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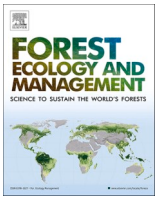

Quantifying minimum site occupancy requirements of common forest tree species in northern New England, USA: Implications for stocking assessment

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ABSTRACT

Minimum stand densities necessary to achieve crown closure is an important aspect of stocking assessment that merits more attention. Managers concerned with optimizing individual-tree and stand-level responses will benefit from improved guidance on minimum densities when designing intermediate silvicultural treatments. To do so we generated a dataset of crown projection areas using previously published crown width models and considered various assumptions about crown packing and the spatial arrangement of stems. Implied stem densities based on predicted crown sizes were used to determine the minimum stand density index (SDI_{MIN}) by species. These values were integrated with published information about maximum stand density index (SDI_{MAX}) providing estimates of minimum relative density (RD_{MIN}=SDI_{MIN}/SDI_{MAX}). Mixed-effects models were used to predict RD_{MIN} and determine the slope of the minimum size-density relationship (mSDR) for common softwood and hardwood species in northern New England, USA. Large differences in crown-stem allometry were revealed between open- and forest-grown trees (ΔRD ~0.2). Hardwoods occupied more growing space than softwoods (ΔRD ~0.05), a finding primarily attributed to differences in crown architecture, though species shade-tolerance may also play a role. Minimum stem densities capable of achieving crown closure span a wide range determined by species composition and stand history. Importantly, the implied slope of mSDR (~ −1.0) differed substantially from that of the benchmark maximum size-density relationship (MSDR; −1.605), corresponding to lower values of RD_{MIN} for smaller-sized stems and earlier in stand development than when stems are larger and older. Our models and resulting estimates of RD_{MIN} can be used to locate the lower boundary of stocking space on size-density diagrams.

1. Introduction

Assessing maximum size-density relationships (MSDR) in forest stands remains an active area of research (Andrews et al., 2018; Bravo-Oviedo et al., 2018; Burkhart, 2013). Broad based synthesis of this topic has generally pointed to an approximate universality of the self-thinning slope defining the MSDR (Enquist et al., 1998; Reineke, 1933; Westoby, 1981), though results from more narrowly focused studies have revealed notable exceptions (e.g., Pretzsch and Biber, 2005; Zeide, 1987). In general, the location of the intercept for the MSDR is reasonably well characterized for most commercially important tree species in the United States (Dixon, 2002; Woodall and Weiskittel, 2021; Yang and Brandeis, 2022). In contrast, the challenge of establishing minimum density levels to meet specific silvicultural objectives (Drew and Flewelling, 1979; Gingrich, 1967), arguably of comparable importance to the maximum density line, has received much less attention.

Two parallel graphical approaches, stocking guides (SGs) and density management diagrams (DMDs), were developed to encompass the possible combinations of stem numbers and average stem size, i.e., stocking space. Both seek to establish an upper limit of stand density

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(subordinate to the MSDR) that minimizes losses attributable to density-dependent mortality, and a lower limit intended to ensure full site occupancy (Ray et al., 2023). Both approaches assume that maintaining stand density within these bounds will result in high net periodic annual increment (PAI) for a given combination of size and density (Long, 1985). Regionally, SGs (Gingrich, 1967) have served this purpose in the eastern US, whereas DMDs (Drew and Flewelling, 1979) have been favored in the western US. While different techniques and terminology were used to characterize the inner workings of these graphical approaches, both seek to convey similar information related to minimum densities to achieve full site occupancy and maximum densities to avoid mortality. Newton (1997, 2021) provides comprehensive reviews the historical development of DMDs including recent innovations (i.e. dynamic and structural model variants) and suggests ways forward for this well-established analytical framework.

Conceptually, the so-called B-line on SGs corresponds to the level of stocking where the crown competition factor (CCF) (Krajicek et al., 1961) equals 100 % and as such is intended to portray the minimum stem density at a given average size, or stage of development, that is capable of fully occupying the above-ground growing space assuming the realization of fully developed crowns. Essentially, this approach uses diameter-based regression models to fit the crown projection area (CPA) of open grown trees with the assumption of no interstitial spaces between adjacent crowns to determine implied stem densities. The crown-stem allometry of the B-line on the original Gingrich (1967) SG for upland oaks (*Quercus* spp.) equates to 58 % of full stocking (the ratio of A-line to B-line density across a range of stand quadratic mean diameter [QMD]), though that value should not be viewed as universal (Roach, 1977). Drew and Flewelling (1979) derived a crown closure (CC) line for their DMD by fitting a diameter-based crown width model, and assuming circular crowns and triangular spacing, corresponding to ~9 % interstitial space. Because relative densities ($RD=TPH_{OBS}/TPH_{MAX}$, where TPH = trees per ha) varied little according to their analysis, ranging from 0.13 to 0.17 at CC for the youngest/densest (1483 TPH) and the oldest/sparsest (247 TPH) stand conditions, respectively, those authors established their CC-line at a constant value of 0.15 RD. Importantly, these authors went on to make a distinction between stand-level production and individual-tree growth, noting that whereas the later could be maximized at e.g., RD=0.15, the former is realized at considerably higher densities, e.g., RD=0.4; also see related treatment by Long (1985). Effectively, this distinction presents two alternative definitions of full site occupancy, with their relevance determined by management objectives. The DMD framework introduced to North America by Drew and Flewelling (1977) can be traced to the work of earlier Japanese scientists, where Ando (1962) (reviewed by Newton, 2021) is attributed with identifying the 'beginning curve of competition', which corresponds to the notion of stand crown closure, and thus the CC-line.

Depiction of B-line stocking is central to SG development (reviewed by Seymour and Smith, 1987). In contrast, the inclusion of a CC-line on DMDs using measurements of crown allometry is uncommon, with some notable exceptions (Newton, 2009; Newton and Weetman, 1993; Smith, 1989; Wilson et al., 1999). This convention, presumably initiated by the approach taken by Drew and Flewelling (1979), has led to a 'recycling' of similar values (i.e., 0.15–0.25 RD) to characterize CC on DMDs. More important here is the fact that DMDs tend not to use the CC-line as a benchmark for management recommendations. In fact, recommendations for managing down as low as even 0.25 RD are uncommon, and presented with the caveat that stand-level growth will be sacrificed to speed diameter growth of individual-trees (Long, 1985). Further, different methodologies employed by the two graphical approaches have resulted in some confusion regarding the disparity between what intuitively should be similar estimates of minimum stocking percent and RD (if multiplied by 100). For example, cross walking benchmark values for the B-line and CC-line gives disparate values (e.g., 55–58 % stocking vs 0.15–0.25 RD, respectively) owing to the different ratio denominators used, i.e., SGs use an average maximum density (A-line) whereas DMDs use a true upper boundary (Drew and Flewelling, 1979; Gingrich, 1967; Ray et al., 2023).

In contrast to the biologically determined upper boundary of stand density, the effective lower boundary, hereafter the minimum size-density relationship (mSDR), may be influenced by factors related to *stand history*. We use this term broadly to refer to aspects encompassing stem density and spatial distribution at stand origin, as well as timing and intensity of intermediate silvicultural treatments e.g., thinning, or exploitative partial cutting (Nyland, 1992), and natural disturbances. Collectively, these factors exert a strong influence over the capacity of tree crowns to occupy growing space (Oliver and Larson, 1996; Seymour and Smith, 1987). In recognition of this influence, Leak and Lamson (1999) presented two B-lines on their revised SG for white pine (*Pinus strobus*), one for unmanaged and another positioned at lower level for previously managed stands, where the latter formulation acknowledges the increased capacity for those trees to develop larger crowns (Seymour and Smith, 1987). Recent work by Pretzsch (2019) using models of crown-stem allometry to describe patterns of growing space occupancy in forest stands reinforces the continued relevance of this longstanding approach.

Given these ambiguities and the modest amount of attention that has been paid to this topic, our work seeks to provide more robust estimates of minimum stem densities required to achieve canopy closure. To do so we focus on two related questions: 1) Is there a broadly applicable value of RD (or stocking percent) that can be used to characterize mSDR, and if not, what factors drive observed differences (e.g., species, species groups, shade tolerance)? And 2) Is there parallelism between MSDR and mSDR, or do these relationships diverge in a biologically meaningful way? Our findings are presented in the context of developing more informative size-density management charts (i.e., SGs and DMDs), and we suggest ways that forest managers can use this information.

2. Materials and Methods

2.1. Study area and dataset

We define the study area as encompassing the overlapping distributional ranges of the study species in the northern New England states of Maine, New Hampshire, and Vermont USA. The regional climate corresponds to Dfb (warm-summer humid continental) designation following the Köppen system. Temperatures range from −7.4–20 °C, and annual precipitation is ~1110 mm/yr. Soils across the region are of glacial till origin with properties ranging from well-drained loams and sandy loams on the ridges to poorly and very poorly drained loams on the flatter and lower lying areas. Prominent forest types in this region include spruce-fir (*Picea-Abies*), hemlock-northern hardwood (*Tsuga-Fagus, Betula, Acer*), aspen-birch (*Populus-Betula*), and oak-pine (*Quercus-Pinus*). A long and active history of forest management in this region has interacted with natural disturbances, giving rise to forest stands that exhibit a high degree of compositional and structural diversity (Loo and Ives, 2003; Seymour, 1995; Janowiak et al., 2018). The allometric relationships derived from datasets described in the following paragraph are broadly representative of contemporary stand conditions.

The dataset was assembled from previously published sources, including crown width models presented by Russell and Weiskittel (2011), and estimates of maximum stand density index (SDI_{MAX}) from Woodall and Weiskittel (2021) and the Northeast Variant of the Forest Vegetation Simulator (FVS) (Dixon and Keyser, 2021) (Table 1). Two estimators of crown size were available, maximum crown width (MCW) representing biological maximum size (i.e., open-grown) and largest crown width (LCW) representing the average forest grown condition; both use diameter at breast height (DBH) as the predictor variable (Russell and Weiskittel, 2011). The LCW regression model includes an option to incorporate live crown ratio (CR) as a covariate, but the authors reported that this did not improve performance substantially; we

Table 1
Description of the species characteristics used to conduct the analysis. Shade tolerance scores (TOL) are from Niinemets and Valladares (2006), crown projection areas (CPA) were determined using models from Russell and Weiskittel (2011) for maximum crown width (MCW) and largest crown width (LCW), and multiple estimates of maximum stand density index (n) came from Woodall and Weiskittel (2021) and the Northeast Variant of the Forest Vegetation Simulator (FVS; Dixon and Keyser, 2021).

					CPA at QMD=25-cm			Maximum SDI	
GRP	Species	Code	Common name	TOL	MCW (m^2)	LCW (m^2)	LCW/MCW	n	Avg±SD (TPH)
SW	*Abies balsamea*	BF	balsam fir	5.01	58.63	13.46	0.23	5	1430 ± 193
SW	*Tsuga canadensis*	EH	eastern hemlock	4.83	64.61	25.88	0.40	7	1398 ± 120
SW	*Picea rubens*	RS	red spruce	4.39	49.51	14.45	0.29	6	1438 ± 133
SW	*Thuja occidentalis*	WC	northern white-cedar	3.45	34.52	12.07	0.35	6	1635 ± 168
SW	*Pinus strobus*	WP	eastern white pine	3.21	52.17	20.27	0.39	8	1414 ± 98
SW	*Picea glauca*	WS	white spruce	4.15	43.01	15.34	0.36	5	1116 ± 251
HW	*Fagus grandifolia*	AB	American beech	4.75	110.29	31.67	0.29	9	*1191 ± 132
HW	*Betula papyrifera*	PB	paper birch	1.54	94.86	26.97	0.28	7	1327 ± 173
HW	*Populus tremuloides*	QA	quaking aspen	1.21	58.63	22.90	0.39	7	1333 ± 332
HW	*Acer rubrum*	RM	red maple	3.44	87.25	29.51	0.34	15	1088 ± 216
HW	*Quercus rubra*	RO	red oak	2.75	96.25	32.98	0.34	2	1369 ± 490
HW	*Acer saccharum*	SM	sugar maple	4.76	85.11	30.19	0.35	9	*1193 ± 127
HW	*Betula alleghaniensis*	YB	yellow birch	3.17	93.14	34.52	0.37	9	*1193 ± 128

* Indicates SDI_{MAX} values from Woodall and Weiskittel (2021) corresponding to the northern hardwood type, i.e., beech-birch-maple.

used the DBH-only model in this work. Multiple estimates of SDI_{MAX} were available for most species for the study region (Dixon and Keyser, 2021; Woodall and Weiskittel, 2021). We present the ratio of LCW to MCW as a succinct indictor of the magnitude of the difference between the two estimates of crown size (Table 1).

A range of DBH values between 10 and 40 cm by 5-cm intervals (n=7 classes) was used to generate point estimates of MCW and LCW for each species, closely approximating the full range of the original data. Crown widths were converted into CPA assuming a circular crown shape. The resulting CPAs for each DBH class and species were divided into the area of one hectare to derive stem density (TPH). Stem densities associated with three alternative stem spacing and crown packing assumptions were determined: 1) *full* canopy cover with no gaps or 100 % canopy cover; 2) *square* spacing equating to 79 % canopy cover; and 3) *equilateral* spacing equating to 91 % canopy cover. Thus, corresponding estimates for TPH are full>equilateral>square for a given DBH and species. The predicted minimum stem densities to achieve full site occupancy (TPH_{MIN}) flow directly from the estimates of CPA, though different assumptions about crown packing and stem spacing contribute to uncertainty in those values (refer to Fig. 1). The intermediate case of equilateral spacing was used to carry out statistical analyses, but we present these comparisons to gauge the magnitude of the differences, as certain assumptions may be more or less realistic in different settings, e.g., planted vs natural stands.

The square (four adjacent competitors) and equilateral (or hexagonal, six adjacent competitors) spacings are as depicted in Smith (1986, p. 123), and full spacing approximates the estimate of TPH that would be obtained for 100 % CCF (Krajicek et al., 1961). Empirical evidence presented by Pretzsch (2019) and derived from fully stocked stands at QMD=25 cm indicated an average crown cover of 88 % (or 12 %

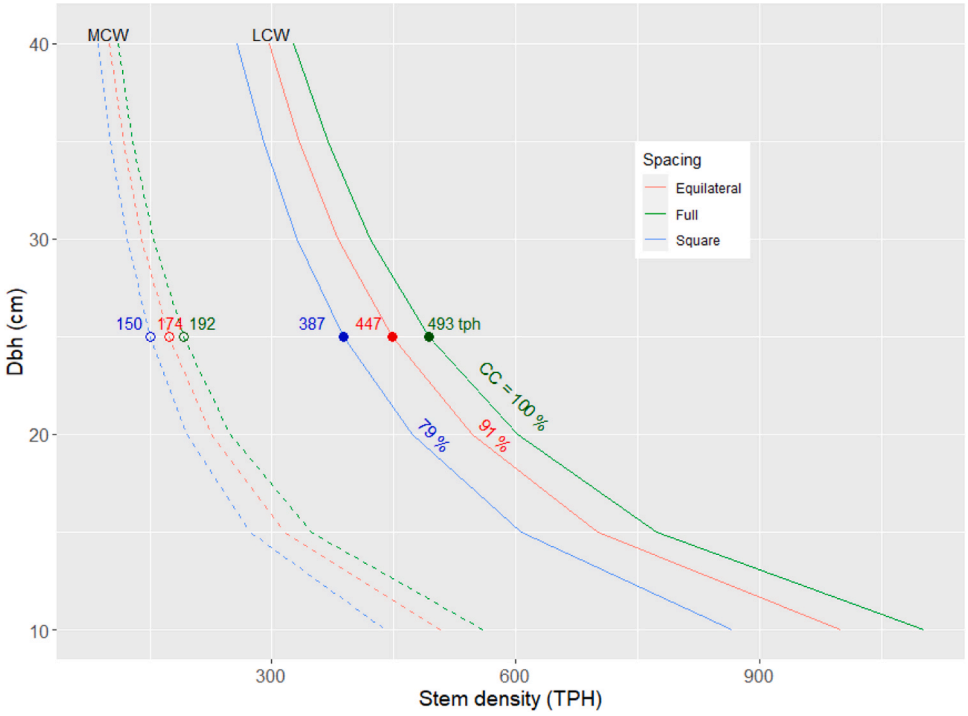

Fig. 1. The relationship between stem density (TPH) and average size (DBH) for eastern white pine corresponding to crown projections areas (CPA) determined by the two crown width models (MCW, LCW) and three assumptions of crown packing (Full, Equilateral, Square). Values of TPH are annotated for DBH=25-cm, and the implied crown cover (CC) for the LCW models (the same values apply to the corresponding MCW models).

interstitial space), which he attributed to mechanical abrasion or 'crown shyness' (Oliver and Larson, 1996; Rudnicki et al., 2003). A further simplification used in this analysis holds that DBH may be interchanged with average stand diameter (QMD, cm). This assumption has previously been adopted in this type of work because plot-based information is typically not available for establishing stem densities at canopy closure, in contrast to the determination of MSDR (e.g., Zhang et al., 2005). The reasonableness of this assumption is further supported by the expectation that evenly spaced planted stems should exhibit an approximately normal diameter distribution prior to crown closure and onset of competition effects.

2.2. Refining the research question

To address our overarching research question concerning the generalization of minimum stem densities to achieve canopy closure, we conducted two related analyses. To assess the appropriateness of interpreting SDI_{MIN} as representing an approximately constant value of RD, e.g. the reference value of 0.15 (Drew and Flewelling, 1979), we analyzed point estimates of TPH_{MIN} determined at DBH (~QMD) of 25 cm (i.e., Reineke's diameter). To assess parallelism of the relationship between MSDR and mSDR we used the full range of DBH by TPH_{MIN} estimates. For both analyses we define species group (GRP) as a class variable, with softwoods (SW=*Gymnosperms*) and hardwoods (HW=*Angiosperms*) constituting a phylogenetic dichotomy in crown architectures and thus crown-stem allometry. Similarly, shade tolerance (TOL), was included as a covariate in both analyses in recognition that it may be related to crown size (Bragg, 2001; Russell and Weiskittel, 2011). The first analysis also includes a covariate representing the range in SDI_{MAX} encountered per species, which, given a fixed crown-stem allometry as defined by the crown width models, quantifies variability in site occupancy attributable to other factors including site quality and growing season length, among others (Andrews et al., 2018; Bravo-Oviedo et al., 2018; Weiskittel and Kuehne, 2019). The second question was addressed consistent with the original size-density analysis of Reineke (1933), where ln(TPH) = f(species/stand-type-specific parameters, ln(QMD)).

To place this work in a context most directly related to stocking assessment, we use RD to standardize estimates of minimum stem densities (i.e., TPH_{MIN}) across species and species groups. Specifically, we express TPH_{MIN} as the minimum value of RD, where $RD_{MIN}=SDI_{MIN}/SDI_{MAX}$; estimates of SDI_{MIN} are derived from TPH_{MIN} provided by the crown width models (MCW and LCW) under the assumption of equilateral spacing, i.e., $SDI_{MIN} = TPH_{MIN}(DBH/25)^{1.605}$ (Reineke, 1933). RD_{MIN} was used as the dependent variable in the first analysis, with differences assessed in relation to the behavior of the GRP, SDI_{MAX}, and TOL covariates. When addressing the second question we assessed the slope parameter of the minimum size-density relationships as indistinguishable from the reference value of −1.605 if the the ±95 % CI of our estimates encompassed that value.

2.3. Statistical analysis

Linear mixed-effects regression models were used to evaluate both research questions. Specifically, the lme function in the nlme package in R (Pinheiro et al., 2021) was chosen because it allows specification of error structures useful for normalizing residuals, providing flexibility in satisfying assumptions of the analysis. This approach was taken to accommodate the hierarchical structure of the data, where individual species exist within one of two groups (Table 1). While our primary interest was to assess general trends exhibited by these distinctive crown architectures (SW vs HW) this modeling framework also provides species-specific coefficients as random effects. Quantitative covariates, including SDI_{MAX} (Dixon and Keyser, 2021; Woodall and Weiskittel, 2021) and TOL (Niinemets and Valladares, 2006), were treated as additive, absent any established biological rationale for their interaction. We compared model fits including random intercepts with those containing random intercepts and slopes using AIC and selected the better performing specification (Δ AIC<2). The general form of both regression models is given below, where the numbering sequence corresponds to the research questions described in the previous section:

[1] $RD_{MIN} = GRP + SDI_{MAX} + TOL$, errors

[2] $\ln(TPH_{MIN}) = \ln(DBH) + GRP + TOL$, errors

Regression weights were specified using the varPower option, with form = SDI_{MAX} and ln(DBH) for models [1] and [2], respectively. Both models were fit to the three estimates of site occupancy derived from MCW, LCW, and MID. Residuals associated with fixed and random effects (species) were assessed visually and deemed consistent with assumptions of both analyses.

Model 1 contains information about SDI_{MAX} on both sides of the equation, where RD_{MIN} is derived with respect to SDI_{MAX} through its relationship to TPH_{MAX}. Nonetheless, we include it because it uniquely enables estimation of the variable of interest across the range of conditions determining those values. Whereas the conventional approach to analyzing maximum size-density relationships involves identifying the boundary condition (e.g., Zhang et al., 2005), in the case of mSDR the average condition was fit. Because the data being analyzed came from model predictions the species level size-density relationships exhibit perfectly linear correspondence when log-transformed, further motivating our conducting the analysis at the higher level of species group.

2.4. Portraying a middle ground

As noted previously, the data used in this analysis (Russell and Weiskittel, 2011) provide two contrasting estimates of growing space occupancy, i.e., CPA based on MCW and LCW. Owing to the methods used for their determination, we view these estimates as providing approximate threshold boundaries for the range of CPA and thus mSDR. Viewed in the context of conventional forest management, estimates provided by MCW may be of limited use because they describe open-grown conditions and therefore would be considered sub-optimal for stand-level production and bole quality of individual trees. In contrast, estimates provided by LCW models correspond to the average forest-grown condition, including information about stems spanning all crown classes, and thus likely underestimate site occupancy characteristics of dominant and codominant crown class stems that are the focus of most conventional commercial thinning regimes (Ashton and Kelty, 2018; Nyland et al., 2016). To better satisfy our objective of providing reference lines depicting canopy closure for upper-canopy, large-crowned forest-grown trees, we also present a 'middle-ground' estimate based on the average of MCW and LCW crown width estimates, hereafter referred to as MID. We believe this value represents a more realistic benchmark for designing thinning interventions and provides needed context to the threshold values represented by MCW and LCW. A recent data publication (Jucker et al., 2022) presenting allometric data for these same species provided an opportunity to visually compare this largely independent source (~30 % from a common source, USDA Forest Service, Forest Inventory and Analysis Forest Health Monitoring plots) in relation to our model-based estimates (Fig. 2).

3. Results

3.1. Characteristics of the dataset

Approximately equal numbers of softwood (SW, n=6) and hardwood (HW, n=7) species are represented in the dataset (Table 1). Assessed at 25-cm DBH, the midpoint of the size range analyzed, predicted CPA values were ~43 % lower for SW than HW groups, averaging 50.5 ± 10.8 (StdDev) m^2 for SW and 89.4 ± 15.8 m^2 for HW according to the MCW model, and 16.9 ± 5.2 m^2 for SW and 29.8 ± 3.9 m^2 for HW for the LCW model. The ratio of CPAs derived from LCW to MCW averaged 0.34 for both species groups. Consistent with group differences for CPA, estimates of SDI_{MAX} obtained from the literature tended to be higher for

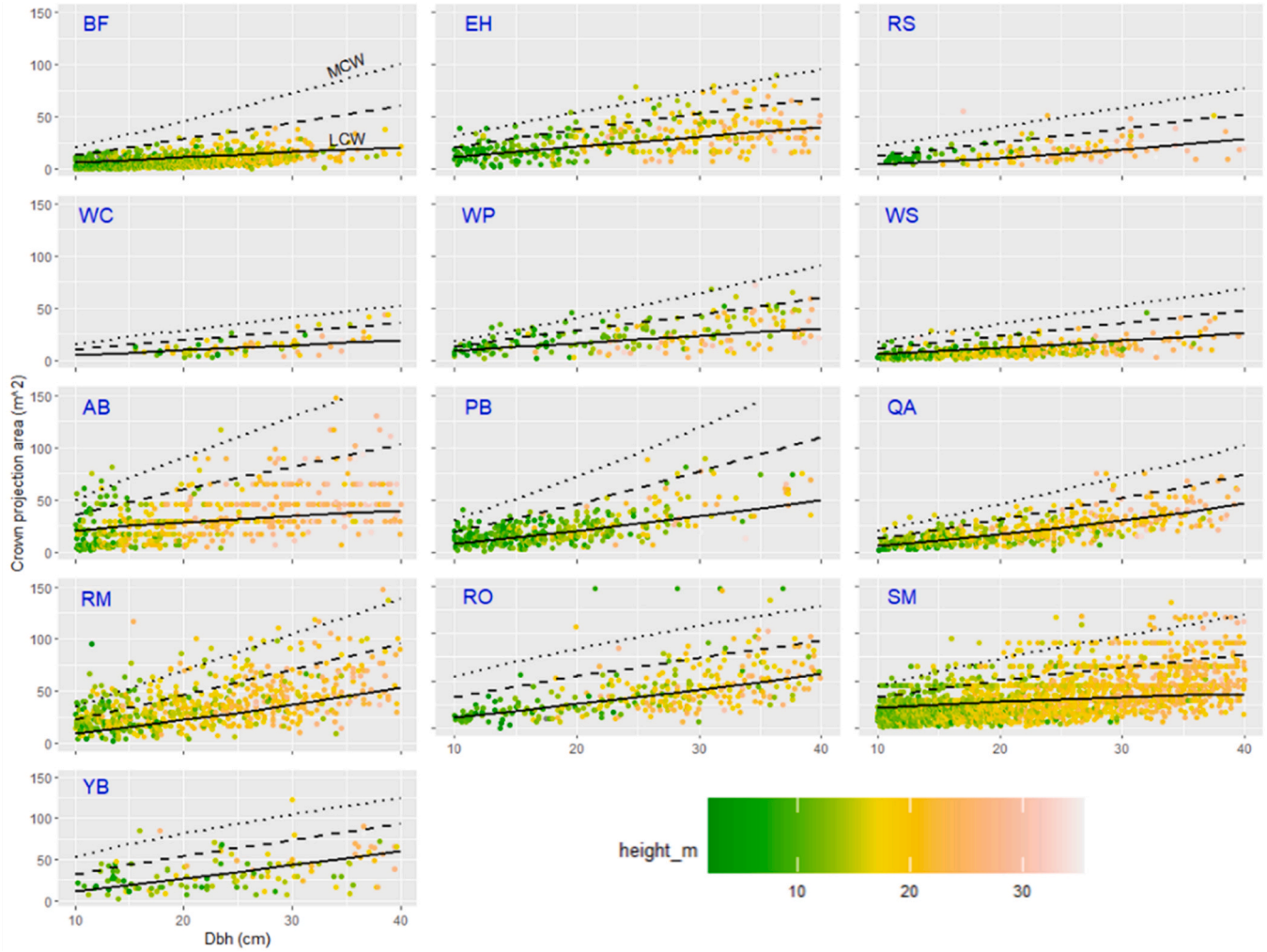

Fig. 2. Relationship between stem diameter (DBH) and crown projection area (CPA) for the species included in this study (refer to Table 1 for species codes). Fits provided by the MCW (dotted line), LCW (solid), and MID (dashed) crown width models are shown in relation to a primarily independent dataset (Jucker et al., 2022). The data points are shaded by total height (m).

SW than for HW species (~18 %), averaging 1384 ± 270 and 1173 ± 285 TPH respectively (Table 1). Among the SW species, white spruce (*Picea glauca*) exhibited the widest range in SDI_{MAX} (855–1490 TPH), while for the HW group, quaking aspen (*Populus tremuloides*) was most variable (1132 to 2055 TPH). For this dataset the average value of TOL was higher for SW (4.2 ± 0.7) than HW (3.1 ± 1.4) species (Table 1), but HWs spanned a wider range of TOL than SWs, at 3.6 vs 1.8 units, respectively.

3.2. Point estimates of minimum relative density (RD_{MIN}) at crown closure

Evaluated at Reineke's (1933) reference diameter of 25 cm, the implications of the model fits were similar for MCW and LCW (Table 2). Initial comparisons between candidate regressions including random intercepts or random intercepts and slopes indicated the latter specification was strongly preferred (ΔAIC ~-90). The random effects of species (intercept) and species by SDI_{MAX} (slope) accounted for a substantial portion of overall variability, supporting the approach taken (Table 2). Parameter estimates for the fixed effects suggest an expectation of higher values for RD_{MIN} among SW species, whereas increases in SDI_{MAX} or TOL were associated with decreases in RD_{MIN} independent of species group. The importance of the TOL variable differed substantially between the MCW and LCW models.

Assuming equilateral spacing and holding fixed effects constant at their means by species group, predicted values of RD_{MIN} were SW=0.126 (95 % ci: 0.111–0.140) and HW=0.101 (95 % ci: 0.085–0.116) according to the MCW model, and SW=0.371 (95 % ci: 0.319–0.424) and HW=0.310 (95 % ci: 0.254–0.366) for the LCW model. This finding suggests that the open-grown trees are capable of occupying roughly three times more growing space than their forest-grown counterparts evaluated at the mid-point diameter of 25-cm DBH, and independent of species group. Further, on average SW species exhibited a 23 % higher RD_{MIN} than did HW according to both models. Estimates of RD_{MIN} from the MID model were SW=0.282 (95 % ci: 0.242–0.321) and HW=0.228 (95 % ci: 0.187–0.269). The influence of TOL scores on estimates of RD_{MIN} (MID model), constrained by the range of values represented in the dataset and applying the average value of SDI_{MAX}, indicated a range of 0.304–0.264 RD for the least to most shade-tolerant SW and 0.270–0.191 RD for HW species.

The influence of SDI_{MAX} on estimates of RD_{MIN} for species and species groups is depicted in Fig. 3. Estimates of RD_{MIN} associated with species having particularly wide (e.g., quaking aspen, 1132 to 2055 TPH) or narrow (e.g., white pine, 1269 to 1534 TPH) ranges of SDI_{MAX} were assessed by applying their respective random effect coefficients (see Supplemental Materials). Thus, based on estimates from the MID model, RD_{MIN} for quaking aspen ranged from a high of 0.197 down to 0.096, and for white pine from 0.223 to 0.182. Note that higher values of RD_{MIN} correspond to lower values of SDI_{MAX}.

Table 2
Parameter estimates and statistics for Model 1 used to predict minimum relative density (RD_{MIN}) at 25-cm diameter at breast height (DBH) by crown width equation including maximum (MCW), largest (LCW), and at their midpoint (MID). GRP is species group and SW is softwood. SDI_{MAX} is the maximum value for stand density index used to determine RD. TOL is shade tolerance score. Variance percents for the fixed and random effects were: MCW=50.4, 48.2; LCW=46.3, 52.8; MID=48.4, 50.0. Random effects coefficients for species specific intercepts and slopes adjusted by SDI_{MAX} can be found in Supplemental Materials (Table S.2).

MCW crown model					
Param	Value	Std.Error	DF	t-value	p-value
Intercept	0.2266	0.0208	81	10.91	<0.001
GRP (SW)	0.0541	0.0114	10	4.74	0.001
SDI_{MAX} (TPH/1000)	-0.0749	0.0064	81	-11.67	<0.001
TOL	-0.0122	0.0048	10	-2.55	0.029
LCW crown model					
Param	Value	Std.Error	DF	t-value	p-value
Intercept	0.6645	0.0700	81	9.49	<0.001
GRP (SW)	0.1407	0.0382	10	3.68	0.004
SDI_{MAX} (TPH/1000)	-0.2251	0.0197	81	-11.41	<0.001
TOL	-0.0291	0.0160	10	-1.82	0.099
MID crown model					
Param	Value	Std.Error	DF	t-value	p-value
Intercept	0.4946	0.0492	81	10.06	<0.001
GRP (SW)	0.1135	0.0273	10	4.16	0.002
SDI_{MAX} (TPH/1000)	-0.0222	0.0114	10	-1.95	0.080
TOL	-0.1684	0.0143	81	-11.79	<0.001

3.3. Slope of the minimum size-density relationship (mSDR)

Evidence provided by this analysis indicates that the slope parameter for the mSDR diverges substantially from that of MSDR, assumed here to be −1.605 (Reineke, 1933). As for the point estimates, mixed-effects models containing random intercepts and slopes provided the best fits (Δ AIC = −597.9 for MCW and −563.7 for LCW) (Table 3). Estimates of the slope coefficients for mSDR were −0.933 (95 ci: from −1.046 to −0.821) for MCW and −1.049 (95 ci: −1.226 to −0.872) for LCW, both converging on values of around −1. As expected, the intercept term was larger for the LCW than MCW models, and the SW group had a larger intercept than the HW group according to both models. There was less agreement regarding the importance of the TOL covariate between the MCW and LCW models for the slope than was indicated for the point estimates, where TOL corresponded to p-values of 0.023 vs 0.531, respectively (Table 2, Table 3).

The divergent slope coefficients between mSDR and MSDR are usefully viewed in relation to RD. For this assessment we used the average values of SDI_{MAX} and TOL by species group as inputs to the MCW and LCW models (Table 3) to estimate RD across the range of DBH. Owing to the different slopes, and the stem densities they imply, the values of RD

Table 3
Parameter estimates and related statistics for Model 2 used to estimate the slope (and intercept) of the size-density relationship evaluated at minimum relative density (RD_{MIN}) by crown width equation including maximum (MCW), largest (LCW), and midpoint (MID). GRP is species group and SW is softwood. QMD (~DBH) is average stand diameter in units of cm. TOL is shade tolerance score. Variance percents for the fixed and random effects were: MCW=90.2, 9.8; LCW=83.9, 16.1; MID=86.0, 14.0. Random effects coefficients for species specific intercepts and slopes adjusted by QMD can be found in Supplemental Materials (Table S3).

MCW crown model					
Fixed	Value	Std.Error	DF	t-value	p-value
Intercept	7.9880	0.2297	77	34.78	<0.001
GRP (SW)	0.7143	0.1019	10	7.01	<0.001
ln(QMD)	-0.9332	0.0573	77	-16.28	<0.001
TOL	-0.1148	0.0430	10	-2.67	0.023
LCW crown model					
Fixed	Value	Std.Error	DF	t-value	p-value
Intercept	9.2049	0.3625	77	25.39	<0.001
GRP (SW)	0.6294	0.1339	10	4.70	<0.001
ln(QMD)	-1.0491	0.0903	77	-11.42	<0.001
TOL	-0.0329	0.0565	10	-0.58	0.531
MID crown model					
Param	Value	Std.Error	DF	t-value	p-value
Intercept	8.7242	0.3077	77	28.35	<0.001
GRP (SW)	0.6237	0.1205	10	5.18	<0.001
ln(QMD)	-0.9848	0.0735	77	-13.17	<0.001
TOL	-0.0356	0.0508	10	-0.70	0.452

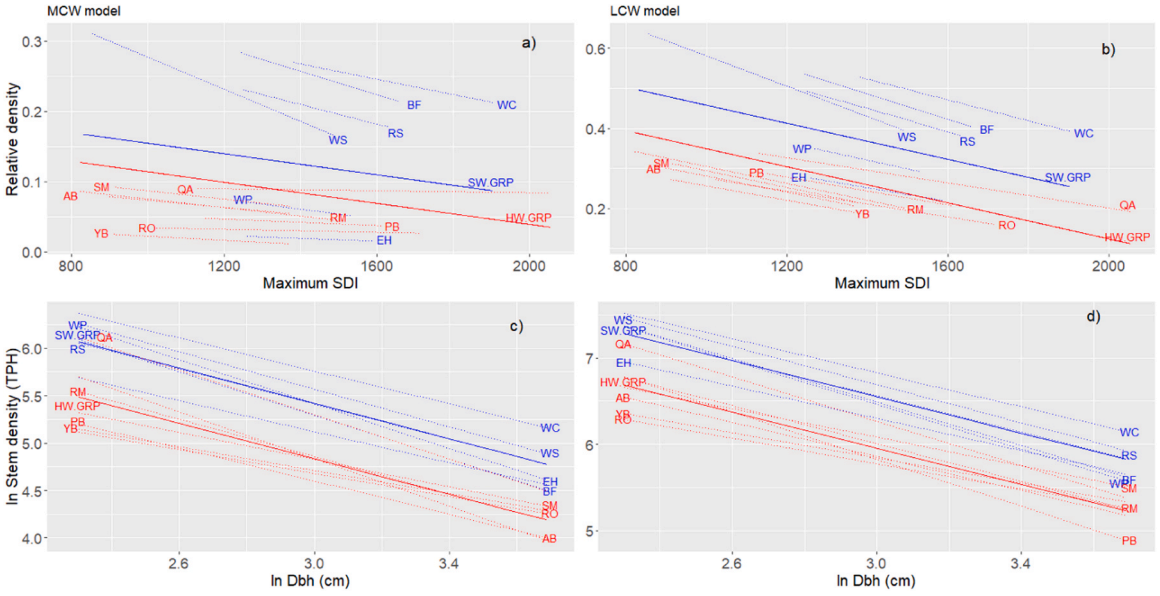

Fig. 3. Model-based representations of growing space occupancy according to the two crown width equations, maximum crown width (MCW, left column, panels a and c) and largest crown width (LCW, right column, panels b and d). The main-effect of species group is depicted as a solid line and labeled as SW.GRP (blue) and HW.GRP (red), and individual species random effects are plotted as dotted lines and labeled with species codes (Table 1). The relationships presented in the first row of panels are for the point estimates of RD_{MIN} (at 25-cm DBH) across a range of SDI_{MAX} adjusted for shade tolerance scores (Table 2), and the second-row panels correspond to the M_{IN}SDR analysis (Table 3).

differ substantially in relation to average stem size (Fig. 3). For example, evaluated at the smallest average size (10 cm DBH), RDs corresponding to the mSDR were less than half those of the largest size (40 cm DBH). For the SW group those values range from 0.07 to 0.18 RD for MCW and 0.23–0.51 RD for LCW, and for the HW group 0.05–0.12 RD for MCW and 0.15–0.33 RD for LCW. On average, values of RD_{MIN} were 50 % higher for SW than HW. Thus, relatively fewer stems are required to achieve canopy closure when their average size is small compared to when large, in contrast to the parity implied by assuming parallel mSDR and MSDR slopes.

4. Discussion

We used tree-level allometric relationships (crown width predicted from DBH) in conjunction with assumptions about crown packing and stem spacing to generate estimates of minimum stem densities to accomplish crown closure in forest stands. To do so we focused on the linkage between stem diameter (DBH) and crown area (CPA), the former easily measured and the latter a proxy for occupied growing space. This approach is well established in the literature (Drew and Flewelling, 1979; Gingrich, 1967; Newton and Weetman, 1993), yet arguably focuses narrowly on above ground competition for light resources. We acknowledge that research has revealed additional drivers of site occupancy relationships, including in relation to belowground competition (e.g., W. Zhang et al., 2011), resulting from crown-crown interactions as trees become tall (Rudnicki et al., 2003), and attributable to differences in site-productivity (e.g., Bi, 2001). Nevertheless, our interpretation of previous efforts, as they relate to integration of this information with size density management charts (i.e., SGs and DMDs), is that insufficient attention has been directed at determining minimum values. The present work aims to address this knowledge gap by advancing a generalizable approach to addressing the problem and provide updated benchmark values potentially useful for integration with existing frameworks. We chose to express density in relative terms, i.e., as RD, because it represents a consistent metric for communicating this information, in contrast to other common measures of stand density (Curtis, 1982; Long, 1985; Ray et al., 2023; Woodall et al., 2006).

Our research questions addressed: 1) the existence of a constant value of RD that may be used to represent minimum stem densities to achieve canopy closure, and 2) whether the slopes of the MSDR and mSDR are approximately parallel. We acknowledge that these questions are interrelated, at least in the sense that if Q2 is rejected then the premise of Q1 cannot logically be accepted. The preponderance of evidence led us to reject the null hypotheses underlying both questions, which we address in the following sections. Additional coverage is devoted to facilitating the application of this information.

4.1. Minimum size-density relationships (mSDR)

The MSDR provides important context for evaluating mSDR. We found that, on average, SDI_{MAX} was ~15 % higher for SW (1381 ± 226 TPH) than HW (1204 ± 212 TPH) species (Table 1). These values capture the implicit relationship between stem density and average crown size at biological carrying capacity (i.e., MSDR), indicating that SW crowns tend to be smaller than those of HWs. We summarized all SDI_{MAX} values used in the Northeast Variant of the FVS model (Dixon and Keyser, 2021) and found the average difference in SDI_{MAX} values between SW (n=16) and HW (n=58) species (excluding those 'mapped' to other species) was 22 % higher for SW species. Similarly, the effect of species group (GRP) on mSDR indicated that SW crowns were generally smaller, expressed here in terms of RD (Fig. 3a and b). Further, we found the magnitude of this difference was considerably larger than at MSDR, with SW vs HW CPAs being on average 44 % lower for MCW and LCW models alike; the ratio of HW to SW stem density (TPH) at MSDR was 0.87 whereas at mSDR that value was 0.55. Bragg's (2001) analysis of crown stem allometry found that crown width was significantly influenced by crowding, quantified as local basal area, for most of the species he studied. Our results highlight the plasticity of tree crowns generally (Jucker et al., 2015; Purves et al., 2007; Vincent, 2008), and suggest that a wider range is exhibited by HW than SW species. Smith and Hann (1986) reported RDs corresponding to crown closure of 0.09 for red alder (*Alnus rubra*, a HW), and 0.12 for red pine (*Pinus resinosa*, a SW). These findings are consistent with underlying differences in crown architecture related to generally strong (SW) vs weak (HW) epinastic control or phototropism, known to regulate development of subordinate side branches as trees grow taller (Oliver and Larson, 1996; Wilson, 1984).

While it may be logical to suggest that TPH_{MIN} is best represented by stem densities predicted by the MCW model, because they derive from open-grown trees and thus the biological maximum crown extent for a given species and stem size, there are also some drawbacks to using this value. From a forest management standpoint MCW may not represent a broadly workable benchmark owing to the implications for branch retention and wood quality, particularly among hardwood species (Heitzman and Nyland, 1991; Miller et al., 2007; Perkey et al., 1993). Conversely, the average forest-grown estimate provided by the LCW model is prone to erring in the other direction, discounting approaches to low-density management that seek to maintain large crowns for rapid growth of individual trees for quality sawlogs (Seymour, 2007; Seymour and Smith, 1987), or perhaps to address emerging forest health concerns (Leak and Yamasaki, 2013; Livingston and Kenefic, 2018). In recognition of this tension we advocate viewing RD_{MIN} as a zone bounded by the MCW and LCW models, hereafter referred to as the zone of minimum density management (ZmDM). Importantly, we suggest that the trajectory of RD described by the MID model serve as a benchmark value located centrally within this zone. Representing the mSDR as a zone of RD (i.e., ZmDM) will require more nuanced field-based observations be made by forest managers, but also represents a more realistic approach to assessing stand conditions and should increase the potential to achieve management objectives in situations where stocking control is being guided by these types of graphical tools.

4.2. Model covariates and random effects

Our analytical approach was geared to producing generalizable findings. For example, species group (SW vs HW) was treated as a fixed effect, whereas individual species were viewed as random effects. In addition, quantitative covariates, including shade tolerance scores (TOL) and SDI_{MAX}, express a range of values that are either relatively fixed (e.g., TOL) or highly variable (e.g., SDI_{MAX}) for a given species (Table 1, Fig. 3). In the following sections, we discuss the influence these covariates had on estimation of crown closure, and how field based observations may be brought to bear in refining them for use in the context of size-density management charts.

4.2.1. Estimates of maximum density (SDI_{MAX})

The justification for including SDI_{MAX} as a covariate centers on the fact that unlike SDI_{MIN}, there are multiple estimates of SDI_{MAX}, and thus RD_{MIN}, available for each species. Species with wide geographic distributions and that are competitive across a broad range of site conditions tend to exhibit higher variability in estimates of SDI_{MAX} (Andrews et al., 2018; Bravo-Oviedo et al., 2018; Woodall and Weiskittel, 2021). In contrast, we assumed that the relationship between site factors and crown-stem allometry was fixed for a given species, though acknowledge that some limited evidence suggests that climatic factors e.g., temperature, wind, and solar radiation may influence crown width independent of DBH (Wang et al., 2022).

The inverse relationship we found between SDI_{MAX} and RD_{MIN} (Fig. 3a and b) was expected and tends to be proportional to the range in SDI_{MAX} exhibited by the individual species (Table 2). The contrasting behaviors of white spruce (SW) and quaking aspen (HW) highlight this (Fig. 3a). Whereas both species exhibit a fairly wide range of SDI_{MAX},

only for white spruce does this also result in substantial differences in RD_{MIN}, as quaking aspen remains relatively flat according to the MCW model; we attribute this difference to the influence of GRP and TOL. Conversely, white pine and Eastern hemlock (*Tsuga canadensis*), both SW, span a narrow range of SDI_{MAX} and only exhibit small differences in RD_{MIN}. Thus, particularly for species that exhibit a wide range of SDI_{MAX}, obtaining the best available estimates is recommended when planning density management regimes.

4.2.2. Species groups (GRP)

The CPA of SW species tended to be smaller than those of HWs at the same average DBH (Table 1, Fig. 3). Consequently, estimates of minimum stem densities to achieve canopy closure are higher for SW than HW groups. In their analysis of crown architecture of common urban tree species, Pretzsch et al. (2015) distinguished among various allometric types, suggesting these relationships are more complex than the phylogenetic dichotomy followed here, though they did report that the largest crowns at a given DBH were associated with HW species. The behavior of two of the six SW species included in this study, white pine and hemlock, points to substantial within-group differences, particularly when considering the open-grown condition, i.e., the MCW model (Fig. 3a).

Evaluated by GRP, the average ratio between CPA of open- and forest-grown stems was similar, suggesting a strong and proportional effect of crowding on crown size. The negative influence of increasing stand density on crown size is well established (Bragg, 2001; Krajicek et al., 1961; Saarinen et al., 2022), although here too there was notable variability among species within our dataset. For example, hemlock (SW) exhibited a larger crown-stem size ratio than quaking aspen (HW); these also happen to be among the most and least shade-tolerant species within the dataset, respectively. When expressed in terms of RD and evaluated at 25-cm DBH, minimum densities for SW species average 0.15 and 0.35 for open- and forest-grown stems, respectively, and 0.10 (MCW) and 0.30 (LCW) for HW. Thus, we infer approximately 0.05 difference in RD attributable to species group, but 0.2 RD units related to crowding effects. As a point of reference, Drew and Flewelling (1979) represented the crown-closure line on their DMD for Douglas-fir (*Pseudotsuga menziesii*) as a constant value of 0.15 RD which falls at the low end of our range for SWs. Because these models were based on the allometries associated with individual species we suggest that is how they should be interpreted and used. While it may be tempting to make inferences about the density management of mixed species stands based on the blending of species estimates included in the larger models, such extension of this information is not recommended at this point.

4.2.3. Shade tolerance (TOL)

Based on reports from previous work (Bragg, 2001; Russell and Weiskittel, 2011) we did not expect to find a strong relationship between TOL and mSDR. Nonetheless, our rationale for including this functional trait was motivated by speculation about its role provided by those studies, as well as evidence provided by stocking assessments made in Allegheny northern hardwoods (Roach, 1977; Stout and Nyland, 1986). Our analysis revealed a nuanced relationship between TOL and mSDR, where in composite the behavior of all species supports interpretation of a slightly negative relationship, yet, and most importantly, when isolated within each species group the trend was positive and stronger (Fig. 4). This finding of a generally positive relationship between TOL and crown size is consistent with previous studies (Bragg, 2001; Stout and Nyland, 1986), but requires proper model specification, i.e., explicit consideration of species groups to resolve, possibly helping to explain why Russell and Weiskittel (2011) reported no significant relationship.

Comparison between MCW- and LCW-based models suggest the influence of TOL was stronger for the former than latter, and primarily in relation to the SW group (Tables 2 and 3). This finding suggests that species differences in CPA related to TOL may be more fully expressed among open-grown trees, and conversely that crowding diminishes the effect. While other studies have explored the relationship between shade tolerance and crown plasticity generally (Jucker et al., 2015; Longuetaud et al., 2013), we are not aware of any that demonstrate a systematic influence on site occupancy as implied by crown cover. These other studies did, however, report that crown plasticity was predominantly a feature of less shade-tolerant species they studied, suggesting less tolerant species are most responsive to crowding. In sum, TOL scores appear to represent a moderately influential covariate for predicting growing space requirements, and perhaps more so in situations where low-density management is contemplated.

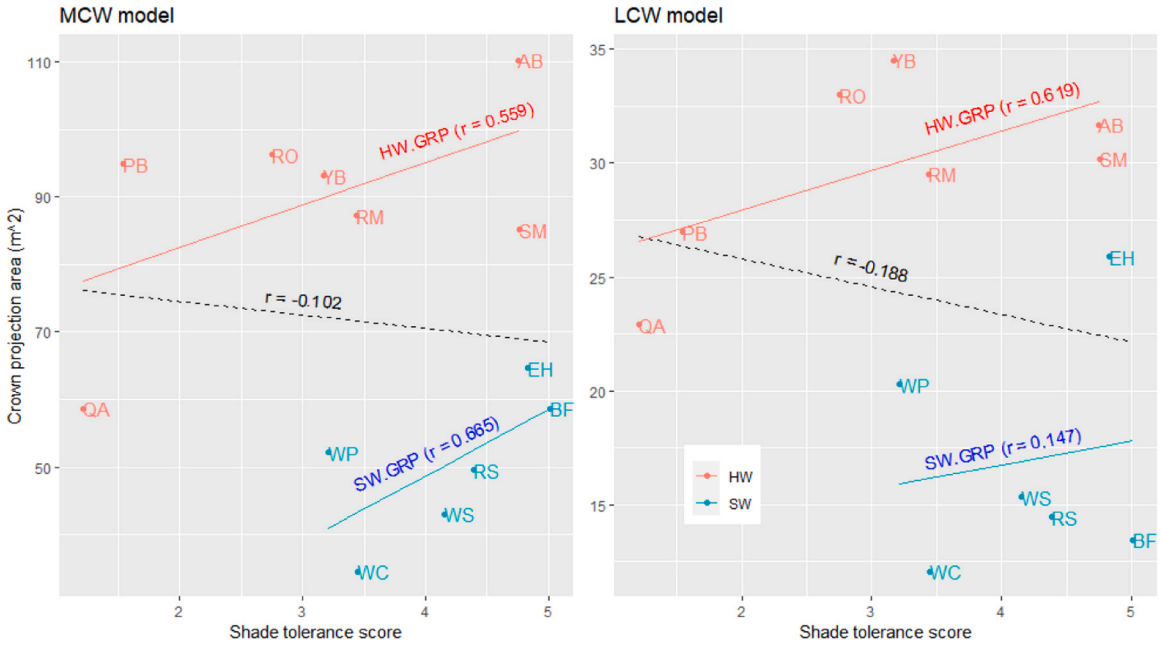

Fig. 4. Relationship between shade tolerance scores (x-axis) from Niinemets and Valladares (2006) and crown projection area (CPA, y-axis) according to both crown width models, MCW (left column) and LCW (right column). The dashed black line is a linear smoother applied across all species, whereas the blue and red lines correspond to the SW and HW species groups, respectively. Pearson correlation coefficients (r) are reported for each relationship. See Table 1 for species codes.

4.3. Slope of the minimum size-density relationship (mSDR)

The question of whether the slope of mSDR runs parallel to the MSDR determines how crown closure is portrayed on size-density management charts, and may also have implications for the design and implementation of thinning regimes (Drew and Flewelling, 1979; McCarter and Long, 1986; Dean and Baldwin, 1993; Wilson et al., 1999). Accurate portrayal of mSDR is most relevant to management approaches that favor the growth of individual trees (Long, 1985; Seymour, 2007). This analysis provides strong evidence that the crown-closure line, or mSDR, as inferred from crown width models, diverges substantially from the MSDR reference value of −1.605 (Reineke, 1933). Our estimates of the slope coefficients for mSDR converge on approximately −1 for both crown width models, i.e. MCW and LCW. The relationship portrayed in Fig. 5 illustrates the nature and magnitude of the difference between mSDR and MSDR slopes. An interesting aspect of the relationship between mSDR and MSDR as portrayed in these figures involves the encroachment of ZmDM into what might be considered relatively high levels of RD with increasing stem size, most notably for the SW group. To some extent this outcome is an inevitable consequence of the different slopes, yet the underlying differences in stem-crown allometry are biologically based. Furthermore, the range of tree sizes (DBH) represented were well represented within the dataset. We speculate this behavior may be partially attributed to a larger crown-stem allometric ratio being exhibited by trees when young and small, based on limited evidence from developing northern hardwood stands (Ray et al., 2011). This could help explain the different trajectories for mSDR vs MSDR, but apparent differences in growing space occupancy between SW and HW groups is expected to self-calibrate on the basis of underlying differences in SDI_{MAX}, as discussed earlier. This is an area worthy of further investigation, assuming our estimates of these quantities based on measurements of individual trees can be shown to correspond to observed behaviors at the stand level.

Minimum stem densities (TPH_{MIN}) presented in Table 4 bracket the range of values necessary to achieve crown closure for the SW and HW groups included in this study. As we have shown, these values, when expressed as RD, become larger with increasing average size (i.e., DBH, Fig. 5). This contrasts with the fixed relationship implied by establishing parallel and subordinate isolines of RD determined by the MSDR. For example, on average TPH_{MIN} declines by 24.8 % as average size increases from 15 to 20 cm DBH following mSDR slope ~-1.0 whereas the corresponding diminution in TPH following the MSDR slope of −1.605 is 37.0 %. Thus, this trend is not readily generalized across the span of TPH because of how RD is defined, as the ratio of observed to maximum stem density following the MSDR slope. Our estimates indicate an approximate doubling of RD_{MIN} between the smallest (10-cm) and largest (40-cm) size classes (Table 4). Another important finding involves the wide range of minimum density estimates encompassed by the MCW (open grown) and LCW (forest grown) models, referred to here as the ZmDM (Fig. 5). Averaged across species group and size class our models suggest approximately one third as many open-grown trees are capable of fully occupying an area compared to the allometry that develops under crowding, i.e., when trees are forest grown.

Our findings are consistent with graphical displays of CC-lines on some previously published DMDs. For example, Wilson et al. (1999) present a CC-line for eastern spruce-fir and reported values at QMD=5.1 and 20.3-cm of 0.11 and 0.32 RD, respectively. We arrive at estimates between 0.04 and 0.19 (5.1-cm QMD), and 0.11 and 0.40 (20.3-cm QMD) for red spruce (*Picea rubens*), and 0.04 and 0.20 (5.1-cm DBH), and 0.09 and 0.41 (20.3-cm DBH) for balsam fir according to the MCW and LCW model estimates, respectively. Smith (1989) presented a CC-line on a DMD for western red cedar (*Thuja plicata*) that assumed square spacing (~79 % crown closure) and which portrayed a divergent slope from that of the MSDR. He explicitly noted the steepness of the slope, where RD at QMD=10-cm was 0.10 and at 40-cm 0.24. Despite representing their CC-line for Douglas-fir as a constant value of 0.15 RD, Drew and Flewelling (1979) described a range of 0.13 RD (smallest QMD) to 0.17 RD (largest QMD) in their paper. In all cases, these researchers offered the caveat that their CC-lines were based on limited data, and as such should be viewed with some caution. Our estimates of mSDR derived from a large dataset representing a wide range of species and crown architectures (Russell and Weiskittel, 2011), and which is broadly consistent with other published data (Fig. 2), agrees with portrayals of mSDR from these studies.

DMDs that do not explicitly present CC-lines may reflect a perception that low-density management regimes lack relevance in the context of these graphical tools, or perhaps as a tacit acknowledgement that a constant RD of ~0.15–0.25 (Drew and Flewelling, 1979; Jack and Long, 1996; McCarter and Long, 1986) provides an adequate approximation of CC. In either case, because contemporary approaches to stand

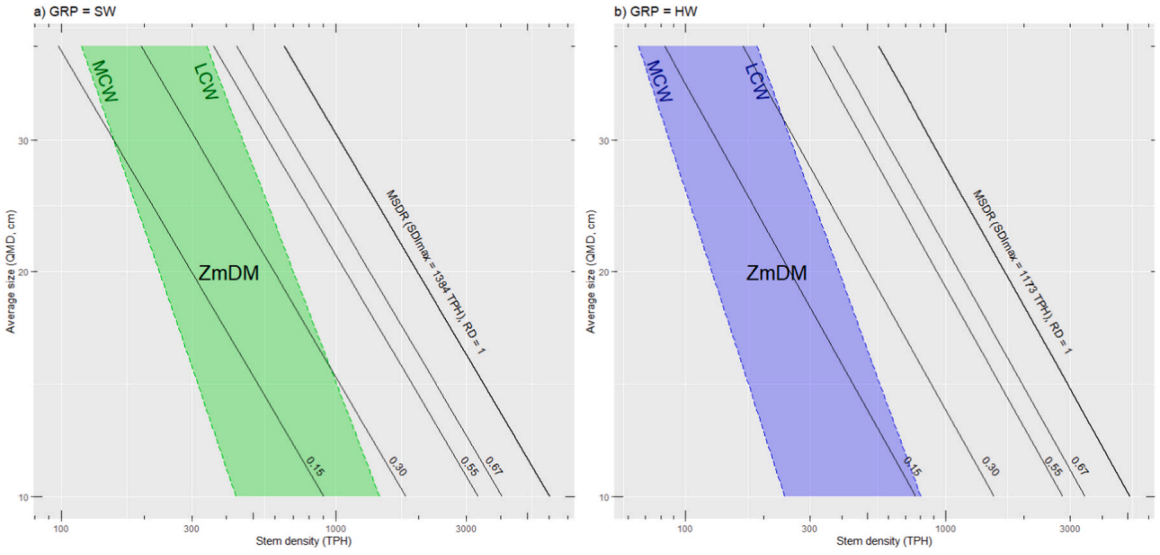

Fig. 5. Generic size density management charts for a) softwood (SW) and b) hardwood (HW) species represented in this study. Average values of SDI_{MAX} and TOL were used to determine the MSDR and MCW and LCW isolines. Selected values of relative density (RD) are plotted along the bottom where 0.67 represents the self-thinning trajectory of an 'average' stand, 0.55 and 0.3 are theoretical upper and lower boundaries of 'full stocking', respectively, and 0.15 crown closure. A zone of minimum density management (ZmDM) is introduced as described in the text.

Table 4
Estimates of minimum densities (TPH) with associated relative densities (RD) in parenthesis to achieve canopy closure according to the three crown width models (MCW=maximum crown width, LCW=largest crown width, and MID=is the midpoint) at different average size (i.e., QMD~DBH). Values correspond to predictions for softwoods (SW) and hardwoods (HW) determined using the average values for shade tolerance (TOL) and maximum stand density index (SDI_{MAX}) by species group (GRP). Corresponding estimates for the individual species are provided in Supplemental Materials (Table S.4.).

Dbh (cm)	MCW, GRP=SW	MCW, GRP=HW	LCW, GRP=SW	LCW, GRP=HW	MID, GRP=SW	MID, GRP=HW
10	433 (0.072)	241 (0.046)	1452 (0.242)	802 (0.153)	1033 (0.172)	572 (0.109)
15	297 (0.095)	165 (0.06)	949 (0.303)	524 (0.192)	690 (0.22)	382 (0.14)
20	227 (0.115)	126 (0.073)	701 (0.355)	388 (0.225)	519 (0.263)	287 (0.167)
25	184 (0.133)	102 (0.085)	555 (0.402)	307 (0.255)	415 (0.301)	230 (0.191)
30	155 (0.151)	86 (0.096)	458 (0.445)	253 (0.282)	346 (0.337)	192 (0.214)
35	135 (0.167)	75 (0.107)	390 (0.485)	215 (0.307)	298 (0.37)	165 (0.235)
40	119 (0.183)	66 (0.117)	339 (0.522)	187 (0.331)	261 (0.402)	144 (0.255)

management (e.g., Ashton and Kelty, 2018; Nyland et al., 2016; Palik et al., 2021) have come to encompass a broader array of objectives, including justifications for managing stands at lower than conventional densities to address forest health issues (Chavardes et al., 2022; Livingston and Kenefic, 2018; McIntire et al., 2018), reduce drought stress (D'Amato et al., 2013), or achieve restoration objectives (e.g., Dey et al., 2017), developing more accurate portrayals of mSDRs is desirable.

4.4. Leveraging information about stand history

Viewing minimum stem densities to achieve canopy closure as existing within a range of RD, i.e., as a zone of minimum density or ZmDM (Fig. 5), acknowledges the influence of stand history on the allometry of individual trees within forest stands. For example, upper canopy trees in stands maintained at lower densities will have higher crown ratios and lower height to diameter ratios (Berrill et al., 2012; Rudnicki et al., 2004). Oliver and Larson (1996) describe the developmental constraints imposed on trees growing in stands in relation to differences in growing space availability during the stem-exclusion stage of stand development. Initial stem densities coupled with patterns of density reduction as stand development progresses (self-thinning, intermediate silvicultural treatments, or natural disturbances), interact to determine the crown sizes that trees can develop, and thus the amount of growing space they are capable of occupying.

To further develop these ideas, the threshold boundaries of the ZmDM defined by the MCW and LCW models can be thought of as representing a range of average live crown ratios (LCR). For open-grown trees (MCW) that value might approach 100 % LCR, while for forest grown (LCW) it would likely be closer to 40 % LCR for upper canopy trees (DOM and CoDOM), a value that Long (1985) reported for western conifers in stands growing at ~0.5 RD. Given the wide range of RD values encompassed by the ZmDM, current and anticipated crown size can be used to help navigate where within that range to target management. Qualitatively, if the intervention being contemplated takes place early in stand development, average crown size of stems being retained is relatively large (e.g., >0.4 LCR), and rapid growth of individual trees is being sought, then favoring the lower bound of the ZmDM (MCW) may be justified (see Supplemental S.1). Conversely, if the intervention takes place later in the rotation, when the potential for additional height growth is limited and average LCR is relatively small, then favoring the upper end of ZmDM (LCW) is more rational. From this perspective, the trajectory portrayed by the MID line provides a useful benchmark for evaluating current conditions, and depending on developmental stage and management objectives, charting a rational path forward in terms of of stand density management.

Jack and Long (1996) discuss the allometric relationships underpinning the construction and use of DMDs and express the view that stand history, specifically related to past management, does not generally limit their use. In fact, this position may be considered central to their utility, i.e., the relationships portrayed are robust to a wide range of stand conditions. While that may be a useful generalization, we suggest that their utility may be improved by considering information about stand history, even if primarily qualitative in nature. This caveat is especially true at the outer boundaries of the RD space considered, i.e., the region of density management approaching the zone of imminent competition mortality (ZICM) and within the area between MCW and LCW estimates (ZmDM), where less nuanced interpretations could lead to unintended consequences in terms of mortality losses or underutilized growing space, respectively. That said, we believe that competent forest managers are already doing this part intuitively, but that more explicitly acknowledging the need to do so can help frame expectations about what information these tools (DMDs and SGs) are capable of providing (Ray et al., 2023).

4.5. Relevance to planting, early stand tending, and intermediate treatments

Here we point to some potential areas of application for this information. Forest management activities including tree planting and enhancing the productivity of established forest stands are widely recognized as representing natural solutions for mitigating climate change (Chapman et al., 2020; Domke et al., 2020; Griscom et al., 2017), the potential unintended consequences of certain tree planting proposals notwithstanding (Fleischman et al., 2020; Holl and Brancalion, 2020). Likewise, approaches to stand density management aimed at alleviating drought stress to avoid mortality can be informed and potentially mitigated by maintaining stands at lower densities (Clark et al., 2016; Dagley et al., 2023; Sohn et al., 2016). We suggest that information about mSDR and ZmDM can be used to help guide these types of decisions, as well as to address more conventional timber management objectives, e.g. pre-commercial thinning (PCT) (Wagle et al., 2022). Our estimates of minimum stem densities required to achieve full site occupancy, i.e., TPH_{MIN} when stands reach commercial size e.g., QMD 12–25-cm, provide target densities for planting or PCT operations. For this application we would use the range of current forest products markets in northeastern North America, and consistent with mensuration practice on permanent inventory systems. Size-density information represented by SGs and DMDs has previously been suggested as useful for this purpose (e.g., Scenario 2 presented in Wilson et al., 1999).

When applied in these contexts, densities associated with the MCW models would be the most economical, but also risky, because any unanticipated losses to mortality would result in underutilized growing space, and issues with wood quality related to branch retention should be anticipated. Alternatively, densities corresponding to the LCW models may be viewed as unnecessarily high and therefore not economically justified, most notably early in stand development. Thus, we tentatively recommend using estimates generated by the MID model for most such purposes (Table 4 and Supplemental Materials, Table S.2), though considerations related to specific management objectives and available resources should ultimately determine which benchmark is more appropriate. As one example, and focusing on white pine, taking this approach would lead to planting or releasing ~550 TPH, according to the MID model evaluated at ~20-cm QMD; see Supplemental Materials S.1 for a more detailed description of a low-density management

regime being implemented over the course of stand development and in relation to ZmDM. By extension these same estimates may be used as benchmarks when carrying out regeneration stocking assessments, with TPH_{MIN} at minimum commercial size representing the target density, and the associated spacing (~4.3 m between adjacent stems, consistent with the above example) could be used to inform the radius of the plots used to carry out the survey.

5. Conclusion

Establishing minimum stem densities to achieve canopy closure has received inadequate attention, despite its importance for informing stocking sufficiency and devising intermediate silvicultural prescriptions to achieve diverse management objectives. Our assessment of this topic focusing on common softwood and hardwood species in northern New England, USA, presents a generalizable framework for establishing a zone of minimum density management (ZmDM) to help guide related aspects of stand management. We present this zone as encompassing the lower bound of the density management zone (DMZ) or analogous zone of optimal density management (ZODM) typically portrayed on density management diagrams, and by analogy with reference to the B-line on stocking guides. Realizing the utility of the ZmDM will require that forest managers interpret relevant aspects of stand history, exhibited as average live crown ratio or height to diameter ratio of the upper canopy stems, and further to evaluate that information in the context of stand developmental stage.

While our estimates of RD_{MIN} and slope of mSDR should be further validated using information from independent datasets and tested against field-based measurements of stocking and growth responses, we believe they provide credible initial estimates that can help inform stocking assessment. Characteristic patterns of growing space occupancy exhibited by softwood (SW) and hardwood (HW) species groups may be used to provide reasonable estimates of minimum stocking for mixed composition stands, based on predominant crown architecture. Integration of these estimates with DMDs and SGs could help facilitate contemporary forest management paradigms that encompass but also extend beyond the optimization of timber production to address broader issues of forest health, drought-stress reduction, and help inform planting and release operations.

CRediT authorship contribution statement

John-Pascal Berrill: Writing – review & editing. **Shawn Fraver:** Writing – review & editing. **Robert Seymour:** Writing – review & editing, Conceptualization. **David Ray:** Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Aaron Weiskittel:** Writing – review & editing, Conceptualization. **Nicole Rogers:** Writing – review & editing. **Laura Kenefic:** Writing – review & editing.

Declaration of Competing Interest

The authors declare no competing interests.

Data Availability

Data will be made available on request.

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Data statement

All data used in this paper were obtained from published sources with references provided herein.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122057.

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