



Predicting longleaf pine coarse root decomposition in the southeastern US

Peter H. Anderson^{a,*}, Kurt H. Johnsen^b, John R. Butnor^c, Carlos A. Gonzalez-Benecke^d,
Lisa J. Samuelson^e

^a USDA Forest Service, Southern Research Station, 3041 E Cornwallis Rd., Research Triangle Park, NC 27709, USA

^b USDA Forest Service, Southern Research Station, 1577 Brevard Rd, Asheville, NC 28806, USA

^c USDA Forest Service, Southern Research Station, University of Vermont, 81 Carrigan Drive, Aiken Center, Burlington, VT 05405, USA

^d Department of Forest Engineering, Resources and Management, 280 Peavy Hall, Oregon State University, Corvallis, OR 97331, USA

^e School of Forestry and Wildlife Sciences, Auburn University, 3301 SFWS Building, Auburn, AL 36849, USA



ARTICLE INFO

Keywords:

Longleaf pine
Decomposition rate
Carbon
Nitrogen
Coarse root
Loblolly pine

ABSTRACT

Storage of belowground carbon (C) is an important component of total forest C. However, belowground C changes temporally due to forest growth and tree mortality (natural and via harvesting) and these fluctuations are critical for modeling C in forests under varying management regimes. To date, little progress has been made in quantifying the rate of decay of southern pines in general, and specifically in longleaf pine (*Pinus palustris* Mill.) coarse root systems. Decomposition rates of lateral roots and tap roots of longleaf pine were quantified *in situ* under field conditions across the species' range to create a model for necromass loss. The roots of 37 longleaf pine stumps were excavated from Florida, Georgia, Louisiana, and North Carolina. The age of the trees when cut ranged from 14 to 260 years, and the time since cut ranged from 5 to 70 years. Remaining lateral roots to a 1 m depth plus the entire tap root were removed, dried, weighed and analyzed for C and nitrogen (N) content. Total dry necromass of harvested roots ranged from 8 to 195 kg tree⁻¹. Soil C and N content at 15 cm depth were significantly higher near the stump compared to half-way between and adjacent to the nearest living longleaf pine. A regression model was developed to predict necromass loss. The final model included years since cut, stump diameter, and average minimum monthly air temperature as predictors ($R^2 = 0.83$). For example, a 100-year-old tree would have a predicted root decomposition rate (k) of -0.120 for lateral roots and -0.038 per year for tap roots. Results suggest that longleaf pine coarse roots persist in the environment longer than the tap roots of loblolly pine.

1. Introduction

Interest in ecosystem productivity and carbon (C) sequestration has led to accounting approaches to calculate the amount of biomass and C in longleaf pine (*Pinus palustris* Mill.) and other forest systems (Samuelson et al., 2014). Storage of belowground C in root biomass is an important but difficult to estimate component of total forest C (Radtke et al., 2009). Following tree mortality or harvest, C in root necromass can persist for many years, with decay rates dependent on species, wood chemistry, and climate (Schimel et al., 2001, Silver and Miya, 2001). Coarse root systems may require decades to decompose (Eberhardt et al., 2009, Weedon et al., 2009, Mobley et al., 2012, Palviainen and Finér, 2015). For example, in 10 to 60-year-old loblolly pine (*Pinus taeda* L.) planted in central North Carolina, 50% of the coarse root system decayed within the first 10 years (Ludovici et al., 2002). However, rapid rates of coarse root decomposition (80% in

10 years) were associated with wetter sites in a Monterey pine (*Pinus radiata* D. Don) plantation in New Zealand (Garrett et al., 2008).

Although not a long-term pool of C, root necromass can provide a short to medium term storage pool. Soil C content in the vicinity of old tap roots can stay elevated for at least 50 years (Ludovici et al., 2002, Garrett et al., 2008, Palviainen et al., 2010). Sucre and Fox (2009) found that soil associated with decomposing stumps was 1.2% of total soil volume but accounted for 10% of total soil C in a mature hardwood forest. Wang et al. (2012) determined that after 10 years, decomposing coarse roots of loblolly pine to a 1 m depth represented 13% of belowground C. In middle latitudes, decomposition of coarse roots is more dependent on temperature than decomposition rates of fine roots (Zhang and Wang, 2015). Decomposition of tap roots can be slowed by the buffering of temperature, decreased aeration, and lower population densities of decomposing organisms at depth in the soil profile (Richter and Markewitz, 2001). Decaying root systems play an important role in

* Corresponding author.

E-mail addresses: phanderson@fs.fed.us (P.H. Anderson), kjohnsen@fs.fed.us (K.H. Johnsen), jbutnor@fs.fed.us (J.R. Butnor), carlos.gonzalez@oregonstate.edu (C.A. Gonzalez-Benecke), samuelj@auburn.edu (L.J. Samuelson).

<https://doi.org/10.1016/j.foreco.2018.05.024>

Received 14 December 2017; Received in revised form 8 May 2018; Accepted 12 May 2018

Available online 26 May 2018

0378-1127/ Published by Elsevier B.V.

soil nutrient dynamics, C cycling, and thus forest productivity (Jurgensen et al., 1997; Clemmensen et al., 2013). Lower soil bulk density and the presence of macropores associated with decaying stumps provide a matrix for live root proliferation (Angers and Caron, 1998).

This research was part of a larger study that developed C sequestration models for longleaf pine plantations and natural stands (Gonzalez-Benecke et al., 2015) to help guide forest C management across the southeastern U.S. (Samuelson et al., 2014, 2017). Tap roots of old longleaf pine have been observed to last intact for many decades, showing little visual evidence of decay and are harvested as a source of quality kindling commonly called “fatwood” or “lighter wood”. Despite the general acceptance that dead longleaf pine tap roots can persist for decades, there is no quantitative data available for C sequestration models. An average root:shoot mass ratio of 0.43 was reported for longleaf pine trees older than 50 years of age (Samuelson et al., 2017), which is higher than many other conifers (Levy et al., 2004). Greater relative C allocation to roots in longleaf pine may lead to a larger live and dead belowground C pool compared to other species. Therefore, our objectives were to: (1) quantify C storage in decaying longleaf pine roots across a range of tree ages at time of harvest and times since harvest, and (2) develop a predictive model for longleaf pine coarse root decomposition that can be incorporated into C sequestration models. We hypothesized that coarse roots of longleaf pine decay at a slower rate than decay rates reported for other southern pines.

2. Materials and methods

2.1. Study sites

Based on access and degree of documentation of stand age and years since tree harvest, 11 locations were selected across the east–west range of the longleaf pine, from Louisiana to North Carolina (Fig. 1). Stump location, age of the tree when cut (Age), and years since cut (YSC) were determined with the help of on-site land managers and land use records. Stumps selected for this study were from trees cut either for production harvest or research. Those that died naturally (i.e. not cut) were not selected. A total of 37 stumps were identified and excavated (Fig. 1). Age ranged from 14 to 260 years and YSC ranged from 5 to

70 years (Table 1). Average minimum monthly air temperature value (T_{min}) was assigned to each site using the USDA Plant Hardiness Zone map (PHZ) (Table 1).

2.2. Stump collection

After identifying stumps, underbrush and leaf litter were removed from the soil surface. A square pit 1 m from the stump edge was then laid out. The area of these pits ranged from 4.7 to 6.8 m², depending on stump diameter. For stumps decayed at the ground line, the remaining bark ring was used to estimate the diameter of the stump (DS). Remaining lateral roots were hand excavated and sorted by depth (0–10, 10–20, 20–30, 30–50, and 50–100 cm). Soil from the pit was sifted through a 6 mm screen. Few lateral roots were found below 30 cm. A small backhoe was used to loosen soil and remove the tap root. Tap roots were taken to the laboratory, cleaned, and cut at ground level and by depth (0–10, 10–20, 20–30, 30–50, 50–100 cm and every 50 cm below 100 cm). All woody components were dried at 65 °C to a constant mass and weighed. Samples were then ground using a wood chipper. Subsamples were taken from the chipped material and ground using a Wiley mill. Wood C and nitrogen (N) concentrations were determined by dry combustion with detection by thermal conductivity (Flash EA 1112 series CN analyzer, Thermo Finnigan Instruments, Milan, Italy). To correct for mineral soil contamination, loss on ignition was measured on all samples.

2.3. Total soil C, N, and bulk density

To characterize spatial variation in soil C and N contents and soil bulk density proximal to stumps and residual live trees, two linear transects 90° apart were run from each stump to the nearest live trees. In plantations, the transect distance was consistent, but in older, naturally regenerated stands, the distance was variable. Prior to excavation, two samples were taken at a distance 0.5 m from the stump. Two samples were also taken 0.5 m from the nearest live tree and another two from the mid-point between the stump and the nearest living tree. Samples for determination of soil C and N, concentration and soil bulk density were collected at five depths (0–10, 10–20, 20–30, 30–50, 50–100 cm). Soil was air-dried to a constant mass and passed through a

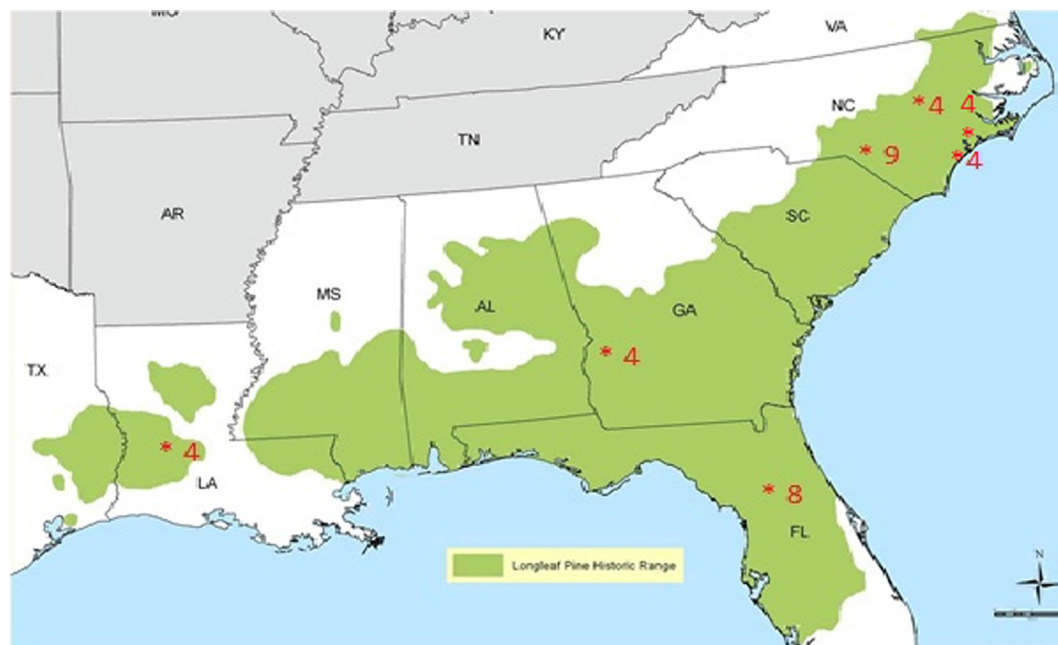


Fig. 1. Map of longleaf pine range in the southeastern US (<http://www.fws.gov/news/blog/images/range500.gif>). Asterisks represent sites where tap roots were removed and the number removed from each site.

Table 1

Site and sampling descriptions for excavated longleaf pine tap roots including the age of the tree when cut (AGE), years since cut (YSC), USDA plant hardiness zone (PHZ), and average monthly minimum temperature (T_{\min} , °C) as per PHZ.

Site	State	Latitude/Longitude	# of Tap roots	AGE	YSC	PHZ	T_{\min}
Camp Lejeune	NC	34.700/–77.301	4	61	18	8A	13.5
Croatian NF	NC	34.708/–77.028	4	52	29	8A	14.1
Duke Forest	NC	36.025/–78.990	2	64	10	7B	7.7
Duke Forest	NC	36.025/–78.990	2	54	20	7B	7.7
Fort Benning	GA	32.389/–89.793	4	14	7	8A	14.4
Kisatchie NF	LA	31.182/–92.743	4	61	15	8B	18.3
Sandhills Gamelands	NC	35.113/–79.667	4	65	14	8A	10.6
Sandhills Gamelands	NC	35.102/–79.665	4	45	30	8A	10.6
Sandhills Gamelands	NC	34.915/–79.578	1	260	70	8A	10.3
University of Florida	FL	29.742/–82.219	4	75	5	9A	20.9
University of Florida	FL	29.742/–82.222	4	65	15	9A	20.9

2 mm sieve to remove roots and rocks. Percent soil C and N concentrations were determined by dry combustion with detection by thermal conductivity as described previously. Soil bulk density samples were collected using a 5.7 cm diameter soil core. Total soil C and N contents (kg ha^{-1}) were calculated as the product of percent concentration and soil bulk density.

2.4. Modeling and statistics

To estimate root decay rate as a function of YSC, we used an equation developed for lodgepole pine (*Pinus contorta* Dougl. ex Loud.) described by Yavitt and Fahey (1982):

$$RW_t = RW_i \cdot \exp(-k \cdot YSC) + \varepsilon_1 \quad (1)$$

where RW_t is the root mass remaining at time t , RW_i is the initial root mass, k is the decomposition rate (year^{-1}), and ε_1 is the error term, with $\varepsilon_1 \sim N(0, s_1^2)$. The model assumes that decomposition is proportional to the amount of mass remaining, and remaining root mass could be predicted only as a function of YSC. Since xylem structure changes as trees mature, k may also depend on tree age. Therefore, we modified the equation so that k was a linear function of tree age ($k = a_1 + a_2 \cdot \text{AGE}$):

$$RW_t = RW_i \cdot \exp((a_1 + a_2 \cdot \text{AGE}) \cdot YSC) + \varepsilon_2 \quad (2)$$

where a_1 and a_2 are fit parameters, and ε_2 is the error term, with $\varepsilon_2 \sim N(0, s_2^2)$. Separate mass models were fit to the lateral root wood (LR), tap root wood (TR), and total coarse roots (CR, lateral + tap).

Initial LR and TR mass (kg) were determined for each tree using the functions reported by Samuelson et al. (2017) for longleaf pine, and CR was determined as sum of predicted LR and TR biomass. As the equations reported in Samuelson et al. (2017) used diameter at breast height (DBH) as predictor, DBH was determined from DS to DBH function fitted using data collected by Samuelson et al. (2014). The 22 sample trees ranged in Age, DS (measured at 20 cm height) and DBH (measured at 137 cm height) from 12 to 87 years, 4.7 to 66.1 cm, and 2.9 to 48.6 cm, respectively. The final model was: $\text{DBH} = 0.1233 + 0.6959 \cdot \text{DS}$ ($p < 0.001$; $R^2 = 0.98$).

Necromass loss, and root C and N contents were estimated as follow:

$$RW_t = \exp(b_1 + b_2 \cdot YSC) + \varepsilon_3 \quad (3)$$

where b_1 and b_2 are fit parameters, and ε_3 is the error term, with $\varepsilon_3 \sim N(0, s_3^2)$. In addition to YSC, other variables were included as covariates in the above model to improve the mass loss equation. The variables considered included AGE, DS and T_{\min} . To determine which variables should be included in the final model, all variables were first log transformed then a stepwise procedure was used with a threshold significance value of 0.15 as the variable selection criteria. The variance inflation factor (VIF) was monitored to detect multicollinearity between explanatory variables. All variables included in the model with VIF larger than 5 were discarded, as suggested by Neter et al. (1996). The

logarithm transformation was preferred as it allows for control of heterogeneity of variances, approximates normality, and uses the linear model framework to select the variables.

Explanatory variable selection and model fitting were performed using Proc Reg. Parameter estimates for intercepts in equations for remaining necromass and root C and N contents (b_1 , c_1 and d_1) include the correction proposed by Snowdon (1991) for logarithm transformation of the response variable. For the root decay rate, model fitting was performed using Proc Nlin. Three measures of accuracy were used to evaluate the goodness-of-fit between observed and predicted values for each variable based on the model evaluation dataset: (i) root mean square error (RMSE); (ii) mean bias error (Bias); and (iii) coefficient of determination (R^2). The residuals were examined by plotting them over the predicted and dependent variables for each model.

Position differences in soil C and N contents by soil depth were analyzed using Proc Mixed. Means separation by position was performed by the Tukey's procedure. All model fitting and statistical analyses were performed using SAS 9.3 (SAS Inc., Cary, NC, USA).

We compared predictions of remaining necromass over time for longleaf and loblolly pine. Our model was used for longleaf pine and a model developed by Ludovici et al. (2002) was used for loblolly pine. The model developed for loblolly pine included DS and YSC as predictive variables. Although these are not direct species comparisons, we set the parameters for the longleaf pine model to match the PHZ for the location of the loblolly pine trees sampled in Ludovici et al. (2002) (Duke University Forest, Durham, NC) and set the initial tree size to 60 cm in both models. In the simulation, tree age was 50 years at time of cut, the necromass of the tap root was set to 80% and lateral necromass was set to 20%.

3. Results

3.1. Root necromass, C and N

Mean tap root and lateral necromass decreased with soil depth at each site. Tap root length ranged from 60 to 340 cm in the 14 and 61 year-old trees, respectively. Lateral root necromass ranged from 0 to 66% of total necromass with a mean of 19.2%. Lateral root necromass ranged from 0 to 68.1 kg tree^{-1} while tap root necromass ranged from 8.6 to 125.2 kg tree^{-1} . A summary of lateral, tap and coarse root necromass is shown in Table 2. Total root C concentration ranged from 42.5 to 57.8% with a mean of 53.2% (data not shown). Total root N concentration ranged from 0.05 to 0.27% with a mean of 0.11% (data not shown).

3.2. Soil C, N, contents and soil bulk density

Total soil C content at the stump was significantly greater ($p < 0.05$) than at the middle of the transect at 10–20 and 20–30 cm depths (Fig. 2A). Soil C content at the stump was also significantly

Table 2
Number of taproots excavated (N), average stump diameter (DS, cm), diameter at breast height (DBH, cm), and necromass of the lateral (LR_M; kg tree⁻¹), tap (TR_M; kg tree⁻¹) and coarse (CR_M, tap + laterals; kg tree⁻¹) roots at each sampling site. Mean of necromass is followed by standard error.

Site	State	N	AGE	DS	DBH ^a	LR _M	TR _M	CR _M
Camp Lejeune	NC	4	61	42.8	29.5	3.8 (1.3)	50.5 (10.1)	54.3 (11.3)
Croatan NF	NC	4	52	53.8	37.1	9.7 (2.7)	41.8 (5.6)	51.5 (8.1)
Duke Forest	NC	2	64	55.0	37.9	5.4 (3.5)	41.1 (4.8)	46.5 (8.3)
Duke Forest	NC	2	54	44.3	30.5	0.0	14.7 (2.3)	14.7 (2.3)
Fort Benning	GA	4	14	20.3	14.0	0.0	11.8 (1.9)	11.8 (1.9)
Kisatchie NF	LA	4	61	63.0	43.4	35.1 (13.9)	134.3 (17.1)	169.4 (12.5)
Sandhills Gamelands	NC	4	65	53.0	36.6	25.4 (10.0)	60.6 (18.7)	86.0 (26.1)
Sandhills Gamelands	NC	4	45	48.2	33.2	1.0 (0.8)	38.3 (19.6)	39.3 (19.0)
Sandhills Gamelands	NC	1	260	65.5	45.2	6.9	38.8	45.7
University of Florida	FL	4	75	43.0	33.6	37.1 (17.1)	94.0 (21.2)	131.1 (34.6)
University of Florida	FL	4	65	44.3	30.5	14.0 (5.3)	49.7 (6.1)	63.7 (11.1)

^a DBH was estimated using a DS-DBH function (Samuelson et al., 2014).

greater than at the live tree at the 10–20 cm depth (Fig. 2A). There was no significant difference in soil C content between the midpoint location and the live tree at any depth (Fig. 2A). Total soil N content at the 10–20 cm depth was significantly higher adjacent to stumps than at the midpoint position or at the live tree (Fig. 2B). Soil bulk density at the 0–10 cm depth was significantly ($p < 0.05$) higher at the middle of the transect than at the stump or at the live tree (Fig. 2C). At the 10–20 cm

depth, soil bulk density was higher in the middle of the tree position ($p < 0.05$) relative to soil bulk density at the stump (Fig. 2C).

3.3. Model fitting

Model parameter estimates for functions to estimate the proportion of initial coarse root (tap + lateral) mass remaining after YSC (CR_{prop}),

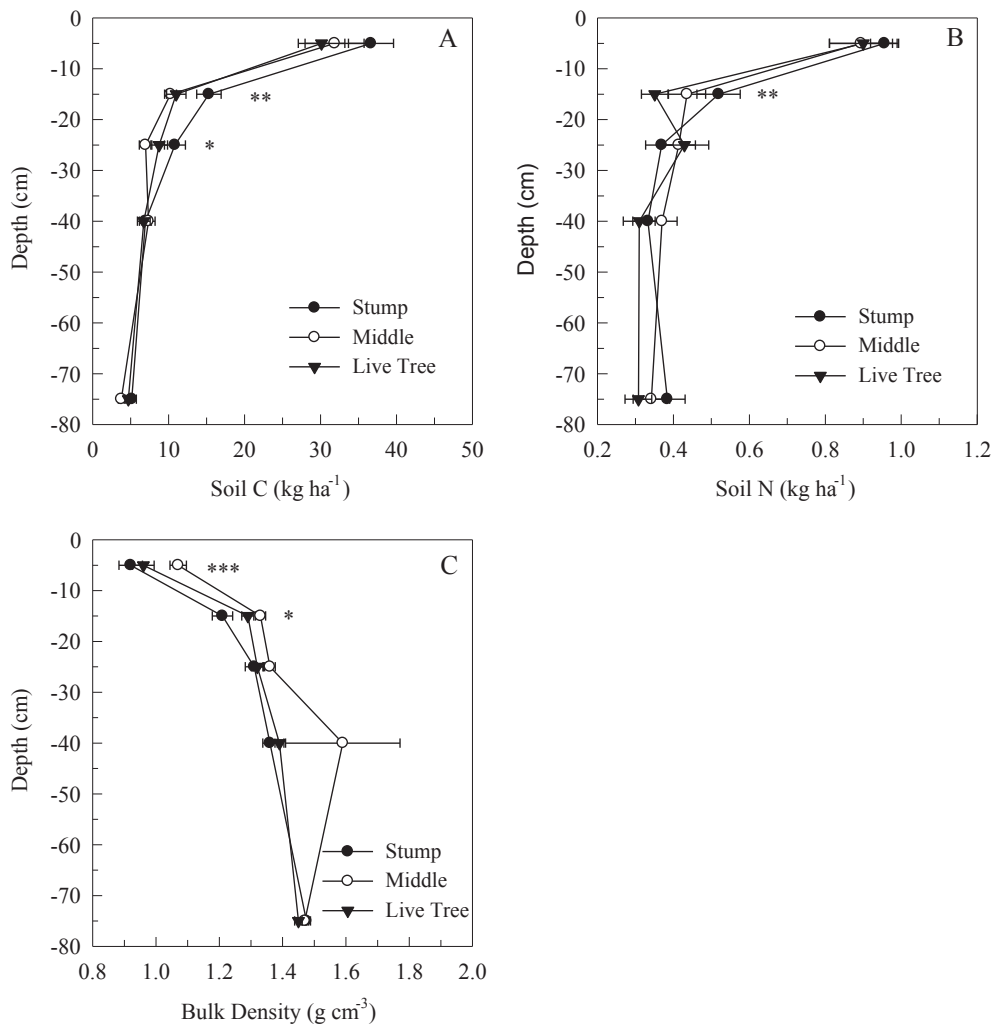


Fig. 2. Mean soil carbon content (A), nitrogen content (B), and soil bulk density (C) by depth and position along transects between the longleaf pine stump and nearest live tree. Soil samples were taken 0.5 m from the stump and live tree. The middle position was halfway between the stump and nearest live tree. * Represents a significant ($p < 0.05$) difference between the stump and middle position. ** Represents a significant ($p < 0.05$) difference between the stump and live tree. *** Represents a significant ($p < 0.05$) difference between the middle and stump and live tree positions.

Table 3

Parameter estimates and fit statistics of the selected functions to estimate decay rate for and predict remaining root necromass of longleaf pine coarse roots. Notation: CR_{Prop} is the proportion of initial coarse root (tap + lateral) mass remaining after years since cut (YSC); CR_M is the necromass of the coarse roots (tap + lateral; kg) after YSC; CR_C is the remaining carbon content of the coarse roots (tap + lateral; kg) after YSC; CR_N is the nitrogen content of the remaining coarse roots (tap + lateral; kg) after YSC; AGE is age when tree was cut (years); DS is stump diameter over bark (cm); T_{min} is average minimum monthly temperature of plant hardiness zone (°C).

Variable	Model	Parameter	Parameter Estimate	SE	R ²	Partial-R ²	RMSE	CV%
CR_{Prop}	$= \exp^{(k + a2 \cdot AGE) \cdot YSC}$	k	−0.0578	0.00615	0.897		0.167	35.2
		a_2	0.00013	0.00005				
CR_M	$= \exp^{(b1 + b2 \cdot \ln(YSC) + b3 \cdot \ln(DS) + b4 \cdot \ln(T_{min}))}$	b_1	−7.20281	0.82537	0.864		0.361	9.3
		b_2	−0.45562	0.11540		0.0650		
		b_3	2.39777	0.20848		0.521		
		b_4	1.21002	0.19977		0.278		
CR_C	$= \exp^{(c1 + c2 \cdot \ln(YSC) + c3 \cdot \ln(DS) + c4 \cdot \ln(T_{min}))}$	c_1	−8.19983	0.80458	0.884		0.344	10.5
		c_2	−0.48931	0.11030		0.072		
		c_3	2.59934	0.19913		0.595		
		c_4	1.09425	0.20103		0.217		
CR_N	$= \exp^{(d1 + d2 \cdot \ln(YSC) + d3 \cdot \ln(DS))}$	d_1	−8.12023	0.98222	0.562		0.525	16.8
		d_2	−0.75289	0.15555		0.311		
		d_3	1.84877	0.29651		0.251		

SE: standard error, R²: coefficient of determination, RMSE: root mean square error, CV%: coefficient of variation as percent (100·RMSE/mean). For all parameter estimates: $P < 0.05$.

Table 4

Parameter estimates and fit statistics of the selected functions to estimate decay rate for and predict remaining lateral root necromass of longleaf pine lateral roots. Notation: LR_{Prop} is the proportion of initial lateral roots mass remaining in the years since cut (TSC); LR_M is the necromass of the lateral roots (kg) after YSC; LR_C is the remaining carbon content of the lateral roots (kg) after YSC; LR_N is the nitrogen content of the remaining lateral roots (kg) after YSC; Age is age when tree was cut (years); DS is stump diameter over bark (cm); T_{min} is average minimum temperature of plant hardiness zone (°C).

Variable	Model	Parameter	Parameter Estimate	SE	R ²	Partial-R ²	RMSE	CV%
LR_{Prop}	$= \exp^{((k + a2 \cdot AGE) \cdot YSC)}$	k	−0.1197	0.02260	0.45		0.314	47.4
		a_2	0.000366	0.00012				
LR_M	$= \exp^{(b1 + b2 \cdot \ln(YSC) + b3 \cdot \ln(DS) + b4 \cdot \ln(T_{min}))}$	b_1	−18.35247	3.54689	0.640		1.388	37.4
		b_2	−0.70000	0.26265		0.0980		
		b_3	4.53677	0.77900		0.247		
		b_4	1.75683	0.53065		0.295		
LR_C	$= \exp^{(c1 + c2 \cdot \ln(YSC) + c3 \cdot \ln(DS) + c4 \cdot \ln(T_{min}))}$	c_1	−18.96912	3.39184	0.661		0.880	50.8
		c_2	−0.69692	0.25117		0.100		
		c_3	4.50188	0.74495		0.247		
		c_4	1.79640	0.50746		0.314		
LR_N	$= \exp^{(d1 + d2 \cdot \ln(YSC) + d3 \cdot \ln(DS))}$	d_1	−17.06214	3.84098	0.445		1.813	23.7
		d_2	−1.23034	0.32889		0.288		
		d_3	4.06652	1.03927		0.158		

SE: standard error, R²: coefficient of determination, RMSE: root mean square error, CV%: coefficient of variation as percent (100·RMSE/mean). For all parameter estimates: $P < 0.05$.

Table 5

Parameter estimates and fit statistics of the selected functions to estimate decay rate for and predict remaining tap root necromass of longleaf pine tap roots. Notation: TR_{Prop} is the proportion of initial tap root mass remaining after years since cut (YSC); TR_M is the necromass of the tap roots (kg) after YSC; TR_C is the remaining carbon content of the tap roots after YSC (kg); TR_N is the nitrogen content of the remaining coarse roots (kg) after YSC; Age is age when tree was cut (years); DS is stump diameter over bark (cm); T_{min} is average minimum temperature of plant hardiness zone (°C).

Variable	Model	Parameter	Parameter Estimate	SE	R ²	Partial R ²	RMSE	CV%
TR_{Prop}	$= \exp^{(k \cdot YSC)}$	k	−0.0376	0.00556	0.834		0.270	56.9
		a_2	−5.80205	0.86935	0.807		1.074	10.2
TR_M	$= \exp^{(b1 + b2 \cdot \ln(YSC) + b3 \cdot \ln(DS) + b4 \cdot \ln(T_{min}))}$	b_1	−0.37384	0.12155		0.055		
		b_2	2.03429	0.21959		0.486		
		b_3	1.05985	0.21042		0.266		
		b_4	1.05985	0.21042		0.266		
TR_C	$= \exp^{(c1 + c2 \cdot \ln(YSC) + c3 \cdot \ln(DS) + c4 \cdot \ln(T_{min}))}$	c_1	−8.19983	0.80458	0.883		0.344	10.5
		c_2	−0.48931	0.11030		0.072		
		c_3	2.59934	0.19913		0.595		
		c_4	1.09425	0.20103		0.217		
TR_N	$= \exp^{(d1 + d2 \cdot \ln(YSC) + d3 \cdot \ln(DS))}$	d_1	−6.42584	0.9257	0.385		1.130	14.6
		d_2	−0.53357	0.1466		0.247		
		d_3	1.17716	0.27945		0.138		

SE: standard error, R²: coefficient of determination, RMSE: root mean square error, CV%: coefficient of variation as percent (100·RMSE/mean). For all parameter estimates: $P < 0.05$.

and remaining necromass and C and N content for roots of longleaf pine trees are reported in Tables 3–5. CR_{prop} slightly decreased as trees aged (Table 3). For example, for a 10-year-old tree, CR_{prop} was -0.057 year^{-1} , while for a 100-year-old tree, CR_{prop} was -0.045 year^{-1} . The necromass of CR after harvest (CR_M) depended on YSC, DS, and T_{min} . The final model explained 86% of CR_M variability. The amount of CR_M was mainly controlled by DS (partial $R^2 = 0.52$) followed by T_{min} (partial $R^2 = 0.28$) and YSC (partial $R^2 = 0.06$). The amount of C content remaining after harvest (CR_C) also depended on YSC, DS, and T_{min} . CR_C was mostly explained by DS (partial $R^2 = 0.60$) and to a lesser extent T_{min} (partial $R^2 = 0.22$) and YSC (partial $R^2 = 0.07$). The amount of N content remaining after harvest (CR_N) was related only to DS and YSC. CR_N was mostly explained by YSC (partial $R^2 = 0.31$) and DS (partial $R^2 = 0.25$). Scatter plots of residuals showed no evidence of bias for any of the final models.

The proportion of lateral root remaining after YSC (LR_{prop}) decay rate slightly decreased as trees aged (Table 4). For example, for a 10-year-old tree, the $LR_{prop} = -0.120 \text{ year}^{-1}$, while for a 100-year-old tree, the $LR_{prop} = -0.083 \text{ year}^{-1}$. Similar to CR_M , LR_M depended on YSC, DS, and T_{min} (Table 4). The final model explained 64% of LR_M variability. The amount of LR_M was mainly controlled by T_{min} (partial $R^2 = 0.30$) and DS (partial $R^2 = 0.25$) followed by YSC (partial $R^2 = 0.10$). Similar to LR_M , LR_C also depended on YSC, DS, and T_{min} . Variability in LR_C was mostly explained by T_{min} (partial $R^2 = 0.31$) and DS (partial $R^2 = 0.25$) and to a lesser extent YSC (partial $R^2 = 0.10$). Also similar to CR_N , LR_N depended only on DS and YSC (Table 4). LR_N was mostly explained by YSC (partial $R^2 = 0.29$) followed by DS (partial $R^2 = 0.16$). Scatter plots of residuals showed no evidence of bias for any of the final models selected.

The proportion of tap root remaining after YSC (TR_{prop}) decay rate k was not affected by tree age. The tap root k was -0.038 year^{-1} (Table 5). Similar to CR_M and LR_M , TR_M depended on YSC, DS, and T_{min} . The model selected explained 81% of TR_M variability. The amount of TR_M was mainly controlled by DS (partial $R^2 = 0.49$) followed by T_{min} (partial $R^2 = 0.27$) and in a lesser extent by YSC (partial $R^2 = 0.06$). Also similar to CR_C and LR_C , TR_C depended on YSC, DS, and T_{min} . TR_C was mostly explained by DS (partial $R^2 = 0.59$) and T_{min} (partial $R^2 = 0.22$) and to a lesser extent YSC (partial $R^2 = 0.07$). Also similar to CR_N and LR_N , TR_N depended only on DS and YSC. TR_N was mostly explained by YSC (partial $R^2 = 0.25$) followed by DS (partial $R^2 = 0.14$). Scatter plots of residuals showed no evidence of bias for any of the final models (data not shown).

When comparing predictions of remaining necromass over time for longleaf pine (using the model reported in this study) and for loblolly pine (using the model developed by Ludovici et al., 2002), we observed that even though both the longleaf pine and loblolly pine model simulations show similar decay rates in the early years following cutting (at 10 years, 59% remained for longleaf pine and 64% remained for loblolly pine), the longleaf pine model indicated that the longleaf pine tap root persisted in the environment longer than the loblolly pine tap root. After 60 years, 30% of the tap root necromass of longleaf pine remained compared to 5% remaining in loblolly pine. One hundred years after cutting, the model predicted that 25% of longleaf tap root necromass remained (Fig. 3).

4. Discussion

Belowground dead wood is an important component of total forest C. As an example, Petersson and Merlin (2010) suggested that five times more C was stored in stump dead wood than in aboveground dead wood in forests in Sweden. Wang et al. (2012) estimated that decaying roots of loblolly-shortleaf pine forests harvested between 1995 and 2005 in South Carolina stored 7.1 Tg C. However, most forest C assessments do not consider C in decomposing roots, because of the paucity of data on coarse root decay and variability in reported decay rates among species and climates. For instance, in Australia, 20% of Monterey pine coarse

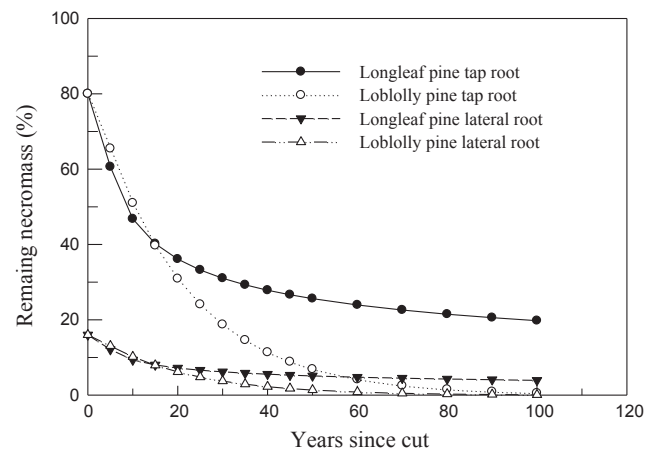


Fig. 3. Predicted necromass by years since cut for tap root and lateral components for a longleaf pine tree simulated using equations developed in this work and for a loblolly pine tree using a predictive equation from Ludovici et al. (2002). Age = 50 years and stump diameter = 60 times of cut.

root biomass remained 25 years after harvest whereas 80% of cypress pine (*Callitris glaucophylla* J. Thomp and L. Johnson) root biomass remained after 50 years (Ximenes and Gardner, 2006). In Norway, a study of stump decomposition at ground level reported k of -0.048 and -0.052 year^{-1} for Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.), respectively (Shorohova et al., 2008). Based on a $k = -0.046 \text{ year}^{-1}$, Melin et al. (2009) predicted the time required for the loss of 50% and 95% of the coarse root wood of Norway spruce in Sweden was 15 and 64 years, respectively. In Wyoming, Yavitt and Fahey (1982) reported a $k = -0.051 \text{ year}^{-1}$ for roots with a diameter of 2–5 cm for lodgepole pine (*Pinus contorta* Dougl. ex Loud.) seven years after harvest.

In the southern United States, Ludovici et al. (2002) examined the decay rate of loblolly pine and found a necromass loss of 50% after 10 years and that less than 5% of coarse root necromass persisted 60 years after harvest. Wang et al. (2012) estimated that 35% of root necromass of loblolly pine trees in South Carolina remained 10 years after harvest and 12% remained after 20 years. Our total coarse root model (lateral + tap root, $k = -0.058 \text{ year}^{-1}$) predicted 54% of longleaf pine necromass remaining after 10 years and 17% present after 60 years. When the total necromass model was separated by component, we found that there was a rapid decrease in lateral root necromass ($k = -0.120 \text{ year}^{-1}$). In 10 years, 26% of lateral root remained and after 60 years only 8% remained. The tap root had a much lower decomposition rate ($k = -0.038 \text{ year}^{-1}$) than lateral roots and constituted the majority (80%) of initial necromass. Simulations of root necromass of longleaf pine compared to loblolly pine indicated that the tap root of longleaf pine persisted in the environment longer as the longleaf pine tap root decomposed more slowly than the rate for loblolly pine. Therefore, necromass could be a significant contributor to C sequestration in longleaf pine forests, particularly given the high total root:shoot ratio reported for longleaf pine (Samuelson et al., 2017) as well as the tap root data as described in our study.

It is generally thought that conifer coarse roots have slow decomposition rates and therefore are a potential sink for C and N storage (Silver and Miya, 2001). Chen et al. (2001) found that western U.S. conifer species with resin ducts present in coarse roots. (Douglas-fir, *Pseudotsuga menziesii* (Merb.) Franco) had lower decomposition rates compared to species where resin ducts were absent (ponderosa pine, *Pinus ponderosa* (P. Laws ex C Laws)). Longleaf pine root systems are thought to be more resistant to decay than other tree species. Longleaf pine has been historically valued for its turpentine production (Gardner, 1989). As turpentine evaporates in root systems, a physical barrier is created hindering access from foraging insects such as

termites (Phillips and Croteau, 1999). However, turpentine is only a small component of a range of compounds collectively termed oleoresins that are produced by longleaf pine and other conifers (Vikström et al., 2005; Eberhardt et al., 2009). Components of oleoresin have been shown to increase wood's resistance to microbial decay and insect infestation (Hart and Shrimpton, 1979; Klepzig et al., 1996; Nerg et al., 2004; Eberhardt et al., 2009). Eberhardt et al. (2009) showed that monoterpenes persist for long periods in heartwood and sapwood of longleaf pine tap roots.

Decomposing root systems provide many benefits to forests including carbon sequestration as well as a favorable soil matrix for live root development, because of decreased soil bulk density and increased water and nutrient availability adjacent to the stumps. Loblolly pine trees growing in natural stands in close proximity to old stumps showed an increase in productivity of 28% compared to trees growing farther from old stumps (Van Lear et al., 2000) presumably due to decreased soil bulk density near the stump ("relic root channels") where live trees root systems could better infiltrate. In the present study, live roots were observed growing in relic root channels, but we did not quantify the extent of live root occupation in root channels. In the soil surrounding decomposing stumps in a naturally regenerated loblolly pine stand in South Carolina, increases in soil N and soil C contents and increased live root density were found 16 years following tree cutting (Van Lear et al., 2000). Increased soil N and soil C contents were found in proximity to stumps in 100-year-old mixed oak/maple stands in the Appalachians of Virginia (Sucre and Fox, 2009). In our study, soil N content at the 10–20 depth was 16% higher adjacent to the stump compared to the midpoint location between the stump and nearest tree, indicating that decaying stumps may improve soil fertility. Soil C content was 32% higher at the stump compared to mid-point at the 10–20 depth and 35% higher at the stump than the mid-point position at the 20–30 cm depth. At the 0–20 cm depth, soil bulk density was highest at the mid-point compared to the stump which affected the total soil C and N content values. Thus, higher soil C content associated with the area surrounding stumps also has implications for soil C sequestration; not only is C stored within the decaying stump but decaying stumps also contribute C to the surrounding soil matrix.

5. Conclusions

The decay models developed by this work provide new tools to estimate longleaf pine coarse root necromass and C storage in decomposing roots in longleaf pine forests across the species' range. Our results demonstrate that the persistence of longleaf pine coarse root necromass makes decaying tap roots an important contribution to C sequestration in longleaf pine forests. For instance, C sequestered in residual longleaf pine tap roots from previous harvests or mortality may account for majority of C stocks in young stands (Samuelson et al., 2014). In addition, lower soil bulk density adjacent to the stumps provides a potential conduit for root infiltration. Increased soil C and N contents near stumps may enhance long term soil productivity. As hypothesized, tap root decomposition rates were lower than reported for loblolly pine, at least on one site, indicating that tap root necromass is more important to long-term forest C sequestration in longleaf pine forests than in loblolly pine forests. Further research with loblolly pine might further support our observation.

Acknowledgements

This research was supported wholly (or in part) by the US Department of Defense through the Strategic Environmental Research and Development Program (SERDP). The authors wish to thank Jason Jackson, Shelly Hooke, Robert Eaton, Tom Christensen, Joel Burley, Lance Kress, and Karen Sarsony for assistance in sample collection, preparation, and analysis. We would also like to thank Brian Waldrep from Fort Benning, Land Management Division, Lyn McDonald, USDA

Forest Service, Kisatchie National Forest Calcasieu Ranger District, the North Carolina Wildlife Resources Commission, the staff of the Austin Cary Forest, Doug French, USDA Forest Service Croatan National Forest, Susan Cohen, and Austin Powell from Camp Lejeune, Forest Management Program for their assistance.

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