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Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA

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ABSTRACT

Factors influencing tree growth in structurally complex forests remain poorly understood. Here we assessed the influence of competition on *Pinus resinosa* ($n = 224$) and *Pinus strobus* ($n = 90$) growth in four old-growth stands in Minnesota, using mixed effects models. A subset of trees, with accurate age estimates, was used to further test the influence of tree age. Our analyses included the weighted Voronoi diagram (WVD) as a novel competition index, representing a detailed description of the spatial structure of a tree's neighborhood.

Competition was variably expressed depending on stand developmental history and tree species. For *P. resinosa* in single-cohort stands, and *P. strobus* in multi-cohort stands, tree size relative to the population mean size best predicted tree growth. In contrast, for *P. resinosa* in multi-cohort stands, the spatial configuration of competitors became important, as shown by the superior performance of the WVD index. Surprisingly, while tree age had a negative influence on growth, it did not influence the intensity of competition.

Our results highlight the importance of considering stand developmental history and tree age in analyses of tree growth and competition, and the potential for improving assessments of competition in complex stands, using detailed quantification of neighborhood structure.

1. Introduction

In natural forests, tree-to-tree variation in growth can be considerable, and it results from, as well as promotes, the structural and compositional complexity that often characterize these forests (Coomes and Allen, 2007; Parish and Antos, 2004). Understanding the factors influencing this variability is essential for predicting forest responses to environmental changes, and it also has direct application to forest management, as management strategies based on natural stand dynamics require an understanding of tree growth responses under a variety of environmental and structural conditions (Roberts and Harrington, 2008).

A number of factors interact to influence tree growth. For example, the influence of neighborhoods depends on characteristics of both the individual (focal) trees and their neighboring trees. These characteristics include species, size and location of a tree relative to its neighbors, as well as their interaction (Canham et al., 2004, 2006; Lorimer, 1983). Most studies agree that these neighborhood effects on individual tree growth are primarily negative, owing to competition for limiting resources (Burton, 1993).

Tree age is also expected to influence growth rates (Johnson and Abrams, 2009; but see Mencuccini et al., 2005; Yoder et al., 1994). Whether these effects are due to tree size rather than age has been debated, and the exact mechanisms governing the age-related reductions in tree growth remain elusive (Li et al., 2012; Mencuccini et al., 2005; Ryan et al., 2004). Another confounding factor is that comparing growth among even-aged stands has made it difficult to disentangle age-effects from edaphic factors, as soils are undergoing concomitant changes (Martinez-Vilalta et al., 2007). In general the influence of tree age on growth, and particularly its relationship to competition, remains poorly studied.

Most studies of competition and tree growth have focused on plantations, managed forests, and even-aged, relatively young natural forests (Woodall et al., 2003; but see Contreras et al., 2011; Kubota and Hara, 1995; Hartmann et al., 2009). Because the factors influencing tree growth, such as tree sizes, ages, and neighborhood structure and composition change through stand development, it is unclear how inferences from studies of early phases of stand development apply to structurally and compositionally different stages of development, especially structurally diverse uneven-aged old-growth forests.

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Tree-tree competition is typically assessed using indices that mathematically express a focal tree's competitive status relative to neighboring trees and/or the degree of localized resource competition that a given focal tree experiences. Indices differ in the various aspects of competition they intend to express, and as such, their performance in predicting tree growth has varied among studies (e.g., D'Amato and Puettmann, 2004; Kunstler et al., 2011). Several previous studies report that indices lacking tree spatial location have performed well, at times even better than more complex spatial indices, in describing competitive interactions (e.g., Lorimer, 1983). This insignificance of tree spatial locations is attributed in part to the studies having been conducted in evenly-spaced plantations (Hartmann et al., 2009). Few studies have addressed these relationships in structurally diverse, old-growth systems that include highly variable and heterogeneous spatial arrangements and sizes of trees.

Despite the sometimes poor performance of indices incorporating tree spatial location, competition for resources affecting tree growth is generally assumed to be a spatially-explicit process. When modeled, competition for resources is typically assumed to occur within a circular neighborhood centered on the focal tree (Burton, 1993). However, the spatial variation in tree architecture (e.g., root and crown distributions) and resource availability in natural populations would suggest that the zone of perception need not be circular (Simard and Sachs, 2004). An alternative neighborhood characterization is the 'area potentially available', defined as a typically irregularly shaped polygon constructed around each focal tree such that no other trees are included within the polygon (Moore et al., 1973). We propose that such an index could better capture and explain competitive effects in structurally heterogeneous old-growth forests where trees exhibit irregular spatial patterns.

Our objective was to quantify the influence of competition on tree growth in structurally heterogeneous old-growth forests, and its relationship to tree ages. We address this objective using a novel approach to neighborhood characterization, namely the multiplicatively weighted Voronoi diagram (WVD), which represents a more detailed description of the spatial relationship of trees within stands compared to traditional indices of neighborhood conditions. We believe this approach will better capture the competitive environment in structurally heterogeneous conditions. The polygon-approach is intuitively appealing because it considers the entire neighborhood structure simultaneously and seamlessly (as opposed to tree-by-tree search radii), such that the size and location of one neighbor appropriately influences the competitive influence of other neighbors. Further, this approach allows for asymmetric partitioning of the growing space, rather than assuming isotropy and uniform shape of the focal tree's growing space. We expected that tree growth in structurally complex forests would be influenced by characteristics of a focal tree's competitive neighborhood, as well as characteristics of the focal trees themselves (including species, size and age) and their interaction. Moreover, we further hypothesized that the characteristics of competition would differ among populations according to stand developmental history, such that spatial structure is of increasing importance in uneven-aged, old-growth forests. We test these hypotheses for the dominant conifers *Pinus resinosa* (red pine) and *Pinus strobus* (white pine) in four structurally heterogeneous old-growth stands in northern Minnesota using the novel WVD approach in combination with six commonly used competition indices. Though applied here to just one forest type, we believe our approach provides an improved framework for assessing the influence of spatial structure on tree growth in other structurally heterogeneous forest systems.

2. Materials and methods

2.1. Study area, plots and field measurements

Our study builds on data from Fraver and Palik (2012), who investigated cohort age structures of four remnant old-growth *P. resinosa*-dominated forests in northern Minnesota. These sites (Itasca State Park, Scenic State Park, Sunken Lake, Pine Point) are located in the Minnesota Drift and Lake Plains (according to the national hierarchical framework of ecological units; Cleland et al., 1997). The area has typically deep soils, consisting of complex juxtapositions of ice contact, fluvio-glacial and lacustrine deposits. Fraver and Palik (2012) showed that *P.resinosa* on two of these sites (Itasca and Scenic State Parks) consists of a single cohort that likely regenerated following a stand-replacing disturbance. On the other two sites (Sunken Lake and Pine Point), *P. resinosa* has a more complex age structure, forming two or more cohorts, reflecting a more complex history of stand development. All four sites are dominated by *P. resinosa*, but *P. strobus* represents a considerable proportion of basal area in the two multi-cohort sites. Other species in these stands included *Abies balsamea*, *Picea glauca*, *Betula papyrifera*, *Acer rubrum*, *Populus* spp., and *Quercus* spp.

Each site included a square plot, which consisted of an inner core area of 70.7 $\times$ 70.7 m (0.5 ha) and a surrounding 10-m buffer area (see Fraver and Palik (2012), for further details of plot establishment). Within the entire plot, diameter at breast height (DBH, 1.37 m), species, and *X* and *Y* coordinates for all living and standing dead trees (stems $\geqslant$ 10 cm DBH) were recorded. Trees in the buffer were inventoried to provide a full set of potential competitors for focal trees located within the core area.

2.2. Tree ring data, basal-area increments and tree ages

Using cross-dated tree-ring data from Fraver and Palik (2012), we calculated annual basal-area increments for each focal tree ($n = 224$ for *P. resinosa*, $n = 90$ for *P. strobus*). By convention, these increments included bark thickness, which was estimated for each year, following Fowler and Damschroder (1988). We used the mean annual basal area increment over the most recent 20 years (see below) as our metric of growth in all subsequent analyses. Although non-pines were present at each site, we focused our analyses on the dominant conifers *P. resinosa* and *P. strobus* located within the 0.5 ha inner core area. Tree ages were also determined from these same tree-ring data, with age estimates refined following methods outlined in Fraver et al. (2011).

2.3. Competition indices

We selected indices for initial testing based on their favorable performance in earlier studies and considering the differences in the nature of competition they represent. Seven indices from four categories were selected (Table 1): (1) relative dominance (representing focal tree's population-level competitive status), (2) distance-independent (competitive effect is strictly related to focal tree and neighbor sizes), (3) two variants of distance-dependent indices, (competitive effect is a function of size of and distance to the neighbors, or the function of focal tree size relative to competitor sizes and distances to them), and (4) the WVD growing-space polygon (resource availability is spatially restricted based on neighbor location, density and size). In addition to these, and for a more detailed assessment of the performance of the WVD, we also included the original, unweighted Voronoi diagram (alternatively known as Dirichlet tesselation or Thiessen polygons). All indices were tested by regression analysis for their influence on basal-area increment. Included in the analyses was a null model that