



Separating effects of crown structure and competition for light on trunk growth of *Sequoia sempervirens*



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ABSTRACT

Tree-level productivity is largely determined by crown size and aboveground vigor, but light availability ultimately controls growth. Competition indices are typically used in modeling instead of actual measurements of light. Our goals were to determine which measure of light best predicts trunk growth increments of *Sequoia sempervirens*, to quantify the amount of growth variation explained by light after accounting for effects of tree structure, and to compare model fitness of various competition indices. Twenty-four trees spanning a wide range of light environments were randomly selected from stands of different ages, including trees 23–72 m tall and 20–560 years old. Tree structure and trunk growth increments were quantified via direct measurements of all branches and coring main trunks at multiple heights. Light availability was quantified via hemispherical photography throughout tree crowns. Competition indices were computed by measuring the size and distribution of neighboring trees. The largest tree had 69 m³ of wood and bark, 3208 m² of leaf area, and produced 1.04 m³ yr⁻¹ of wood in the main trunk, whereas the smallest tree had less than 1 m³ of wood and bark, 134 m² of leaf area, and produced 0.04 m³ yr⁻¹ of wood in the main trunk. After accounting for tree structure, light availability explained an additional 10% of variation in trunk wood volume increment. Light availability alone explained 49% of the variation in wood volume increment, while tree size alone explained 41%. The growth model with average mid-crown openness as the measure of light availability was 19 times more likely than the model without a term for light. A distance-dependent competition index computing neighboring tree crown volume (DDCV) was >1200 times more likely than any other competition index in the best growth model. Together with tree size and aboveground vigor, DDCV explained 91% of variation in trunk wood volume increment.

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1. Introduction

The growth rate of a tree is largely determined by its size. If radial increment and height growth are used to evaluate growth rate, it could appear as if growth rates decline with increasing size, because radial increments at breast height tend to decrease as trunk circumference increases, and height increments decline as trees approach maximum height (Bowman et al., 2013; Koch et al., 2004; Krumland and Eng, 2005). Despite these facts, annual mass increments increase continuously with tree size (Enquist et al., 1999; Sillett et al., 2015a,b). This holds true for the largest trees of at least 367 species (Stephenson et al., 2014). Simply put, a tree with more leaves has more photosynthetic capacity to support growth.

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Secondary to size, the ratio of a tree's aboveground respiratory demands to its photosynthetic capacity (i.e., aboveground vigor) explains significant variation in growth increments (Sillett et al., 2015a). Wood and bark production, heartwood formation, and maintenance respiration are some of the cellular processes in trees that consume carbohydrates produced in leaves via photosynthesis (Kozłowski, 1992). The balance between respiring and photosynthesizing tissues is independent of tree size (Litton et al., 2007; Van Pelt and Sillett, 2008; Sillett et al., 2010). Ratios of cambium area to leaf area and heartwood deposition area to leaf area are measures of tree structure independent of size (Sillett et al., 2010, 2015a). A tree with less respiring tissue per unit leaf area will have relatively more fixed carbon available for growth and other biological functions (e.g., reproduction, mycorrhizae). Trees with full crowns have higher aboveground vigor and produce wood faster than trees with sparse crowns (Van Pelt and Sillett, 2008; Sillett et al., 2015a,b).

Another determinant of tree growth is light availability, which depends on the tree's crown position (e.g., dominant or suppressed) and how foliage is distributed among neighboring crowns in the forest. Light availability generally increases exponentially with height in the canopy, so tree size and light availability are often correlated within a forest (Parker, 1997). Tall, dominant trees generally experience greater light availability than shorter, subordinate trees. As light penetrates a forest, it is absorbed and diffused by various layers of leaves, branches, and trunks that compose the canopy and can be modeled via Beer's law (Binkley et al., 2013; Hale, 2003). However, leaf size, shape, inclination, clumping, and leaf area density (leaf area per unit crown volume) within tree crowns affect light availability differently depending on light's path to any given location in the forest (Stadt and Loeffers, 2000; Wang and Jarvis, 1990). Moreover, as the sun's position in the sky is constantly changing, light availability of individual branches within crowns fluctuates widely. Hemispherical photography can quantify the amount of direct radiation (direct site factor, DSF) and indirect radiation (indirect site factor, ISF) relative to an open sky at any given location, but it remains unclear which measure of light availability—openness, DSF, ISF, or total radiation (total site factor, TSF)—best reflects tree-level productivity in forests. The enormous effort necessary to quantify crown-level light environments helps explain why individual-tree growth models rely on competition indices.

Distance-independent competition indices have some success explaining variation in trunk growth. Basal area of trees at breast height per unit area (BA) explains ~10% of the variation in trunk growth for 16 tree species in a temperate forest, ranging from 18% for *Picea abies* to 1% for *Quercus ilex* (Kunstler et al., 2011). In an even-aged forest, including BA in a trunk growth model reduces mean square error by 24% (relative to a model without a competition term) for *Abies concolor* but is unable to improve predictions for *Pinus ponderosa* (Biging and Dobbertin, 1995). Stand density index (SDI) or cohort specific SDI (Berrill et al., 2013; Reineke, 1933), and BA of trees larger than the subject tree (BAL) are stand-level measures of competition capable of improving model predictions (Coomes and Allen, 2007; Juma et al., 2014; Pukkala et al., 2009; Rivas et al., 2005). However, neither SDI nor BAL improves trunk growth predictions of *Pinus ponderosa* or outperforms BA for predicting *Abies concolor* trunk growth in the mixed conifer forests (Biging and Dobbertin, 1995). Another stand-level index evaluates a crown attribute (e.g. cross-sectional area) of trees in the neighborhood at a height relative to the subject tree's height. For example, *A. concolor* trunk growth is best predicted with the per unit area sum of crown cross-sectional areas evaluated at 66% of tree height, resulting in a 37% lower mean square error, and *P. ponderosa* trunk growth is best predicted with the per unit sum of crown surface areas evaluated at 75% of tree height, resulting in 19% lower mean square error (Biging and Dobbertin, 1995). Competition indices that use spatial data can improve predictions in more complex forests.

Tree-level productivity in stands with horizontally or vertically heterogeneous structure is best predicted using distance-dependent competition indices that consider distances between a subject tree and its competitors. A horizontal angle (i.e., variable radius plot) can be used to select competitors so that a tree's trunk diameter relative to its distance is considered (Contreras et al., 2011). Alternatively, a vertical angle emanating from the crown of the subject tree can be used to delineate a cone of influence (Rivas et al., 2005), although the explanatory power of these search cones decreases with increasing height in the tree (Seidel et al., 2015). In structurally complex forests, distance-dependent indices may be better at predicting trunk growth increments than distance-independent indices or measures of light availability (Contreras et al., 2011). Indeed, predicted trunk growth increments

in a multi-story forests have lower standard error when modeled with a distance-dependent index than with distance-independent indices (Schröder et al., 2007). We expect competition indices that use spatial data to perform better than distance-independent indices for tall species in multiage forests.

Sequoia sempervirens is currently the world's tallest species (Sillett et al., 2015a) and is considered shade tolerant (Baker, 1949). Accordingly, *S. sempervirens* can be examined across wide gradients of both size and light availability. The shade tolerance of this decay- and fire-resistant tree gives it great potential for uneven-aged management. Here we investigate three measures of trunk growth—volume increment, radial increment, and main trunk growth efficiency—of *S. sempervirens* across gradients of tree size, aboveground vigor, light availability, and competition commonly found in re-growth forests. We have three main objectives: (1) to determine which measure of light availability (openness, DSF, ISF, or TSF) best predicts trunk growth, (2) to use the best light availability metric to quantify how much variation in trunk growth is attributable to light availability before and after accounting for effects of size and aboveground vigor, and (3) to compare predictive capacities of competition indices after accounting for effects of tree size and aboveground vigor. Our goal is to improve modeling of tree-level performance in managed *S. sempervirens* forests.

2. Materials and methods

2.1. Tree selection

Trees were selected randomly from multiple height classes and crown positions. Since trees in the same stand that experience different light availability are often different sizes, selecting trees from a single stand would confound the effects of size and light availability. To avoid this, trees experiencing both low and high light availability were selected from stands of different ages to include 20–30, 40–50, and 60–70 m height classes (Table 1). These height classes represent dominant trees growing on a location with site index 120 and ages at breast height of 23–38, 57–87, and 117–170 years respectively (Krumland and Eng, 2005). Dominant trees were the tallest in the stand, while subordinate trees were shorter with over-topped crowns. Except for the northern stand used to select the 20–30 m dominant trees, a wide range of tree heights was present in each stand. Ten dominant and ten subordinate trees within each height class were located while exploring each stand. For each height class and crown position, two trees were randomly selected from stands in both southern and northern portions of the northern range of *S. sempervirens*, yielding a total of 24 trees. No subordinate trees were tallied in the re-growth forests used to select 20–30 m dominant trees, and no dominant trees were tallied in the old-growth forests where 60–70 m subordinates were found. Trees growing on either alluvial or xeric sites were excluded to minimize site quality effects (Noss, 2000). A wide gradient of aboveground vigor was ensured by randomly selecting dominant and subordinate trees from larger populations.

2.2. Tree structural attributes

Main trunks and all appendages (i.e., branches and segments) of the 24 trees were measured in a three-dimensional framework (Sillett et al., 2010, 2015a). We climbed trees with arborist-style rope techniques (i.e., no spikes). Ground level of each tree was determined by averaging vertical distances from the highest and lowest points where the trunk intercepted mineral soil to an arbitrary point on the trunk. A fiberglass tape was strung from ground level to near treetop to serve as a reference for all height measurements. We measured all live branches greater than a minimum

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