



Process-based size-class distribution model of trees within forest plantations: A hierarchical modeling approach



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ARTICLE INFO

Article history:

Received 19 November 2014

Received in revised form 9 February 2015

Accepted 11 February 2015

Available online 27 February 2015

Keywords:

Diameter

Height

Pinus radiata

Eucalyptus globulus

Variability

Silviculture

ABSTRACT

Prediction of stand structure, and how it varies with climate, disturbance and silviculture, can assist the design of adaptation options to climate change, aid silviculture response to storm damage or pest attack, and help stand managers meet product delivery schedules and maximize wood value. Making these predictions with process-based models typically requires detailed data on the existing tree population structure from which to initiate projection, or alternatively highly complex, and difficult to parameterize, models of inter-tree competition. This paper introduces a hierarchical modeling approach to address this problem. In this approach, the stand-level outputs of a process-based model, CABALA, are disaggregated among individual trees within a stand according to simple rules to provide individual tree sizes and growth trajectories. The model, designed for single-species, evenly-spaced stands, is based on a number of assumptions including: stand level allometrics can be scaled to individual trees; above-ground competition for space and resources can be used as a guide to overall inter-tree competition; trees within a stand start with a distribution of sizes as well as variation in intrinsic productive potential.

The output of the model was tested across a wide range of site types for two species, *Pinus radiata* and *Eucalyptus globulus*, over a range of thinning and fertilization treatments, and for stands of ages between 2 and 27 years. Across these conditions, predicted and observed distributions were statistically similar ($p = 0.05$) in 38% of the 280 *E. globulus* height distribution, in 47% of the 280 *E. globulus* diameter distribution and in 85% of the 53 *P. radiata* diameter distribution comparisons. Overall, predictions were better for *P. radiata* than *E. globulus*, and for both species were better for older stands than young. Spatial patterns were similar: neither predicted nor observed spatial distributions exhibited spatial auto-correlation.

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1. Introduction

Forests are complex and richly-linked systems where the emergent stand-level processes of thinning, leaf area index, current annual increment of wood, water-use and the distribution of trees of different sizes, are the result of the individual interactions of the many trees that compose the forest. Confronted with such complexity, most process-based forest growth models (Landsberg and Waring, 1997; Kirschbaum, 1999; Battaglia et al., 2004) utilize stand-level emergent relations (e.g. the self thinning law, linear relationship between intercepted radiation and net primary production, etc.) to simulate stand-level growth. Individual trees within the forest, if considered at all, are then treated as identical to the mean tree of the stand.

Modeling of forest production at the stand level is pragmatic. Relationships that are often complex and non-linear at fine-scales can, in some instances, be simplified when averaged across space and time, and when real-world heterogeneity is ignored. However, representation of stand-level phenomena alone limits the usefulness of these models. For example, existing stand-level models are of limited use in predicting tree size-class distributions and the sizes of logs obtainable from harvests. This reduces the utility of models for economic forecasting. Wood quality too, is strongly dependent on individual tree size and not stand level attributes (Downes et al., 2006). These limitations restrict the application of models to the simulation of stands in which all trees can be approximated as identical, or uniformly spaced. The use of these models is generally restricted to young, single-species stands, and to situations in which silvicultural practices, such as pruning, are applied to all trees and not just to the selected final crop-trees.

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As forests, including plantations, get older the trees within the stand differentiate in size so that even homogeneous plantations become more structurally complex (for example see (Binkley et al., 2002)). Disease, mammalian browsing and events such as drought and frost can accelerate the introduction of heterogeneity into forest stands. It is clear that tree size affects tree functioning, in particular fluxes of water and carbon (e.g. Ryan et al., 2000), and that this may affect growth efficiency (Stoneman and Whitford, 1995; Binkley et al., 2004).

Few process-based models have attempted to build forest stands from the bottom-up (but see West, 1987, 1993; Franc, 1999; Brotsma et al., 2010) as the aggregate of individual trees competing for resources. Such models usually involve lengthy lists of inputs and considerable algorithmic complexity (e.g. Mitchell, 1975). They are often less accurate than whole stand distribution models (Daniels et al., 1979). These models may need the imposition of constraining relationships to prevent run-away behavior (e.g. Mowrer, 1989) and may use site level factors such as site index to constrain height growth (West, 1987). Furthermore, despite aspects of their complexity, in many cases these models incorporate competition indices based on fairly simple assumption such as distance dependent competition strength (Larocque et al., 2012).

Complex systems, however, can be simulated with simple algorithms. The application of cellular automata models for the simulation of size class distribution in forest stands has been demonstrated (Franc, 1999). In such a system, the forest is represented as a lattice of connected cellular automata. Each automata or node on the lattice represents an individual tree. Simple rules govern the interaction between nodes and stand level phenomena such as self thinning emerge from these simple interactions. Similar principals can be applied in simulations with a more relaxed spatial structure (McMurtrie, 1981; Korol et al., 1991, 1995; Running and Milner, 1995; Korol et al., 1996).

This approach is relatively unexplored in forest growth and yield modeling, although it has seen extensive application in ecological studies to characterize species distribution and patterns (Manrubia and Sole 1997; Lett et al., 1999; Cumming et al., 2000; Ostendorf et al., 2001), to model individual tree structure (Perttunen et al., 1996; Makela, 2003) and to explore theoretical patterns of tree competition and distribution (Gates 1978, 1982). Where the technique has been applied in forest growth and yield modeling, verification and validation has been limited, raising concern about the generality of the rules governing interactions between individuals. Critical for such verification is the validation of size class distributions over time drawn from stands that have been subjected to a range of conditions (Larocque et al., 2012).

Review has suggested that soundly-based, mechanistic-modeling of this kind warrants investigation (Vanclay, 1994; Larocque et al., 2012). In simple form, these models require the user to define an initial matrix of site and plant conditions (height, leaf area and vigor) and a few simple rules of how individuals interact. Critical for successful application of the method is a simple definition of ecological interaction (Iwasa, 1998) and an analysis of demographic structure in relation to the partitioning of space inherent in the array structure (Bian, 2003). Plantations in which the initial spacing of trees is predetermined provide an ideal system to test the usefulness of these approaches. The hierarchical approach of linking models across different scales utilizes the structural complexity implicit, and emergent properties observed, in many ecological systems (Allen and Starr, 1982).

There is emerging evidence that neighborhood uniformity is a factor in determining competition strength (Luu et al., 2013). In this work, we adopt this approach and introduce additional novelty by considering the role of genetic variability between individuals within a stand. Plantations established with seedlings will

comprise two distinct populations, out-crossed and self-fertilized seedlings ('selfed'), with different performance attributes and different population variability (Costa e Silva et al., 2010). One tool available to siviliculturalists to improve production (Binkley et al., 2010), and determine the subsequent development of size class distributions, will be the intrinsic genetic variability of the stand. At one end of the scale are clonally propagated plantations, and at the other those plantations established with seed from wild populations, or poorly managed seed orchards, in which high rates of self-fertilization can markedly depress plantation performance (see Harwood et al., 2004 for example).

In this work we use stand-level production estimates from the stand model CABALA (Battaglia et al., 2004) to bound, or apply upper level constraints to, forest growth and water-use. While we use CABALA in this instance, any process-based model (3PG (Landsberg and Waring, 1997) for example) that can provide a time stream of the requisite inputs could be used. Then the approach of Korol et al. (1995) and Sievänen and Burk (1993) is used to define inter-tree interaction and disaggregate stand level production and respiration derived from CABALA. By allowing for neighborhood effects this approach allows for the observation that large trees are not only those that have intrinsically superior growth but are also those that are favored by proximity to inferior rather than co-dominant trees (McMurtrie, 1981).

We use the well studied, but phylogenetically and physiologically contrasting, *Eucalyptus globulus* and *Pinus radiata* plantation systems to test the modeling approach. The CABALA model has been well validated for these two species (Battaglia et al., 2009; Miehle et al., 2010), and they collectively make up more than 70% of the Australian plantation industry and are both planted widely around the world. Competitive interactions between trees of different sizes have been defined under conditions of varying water and nutrient stress (O'Grady et al., 2008, 2010). At different levels of thinning and fertilization, height and diameter distributions for *E. globulus*, at various ages between 2 and 10 years (White et al., 2009), and for diameter distributions for *P. radiata*, between ages 8 and 27 years (Carlyle and Bruce, 2001), are available for model validation.

2. Methods

2.1. The model

2.1.1. General assumptions

It is assumed, for modeling, that tree-scale allometrics and physiological functions are scalable from the tree to the stand. To ensure consistency between stand, and tree, models, at the start of a model time-step, total production, leaf area, biomass loss and respiration are disaggregated among trees to simulate individual tree growth, and then at the end of the time-step the dimensions and survival of the individual trees are summed and averaged to provide height, diameter and stocking for the stand level model. Tree and stand-level models communicate on a monthly basis in the current implementation to reduce computational time. A consequence was that the only additional parameters needed for the model are those that define variability between trees in initial size and genetic performance, and those that determine tree mortality from carbon starvation (and if the later is not of interest these can be ignored).

A second assumption is that above-ground competition for space and resources can guide overall inter-tree competition. The model partitions net primary production (NPP) as a function of individual tree light interception, which is determined by the canopy extent and shading of the tree by neighbors. At the stand-level, both water stress and nutrient stress reduce the

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