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Effects of climate on maximum size-density relationships in Western Canadian trembling aspen stands

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ABSTRACT

Maximum size-density relationships (MSDR) are examined in stands of trembling aspen (*Populus tremuloides* Michx.) in the boreal forest region of Alberta and Saskatchewan, Canada. Stochastic frontier function regression was used to develop the static self-thinning line, and a linear mixed-effects model was used to estimate the average dynamic self-thinning line from repeated measurements. Climate variables obtained from Climate WNA were included in our models. The static self-thinning line was steeper than Reineke's slope (−1.605), while the average slope value of the dynamic self-thinning line was not different from −1.605. Increasing frost free period, summer heat moisture index, and mean coldest month temperature move the static self-thinning line downwards because these climate variables are linked to increases in evapotranspiration and drought exposure. For the average dynamic self-thinning line, degree days above 5 °C positively increases the intercept and summer heat moisture index has a negative effect on the intercept, but no effect on the slope for both climate variables. Results suggest that increasing summer dryness related to climate change may decrease the carrying capacity and productivity of aspen stands in portions of this region.

1. Introduction

Maximum size-density lines, based on Reineke's rule (Reineke, 1933) and the −3/2 power law (Yoda et al., 1963), define the maximum number of trees that can be supported in a stand when trees are any particular size. Several studies indicate that the slope and intercept of this relationship fit on log-transformed data vary between species (Weller, 1987; Pretzsch and Biber, 2005; Charru et al., 2012; Vospernik and Sterba, 2015), and are also influenced by stand origin (Weiskittel et al., 2009), site quality (Bi, 2001; Weiskittel et al., 2009), climate (DeBell et al., 1989; Comeau et al., 2010), and nutrient level (Morris, 2003; Reyes-Hernandez et al., 2013). Variation between species reflects differences in resource requirements (e.g., shade tolerance, drought tolerance and packing capacity) (Zeide, 1985; Pretzsch and Biber, 2005; Charru et al., 2012). In general, shade tolerant species show higher "stockability" (i.e., for any given average size, maximum densities are higher) than shade intolerant species (Pretzsch and Biber, 2005; Charru et al., 2012). Plantation origin stands have been reported to have a lower intercept and a flatter slope than natural stands (Weiskittel et al., 2009; Charru et al., 2012). Increases in site quality or nutrient regime lead to increases in the intercept value (Westoby, 1984; Bi, 2001; Weiskittel et al., 2009; Reyes-Hernandez et al., 2013). DeBell et al. (1989) reported that climate can influence the stockability of loblolly pine (*Pinus taeda* L.) stands, with stands in Hawaii carrying higher density and basal area at any given sizes than stands in the southeastern United States.

Analysis of maximum size-density relationships has focused primarily on static self-thinning lines defined using the upper boundary points from a large number of crowded stands (Osawa and Sugita, 1989; Weller, 1990). The static self-thinning line provides a general boundary limit for the species in a region (Weller, 1990; VanderSchaaf and Burkhart, 2007), so the species boundary line can be used in developing stand density management diagrams, stocking guides, and in growth models (Drew and Flewelling, 1979; Weller, 1990; Jack and Long, 1996; Yang and Titus, 2002). Dynamic self-thinning lines use data from re-measurements of permanent sample plots to examine the behavior of individual crowded stands over time (Weller, 1987). Dynamic self-thinning lines are more sensitive to effects of site quality, silvicultural treatments and other factors (Westoby, 1984; Weller, 1990; VanderSchaaf and Burkhart, 2007). VanderSchaaf and Burkhart (2007; 2008; 2010) used a mixed effects model to better reflect behavior of individual self-thinning stands and develop an average dynamic thinning line for loblolly pine.

Trembling aspen (*Populus tremuloides* Michx.) is a prominent and widespread tree species in Canada and in the central and northern United States. This species grows on well drained, loamy, and high organic matter soils, and can also be found on shallow and rocky sands and heavy clays (Perala, 1990). As a shade intolerant and pioneering species, it regenerates in abundance from living roots left behind after fire or harvesting and

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grows rapidly. Aspen is found in single species stands throughout its range, and in the Canadian boreal forest it is also found in mixture with conifers, particularly white spruce (*Picea glauca* (Moench) Voss). Due to the regeneration from sucker roots, aspen seedlings can exceed 100,000 stems per hectare at age 2 when conditions are suitable (Steneker, 1976; Bella, 1986). Given these high densities of regeneration, self-thinning begins at early ages due to the intraspecific competition for resources (light, water, and nutrients) and space, and senescence causes the mortality in the late successional stage (Senecal et al., 2004; Luo and Chen, 2011; Bell et al., 2014). In addition, mortality in aspen stands can be accelerated by insect attacks (e.g., Forest tent caterpillar (*Malacosoma disstria* Hübner)), diseases (e.g., Shepherd's crook), drought, wildfire, and herbivores.

Lieffers and Campbell (1984) estimated the self-thinning line using biomass and density in young aspen stands and obtained a slope of −0.962 which differs from Yoda's boundary thinning line. Yang and Titus (2002) developed maximum size-density functions for mixed species including trembling aspen and found no effect of site quality (site index) on the static size-density relationship. Bokalo et al. (2007) developed size-density equations for young-regenerated aspen stands and found that the slope of the maximum density-quadratic mean root collar diameter line was -1.408. In a recent study, Reyes-Hernandez et al. (2013) estimated the static and dynamic self-thinning lines for mature mixed stands of aspen and white spruce and examined the effects of stand composition, age, and site quality indicators (soil moisture regime and soil nutrient regime). While they found that the slope of the static line became steeper as aspen proportion increased, there was no effect of site quality on the static line. With regard to the dynamic line, the intercept decreased with increasing proportion of aspen and increased with increasing nutrient regime.

Maximum size density lines have been developed for trembling aspen in this region and effects of stand age, site quality, and soil water and nutrient regime have been examined, but these studies have not examined effects of climate. Climate, particularly drought, is important to tree growth and survival (Suarez et al., 2004). Western Canadian boreal forests have short growing seasons and low mean annual precipitation ranging between 472 and 620 mm based on 1961–1990 climate normal data (Gray et al., 2011; Price et al., 2013). Drought stress is considered to be an important factor causing mortality of trembling aspen (Hogg et al., 2002; Allen et al., 2010; Michaelian et al., 2011; Peng et al., 2011; Hogg et al., 2013; Worrall et al., 2013).

The purpose of this study was to use data from Alberta and Saskatchewan to determine whether a single regional maximum size-density relationship can be used or if it is necessary to incorporate climate into the models. In this study we evaluate effects of climate on both the static and dynamic self-thinning lines for trembling aspen.

2. Materials and methods

2.1. Data

The study plots are mostly located in the boreal plains ecozone across Alberta and Saskatchewan (Fig. 1). The Boreal plains ecozone has 0.2 °C mean annual temperature and 472 mm annual precipitation (Price et al., 2013), and despite the low precipitation this ecozone is considered to have a moist climate because of cold winters and moderately warm summers (Wiken and Canada, 1986). Under these climatic conditions and forested lands, gray Luvisolic soils predominate (Wiken and Canada, 1986; Lavkulich and Arocena, 2011). The boreal plains ecozone has a frost free period of 80–130 days and 1000–1250 degree-days above 5 °C for the growing season, where trembling aspen, balsam poplar, white birch, white and black spruce, jack pine and tamarack are found in pure or mixed stands (Wiken and Canada, 1986).

344 aspen dominated permanent sample plots established by government agencies and forest industry were measured and used for this analysis. Alberta government (ESRD), Alberta-Pacific Forest Industries Inc. (ALPC), and Weyerhaeuser Company Ltd. (WEYR) meet the minimum standards of Provincial Growth and Yield Initiative (PGYI) to measure permanent sample plots. In general, trees where a diameter is bigger than 9.1 cm were measured in 400 m^2 and plot size varied from 400 to 1000 m^2 depending on agency. Saskatchewan government measures trees larger than 7.1 cm and plot size varies from 600 to 1000 m^2. In order to unify the dataset, only trees bigger than 9.1 cm were used for the analysis. In all of these plots, aspen comprised at least 80% of plot basal area. These permanent sample plots varied in elevation, tree size, and density and included between one and five measurements (Table 1).

2.2. The static self-thinning line

Stochastic frontier function (SFF) regression was used to develop the static self-thinning boundary lines. SFF directly determines boundary lines and accommodates inclusion of covariates (Bi et al., 2000; Zhang et al., 2005; Weiskittel et al., 2009; Reyes-Hernandez et al., 2013). The self-thinning boundary line was fit, using stand density (TPH) as the dependent variable and quadratic mean diameter (QMD) as the independent variable. Even though SFF allows observations to depart from the frontier line, low values for TPH on the left or right side can influence the estimates of slope and intercept. Consequently, we removed measurements where relative density (Curtis, 1982) was below 0.4. This left 344 plots from 4 agencies for fitting the SFF (Table 2). For this analysis, only a single measurement (the highest measurement of basal area) was included for each plot to avoid issues arising from repeated measurements. The equation for the self-thinning boundary line is:

$$\ln(\mathrm{TPH}) = \beta_0 + \beta_1 \times \ln(\mathrm{QMD}) + \varepsilon(=\nu - u), \quad (1)$$

where ln is the natural logarithm, TPH is trees/ha, QMD is quadratic mean diameter (cm), β_0 is the intercept value, and β_1 is the slope value. ε consists of two error terms where the first error term (ν) is the effect of random factors influencing stand density, such as external disturbances or environmental influences and the second error term ($u \geq 0$) is a non-negative random variable related to site occupancy (Bi et al., 2000; Bi, 2004; Zhang et al., 2005). Climate variables were added as separate variables to test the effects of climate variables on the intercept and also as interaction terms with ln(QMD) to evaluate their influence on the slope of the maximum size-density line. The equation is:

$$\ln(\mathrm{TPH}) = \beta_0 + \beta_1 \times \ln(\mathrm{QMD}) + \beta_2 \times \text{Climate variable} + \beta_3 \times \ln(\mathrm{QMD}) \times \text{Climate variable} + \varepsilon, \quad (2)$$

where β_2 is the coefficient of climate variable and β_3 is the coefficient of the interaction term between ln(QMD) and climate variable. To develop better models, one climate variable to three climate variables were added with the interaction term (β_3) to the basic model. Parameters for stochastic frontier function were estimated using the frontier package (Coelli and Henningsen, 2013) of R version 3.0.3 (R Core Team, 2016).

2.3. The dynamic self-thinning line

To assess dynamic self-thinning lines, at least 2 measurements of each plot are required to track the behavior of a stand. Out of the 407 plots (699 measurements) available for fitting of static lines, 41 plots had two or more measurements. 15 plots not undergoing self-thinning over time and not being within the zone of imminent competition mortality (i.e., relative density was below 0.55) were removed (Drew and Flewelling, 1979; Newton, 1997; Reyes-Hernandez et al., 2013). 26 plots (62 observations) having two or more re-measurements were used to develop and evaluate dynamic self-thinning lines (Table 2). Dynamic maximum size-density lines were fit using logarithm of stand density (TPH) as the dependent variable and logarithm of quadratic mean diameter (QMD) as the independent variable, and plot and log-quadratic mean diameter were used as random intercept and slope. Because re-measurements of plots were correlated and all plots were independent, a linear mixed-effects model was used (VanderSchaaf and Burkhart, 2007; Vanderschaaf, 2010). An unstructured variance-covariance matrix was assumed for developing the