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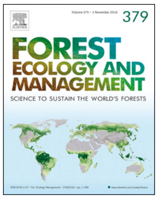

A common garden experiment examining light use efficiency and heat sum to explain growth differences in native and exotic *Pinus taeda*

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ABSTRACT

Previous work indicates that *Pinus taeda* L. grows faster and has a higher carrying capacity when grown outside its native range. We were interested in examining the hypotheses that growth, light use efficiency (volume growth and absorbed photosynthetically active radiation relationship, LUE) and volume growth per unit heat sum is the same for native and exotic plantations. To test these hypotheses, we installed a common garden experiment where the same six genetic entries of *P. taeda* (four clonal varieties, one open pollinated family and one control mass pollinated family) were planted at three densities (618, 1235, and 1853 stems ha^{-1}) with three or four replications at three sites (Virginia (VA), and North Carolina (NC) in the United States and Paraná State in Brazil (BR)). The VA and BR sites were outside the native range of *P. taeda*. After five years of growth, the BR site had larger trees and stand scale basal area and volume were increasing faster than the other sites. Site did not affect LUE but density and genetic entry did. The sites were at different latitudes but the average photosynthetically active radiation at the top of the canopy was similar for the years when all sites were operational, likely because the BR site receives more rain annually and the cloudiness associated with the rain may have reduced available light. We estimated an hourly heat sum where the daytime temperature was between 5 and 38 °C, hours where vapor pressure deficit exceeded 1.5 kPa and days following nights where nighttime temperatures were less than 0 °C were excluded. Site was significant for the cumulative volume and heat sum relationship, for a given level of cumulative degree hours the sites ranked BR > VA > NC in cumulative volume. The different growth per unit of degree hours for each site indicated that something other than the heat sum was causing the observed difference in growth. Other factors including respiration and extreme climatic conditions may contribute to growth differences per unit degree hour and including these differences in the analysis would require a more detailed modeling effort to examine. The sites used in this study are ideally suited to continue testing additional hypotheses to explain the different growth between native and exotic *P. taeda* plantations because they have the same genotypes at all sites and consequently eliminate differences in genetics as a potential explanation for observed growth differences.

1. Introduction

Environmental variables have large effects on tree growth. Trees intercept light and transform light energy into biomass and this transformation is limited by environmental factors affecting photosynthesis (Cannell, 1989b) and light interception is controlled by leaf area (Vose and Allen 1988). Growth per unit intercepted light (light use efficiency (LUE)) has been used to understand how treatments, and

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changes in climate and location influence growth (Albaugh et al., 2016; Monteith 1977; Waring et al., 2016). Heat units have been used since the 1700s to predict development and growth in crop species (e.g. (McMaster and Wilhelm 1997)) and more recently in tree species (e.g. (Way and Oren 2010)). Heat units can be simply summing of temperatures within a specific threshold or they may include other variables to limit the summing (e.g. vapor pressure deficit (VPD) (Sangines de Carcer et al., 2017) when it is compared to some point of development or cumulative growth. The amount and quality of light and temperature patterns change when moving a species from one location to another. Developing an understanding of how light and temperature affect a given species would help predict how a species will behave in a new environment. For example, the Köppen climate classification system is used to identify similar environmental niches for exotic planting of *Eucalyptus* species to improve the likelihood a species will be planted successfully in other environments (Goncalves et al., 2013). At the other end of the spectrum, there are species that are already planted in exotic locales and do well (e.g. (Waring et al., 2008)). In this case, improving our understanding of conditions that make a species grow better as an exotic may help improve management in the native range. At the same time, identifying driving factors or relationships similar to LUE and heat sums that influence growth will make this analysis applicable to other species. *Pinus taeda* L. is one species that may grow extremely well outside its native range (Wallinger, 2002). This species is one of the world's most important commercial species, a native to North America where it is responsible for about 60% of forestry production in the United States (Prestemon and Abt, 2002). Future climate change may influence the species range in and near its native range (Susaeta et al., 2014). Given that it is already planted extensively in areas where it grows well as an exotic (Argentina and Brazil), *P. taeda* would be a useful test case to compare native and exotic plantings to develop a better understanding of the factors driving growth. Understanding what drives superior exotic growth may permit improvement in silviculture of native grown *P. taeda* and help relieve pressure on the land base from an increasing population and an increase in demand for forest services predicted in the future (Susaeta et al., 2014).

From the 1940's to the 2000's, improvement in silvicultural practices greatly increased estimated productivity of *P. taeda* plantations grown in the species' native range in the southeastern United States (Fox et al., 2007). There is evidence that maximum growth for the species in its native range is about 16 $\mathrm{Mg\,ha^{-1}\,yr^{-1}}$ (mean annual increment) (40 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$, assuming 400 $\mathrm{kg\,m^{-3}}$ wood density (Antony et al., 2014)) given that additional silvicultural inputs do not increase productivity beyond this amount (Zhao et al., 2016). Typical mean annual growth rates for *P. taeda* in the southeastern United States range from 16 to 33 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$ (Zhao et al., 2016). However, the theoretical maximum growth for *P. taeda* was estimated at 30 $\mathrm{Mg\,ha^{-1}\,yr^{-1}}$ mean annual yield (75 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$) (Farnum et al., 1983). When *P. taeda* is grown outside its native range apparent productivity is much higher. For example, *P. taeda* mean annual growth rates of 50, 56 and 59 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$ for stands in Brazil have been reported (Barrichelo et al., 1977; Leite et al., 2006; Wallinger 2002). In Argentina, Pezzutti (2011) reported mean annual volume growth up to 45 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$. Cubbage et al. (2007) estimated that mean annual increments of 40 and 18 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$ were possible in Brazil and the United States, respectively, current annual increments would be higher.

A number of hypotheses to explain better exotic plantation growth have been proposed. Rapid growth in Brazil was attributed to a longer growing season, greater sunlight intensity, better soils and lack of pathogens (Wallinger 2002). Harms et al. (1994) suggested that high solar radiation intensities and high sun angles may be responsible for better growth and noted that genetic characteristics may play a role in the differences observed between native and exotic plantations. Physiological assessments (leaf light-saturated net photosynthesis, dark respiration, stomatal conductance and quantum yield) completed on *P. taeda* trees in exotic locations (Hawaii and Brazil) were comparable to those reported in the native range (Samuelson et al., 2010). Samuelson et al. (2010) suggested that better growth in Hawaii may be related to a more favorable climate permitting year-round growth, high nutrient availability, increased flushing and less belowground allocation.

However, few hypotheses have been tested to explain the different growth between native and exotic plantations. Foliage longevity was examined for *P. taeda* in North Carolina and in Corrientes, Argentina. More foliage was displayed for a shorter time per fascicle in Argentina and while study inference was limited (only one exotic and one native site with different genotypes at each site) most fascicles at both sites survived for two growing seasons, the one in which they were produced and the following one (Albaugh et al., 2010). Waring et al. (2008) used a combination of modeling and direct measurements to determine that summer drought and evaporative demand limitations in native Douglas- fir (*Pseudotsuga menziesii* (Mirb.) Franco), limit growth to 30 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$ in managed plantations in its native range in western Oregon in the United States compared to 50 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$ in exotic plantations in New Zealand from the same seed source that do not experience these moisture limitations. No studies were found in the literature where the same genotypes were planted in the native range and in exotic locations that would permit testing hypotheses to explain the differences in growth and carrying capacity observed between the same species planted in native and exotic locations.

Consequently, we were interested in examining growth, LUE and heat sums in *P. taeda* grown in native and exotic plantations where the genotypes were the same in both locations. Specifically, we examined these hypotheses for *P. taeda*: (1) Growth is the same for native and exotic plantations; (2) LUE is the same for native and exotic plantations (site does not affect the volume growth and absorbed photosynthetically active radiation relationship); (3) heat sum per unit of volume growth is the same for native and exotic plantations (site does not affect the cumulative volume and degree hour relationship).

2. Methods

2.1. Experimental design

We installed a split split-plot design with three or four replications at three sites (Vickers et al., 2011). The first site (NC) with three replications was selected in the Atlantic Coastal Plain of North Carolina, United States in Bladen Lakes State Forest at (34.83133°, −78.5873°) in the native range of *P. taeda* near where the genetic material used in the study was sourced. The second site (VA) had four replications and was in the Piedmont of Virginia, United States at the Reynolds Homestead (36.64232°, −80.1546138°) in an area where *P. taeda* grows successfully but is outside the native range of the species. The third site (BR) was in Paraná State in Brazil (−26.1904805°, −49.49631°) with three replications on land owned by Valor Florestal in an area where *P. taeda* is commonly grown as an exotic species. Whole plot treatments were two levels of silviculture, operational to match current operational practices and intensive, which was designed to achieve near maximum growth for the existing soil and climate. For this analysis, we excluded the operational silviculture treatment because competing vegetation interfered with our ability to estimate peak pine leaf area index in this treatment and three of the genetic entries did not have operational silviculture plots at the BR site due to a space limitation at the site and insufficient seedlings at planting. Consequently, we treated the experiment as a split-plot design. Genetic entry was the main-plot treatment and initial density was the split-plot treatment. There were six genetic entries, four clonal varieties (C1, C2, C3, C4), one open pollinated family (OP) and one control mass pollinated family (MP). There were three initial densities, 618, 1235, and 1853 $\mathrm{stems\,ha^{-1}}$. These treatments yielded six main-plots (genetic entry) each with three subplots (initial density) per replicate.

All plots had a treated area with a smaller measurement plot centered in it. The BR site and three replicates at the VA site had 81 trees (9