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Estimating the self-thinning line from mortality data

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ABSTRACT

Context: Self-thinning is fundamental to modern density-based forest management. The process of self-thinning arises from the dynamic interaction of stand growth and mortality at equilibrium conditions. However, despite the dynamic basis for the self-thinning process, it is typically modeled using static size-density data.
Material and methods: We tested the ability of a simple stand mortality model to estimate the self-thinning line. We used data from long-term silvicultural experiments for six common *Eucalyptus* species in southeastern Australia. Our approach built on existing mortality model structure that predicts survival trajectories that follow a self-thinning line. We used Poisson and negative binomial generalized linear models for count data as well as a non-linear least squares procedure on the integrated scale to calibrate the mortality model. Derived self-thinning parameters were compared to parameters calibrated on the static allometry between quadratic mean diameter (Dq) and stand density (N) using two reference methods (linear model and stochastic frontier analysis).
Results: Our dynamic mortality models provided estimates of the self-thinning line that were as good as or better than those obtained using reference methods; however, this required accounting for overdispersion of mortality count data. We validated survival trajectories using independent data for the three most abundant eucalypt species and found that they showed excellent behavior.
Discussion: Survival trajectories predicted by the mortality models were consistent with, and accurately estimated, the self-thinning line for the eucalypt species in our study. The simplicity of calibrating mortality models using GLM methods raises the possibility of quantifying how environmental drivers influence the dynamic self-thinning equilibrium.

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1. Introduction

Size-density relationships defined by the self-thinning line (also referred to as the maximum size-density limit) describe the maximum number of plants of a given mean size that can be stocked per unit area (Harper, 1977). The concept of self-thinning is foundational to plant ecology, providing an equivalent to the concept of carrying capacity in animal populations, when both number and size are necessary to describe the system (Westoby, 1981; Westoby, 1984). In even-aged forests, self-thinning is an emergent property of the dynamic equilibrium between stand growth and competition-based mortality. As trees get larger, they require more space and resources to grow and survive; smaller trees become progressively suppressed and eventually die as the resources available to them diminish. Self-thinning is of major importance in forest management as it provides the conceptual framework for density-based management (Jack and Long, 1996; Long and

Vacchiano, 2014) and allows for derivation of the relative density index (Reineke, 1933). Self-thinning also provides upper boundary guidelines for projecting tree survival (Monserud et al., 2004; Le Moguédec and Dhôte, 2012; Landsberg and Waring, 1997; Franklin et al., 2009), as well as a benchmark to evaluate mortality models (Monserud et al., 2004; Fortin et al., 2014; Vospernik et al., 2015).

Although the process of self-thinning emerges from the dynamic equilibrium between stand growth and mortality, it is typically calibrated using static data on mean plant size and stand density (Zhang et al., 2005). While self-thinning has been studied in plant populations ranging from annual herbs to long-lived trees (White and Harper, 1970; Drew and Flewelling, 1977; Lonsdale, 1990), our focus is on trees[1]. Considerable research has focused on

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[1] The standard metric for mean size in self-thinning studies of trees is either stem biomass or stem diameter (measured at breast height, 1.3–1.4 m above the ground). Because stem biomass is typically estimated from a diameter-biomass allometry, we focus on the direct measurement, stem diameter, which is commonly obtained as the standard measure of tree size.

the best methods for fitting the self-thinning line to the allometric relationship between quadratic mean diameter (*Dq*) and stand density (*N*, the number of trees per unit area), increasing the objectivity of the method to allow broader application and reproducibility of the research (Bi et al., 2000). Historically, two steps have been involved: (1) a selection of unthinned control plots ranging in *Dq* and *N* and (2) fitting a line to the *Dq-N* allometry on a log-log scale. The earliest approach was simply to hand-fit a line to the plotted data (*e.g.*, Reineke, 1933; Drew and Flewelling, 1977). Subjectivity in parameter estimates in step 2 was subsequently overcome by using statistical methods such as ordinary least square regression (OLS) (Zhang et al., 2005) or by computing the average slope of successive *N* and *Dq* measurements in unthinned control plots (Pretzsch and Biber, 2005; VanderSchaaf and Burkhart, 2007). The need for subjective data selection in step 1 was eliminated by using methods that explicitly model the error distribution in such a way that the estimated line is shifted towards or on to the upper *Dq-N* boundary. This can be achieved with quantile regression (Zhang et al., 2005) or stochastic frontier analysis (SFA) (Bi et al., 2000). Due to its good inferential properties, SFA is widely considered as the current state-of-the-art method for estimating the self-thinning line (Bi, 2001; Zhang et al., 2005; Weiskittel et al., 2009; Charru et al., 2012). While each of these methods can successfully estimate the self-thinning line based on the observed static *Dq-N* data, they provide no insights into the underlying dynamic allocation process that drives self-thinning. In addition, they provide little guidance for projecting tree survival for stand conditions that are not close to the self-thinning frontier (*i.e.*, *Dq-N* boundary), a situation that occurs frequently in forest management. Recognizing that tree mortality occurs away from the maximum size-density limit, some researchers have developed phenomenological piecewise models that smoothly connect the initial stand development phase characterized by an absence of tree mortality to the self-thinning line (Smith and Hann, 1984; Cao and Dean, 2008; Ningre et al., 2016). These piecewise models, however, describe trajectories rather than rate of change (Garcia, 2013b) and might be limited for dealing with stand disturbances (*e.g.*, thinning) or changes in environmental conditions.

Early dynamic models of stand mortality modeled the survival of individuals in *time* as a function of stand *age* and *N* (*e.g.*, Clutter et al., 1980):

$$\frac{\delta N}{\delta t} = exp(\beta_0) \cdot age^{\beta_1} \cdot N^{\beta_2} \qquad (1)$$

This basic model was later extended to include survival functions of varying shapes (Rose et al., 2004), environmental covariates (Thapa and Burkhart, 2015), and the ability to model the error distribution and overdispersion typical of mortality count data (Affleck, 2006). Recently, Garcia (2009) made a significant advance by replacing (1) stand *age* with average tree *size* and (2) the *time* derivative with a *size* derivative (*i.e.*, size increment). This approach, in effect, simulates the conditions that generate the dynamic equilibrium between stand growth and mortality:

$$\frac{\delta N}{\delta size} = exp(\beta_0) \cdot size^{\beta_1} \cdot N^{\beta_2} \qquad (2)$$

By construction, Eq. (2) predicts limiting survival trajectories that converge to a maximum size-density limit. As mortality is inherently noisy and hard to predict, compliance to the maximum size-density limit is often used to test the biological realism and to validate mortality models (Monserud et al., 2004; Fortin et al., 2014; Vospernik et al., 2015).

While trajectories predicted by Eq. (2) are consistent with a self-thinning line, its ability to accurately estimate this line has never been compared against methods usually used to calibrate it.

The overarching goal of this study was to investigate the ability of simple dynamic mortality models such as Eq. (2) to estimate the

self-thinning line and evaluate them against classical methods that use static *Dq-N* data (OLS and SFA). This is also a test of the consistency of the mortality models with a known dendrometric rule. We extend Eq. (2) by using Poisson and negative binomial (NB) error distributions within a GLM framework to account for the error distribution typically arising from modeling count data (Affleck, 2006) and to evaluate its influence on estimates of the self-thinning line. Our data originate from long-term silvicultural thinning experiments for six common *Eucalyptus* species in southeastern Australia. These long-term trials allowed us to explore repeated measurements of mortality and *size* increment across large gradients of *size* and *N* over years to decades.

The three specific aims of the study were:

1. to investigate the ability of mortality models to estimate the self-thinning line;
2. to determine the effect of modeling the error count distribution on self-thinning line estimates; and
3. to provide self-thinning line estimates and stand mortality models that comply with self-thinning rules.

2. Material and methods

2.1. Experimental data

Our study focuses on six eucalypt species that are common and, in some cases, commercially important in southeastern Australia (*Eucalyptus camaldulensis*, *E. delegatensis*, *E. nitens*, *E. obliqua*, *E. regnans*, and *E. sieberi*) (DNRE, 2007). Native forests of *E. camaldulensis* can be found along the rivers and valleys of southeastern Australia. Elevation and rainfalls are generally low and the sites are periodically flooded. *Eucalyptus sieberi*, which is often found in mixtures with other eucalypt species, occupies lowland forests ($< 700m$) in eastern Victoria and southern New South Wales. The four other *Eucalyptus* species can be found in tall open wet forests, most often dominated by a single overstorey species, and occupy mountainous areas of the Central Highlands and East Gippsland in Victoria. These forests are characterized by high rainfall ($> 1000 – 1200mm.year^{-1}$), with *E. delegatensis* found at higher parts of the elevation range and *E. obliqua* found on drier sites and aspects. *Eucalyptus obliqua* can also be found in mixed-species forests at lower elevation and coastal area.

Our data originate from several long-term silvicultural experiments in even-aged stands compiled in a database that was historically curated by the Victorian Department of Environment, Land, Water, and Protection (DELWP) and its various precursor organisations, and is currently maintained by VicForests, the State-Owned Enterprise responsible for forest management on Victoria's State Forests. The objective of these silvicultural experiments, which were established between the 1920s and 1970s, was to study the effect of thinning treatments on stand-level growth and yield. Each experimental series (experimental site) had several permanent plots – typically, but not always, of the same age – that were subjected to varying thinning treatments (namely: no thinning, initial thinning, initial plus frequent thinning). In several of the experimental series the thinning treatments were replicated within the site. Individual trees within the study plots were remeasured for diameter at breast height (1.3 m, *dbh*) and status (alive, dead) at relatively regular intervals of approximately 2–3 years until the late 1990s. Many of the study plots have >10 measurements and the longest series has 19 covering a period of 50 years.

From the database of thinning trials, we selected single-species stands (defined as stands in which the dominant species accounts for >80% of total basal area ($BA, m^2.ha^{-1}$) from large plots ($> 250 \text{ m}^2$) with sufficiently long remeasurement periods