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ORIGINAL ARTICLE

Carbon sequestration and nitrogen uptake in a temperate silvopasture system

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Abstract Agroforestry systems (AFS) have the potential to foster long-term carbon sequestration and nutrient uptake. Yet, information on sequestration rates is still scarce, especially for AFS in temperate regions and for maturing AFS. This study aims to determine the rate and amount of carbon and nitrogen uptake in a 17-year-old northern red oak (*Quercus rubra*)–pecan (*Carya illinoinensis*) silvopastoral planting in Fayetteville, AR, USA. Seven oak and pecan trees were felled to develop AFS-specific allometric equations for above-ground biomass, carbon, and nitrogen. Tree-stand woody biomass (DW_w), carbon (C_w) and nitrogen (N_w) and leaf biomass (DW_L), carbon (C_L), and nitrogen (N_L) were calculated with these equations. Diameter at 1.37 m above ground (DBH) was measured annually, and a non-linear mixed-effect model was used to estimate absolute (AGR) and relative growth rates. DW_w and C_w was 7.1 and 3.4 Mg ha^{-1} for pecan and 26.6 and 12.7 Mg ha^{-1} for oak, which corresponds to a carbon sequestration rate of 0.75 and 0.20 Mg C ha^{-1} yr^{-1}, respectively. Total N uptake was approximately 66 and 71 g N tree^{-1} yr^{-1} for oak and pecan. The mixed-effect model with individual-tree-level random effects for all parameters provided the best representation of DBH growth of oak and pecan, likely due to the high heterogeneity of site characteristics. The AGR explained the non-linear plant growth and reached its

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maximum of 0.017 and 0.0179 m yr^{-1} for oak and pecan, respectively, 11 years after planting. This suggests that carbon and nitrogen uptake also declined after 11 years.

Keywords *Quercus rubra* · *Carya illinoinensis* · Carbon sequestration · Nitrogen uptake · Mixed effect models · Allometric equations

Introduction

In North America, agroforestry systems (AFS) are mainly comprised of riparian forests, alley cropping, forest farming, silvopastures, and windbreaks (Sauer and Hernandez-Ramirez 2011; Schoeneberger 2009). These systems have recently drawn attention as climate-smart production systems for temperate regions, as they can provide high net carbon (C) gains per area (Schoeneberger 2009), and generally occupy a relatively small fraction of the agricultural landscape (Schoeneberger et al. 2012). Nitrogen (N) is an important macro-nutrient for tree growth, and a great share of tree N and C content is stored in the above-ground biomass, which is a relatively reliable pool to calculate (Schoeneberger et al. 2012). While C and N is sequestered long-term in the woody biomass, leaf C and N may be released back to the system when leaves senesce and decompose. AFS also sequester C and N in the below-ground biomass of trees and shrubs and can avoid C and N losses owing to lower CO_2 respiration rates and N leaching from soils (Dixon et al. 1994; Wolz et al. 2018). Recent studies found that AFS have a higher potential for reducing C and N related greenhouse gas emissions from agricultural land (Peichl et al. 2006; Nair 2012; Baah-Acheamfour et al. 2016; Wolz et al. 2018), and can store higher amounts of C (Sharrow and Ismail 2004) compared with open pastures, traditional tree plantations, or field crop systems.

However, there is still a limited understanding of C and N pools and fluxes within AFS in the temperate zone (Nair 2012; Morgan et al. 2010). The vast complexity among various AFS (i.e. climate, species composition, tree pruning, fertilizer application, tree density, and setup) precludes the simple comparison of C and N pools and rates among systems (Nair 2012). Depending on these factors, AFS can range from being a C sink or a source (Dixon 1995). Estimated C sequestration rates for temperate silvopastures (i.e. above- and below-ground biomass, and soil) range from 1.8 to 3.3 Mg ha^{-1} yr^{-1} (Nair and Nair 2002) but may be as high as 6.1 Mg ha^{-1} yr^{-1} (Udawatta and Jose 2012). In addition, knowledge of tree N uptake rates are important in optimizing N requirements and management in temperate AFS over time. Gamble et al. (2016) found mean N uptake between 86 and 233 kg ha^{-1} after approximately 3 years, depending on species and location. The mean sequestration and uptake rates can be calculated as the sum of the biomass C and N stock divided by the tree stand age (Kumar et al. 1998; Nair et al. 2009). This is the absolute growth rate (AGR) of a linear model, i.e.:

$$AGR = \frac{dX}{dt} \tag{1}$$

where *d*X is the difference in C and N pools at the beginning and end of a time period, *d*t. While Eq. (1) is an easy way of estimating sequestration rates, it is not directly applicable to the non-linear nature of individual tree growth. This effect becomes increasingly important as AFS mature. Lee and Dodson (1996) assumed an asymptote for growth e.g. increased rates for the first 25 years with growth plateauing beyond that threshold. Similarly, Merwin et al. (2009) and Ziegler et al. (2016) introduced non-linear tree growth models to estimate C sequestration rates. In addition, tree stand C and N pools in Eq. (1) are often calculated with allometric equations with a non-destructively measured variable (such as diameter at breast height; DBH) as independent and a destructively measured variable (such as C content) as dependent variable (Chojnacky et al. 2014). However, these equations are largely developed for forest stands, and are not accurate for typically wider spaced and fertilized AFS (Schoeneberger 2009). Tree growth is driven by plant-available nutrients, water, and light among other factors, and trees have a high morphological and physiological plasticity to adapt to resource limitations (Grams and Andersen 2007; Lines et al. 2012; Stovall et al. 2013). Resource-competition and mutual shading are greater in dense, unfertilized forest stands compared to AFS. Therefore, trees in AFS can be morphologically and physiologically different to forest trees. AFS-grown trees have larger canopies with higher branch biomass (Zhou et al. 2011; Schroth et al. 2015). To support the additional weight, trees in

AFS develop a different tree taper with higher trunk specific gravity (Zhou et al. 2011). Trees response to fertilizer application and irrigation with increased biomass production (Johnson 1990; Coyle and Coleman 2005; Schroth et al. 2015). Fertilizer application and spacing reportedly affects tree crown shape and biomass (Rance et al. 2017). Leaf chlorophyll content and leaf mass per unit leaf area increases under light competition in order to maximize CO_2 uptake (Grams and Andersen 2007). Shaded trees increase height at the same trunk diameter compared to isolated trees (Harja et al. 2012). Therefore, generalized allometric equations can lead to substantial over- and underestimations of biomass of AFS (Kuyah et al. 2012; Borden et al. 2017). A comparison of AFS and forest allometric equations showed that the latter underestimates AFS tree branch biomass, and over-estimates trunk biomass (Zhou et al. 2014).

It is crucial to estimate C sequestration and N uptake rates with higher precision and accuracy, especially as AFS mature, which requires the development of AFS-specific allometric equations. In addition, nonlinear growth curves can identify changes in growth rates over time (Paine et al. 2012). In this study, AFS-specific allometric equations are developed and C sequestration and N uptake rates are calculated for a 17-year-old pecan (*Carya illinoinensis* [Wangenh.] K. Koch) and northern red oak (*Quercus rubra* L.) tree stand in a silvopastoral setting, and a non-linear mixed effect model is applied to evaluate changes in tree growth rates over time.

Materials and methods

Study site

This silvopasture site was established in 1999 at the University of Arkansas, Agricultural Research and Extension Center, Fayetteville, AR, USA (36.091°N, − 94.190°W; 380 m above sea level). According to the USDA soil taxonomy, soils were identified as Captina silt loam (fine-silty, siliceous, active, mesic Typic Fragiudults), Pickwick silt loam (fine-silty mixed, semiactive, thermic Typic Paleudults), Nixa cherty silt loam (loamy-skeletal, siliceous, active, mesic Glossic Fragiudults) and Johnsburg silt loam (fine-silty, mixed, active, mesic, Aquic Fragiudults) (Harper et al. 1969). The climate is sub-humid with a mean annual (± SD) precipitation of 1094 ± 231 mm and mean annual maximum and minimum air temperature of 20.6 ± 1.0 °C and − 4.7 ± 1.3 °C from 2000 to 2015 (NOAA 2016).

A total of 119 potted pecan trees (‘Kanza’ and ‘Peruque’ cultivars grafted to ‘Colby’ seedling rootstocks; Forrest Keeling Nursery, Elsberry, MO) were planted in six East–West rows with 15 m × 9.1 m spacing, covering an area of 1.84 ha in November 1999. Of the original 119 trees, six trees died without replacement, and 26 have been replaced from 2004 to 2017 and were not considered in this study (n = 87; i.e. 47 trees/ha). In addition, 233 bare-root northern red oak seedlings (Kansas Forest Service, Manhattan, KS) were planted in five East–West rows with an initial spacing of 15 m × 2.4 m in March 2000, covering an area of 1.12 ha. Owing to natural mortality, the total number decreased to 158 trees as of 2016 (141 trees/ha), and within-row tree spacing was uneven with 2.4–12 m. Seven oak trees were excluded from further analyses, because they were above maximum DBH of the sample trees (see “Sample trees” section; Table 1), i.e. n = 151. Alleys were planted with either orchardgrass (*Dactylis glomerata* L. ‘Tekapo’) or a big bluestem mixture (*Andropogon gerardi* L.) and harvested annually for hay in the first few years of the study. The forages were mob grazed mid-June by cattle.

Landscape fabric, mowing, and herbicide application around the trunk base were used for weed control, and plastic tree shelters protected the pecan trees during the first year of growth. The trees were watered as needed during the first two growing seasons. Each tree received an initial mineral N–P–K fertilizer application of 1.6, 0.3 and 0.7 g. The Eastern part of the site received one annual broad spread application of 4.5 Mg ha^{-1} poultry litter (2–3% N), while 56 kg ha^{-1} of mineral NH_4NO_3 fertilizer was applied to the Western part from 2001 to 2007 (Sauer et al. 2015). Beginning from 2004, a slow-release N–P–K fertilizer with 5.6, 2.4, and 4.6 g tree^{-1} was applied annually. Mineral fertilizer with N, P, K, S, and Ca was also applied at a rate of 112, 49, 56, 29, and 41 kg ha^{-1} in March 2016. Trees were pruned periodically to achieve a 2.4 m trunk. Further reading on setup and management of the silvopasture is provided in Thomas et al. (2008, 2015), Sauer et al. (2015), and Adhikari et al. (2018).

Table 1 Mean (± SE) DW_w, DW_L, C_w, C_L, N_w, N_L, DBH, trunk and tree height, as well as specific gravity of harvested oak and pecan sample trees (n = 6/7) and total tree stand (n = 151/87) in 2016

Variables	Oak		Pecan	
	Sample trees	Tree stand	Sample trees	Tree stand
DW_w (kg)	166.5 ± 49.4	198.3 ± 8.1	230.0 ± 50.5	150.9 ± 8.7
DW_L (kg)	15.1 ± 3.7	15.5 ± 0.5	38.4 ± 5.6	29.4 ± 1.0
$\%C_w$	47.9% ± 0.1%	–	47.3% ± 0.2%	–
$\%C_L$	48.4% ± 0.2%	–	45.1% ± 0.3%	–
$\%N_w$	0.44% ± 0.01%	–	0.49% ± 0.01%	–
$\%N_L$	2.04% ± 0.07%	–	1.78% ± 0.05%	–
C_w (kg)	79.9 ± 23.8	95.1 ± 3.9	109.5 ± 24.6	71.3 ± 4.2
C_L (kg)	7.3 ± 1.8	7.5 ± 0.3	17.4 ± 2.6	13.3 ± 0.5
N_W (kg)	0.68 ± 0.2	0.80 ± 0.03	1.05 ± 0.24	0.68 ± 0.04
N_L (kg)	0.30 ± 0.1	0.31 ± 0.01	0.70 ± 0.1	0.52 ± 0.02
DBH mean (m)	0.174 ± 0.027	0.196 ± 0.004	0.237 ± 0.014	0.208 ± 0.003
DBH range (m)	0.076–0.279	0.065–0.279	0.185–0.295	0.125–0.295
Specific gravity (kg m^{-3})	0.63 ± 0.01	–	0.55*	–
Trunk height (m)	3.5 ± 0.9	–	1.8 ± 0.1	–
Tree height (m)	10.7 ± 0.6	9.9 ± 0.1	9.6 ± 0.5	8.6 ± 0.1

DW_w, calculated woody dry weight; DW_L, calculated leafy dry weight; C_w, carbon content of woody material; C_L, carbon content of leafy material; N_w, nitrogen content of woody material; N_L, nitrogen content of leafy material; DBH, diameter at breast height

*Measured on one pecan tree only

Sample trees

Seven pecan trees and six oak trees were felled between August and October 2016, and a seventh oak tree was additionally felled in February 2017 after leaf senescence (i.e. n = 6 for oak leaf analysis). The sample trees were chosen to cover a wide DBH range to be able to generate log–log models for the whole tree stand (Table 1), and without affecting the original experimental setup. The trees were subdivided into leaves, twigs (< 0.025 m diameter), stems (> 0.025 m diameter), and trunk, and fresh weight (FW) of all components was measured in the field (accuracy: ± 0.1 kg). One leaf sample, one twig sample, three to six stem samples, and two to six trunk samples per tree were taken, weighed in the field (accuracy: ± 0.01 kg and 0.1 g for large and small samples, respectively), and stored cool until further processing. Leaves, twigs and stem samples were randomly taken from within the canopy and made up 0.6–13.9% of the total tree weight. Pecan and oak woody biomass samples were oven-dried at 100 °C and 70 °C, respectively, while leaf samples were dried at 66 °C. The oven-dried stem samples were 39–60 mm long with a 29–129 mm diameter, and the trunk samples were 31–65 mm long with a 40–360 mm diameter. An additional set of nine duplicate samples from each species was oven-dried at 70 and 100 °C to evaluate the impact of different temperatures on C and N analysis. All oven-dried samples were weighed, ground to 2 mm, and thereafter a subsample was fine ground for analysis of C and N concentration (i.e. %C and %N) using a C:N Analyzer (Flash 1112, Thermo Finnigan, San Jose, CA).

The total tree dry weight of woody material (DW_w) and leaves (DW_L) was calculated as the total tree FW multiplied by the DW–FW ratio. The leaf carbon (C_L) and nitrogen (N_L), and woody C and N content (C_W, and N_W) were calculated as DW_w and DW_L multiplied by the corresponding C and N concentration.

Further measurements on the sample trees included DBH (1.37 m above soil level), trunk height (distance from the ground to the first stem) and total height.

Specific gravity (kg m^{-3}) was calculated from stem and trunk samples as DW divided by fresh sample volume.

Total tree stand estimates

Allometric relationships for the sample trees were developed with a log–log model, where DBH is the independent variable and DW_L, C_L, N_L as well as DW_w, C_W, and N_W of oak and pecan were dependent variables:

$$ln(y) = ln(a) + m * ln(DBH) \tag{2}$$

where y = the dependent variable of interest (in kg); DBH = diameter at breast height (m).

The log–log model is commonly used to model allometric relationships and calculate biomass for tree stands (Chojnacky et al. 2014). The back-transformation of the log-transformed data to the metric scale requires a correction factor to minimize the bias induced by logarithmic transformation (Baskerville 1972). In this study, the correction factor proposed by Shen and Zhu (2008) was used as a multiplier, which reportedly yields reliable estimates and predictions (Clifford et al. 2013). Note that Shen and Zhu's (2008) correction factor is not a constant, but changes with the independent variable. Significance of the log–log model was tested with the F-test for linear regression at a Type I error rate of 5%. The root mean square error (RMSE) between measured and calculated C and N values among sample trees was calculated.

Tree stand DW, C, and N parameters were calculated with Eq. (2), the sample tree log–log parameters, and tree stand DBH from 2016 (see also "Tree growth rates and mixed effect model development" section). The tree stand C and N stock was calculated per area (in Mg ha^{-1}) and in individual trees (in kg $tree^{-1}$). The C sequestration and N uptake rates were calculated using Eq. (1), where dX and is the difference between C_W, N_W, C_L, and N_L in 2016 [estimated with Eq. (2)] and 1999 (set to zero at time of new tree planting), and dt is the number of years after planting (YaP; i.e. 17 years).

Tree growth rates and mixed effect model development

Annual DBH measurements were taken on all oak and pecan trees from 2005–2016 to 2004–2016 (excluding 2007 and 2013), respectively. Outlier and unreasonable DBH values were excluded. Additional diameter measurements on pecan were taken 0.25 m above the graft union from 2001 to 2010 to record the growth of the grafted scion. These measurements were converted to DBH using a linear regression model ($y = 0.86x$; $R^2 = 0.98$, $p < 0.01$; n = 521 measurements on 117 trees over 5 years).

The AGR and relative growth rate (RGR) were calculated with a non-linear mixed effect model. Mixed effect models consist of fixed effects (whole population) and random effects (individual tree). Random effects also acknowledge the non-independent nature of individual tree measurements (West et al. 1984; Adame et al. 2008). Mixed effect models have previously been applied to calculate tree growth rates in forest stands (Adame et al. 2008) and coffee-agroforestry systems (Nath et al. 2011). The model development was done with the *nlme*-package (Pinheiro and Bates 2000) and R software (R Development Core Team 2011). The development of the mixed effect model started with a graphical examination of the combined oak and pecan DBH data. A self-starting three-parameter logistic model was chosen with DBH as the dependent and YaP as the independent variable and was implemented with the *SSlogis*-command. First, individual models for each oak and pecan tree were established with the *nlsList*-command. Then, the development of a more parsimonious model started with all parameters being random effects using the *nlme*-command. The within-group heteroscedasticity structure was described with the *varPower*()-argument within the *nlme*-command, which accounted for the natural occurrence of increasing variance in DBH as trees age. Thereafter, models with different combinations of fixed and random parameters were established, and the best combination was selected according to the Akaike Information Criterion (AIC) using the *anova*-command. Thenceforth, the dependence of the parameters to tree species as covariate was analyzed, using the *fixed*-argument in the *nlme*-command. The best model was again determined by AIC comparison, and the significance of tree species on the parameters was analyzed with the *anova*-command. The AGR and RGR were calculated with the mean parameter values of the best fit model following Paine et al. (2012). All graphs were developed with R.

Results

Above-ground biomass and C and N content of sample trees

Above-ground biomass was estimated with FW samples from seven trees each. Sample FW was up to 14% of the total tree FW, and DW–FW ratio ranged from 1.44 to 2.84 kg kg^{-1}. Calculated oak and pecan DW_w (as the sum of woody tree components) ranged from 18.1–370.8 to 96.8–499.3 kg, respectively. Oak DW_L was lower and ranged from 3.6 to 28.0 kg, compared to pecan with 24.4–68.4 kg, respectively. The mean C concentration of woody and leafy tissue was below 50% in both tree species, and leafy N was higher than woody N concentration (Table 1). Note, that there were few differences in C in N concentration at different oven temperatures, however we did not compare the two temperatures statistically owing to the small sample size.

The calculated C_w of oak and pecan ranged from 8.8 to 178.9 kg and from 45.7 to 241.5 kg, respectively. The calculated C_L of oak and pecan ranged from 1.8 to 13.7 kg and from 11.1 to 31.7 kg, respectively. Pecan total height, trunk height, and specific gravity of wood was smaller compared to oak. The calculated N_w of oak and pecan ranged from 0.08 to 1.51 kg and from 0.45 to 2.38 kg, respectively. The calculated N_L of oak and pecan ranged from 0.08 to 0.61 kg and from 0.41 to 1.35 kg, respectively (Table 1).

The allometric relationship between DBH as the independent variable and DW, C, and N components as dependent variable was significant ($p < 0.05$), explaining 79–99% of the variation. The pecan log–log models had higher slopes and lower intercepts than the oak log–log model (Figs. 1, 2). The RMSE of measured and calculated parameter values of the sample trees are presented in Table 2.

Total tree stand above-ground biomass and C and N contents

The allometric DBH relationships were used to calculate total tree stand and mean oak and pecan stand DW, C and N of woody and leafy plant tissue. The correction factor used for back-transformation ranged from 1.0004 to 1.009. Tree stand mean values in comparison to sample trees can be found in Table 1. Total pecan tree stand DW_w, C_w, and N_w was estimated to 7.1, 3.4 Mg ha^{-1} and 32.5 kg ha^{-1}. Total oak tree DW_w, C_w, and N_w was estimated to 26.6 and 12.7 Mg ha^{-1} and 107.5 kg ha^{-1}. Total pecan DW_L, C_L, and N_L was estimated to 1.4 and 0.6 Mg ha^{-1} and 24.5 kg ha^{-1}. Total oak tree DW_L, C_L, and N_L was estimated to 2.1 and 1.0 Mg ha^{-1} and 42.6 kg ha^{-1}.

Carbon sequestration, nitrogen uptake, and DBH growth rates

Carbon sequestration and N uptake rates were calculated for woody and leafy above-ground biomass with Eq. (1). Tree stand and tree average rates are presented in Table 3. The C sequestration rates were higher in oak than in pecan for both tree stand and individual tree averages. For example, C_w sequestration rate was 0.75 and 0.20 Mg C ha^{-1} yr^{-1} for oak and pecan, respectively. Nitrogen uptake was also higher in oak than in pecan, except for tree average N_L, where pecan N uptake was 30.44 g tree^{-1} yr^{-1} compared to oak N uptake with 18.68 g tree^{-1} yr^{-1}.

Mean (± SE) pecan DBH increased from 0.015 ± 0.004 m in 2001 to 0.208 ± 0.033 m in 2016, while oak DBH increased from 0.033 ± 0.019 to 0.201 ± 0.052 m. This dataset was used to analyze DBH growth with a three-parameter logistic mixed effect model (Fig. 3). The parameters of the model of best fit (i.e. lowest AIC) are presented in Table 4. Model analysis showed that a logistic model with individual-level random effects for all three parameters provided the best representation of DBH growth, i.e. all parameters varied among trees. The tree species had a significant effect on DBH growth ($p < 0.05$). The parameters *scal* and *xmid* were significantly different between oak and pecan, while no difference was found for the *Asym*-parameter. The mean three-parameter logistic model fit is shown in Fig. 3. The overall mean asymptote (*Asym*) was at 0.216 ± 0.003 m for both, pecan and oak. The mean time at which half of the asymptotic DBH was reached (*xmid*), was estimated to 10.67 ± 0.10 and 10.31 ± 0.15 YaP for oak and pecan, respectively. The mean elapsed time where trees increased from half to ~ 3/4 of the asymptotic DBH (*scal*) was estimated at 3.18 ± 0.05 and 3.02 ± 0.06 years.

Maximum AGR of oak DBH was 0.017 m yr^{-1} in ~ 11.1 YaP, while for pecan it was 0.0179 m yr^{-1}

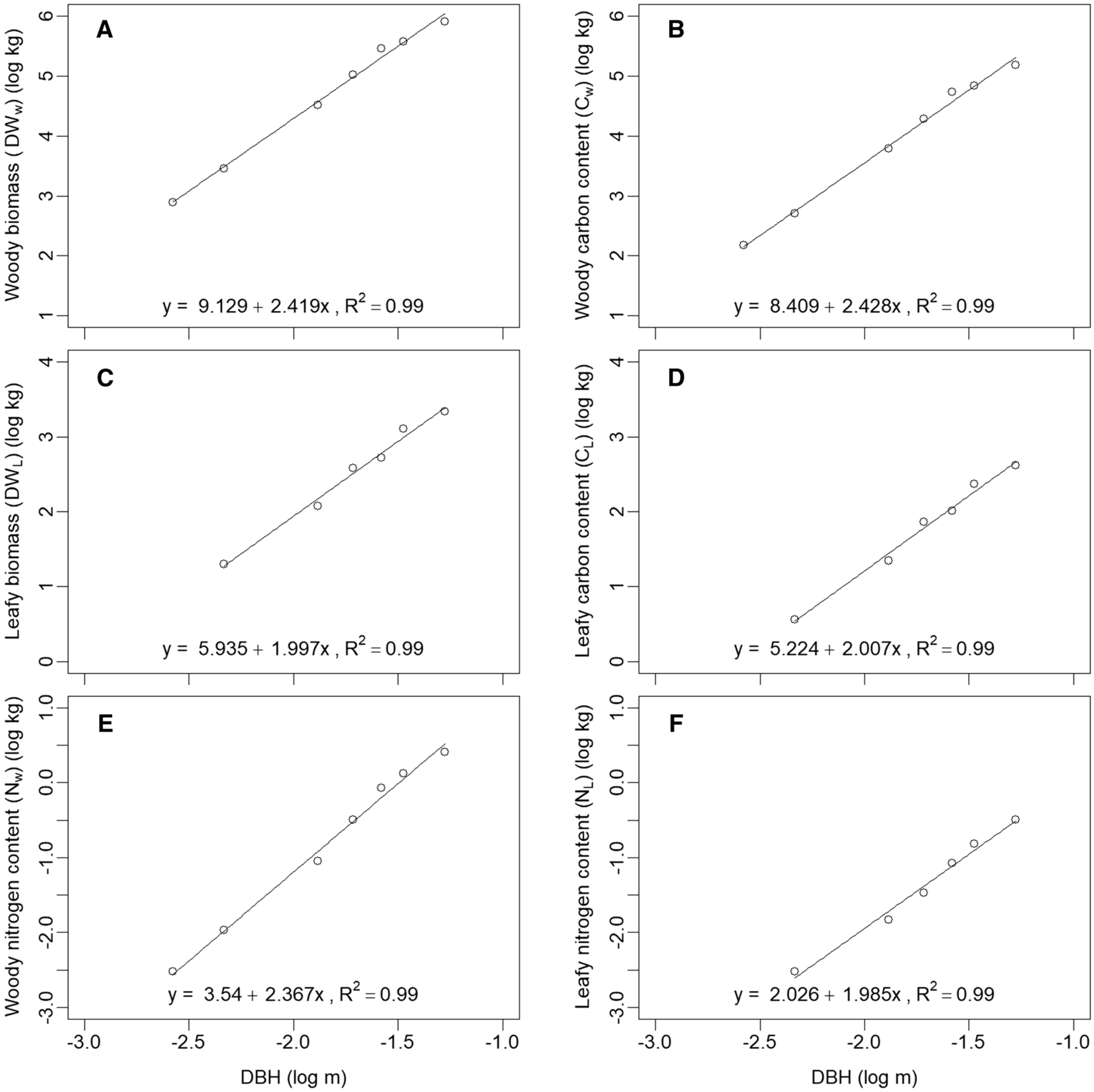

Fig. 1 Log–log model with diameter at breast height (DBH) as independent variable and woody (DW$_w$) and leafy (DW$_L$) biomass and carbon (C$_w$, C$_L$) and nitrogen (N$_w$, N$_L$) content as dependent variables of oak sample trees (n = 6/7)

in ~ 11.3 YaP (Fig. 4a). The RGR of oak DBH steadily decreased from 0.26 to 0.04 m m^{-1} yr^{-1} during the time period of 6–17 YaP and with a model predicted DBH mean of 0.04–0.19 m for the same period of time, while pecan RGR steadily decreased from 0.31 to 0.03 m m^{-1} yr^{-1} during the period of 2–17 YaP and with a predicted DBH of 0.013–0.195 m (Fig. 4b, c).

Discussion

Allometric relationships, C and N concentration

In this study, AFS-specific allometric equations were developed to estimate total tree stand above-ground biomass, C and N content. Allometric relationships are commonly used to calculate biomass and C pools and fluxes, and is preferred over destructive sampling in

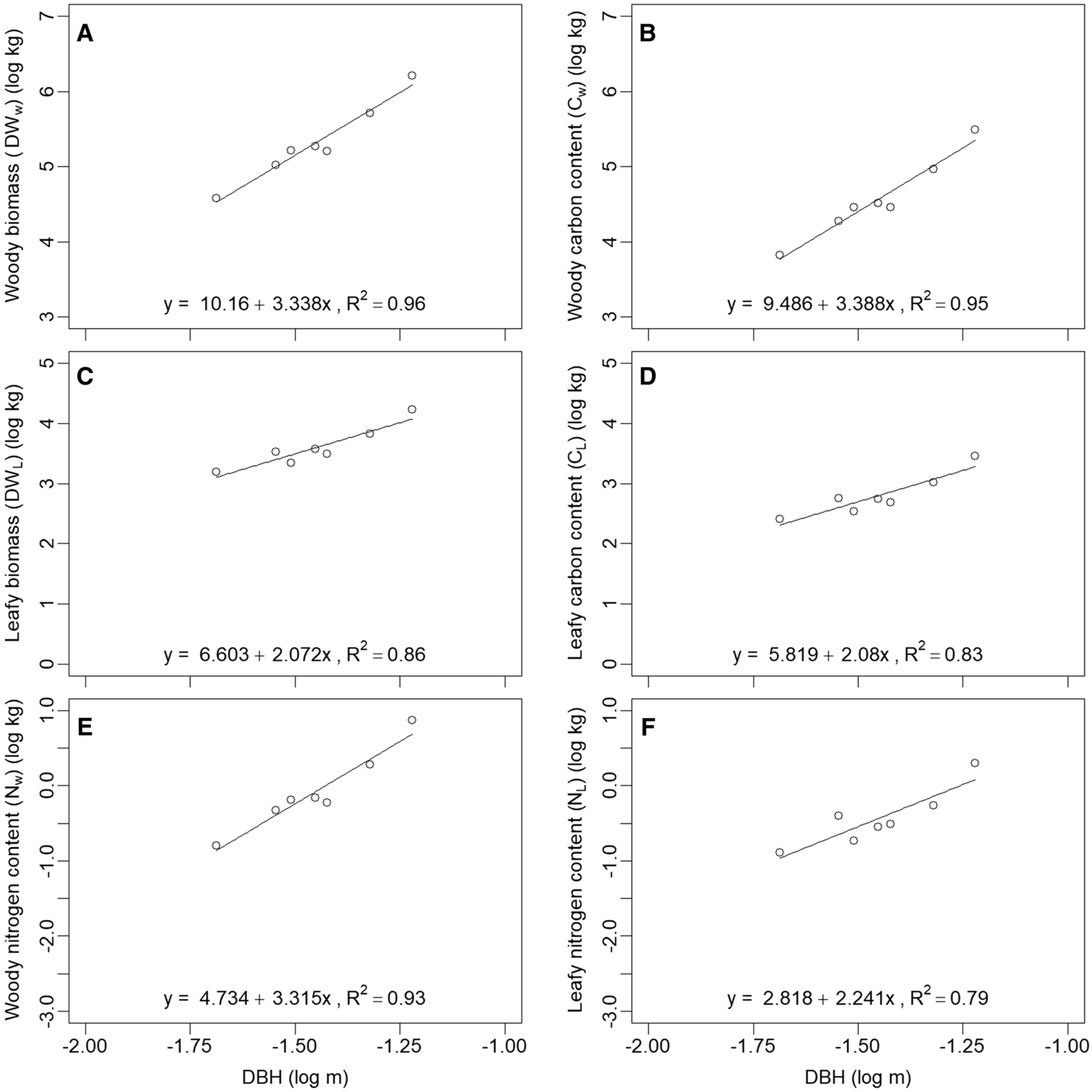

Fig. 2 Log–log model with diameter at breast height (DBH) as independent variable and woody (DW_w) and leafy (DW_L) biomass and carbon (C_w, C_L) and nitrogen (N_w, N_L) content as dependent variables of pecan sample trees (n = 7)

AFS and forests (Jenkins et al. 2004; Nair 2012; Chojnacky et al. 2014). However, as tree density is typically lower in AFS, and AFS are managed systems with weeding, fertilizer application etc., forest derived allometric equations may not be applicable (Schoeneberger et al. 2012), and AFS-specific estimates are needed. In this study, a long-term impact of fertilizer (Stovall et al. 2013; Johnson 1990; Coyle and Coleman 2005; Schroth et al. 2015) and plant density (Rance et al. 2017; Harja et al. 2012) on tree allometry could be expected. Log–log model parameters similar to those in this study have previously been reported for a pecan orchard of similar age, however with smaller area per tree and different genotypes (Smith and Wood 2006). As for northern red oak, the slope and intercept of this study fit well with a generalized model for forest applications (Chojnacky et al. 2014). The tree density of the studied northern red oak in this study

Table 2 The root mean square error (RMSE) (kg) of measured and calculated DW_w, DW_L, C_w, C_L, N_w, N_L of oak and pecan sample trees (n = 6/7)

Variables	Oak	Pecan
DW_w	21.67	22.18
DW_L	1.32	3.74
C_w	10.26	10.89
C_L	0.57	1.87
N_W	0.08	0.13
N_L	0.02	0.09

DW_w, calculated woody dry weight; DW_L, calculated leafy dry weight; C_w, carbon content of woody material; C_L, carbon content of leafy material; N_w, nitrogen content of woody material; N_L, nitrogen content of leafy material

was higher than usual for a silvopastoral system, which may have led to forest-like growth behavior and biomass production. Oak tree height was significantly negatively related to within-tree distance (Spearman r = − 0.83, n = 8, $p < 0.05$), i.e. trees nearer to each other tend to be higher. This indicates morphological adaptation to planting density. Trees in dense stands or under mutual shading compete for light and have greater tree height than isolated trees (Rance et al. 2017; Harja et al. 2012). This morphological adaptation enables trees to capture a greater share of available solar radiation and cast shade on their competitor neighboring trees (Grams and Andersen 2007). Also note that sample size used to develop the allometric equations was low, as mature trees were selected for destructive sampling in this study. A low sample size can lead to substantial over- and underestimations of tree stand DW, C and N content, and eventually C sequestration and N uptake rates (Roxburgh et al. 2015). This is also reflected in the relatively large RMSE (Table 2). The log–log models for pecan were poorer compared to oak because of one pecan sample tree with lower DW at higher DBH than the other sample trees (Figs. 1, 2).

The estimation of above-ground C content in woody biomass requires an estimate of C concentration. When an estimate is not available, 50% C is often assumed for C pool and sequestration rate estimations (e.g. Udawatta and Jose 2012; Merwin et al. 2009). However, the C concentration of trees can differ widely among species and may be below the anticipated value of 50% as shown in this study and others (Martin and Thomas 2011; Nair 2012). This can lead to the overestimation of C pools and fluxes. For example, the perennial C pool of oak and pecan in this study would have been overestimated by 0.54 and 0.20 Mg ha^{-1}, respectively. Hence, a conservative estimation (i.e. underestimation, say 45% C) may be more appropriate to calculate C pools and sequestration rates in AFS (see also Schoeneberger 2009), especially for an application on a regional or national level. The same is probably true for N concentrations and N uptake calculations. Gamble et al. (2016) found N concentration values 0.43–0.44% for poplar and willows, which is similar to oak N in this study, but lower than in pecan. While the N concentration in woody biomass is low, the N content and N uptake rates can be higher owing to the higher amount of woody biomass.

Carbon sequestration, nitrogen uptake, and DBH growth rates

Sequestration rates of C and uptake rates of N were calculated with Eq. (1) as the AGR of a linear model.

Table 3 C_w, C_L, N_w, and N_L sequestration rates from oak and pecan during the 17-year-period

Variables	Oak		Pecan	
Units	Mg ha^{-1} yr^{-1}	kg $tree^{-1}$ yr^{-1}	Mg ha^{-1} yr^{-1}	kg $tree^{-1}$ yr^{-1}
C_w	0.75	5.59	0.20	4.20
C_L	0.06	0.44	0.04	0.78
Units	kg ha^{-1} yr^{-1}	g $tree^{-1}$ yr^{-1}	kg ha^{-1} yr^{-1}	g $tree^{-1}$ yr^{-1}
N_W	6.32	47.20	1.91	40.48
N_L	2.51	18.68	1.44	30.44

DW_w, calculated woody dry weight (kg); C_w, carbon content of woody material; C_L, carbon content of leafy material; N_w, nitrogen content of woody material; N_L, nitrogen content of leafy material

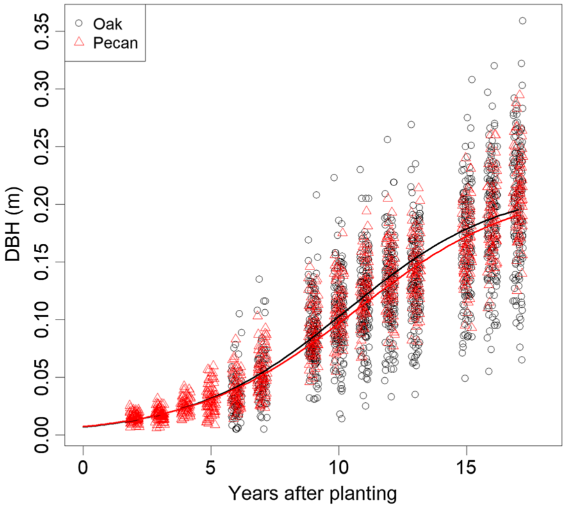

Fig. 3 Scatter plot with years after planting as independent and DBH (m) as dependent variable for oak (black circles) and pecan (red triangles). The lines show the overall (mean) prediction of the oak (black) and pecan (red) three parameter logistic model. (Color figure online)

Table 4 Mean (± SE) parameters (*Asym*, *scal*, and *xmid*) of the 3-parameter logistic mixed effect model with YaP as independent and DBH of oak and pecan as dependent variable

Logistic model parameters	Oak	Pecan
Asym	0.216 ± 0.003**	
Scal	3.18 ± 0.05**	3.02 ± 0.06*
Xmid	10.67 ± 0.10**	10.31 ± 0.15*

Asym, upper asymptote of the model; xmid, time, at which half of the asymptotic DBH is reached; scal, time elapsed between half and ~ ¾ of asymptotic DBH

*$p < 0.05$; **$p < 0.0001$

The total tree stand C_W and N_W rates were lower for pecan, partly due to the lower tree density. Similarly, mean tree C_W and N_W rates were lower, showing that C and N uptake also differed among species. The rates of C and N calculated in this study depend on the log–log models used to substitute DBH with C and N. While the slope of the pecan log–log model was higher (i.e. more C and N per unit DBH), the intercept was lower than that of oak (i.e. subtracting a higher constant from C and N), which eventually led to lower C sequestration and N uptake rates for the studied range of DBH. In contrast, mean tree C_L and N_L rates were higher in pecan, and slope and intercept were slightly higher than in oak. This may reflect pecan tree habitus with lower trunk and total height, as well as lower specific gravity, but more foliage compared to northern red oak (Table 1).

While the northern red oak stand in this study was within the range of previously reported C sequestration rates, pecan rates were lower on a tree stand and individual tree basis. Sharrow and Ismail (2004) found above-ground woody C sequestration rates of 0.9 Mg ha^{-1} yr^{-1} in an 11-year *Pseudotsuga-menziesii*-silvopastoral-system, and Swan et al. (2015) reported woody above-ground biomass C rates of 0.31–1.25 Mg ha^{-1} yr^{-1} for temperate silvopastures.[1] These findings demonstrate how difficult the comparison among AFS and in comparison to natural forests is, even within the subgroup of silvopasture systems. Tree density, tree age, tree and forage species, management, site characteristics, among other factors can influence allometric equations and hence, the rate of C sequestration and N uptake (see "Allometric relationships, C and N concentration" section).

Nutrient analysis in plant tissues is important to estimate nutrient uptake and fertilizer requirements of plants (Sauer et al. 2015). In this study, oak and pecan had N uptake rates of approximately 66 and 71 g N tree^{-1} yr^{-1} for leaves and above ground woody biomass combined (Table 3). Note that we lack information on below-ground biomass and N removal of harvested pecan nuts, hence, N uptake and requirement is higher. The actual fertilizer application is also higher, as only a small portion of applied fertilizer is taken up by pecan (Smith et al. 2007). Also, the amount of N uptake differs over time, as plant growth rates followed a non-linear trend as shown in Figs. 3 and 4.

The mixed effect model showed the magnitude of heterogeneity of growth among individual trees, as all three parameters of the logistic model of best fit were random effects (Table 4). This could be connected to the unequal tree spacing due to natural mortality in the northern red oak stand, which may have led to variable intraspecific competition. In addition, other factors such as soil conditions, nutrients, and soil water content deviated within the tree stand, which influenced tree growth. For example, some trees grew poorly and eventually died due to unfavorable local

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[1] COMET-Planner, see: Silvopasture Establishment on Grazed Grasslands, Conservation Practice Standard 381.

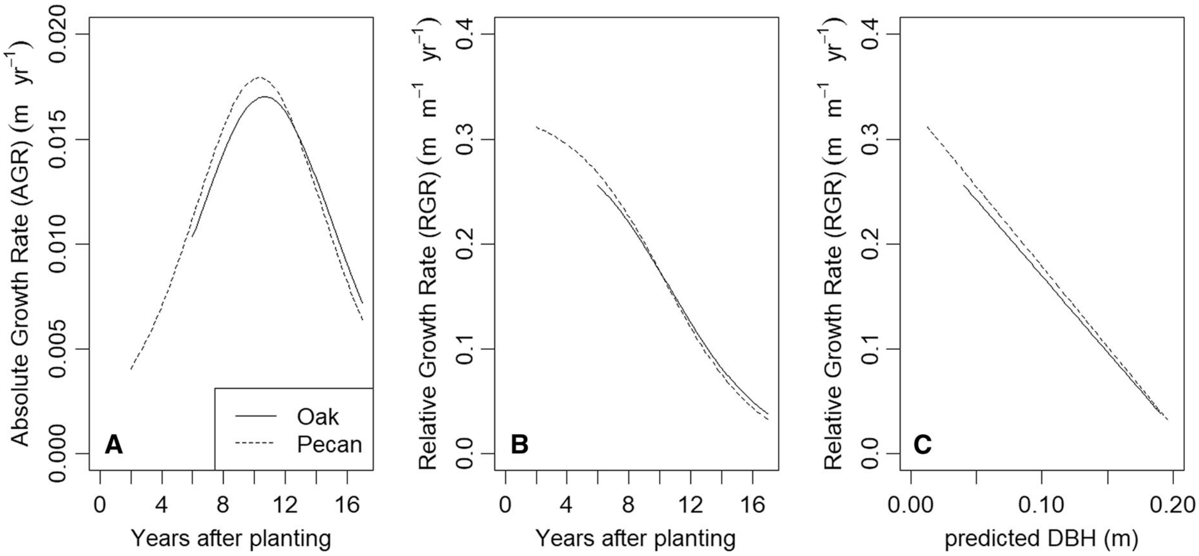

Fig. 4 Relative (RGR) and absolute (AGR) growth rates of DBH plotted against time (**a**, **b**), predicted DBH (**c**) for oak (solid line) and pecan (dashed line)

soil conditions including a high water table, while others exceeded mean tree growth substantially (Fig. 3).

The significantly different parameters *xmid* and *scal* among species showed that the pecan reached half of the asymptotic DBH (*xmid*) significantly faster, and the time elapsed between half and ~ ¾ of DBH asymptote (*scal*) was significantly shorter (Table 4). That resulted in slightly higher AGR and RGR values for pecan (Fig. 4) and may reflect the favorable growth conditions for pecan with wider tree spacing and different soil conditions. Note that the calculation of RGR allows for growth rate comparisons among species within the same reference size (Rees et al. 2010), or when plotted against model predicted mean variables of interest (Paine et al. 2012) to overcome bias of differences of initial size among species. In this study, pecan should have had slightly higher growth rates compared with oak at lower DBH, and similar rates from DBH ~ 0.19 m (Fig. 4c) but may not have differed significantly due to the high heterogeneity of individual trees. The comparison of RGRs could assist in analyzing significant differences among tree species in AFS for their capability to sequester C, or to compare sequestration rates among different AFS management schemes. Note that the applied model cannot predict future growth, but rather explains the non-linear plant growth within the first 17 years after planting.

However, faster DBH growth did not result in higher C_W and N_W uptake, as reflected in the lower C sequestration and N uptake rates of pecan. That is probably connected to the lower specific gravity (i.e. less biomass per volume), and lower trunk and tree height of pecan (Table 1); which demonstrates the limitation of non-destructive growth measurements, as well as the need for estimations of C_w over time to accurately estimate C sequestration. This would require temporal destructive sampling campaigns (Philipson et al. 2012), or chronosequence studies with several sites of known age (Saldarriaga et al. 1988).

While the magnitude of C sequestration and N uptake rate may differ from DBH growth, the overall trend of the calculated AGR and RGR of DBH reinforces the non-linear behavior of tree growth, and hence, C sequestration and N uptake. The reduction of AGR and RGR is connected to changes in plant physiology with tree age, mutual competition, and the growing demand of nutrients for the constantly increasing standing biomass (Rees et al. 2010; Paine et al. 2012). Similar effects may have occurred in this study, where oak trees grew under high self-competing conditions, and pecan reached its reproductive stage. Assuming that C sequestration and N uptake rates of oak and pecan follow similar trends as AGR of DBH, trees in this study would have sequestered C and taken up N at increasingly higher rates during the first ~ 11 YaP, with sequestration and uptake plateauing thereafter. In contrast, the C sequestration and N uptake rate calculated with Eq. (1) represents a constant, "mean" rate. Applying this rate for the beginning or end of a certain growth period may lead to substantial under- or overestimation of sequestered C and N uptake.

Conclusion

In this study, allometric equations and non-linear mixed effect models were applied to analyze C sequestration and N uptake of a silvopastoral system over 17-years. The developed allometric equations are AFS-specific and may be applicable in other silvopastures with similar management, climatic conditions, and DBH range. Yet, the small sample size led to a relatively high RMSE, which should be considered for future use. Non-linear mixed effect models are appropriate to estimate growth rates in AFS and allow for more dynamic predictions compared with linear approaches. The DBH growth rate suggested a non-linear C sequestration and N uptake rate with its predicted peak occurring 11 YaP. Hence, a linear model can lead to substantial over- or underestimation, especially for regional and national estimations, and depending on tree age, species, and density. The calculation of mixed effect model derived relative growth rates also allows for the comparison of C sequestration and N uptake among species. However, that would require biomass estimations over time. Therefore, further long-term research and a re-evaluation of existing data are needed to analyze the non-linear behavior of C sequestration, N uptake, and plant growth in AFS.

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