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Neighborhood uniformity increases growth of individual *Eucalyptus* trees

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ABSTRACT

Competition is a crucial factor in determining stand structure and productivity. Competition entails complex interactions that depend on spatial arrangement of trees, resource supplies, and the efficiency of using resources. The net outcome of competition may be characterized by the sizes and distances of trees in a neighborhood around a focal tree. We tested a hypothesis that higher variability in tree sizes within the neighborhood (=low uniformity) would directly reduce growth of individual trees. Neighborhood models tested the influence of focal tree size and neighborhood competition on focal tree growth, and whether further inclusion of a uniformity measure would improve model performance. We modeled growth of 8800 focal clonal trees in a 9 ha operational, clonal plantation of *Eucalyptus grandis* x *urophylla* to test our hypothesis by estimating the effects of size, and neighborhood competition and uniformity. The growth of a focal tree was strongly related to the tree's size and to the neighborhood competition index that combined the sizes and distances of neighboring trees (within 8 m of the focal tree). For a given size focal tree and a given level of neighborhood competition, the uniformity of neighborhood trees influenced potential growth by −2% (very uniform neighborhoods) to −10% (for heterogeneous neighborhoods), for an overall reduction in potential stand growth of 4.3%. Higher growth of larger trees did not compensate for lower growth of smaller trees, and silviculture systems that maximize stand uniformity may lead to measurable increases in stand-level growth.

1. Introduction

Understanding the factors that control stem growth is central to forest ecology (Uriarte et al., 2004; Canham et al., 2006; Grams and Andersen, 2007; Coomes and Allen, 2007), providing quantitative insights into biomass and stem quality in intensively managed plantations (Boyden et al., 2008; Stape et al., 2010; Asoubwall et al., 2011). The growth of trees depends in part on obtaining resources from the environment (Binkley et al., 2004), and the success of each tree in obtaining resources depends on the level of competition with neighborhood trees (Grace and Tilman, 1990, Wilson and Tilman, 2002). Competition for resources likely becomes more severe as the number and size of nearby trees increases (Bonan, 1988; Weiner et al., 2001; Canham et al., 2004; Uriarte et al., 2004; Boyden et al., 2005, 2008; Sabatia and Burkhart, 2012). The positive feedbacks of competition typically lead to increasing variance of tree sizes within a stand over time (Bonan, 1988; Weiner et al., 2001), and increasing variation in tree sizes may alter both tree-to-tree competition and stand-level production. Even a highly uniform, operational plantation of clonal *Eucalyptus* has substantial variance in tree sizes and growth (Figs. 1 and 2; see also Ryan et al., 2010; Stape et al., 2010).

The mechanisms giving rise to the patterns of competition are variable (Schwinning and Weiner, 1998; Weiner et al., 2001; Sabatia and Burkhart, 2012), and the relative importance of features such as "size-asymmetry" (Weiner, 1990; Schwinning and Weiner, 1998), "size-symmetry" (Lundqvist, 1994), and "neighborhood competition" (Bonan, 1991) differ among case studies. A given level of competition may also have varying effects on different focal trees. For example Boyden et al. (2008), examined the effects of competition on stem growth of individual trees of a single clonal genotype, and from seeds in intensively managed 4-year-old *Eucalyptus* plantations. Medium-size focal trees (75 kg wood mass) in single-clone plots grew faster than same-size trees in seed-origin plots when competition was low or moderate, but clones were more sensitive to intense competition than seed-origin trees.

The growth of a focal tree is usually sensitive to the sizes and distances of neighboring trees, often combined into a neighborhood competition index (e.g. Canham et al., 2004); a neighborhood competition index may relate to the supply of resources available to a focal tree. An additional feature may contribute to competition: the influence of neighboring trees on the ability of a focal tree to use resources efficiently in producing wood. Binkley et al. (2010) showed that exponentially increasing rates of growth by larger

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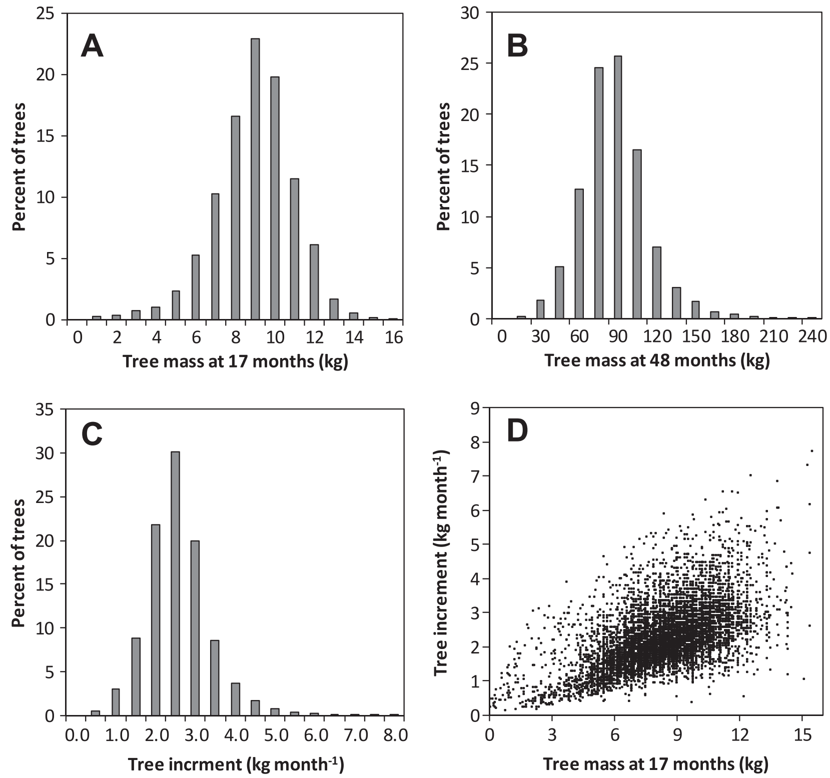

Fig. 1. The size and growth of trees can be examined as distributions in a stand, without regard for spatial location or patterns. At 17 months, trees in a 9 ha portion of the plantation studied in this project averaged about 9 kg of stem mass (A) increasing by 10-fold at 48 months (B). At both ages, the 30% tile tree was about 25% smaller than the 70% tile tree. Increment averaged about 2.5 kg month^{-1} between these two ages (C), and larger trees grew faster, on average, than smaller trees (D). Increments showed very large variations (residuals) for any size class; spatially explicit approaches to evaluating individual tree growth offer the possibility of accounting for more of the variance.

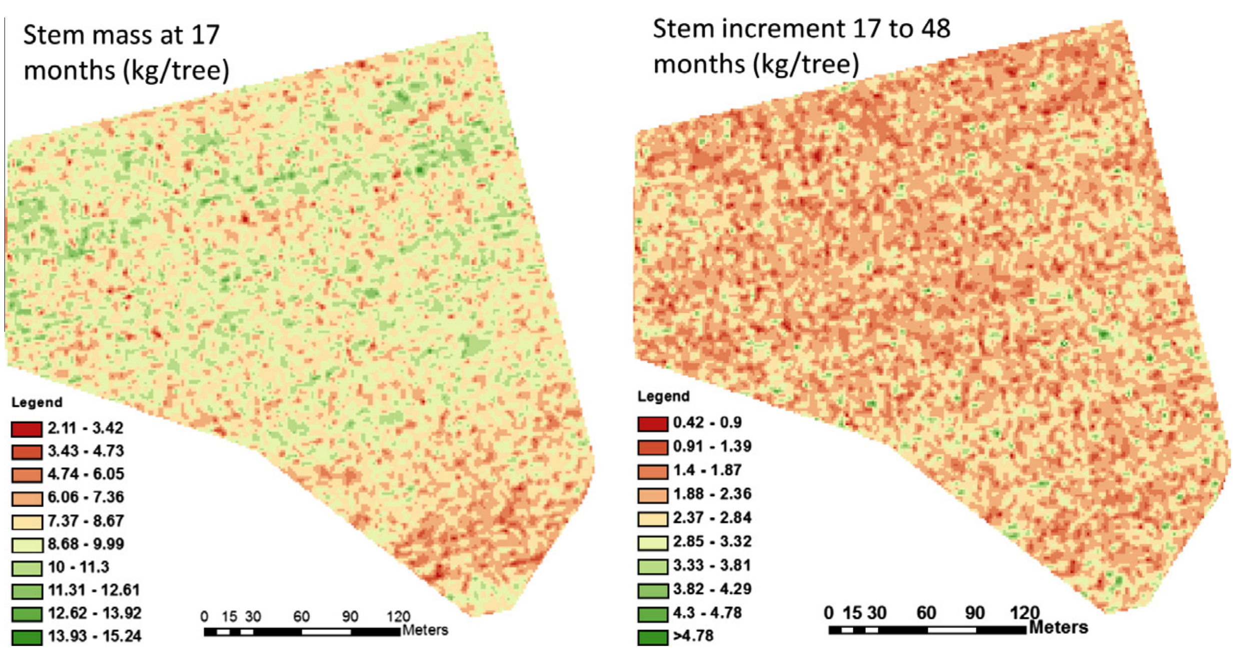

Fig. 2. Map of pattern of tree mass at 17 months (left), and tree increment from 17 to 48 months (right).

trees within *Eucalyptus* plantations was driven about equally by linear increases in light interception and linear increases in efficiency of using light to produce wood. In the same experiment, Stape et al. (2010) highlighted the importance of stand uniformity on stand-level growth; trees grew an average of 13% more in plots with very uniform tree sizes than in plots designed with higher variation among tree sizes. The pattern of uniformity and growth is clear, but the mechanisms remain largely unknown.

These insights on individual-tree competition and stand-level production led us to hypothesize that the uniformity of trees within a neighborhood would influence focal tree growth in operational plantations. Specifically, we hypothesized that the growth of a