Forest Ecology and Management 386 (2017) 51–61

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Climate and species functional traits influence maximum live tree stocking in the Lake States, USA

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ARTICLE INFO

*Article history:*
Received 22 August 2016
Received in revised form 7 December 2016
Accepted 9 December 2016
Available online 22 December 2016

*Keywords:*
Competition
Stand density management
Relative density
Stocking
Functional traits
Climate change

ABSTRACT

Quantifying the density of live trees in forest stands and partitioning it between species or other stand components is critical for predicting forest dynamics and responses to management, as well as understanding the impacts of stand composition and structure on productivity. As plant traits such as shade tolerance have been proven to refine understanding of plant community dynamics, we extended a previous model relating maximum stand density to wood specific gravity to incorporate shade tolerance as an additional functional trait. Additionally, we included climatic variables that might influence ecological dynamics and modulate species-specific traits, across a region and also potentially over time under climate change scenarios. We used data from the USDA Forest Service, Forest Inventory and Analysis program for three states in the northern United States (Minnesota, Wisconsin, and Michigan) that reflect strong gradients in climate and species composition, to fit a maximum density model by quantile regression. The resulting strictly additive density measure conforms well to both existing silvicultural guidance and to observed densities of monocultures that lack such guidance. Wood specific gravity appears to interact with precipitation, while shade tolerance interacts with temperature, in driving maximum density relationships. Our proposed maximum stand density model is not only parsimonious for field application in management situations, but also empowers the evaluation of the effects of future climate and tree range scenarios on forest management guidelines.



## 1. Introduction

The assessment of stand density is a critical task for silvicultural diagnosis and prescription, and for strategic-scale assessments of forest characteristics (Long, 1985; Woodall et al., 2005). Stand density is a driving factor in trajectories of stand volume and carbon sequestration due to ordinary stand dynamics (Oliver and Larson, 1996; Pretzsch, 2009), and is a key predictor of wood quality (e.g. Mason, 2012; Groot and Luther, 2015). It can also indicate predisposition to catastrophic changes due to disturbances such as fire (Woodall et al., 2006), wind (Castedo-Dorado et al., 2009; Lindroth et al., 2009; Pretzsch et al., 2015), and insects (Kurz et al., 2008; Zhang et al., 2013), and can modulate forest responses to climatic stress (Trouvé et al., 2014). The archetypal approach to stand density assessment is that of Reineke (1933), while other approaches have built on those of Hart (1928) and Yoda et al. (1963). All of these approaches combine some measure of tree size (diameter, height, or biomass) with an absolute density of trees to establish reference density levels. The original approaches, (e.g., Reineke, 1933) along with most succeeding applications (e.g., Long, 1985), have been designed for single-cohort monocultures.

In many forested regions, mixed-species forests are the rule rather than the exception, while in others (e.g., Europe) they are expanding in prevalence and associated management interest (Bravo-Oviedo et al., 2014; del Río et al., 2016). In regions with relatively complex forests, individual species may be rare, but collectively rare species may be present in a large fraction of stands. Misguided approaches to quantifying total density and its partition among tree species and size classes can lead to erroneous management decisions and ecological inferences (Sterba et al., 2014). However, direct attention to the problem of describing stand density in complex mixed-species, multi-cohort forests in a fashion that accounts for variation in species composition has been limited. Stout and Nyland (1986) and Stout et al. (1987) adapted an early

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http://dx.doi.org/10.1016/j.foreco.2016.12.007
0378-1127/

approach by Chisman and Schumacher (1940) by using broad species groups to develop multi-species stocking indices in the Allegheny region of Pennsylvania. These approaches were highly dependent on observing maximum size density relationships across a population of trees (i.e., a region) which can overlook rare or non-commercial tree species. In contrast, Woodall et al. (2005, 2006), building on work by Dean and Baldwin (1996), proposed an approach where only the average wood specific gravity within a stand was needed to estimate the maximum size/density relationship for any particular combination of tree species. Such national-scale stocking indices enables large-scale evaluation of stand dynamics such as dead wood (Woodall and Westfall 2009) and live tree biomass accretion (Woodall et al. 2015). Ducey and Knapp (2010) further extended Woodall's approach (2005) to develop an additive version of Reineke's (1933) stand density index, similar to the form outlined by Curtis (1971), accounting for interspecific variation using specific gravity as a predictive functional trait. The incorporation of species-specific functional traits in the assessment of stand density paves the way to a more mechanistic explanation of site occupancy in complex forests. However, a single-trait approach, like specific gravity, reduces the maximum density that a stand can support to species tolerance to bending stress (Dean and Baldwin, 1996). In mixed-species forests tolerance to low light intensity could be more influential in size-density relationships than mechanical properties because of the key role of shade tolerance in shaping plant communities (Valladares and Niinemets, 2008). Another approach to capture the interspecific variation in maximum density is that presented by Rivoire and Le Moguedec (2012) based on resource availability for some European mixtures; however, calibration of their approach requires information on monocultures of each species, which is often unavailable for complex mixtures.

Another potential challenge for modeling stand density in complex mixtures is the influence of climate and other environmental factors. Although Reineke (1933) suggested that maximum stand density for a given species might be insensitive to site quality, recent work suggests otherwise. For example, Bi et al. (2000) working in radiata pine (*Pinus radiata*) and Pittman and Turnblom (2003) in Douglas-fir (*Pseudotsuga menziesii*) found that site index influenced maximum species density and individual-stand self-thinning trajectories. Weiskittel et al. (2009) found that stand origin, purity, and site index influenced the maximum density boundary for Douglas-fir and western hemlock (*Tsuga heterophylla*). In addition, they found that soil and climatic variables related to dryness also influenced the boundary for red alder (*Alnus rubra*). At a broad scale, Comeau et al. (2010) suggest climate as a factor driving differences in maximum density for Douglas-fir and Sitka spruce (*Picea sitchensis*) between Canada and the U.K. In mixed-species forests, Reyes-Hernández et al. (2013) identify both species composition and site factors as important drivers of density relationships. In addition, variation of specific wood gravity with site conditions (e.g. temperature and precipitation) has been observed across spatial gradients (Wiemann and Williamson, 2002; Antony et al., 2010) whereas shade tolerance is known to be modulated by climate and soil moisture conditions (Carter and Klinka, 1992; Niinemets and Valladares, 2006). If species composition responds to some of the same environmental drivers as stand density, then the influences of species identity and associated functional traits could be confounded with those of environmental factors that are not incorporated into the analysis. However, the interplay between species specific characteristics (i.e. functional traits) and climate to predict stand density is unexplored.

The overarching goal of this study is the exploration of the relationship between climatic factors, species functional traits (specific gravity and shade tolerance), and stand density for three of the Lake States (Minnesota, Wisconsin, and Michigan) in the north-central United States. The study region features complex species mixtures as well as some monocultures, along with strong climatic and ecological gradients from prairie and open woodland on the western edge, to boreal forest on the north, and mixed hardwoods on the south. Historically, the region has been viewed as a "tension zone" characterized by climatically-driven transitions (Curtis, 1959), and thus serves as a challenging but appropriate test for efforts to incorporate climate into density assessment.

It is hoped that accomplishing this overarching goal could provide a means to update the national-scale stand density approach of Woodall et al. (2005) while adhering to the aspirational goals for a regional or national density measure postulated by Ducey and Knapp (2010):

- The density measure must accommodate a wide range of diameter distributions and species compositions.
- It must be able to incorporate rare species, and species that appear too rarely (if ever) as monocultures to allow separate modeling of their maximum density relationships.
- Where possible, the density measure should be consistent with accepted empirical relationships developed from common monocultures in the region.
- The density measure should be spatially consistent, and avoid arbitrary modifications following artificial boundaries (such as political subdivisions).
- The density measure should have a reasonably simple mathematical form, preferably one that simplifies evaluation of sampling error when used in practice (Ducey and Larson, 1997, 2003).

Addressing species composition, along with climate or other types of environmental variability, could conflict with the overarching goals of simplicity and transparency outlined above. The biology and ecology of species interactions can be complex, even in mixtures containing a small number of species (Forrester, 2014; Pretzsch, 2014). Attempts to quantify a stand's full complexity could render associated stand density measures impractical for broad assessments and/or stand management exercises. Hence, the specific objectives of our study are:

1. To outline a mathematical approach for incorporating multiple species functional traits, including shade tolerance as key functional trait in shaping forest structure and dynamics (Valladares and Niinemets, 2008), and potentially in interaction with climate or other environmental variables, into the mixed-species density model of Ducey and Knapp (2010);
2. To fit the resulting model to inventory data to our study region, evaluating whether common climate variables and functional traits other than specific gravity improve the statistical performance of the model; and
3. To assess the ecological and management implications and limitations of the model.

## 2. Materials and methods

### 2.1. Theory

Reineke's (1933) original stand density index (SDI) for single-cohort monocultures relies on an empirical relationship between number of trees per unit area (N) and the quadratic mean diameter (QMD, typically cm but inches in Reineke, 1933) of normally-stocked stands:

$$\log_{10}\mathrm{N} = -1.605\log_{10}\mathrm{QMD} + \mathrm{k} \quad (1)$$

where k is a constant varying with species. This in turn implies that at maximum stocking