function (SFF) method across multiple years for research plots and individual observations at the time of measurement for FIA plots across California, USA.

used. The SFF yielded slightly higher intercepts and more negative slopes so that the maximum SDI indexed to a QMD of 25.4 cm was smaller than what QR estimated (Tables 2 and 3 and Fig. 3). If we use fitted models without considering the effect of site quality, maximum stand density would be between 1050 and 1250 TPH indexed to a QMD of 25.4 cm. This number is higher than the limiting SDI of 900 TPH suggested by Oliver (1995) and much lower than the SDI of 2000 TPH at a QMD of 25.4 cm visually estimated from Reineke's figure (Reineke 1933). However, it is in the range of SDI from Weller (1987) and under the 1270 TPH reported in pure ponderosa pine stands by Woodall et al. (2005).

The discrepancy between our findings from those established previously in California might be related to several factors. First, Reineke (1933) used density as the dependent variable and QMD as the independent variable. A switch between variables could have yielded a significant difference in fitting a regression line. Second, data used by Reineke (1933) were much more limited than ours in terms of stand diameter and stocking levels (Fig. 2). Third, pure ponderosa pine stands are rare in the southern Sierra Nevada from which Reineke (1933) obtained his data. Therefore, plots were squeezed into a rather small area, which could lead to some erroneous overestimates of stand density. Fourth, the stands used by Reineke (1933) showed no evidence of self-thinning. Using plots that had not started self-thinning would steepen the slope with high density as Fig. 2 suggests (Westoby 1984). Fifth, the 900 TPH suggested by Oliver (1995) was not estimated from his data per se but rather from a slope recalculated from Reineke's data and a visually fitted intercept. The number might be perfect for certain research plots with the largest diameter, but not with a smaller

mean diameter of trees on the plots. Finally, because the current self-thinning line is much flatter than the previous line, the maximum SDI would have been much lower with a QMD greater than 25.4 cm.

The size–density relationship has been examined across the distribution range of ponderosa pine. Weller (1987) found a much steeper slope (-0.72 ± 0.66 SD) between bole biomass and density in a log–log scale by averaging 27 thinning lines established from three yield tables. Using 2% of the highest SDI plots, mostly with a QMD of 25 cm or less, Edmister (1988) found a slope of -0.602 for ponderosa pine in the US Rocky Mountains and Southwest. DeMars and Barrett (1987) obtained -0.566 from a yield table for their yield simulator. All these numbers are much lower than the least slope (-0.474) in this study. To our knowledge, no one has reevaluated the slope for this species with stands over a very broad range of QMDs and densities, measured over multiple years. However, many authors have examined other species with both research plots and (or) FIA plots (Weller 1987; Long and Shaw 2005; VanderSchaaf and Burkhart 2007) and even with uneven-aged or mixed-species stands (Long and Daniel 1990; Solomon and Zhang 2002; Woodall et al. 2003, 2005). As we expected, Reineke's maximum SDI for ponderosa pine was seriously challenged.

Our maximum SDI did not cover the data used by Reineke (1933) in Fig. 2. That the plots were overstocked and small as indicated by Reineke might cause some stands to exceed this line. In fact, we had observed several rather small plots standing alone or adjacent to roads in which SDI reached as high as 1450 TPH. These plots were excluded based on our plot selection criteria. Therefore, a plot in which trees are under intensive competition is most appropriate for establishing a self-thinning boundary line or maximum SDI line. In addition, stands would be the best for maximum SDI if self-thinning had started. Onset of competition could have occurred in the stands with a smaller mean diameter of trees as well as a larger mean diameter of trees. The reason for the falloff in the relative density (Shaw and Long 2010) for the fewer large diameter trees (Fig. 3) could be the lack of intense intertree competition, but appreciable tree-understorey competition (Zhang et al. 2013a).

Another important finding in this study was the significant effect of site quality on the self-thinning lines (Tables 2 and 3), which yielded the self-thinning planes (Fig. 4). Results showed that maximum SDI was much lower at a lower SI than SDI at a higher SI (Fig. 5). Similar to the reduced model earlier (eq. (4.1)), no substantial difference was found in model fits by using data from both research plots and all plots regardless of whether the QR or SFF method was used. However, because only 59 plots were included, the parameter estimates from FIA plots alone yielded immense variation, from which no common result could be generated (Figs. 4 and 5).

The effect of site quality on size–density relationships has been previously reported. DeBell et al (1989) found that mortality in *Pinus taeda* L. plantations was considerably lower for a given density in Hawaii with an SI of 25 m at 25 years than in the southeastern US with an SI of 21 m, although the trees were larger in Hawaii.

A similar trend with site quality also was found in ponderosa pine grown in California compared with plots in southeast Oregon (Zhang et al. 2013b). Bi (2001) reported a significant relative SI effect on the self-thinning surface for *Pinus radiata* D. Don. Later, Bi (2004) found that soil fertility increased the intercept of the self-thinning line in *Erigeron canadensis* L. With both reports, Bi presented clear evidence that site quality increased site-carrying capacity or occupancy, which increased the intercepts of the self-thinning boundary line. This phenomenon was also found in *Pseudotsuga menziesii* (Mirb.) Franco, *Tsuga heterophylla* (Raf.) Sarg., and *Alnus rubra* Bong. (Weiskittel et al. 2009) and reviewed by Morris (2003). In this study, we did not separate fertilized plots from others, although the effect of fertilization on site quality was reflected in the calculation of plot-level SI. In fact, our estimate of SI considered all factors that influence tree height growth on each plot. A significant effect of site quality on the self-thinning boundary line was demonstrated (Figs. 4 and 5).

A remaining issue is that we could not statistically estimate “a threshold for a zone of imminent mortality” as Oliver (1995) established. One possibility is to use the site occupancy of 0.75 to be a reference SDI (Fig. 6). If 1060 TPH was the maximum SDI for near 100% site occupancy, an SDI of 800 TPH would approximate the onset of mortality for a stand. Obviously, numbers would vary with SIs.

The suggested maximum SDI will cover tree mortality caused by any stress including insects and pathogens. In fact, considerable mortality was caused by *Dendroctonus* spp. (Oliver 1995). Because these create very high stress in forests of North America (Fettig et al. 2007), stands with lower densities have low probabilities of mortality (Oliver 1995, 1997).

Acknowledgements

We thank all who designed, installed, maintained, and measured these plots during the last 50 years. Thanks also to Dr. Lianjun Zhang for suggesting the use of quantile regression analysis and to Dr. Jim Baldwin, our station statistician, for helping in the stochastic frontier regression and boot strapping to approximate the confidence intervals. The suggestions for improving the manuscript from Dr. Haiganoush Preisler, Dr. Mark Kimsey, and the anonymous reviewers are greatly appreciated. Sierra Cascade Intensive Forest Management Research Cooperative provided partial financial support for the last measurements. Use of trade names in this paper does not constitute endorsement by the United States Forest Service.

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