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Scientific paper

Differences in the maximum size–density relationship of *Pinus occidentalis* Swartz, within three humidity gradients

Running head: Maximum Size–Density of *Pinus occidentalis*

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Abstract

Introduction. The maximum size–density relationship (MSDR) establishes self-thinning thresholds in forest stands. For *Pinus occidentalis* Swartz, responses to humidity gradients across ecological zones in La Sierra, within the northcentral portion of Cordillera Central of the Dominican Republic, remain poorly understood.

Objectives. We aimed to (1) quantify MSDR across dry, intermediate, and humid ecological zones within La Sierra region, Santiago Province, Dominican Republic; (2) test whether slopes and intercepts of the natural log-transformed Quadratic Mean Diameter

and stand density in terms of trees per hectare by ecological zone [ln(QMD)–ln(TPH)] relationships differ among ecological zones; and (3) compare Reduced Major Axis (RMA) with Ordinary Least Squares (OLS).

Materials and methods. Quadratic mean diameter (QMD) and stand density in terms of trees per hectare (TPH) from even-aged *P. occidentalis* plots across dry, intermediate, and humid zones were log-transformed. Analyses were limited to plots with relative density > 0.7. MSDR were estimated using RMA regression in reciprocal form, with delta-method confidence intervals. OLS models observed–fitted comparisons, and mean absolute error were used for benchmarking.

Results. RMA slopes steepened from dry (−0.510) to intermediate (−0.669) and humid zones (−0.894), indicating stronger self-thinning under humid conditions, though slope differences were not significant. Intercepts differed significantly among zones ($p < 0.001$), revealing vertical shifts in size–density trajectories. RMA slopes exceeded OLS estimates, while observed–fitted patterns and mean absolute error were comparable across methods.

Conclusions. While slopes correspond with classic self-thinning theory, intercept shifts indicate ecological effects on growth potential. Results support using RMA for estimating size–density relationships in forest stands where both variables show variability and assist with zone-specific silvicultural density management.

Keywords: allometry, ecological gradients, forest productivity, self-thinning, silviculture.

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Introduction

Maximum size–density relationships (MSDR) are essential for understanding forest dynamics and informing silvicultural practices (Lee & Choi, 2019; Lee et al., 2025). They establish the upper limit of stand density for a specific tree size, according to the self-thinning rule (Reineke, 1933; Yoda et al., 1963), which predicts a decline in tree density as the average tree size increases. Conventional models like Reineke's, which utilizes quadratic mean diameter (QMD), and Yoda's, which uses total aboveground biomass per tree or stand, typically assume a consistent slope close to -3/2.

Ordinary least squares (OLS) and reduced major axis (RMA) regressions use different statistical approaches: OLS minimizes vertical deviations under a stochastic error model for the response variable, whereas RMA estimates a structural relationship by treating variability in both variables symmetrically (Smith, 2009; Sokal & Rohlf, 1981). RMA regression offers a more suitable approach, treating both variables equally, ensuring scale invariance, and allowing it to reflect biological constraints more accurately, rather than merely predicting one variable based on another (Smith, 2009). Scale invariance here refers to the property that RMA slope estimates remain unchanged under linear rescaling of either variable.

Reineke's stand density index and Yoda's −3/2 self-thinning rule are best viewed as empirically derived size–density relationships that are guided more by ecological and geometric principles than by strict theoretical models. In even-aged forests, the link between stand density and tree size has been described through various empirical formulas, each calibrated with observational data and predicting different slopes in ln-transformed form (West & Ratkowsky, 2025; Zhang et al., 2022). Consequently, these models not only suggest different expected slopes but also highlight variations in their foundational assumptions about size metrics, stand structure, and scaling behavior. This emphasizes the need to consider their conceptual background when interpreting size–density relationships. These different formulas stem from varied assumptions regarding tree size metrics, stand structure, and scaling behavior, yet they all describe the same fundamental self-thinning process.

Two classical models describe self-thinning relationships. Reineke's Stand Density Index predicts a slope of −1.605 when ln (TPH) is expressed as a function of ln (QMD).

The −3/2 power law proposed by Yoda et al. (1963) predicts a slope of −1.5 when biomass is related to density. When expressed in reciprocal form as ln (QMD) versus ln (TPH), these values correspond approximately to −0.623 and −0.667, respectively. These figures are indicative of differing assumptions regarding tree geometry, growth limitations, and resource distribution (Pretzsch et al., 2024). Reineke's Stand Density Index (SDI) is grounded in empirical data that associate stem density, as a response variable, with QMD, as an explanatory variable, underscoring the structural constraints on stand occupancy. In contrast, the -3/2 Power Law, based on metabolic scaling theory, examines the relationship between biomass production and mortality. As a result, these models suggest different expected slopes and also highlight variations in their fundamental assumptions regarding size metrics, stand structure, and scaling behavior. This emphasizes the need to understand their conceptual basis when analyzing size–density relationships.

Environmental context also plays a vital role. Holdridge's (1987) life zone classification uses temperature, precipitation, and evapotranspiration to establish ecologically relevant units. These zones reflect climatic factors that affect tree growth, competition, and mortality, thereby enhancing the accuracy of MSDR by integrating site-specific environmental differences. Within the study area, five Holdridge life zones are present; three were selected for this analysis based on the distribution of *P. occidentalis*. These include: the Dry Ecological Zone (DEZ), corresponding to Subtropical Dry Forest; the Intermediate Ecological Zone (IEZ), representing Subtropical Humid Forest; and the Humid Ecological Zone (HEZ), classified as Very Humid Subtropical Forest.

P. occidentalis is an ecologically and economically important species of Hispaniola Island, for which no species-specific MSDR has ever been established. It is the most abundant species capable of successfully growing in and protecting the acidic, shallow, and infertile sandy soils that characterize the steep slopes of the mountain ranges (Bueno-López et al., 2024).

Although the MSDR has been widely applied in temperate and boreal forests, species-specific MSDR remain poorly documented for tropical pines. In particular, no MSDR has previously been established for *P. occidentalis*, an ecologically dominant species in the Cordillera Central of Hispaniola. Moreover, few studies have explicitly examined whether

ecological gradients modify the position or geometry of self-thinning lines in tropical systems. Addressing this gap is essential for developing ecologically sound density-management guidelines and for understanding how site productivity and moisture availability influence competitive dynamics in tropical pine forests.

Our objectives were: 1) to model the MSDR of *P. occidentalis* using RMA regression models across dry (DEZ), intermediate (IEZ), and humid (HEZ) ecological zones, within La Sierra region, Santiago Province, Dominican Republic; 2) test whether slopes and intercepts of the natural log-transformed Quadratic Mean Diameter and stand density in terms of trees per hectare by ecological zone [ln(QMD)–ln(TPH)] relationships differ among ecological zones; and 3) to compare the performance and estimates of RMA and OLS regression methods in modeling the size–density relationship under measurement error in both variables.

Materials and Methods

Study area

The study area is located within La Sierra region, Santiago Province, Dominican Republic, in the north-central part of Cordillera Central, DR, covering approximately 1 800 km^2 (Figure 1). Even-aged natural stands of *P. occidentalis* in the study are located within three ecological zones (EZs) according to the Holdridge (1987) classification system, which incorporates climatic variables including mean annual biotemperature, total annual precipitation, and potential evapotranspiration. These include Dry Ecological Zone (DEZ), corresponding to Subtropical Dry Forest; the Intermediate Ecological Zone (IEZ),

representing Subtropical Humid Forest; and the Humid Ecological Zone (HEZ), classified as Very Humid Subtropical Forest are found at average elevations of 500, 650, and 800 m, respectively (Bueno-López, 2024). The average annual temperatures are 24 ºC in DEZ, 24 ºC in the IEZ, and 22 ºC in the HEZ. Following the same order, their typical yearly rainfall ranges from 800 to 1 000 mm, 1 000 to 2 000 mm, and 1 200 to 1 600 mm. These forests usually develop in shallow, carbonate, lateritic, low-producing soils with rugged topography. Plots were assigned to zones based on their georeferenced location and corresponding climatic data using GIS overlays of Holdridge life zones.

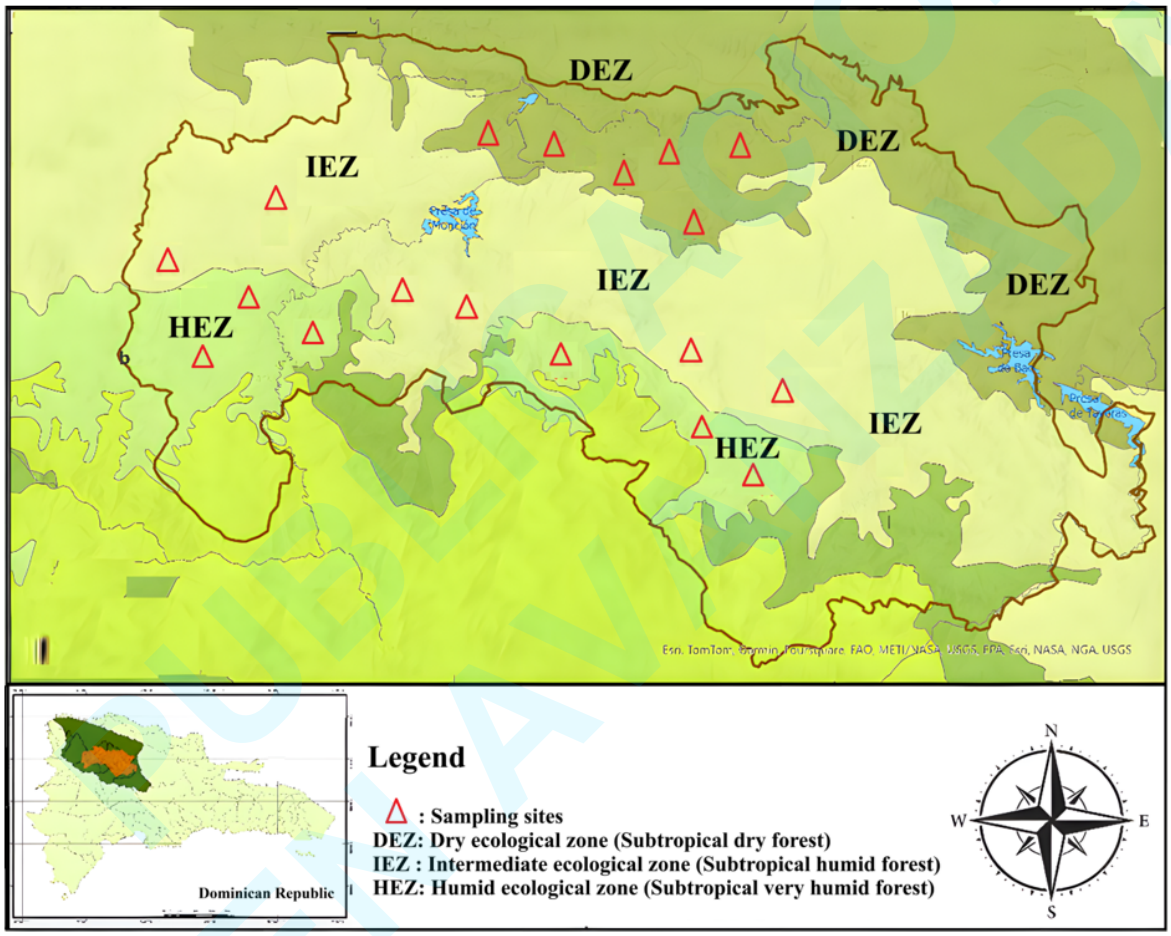

Figure 1. Sampling sites within La Sierra, Dominican Republic, across Dry, Intermediate, and Humid ecological zones used to compare natural log-transformed Quadratic Mean Diameter [ln (QMD)] and stand density in terms of trees per hectare [ln (TPH)] of *Pinus occidentalis* self-thinning relationships under contrasting humidity gradients.

Data sources

In each ecological zone (DEZ, IEZ, and HEZ), six even-aged forests dominated by *P. occidentalis* were randomly selected. Each forest comprised multiple stands of similar age and structure. Within each forest, between one and five temporary circular plots (350 m²) were established, resulting in a total of 64 plots in the DEZ, 63 plots in the IEZ, and 60 plots in the HEZ.

Within each plot, all trees with diameter at breast height (dbh) ≥ 10 cm were measured. Measurements included dbh, from which quadratic mean diameter (QMD) was calculated, and tree counts used to derive stand density (trees·ha^{-1}, TPH). All trees present in each plot were included; no trees were excluded based on health status or crown class, as MSDR analysis requires full representation of stand structure. Descriptive statistics for the plots in each EZ are presented in Table 1.

Table 1. Descriptive statistics of *Pinus occidentalis* stand variables in the dry ecological zone (DEZ), intermediate ecological zone (IEZ), and humid ecological zone (HEZ) in La Sierra, Dominican Republic.

Ecological Zone	Number of stands	Variables	Mean	SD	Minimum	Maximum
DEZ	64	TPH (trees·ha^{-1})	344	191	114	1238
		BA (m^2·ha^{-1})	12.31	4.43	4.36	26.41
		QMD (cm)	22.25	4.17	14.25	35.01
IEZ	63	TPH (trees·ha^{-1})	627	400	200	2 400
		BA (m^2·ha^{-1})	22.84	6.69	14.39	50.44
		QMD (cm)	23.49	6.03	11.27	36.93
HEZ	60	TPH (trees·ha^{-1})	822	522	276	2603
		BA (m^2·ha^{-1})	30.12	12.25	14.75	84.62
		QMD (cm)	23.83	6.77	11.36	37.97

SD: standard deviation, TPH: trees per ha, BA: total basal area, QMD: quadratic mean tree diameter.

Maximum size-density relationships

Data Transformation

To evaluate the relationship between stand structure and density, the QMD (cm) and stand density (trees per hectare, TPH) were transformed using the natural logarithm. This transformation was applied to linearize the allometric relationship between tree size and stand density and to stabilize variance across the dataset. In the reciprocal formulation adopted here, ln(QMD) was treated as the response variable and ln(TPH) as the explanatory variable.

Regression Approach

Although Reineke's (1933) original formulation expresses ln(TPH) as a function of ln(QMD), the reciprocal formulation—ln(QMD) as a function of ln(TPH)—was adopted in this study. This transformation is algebraically equivalent and has been widely used in diameter-based MSDR analyses to facilitate interpretation of vertical shifts in size–density trajectories. Importantly, this formulation does not imply a causal direction from density to diameter, but represents the same self-thinning boundary expressed in reciprocal form. RMA regression was used to estimate MSDR because both ln (QMD) and ln (TPH) reflect random variability in the relationship and biological variability. RMA is therefore appropriate for estimating structural allometric boundaries rather than predictive relationships. While no single method is universally optimal, RMA provides a transparent and biologically interpretable framework consistent with much of the MSDR literature.

The RMA model tested was:

$$\ln(QMD) = \hat{\alpha}_{RMA} + \hat{\beta}_{RMA} * ln(TPH) + \varepsilon$$

Where, ϵ is error term representing stochastic variability, $\hat{\alpha}_{RMA}$ is the RMA intercept and $\hat{\beta}_{RMA}$ is the RMA slope. The intercept was calculated using the mean-centered formulation: $\hat{\alpha}_{RMA} = \overline{\ln(\mathrm{QMD})} - \left(\hat{\beta}_{RMA} * \overline{\ln(\mathrm{TPH})}\right)$. The RMA slope was calculated as $\hat{\beta}_{RMA} = \mathrm{sign(r)} * {S_y}/{S_x}$; where, r is the Pearson correlation coefficient between ln (QMD) and ln (TPH), $S_{\ln(\mathrm{QMD})}$ and $S_{\ln(\mathrm{TPH})}$ are the sample standard deviations (Solomon & Zhang, 2002). The standard error (SE) of the RMA slope was estimated using the delta method as:

$$SE\left(\hat{\beta}_{RMA}\right) = \hat{\beta}_{RMA} * \sqrt{\frac{(1-r^2)}{(n-2)}}$$

This approach provides an approximation of the variance of the slope accounting for sampling uncertainty (Sokal & Rohlf, 1981). Ninety-five percent confidence intervals were computed using the t-distribution with n-2 degrees of freedom.

Statistical Comparisons

To assess the differences in self-thinning trajectories among ecological zones, pairwise comparisons of RMA slope and intercept estimates were conducted using independent-sample t-tests following methods outlined in Sokal and Rohlf (1981). These tests were employed to determine whether the observed disparities in scaling relationships between zones were statistically significant.

Additionally, OLS regressions were conducted for comparison with the RMA models to assess differences in slope estimates and their uncertainties. While OLS aims to minimise deviations in the response variable, RMA estimates a symmetric structural relationship. Consequently, differences in the slopes highlight the different statistical goals of each method rather than issues with model assumptions.

To express the relationship between ln (QMD) and ln (TPH) the OLS regression model used in each zone was:

$$\ln\ (QMD) = \ \hat{\alpha}_{OLS} + \hat{\beta}_{OLS} * \ln(TPH) + \ \varepsilon$$

where, $\hat{\alpha}_{OLS}$ is the OLS intercept, $\hat{\beta}_{OLS}$ is the OLS slope, and ϵ is error term representing stochastic variability.

All analyses were performed on the same subset of plots with relative density values exceeding 0.7, approaching full site occupancy. Relative density was calculated as the ratio between observed stand density and the estimated maximum stand density derived from the self-thinning boundary. Model diagnostics involved residual inspection and comparison of observed versus fitted values. The Absolute Mean Error (MAE) was used as a descriptive measure of model performance.

Residual analyses were conducted to assess model fit and detect potential outliers or violations of model assumptions. Plots of residuals versus fitted values were inspected for each zone to confirm homoscedasticity and linearity.

This same subset of plots was used consistently for both RMA and OLS regression analyses to ensure direct comparability of slope estimates.

All analyses were conducted using IBM SPSS (IBM Corp., 2020) and Microsoft Excel (Microsoft 365 Subscription). Figures and regression plots were generated with these two software programs.

Results and discussion

Reduced major axis regression intercepts and slopes comparison among ecological zones

Table 2 presents the descriptive statistics of the natural log-transformed Quadratic Mean Diameter [ln(QMD)] and stand density, represented by trees per hectare [ln(TPH)], for plots with a relative density (RD > 0.7), which are assumed to be experiencing self-thinning. It provides context for the variability and range of input values used in the RMA regression analyses.

Table 2. Descriptive statistics of natural log-transformed Quadratic Mean Diameter [ln (QMD)] and stand density in terms of trees per hectare [ln (TPH)] by ecological zone in La Sierra, Dominican Republic.

		ln (QMD)				ln (TPH)			
Zone	**n**	**Mean**	**SD**	**min**	**max**	**mean**	**SD**	**min**	**max**
DEZ	5	3.09	0.33	2.70	3.47	6.40	0.64	5.69	7.12
HEZ	4	2.99	0.28	2.71	3.38	7.51	0.32	7.13	7.86
IEZ	7	3.07	0.43	2.42	3.61	6.88	0.64	5.98	7.78

Values represent sample size (n), mean, standard deviation (SD), minimum, and maximum. Ecological zones: dry (DEZ), intermediate (IEZ), and humid (HEZ).

Table 3 presents the slope and intercept coefficients from RMA regression models that describe the relationship between ln(QMD) and ln(TPH) for fully stocked, even-aged *P. occidentalis* plots with a RD > 0.7 across the three ecological zones. Across zones, the RMA slopes indicate a progressively stronger negative size–density relationship from the DEZ to the HEZ. This pattern suggests increasingly pronounced self-thinning dynamics under more humid conditions. Differences in intercepts further indicate vertical shifts in the ln(QMD)–ln(TPH) relationship among ecological zones, reflecting larger average tree sizes at comparable stand densities in more humid environments.

Table 3. Estimated slope and intercept parameters of the maximum size–density relationship between natural log-transformed quadratic mean diameter [ln QMD, response variable) and stand density in terms of trees per hectare (ln TPH, explanatory variable) across the three ecological zones of *Pinus occidentalis*, obtained using reduced major axis regression.

Ecological Zone	Parameter	Coefficient	Standard Error	95 % Confidence Interval
DEZ	Intercept	6.355	—	—
	ln (TPH)	−0.510	0.043	[−0.648, −0.371]
IEZ	Intercept	7.671	—	—
	ln (TPH)	−0.669	0.058	[−0.818, −0.521]
HEZ	Intercept	9.706	—	—
	ln (TPH)	−0.894	0.157	[−1.568, −0.221]

DEZ: dry ecological zone, IEZ: intermediate ecological zone, HEZ: humid ecological zone.

Table 3 summarizes the estimated RMA regression parameters for each ecological zone (DEZ, IEZ, and HEZ). RMA slope standard errors and confidence intervals were estimated using the delta method and intercepts were derived from the slope and the means of ln(QMD) and ln(TPH). The estimated slope for the DEZ was −0.510, indicating a moderate inverse relationship between stand density and QMD. In the IEZ, the slope was −0.669, reflecting a stronger inverse relationship, while the steepest slope was observed in the HEZ (−0.894), indicating a more pronounced decline in average tree size with increasing stand density.

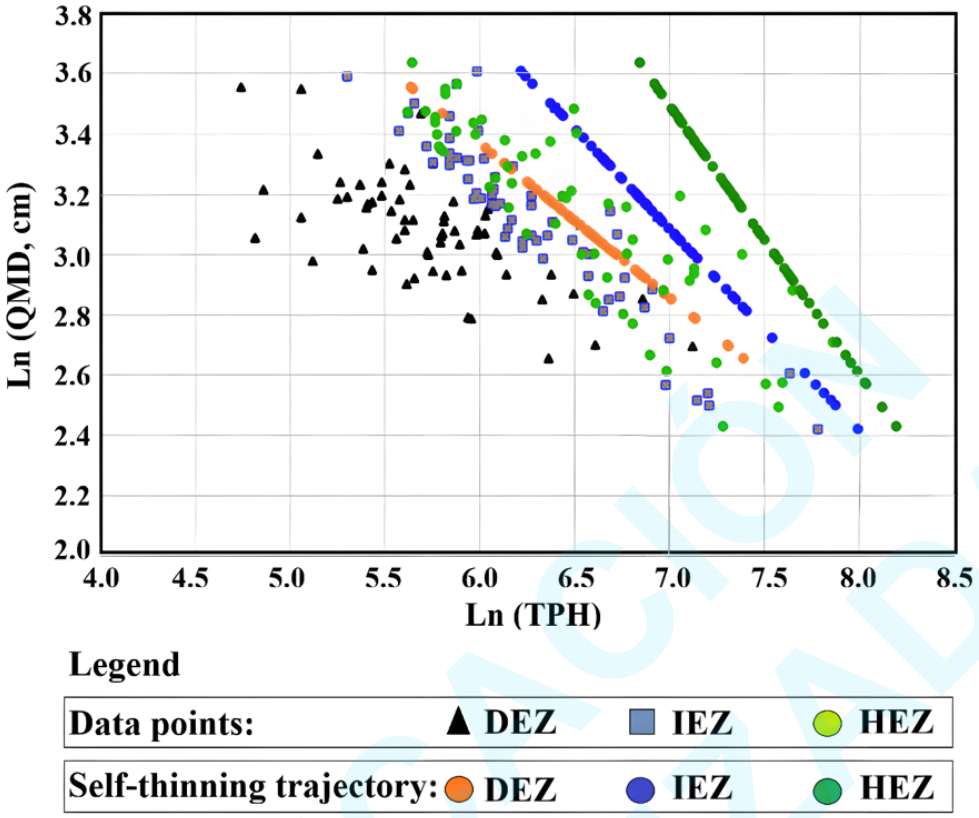

Figure 2. Relationship between natural log-transformed quadratic mean diameter [ln(QMD)] and stand density in terms of trees per hectare [ln(TPH)] across ecological zones for *Pinus occidentalis*. Data points represent plots within the DEZ (dry), IEZ (intermediate), and HEZ (humid) ecological zones in La Sierra, Dominican Republic. Consecutive lined points indicate the zone-specific self-thinning trajectories derived from reduced major axis regression models.

The relationship between ln(QMD) and ln(TPH) was further examined visually across ecological zones, first including all plots in each zone (Figure 2) and second, only considering plots with RD > 0.7 (Figure 3). Both figures visually illustrate the RMA regression lines for the relationship between ln(QMD) and ln(TPH) across the three ecological zones: DEZ, IEZ, and HEZ. Distinct scatter points and corresponding RMA regression lines represent each zone. The steeper slope in the HEZ confirms corresponding coefficient values that indicate a more pronounced decline in mean tree size with increasing stand density, consistent with self-thinning dynamics in more humid environments.

Figure 3 corroborates what is already depicted in Figure 2; the steeper slope in the HEZ suggests a more pronounced decline in mean tree size with increasing stand density, consistent with self-thinning dynamics in more humid environments.

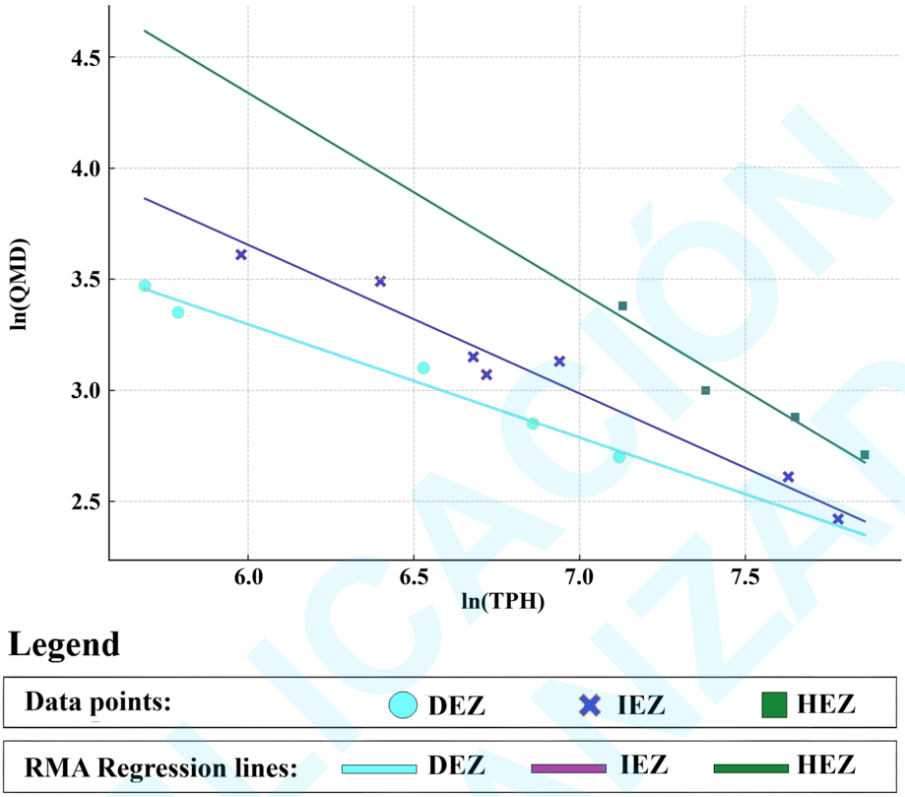

Figure 3. The relationship between natural log-transformed tree size in terms quadratic mean diameter [ln(QMD)] and stand density in terms of trees per hectare [ln(TPH)] across three ecological zones was estimated using reduced major axis (RMA) regression. Each colored line indicates the zone-specific RMA fit for the dry (DEZ), intermediate (IEZ), and humid (HEZ) ecological zones of *Pinus occidentalis*. Variations in the slopes among these zones highlight differences in size–density relationships, aligning with self-thinning patterns observed under different moisture conditions.

Differences in self-thinning relationships among ecological zones

Pairwise comparisons of RMA slopes revealed no statistically significant differences between zones at the α = 0.05 level (Table 4). For instance, the slope for the IEZ (−0.669) did not differ significantly [t (3) = 2.21, p = 0.115] from that of the DEZ (−0.510). Similarly, comparisons between the HEZ (−0.894) and both the DEZ and IEZ yielded non-significant results (p = 0.142 and 0.310, respectively), providing no statistical evidence of differences in slope among ecological zones.

Pairwise comparisons of the RMA regression intercepts showed significant differences between ecological zones (Table 4). The intercept for the IEZ (7.671) was significantly higher [t (3) = −34.42, p < 0.001] than that of the DEZ (6.355). Similarly, the HEZ had a significantly greater intercept (9.706) than both the DEZ [t (2) = −80.73, p < 0.001] and IEZ [t (2) = −42.81, p < 0.001]. These differences reflect upward vertical shifts in the ln (QMD)–ln (TPH) relationship, consistent with higher mean tree sizes at equivalent stand densities in more humid zones.

The slopes reported here are expressed using the reciprocal formulation of the size–density relationship, with ln(QMD) modeled as a function of ln(TPH). In this formulation, the classic Reineke self-thinning slope of −1.605 for ln(TPH) versus ln(QMD) corresponds to a reciprocal slope of approximately −0.623 when expressed as ln(QMD) versus ln(TPH). The RMA slope estimates obtained for the DEZ (−0.510), IEZ (−0.669), and HEZ (−0.894), therefore, fall within, or reasonably close to, the range expected from established self-thinning theory, particularly given ecological variability and sample size limitations. Comparable reciprocal slopes have been reported for conifer-dominated stands in temperate systems, including values between −0.59 and −0.78 for *Pseudotsuga menziesii* (Mirb.) Franco, *Tsuga heterophylla* (Raf.) Sarg., and *Cunninghamia lanceolata* (Lamb.) Hook. forests (Han et al., 2024; Heiderman & Kimsey, 2021). Expressing slopes in reciprocal form does not alter the underlying biological interpretation of self-thinning; rather, it provides an alternative representation of the same boundary, facilitating comparisons of vertical shifts in size–density trajectories across ecological gradients.

Table 4. Summary of the independent *t*-tests comparing reduced major axis slopes and intercepts between dry (DEZ), intermediate (IEZ) and humid (HEZ) ecological zones of

Pinus occidentalis for the natural log-transformed quadratic mean diameter [ln(QMD)] and stand density in terms of trees per hectare [ln(TPH)] relationships.

Comparison	Slope 1	Slope 2	SE of Difference	*t*(df~3)	*p*-value	*t*(df~2)
DEZ vs. IEZ	-0.509	-0.669	0.072	2.206	0.115	
DEZ vs. HEZ	-0.509	-0.894	0.163		0.145	2.367
IEZ vs. HEZ	-0.669	-0.894	0.167		0.310	1.348
Comparison	**Intercept 1**	**Intercept 2**	**SE of Difference**	***t*(df~3)**	***p*-value**	***t*(df~2)**
DEZ vs. IEZ	6.355	7.671	0.038	-34.419	0.0001	
DEZ vs. HEZ	6.355	9.705	0.042		0.0002	-80.731
IEZ vs. HEZ	7.671	9.705	0.048		0.0005	-42.815

SE: standard error; t: Student's t distribution; df: degrees of freedom.

OLS vs. RMA Slope Differences

Table 5 below provides the Ordinary Least Squares (OLS) regression summary for plots with RD > 0.7 in each ecological zone (DEZ, IEZ, HEZ). It includes estimated coefficients, standard errors, and R^2 values, which allow direct comparison with the RMA regression results (Table 6). The comparison of OLS (Table 4) and RMA slopes (Table 2) indicated that RMA estimates were consistently steeper because this method considers the variance in both variables. The differences in slope estimates between OLS and RMA in this study arise from their distinct statistical objectives, not from conflicting biological meanings (Smith, 2009). OLS determines regression parameters by minimizing vertical differences in the response variable, assuming a stochastic error model (Sokal & Rohlf, 1981), while RMA captures a symmetric relationship by considering variability in both ln(QMD) and ln(TPH) (Warton et al., 2006). The choice of model form and fitting approach is known to influence coefficient estimates and derived stand density indices, particularly when nonlinear relationships are linearized, as shown through simulation studies of stand density models (Marchi, 2019). As a result, the two methods naturally produce different slopes when both variables vary, which is common in forest inventory data. Here, OLS

serves as a reference point, whereas RMA helps define the structural boundary of the size–density relationship, aligning with prior MSDR research focused on boundary estimation rather than prediction (Solomon & Zhang, 2002).

Table 5. Ordinary Least Squares (OLS) regression results for the relationship between natural log-transformed quadratic mean diameter [ln(QMD)] and stand density in terms of trees per hectare [ln(TPH)] by ecological zone of *Pinus occidentalis*.

Zone	Intercept	Intercept SE	Slope	Slope SE	R^2	n
DEZ	6.319	0.279	-0.504	0.043	0.978	5
IEZ	7.584	0.399	-0.657	0.058	0.963	7
HEZ	9.497	1.176	-0.867	0.157	0.939	4

SE: standard error; R^2: coefficient of determination, n: sample size.

Table 6. Ordinary least squares (OLS) and reduced major axis (RMA) regressions results for the relationship between natural log-transformed quadratic mean diameter [ln(QMD)] and stand density in terms of trees per hectare [ln(TPH)] by ecological zone of *Pinus occidentalis*.

Zone	OLS	RMA
DEZ	ln (QMD) = 6.319−0.504*ln (TPH)	ln (QMD) = 6.355−0.510*ln (TPH)
IEZ	ln (QMD) = 7.584−0.657*ln (TPH)	ln (QMD) = 7.671−0.669*ln (TPH)
HEZ	ln (QMD) = 9.497−0.867*ln (TPH)	ln (QMD) = 9.706−0.894*ln (TPH)

DEZ: dry ecological zone, IEZ: intermediate ecological zone, HEZ: humid ecological zone.

In Figure 4, the consistently steeper RMA slopes indicate how the method accommodates variance in ln (QMD) and ln (TPH), providing a more accurate estimate of the size–density relationship in forest stands.

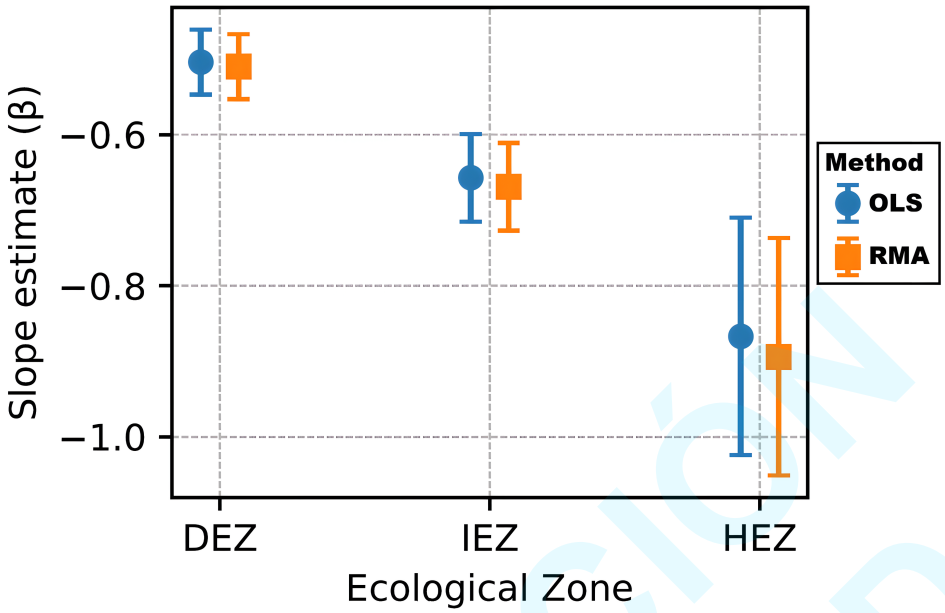

Figure 4. Comparison of slope estimates and standard errors (vertical bars) from ordinary least squares (OLS) and reduced major axis (RMA) regression across ecological zones (DEZ: dry ecological zone, IEZ: intermediate ecological zone, HEZ: humid ecological zone) of *Pinus occidentalis*.

Residual Analysis and Model Fit

Pearson correlation coefficients (r) were above 0.96 in all zones, indicating strong linear relationships. Residual plots (Figure 5) displayed no significant heteroscedasticity or outliers. The high degree of explained variance and the linearity of the fitted relationships support the appropriateness of the RMA approach for this data.

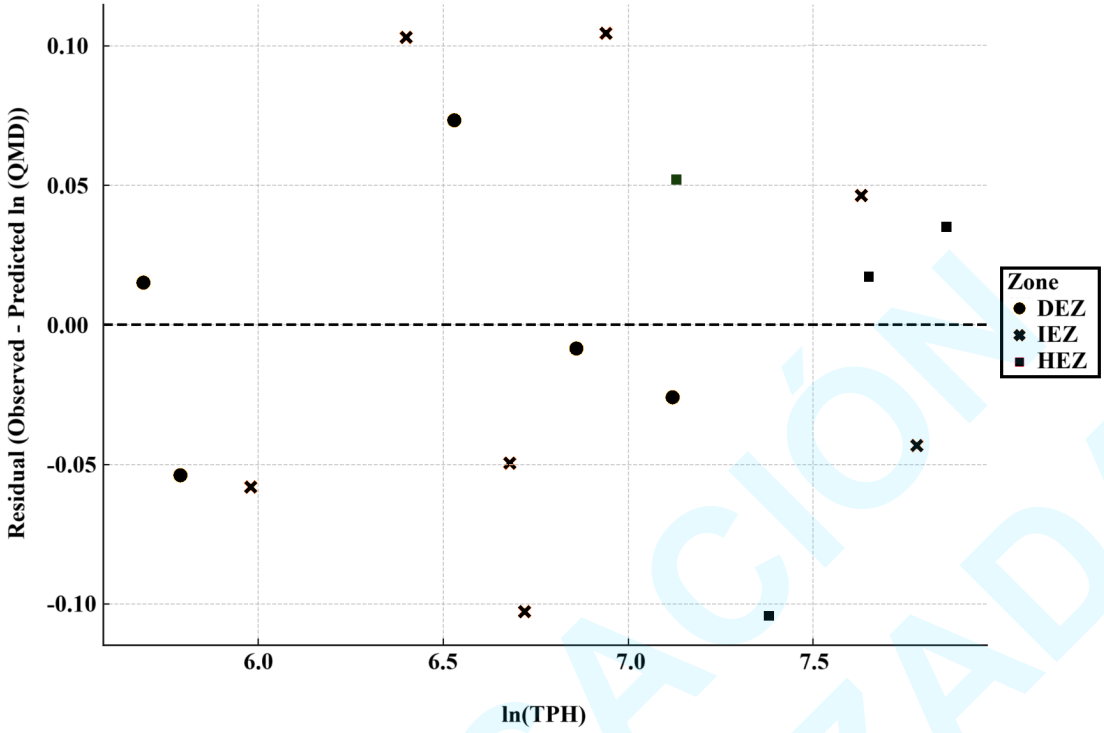

Figure 5. Residuals of the reduced major axis (RMA) regression for the natural log-transformed quadratic mean diameter [ln(QMD)] and stand density in terms of trees per hectare [ln(TPH)] by ecological zone of *Pinus occidentalis* were calculated as the difference between observed and predicted ln (QMD) values. DEZ: dry ecological zone, IEZ: intermediate ecological zone, HEZ: humid ecological zone.

The increasingly pronounced slopes from DEZ to HEZ indicate a heightened presence of self-thinning dynamics in more humid environments. The more pronounced slope observed in HEZ suggests that increases in stand density have led to more significant reductions in average tree size. Marked differences in intercepts indicate that, at a specified density, trees located in humid zones tend to achieve greater sizes. These findings align with ecological theory, which asserts that resource-rich environments foster the growth of larger trees under comparable competitive pressures.

Pairwise comparisons of RMA slopes revealed no statistically significant differences among zones at the $\alpha = 0.05$ level, aligning with the hypothesized value of -0.625 proposed by Reineke (1933) in his Stand Density Index (SDI). Similarly, Yang and

Brandeis (2022) reported that the slope coefficient did not differ significantly among physiographic zones for forest types in the eastern United States.

Reineke's rule indicates that the classic self-thinning slope is approximately -1.605 when considering ln (TPH) as the response variable and ln (QMD) as the predictor. Conversely, this corresponds to a slope of about -0.625 when ln (QMD) serves as the response and ln (TPH) as the explanatory variable. When the variables are switched, the slope value becomes its reciprocal. Thus, the slopes found for the DEZ, IEZ, and HEZ in the ln (QMD) versus ln (TPH) relationship correspond to -0.625, aligning with the reciprocal of -1.605. These results are consistent with the historically influential Reineke empirical value and with most empirical studies (Long et al., 2022, 2025), reflecting established findings in forest stand dynamics.

Han et al. (2024) reported slopes for ln(TPH) versus ln(QMD) ranging from −1.28 to −1.70 in mixed forests dominated by *C. lanceolata* in China, corresponding to reciprocal slopes between −0.781 and −0.588 when expressed as ln(QMD) versus ln(TPH). Similarly, Heiderman and Kimsey (2021) reported a self-thinning slope of −1.517 for stands dominated by *P. menziesii* and −1.461 for stands dominated by *T. heterophylla*, with reciprocal slopes of −0.659 and −0.684, respectively.

The analysis of Ordinary Least Squares (OLS) and Reduced Major Axis (RMA) regression revealed notable disparities in slope estimates across different ecological zones. OLS slopes ranged from −0.504 in the DEZ to −0.867 in the HEZ. Compared to OLS slopes, RMA slopes were consistently steeper, with values between −0.510 and −0.894 across ecological zones. These variations result from the different mathematical properties of each method, not from statistical significance or biological conflicts. Since OLS and RMA adapt different fitting criteria, the slope differences alone do not signal which model is better. To allow direct comparison, observed ln(QMD) values were contrasted with estimates from both approaches, and model accuracy was measured using the Mean Absolute Error (MAE), highlighting deviations between observed and fitted data. Consequently, RMA is better suited for scenarios where both ln (QMD) and ln (TPH) face measurement error or natural variability (Smith, 2009).

Observed–Fitted Comparison and Descriptive Error Metrics

Because differences between OLS and RMA slope estimates represent numerical properties of the fitting methods rather than inferential statistics, additional diagnostics were used to compare how each approach represents the observed data. Observed ln(QMD) values were plotted against values estimated by both OLS and RMA regressions for plots with RD > 0.7 (Figure 6). In addition, model performance was summarized using the Mean Absolute Error (MAE), which quantifies the average absolute deviation between observed and fitted values without relying on distributional assumptions.

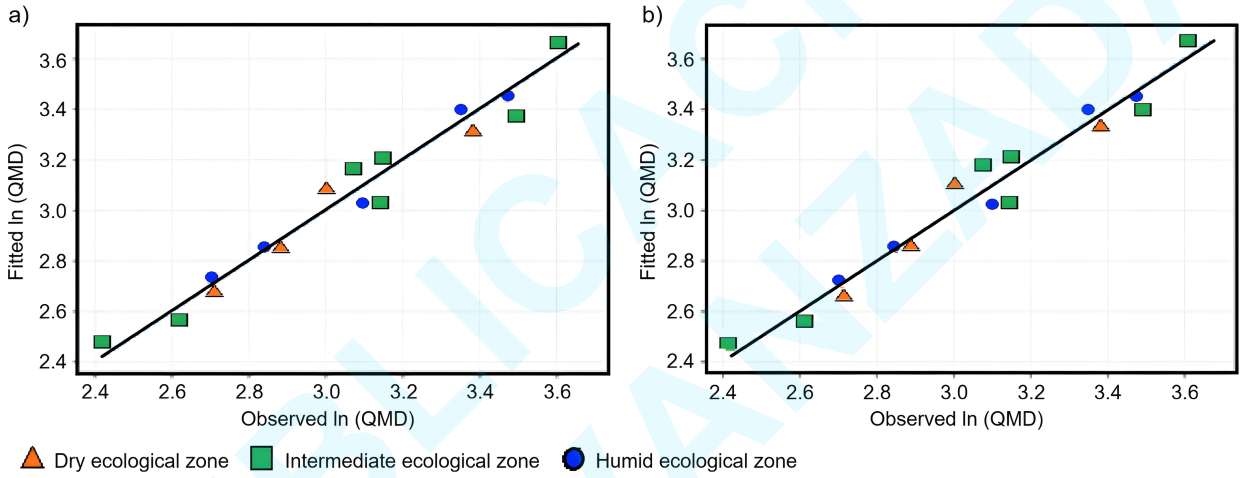

Figure 6. Observed versus fitted ln(QMD) values are shown for both Ordinary Least Squares (OLS) (panel a) and Reduced Major Axis (RMA) regressions (panel b) across three ecological zones. The points represent observed ln(QMD) values, while the fitted ones come from regression models based on plots with relative density (RD) greater than 0.7. The solid 1:1 line provides a reference for agreement between observed and predicted values; departures from this line indicate residual error and model dispersion.

Mean Absolute Error by zone

Across ecological zones, RMA produced slightly lower MAE values than OLS in the DEZ (0.0349 vs. 0.0368) and HEZ (0.0501 vs. 0.0516), while MAE values were comparable between methods in the IEZ (0.0728 vs. 0.0710). These results indicate a marginally improved representation of the size–density boundary by RMA rather than superior predictive accuracy.

In ecological research on allometry and size–density relationships, RMA regression is typically favored due to its lack of directional assumptions regarding variable error structures (c). Considering the biological characteristics of forest inventory data, where both tree size and density are subject to the variability inherent in ecological data rather than imprecision in the field measurements, RMA enhances the robustness of inferences regarding the structural dynamics at play. The steeper slopes found in the RMA models across all zones indicate a greater density-dependent limitation on tree size compared to the insights derived solely from OLS models.

The steady increase in slope steepness from dry to humid zones observed in both modeling methods suggests that resource availability, particularly moisture, intensifies competitive interactions. This results in more pronounced declines in average tree size as stand density rises. Site quality is known to affect maximum size-density relationships (Ray et al., 2023), with warmer and drier conditions leading to lower maximum densities (Kweon & Comeau, 2021). Flatter slopes imply a greater resilience of a stand to low-density conditions, where diameter growth is more pronounced, while indicating trees' reduced capacity to endure crowding (Han et al., 2024). Forest site productivity impacts the intercepts of self-thinning lines (Seo et al., 2025), consistent with our findings that mesic environments can support larger trees at any given density.

Pairwise comparisons of the RMA regression intercepts revealed significant differences among ecological zones. According to Zhang and Chen (2021), although the slope of self-thinning lines tends to remain consistent (Walker et al., 2020), the intercepts differ across sites, thereby supporting our findings on how ecological zones influence tree size-density relationships. The findings of Li and Wang (2020) show that environmental factors and stand development stages affect the intercepts of self-thinning lines, further confirming our observations of differences across ecological zones.

Recent studies support the idea that although the slope of self-thinning lines tends to be consistent across various ecological conditions, the intercepts can differ considerably depending on factors like site productivity, species composition, and environmental gradients (Kweon & Comeau, 2021). Our results corroborate this research, indicating that ecological zones affect the maximum possible tree size at a specific density.

Our findings support the ecological gradient identified and substantiate the use of RMA as a more cautious and realistic modeling method for analyzing forest structure. This conclusion aligns with recent research suggesting that the intercept and slope of the self-thinning line can be influenced by factors like topography, climate, soil, and other site-specific variables (Brunet-Navarro et al., 2016; Heiderman & Kimsey, 2021; Looney & Shaw, 2025).

Alternative statistical methods, such as mixed-effects models, quantile regression, and stochastic frontier analysis, have also been used to estimate maximum size–density boundaries. These approaches can explicitly handle hierarchical data, unbalanced sampling, and upper-bound behavior. Applying these methods to *P. occidentalis* in future studies would enable formal testing of random-site effects and comparisons of boundary estimation techniques, complementing the traditional RMA framework used here.

Conclusions

This study explored the size–density relationship of *Pinus occidentalis* across various ecological zones in La Sierra, Dominican Republic, utilizing Reduced Major Axis (RMA) regression. Self-thinning slopes increased from the dry to the humid ecological zone, suggesting stronger density-dependent competition under higher moisture availability, although the differences were not statistically significant. Intercepts differed significantly across zones, indicating vertical shifts in the ln(QMD)–ln(TPH) relationship and

suggesting that trees in more humid environments attain larger sizes at comparable stand densities. These differences suggest that maximum stand density and thinning thresholds need to be tailored to different site productivity levels and should be adjusted based on ecological zones. RMA produced steeper slopes than Ordinary Least Squares (OLS), highlighting the importance of accounting for variability in tree size and stand density. Overall, moisture gradients influence stand structure and provide a quantitative basis for zone-specific density management in tropical pine forests.

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Conflicts of Interest

The authors declare that we have no financial conflicts of interest or known personal relationships that could have influenced the work presented in this article.

Artificial Intelligence (AI) Use Statement

The authors declare that they have not used generative AI or AI-assisted technologies for the development of this manuscript.

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