

RELATIONSHIP BETWEEN FOREST ABOVEGROUND BIOMASS GROWTH AND TREE SPECIES RICHNESS, IDENTITY, AND STRUCTURE

Santosh Ojha and Luben Dimov*

Department of Biological and Environmental Sciences, Alabama A&M University, Normal AL 35762, USA. E-mails: santoshdfers@gmail.com, Luben.Dimov@gmail.com*

Received: 28 July 2017

Accepted: 14 November 2017

Abstract

The effects of stand structure and species composition on the forest diversity-productivity relationship have received much attention during the last few decades. The objective of this study was to compare dry live aboveground biomass (AGB) growth among species structures (pure hardwood, mixtures of hardwoods, mixtures of pines, mixtures of pines with hardwoods, and pure pine) for different stand age, stand stocking, and site productivity classes. We also examined the relationship between AGB growth and the predictors species richness, quadratic mean diameter, height, compacted crown ratio, relative density, slope, aspect, precipitation, and elevation. We used data from 2554 USDA Forest Inventory and Analysis (FIA) plots in Alabama. Tukey-Kramer procedure with multiplicity adjustment was applied to compare AGB growth among the five species structures. Species richness was 1–17 and AGB growth was 0.01–15.68 Mg ha⁻¹ yr⁻¹ across the plots. For the pooled data, there was a weak overall correlation between AGB growth and species richness ($r=0.07$, $p=0.001$). The AGB growth of pure and mixed stands was statistically the same. In high-stocked stands productivity (AGB growth) was statistically the same in the different structures. There was no difference between the AGB growth rate of pure pine stands and mixtures that contained pine. However, pure pine stands outperformed mixed stands that did not contain pines in the mix. Species identity was an important factor for AGB growth in pure and mixed stands. As stocking increased, species structure became less important for the AGB growth rate. Among stands with high-stocking, pure stands were as productive as mixtures with no overall growth benefit of monocultures. If high or medium stocking level is maintained, there is no obvious growth benefit from monocultures or mixtures. In stands with low-stocking however, there appeared to be a benefit to having multiple species in the composition.

Key words: aboveground biomass growth; FIA; species richness; species structures; stand stocking.

Introduction

The quantitative relationship between biodiversity and ecosystem function has been investigated for decades (Huston et al. 2000, Nadrowski et al. 2010). The question of whether plant diversity promotes

aboveground biomass productivity has been a matter of much interest and experimentation (Vilà et al. 2003, Paquette and Messier 2011). Grassland studies, conducted as controlled manipulative experiments, have found conclusive evidence that plant diversity increases and

stabilizes productivity (Tilman and Downing 1994, Tilman et al. 1996, Tilman 1999, Cardinale et al. 2006), nutrient retention, stability of multiple functions such as soil microbial activity and nutrient cycling, and soil carbon sequestration (Nadrowski et al. 2010). There are no such rigorous experiments showing whether a positive diversity-productivity relationship is also present in naturally regenerated forests, where the relationship is not necessarily the same as in plantations (Firn et al. 2007).

Several studies of naturally regenerated forests found species diversity as a significant factor for aboveground biomass productivity (Caspersen and Pacala 2001, Liang et al. 2007, Vilà et al. 2007, Paquette and Messier 2011, Ojha 2015, Liang et al. 2016), while others showed stronger effects of species identity (referring to which (set of) species are in the community) than diversity (Nadrowski et al. 2010). The mechanisms explaining patterns of diversity-productivity relationships in many ecosystems depend on complex interactions between spatial covariance and ecological parameters (Belote et al. 2011). Several factors can have an influence on the species diversity-productivity relationships in forests, such as plant density (He et al. 2005, Potter and Woodall 2014), site quality (Rodríguez-Loínaz et al. 2008, Thoms et al. 2010, Paquette and Messier 2011, Potter and Woodall 2014), environment (Hooper et al. 2005, Vilà et al. 2005, Ma et al. 2010, Paquette and Messier 2011), seed dispersal limitation (Pärtel and Zobel 2007), evolutionary history and latitude (Pärtel et al. 2007), successional status (Caspersen and Pacala 2001, Vilà et al. 2003), anthropogenic disturbances (Lorimer and White 2003, Tenzin and Hasenauer 2016), and spatial scales (Chase and Leibold 2002, Belote et al. 2011).

In forest dynamics, the biotic tree-to-tree interactions (competitive or facilitative) are important structural mechanisms that have been found to vary across environmental gradients and tree growth stages (Fichtner et al. 2015). Many processes, such as competition reduction or facilitation, take place due to interspecific differences in physiology, phenology, or morphology. These and other interspecific interactions among species may influence the diversity-productivity relationships in forests (Forrester and Bauhus 2016).

Mixed species forests have sometimes been found more productive than monocultures due to the complementarity interactions among species, but the important factors that influence the diversity-productivity relationships are stand structural attributes, resource availability, resource uptake, and resource use efficiency (Forrester and Bauhus 2016). While the relationship between species diversity and productivity has received a lot of attention in many recent studies, we found far less information about the effects of stand and site characteristics and of species structures (e.g., pine, hardwood, mix) on aboveground biomass productivity.

Our knowledge of the diversity-productivity relationships in forest ecosystems is essential for the sustainable management and conservation of biodiversity (Mittelbach et al. 2001). There are several studies that used a large number of permanent plots in stands of all ages to study the relationships between tree species diversity and productivity (Caspersen and Pacala 2001, Liang et al. 2007, Vilà et al. 2007, Moser and Hansen 2009, Paquette and Messier 2011, Woodall et al. 2011, Potter and Woodall 2014). However, there is a lack of studies that compared pure and mixed stands consisting of various species structures (conifers, hardwoods,

mixtures of conifers and hardwoods) for different age classes, stand stocking classes, and site productivity classes.

Understanding the relationship between stand structure, species composition, and aboveground biomass productivity, as well as its relation to ecosystem function, are crucial for management, so that we can manipulate the number of species to achieve greater aboveground biomass production and carbon sequestration (Woodall et al. 2011) while maintaining other important ecosystem services and functions.

Our study aimed to evaluate dry live aboveground biomass (AGB) growth among species structures (pure hardwood, mixtures of hardwoods, mixtures of pines, mixtures of pines with hardwoods, and pure pine). The study objectives were to investigate if 1) there is a difference in AGB growth among the species structures, 2) there is a difference in AGB growth among species structures for a range of species richness levels in different stand age, stand stocking, and site productivity classes, and 3) there is a difference in AGB growth between pure and mixed stands of the two most dominant tree species. We also examined the bivariate correlation between AGB growth, species richness, quadratic mean diameter, height, compacted crown ratio, relative density, slope, aspect, precipitation, and elevation.

Materials and Methods

Study area

The study area was the state of Alabama in the United States. The state represents a southeastern humid subtropical climate under the Köppen climate classification (Zifan 2016). There are about 200 tree spe-

cies and 4000 species of vascular plants including trees, shrubs, vines, grasses, legumes, and ferns in Alabama (Alabama Forestry Commission 2010). The forests in the state cover 9.2 million ha, approximately seventy percent of the land area. It consists of forty-six forest types with the loblolly pine (*Pinus taeda* L.) type being the most common forest type and covering one third of all forested area (Alabama Forestry Commission 2010). Hardwood or mixed pine-hardwood forests comprise fifty-seven percent of the state's forestland. The most common hardwood species of the state are northern red oak (*Quercus rubra* L.), southern red oak (*Quercus falcata* Michx.), white oak (*Quercus alba* L.), hickories (*Carya* spp.), sweetgum (*Liquidambar styraciflua* L.), and yellow poplar (*Liriodendron tulipifera* L.). Ninety-four percent of the forest is owned by private landowners, and plantations occupy about thirty percent of the forest area of the state (Hartsell and Cooper 2013).

The major physiographic areas of Alabama are the Interior Plateau (Highland Rim), Southwestern Appalachians (or Cumberland Plateau), Piedmont, Ridge and Valley, and the East Gulf Coastal Plain (Alabama Department of Conservation and Natural Resources 2006). The average summer temperatures range from 21 to 32 °C, and average winter temperatures range from -1 to 10 °C (Alabama Department of Conservation and Natural Resources 2006). The humid and mild climate of the state is favorable for the growth of many plant species.

Data

We used forest inventory data from the US Forest Service Forest Inventory and Analysis (FIA) database, which is publicly available. The FIA uses a national

standard sampling procedure with a quasi-systematic sampling design and a sampling intensity of one plot for every 2428 hectares (Bechtold and Patterson 2005). The FIA standard plot (size 0.067 ha) consists of four 7.3 m radius subplots (approximately 0.0168 ha) spaced 36.6 m apart in a triangular arrangement with three plots at each corner and one subplot in the center of the triangle. The data from the subplots included all trees of at least 12.7 cm in diameter at breast height (dbh, 1.37 cm

above the ground).

We used plots that were measured during the most recent periodic inventory cycle between 2005 and 2012 in the state of Alabama. There were a total 2554 plots, all of which were classified as forest land with at least ten percent cover by trees and with no visible disturbance since the last measurement or within the last five years due to natural causes. The approximate location of the selected plots in Alabama map is shown on Figure 1.

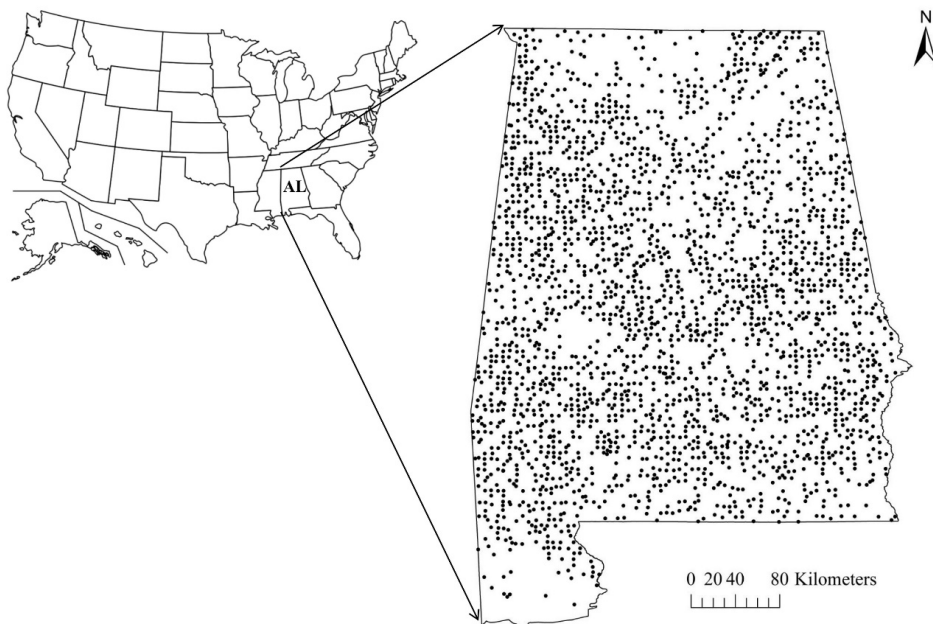


Fig. 1. Map with approximate location of the 2554 FIA plots in Alabama and an inset map of the USA.

About two thirds out of the 2554 plots were naturally regenerated and the remainder were plantations. Almost 98 % of the plots were classified as two-storied stands (two distinct layer of the tree crowns), 1 % were in multistoried stands (three or more canopy layers), and 1 %

were in single-storied stands (single canopy layer). The plots were located in natural stands and plantations under various ownership (private, public (both federal and state government ownership), industrial, and others). About 20 % of the plots experienced management activities such

as clear cut, partial harvest, shelterwood harvest, commercial thinning, timber stand improvement, and salvage cutting since the last measurement.

We used the following variables from the FIA database: species, dbh, height, compacted crown ratio, stand age, slope, aspect, elevation, and site productivity class. We generated the plot level variables species richness, quadratic mean diameter (QMD), dry above ground biomass of live-trees, relative stand density, stand age class, stand stocking class, and species structure class. We use the terms plot and stand interchangeably. Precipitation data were extracted from spatial datasets with resolution of 800 m (PRISM Climate Group 2016). Precipitation value was the 30 year average for the period of 1981 to 2010.

We used primarily species richness (number of species in the plot) among the taxonomic diversity indices to characterize species diversity. To express the average tree diameter, we calculated the QMD for each plot. The mean height of the trees in a plot is the average height of all individual trees in the subplots with dbh of at least 12.7 cm. Compacted crown ratio (CCR) is the percent of the tree bole supporting live, healthy foliage on all sides of the stem (Woudenberg et al. 2010). The mean CCR of a plot is the average CCR of all individual trees in the subplots with dbh of at least 12.7 cm. We used FIA calculated stand age that is an average of the ages of dominant and codominant crown class trees (Stevens et al. 2016), where the age of individual live trees is determined from counting of tree rings on increment cores from breast height. The stand age ranged from 1 to 125 years.

The AGB of a live tree was calculated as the sum of the biomass of the merchantable bole, top of the tree, and tree

stump (Woudenberg et al. 2010). We used the FIA method for estimating AGB (in mega grams per hectare, Mg ha⁻¹) that was based on the published Jenkins biomass equations (Jenkins et al. 2003) with adjustment factors of the tree components (Woudenberg et al. 2010). We define forest productivity as the mean annual increment of AGB, referred hereafter as the 'AGB growth', and expressed it in mega grams per hectare per year (Mg ha⁻¹ yr⁻¹). We computed mean annual AGB growth (Y) of each plot as follows:

$$Y = \frac{\sum_{i=1}^n b_i}{t} \quad (1),$$

where b is the biomass of i_{th} tree of a plot that contains n trees, and t is the mean stand age on the plot.

The FIA manual notes that stand age may have large measurement errors. However, as these errors are likely random, such an error would add noise to the data, which should not conceal a trend or a pattern in the data. In addition, the estimate of AGB growth is likely to be below its true value because similar to other studies (Vilà et al. 2007, Moser and Hansen 2009, Paquette and Messier 2011, Potter and Woodall 2014), we did not account for the biomass that may have been removed since stand establishment – this was impossible to do with the available data.

The Gaussian distribution of AGB growth was left skewed, so a square root transformation was applied to satisfy the normality and homogeneity assumptions (Legendre and Legendre 2012). Thus, the transformed AGB growth is referred hereafter as 'square root AGB growth' which was used only in the Pearson correlation analysis.

The aspect was transformed by modifying the azimuth from 0–360° to values ranging from 0 to 2 (Beers et al. 1966).

A value of 2 corresponds to northeast facing slopes (mesic) and a value of 0 to southwest facing slopes (xeric). We used arcsine transformation for slope and CCR as it is considered an appropriate normalizing transformation for percentages and fractions (Legendre and Legendre 2012).

Relative stand density was calculated by dividing the current stand density index (SDI) by the maximum SDI (Woodall et al. 2005). We used a published regression equation (Woodall et al. 2005) based on wood specific gravity (Miles and Smith 2009) of each tree species in the plot to estimate maximum SDI of each plot. Relative stand density is the stand stocking, defined as the number equivalent of 25-cm diameter trees per unit area in a stand relative to the potential maximum number of trees in the same stand (Woodall et al. 2011). We estimated SDI of each plot based on Reineke (1933) but after a slight modification that is useful for uneven-aged stands, called summation method (Long and Daniel 1990). The equation is expressed as:

$$SDI = \sum_i \text{tph}_i \left(\frac{DBH_i}{25} \right)^{1.6} \quad (2),$$

where tph_i is number of trees per hectare for the i^{th} tree in the stand, and DBH_i is the diameter of the i^{th} tree in the stand (cm).

We evaluated the AGB growth among species structures at various stand stocking, stand age and site productivity classes. The categorical variables stand stocking, stand age, site productivity and stand structures were generated as described below.

All the plots were divided in three stand stocking classes, similar to Long (1985): low stocked (relative density $RD < 0.3$), medium stocked (RD of $0.3-0.6$), and high stocked ($RD > 0.6$). Out of 2554 plots,

about 45 % were less than 25 years old and over 95 % of the plots were under 75 years old. Thus, we formed three stand age classes with adequate sample size in each class: age class I (stand age less than or equal to 25 years), age class II (26 to 50 years), and age class III (more than 50 years).

The FIA uses site index trees to classify the plots based on the productivity of the site in terms of its capacity to grow crops of industrial wood (Woudenberg et al. 2010). The FIA uses seven productivity classes, with class 1 being the most productive. We had plots from all classes except 7. We grouped the FIA site productivity classes into three groups: 1) low (FIA site productivity classes 5 and 6 with wood growth potential less than $5.9 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$), 2) medium (FIA site productivity classes 3 and 4 with wood growth potential between 5.9 and $11.5 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$), and 3) high (FIA site productivity classes 1 and 2 with wood growth potential greater than $11.5 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$).

We first divided all plots into two broad species structures, pure (species richness (SPR) =1) and mixture (SPR >1) and tested whether the AGB growth of pure and mixed stands differ significantly from each other. Secondly, based on species richness, species composition and species taxonomic identity, all the plots were then classified into five separate species structures, namely, 1) pure hardwood (plot contains single hardwood species; $SPR=1$), 2) mixtures of hardwoods (plot comprises two or more hardwood species; $SPR \geq 2$), 3) mixtures of pines (plot comprises of two or more pine species; $SPR \geq 2$), 4) mixtures of pines with hardwoods (plot comprises two or more pine and hardwood species; $SPR \geq 2$), and 5) pure pine (plot contain single pine species; $SPR=1$). It should be noted that the amount of non-pine con-

fers in the data was insignificant, so we refer to the structures containing conifers as simply pine structures.

The AGB growth across the plots consisting of the two most dominant species, loblolly pine and sweetgum, was examined to determine whether it was different in pure stands and in stands where these species grow in mixtures. Three kinds of species composition groups for each species were examined – for loblolly pine: pure loblolly pine ($SPR=1$), loblolly pine and hardwoods ($SPR\geq 2$), and loblolly pine and other pines and hardwoods ($SPR\geq 3$), and similarly for sweetgum, pure sweetgum ($SPR=1$), sweetgum and hardwoods ($SPR\geq 2$), and sweetgum and other hardwoods and pines ($SPR\geq 3$).

Data analysis

To assess the dominance of the species across the plots, we calculated importance value percent (IVP) of each species by averaging relative frequency percent, relative density percent, and relative dominance percent (Curtis and McIntosh 1951). Importance values rank species and give an estimate of influence of a plant species in the community. The benefit of using importance value is that a large size tree or a large number of small trees from a particular species do not influence excessively the importance value of the species (McCune and Grace 2002).

The relationship between AGB growth and stand age as well as between species richness and stand age across the plots was examined using loess smoothing curve fitted with tricube weighting and polynomial regression using 50 % of the data points. Loess is a non-parametric smoothing procedure that displays functional dependencies between the variables (Jacoby 2000). The loess fitting

procedure produces parsimonious graphical summary of the bivariate data and is a fairly direct generalization of traditional least-squares methods for data analysis that tracks the most concentrated areas of data points and ignores the outliers (Jacoby 2000).

We performed analysis of variance (ANOVA) to test whether there were any differences among groups for a given variable. When ANOVA showed an overall significant difference among group means, we ran post hoc tests to check where the differences occurred.

As we divided plots into five species structures that resulted in five unequal group sizes, we used a modified Tukey-Kramer procedure for pairwise comparisons of unequal size samples, as it better addresses the variance heterogeneity of the groups. To handle unequal group sizes and any possible unequal group variances, i.e., data heteroscedasticity, multiplicity adjustments are necessary to take into account the denominator degrees of freedom that are not constant across estimates. Both the Satterthwaite and Kenward-Roger degree of freedom are designed for use in models with unbalanced designs and more complex covariance structures (Bell et al. 2013). They were selected to estimate the degrees of freedom in Tukey-Kramer mean separation. Among them, the Kenward-Roger method adjusts the covariance matrix with a small-sample bias (Bell et al. 2013) and therefore, it was applied when one of the group sizes was too small compared to other group sizes. The estimation method for the covariance parameter in the model was based on residual (restricted) maximum likelihood (REML). SAS[®] PROC mixed procedure with multiplicity adjustment for Tukey was executed to check whether AGB growth least square (LS)

means of the species structures differ significantly.

We used Pearson bivariate correlation to assess the linear relationship between the dependent variable transformed AGB growth and the predictor variables species richness, quadratic mean diameter, mean height, compacted crown ratio, relative density, slope, aspect, precipitation, and elevation.

The descriptive statistics, ANOVA, and multiple comparisons of the means were performed using the IBM SPSS® 21 and SAS® 9.3 statistical packages. Species richness and species IVP were calculated using PC-ORD® Version 6.12.

Results

The forests across the study area were highly diverse with a total of 113 woody species. At the plot level, species richness ranged from 1 to 17. The current AGB ranged from 0.10 to 403.5 Mg ha⁻¹, while AGB growth was from 0.01 to 15.7 Mg ha⁻¹ yr⁻¹ (Table 1).

Based on IVP, the three most important species were loblolly pine (31.58 %), sweetgum (7.97 %), and water oak (*Quercus nigra* L., 4.78 %), all of which are shade intolerant species. The next three most important species were yellow-poplar, white oak, and red maple (*Acer rubrum* L.), with IVP values from 3.08 % to 4.32 %.

The only hardwood species growing as pure stands on more than one plot were sweetgum, water oak, red maple, black gum (*Nyssa sylvatica* Marsh.), mockernut hickory (*Carya alba* Mill.), and sweetbay (*Magnolia virginiana* L.). The other species that were in pure stands, but occurring on only a single plot each were Florida maple (*Acer barbatum* Michx.), sugarberry (*Celtis laevigata* Willdenow), flowering dogwood (*Cornus florida* L.), common persimmon (*Diospyros virginiana* L.), yellow-poplar (*Liriodendron tulipifera* L.), sourwood (*Oxydendrum arboreum* (L.) DC), southern red oak (*Quercus falcata* Michx.), chestnut oak (*Quercus prinus* L.), post oak (*Quercus stellata* Wangenh.), black willow (*Salix nigra* Marshall), winged elm (*Ulmus alata* Michx.), and the non-

Table 1. Mean, standard deviation, minimum and maximum values of the variables across 2554 FIA plots in Alabama.

Variables	Mean	SD	Minimum	Maximum
Quadratic mean diameter, QMD (cm)	23.1	5.73	12.6	94.1
Basal area (m ² ha ⁻¹)	16.2	9.14	0.19	58.96
Height (m)	16.7	3.83	6.1	32.6
Density (stems ha ⁻¹)	392	229	15	1324
Relative stand density	0.4	0.15	0	0.83
Compacted crown ratio	0.39	0.10	0	0.99
Stand age (yr)	34	22	1	125
Total AGB (Mg ha ⁻¹)	82.8	60.4	0.10	403.5
Mean annual AGB growth (Mg ha ⁻¹ yr ⁻¹)	2.7	1.8	0.01	15.7
Species richness (SPR)	5.8	3.36	1	17
Precipitation (cm)	142	8.4	121	172.7
Slope (percent)	12	12	0	85
Elevation (m)	138	90.45	0	677

native chinaberry (*Melia azedarach* L.). The trees recorded in the pure hardwood plots were most likely residuals from a previous rotation, considering that the mean stand age in these plots was only 6 years, the mean density was 29 stems ha^{-1} , but the diameter of the residual trees was over 12.7 cm.

It was surprising that the AGB growth in the very young plots (less than about 5 years) was fairly high. The dbh of the trees in these plots ranged between 12.7 cm and 42.4 cm, suggesting that even in the recently regenerated stands, there was a large amount of unharvested residual trees remaining on site. Stand age of these plots was determined by the FIA based on a large number of small size seedlings and saplings, likely without taking into account the age of the much fewer large-size residual trees (e.g., maximum dbh 42.4 cm at stand age 3) that were present in the plots. Furthermore, the seedlings, saplings, and small trees in these young plots were dominated by loblolly pine, pignut hickory (*Carya glabra* Mill.), sourwood (*Oxydendrum arboreum* L. DC), white oak, scarlet oak (*Quercus coccinea* Muenchh.), and yellow poplar, whereas the residual large trees were primarily loblolly pine, American beech (*Fagus grandifolia* Ehrh.), chestnut oak (*Quercus prinus* L.), red maple, yellow poplar, and water oak. The AGB growth of some young plots is therefore somewhat artificially inflated because the stand

age was recorded as being quite low, but there was actually a rather small number of much older trees present. Therefore, the loess smoothing curve fitting using tricube weight and 50 % of the observations was used to show the relationship between stand age and AGB growth, as well as between stand age and species richness, without the influence of such outliers. The AGB growth rate increased with increasing stand age up to the age of 19 years, and after that, decreased gently with increasing stand age (Fig. 2a). Similarly, species richness increased rapidly with increasing stand age up to the age of 50 years and then slowed down (Fig. 2b).

There was no significant relationship between AGB growth and species richness across the plots (Fig. 3a and 3b).

Moreover, there was no significant AGB growth difference between pure stands (SPR=1) and mixtures (SPR>1, $t_{1, 365.39}=0.016$, $p=0.99$, Fig. 4a). The amount of AGB (not growth), however, of pure and mixed stands was significantly different, with the mixtures containing about twice as much biomass ($t_{1, 563.57}=-18.59$, $p<0.001$) (Fig. 4b), where stand age was a confounding factor. The pure stands ranged from 1 to 78 years and about 91 % of the plots were under the age of 25 years, while the mixed stands ranged from 1 to 125 years and about 61 % of the plots had stand age over 25 years. Pure stands were relatively younger than mixed stands.

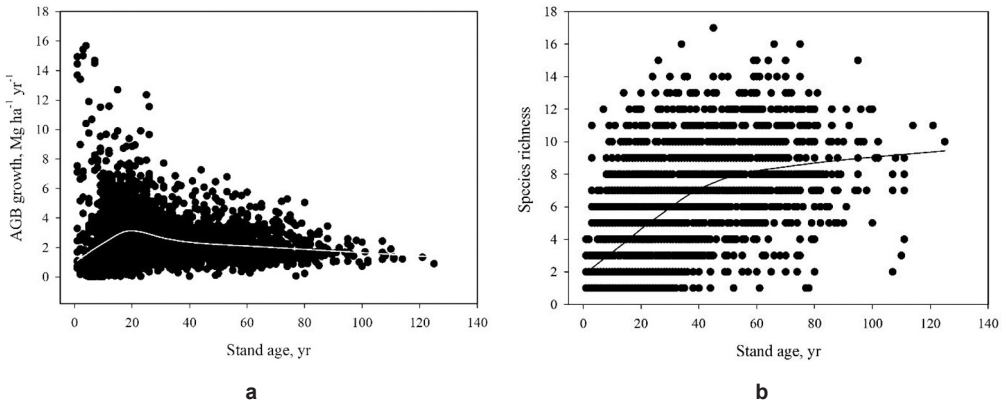


Fig. 2. Scatterplots for (a) AGB growth and stand age, and (b) species richness and stand age, across 2554 FIA plots in Alabama. The loess smoothing curve is fitted with tricube weighting and polynomial regression using 50 % of the data points.

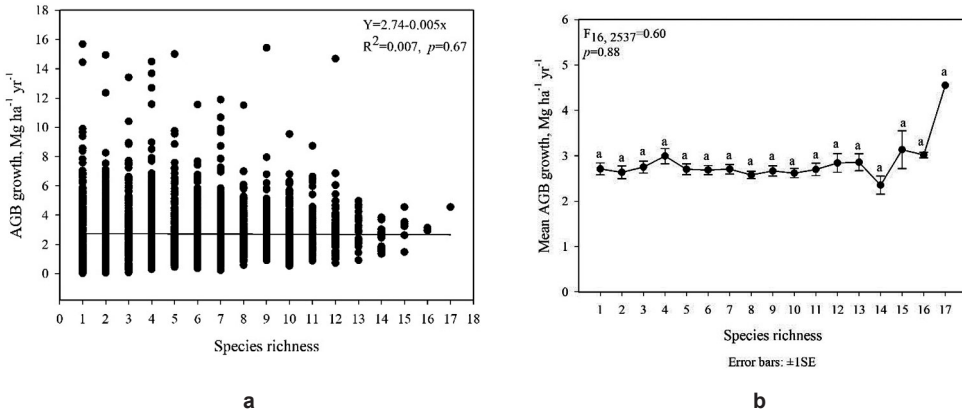


Fig. 3. Relationship between (a) AGB growth and species richness and (b) mean AGB growth and species richness across 2554 FIA plots in Alabama. Means with the same letter are not significantly different at $\alpha=0.05$. The best fitted trendline, equation, R^2 , and p -values show the linear association between the variables.

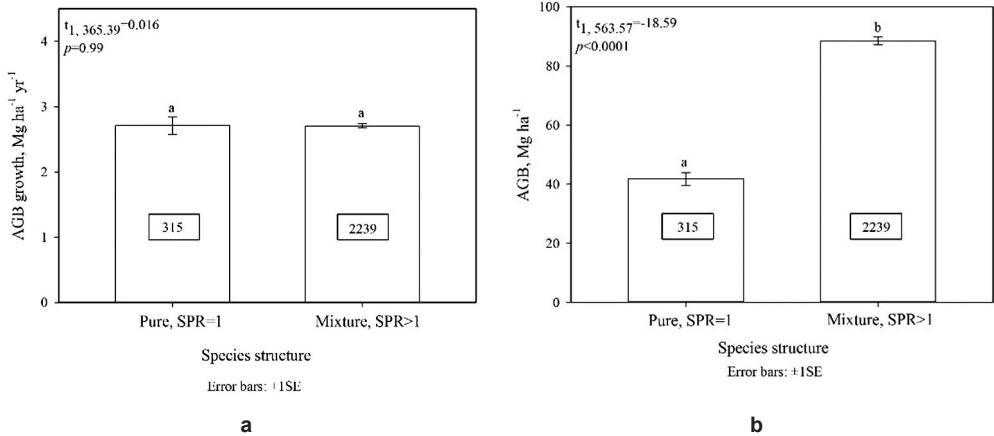


Fig. 4. Welch-Satterthwaite t-test between (a) AGB growth means of pure (species richness (SPR)=1) and mixed species structures (SPR>1), and between (b) current AGB (not growth) of pure and mixed species structures across the 2554 FIA plots in Alabama. Age is confounded with species structure, as the mixtures were generally older than the pure species stands. Means with the same letter are not significantly different at $\alpha=0.05$. The number of plots for each species structure is shown inside each bar.

Species structure and AGB growth

Plots that contained mixture of hardwoods had species richness of 2 to 17 (average 7), while the plots that contained mixtures of pines and hardwoods had richness of 2 to 16 (average 7; Table 2). The mean stand age (6 years) and stand density (29 stems ha⁻¹) of the pure hardwood stands were very low compared to other stand structures.

We found significant difference in AGB growth among the five species structures ($F_{4,2549}=14.65$, $p<0.001$, Fig. 5). The

AGB growth was greatest in pure pine (SPR=1), mixtures of pines with hardwoods, and mixtures of pines. The AGB growth of these three species structures was not significantly different. AGB growth was lowest in pure hardwoods (SPR=1), whose growth was significantly smaller than the growth in the other four groups (Fig. 5). However, it is important to note that the plots with pure hardwoods had at least ten times fewer stems per hectare than any of the other species structures and their mean stand age was only 6 years, compared to 16 to 45 years for the other groups (Table 2).

Table 2. Stand characteristics of the species structure classes across the 2554 FIA plots in Alabama. Minimum and maximum values are in parenthesis.

Variables	Species structure				
	Pure hardwood	Mixtures of hardwoods	Mixtures of pines	Mixtures of pines with hardwoods	Pure pine
Plots	38	458	44	1737	277
Quadratic Mean diameter (cm)	19.4(13.0,94.1)	26.2(12.6,48.0)	20.9(13.8,34.0)	23.1(13.2,56.2)	19.3(12.6,45.2)
Mean stems per ha	29(15,89)	283(30,1100)	379(30,981)	412 (30,1219)	502 (15,1324)
Mean basal area (m ² ha ⁻¹)	0.97(0.21,10.43)	16.31(0.38,53.7)	12.55(0.48,30.91)	17(0.41,58.96)	14(0.19,41)
Mean height (m)	13(7.6,32.6)	18.7(7.9,29.4)	14.2(7.7,26)	16.9(7.2,28.8)	13.6(6.1,31.4)
Mean compacted crown ratio	0.48(0,0.95)	0.39(0.14,0.83)	0.44(0.22,0.75)	0.39(0.16,0.8)	0.44(0.17,0.99)
Relative stand density	0.1(0,0.5)	0.3(0,0.8)	0.3(0,0.7)	0.4(0,0.8)	0.3(0,0.8)
Mean stand age (yr)	6(1, 23)	45(1,114)	21(3,74)	34(1,125)	16(1,78)
Species richness (SPR)	1(1,1)	7(2,17)	2(2,3)	7(2,16)	1(1,1)
Mean AGB growth (Mg ha ⁻¹ yr ⁻¹)	1.02(0.04,14.44)	2.37(0.07,15.43)	2.54(0.11,8.25)	2.8(0.05,15)	2.94(0.01,15.68)

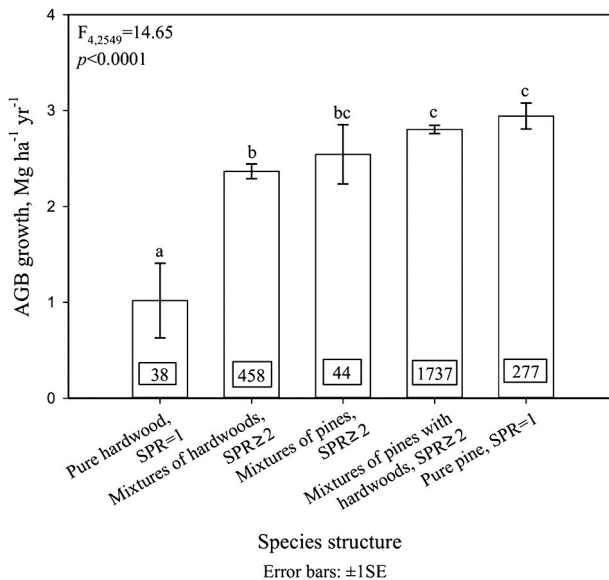


Fig. 5. Multiple comparisons (Tukey-Kramer test) of the AGB growth LS-means among the species structures and species richness (SPR) across the 2554 FIA plots in Alabama. LS-means with the same letter are not significantly different at $\alpha=0.05$. The number of plots for each species structure is shown inside each bar.

Species structure, stand age, and AGB growth

We found significant differences in AGB growth among the five species structures for age class I ($F_{4,1156} = 14.10, p < 0.001$), and for age class III ($F_{3,578} = 4.73, p = 0.0029$), but not for age class II

($F_{3,807} = 0.42, p = 0.73$, Table 3). The majority of the plots (83 %) in age class I were mixtures of pines with hardwoods ($SPR \geq 2$) and pure pine ($SPR = 1$), whereas the plots in age classes II and III were mostly mixtures of pines with hardwoods ($SPR \geq 2$) and mixtures of hardwoods ($SPR \geq 2$).

Table 3. Multiple comparisons (Tukey-Kramer test) between the AGB growth LS-means of the species structures in different stand age, stand stocking, and site productivity classes across the plots in Alabama.

Species structure	Plots	LS- mean			95 % CL			Plots	LS- mean	95 % CL			Plots	LS- mean	95 % CL				
		LB	UB		LB	UB				LB	UB								
Stand age class		Age class I						Age class II						Age class III					
Pure hardwood	38	1.02 ^c	0.30	1.74															
Mixtures of hardwoods	127	2.40 ^b	2.00	2.79	136	2.60 ^a	2.38	2.83	195	2.18 ^a	2.05	2.32							
Mixtures of pines	35	2.80 ^{ab}	2.05	3.56	5	2.05 ^a	0.86	3.23	4	0.88 ^b	-0.07	1.83							
Mixtures of pines with hardwoods	713	3.38 ^a	3.22	3.55	646	2.57 ^a	2.47	2.68	378	2.11 ^{ab}	2.01	2.20							
Pure pine	248	3.00 ^{ab}	2.72	3.28	24	2.76 ^a	2.22	3.30	5	1.00 ^b	0.15	1.85							
Stand stocking class		Low stocked						Medium stocked						High stocked					
Pure hardwood	36	1.05 ^b	0.47	1.63	2	0.39 ^{de}	-1.84	2.62											
Mixtures of hardwoods	180	1.82 ^{ab}	1.56	2.08	254	2.60 ^{ee}	2.40	2.80	24	3.96 ^a	3.06	4.86							
Mixtures of pines	27	1.84 ^{ab}	1.17	2.51	15	3.70 ^{abc}	2.88	4.51	2	3.38 ^a	0.27	6.50							
Mixtures of pines with hardwoods	523	2.16 ^a	2.00	2.31	1130	3.00 ^{bd}	2.91	3.10	84	4.16 ^a	3.68	4.64							
Pure pine	149	1.69 ^b	1.41	1.98	118	4.35 ^a	4.06	4.64	10	4.98 ^a	3.59	6.37							
Site productivity class		Low						Medium						High					
Pure hardwood	23	0.76 ^b	0.12	1.39	15	1.42 ^c	0.44	2.40											
Mixtures of hardwoods	248	2.18 ^a	1.98	2.37	181	2.60 ^{bc}	2.32	2.88	29	2.54 ^b	1.87	3.21							
Mixtures of pines	24	1.97 ^{ab}	1.35	2.59	19	3.30 ^{ab}	2.43	4.18	1	1.89 ^{ab}	-1.71	5.50							
Mixtures of pines with hardwoods	694	2.37 ^a	2.25	2.48	894	3.01 ^{ab}	2.88	3.13	149	3.62 ^a	3.32	3.91							
Pure pine	85	1.93 ^a	1.60	2.25	160	3.25 ^a	2.95	3.55	32	4.11 ^a	3.47	4.75							

Note: LS – least square, LB – lower bound, and UB – upper bound. Blank spaces where data was not available. LS-means with the same letter are not significantly different.

In age class I, the AGB growth of pure hardwood ($SPR = 1$) was significantly lower than the AGB growth of the other four groups. While the plots with mixed hardwoods had slower AGB growth than the plots with a mixture of pines with hardwoods, the pure pine plots had similar

productivity to all other groups (except the pure hardwoods). Unlike age class I, in age class III the AGB growth of the pure pine ($SPR = 1$) was significantly smaller than the AGB growth of the mixtures of hardwoods ($SPR \geq 2$).

Species structure, stand stocking, and AGB growth

We found significant differences in AGB growth among the five species structures in plots with low stand stocking ($F_{4,910} = 5.07$, $p < 0.001$) and medium stand stocking ($F_{4,1514} = 26.40$, $p < 0.001$), but not in plots with high stand stocking ($F_{3,116} = 0.59$, $p = 0.62$, Table 3).

In the low stocked plots, the mixtures of pines with hardwoods ($SPR \geq 2$) had significantly greater growth than both pure hardwoods and pure pine (Table 3). In the medium stocked plots, the AGB growth of pure pine ($SPR = 1$) was the greatest and was significantly more than AGB growth of all other groups, except mixtures of pines with hardwoods ($SPR \geq 2$). However, in high stocked plots all groups had statistically equal rates of growth.

Species structure, site productivity, and AGB growth

We found significant differences in AGB growth among the five species structures

in all three site productivity classes (Table 3). On the low productivity sites, the plots with only pure hardwoods in the composition were again the least productive, and less productive than all but the mixtures of pines. On medium and high productivity sites, the AGB growth of pure pine was greater than the growth of the species structures that did not contain conifers in the composition. On all three productivity sites, the AGB growth of pure pine ($SPR = 1$) was not significantly different than the AGB growth of mixtures of pines ($SPR \geq 2$), and mixtures of pines with hardwoods ($SPR \geq 2$, Table 3).

Dominant species, species composition, and AGB growth

The AGB growth of pure loblolly pine ($SPR = 1$) was not different from the growth of the other two groups (Table 4). The growth of sweetgum, however, was significantly lowered when it grew in pure stands compared to when it grew in any of the two types of mixtures (Table 4).

Table 4. Multiple comparisons (Tukey-Kramer test) between the mean AGB growth among pure (species richness ($SPR = 1$) and mixed ($SPR > 1$) loblolly pine and sweetgum stands across the plots in Alabama.

Species compositions	Plots	LS-mean	LB	UB
Pure loblolly pine vs. mixtures				
Pure loblolly pine ($SPR = 1$)	256	3.06 ^{ab}	2.83	3.28
Loblolly pine and hardwoods ($SPR \geq 2$)	804	3.05 ^a	2.92	3.17
Loblolly pine and other pines and hardwoods ($SPR \geq 3$)	632	2.75 ^b	2.60	2.89

Pure Sweetgum vs. mixtures				
Pure sweetgum ($SPR = 1$)	8	0.45 ^c	-0.68	1.57
Sweetgum and other hardwoods ($SPR \geq 2$)	248	2.57 ^b	2.37	2.77
Sweetgum and other hardwoods and pines ($SPR \geq 3$)	960	2.92 ^a	2.81	3.02

Note: LS – least square, LB – lower bound, and UB – upper bound. LS-means with the same letter are not significantly different.

Correlation of AGB growth with species richness, stand- and environmental variables

We found a stronger association of square root AGB growth with the stand variables than with the environmental variables (Table 5). Square root AGB growth had an extremely weak association with species richness ($r=0.07$, $p=0.001$, Table 5). Square

root AGB growth had high and significant correlation with relative stand density, height, compacted crown ratio, and quadratic mean diameter. Compacted crown ratio, slope, and precipitation had a significant negative correlation with square root AGB growth, but the correlation with slope and precipitation was very weak (Table 5). The aspect and elevation had no correlation with the square root AGB growth.

Table 5. Pearson bivariate correlation between the square root transformed aboveground biomass growth (AGBG) and other variables across the 2554 FIA plots in Alabama.

	AGBG	QMD	SPR	RD	HT	CCR	SL	AS	PPT	ELEV
AGBG	1	0.25**	0.07**	0.46**	0.36**	-0.36**	-0.07**	0.03	-0.08**	-0.02
QMD		1	0.32**	0.15**	0.82**	-0.23**	-0.02	0.06**	-0.04*	0.03
SPR			1	0.39**	0.40**	-0.23**	0.26**	-0.06**	-0.06**	0.19**
RD				1	0.28**	-0.33**	0.09**	-0.01	-0.02	0.12**
HT					1	-0.53**	0.04	0.06**	-0.03	0.04*
CCR						1	-0.01	-0.04	-0.06**	-0.003
SL							1	-0.42**	-0.07**	0.43**
AS								1	0.06**	-0.21**
PPT									1	-0.08**
ELEV										1

Note: The ** and * indicate that the correlation is significant at $\alpha=0.01$ at $\alpha=0.05$ level, respectively. QMD – quadratic mean diameter (cm); SPR – species richness; RD – relative stand density; HT – height (m); CCR – compacted crown ratio; SL – slope (arcsine transformed); AS – aspect (Beers transformed); PPT – mean precipitation (Z-score transformed); ELEV – elevation (Z-score transformed).

Discussion

The results have to be interpreted with these three important considerations: 1) stand age range was fairly large (1 to 125 years) and only trees over 12.7 cm in dbh were used for calculating the AGB growth. Because the plots with stand age of 5 years or younger also contained some large trees (likely residuals from the previous stand), and because stand age was likely determined by the FIA from the age of the seedlings and saplings only, it is likely that there is an overestimation of AGB growth in the plots with stand age 5

years or less; 2) past management could not be taken into account, so it is possible that the rather common and degrading practice of selectively harvesting the largest trees of the most valuable species (often referred to as highgrading), would have resulted in underestimation of the growth in the mixed stands; and last, but certainly not least, 3) the pine stands were generally younger than the hardwood stands, as they are often harvested at a younger age.

When species structure was not taken into account, there was no significant difference between the AGB growth of

pure stands ($2.71 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and mixed stands ($2.70 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). We observed an increase in AGB growth with the change in species structure from pure hardwoods to mixed hardwoods and to a mix of pines with hardwoods, but the pure pines and mixed pines were as productive as the hardwood-pine mixes. Hardwood stands had greater species diversity (up to 17 species) than mixed pine stands (up to only 3 species) and they also contained species with a larger variety of shade tolerances than the pine stands. Facilitation, or resource partitioning due to diversified functional trait variation of the species, should have been stronger in the mixed hardwood stands than in the mixed pine stands. The observed AGB growth rate in our study does not support this hypothesis however – AGB growth of the mixed hardwoods (usually containing shade tolerant and intolerant species) and mixed pines (usually only intolerant species) were not different from each other, even after taking into account stand age, stocking, and site productivity. There was only one exception – at age class III (more than 50 years old) the mixed pine stands grew much slower than the mixed hardwoods, but this result is based only on 4 mixed pine plots (and 195 mixed hardwood plots) and therefore the result is not particularly convincing. Pangle et al. (2009) similarly found nearly identical aboveground net primary productivity (ANPP) in late successional secondary mixed hardwood forests ($11.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and in mature 50 year old white pine (*Pinus strobus* L.) plantations ($10.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) in the southern Appalachian Mountains. Vilà et al. (2007), however, reported that the dominant tree species were an important determinant for wood production in forests across Catalonia, Spain. The identity of the species in the mixture sometimes determines

whether mixed stands are more productive than monospecific stands of similar age, tree density, soil characteristics, and management. In boreal forests for example, the mixture of birch (*Betula* spp.) with spruce (*Picea abies*) exhibits greater productivity than pure spruce stands, but mixture of birch with Scots pine (*Pinus sylvestris*) is less productive than pure pine stands (Vilà et al. 2005). Similar to the total biomass, stemwood production also increased with increasing species richness in *sclerophilous* and conifer forests in Catalonia, Spain, where production increased 19.6 % and 45.8 % in four and five species mixtures, respectively, than in monospecific, two or three species mixtures (Vilà et al. 2005).

Successional stage can have significant effect on forest productivity. The association between species diversity and productivity can be stronger in early successional forests than in late successional forest communities (Caspersen and Pacala 2001) when early successional forest contains multilayered trees with greater species richness than late successional communities that contain monolayered structure with lower species diversity (Sprugel 1985). In our case, at age class I (less than or equal to 25 years), the pure pine stands were as productive, but not more productive, than any of the structures containing a mixture of species (mixed hardwoods, mixed pines, mixed pine-hardwoods). The same was true for the older stands of age class II (26 to 50 years), while for the oldest stands (more than 50 years) this could not be determined with much confidence, as there were too few plots for two of the structures. This was likely due to the high probability of invasion over time by more shade-tolerant species in the pure stands. Thus, in our study, there was no clear importance

of successional stage on productivity of the different types of stands, but it should be noted that the age range was not particularly wide.

At high stocking all structures were equally productive, whereas at low stocking the pure pines were less productive than pine-hardwood mixes. The mixed pines were as productive as pure pines at all stocking levels. Weaker interspecific competition in mixed stands than intraspecific in pure stands has been proposed by others as a possible reason for increased productivity with increasing species diversity (Amaroso and Turnblom 2006). On the other hand, a facilitative-competitive interactions study in old-growth European beech (*Fagus sylvatica* L.) forests reported that the growth rates of trees do not necessarily depend on the density of potential competitors at the intraspecific level, but on the conspecific aggregation of large diameter trees and their functional role (Fichtner et al. 2015). The effects of species mixtures on productivity may vary considerably depending upon the type of mixture and site conditions (Pretzsch 2005). A positive relationship between diversity and productivity is sometimes particularly pronounced in less productive site conditions (Potter and Woodall 2014). The low species richness is commonly found at high resource environments because of the presence of less environmental heterogeneity and fewer niches (Chisholm et al. 2013). Fast growing and highly productive species can dominate and compete well in more productive habitats where the positive association between tree diversity and aboveground biomass may be weaker (Potter and Woodall 2014). Stress-gradient hypothesis is used in many forest studies to explain that complementarity increases with harsher environmental conditions or along

gradients of declining site productivity in forests (del Río et al. 2014, Toigo et al. 2015, Forrester and Bauhus 2016). The low species richness is commonly found at high resource environments because of the presence of less environmental heterogeneity and fewer niches (Chisholm et al. 2013). Fast growing and highly productive species can dominate and compete well in more productive habitats where the positive association between tree diversity and aboveground biomass may be weaker (Potter and Woodall 2014). The low functional trait variation in such cases may lead to competitive exclusion rather than facilitation in pine forests and consequently diversity is not an important factor for productivity.

Our findings showed that, in general, the AGB growth of the pure pine or even pure loblolly pine (the most commonly grown species in the state) stands was not significantly different than the growth of mixed stands that contained pine species. Research in intensive silviculture has shown that the growth of pure stands can increase substantially as a result of various treatments. However, we did not take account of such treatments, which may have been applied in the pure pine stands to increase the productivity. Even though some of these stands may have indeed been fertilized or subjected to early competition control, the overall productivity of pure loblolly pine was still not greater than that of the mixtures. The productivity of some stands that are already near the physiological optimum does not increase with the increase in species or structural diversities because these stands would have already benefitted from management inputs, such as fertilizing or control of pests and invasive species (Forrester and Bauhus 2016). The combined effect of fertilizer and weed control treatments enhanced aboveground

dry biomass growth on average 2 and 2.8 fold for slash and loblolly pine respectively (Jokela et al. 2004).

Sometimes, the beneficial interactions between the species in mixtures do not occur in enough magnitude, or do not even exist, to produce more yield than the monoculture of a highly productive species (Kelty 1992). We found no relationship between diversity and productivity in pine dominated stands where no hardwoods were present. Thus, the pure pine stands were as productive, although not more productive, than the stands with other species in the mix. On the other hand, mixed hardwood stands, as well as pine-hardwood mixtures, were either more productive than or as productive as pure hardwood stands. Moreover, the relationship between species richness and aboveground biomass growth was not significant across the loblolly pine containing plots, but was positive across the sweetgum containing plots. The associations of pines and hardwood species may sometimes help the utilization of limiting resources efficiently, despite the negative effect of interspecific competition, resulting in equal or increased AGB productivity with increasing species richness.

Based on the bivariate correlations, the stand variables density and height, had the greatest association with AGB growth among the selected predictors. The weak correlation of AGB growth with precipitation, slope, aspect, or elevation indicates that environmental factors explain little variation of stand AGB growth, which may be because of relatively low environmental and climatic heterogeneity in the study area. Stand density can significantly affect diversity-productivity relationships, and the complementarity effect increases or decreases with increasing stand density depending on the limiting resources (or

climatic conditions) (Forrester and Bauhus 2016). In a review of large inventory data set studies, Forrester and Bauhus (2016) found stand density to be a stronger determinant of productivity than tree species richness and pointed out the importance of accounting for stand density while analyzing diversity-productivity relationships, as we have done in this paper.

Our study contributes towards the understanding of the relationship between stand composition, structure, and aboveground biomass growth, particularly in southeastern US forests, where loblolly pine is a dominant choice in forestry for commercial wood production. The study results are of significance to forest management strategic planning and biodiversity conservation. Maintaining high productivity is also vital for carbon sequestration and climate change mitigation. If the objective is to maintain both species diversity and optimal aboveground biomass production, maintaining mixed species is crucial.

Conclusion

The dynamics of heterospecific forests are much more complex and difficult to predict than that of conspecific forests, because productivity is related to both population dynamics of the dominant species and differences in resource use among species. In the case of forest ecosystems, higher species diversity may not always or everywhere associate with greater productivity due to the effect of certain environmental, ecological and management factors in the ecosystem processes.

When all data were pooled, species richness was not a significant factor for aboveground biomass growth across the forests of Alabama. The area has little

variability in climatic condition and represents only humid subtropical climate and was dominated by pine stands, particularly loblolly pine. The overall comparison between the five species structures showed that pure pine stands were not more productive than mixed pine stands and pine-hardwood mixtures, but were more productive than mixed hardwoods and pure hardwood stands. If the stands are grown at high stocking however, then all structures (pure, mixed, with or without pine in the composition) were equally productive.

Based on the results for age class I, we conclude that for biomass production on a short rotation, pure pine forests may be as productive as mixed forests, but without the ecological benefits, as well as the economic benefits (but sometimes processing disadvantages) of greater tree species diversity. Further studies need to increase spatial scale to observe the diversity-productivity relationship on a broader geographic scale and in stands that have not experienced harvesting since establishment. Besides the environmental conditions, forest disturbances and management activities have a great influence on forest composition and productivity and they should be accounted for in future studies, analyses, and experimental designs.

Acknowledgements

This material is based upon work supported by the National Science Foundation's Alabama Experimental Program to Stimulate Competitive Research (Alabama EPSCoR) Graduate Research Scholars Program (GRSP) grant round 7, 8 and 9; the National Science Foundation, Center of Research Excellence in Science and

Technology (CREST), Center for Forest Ecosystem Assessment, CREST-CFEA HRD 0420541; and by a United States Department of Agriculture, Forest Service Cooperative Agreement number 06CA11330134074. This work was also supported by the USDA National Institute of Food and Agriculture, McIntire-Stennis projects 1008953 and 0218126. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the funding agencies. The data was acquired through the publicly available database of Forest Inventory and Analysis (FIA) unit of the United States Department of Agriculture, Forest Service. We are thankful to the Alabama Forestry Commission crews who collected the data and to Bill Burkman and Jeff Turner from the FIA for their support in obtaining the data. We thank Dr. Andy Scott, Dr. Callie Schweitzer, Dr. Kozma Naka, Dr. Yong Wang, and two anonymous reviewers for their reviews and valuable suggestions.

References

- ALABAMA DEPARTMENT OF CONSERVATION AND NATURAL RESOURCES 2006. Alabama's comprehensive wildlife conservation strategy. Chapter 2. Wildlife Habitat – Alabama's Ecological Framework. Alabama Department of Conservation and Natural Resources. Available at: <http://www.outdooralabama.com/sites/default/files/Chapter2.pdf>. (Accessed on 4 February 2016).
- ALABAMA FORESTRY COMMISSION 2010. Forests at the Crossroads – Alabama Statewide Forest Assessment and Resource Strategy. Available at: http://www.forestry.alabama.gov/PDFs/Forests_at_the_Crossroads-AL-State_Assessment.pdf. (Accessed on 12 July 2016).
- AMOROSO M.M., TURNBLOM E.C. 2006. Comparing productivity of pure and mixed Doug-

- las-fir and western hemlock plantations in the Pacific Northwest. *Canadian Journal of Forest Research* 36: 1484–1496.
- BECHTOLD W.A., PATTERSON P.L. (Ed.) 2005. The enhanced forest inventory and analysis program-national sampling design and estimation procedures. General Technical Report SRS–80. USDA Forest Service, Southern Research Station: 98 p. Available at: <http://www.treearch.fs.fed.us/pubs/20371>. (Accessed on 17 November 2016).
- BEERS T.W., DRESS P.E., WENSEL L.C. 1966. Aspect transformation in site productivity research. *Journal of Forestry* 64: 691–692.
- BELL B.A., SMILEY W., ENE M., SHERLOCK JR.P.R., BLUE G.L. 2013. An Intermediate Primer to Estimating Linear Multilevel Models using SAS® PROC MIXED. SAS Institute Inc. Available at: <http://analytics.ncsu.edu/sesug/2013/SD-14.pdf>. (Accessed on 23 October 2016).
- BELOTE R.T., PRISLEY S., JONES R.H., FITZPATRICK M., DE BEURS K. 2011. Forest productivity and tree diversity relationships depend on ecological context within mid-Atlantic and Appalachian forests (USA). *Forest Ecology and Management* 261: 1315–1324.
- CARDINALE B.J., SRIVASTAVA D.S., EMMETT DUFFY J., WRIGHT J.P., DOWNING A.L., SANKARAN M., JOUSEAU C. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443: 989–992.
- CASPERSEN J.P., PACALA S.W. 2001. Successional diversity and forest ecosystem function. *Ecological Research* 16: 895–903.
- CHASE J.M., LEIBOLD M.A. 2002. Spatial scale dictates the productivity-biodiversity relationship. *Nature* 416: 427–430.
- CHISHOLM R.A., MULLER-LANDAU H.C., ABDUL RAHMAN K., BEBBER D.P., BIN Y., BOHLMAN S.A., BOURG N.A., BRINKS J., BUNYAVEJCHEWIN S., BUTT N., CAO H., CAO M., CÁRDENAS D., CHANG L.-W., CHIANG J.-M., CHUYONG G., CONDIT R., DATTARAJA H.S., DAVIES S., DUQUE A., FLETCHER C., GUNATILLEKE N., GUNATILLEKE S., HAO Z., HARRISON R.D., HOWE R., HSIEH C.-F., HUBBELL S.P., ITOH A., KENFACK D., KIRATIPRAYOON S., LARSON A.J., LIAN J., LIN D., LIU H., LUTZ J.A., MA K., MALHI Y., McMAHON S., MCSHEA W., MEEGASKUMBURA M., MOHD. RAZMAN S., MORECROFT M.D., NYTCH C.J., OLIVEIRA A., PARKER G.G., PULLA S., PUNCHI-MANAGE R., ROMERO-SALTOS H., SANG W., SCHURMAN J., SU S.-H., SUKUMAR R., SUN I.-F., SURESH H.S., TAN S., THOMAS D., THOMAS S., THOMPSON J., VALENCIA R., WOLF A., YAP S., YE W., YUAN Z., ZIMMERMAN J.K. 2013. Scale-dependent relationships between tree species richness and ecosystem function in forests. (Ed.) D. Coomes. *Journal of Ecology* 101: 1214–1224.
- CURTIS J.T., MCINTOSH R.P. 1951. An Upland Forest Continuum in the Prairie – Forest Border Region of Wisconsin. *Ecology* 32(3): 476–496.
- DEL RIO M., SCHÜTZE G., PRETZSCH H. 2014. Temporal variation of competition and facilitation in mixed species forests in Central Europe. *Plant Biology* 16: 166–176.
- FICHTNER A., FORRESTER D.I., HÄRDLE W., STURM K., VON OHEIMB G. 2015. Facilitative-Competitive Interactions in an Old-Growth Forest: The Importance of Large-Diameter Trees as Benefactors and Stimulators for Forest Community Assembly. *Plos One* 10: e0120335.
- FIRN J., ERSKINE P.D., LAMB D. 2007. Woody species diversity influences productivity and soil nutrient availability in tropical plantations. *Oecologia* 154: 521–533.
- FORRESTER D.I., BAUHUS J. 2016. A review of processes behind diversity – productivity relationships in forests. *Current Forestry Reports* 2: 45–61.
- HE J.-S., WOLFE-BELLIN K.S., SCHMID B., BAZZAZ F.A. 2005. Density may alter diversity – productivity relationships in experimental plant communities. *Basic and Applied Ecology* 6: 505–517.
- HOOPER D.U., CHAPIN III F.S., EWEL J.J., HECTOR A., INCHAUSTI P., LAVOREL S., LAWTON J.H., LODGE D.M., LOREAU M., NAEEM S., SCHMID B., SETALA H., SYMSTAD A.J., VANDERMEER J., WARDLE A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological monographs* 75(1): 3–35.
- HUSTON M.A., AARSSSEN L.W., AUSTIN M.P., CADE B.S., FRIDLEY J.D., GARNIER E., GRIME J.P.,

- HODGSON J., LAUENROTH W.K., THOMPSON K., VANDERMEER J. H., WARDLE D. A. 2000. No consistent effect of plant diversity on productivity. *Science* 289: 1255–1255.
- JACOBY W.G. 2000. Loess: a nonparametric, graphical tool for depicting relationships between variables. *Electoral Studies* 19: 577–613.
- JENKINS J.C., CHOJNACKY D.C., HEATH L.S., BIRDSEY R.A. 2003. National-scale biomass estimators for United States tree species. *Forest Science* 49: 12–35.
- JOKELA E.J., DOUGHERTY P.M., MARTIN T.A. 2004. Production dynamics of intensively managed loblolly pine stands in the southern United States: a synthesis of seven long-term experiments. *Forest Ecology and Management* 192: 117–30.
- KELTY M.J. 1992. Comparative productivity of monocultures and mixed-species stands. In: Kelty M.J., Larson B.C., Oliver C.D. (Eds.). *The Ecology and Silviculture of Mixed-Species Forests: Forestry Sciences* 40. Springer Netherlands: 125–141.
- LEGENDRE P., LEGENDRE L.F.J. 2012. *Numerical Ecology*, Volume 24. Third. Amsterdam: Elsevier. 1006 p.
- LIANG J., BUONGIORNO J., MONSERUD R.A., KRUGER E.L., ZHOU M. 2007. Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality. *Forest Ecology and Management* 243: 116–127.
- LIANG J., CROWTHER T.W., PICARD N., WISER S., ZHOU M., ALBERTI G., SCHULZE E.-D., MCGUIRE A.D., BOZZATO F., PRETZSCH H., DEMIGUEL S., PAQUETTE A., HERAULT B., SCHERER-LORENZEN M., BARRETT C.B., GLICK H.B., HENGEVELD G.M., NABUURS G.-J., PFAUTSCH S., VIANA H., VIBRANS A.C., AMMER C., SCHALL P., VERBYLA D., TCHEBAKOVA N., FISCHER M., WATSON J.V., CHEN H.Y.H., LEI X., SCHELHAAS M.-J., LU H., GIANELLE D., PARFENOVA E.I., SALAS C., LEE E., LEE B., KIM H.S., BRUELHEIDE H., COOMES D.A., PIOTTO D., SUNDERLAND T., SCHMID B., GOURLET-FLEURY S., SONKE B., TAVANI R., ZHU J., BRANDL S., VAYREDA J., KITAHARA F., SEARLE E.B., NELDNER V.J., NGUGI M.R., BARALOTO C., FRIZZERA L., BA AZY R., OLEKSYN J., ZAWI A-NIED WIECKI T., BOURIAUD O., BUSSOTTI F., FINER L., JAROSZEWICZ B., JUCKER T., VALLADARES F., JAGODZINSKI A.M., PERI P.L., GONMADJE C., MARTHY W., OBRIEN T., MARTIN E.H., MARSHALL A.R., ROVERO F., BITARIHO R., NIKLAUS P.A., ALVAREZ-LOAYZA P., CHAMUYA N., VALENCIA R., MORTIER F., WORTEL V., ENGONE-OBIANG N.L., FERREIRA L.V., ODEKE D.E., VASQUEZ R.M., LEWIS S.L., REICH P.B. 2016. Positive biodiversity-productivity relationship predominant in global forests. *Science* 354: aaf8957–aaf8957.
- LONG J.N. 1985. A practical approach to density management. *The Forestry Chronicle* 61: 23–27.
- LONG J.N., DANIEL T.W. 1990. Assessment of growing stock in uneven-aged stands. *Western Journal of Applied Forestry* 5: 93–96.
- LORIMER C.G., WHITE A.S. 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. *Forest Ecology and Management* 185: 41–64.
- MA W., HE J.-S., YANG Y., WANG X., LIANG C., ANWAR M., ZENG H., FANG J., SCHMID B. 2010. Environmental factors covary with plant diversity-productivity relationships among Chinese grassland sites: Diversity-productivity relationships in Chinese grassland. *Global Ecology and Biogeography* 19: 233–43.
- MCCUNE B., GRACE J.B. 2002. *Analysis of Ecological Communities*. MjM Software Design Glenden Beach, Oregon USA. 304 p.
- MILES P.D., SMITH B.W. 2009. *Specific Gravity and Other Properties of Wood and Bark for 156 Tree Species Found in North America*. Research Note NRS-38. Newtown square PA 19073-3294: United States Department of Agriculture Forest Service Northern Research Station. 39 p. Available at: http://www.nrs.fs.fed.us/pubs/rn/rn_nrs38.pdf. (Accessed on 9 February 2017).
- MITTELBACH G.G., STEINER C.F., SCHEINER S.M., GROSS K.L., REYNOLDS H.L., WAIDE R.B., WILLIG M.R., DODSON S.I., GOUGH L. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82: 2381–2396.
- MOSER W.K., HANSEN M. 2009. The relation-

- ship between diversity and productivity in selected forests of the Lake States Region (USA): relative impact of species versus structural diversity. In: McRoberts R.E., Reams G.A., Deusen P.C.V., McWilliams W.H. (eds.) Proceedings of the Eighth Annual Forest Inventory and Analysis Symposium: 414. Monterey, CA: USDA, Forest Service, General Technical Report, WO-79.
- NADROWSKI K., WIRTH C., SCHERER-LORENZEN M. 2010. Is forest diversity driving ecosystem function and service? *Current Opinion in Environmental Sustainability* 2: 75–79.
- OJHA S.K. 2015. Tree diversity-productivity relationships in the forests of Alabama and the eastern United States (PhD). Alabama Agricultural and Mechanical University, Alabama, United States.
- PANGLE L., VOSE J.M., TESKEY R.O. 2009. Radiation use efficiency in adjacent hardwood and pine forests in the southern Appalachians Forest. *Ecology and Management* 257: 1034–1042.
- PAQUETTE A., MESSIER C. 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography* 20: 170–180.
- PÄRTEL M., LAANISTO L., ZOBEL M. 2007. Contrasting plant productivity–diversity relationships across latitude: the role of evolutionary history. *Ecology* 88: 1091–1097.
- PÄRTEL M., ZOBEL M. 2007. Dispersal limitation may result in the unimodal productivity-diversity relationship: a new explanation for a general pattern. *Journal of Ecology* 95: 90–94.
- POTTER K.M., WOODALL C.W. 2014. Does biodiversity make a difference? Relationships between species richness, evolutionary diversity, and aboveground live tree biomass across U.S. forests. *Forest Ecology and Management* 321: 117–129.
- PRETZSCH H. 2005. Diversity and Productivity in Forests: Evidence from Long-Term Experimental Plots. In: Scherer-Lorenzen M., Körner C., Schulze E.-D. (Eds.). *Forest Diversity and Function*, 176. Ecological Studies. Springer Berlin Heidelberg: 41–64.
- PRISM CLIMATE GROUP 2016. Northwest Alliance for Computational Science & Engineering. Available at: <http://www.prism.oregonstate.edu/normals/>. (Accessed on 28 April 2016).
- REINEKE L.H. 1933. Perfecting a stand-density index for even-aged forests. *Journal of Agricultural Research* 46: 627–638.
- RODRÍGUEZ-LOINAZ G., ONAINDIA M., AMEZAGA I., MIJANGOS I., GARBISU C. 2008. Relationship between vegetation diversity and soil functional diversity in native mixed-oak forests. *Soil Biology and Biochemistry* 40: 49–60.
- SPRUGEL D.G. 1985. Natural Disturbance and Ecosystem Energetics. In: Pickett S.T.A., White P.S. (Eds.). *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press Inc. San Diego, California 92101: 335–352.
- STEVENS J.T., SAFFORD H.D., NORTH M.P., FRIED J.S., GRAY A.N., BROWN P.M., DOLANC C.R., DOBROWSKI S.Z., FALK D.A., FARRIS C.A., FRANKLIN J.F., FULÉ P.Z., HAGMANN R.K., KNAPP E.E., MILLER J.D., SMITH D.F., SWETNAM T.W., TAYLOR A.H. 2016. Average Stand Age from Forest Inventory Plots Does Not Describe Historical Fire Regimes in Ponderosa Pine and Mixed-Conifer Forests of Western North America. *PLoS ONE* 11: 1–20.
- TENZIN J., HASENAUER H. 2016. Tree species composition and diversity in relation to anthropogenic disturbances in broad-leaved forests of Bhutan. *International Journal of Biodiversity Science, Ecosystem Services & Management* 12(4): 274–290.
- THOMS C., GATTINGER A., JACOB M., THOMAS F.M., GLEIXNER G. 2010. Direct and indirect effects of tree diversity drive soil microbial diversity in temperate deciduous forest. *Soil Biology and Biochemistry* 42(9): 1558–1565.
- TILMAN D. 1999. The ecological consequences of changes in biodiversity: A search for general principals. *Ecology* 80: 1455–1474.
- TILMAN D., DOWNING J.A. 1994. Biodiversity and stability in grasslands. *Nature* 367: 363–365.
- TILMAN D., WEDIN D., KNOPS J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379: 718–720.
- TOÍGO M., VALLET P., PEROT T., BONTEMPS J.-D., PIEDALLU C., COURBAUD B. 2015. Overyield-

- ing in mixed forests decreases with site productivity. *Journal of Ecology* 103: 502–512.
- VILÀ M., INCHAUSTI P., VAYREDA J., BARRANTES O., GRACIA C., IBÁÑEZ J.J., MATA T. 2005. Confounding Factors in the Observational Productivity-Diversity Relationship in Forests. In: Scherer-Lorenzen M., Körner C., Schulze E.-D. (Eds.). *Forest Diversity and Function- Temperate and Boreal Systems*, 176. *Ecological Studies*. Springer: 65–86.
- VILÀ M., VAYREDA J., COMAS L., IBÁÑEZ J.J., MATA T., OBÓN. B. 2007. Species richness and wood production: a positive association in Mediterranean forests. *Ecology Letters* 10: 241–250.
- VILÀ M., VAYREDA J., GRACIA C., IBÁÑEZ J.J. 2003. Does tree diversity increase wood production in pine forests? *Oecologia* 135: 299–303.
- WOODALL C.W., D'AMATO A.W., BRADFORD J.B., FINLEY A.O. 2011. Effects of stand and inter-specific stocking on maximizing standing tree carbon stocks in the eastern United States. *Forest Science* 57: 365–378.
- WOODALL C.W., MILES P.D., VISSAGE J.S. 2005. Determining maximum stand density index in mixed species stands for strategic-scale stocking assessments. *Forest Ecology and Management* 216: 367–377.
- WOUDENBERG S.W., CONKLING B.L., O'CONNELL B.M., LAPOINT E.B., TURNER J.A., WADDELL K.L. 2010. *The Forest Inventory and Analysis Database: Database description and users manual version 4.0 for Phase 2*. 344 p. Available at: <http://www.treesearch.fs.fed.us/pubs/37446>. (Accessed on 10 February 2017).
- ZIFAN A. 2016. USA map of Köppen climate classification. Available at: https://commons.wikimedia.org/wiki/File:USA_map_of_K%C3%B6ppen_climate_classification.svg. (Accessed on 20 February 2017).