Forest Ecology and Management 289 (2013) 300–311

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

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

Static and dynamic maximum size–density relationships for mixed trembling aspen and white spruce stands in western Canada

Valentin Reyes-Hernandez [*], Philip G. Comeau, Mike Bokalo

Department of Renewable Resources, University of Alberta, 751 General Services Building, Edmonton, AB, Canada T6G 2H1

ARTICLE INFO

Article history:
Received 30 July 2012
Received in revised form 22 September 2012
Accepted 27 September 2012
Available online 28 November 2012

Keywords:
Maximum size–density relationships
Self-thinning
Static thinning line
Dynamic thinning line
Boreal mixedwoods

ABSTRACT

We examine maximum size–density relationships (MSDR) of pure and mixed stands of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss.) in the Boreal Forest Natural Region of Alberta, Canada. Stochastic frontier function regression was used to estimate the MSDR species boundary or static line and mixed models were used to investigate how individual stands self-thin (dynamic thinning line). Effects of age, stand composition, soil nutrient regime and soil moisture regime were also evaluated. A steeper slope was obtained for the dynamic than for the static thinning line, and both MSDR lines slopes are statistically different from the theoretical value proposed by Reineke (1933). The deciduous component (percent of stand total basal area that is deciduous) has a negative effect on the slope and a positive effect on the intercept of the static line. Composition (increasing aspen basal area) also has a negative effect on the intercept of the dynamic line although no effect was detected on the slope. Soil nutrient regime has a positive effect on the intercept and a negative effect on the slope of the dynamic thinning line. Results suggest that local differences such as site quality and stand composition are important factors in determining maximum size–density relationships for these mixedwoods stands and how individual stands develop and self-thin.

1. Introduction

Relationships between the number of individuals per unit area and their average size have been used to explore stand dynamics, self-thinning and also in the development of relative density indices and density management diagrams in forest management (Lhotka and Loewenstein, 2008). The boundary line for tree size–density relationships has also been used as a measure of maximum stockability which is defined as the maximum number of trees that a site with particular conditions can grow to a given size (DeBell et al., 1989; Harms et al., 1994). A relationship between quadratic mean tree diameter (D_q) and number of trees per hectare (TPH) has been widely used in forestry based on Reineke's work (1933), in which the upper boundary is a straight line on logarithmic scales and is given by:

$$\ln(\mathrm{TPH}) = \beta_0 + \beta_1 \ln(D_q) \tag{1}$$

where β_0 and β_1 are the intercept and slope of the self-thinning line, respectively. Reineke (1933) investigated this relationship for 14 tree species growing in pure stands under different conditions and proposed application of this relationship in characterising a 'Stand Density Index' (SDI), defined as the number of trees in a site at a reference diameter of 25.4 cm (10 in.). SDI can be calculated using the equation:

$$\mathrm{SDI} = \mathrm{TPH}(D_q/25.4)^r \tag{2}$$

where SDI = Stand Density Index, $r = -1.605$.

Japanese researchers demonstrated a similar relationship between mean plant biomass and density for a number of plant species (Kira et al., 1953; Shinozaki and Kira, 1956), which was further developed by Yoda et al. (1963), and is given by:

$$w = KN^{-a} \tag{3}$$

where w is mean plant biomass; N is plant density, and 'K' and 'a' are constants. The value of 'a' was empirically found to be -1.5. This relationship has been known as the $-3/2$ power law or self-thinning law, and states that the mean plant biomass in a mono-specific crowded population is related to the mean density by a power approximation. The maximum size–density relationship (MSDR) represents a limit for the amount of biomass that can be supported by the available resources of the site (Lonsdale and Watkinson, 1982) such that for a population at the carrying capacity, individual growth will continue only if the density is reduced (Kimmins, 2004).

Whether the slope and intercept values of the self-thinning line are invariant has been a matter of discussion for many years. Some

---

[*] Corresponding author. Tel.: +1 780 492 1879; fax: +1 780 492 4323.
E-mail addresses: reyesher@ualberta.ca (V. Reyes-Hernandez), phil.comeau@afhe.ualberta.ca (P.G. Comeau), Mike.Bokalo@ales.ualberta.ca (M. Bokalo).

0378-1127/$ - see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2012.09.042

studies show that the slope can change with species, age, tree size and other variables (Weller, 1987; Zeide, 1985, 1987). Site quality (water, nutrients and light availability) can also influence the intercept of the size–density line (Harper, 1977; White, 1980). Site index (Bi, 2001), nutrient availability (Morris, 2003), climate (DeBell et al., 1989; Comeau et al., 2010), and stand age (Ogawa, 2005; Zeide, 2005) have also been shown to influence the intercept and slope. In a recent study, site index, stand origin, and stand composition (measured as the proportion of basal area of the leading species) influenced the position and/or the slope of self-thinning lines of Douglas-fir and western hemlock in the Pacific Northwest of North America (Weiskittel et al., 2009). Although for some tree species the slope seems to agree with the theoretical values proposed by Reineke (1933) or Yoda et al. (1963), the idea of a universal slope value that fits for all tree species seems to be untenable, and gives scope to species-specific variation in its value (Pretzsch and Biber, 2005; Pretzsch, 2006). Crown and canopy architecture may be important factors in determining self-thinning lines, because they might influence the biomass that can be packed into a specified volume, the pattern of light penetration through the canopy and light utilisation (Lonsdale and Watkinson, 1983). Several other reasons that have been proposed for these deviations include: differences in tolerance and light capture by tree crowns (Zeide, 2005); that relationships between leaf area index and tree size may change with species, age and other factors (Franco and Kelly, 1998); and, that sun angle and growing season length may influence survival and growth through effects on net annual carbon uptake, crown depth, and other factors (Harms et al., 1994, 2000).

Weller (1987, 1990) suggests that controversial results had been due to the application of two different concepts which he further defined as the static and the dynamic thinning lines. The static thinning line (also called the species boundary line) operates in all stands of a species across sites, tree sizes, genetics, thinning, etc. In this case, maximum tree densities across an array of average tree sizes are delimited with a line of constant slope notwithstanding all of the factors mentioned above. Observations used to derive the static thinning line are not necessarily from the same stand, rather they can be a collection of observations obtained from many different stands (VanderSchaaf and Burkhart, 2007b). The dynamic thinning line on the other hand, is a limit that operates in an individual crowded stand (VanderSchaaf and Burkhart, 2007a), and represents how each individual site self-thins. As a consequence, each MSDR dynamic thinning line has its own slope and intercept value. Much of the past work on the analysis of MSDR has been based on the delimitation of a static thinning line, and although both limits can coincide this is not necessary. In contrast to the static thinning line, which is proposed to be a constant for all the stands of a certain species, the slope and intercept values of the dynamic thinning line can be affected by a number of factors such as light availability, climate, site quality, initial density and spatial arrangement of individuals (Weller, 1990). VanderSchaaf and Burkhart (2007b) further expanded this concept and proposed species boundary line II, which is obtained from multiple observations coming from crowded stands experiencing density-dependent mortality (such as the dynamic thinning line), and its slope would represent on average how all those stands self-thin.

Although the concepts of MSDR and self-thinning were developed and applied to mono-specific, even-aged plant stands, attempts have been made to apply them in mixtures of species and in uneven-aged stands of trees (Puettmann et al., 1992; Torres-Rojo and Velázquez-Martínez, 2000; Woodall et al., 2005; Ducey and Knapp, 2010a,b). These and other studies have emphasised that both concepts should hold for the entire stand and not for each separate species (Yang and Titus, 2002). Since species mixtures can be more productive, in some cases, than monocultures (Man and Lieffers, 1999; Chen et al., 2003; Pretzsch et al., 2010), an effect of stand composition on the MSDR for mixed species stands would be anticipated when species with differences in shade tolerances and resource requirements grow together. However, this effect can be verified only if information on stand composition is available and tested for (Puettmann et al., 1992). The development of MSDR requires objective selection of data points, use of appropriate data and proper analyses. The statistical techniques used to develop MSDR have varied among studies and include ordinary least squares regression (OLS), reduced major axis, quantile regression, first difference models and mixed models (Zhang et al., 2005; VanderSchaaf and Burkhart, 2007b). Regression using an OLS approach is sensitive to data selection and may produce self-thinning lines with inappropriate slopes, and techniques such as quantile regression, deterministic frontier and stochastic frontier function (SFF) regression are currently preferred over OLS for this type of analysis (Zhang et al., 2005). SFF is useful to perform statistical inferences on the model parameters, as well as to test for the effects of covariates and deal with some of the problems associated with data that might have autocorrelated errors (Zhang et al., 2005; Weiskittel et al., 2009). In contrast to techniques such as OLS that intersect data, SFF encloses or envelops data which enhances its power in defining the frontier (Bi, 2004). On the other hand, mixed modelling is considered to be the best approach for examining data that could show autocorrelated errors and heteroscedasticity (Littell et al., 2006) as may be the case when using repeated measurements coming from remeasured permanent sample plots. This approach also allows testing for effects of site, age and other factors on size–density relationships.

The boreal forest is the largest forested area in Canada in which trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss.)) can grow either in pure or in mixed stands, with variable proportions of other tree species such as balsam poplar (*Populus balsamifera* L.), white birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* (Mill.) BSP.) and balsam fir (*Abies balsamea* (L.) Mill.) (Rowe, 1972). The boreal mixedwoods, as they are commonly known, are generally found in upland mesic to subhygric (well to moderately well drained) sites in western Canada (Lieffers et al., 1996) and represent an ecologically and economically important component of the landscape. Until the 1990s, boreal mixedwoods were generally managed to harvest the white spruce (Andison and Kimmins, 1999). The replacement of mixed stands by a more desirable softwood stand was a common trend in the western Provinces (Lieffers and Beck, 1994) through the 1990s. Currently there is an increasing interest in regenerating and maintaining mixtures and is being attempted in many areas. Successful establishment of pure white spruce stands, generally requires site preparation to deal with flooding and cold soils and follow up control of competition from grasses and intolerant tree species such as trembling aspen (Lieffers and Beck, 1994). It is suggested that mixed stands have many advantages over the conversion to either pure aspen or pure spruce stands (Comeau et al., 2005). Higher diversity and productivity, as well as less damage due to partial disturbances have been suggested for boreal mixedwoods than for mono-specific stands (Comeau, 1996), although some challenges related to finding a balance between the competitive and beneficial effects of aspen on white spruce, as well as the economical advantages of mixtures of these two species in the long term, remain only partially answered. Since any tending of mixedwoods to improve or accelerate spruce growth requires selective treatments, costs can quickly exceed those for pure spruce plantations, with at best small gains in wood fibre yield.

Analyses of MSDR for western Canada boreal tree species have been previously developed. Lieffers and Campbell (1984) reported that the slope of the relationship between tree biomass and density for 23–57 year-old trembling aspen stands was found to be flatter than the theoretical value suggested by the self-thinning law. Yang