Trees (2006) 20: 176–185
DOI 10.1007/s00468-005-0024-4

ORIGINAL ARTICLE

Timothy J. Albaugh · H. Lee Allen · Lance W. Kress

Root and stem partitioning of *Pinus taeda*

Received: 7 February 2005 / Accepted: 8 August 2005 / Published online: 2 December 2005
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Abstract We measured root and stem mass at three sites (Piedmont (P), Coastal Plain (C), and Sandhills (S)) in the southeastern United States. Stand density, soil texture and drainage, genetic makeup and environmental conditions varied with site while differences in tree size at each site were induced with fertilizer additions. Across sites, root mass was about one half of stem mass when estimated on a per hectare basis. Stem mass per hectare explained 91% of the variation in root mass per hectare, while mean tree diameter at breast height (*D*), site, and site by measurement year were significant variables explaining an additional 6% of the variation in root mass per hectare. At the S site, the root:stem ratio decreased from 0.7 to 0.5 when mean tree *D* increased from 10 to 22 cm. At the P and C sites, where mean root:stem ratios were 0.40 and 0.47, respectively, no significant slope in the root:stem to mean tree *D* relationship was found over a more narrow range in mean tree *D* (12–15 and 12–18 cm, respectively). Roots were observed in the deepest layers measured (190, 190, and 290 cm for the P, C, and S sites, respectively); however, the asymptotically decreasing root mass per layer indicated the bulk of roots were measured. Root growth relative to stem growth would need to change with increased mean tree *D* to explain the results observed here. While these changes in growth rate among plant components may differ across sites, stem mass alone does a good job of estimating root mass across sites.

Keywords Rooting depth · Soil characteristics · Tree diameter · Site

T. J. Albaugh (✉) · H. L. Allen
Department of Forestry, North Carolina State University,
Box 8008, Raleigh, NC 27695-8008, USA
e-mail: tim_albaugh@ncsu.edu
Tel.: 919-515-3500
Fax: 919-515-6193
e-mail: lee_allen@ncsu.edu

L. W. Kress
USDA Forest Service,
3041 Cornwallis Road, RTP, NC 27709, USA
e-mail: lkress@fs.fed.us

Introduction

Loblolly pine (*Pinus taeda* L.) stem growth per unit of leaf area (growth efficiency) varies across the southeastern United States and this variation may be at least partly a result of altered carbon partitioning where site conditions result in greater below ground biomass production per unit of above ground production (Sampson and Allen 1999; Jokela et al. 2004). Loblolly pine is the primary commercial tree species in the region and interest in quantifying total carbon accumulation, both above and below ground, across its range is growing given the emerging desire to understand and possibly manipulate carbon sequestration to manage national global policy commitments (Johnsen et al. 2001). Throughout the region, accurate estimates of above and below ground biomass at the stand level are necessary to understand the observed differences in growth efficiency and the concomitant changes in carbon accumulation. A robust understanding of how above and below ground biomass and hence carbon accumulation may vary across site types is a first step needed to address both issues.

Above and below ground development in all plants has been linked theoretically with a biophysical model of resource transport (West et al. 1999). The model describes stem and root allometry and works remarkably well given a tremendous range in plant species and sizes. While the model is useful examining global patterns it may not work well for a given species and location; it has been used to examine limitations in available data. For example, Robinson (2004) reported the model overestimated below ground mass in forests by 40% when compared with current root biomass data. Potential sources of error in estimating root mass were in extracting all roots from the soil (Friend et al. 1991), in handling after separation from the soil (Robinson 2004), and failure to sample roots deep in the soil profile (Stone and Kalisz 1991; Schenk and Jackson 2002).

Above and below ground biomass estimates are available across the loblolly pine range on a variety of sites (Wells et al. 1975; Pehl et al. 1984; Van Lear and Kapeluck 1995; Albaugh et al. 1998, 2004a; Retzlaff et al. 2001;

Adegbidi et al. 2002; Samuelson et al. 2004). Above ground biomass estimates should be reasonably robust because calculation of above ground biomass accumulation is relatively straightforward and relatively little error in estimation would be expected (Robinson 2004). On the other hand, the methods used to estimate below ground mass vary substantially and may not consistently or effectively quantify roots under all conditions. The methods used to estimate root mass include direct excavation of individual tree roots (Wells et al. 1975; Albaugh et al. 1998; Retzlaff et al. 2001) coupled with soil coring (Pehl et al. 1984) or excavation of coarse roots located away from tree stumps (Albaugh et al. 2004a), other methods included excavation using air (Samuelson et al. 2004) or water (Kapeluck and Van Lear 1995), the latter coupled with dimensional measures to estimate lateral root mass and additional coring to capture roots less than 6 mm in diameter. Methodological differences arise from the distinction between stem and roots, where some have considered all material below the stump as root (Van Lear and Kapeluck 1995) rather than below ground (Wells et al. 1975; Pehl et al. 1984; Albaugh et al. 1998, 2004a; Retzlaff et al. 2001; Samuelson et al. 2004) and the distinction between coarse roots and fine roots which ranged from 2 to 6 mm among these studies. Determining the best method is problematic without an independent verifiable root mass estimate and, consequently, the method utilized will be determined from personal preference, experience, equipment, and resources (Vogt et al. 1998).

Limitations in estimating loblolly pine root mass across the region from the existing studies may result from factors other than methodology. Stand age, site quality, and stocking are factors that may affect comparison from study to study (Van Lear and Kapeluck 1995). Site specific soil physical and morphological characteristics (Parker and Van Lear 1996; Schenk and Jackson 2002; Bongarten and Teskey 1987), as well as rooting zone restrictions (Nicoll and Ray 1996), may influence the growth of roots. Wind stresses may alter root morphology and the number and size of windward lateral roots (Telewski 1995; Stokes et al. 1995; Nicoll and Ray 1996). The above ground developmental pattern and resulting canopy position of individual trees may also affect root growth (Kapeluck and Van Lear 1995). Root sampling in existing studies has focused on relatively shallow roots (1 m or less in depth), while measurement to greater depths (2 m or more) may be required to insure an adequate accounting of all roots (Stone and Kalisz 1991; Hacke et al. 2000; Schenk and Jackson 2002). In addition, genetic makeup may further compound the difficulty in quantifying below ground mass as above and below ground biomass allocation have been found to differ between fast and slow growing loblolly pine families in some studies (Li et al. 1991; Bongarten and Teskey 1987) but not in others (Retzlaff et al. 2001).

Table 1 Number of samples and timing for above and below ground biomass assessments

Parameter	Site		
	Piedmont	Coastal plain	Sandhills
Individual tree sampling used for developing predictive equations for SM, RT, RN[a]			
Sample years	2002	1999	1992, 1994, 1996, 1998, 2003
Number of trees	15	15	16, 16, 16, 16, 4
Number of tap and coarse root pits[b]	15	15	0, 7, 16, 16, 4
Root sampling away from trees			
Sample years	2002, 2003	1999, 2003	1996, 2003
Number of sample pits	36, 6	36, 1	16, 32
Pit depth (cm)	50, 190	50, 190	50, (50, 290)[c]

[a]SM, stem mass per hectare; RT, tap root mass; RN, roots in square meter centered on each tree

[b]At the S site in 1992 no below ground samples were collected

[c]At the S site in 2003 for the root sampling away from the trees, eight of the 32 excavated pits were to 290 cm and the remaining 24 were to 50 cm

Table 2 Study site characteristics

Parameter	Site		
	Piedmont	Coastal plain	Sandhills
Annual precipitation (mm)	1092	1219	1220
Mean annual temperature (°C)	14.2	16.8	16.9
Annual number of frost free days	266	280	303
Mean wind speed (m s^{-1})	1.7	1.6	1.6
Planting year	1993	1992	1985
Tree family origin	Piedmont	Atlantic Coastal Plain	Piedmont
Site index (m at 25 years)	16.8	18.3	16
Soil texture	Clay	Clay	Sand
Drainage	Well-drained	Poorly-drained	Well-drained

Table 3 Stand characteristics in the years coarse roots were sampled between trees

Site	Height (m)				Diameter (cm)			Basal area (m^2 ha^{-1})			Stand density (stems ha^{-1})		
	Year	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum
Sandhills	1995	7.1	8.5	5.7	12.1	15.4	9.9	14.1	21.8	8.2	1,160	1,267	1,017
	2002	12.3	15.2	8.7	17.7	22.2	14.1	29.2	42.8	16.2	1,115	1,244	990
Piedmont	2001	8.7	9.5	7.9	13.2	14.8	12.2	22.7	27.9	19.6	1,616	1,761	1,449
	2002	9.2	9.4	8.9	14.5	15.4	13.8	26.2	27.7	25.2	1,556	1,656	1,449
Coastal	1998	8.0	8.7	7.4	12.6	13.4	11.8	16.9	20.3	14.0	1,308	1,409	1,211
Plain	2002	12.4	12.4	12.4	17.9	17.9	17.9	35.9	35.9	35.9	1,359	1,359	1,359

To address the limitations of the previously reported work and to improve our understanding of how loblolly pine biomass partitioning varies across the region, our objectives were to quantify above and below ground biomass on different site types at different stand developmental stages using the same methodology.

Methods

Study sites

We selected three study sites in the southeastern United States (US) with a range of tree and stand developmental stages induced by fertilizer application and estimated above and below ground biomass at two different times at each site. The study plots at the sites were used as individual stands for our assessments. One site was in Brunswick County in the southern Virginia Piedmont (P) on a well drained clay soil (Typic Kanhapludult) (36.68°N latitude, 77.99°W longitude), a second site was in Craven County in the eastern North Carolina Lower Coastal Plain (C) on a poorly drained clay soil (fine, mixed, active, thermic Typic Albaquult) (35.11°N latitude, 76.58°W longitude) and the third site was in Scotland County in the southern North Carolina Sandhills (S) on a well drained sandy soil (siliceous, thermic Psammentic Hapludult) (34.91°N latitude, 79.48°W longitude) (Albaugh et al. 1998, 2004a).

All sites had pine plantations as the previous crop and had vegetation control at time of planting of the current rotation. Long term (1960–2000) meteorological data (average annual precipitation, mean annual temperature and number of frost free days) were acquired from the US National Oceanic and Atmospheric Administration weather station closest to each site. The weather stations for long-term data were 16, 21, and 24 km from the S, P, and C sites, respectively. Wind speed was measured at each site.

Tree and stand measurements

In the dormant season (December–February) measurements of diameter at breast (1.4 m) height (*D*), and height (*H*), and mortality assessments were made on all living trees in each plot at each site. Basal area was calculated for each tree, summed to the plot level, and scaled to determine basal area per hectare.

Biomass estimation

We estimated biomass (dry weight of living tissue) of stem and roots >2 mm on an area basis. Stand level root biomass to depth (RM) was the sum of stand level estimates of tap root mass (RT), coarse root mass in the square meter centered on each tree (roots near the tree, RN) and coarse root mass outside the square meter centered on each tree (roots away from the tree, RA). Stem biomass, RT and RN were calculated from tree dimensional measures which

Table 4 Coarse root mass (g m^{-2}) and standard error by depth (cm) for pits excavated to the maximum depth at each site. All maximum depth pits were centered between four trees

Sample depth		Sandhills site		Piedmont site		Coastal plain site	
From	To	Root mass	SE	Root mass	SE	Root mass	SE
0	15	479	47	410	50	208	NE
15	30	190	40	110	25	132	NE
30	50	122	31	56	14	382	NE
50	70	167	61	75	17	117	NE
70	90	161	40	32	12	58	NE
90	110	227	111	41	28	60	NE
110	130	53	13	3	1	37	NE
130	150	35	8	4	1	36	NE
150	170	42	19	7	4	6	NE
170	190	24	8	3	2	5	NE
190	210	20	7	NM	NM	NM	NM
210	230	27	9	NM	NM	NM	NM
230	250	16	5	NM	NM	NM	NM
250	270	15	6	NM	NM	NM	NM
270	290	15	6	NM	NM	NM	NM

Note. NE is no estimate available, depths where only one sample was available. NM is not measured

were collected each year; however, RA was not associated with tree dimensional measures so our comparisons were limited to those years in which we sampled RA (Table 1).

Stand level biomass estimates for stem wood were calculated from site- and plot specific regression equations applied to all trees and then scaled to an area basis for each plot. The stem regression equations were developed following the methods presented in Albaugh et al. (1998) and (2004a), were based on destructive harvests and included *D* and *H* as independent variables. Destructive sampling for stem mass was completed in the dormant season (January and February) in several years on a total of 68 trees at the S site and on 15 trees at each of the P and C sites (Table 1). Trees were selected to represent the range in *H* and *D* at the time of sampling. All trees were cut at soil level, the branches were removed and the stem wood was dried at 65°C to a constant weight.

Site- and plot specific regression equations were developed to estimate tap root mass and coarse root mass in the square meter centered on the tree from measures of individual tree *D* and *H*. These equations were applied to all trees, scaled to an area basis for each plot and equaled RT and RN, respectively. The root regression equations were developed following the methods presented in Albaugh et al. (1998) and (2004a) from a subset of trees used in the destructive stem harvests on 43, 15, and 15 tap root and coarse root systems at the S, P, and C sites, respectively (Table 1). At the P and S sites, the entire tap root to depth (in some cases to 3 m) was removed by hand excavation. Also at the P and S sites, all live coarse roots found in a square meter centered on the tree stump down to 50 cm in the soil were removed by hand excavation. Excluding the tap root, coarse roots in the square meter centered on the tree were generally found in the surface 50 cm with very few found at greater depths. At the C site, the tap root and all attached live coarse root material were excavated mechanically (pulled out by a backhoe tractor), and separated into tap and coarse root. The actual area sampled at the C site closely approximated 1 m^2. The roots were readily extracted from the soil and additional hand excavation of the soil volume from which the excavated roots were removed indicated that this method yielded similar results when compared to the hand excavation method at the other sites. All excavated roots were dried to a constant weight at 65°C.

To estimate root mass outside the 1 m^2 centered on a tree, excavations centered between four trees were completed in 2 years at each site (Table 1). Forty-eight, 42, and 37 pits were hand excavated to at least 50 cm at the S, P, and C sites, respectively. Of these pits, eight, six, and one pit(s) at the S, P, and C sites, respectively, were excavated to 290 cm at the S and 190 cm at the P and C sites. All pits were hand excavated by layer (0–15, 15–30, 30–50 cm and then by 20 cm increments to the maximum depth). Surface dimensions of the pits were 1 m × 1 m at the flat planted S and P sites and 0.5 m × 2 m at the bedded C site. Roots were separated from the soil and dried at 65°C to a constant weight. Excavations were completed to the deeper depths on only a portion of the pits because of limited resources; however, site specific regression equations were developed

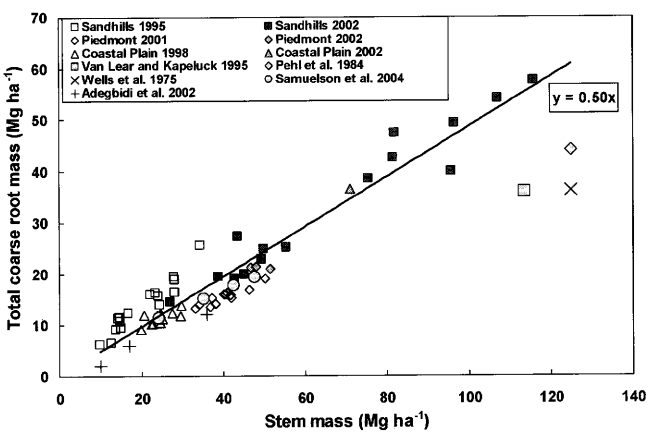

Fig. 1 Total coarse root mass (Mg ha^{-1}) and stem mass (Mg ha^{-1}) for all stands measured each year at the three sites. Data from the literature are included for comparison. Regression line includes only data from this study

Table 5 Statistics (parameter estimates for the independent variables, standard error of the parameter estimate, sample size and mean square error) for the models used to explain variation in the dependent variables root mass and root:stem

Dependent variable	Model[a] or site	Independent variable	Measurement year	Parameter estimate	Standard error	*N*	Mean square error
Root mass	Reduced	Stem mass	All	0.50	0.010	60	13.3
Root mass, log scale	Full	Stem mass, log scale	All	0.70	0.13	60	0.007
		Mean tree *D*		0.05	0.02		
		S site		−0.36	0.20		
		P site		−0.43	0.22		
		C site		−0.33	0.22		
		S site ∗ 1995[b]		0.24	0.06		
		P site ∗ 2001[b]		−0.11	0.06		
		C site ∗ 1998[b]		−0.14	0.10		
Root mass	Sandhills	Stem mass	1995	0.69	0.018	16	2.3
Root mass	Sandhills	Stem mass	2002	0.52	0.010	16	7.0
Root mass	Piedmont	Stem mass	2001	0.38	0.005	12	0.5
Root mass	Piedmont	Stem mass	2002	0.43	0.015	3	1.5
Root mass	Coastal Plain	Stem mass	1998	0.46	0.013	12	1.2
Root mass	Coastal Plain	Stem mass	2002	–[c]	–	1	–
Root:stem	Sandhills	Mean tree *D*	1995 and 2002	−0.02	0.005	32	0.008
Root:stem	Piedmont	Mean tree *D*	2001 and 2002	NS[d]	–	15	0.0008
Root:stem	Coastal Plain	Mean tree *D*	1998 and 2002	NS	–	13	0.002

Note. See the text for specific information regarding model development

[a]All models explaining root mass or root mass log scale have intercept = 0

[b]The parameter estimate for the site and measurement year combinations of S∗2002, P∗2002, and C∗2002 =0

[c]A slope calculated between the one measured point and the origin would be 0.52

[d]NS, non-significant slope

to scale shallow pit data to the maximum depth measured (290 cm at S site and 190 cm at the P and C sites) as a function of the pit root mass to a depth of 50 cm and the plot basal area. These equations were applied to all pits that did not reach the site maximum pit depth. The number of square meters within a plot not occupied by trees multiplied by the root mass to the maximum depth was scaled to an area basis and equaled RA.

Statistical analyses

Analysis of variance (ANOVA) (SAS, 1988) was used to examine independent variables influencing root mass. First we calculated parameter estimates for a simple model:

$$RM = SM \quad (1)$$

where RM was root mass per hectare and SM was stem mass per hectare. This simple model was quantified for all data and for each site and year combination. Second, we identified significant independent variables and estimated parameters for a more complex model explaining RM:

$$RM = SM\ SITE\ TSIZE\ MY \quad (2)$$

where RM and SM were as before, SITE indicated study site, TSIZE was mean tree *D* for the plot, and MY was measurement year. The SITE and MY variables were treated as dummy variables with a mean of zero. The full model included each variable alone and all possible interactions. Non-significant individual terms were dropped from the model until all remaining terms were significant. Additionally, ANOVA was used to find the slope of the RM-to-SM ratio (RM:SM) to mean tree *D* relationship for the S site. All significance levels were <0.05.

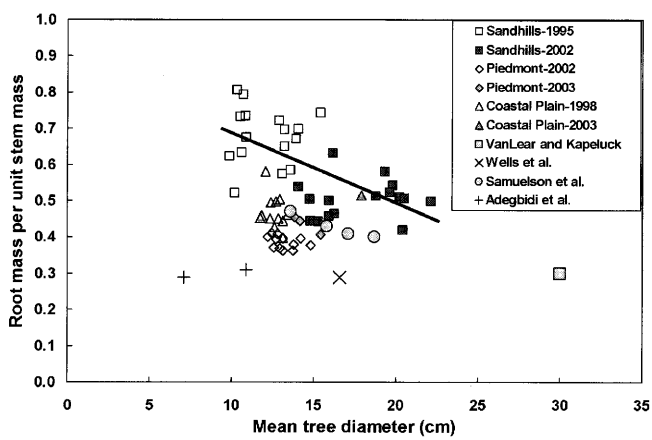

Fig. 2 Root mass per unit stem mass and mean tree *D* (cm) for all stands measured each year at the three sites. Data from the literature are included for comparison. Regression line describes data from the Sandhills site; the other sites did not have significant slopes

Table 6 Summary of stem and root mass data previously reported for loblolly pine in the southeastern United States

Study	Soil	Location	Stem v mass (Mg ha^{-1})	Root mass (Mg ha^{-1})	Estimated R:S ratio	Basal area (m^2 ha^{-1})	Mean tree D[a] (cm)	Age (years)	Stem density[b] (stems ha^{-1})	Thinning	Notes
Pehl et al. (1984)	Arenic Paleudult, loamy, siliceous, thermic	TX	125	44	0.35	NR[c]	NR	25	1175	No	Root mass reported here assumes one half of lateral root size class <0.5 cm reported in Pehl et al. is >2 mm
Van Lear and Kapeluck (1995)	Pacolet thin fine sandy loam overlying clay and clay loam (clayey kaolinitic thermic Typic Kanhapludult)	SC	114	34	0.30	19.1	30.0	48	437	Twice	Root mass reported here assumes one half of lateral root size class <0.6 cm reported in Van Lear and Kapeluck is >2 mm
Wells et al. (1975)	Granville coarse sandy loam Typic Hapludult, fine loamy, siliceous, thermic	NC	125	36	0.29	49.0	16.6	16	2243	No	
Samuelson et al. (2004)	Well drained Grossarenic Paleudult, argillic horizon at 1 m	GA	24	11	0.47	14.0	13.6	6	960	No	Weed control
			35	15	0.43	18.5	15.8	6	945	No	Weed control, irrigation
			43	18	0.41	22.0	17.1	6	960	No	Weed control, irrigation, fertilization

Table 6 Continued.

Study	Soil	Location	Stem v mass (Mg ha^{-1})	Root mass (Mg ha^{-1})	Estimated R:S ratio	Basal area (m^2 ha^{-1})	Mean tree D[a] (cm)	Age (years)	Stem density[b] (stems ha^{-1})	Thinning	Notes
			48	19	0.40	24.9	18.7	6	910	No	Weed control, irrigation, fertilization, pest control
Adegbidi et al. (2002)	Spodosol with argillic horizon (sandy, siliceous, thermic Ultic Alaquod and Oxyaquic Alorthod)	GA	10	2	0.20	NR	NR	2	1420	No	Root mass includes fine roots
			17	5	0.29	5.6	7.1	3	1420	No	Authors root:stem ratio of 0.35 included fine roots, this estimate assumes 1 Mg ha^{-1} fine roots
			36	11	0.31	13.2	10.9	4	1420	No	Authors root:stem ratio of 0.34 included fine roots, this estimate assumes 1 Mg ha^{-1} fine roots

[a]Mean tree diameter estimated from basal area and stem density for Samuelson et al. and Adegbidi et al.
[b]Stem density for Adegbidi et al. estimated assuming 95% survival from planting density of 1,495
[c]NR indicates data not reported

Results

The P site was cooler and drier than the C and S sites with shorter summers, lower mean annual temperature and less annual precipitation (Table 2). Site index at the C site was about 2 m greater than the other sites. Stand ages when the assessments were completed were 11 and 18, 9 and 10, and 7 and 11 years for the S, P and C sites, respectively. Mean wind speeds were similar at all sites. The ranges in tree size (*H* and *D*), and stand basal areas among the sites were overlapping (Table 3). The S site had 28 and 15% fewer trees per hectare than the P and C sites, respectively. Little mortality was observed during the years of the study.

Pits excavated to the maximum depth at each site (290 cm at the S site and 190 cm at the P and C sites) showed an asymptotic relationship between cumulative root mass and depth (Table 4). At least 95% of the total root mass found in the deep pits occurred in the surface 230, 110 and 130 cm, at the S, P and C sites, respectively (Table 4). Consequently, at all sites, very little (less than 1%) of the total root mass in the deep pits was found in the last 20 cm sampling horizon (270–290 cm at the S and 170–190 at the P and C sites).

Across all sites and measurement years, total coarse root biomass per hectare was about 50% of stem biomass per hectare (R^2=0.91) (Fig. 1). Stem mass, mean tree *D*, site, and measurement year by site were significant independent variables in a more comprehensive model explaining 97% of the variation in root mass (Table 5). Slopes of the root mass per unit of stem mass relationship between any pair of site and measurement year combinations differed by up to 80% (Table 5). Across the mean tree *D* (10–22 cm) examined here, corresponding to a stand basal area of 8–43 m^2 ha^-, the root:stem ratio varied from 0.36 to 0.81 (Fig. 2). Only the S site had a significant slope for the root:stem ratio to mean tree *D* relationship; the root:stem ratio was reduced as mean tree *D* increased at the S site (Table 5 and Fig. 2).

Discussion

Loblolly pine root mass was found to be about one half of stem mass across three sites with a range of tree sizes and stand basal area. Retzlaff et al. (2001) and Ludovici et al. (2002) suggested that the root:shoot ratio in loblolly pine is about 0.43 (30% root and 70% shoot, where shoot equals the sum of stem, branch and foliage biomass). Adjusting their estimates to include only perennial tissues (coarse root and stem) will result in a smaller denominator because fine root mass is likely to be less than the sum of branch and foliage mass (Albaugh et al. 1998) and would give a root:stem ratio closer to the 0.5 found in this study. This estimate is also in agreement with Robinson's (2004) estimate of the root to stem mass relationship for all vegetation. As an initial approach, then, this relationship should be useful for calculation of regional estimates of below ground carbon stocks associated with loblolly pine.

However, for the purpose of understanding differences in growth efficiency at specific sites and how they may be affected by above and below ground partitioning, the observed variation around the more regional root to stem relationship is equally interesting. While stem mass explained most of the variation in root mass, both tree size and site were also significant factors influencing root mass. In loblolly pine (Albaugh et al. 1998, 2004a; Samuelson et al. 2004; Jokela et al. 2004) and other species (*P. radiata*: Albaugh et al. 2004b; Linder et al. 1987; *P. sylvestris*: Linder 1987; *Picea abies*: Bergh et al. 1998) trees may reach different developmental stages (tree size, accumulated mass) at the same age depending on the silvicultural regime imposed, environmental conditions and the native ability of a given site to supply resources. For a given measurement year, the range in tree *D* and stand basal area at all sites was induced by fertilization. King et al. (1999) reported a small but significant increase in perennial root tissue (coarse roots) relative to perennial above ground tissue (stem and branches) at the S site with fertilization. The significant tree *D* effect on the root to stem relationship likely represents the fertilization effect found by King et al. (1999).

The site factor would include stand age, stocking, environmental conditions, site quality (available resources), soil characteristics, and genetic makeup. Of these factors, stand age and environmental conditions are least likely to contribute to variation between the sites. There was overlap in stand age for the measurement years and the magnitude of climatic difference would not likely influence root development (rooting depth) (Schenk and Jackson 2002).

Differences in stocking, soil characteristics (texture and drainage) and genetic makeup may have influenced relative root and stem development. The S site soil had lower stand density and more root mass than the P and C sites in agreement with Shelton et al. (1984) who found more root mass in stands with lower density. The S site had relatively low mechanical resistance, low soil water potential (Hacke et al. 2000; Ewers et al. 1999) and greater root mass relative to stem mass in stands with small tree *D* compared to the P and C sites which had higher soil mechanical resistance and higher soil water potential which was similar to other studies (Torreano and Morris 1998; Zou et al. 2001). However, with larger tree *D* (>15 cm) at the S site, the root mass to stem mass ratio was reduced even though soil characteristics remained unchanged. The C site had a coastal family on a poorly drained soil and produced less root mass per unit stem mass in agreement with Bongarten and Teskey's (1987) work in seedlings. However, based on Bongarten and Teskey's (1987) study and given the continental sources at the P and S sites, one would expect a higher root:stem ratio at the slightly drier P site but this pattern was not observed here. The observed patterns of root and stem mass were an integration of these factors but it would not be possible to determine which factor was most influential at a given measurement period.

More root mass was found at greater soil depth at the S site than at the P and C sites in agreement with Schenk and Jackson's (2002) analysis of root biogeography where

deeper rooting depths were found in sandy soils relative to clay or loam soils. Root mass at all sites decreased with soil depth similar to other studies (Kapeluck and Van Lear 1995; Parker and Van Lear 1996; Van Lear et al. 2000; Schenk and Jackson 2002). While roots were observed at the greatest measured depths, the root mass found in the deepest layers was low, less than 1% of the total found in the profile. If sampled, roots are likely to be found at even greater depths (Stone and Kalisz 1991) following root channels from previous rotations (Van Lear et al. 2000; Ludovici et al. 2002) or soil physical features like fractures or rock faces (Parker and Van Lear 1996). The contribution to total root mass from these deeper roots is unknown. Robinson (2004) calculated that root mass may be underestimated as much as 40% in root studies using excavation techniques. The asymptotically decreasing root mass per layer gave confidence that we captured the bulk of the roots in the profile (Schenk and Jackson 2002).

Across the stand conditions (8–43 m^2 ha^{-1} basal area, 7–18 years of age, 1100–1600 stems ha^{-1}) represented here the root:stem ratio ranged from 0.36 to 0.80. Samuelson et al. (2004) and Pehl et al. (1984) reported similar loblolly pine root:stem ratios (0.40–0.47 and 0.35, respectively) while Wells et al. (1975), Van Lear and Kapeluck (1995), and Adegbidi et al. (2002) reported lower root to stem mass ratios of 0.29, 0.30, and 0.20–0.31, respectively (Table 6). The low root:stem ratio of the stand measured by Wells et al. (1975) may have been related to its high stocking (>2200 stems ha^{-1}) (Shelton et al. 1984). Also, root mass was measured on only two trees in Wells et al. (1975) making sampling error a possible contributor to the observed differences. Van Lear and Kapeluck (1995) measured a stand on a well drained clay soil that was older (48 years old), had larger trees (30 cm average diameter) and had been thinned twice. If the pattern of reduced root:stem ratio with increased tree size and age we found on the S site is common to all sites then it is reasonable to expect a low root:stem ratio for a stand with trees of that age and size. On the other hand, it is possible that root mass was underestimated in Van Lear and Kapeluck (1995) given the Retzlaff et al. (2001) caution against assuming that root:stem ratio declined with age (larger trees) simply because of the difficulty in measuring large tree roots. Adegbidi et al. (2002) examined young stands on poorly drained sandy loam soils with an argillic horizon; here the possibility of root mass underestimation should be less because the small tree size facilitates root measurement. Hence, the low root:stem mass ratio relative to our study may be related to the poor drainage and the relatively small tree size.

At the S site, where the root:stem to mean tree D relationship had a negative slope, stands with small D trees had a high (0.6–0.8) root:stem ratio, while trees with larger D had a lower root:stem ratio (0.4–0.6). For this pattern to be observed, the relative growth rate of root and stem biomass would shift as tree D increased. During the first 11 years, root growth was rapid relative to stem growth. In the next 7 years, root growth relative to stem growth would need to slow considerably for the point in time root:stem ratio to shift from 0.6–0.8 to 0.4–0.6. The shift from relatively rapid root growth to slower root growth may have actually occurred prior to the year 11 sampling period. A pattern of changing root:stem ratio with increasing tree D was observed by Ovington (1957) in a chronosequence study on *P. sylvestris* where root:stem ratio increased through age 7 (D=0.5 cm) and then generally decreased through age 55 (D=23 cm). For the P and C sites, the root:stem to mean tree D relationship did not have a significant slope; however, the range in mean tree D was less at the P and C sites compared to the S site and may have been too small to observe changes. In their study of trees with smaller mean tree D (7.1–10.9 cm), Adegbidi et al. (2002) reported that root mass increased from 20 to 32% of total mass for trees 1–2 and 3 years old, respectively. Apparently, changes in root:stem ratios from year to year are possible at least for small trees and may occur throughout the life of a stand (Ovington 1957; Causton and Venus 1981).

If relative root and stem growth change throughout stand development, understanding the cause and timing of these changes will be critical to applying data from this study to individual sites across the broader landscape. This work showed that tree size and site (soil texture and drainage, genetic makeup, stem density) influence the root and stem mass relationship. It is likely that the observed changes through time are the net result of the interaction of these factors. The point in time measures used here integrate these effects so the importance of any one component could not be isolated. However, we have demonstrated that the bulk of variation in loblolly pine root mass across sites may be explained by stem mass and this may be the best estimate available until experiments are installed to tease out the influence of the various site components.

Acknowledgments This work contributes to the Global Change and Terrestrial Ecosystem (GCTE) core project of the International Geosphere-Biosphere Program (IGBP). We gratefully acknowledge the support provided by the USDA Forest Service Southern Forest Experiment Station, the Southern Global Change Program, the Department of Forestry, North Carolina State University, and members of the Forest Nutrition Cooperative. This paper has not been subject to USDA Forest Service policy review and should not be construed to represent the policies of that Agency. The use of trade names in this paper does not imply endorsement by the associated agencies of the products named, or criticism of similar ones not mentioned.

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