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REGULAR ARTICLE

Longleaf and loblolly pine seedlings respond differently to soil compaction, water content, and fertilization

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Abstract

Aims Longleaf pine (*Pinus palustris* Mill.) is being restored across the U.S. South for a multitude of ecological and economic reasons, but our understanding of longleaf pine's response to soil physical conditions is poor. On the contrary, our understanding of loblolly pine (*Pinus taeda* L.) root and shoot growth response to soil conditions is well established.

Methods We performed a comparative greenhouse study which modeled root length density, total seedling biomass, and the ratio of aboveground:belowground mass as functions of volumetric water content, bulk density and soil fertility (fertilized or not).

Results Root length density was about 35 % greater in longleaf pine seedlings compared to loblolly pine seedlings, and was reasonably well modeled (R^2=0.54) for longleaf pine by bulk density (linear), volumetric water content (quadratic), soil fertility, and the interactions of bulk density, volumetric water content, species, and soil fertility. The aboveground:belowground mass ratio (ABR) increased at both extremes of water content.

Conclusions This research indicates that young longleaf pine seedling root systems respond more negatively to extremes of soil physical conditions than loblolly pine, and compacted or dry loamy soils should be ameliorated in addition to normal competition control, especially on soils degraded by past management.

Keywords Longleaf pine · Loblolly pine · Bulk density · Soil water content · Root length density

Introduction

Longleaf pine (*Pinus palustris* Mill.) once occupied 37 million ha across the southeastern U.S. from Virginia to Texas, but currently occupies about 1 million ha due to widespread harvesting and subsequent regeneration failures, feral hog predation, and especially fire suppression (Frost 2006). Longleaf pine ecosystems are exceptionally biologically diverse, both in terms of flora and fauna. They provide sustainable income to landowners, especially when cost-share programs and non-traditional forest markets such as pine straw and agroforestry (Stainback and Alavalapati 2004) are considered. Finally, longleaf ecosystems are resistant to myriad natural disturbances such as southern pine beetle (*Dendroctonus frontalis* Zimm.) outbreaks, wildfire, and hurricanes (Johnsen et al. 2009). Efforts are currently underway to restore longleaf pine ecosystems within their former range, e.g., America's Longleaf Restoration Initiative (America's Longleaf 2009), but many soils suitable for longleaf restoration have been degraded or altered through past agriculture or other management activities. Longleaf restoration success is hindered in part by a relative lack of detailed information on seedling responses to environmental conditions such as soil properties.

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While longleaf pine is relatively drought-tolerant and competes well on xeric, sandy soils, it also is native to wet flats where fire reduces loblolly pine (*Pinus taeda* L.) encroachment. Sites across this range of soil moisture may be eroded, compacted, or have altered fertility from previous agricultural land use or from various forest management activities. Compacted soil affects the ability of roots to exploit the soil volume for water and nutrient uptake, and exacerbates growth retardation in infertile soils (Greacen and Sands 1980; Worrell and Hampson 1997). In general, root growth opportunity is diminished proportionally with increasing soil density due to excessive soil strength as a soil dries, or inadequate aeration when a soil becomes too wet (Siegel-Issem et al. 2005). Therefore, it is critical to thoroughly understand compaction processes, their effects on soil and plant growth, and the extent to which negative effects of compaction can be minimized.

Prescribed fire is essential for maintaining the open herbaceous understory commonly desired in longleaf forests for providing the plant and animal diversity characteristic of the longleaf pine ecosystem. However, prescribed fire can compact surface soils (Boyer and Miller 1994; Moehring et al. 1966). Longleaf pine has been shown to have reduced growth following repeated prescribed burns (Boyer 1987; Haywood and Grelen 2000), but little is known about the causes of this reduced growth. Defoliation through crown scorch (Sword Sayer and Haywood 2009), fine root mortality (Sword Sayer and Kuehler 2010) and soil physical property changes (Sword Sayer 2007) have all been suspected, but few studies have isolated any one of these three factors with respect to longleaf seedling response.

Not only do soil physical parameters interact to control root growth opportunities but changes in soil water and aeration can directly affect nutrient availability. In very dry conditions, availability of nutrients such as N, P, K, and Ca are limited due to a lack of soil solution for mass flow or diffusion, as well as reduced mineralization rates. In very wet conditions, changes in aeration and redox potentials alter mineralization and mineral nutrient availability. Fertilization with phosphorus (P) has been noted as an ameliorative treatment for tree growth on physically impaired soils (Aust et al. 1998) due to increased anaerobic root metabolism in high-P conditions, but restoration objectives could actually be hindered by elevated soil fertility levels that encourage competitors (Maron and Jefferies 2001).

Our knowledge of loblolly pine response to environmental conditions, such as soil properties and processes, is substantial. Since we know loblolly pine's field-based responses to soil compaction and water availability quite well, we can use comparative research on both species to make broader implications on longleaf response to field conditions than from one limited study.

Accordingly, our research objectives were to (1) model root length density and seedling biomass growth as functions of soil bulk density (ρ_b) and volumetric water content (θ_v) for loblolly and longleaf pine for the Freest soil series, a common Gulf Coastal Plain soil; and (2) determine the extent to which soil fertility modifies these models by altering root nutrient uptake opportunity. We hypothesized that belowground and aboveground growth would be reduced by the extremes of density and water content, but that soil fertility would attenuate these reductions in growth by reducing nutrient stress associated with limited root uptake capacity. We further hypothesized that a higher level of soil fertility would attenuate these growth reductions to a greater degree in wet conditions due to P influence on anaerobic metabolism.

Methods and materials

Site and soil descriptions

We collected soil for this study from the surface 20 cm in a single 25-m^2 area in the border row of one plot of the Mississippi installation (MS 2) of the Long-Term Soil Productivity Study (Scott and Dean 2006). This area is located in a prime longleaf pine habitat, yet has been dominated by either loblolly or slash pine (*Pinus elliottii* Engelm.) for approximately 65 years. The surrounding area is dominated by either loblolly or longleaf pine, inkberry (*Ilex glabra* (L.) A. Gray), and various herbaceous plants (Stagg and Scott 2006). The soil is a Freest series and is a fine-loamy, siliceous, thermic Aquic Paleudalf (Davis et al. 1986) formed from loamy and clayey sediments of the Hattiesburg formation (Moore 1985).

Soil analyses were conducted on samples collected from the A and E horizons (0–12 and 12–22 cm, respectively) of a soil pit at the general research site to provide general characterization data. Samples were air-dried, crushed with a wood cylinder, and sieved through a 10-mesh sieve to remove coarse fragments larger than 2 mm (USDA Soil Survey Staff 1992). Particle size distribution was determined by hydrometer method and sieving (Day 1965). Organic matter was determined by wet combustion procedure (Allison 1935). Exchangeable base cations were extracted with neutral N NH_4OAc and determined by atomic adsorption spectrometry (USDA Soil Survey Staff 1992). Soil pH was measured in 1:1 soil-to-water ratio. Available P was determined by the dilute double acid (Mehlich I) extraction (Olson and Dean 1965). Water retention characteristics were determined with the pressure membrane method (Richards 1949) on natural aggregates of non-disturbed cores.

Soil compaction treatment

Soil was air dried and sieved (2 mm) to obtain the fine-earth fraction and to remove old roots. We added water to bring the soil to its optimum water content for compacting, 23 % w/w, which was determined by Proctor test following Siegel-Issem et al. (2005) (data not shown). We then added loose, moist soil to the PVC cylinders, settled and smoothed the surface, and then compacted the soil with a predetermined number of hammer blows to achieve a range of ρ_b (Table 1). The target ρ_b were based on maximum and minimum soil bulk densities achievable for this soil. Soil volume, mass, and water content were measured and oven dry weight and actual ρ_b were determined for each core.

Soil water gradient

A θ_v gradient ranging from near-permanent wilting point to near-saturation was established and maintained based on water retention characteristics (Table 1). The weight of each pot associated with the target θ_v was calculated. All pots were weighed and watered as necessary to maintain the target θ_v as closely as possible. Watering frequencies ranged from daily (or more frequently) to several days between watering. Wet conditions in the very low density cores, i.e., those with high conductivity rates, were maintained by keeping the pots within a shallow plastic tub with water in the tub; otherwise these cores achieved field capacity very rapidly (within minutes to hours). Fertilized and unfertilized cores were maintained in separate tubs to avoid contamination.

Soil fertilization treatment

Fertilization treatments were initiated 2 weeks after planting coincident with the start of water content treatments. A commercial complete fertilizer solution containing 710 mg kg^{-1} N, 610 mg kg^{-1} P, 590 mg kg^{-1} K, 7 mg kg^{-1} Fe, 3 mg kg^{-1} Cu, 3 mg kg^{-1} Zn, 2 mg kg^{-1} Mn, 0.9 mg kg^{-1} B, and 0.02 mg kg^{-1} Mo was applied in 4.5 mL of water to the soil every 3 weeks (three applications) to half of the seedling cores.

Seedling establishment and growth

Loblolly and longleaf pine seed of unimproved seed stock appropriate to the areas from which our soils were collected were used. The seeds were germinated on a potting soil and sand mixture in shallow pans. Root length, number of lateral roots, and length of loblolly shoots (root collar to base of needles) were determined. Longleaf seedlings have no shoot due to their grass stage. Roots longer than 10 cm were pruned to 10 cm to avoid J-rooting.

A 1-cm diameter hole was drilled in the center of each packed soil column to within 3.5 cm of the bottom. The seedlings were carefully planted in the center of each pot. Washed silica sand was used to fill the 1-cm hole in the core and also added to the top of the soil to prevent soil surface disturbance from the watering treatments. Landscape cloth was attached to the bottom of each core to prevent the loss of soil and allow water drainage. After a 2-week establishment period in which θ_v was maintained at approximately 16 % (field capacity), seedlings were grown for the experimental period of approximately 11 weeks, at which point roots of some seedlings were exceeding the core volume. Seedlings that died during the establishment period were replaced. Seedlings that died after the establishment period were not replaced but were noted as such and mortality data was recorded. Greenhouse temperature was measured whenever seedlings were watered.

After the growing period, seedling heights (root collar to base of needles) were measured with calipers on all living seedlings. Each core was then deconstructed and root systems separated from the soil by carefully washing with water. The seedlings were separated at the root collar. Root length and surface area were determined for the entire root system with a computer imaging analyzer (Delta T Scan, Delta T Devices, LTD, Burwell, Cambridge, England). Root length density

Table 1 Mean bulk density (ρ_b), volumetric water content (θ_v), and approximate water potential (ψ) of soil cores constructed to grow loblolly and longleaf seedlings ($n=196$)

Nominal compaction level	Mean actual ρ_b Mg m^{-3} (std. dev.)	Water level	Target θ_v % (v/v)	Approximate ψ (MPa)
1[a]	1.13 (0.037)	1	8	−1.5
2	1.24 (0.020)	2	12	−0.6
3	1.35 (0.021)	3	16	−0.3
4	1.44 (0.017)	4	20	−0.03
5	1.49 (0.016)	5	26	−0.015
6	1.56 (0.019)	6	34	−0.005
7	1.64 (0.019)	7	42	0

[a] Compaction level 1 consisted of loosely filling soil in core with no mechanical compaction and represented the lowest bulk density achievable for this sieved soil

(RLD) (sum of all root lengths per unit volume of soil) was determined. Needles, stems (for loblolly pine), and roots were oven dried at 72 °C for 3 days, and biomass was measured. Because all soil was previously washed from the root samples, dry-ashing was not needed for mineral-free biomass.

Model development and statistics

We created separate multiple linear regression models for RLD, total seedling biomass, and the aboveground:belowground biomass ratio (ABR) to test these hypotheses:

We hypothesized that root growth (and by extension aboveground growth) would decrease from optimum at both the wet and dry extremes and that this relationship could be depicted mathematically as a quadratic function.

We hypothesized that root growth would decrease linearly with increasing ρ_b (Foil and Ralston 1967; Mitchell et al. 1982).

We hypothesized that responses on fertile soils would be greater than on infertile soils but the relationships among growth, bulk density, and water content would be similar, i.e., no significant fertilization by bulk density or water content interactions, but models would have a higher intercept. We hypothesized that seedlings would alter their biomass allocation in response to soil conditions.

Full models included parameters for bulk density (ρ_b), linear and quadratic terms for volumetric water content (θ_v), soil fertilization (unfertilized = 0 and fertilized = 1), species (loblolly = 0, longleaf = 1), and all interactions. The soil water gradient consisted of seven values of θ_v ranging from 8 % to 42 %. Seven seedling cores were used for each level of θ_v. Bulk density of the cores in each level of θ_v ranged from 1.13 to 1.64 Mg m^{-3} (Table 1). We used backwards stepwise model selection with $p<0.10$ and C(p) to determine the final model for each response value.

Field compaction and seedling response

To ensure greenhouse conditions were relevant to field conditions for this soil, we also collected data from the larger field experiment from which the soils were collected. Details on the field study have been previously described (Scott and Dean 2006). Briefly, nine 0.4 ha plots were established on each of three replicate blocks of the Freest soil. On these plots, three levels of harvest intensity and three levels of experimental soil compaction were applied. Compaction levels consisted of no compaction (no mechanical equipment was allowed on plots during harvest), moderate and severe compaction, which were accomplished by pulling a weighted road compactor across the plots six times. Compactor weights were determined by field-based Proctor tests and intended on achieving 80 % of the root-growth limiting bulk density (Daddow and Warrington 1983) for the severe treatment and a mid-way bulk density for the moderate treatment. Harvest intensity levels consisted of bole-only harvest, whole-tree harvest, and complete aboveground organic matter (forest floor included) harvest. The 0.4 ha plots were split, with one half of the plot receiving herbicide to control competition while the other side received no herbicide. Following treatments, containerized loblolly pine were planted on a 2.5 by 2.5 m spacing. For this study comparison, we used only the non-herbicided, complete organic matter removal treatment to compare directly to the soil used in the greenhouse study. We measured bulk density of the 0–10 cm soil depth just

Table 2 Initial characteristics of loblolly and longleaf pine seedlings (n=196) before planting in constructed soil cores with gradients of bulk density and volumetric water content

Parameter	Root length (mm)	Shoot length (mm)	Seedlings with lateral roots (n)	Pruned seedlings (n)
Loblolly pine (n=98)	81.4 (2.57)	34.0 (0.42)	0	47
Longleaf pine (n=98)	57.7 (2.61)	n/a	15	0

Values are means with standard errors in parentheses unless noted

following the compaction treatments by the core method (Grossman and Reinsch 2002) on 10 subsamples per 0.1 ha measurement plot and the height of the seedlings following one full growing season. Means for each are reported based on three replicate blocks of the three treatments.

Results

The soil used was a silt loam (40 % sand, 52 % silt, 8 % clay), had relatively little organic matter (2.5 %), and was very infertile with respect to double-acid extractable P (0.64 mg kg^{-1}). Soil basic cations were moderate; Ca, Mg, and K were 200, 36, and 25 mg kg^{-1}, respectively. The soil was moderately acid for a coastal plain forest soil, with pH of 4.76. Water retention at field capacity and permanent wilting point was approximately 16 % and 8 % by weight, respectively. In summary, this surface soil was very representative of medium-textured forest soils throughout the Pleistocene to Miocene-aged terraces of the western Gulf Coastal Plain upon which longleaf pine would have historically predominated but which now are covered with vast acreages of loblolly pine.

After 13 weeks (11 weeks of water treatments), 11 of the 196 seedlings died, primarily from the driest cores. Five longleaf pine seedlings died, with four from the driest cores and one from the wettest. Six loblolly pine seedlings died from the two driest sets of cores. Bulk density had less impact on survival; seedlings died at almost all compaction levels. Fertilization had mixed effects on survival; all dead longleaf pine seedlings were in fertilized cores, whereas all but two dead loblolly pine seedlings were in unfertilized cores. Greenhouse temperatures were maintained at an average of 33 °C for the duration of the study, with daily minimum temperatures averaging 23 °C and daily maximum temperatures averaging 43 °C.

Following initial germination but before planting in the cores, the loblolly and longleaf seedlings were quite different in character (Table 2). Loblolly seedlings had about 40 % longer taproots than longleaf seedlings (8.1 to 5.8 cm, respectively), and 15 % of the loblolly pine seedlings had a single lateral root formed (no seedlings had more than one lateral root). About half the loblolly pine seedlings were root-pruned to 10 cm to avoid J-rooting within the core, while none of the longleaf pine seedlings had lateral roots or taproots longer than 10 cm. Loblolly pine shoot length (measured from root collar to base of needles) averaged 3.4 cm.

Contrary to initial (pre-plant) seedling root lengths, longleaf seedlings had more root length density and more total (shoot + root) biomass in 11 weeks than loblolly pine seedlings under all conditions (Table 3). Aboveground biomass (needles of longleaf pine seedlings and needles and stem of loblolly pine seedlings)

Table 3 General seedling response by species and fertilization across all combinations of compaction and water content

Species	Fertilization	Seedlings (n)	Aboveground mass (g)	Root mass (g)	Root length density (cm cm^{-3})	ABR[a]
Loblolly pine	Unfertilized	45	0.140 (0.006)	0.071 (0.012)	0.241 (0.017)	2.46 (0.13)
	Fertilized	47	0.207 (0.011)	0.084 (0.006)	0.321 (0.027)	2.94 (0.20)
Longleaf pine	Unfertilized	49	0.243 (0.012)	0.162 (0.010)	0.325 (0.021)	1.62 (0.07)
	Fertilized	44	0.347 (0.019)	0.209 (0.015)	0.446 (0.037)	1.87 (0.10)

Values are means with standard errors in parentheses

[a] ABR is aboveground:belowground mass ratio

was about 70 % greater for longleaf seedlings, while root biomass was more than twice as great in longleaf seedlings as in loblolly seedlings. Root length density of longleaf pine seedlings was 36 % greater than that of loblolly pine seedlings. Fertilization had a similar effect on growth of both species. Aboveground mass, root mass, total mass, and root length density were all about 20-40 % greater in fertile soils than infertile soils with species combined.

RLD was reasonably well modeled by bulk density (linear) and volumetric water content (quadratic) for unfertilized and fertilized loblolly and longleaf pine ($R^2=0.54$) (Table 4). Unfertilized loblolly pine RLD was not affected by bulk density but did significantly respond to water content as expected (Fig. 1). Longleaf pine responded significantly and as hypothesized to both bulk density and water content (Fig. 1). Unfertilized longleaf and loblolly pine RLD responded similarly to water content. Fertilization had no influence on the RLD response to bulk density for either species (Fig. 2). Loblolly pine RLD greatly increased in fertilized, mesic soils while longleaf pine RLD increased in fertilized soils but to a lesser degree.

We hypothesized that seedlings would alter their biomass allocation in response to soil conditions, and we

Table 4 Regressor coefficients and multiple linear regression model statistics for root length density (RLD), total seedling biomass, and aboveground:belowground mass ratio (ABR) of loblolly and longleaf seedlings in response to gradients of soil bulk density, water content, and fertilization

Parameter	RLD	$P > F$	Partial R^2	Biomass	$P > F$	Partial R^2	ABR	$P > F$	Partial R^2
β_0 Intercept	−0.062	0.3258		0.213	<0.0001		2.971	<0.0001	–
β_1 Bulk density (ρ_b)		0.3979			0.7157			0.8189	–
β_2 Water content (θ_v)		0.4176			0.5819		19.274	0.0584	0.0934
β_3 θ_v^2	0.062	0.0005	0.0030		0.8666		−78.905	0.0052	0.1516
β_4 $\rho_b \times \theta_v$	1.816	<0.0001	0.0003		0.4870		−19.980	0.0029	0.0588
β_5 $\rho_b \times \theta_v^2$	−8.334	<0.0001	0.1799		0.5488		72.316	0.0002	0.0042
β_6 Fertilization (F)		0.1130			0.5423			0.7576	–
β_7 F × ρ_b		0.3107		−0.194	0.0067	0.0715	1.867	<0.0001	0.0446
β_8 F × θ_v	8.538	<0.0001	0.0466		0.5439		−45.151	0.0002	0.0028
β_9 F × θ_v^2	−24.423	<0.0001	0.0605		0.9942		123.777	0.0003	0.0457
β_{10} F × ρ_b x θ_v	−5.274	0.0002	0.0123	2.255	0.0004	0.0092	14.829	0.0735	0.0023
β_{11} F × $\rho_b \times \theta_v^2$	15.542	0.0004	0.0604	−4.146	0.0007	0.1063	−50.350	0.0316	0.0079
β_{12} Species (S)	1.539	<0.0001	0.0718	1.235	0.0003	0.3331	−4.817	0.0043	0.1877
β_{13} S × ρ_b	−0.979	<0.0001	0.0319	−0.976	<0.0001	0.0319	3.056	0.0107	0.0011
β_{14} S × θ_v	−4.413	0.0079	0.0064	−3.104	0.0188	0.0135	12.231	0.0665	0.0185
β_{15} S ×s θ_v^2		0.8405			0.1054			0.4431	–
β_{16} S × $\rho_b \times \theta_v$	2.929	0.0119	0.0097	4.250	0.0001	0.0062	−9.604	0.0398	0.0113
β_{17} S × $\rho_b \times \theta_v^2$		0.2600	–	−3.550	0.0019	0.0339		0.8804	–
β_{18} S × F	−0.502	0.0002	0.0001	−2.296	0.0181	0.0047		0.6309	–
β_{19} S × F × ρ_b		0.6722		1.708	0.0163	0.0012	−1.121	0.0386	0.0017
β_{20} S × F × θ_v		0.9528		18.998	0.0195	0.0003	17.330	0.0075	0.0047
β_{21} S × F × θ_v^2	8.029	0.0423	0.0001	−29.417	0.0552	0.0005	−39.629	0.0016	0.0212
β_{22} S × F × $\rho_b \times \theta_v$	3.447	<0.0001	0.0186	−13.676	0.0214	0.0097		0.9464	–
β_{23} S × F × ρ_b x θ_v^2	−12.373	0.0005	0.0343	20.958	0.0610	0.0078		0.6540	–
Final R^2	0.5358			0.6297			0.6575		
C(p)	14.3			10.6			11.2		

Full model was of the form Response$=\beta_0+\beta_n X_n+$error where X_n = parameters listed. Model parameters included in final model were selected through multiple regression using backwards selection with each regressor evaluated at $p<0.10$

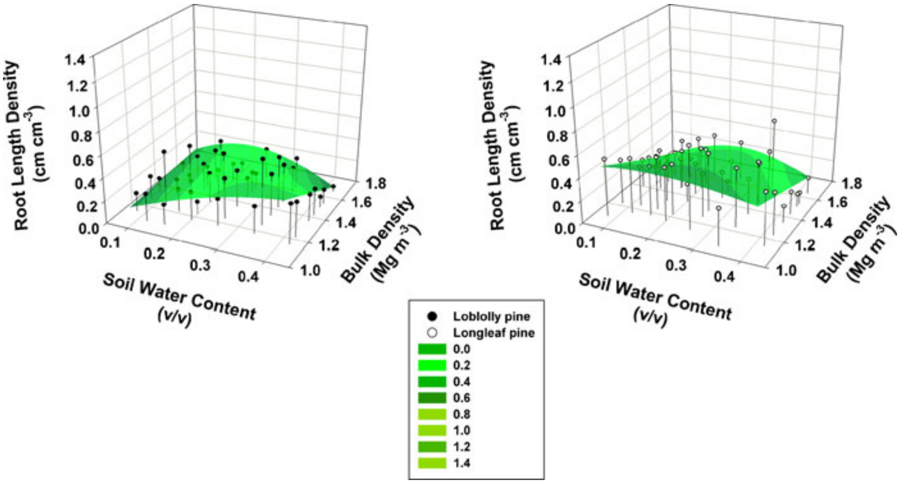

Fig. 1 Root length density of unfertilized loblolly (*P. taeda* L.) and longleaf (*P. palustris* Mill.) pine seedlings subjected to a range of bulk density values and seven levels of water content for 11 weeks

tested this by modeling the aboveground:belowground biomass ratio (ABR). We used aboveground mass instead of shoot mass since longleaf seedlings had no shoots yet and most of the aboveground mass was in foliage. Generally, we observed opposite relationships of ABR to bulk density and water content than we did in seedling biomass growth and root length density (Table 4). ABR increased linearly with respect to bulk density except for unfertilized loblolly pine (Fig. 3), and increased at both extremes of water content regardless of species or fertilization level (Figs. 3 and 4). Both species behaved similarly in response type. Soil fertilization had less effect on ABR in longleaf pine seedlings but greatly increased the responses for loblolly pine seedlings (Fig. 4).

In the field test of loblolly pine response to soil compaction, bulk density averaged 1.30 Mg m^{-3} in the uncompacted soils and 1.44 Mg m^{-3} across both compaction treatments, respectively (Fig. 5). Both compaction levels significantly increased bulk density ($p<0.05$) but were similar to each other. First-year seedling heights averaged 49.4 cm for the uncompacted soil and 48.8 cm for the compacted soils, respectively, but were not significantly different.

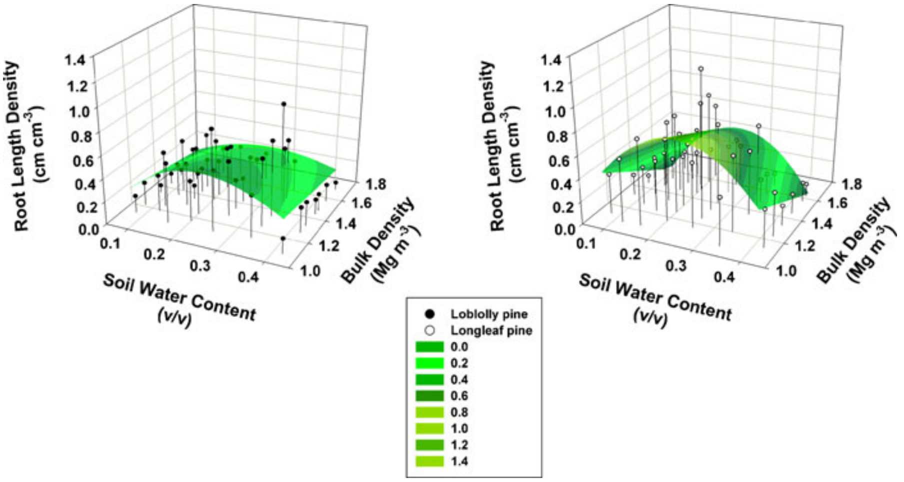

Fig. 2 Root length density of fertilized loblolly (*P. taeda* L.) and longleaf (*P. palustris* Mill.) pine seedlings subjected to a range of bulk density values and seven levels of water content for 11 weeks

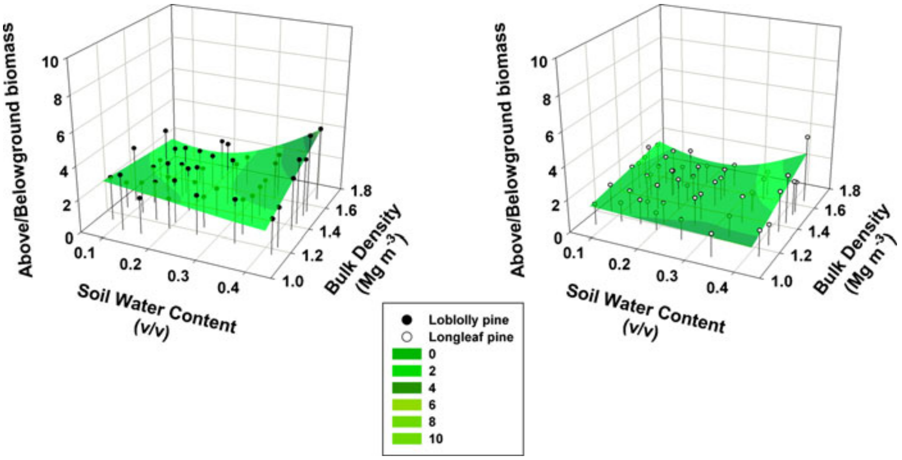

Fig. 3 Aboveground:belowground seedling mass ratio of unfertilized loblolly (*P. taeda* L.) and longleaf (*P. palustris* Mill.) pine seedlings subjected to a range of bulk density values and seven levels of water content for 11 weeks

Discussion

Our greenhouse study encompassed an even greater range of conditions than would be expected in field conditions. First, greenhouse temperatures were very similar to those expected in late spring to summer at similar field locations. Mean daily minimum temperatures for the field location in winter are 4 °C, while mean daily maximum temperatures for summer are 33 °C (Davis et al. 1986). Loblolly pine germinates in the spring, so greenhouse conditions would be similar to field conditions for naturally regenerated loblolly pine. Longleaf pine seed germinates in autumn following seedfall, so our greenhouse conditions would not be similar to those in field conditions for longleaf. The planting season for longleaf, however, ranges from July to March (summer through spring) when soil moisture is adequate (Brockway et al. 2006) thus the greenhouse conditions provided a good test of harsh but reasonable field conditions for planted seedlings of either species. Secondly, the bulk density of the field study averaged 1.3–1.5 Mg m^{-3} in uncompacted and compacted states, respectively while our cores achieved a range of 1.13 to 1.65 Mg m^{-3}. Thus, our greenhouse

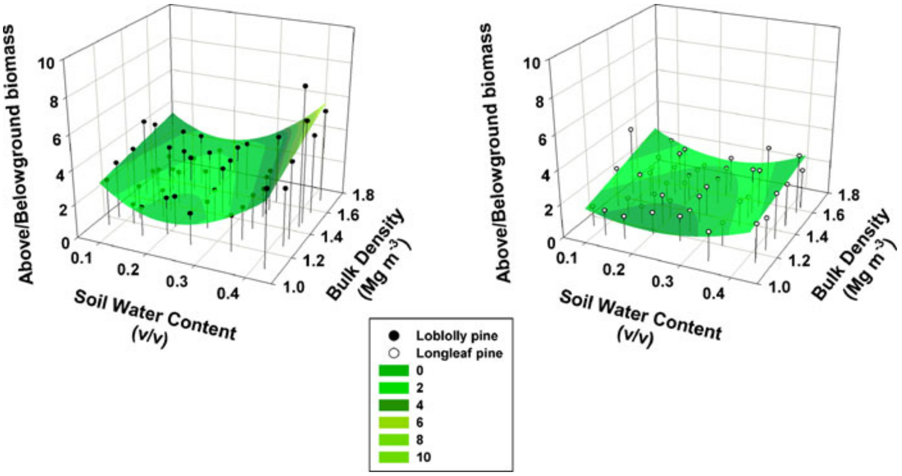

Fig. 4 Aboveground:belowground seedling mass ratio of fertilized loblolly (*P. taeda* L.) and longleaf (*P. palustris* Mill.) pine seedlings subjected to a range of bulk density values and seven levels of water content for 11 weeks

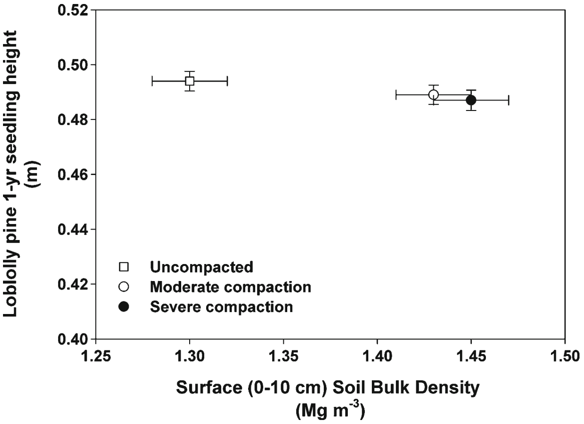

Fig. 5 Surface (0–10 cm) soil bulk density and first-year seedling heights of loblolly pine in uncompacted and compacted field soils

conditions extend to potential soil conditions beyond that which were achieved in the field for this soil. Finally, while our soil water conditions were similar to those found naturally for this soil, field conditions would rarely stay as wet or dry for a similar length of time, as precipitation is distributed throughout the year in this region. Thus, our greenhouse conditions provide a reasonable approximation of the most severe conditions either species would likely face on similar soils.

Many studies have shown cases in which soil disturbance negatively affects loblolly pine growth (Miwa et al. 2004), but in most cases more severe soil disturbance has occurred than simple compaction. Siegel-Issem et al. (2005) found that of four species, loblolly pine responded least to similar gradients in bulk density and water content as in this study. The field study showed that while the surface soils were significantly compacted, first year growth of loblolly pine was not significantly reduced. Thus, the results of our greenhouse study mirror that of our field study for loblolly pine, which suggest that on similar soils, longleaf pine may be more negatively affected by higher bulk densities. Specifically, bulk densities above 1.5 on dry or wet site conditions were highly deleterious to longleaf pine growth, and restoration projects should consider surface tillage or mechanical planting on compacted sites even where such tillage might not be required for loblolly pine plantings. Our field study showed these root-growth limiting bulk densities could easily be attained. While loblolly pine showed no negative first-year growth on these compacted soils, the greenhouse results show that longleaf would likely be susceptible to reduced root growth on these same soils.

Longleaf has been shown to be more sensitive to herbaceous plant competition for water resources than loblolly pine, especially on drier sites (Barnett 1989), but in controlled conditions it has been shown to be more resilient to water stress (Sword Sayer et al. 2005) than loblolly pine. The latter study was conducted on 6 to 8 month-old seedlings over a 28-day period. It is possible that physiological differences exist between very young seedlings and older, established seedlings, which would indicate that maintaining an uncompacted soil would be of even greater importance for naturally regenerated or direct-seeded longleaf communities on dry sites, especially for initial plantation success.

Soil fertilization altered the relationships among growth and soil physical conditions in loblolly pine, but these interactions may be partly caused by the study duration. Although loblolly pine seedling root length density was significantly related to bulk density and water content, total seedling mass was only related to water content in fertile soils. This lack of relationship among total seedling mass, soil bulk density, and water content was likely due to low overall growth of the unfertilized loblolly seedlings and may not be indicative of longer-term responses. However, (Siegel-Issem et al. 2005) found that loblolly pine responded weakly to water content gradients in a similar study. For longleaf pine and loblolly pine total seedling biomass, the negative quadratic relationships among seedling biomass and root length density and water content were more pronounced in fertile soils; seedlings did not perform appreciably better at either extreme of soil water content but performed much better in moderate soil water conditions. These relationships are important because it suggests that fertilizer does not improve seedling growth under dry or wet conditions but only under moderate soil water conditions.

Green et al. (1994) found that in infertile soils, initial differences in root:shoot ratio in loblolly pine were eliminated by imposing a drought. Our results (Figs. 3 and 4) indicate that aboveground growth is retarded less than belowground growth in poor soil conditions (compacted and too wet or too dry). Ludovici (2008) found similar results in a loblolly pine study on compacted and uncompacted soils in North Carolina. Since fine root mortality had yet to occur, the change in relative biomass allocation of loblolly pine in response to fertilization supports the divergent allocation hypothesis (Gower et al. 1992), which states that as N availability increases, C allocation to roots decreases. Jackson et al. (2012) found a similar response in newly germinated longleaf seedlings. However, this may be a seedling-specific response, as Carter et al. (2004) found the opposite in a mature longleaf forest.

Many longleaf pine restoration problems occur on more fertile soils. Fertile soils often promote herbaceous and woody competition, which is a primary reason for failure on high quality sites. If longleaf pine seedlings were to allocate more carbohydrate aboveground in extreme soil water conditions, especially on fertile soils, and then the aboveground portion is repeatedly burned, the root systems may not develop well enough for future competitiveness. If these fertile sites are also compacted or undergo a drought, longleaf pine could reallocate resources to the needles, which then may be burned off.

Conclusions

Restoring longleaf pine requires an understanding of how the tree will respond to various conditions, yet our vast research experience with loblolly pine need not be repeated if we can adapt our knowledge of loblolly pine responses to soil conditions and management. Initial growth and biomass allocation patterns for longleaf pine in response to soil compaction, drought, and different fertilization levels were similar to those of loblolly pine, but more magnified. Longleaf pine growth was retarded to a greater degree than loblolly pine in response to soil compaction and to extremes in soil water content, which combined to alter aeration and soil strength. Soil fertilization did not generally affect the direction of responses to soil physical conditions, but did tend to magnify responses. Finally, both loblolly and longleaf pine root length density and seedling mass corresponded well to our model hypothesis which was that root length density would be linearly reduced by increases in bulk density and be reduced by extremes in water content.

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References

Allison LE (1935) Organic soil carbon by reduction with chromic acid. Soil Sci 40:311–320

America’s Longleaf (2009) Range-wide conservation plan for longleaf pine. http://americaslongleaf.org Accessed May 6, 2013 52p

Aust WM, Burger JA, McKee WH Jr et al (1998) Bedding and fertilization ameliorate effects of designated wet-weather skid trails after four years for loblolly pine (*Pinus taeda*) plantations. South J Appl For 22:222–226

Barnett JP (1989) Site preparation, containers, and soil types affect field performance of loblolly and longleaf pine seedlings. In: Miller JH (ed) Proceedings of the 5th biennial southern silvicultural research conference. Gen. Tech. Rep. SO-74. U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, LA, pp 155–158

Boyer WD (1987) Volume growth loss: a hidden cost of periodic prescribed burning in longleaf pine? South J Appl For 11:154–157

Boyer WD, Miller JH (1994) Effect of burning and brush treatments on nutrient and soil physical properties in young longleaf pine stands. For Ecol Manag 70:311–318. doi:10.1016/0378-1127(94)90096-5

Brockway DG, Outcalt KW, Boyer WD (2006) Longleaf pine regeneration ecology and methods. In: Jose S, Jokela EJ, Miller DL (eds) The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, New York, pp 95–133

Carter DC, Hendricks JJ, Mitchell RJ, Pecot SD (2004) Fine root carbon allocation and fates in longleaf pine forests. For Sci 50:177–187

Daddow RL, Warrington GE (1983) Growth-limiting soil bulk densities as influence by soil texture. WSDG Report WSDG-TN-00005, U.S. Department of Agriculture, Forest Service. Ft. Collins, CO, 17pp

Davis RE, Kilpatrick TT, McArthur ML, Weeks ML (1986) Soil survey of Jones County, MS. U.S. Department of Agriculture, Soil Conservation Service

Day PR (1965) Particle fractionation and particle size analyses. In: Black CA (ed) Methods of Soil Analysis, Part 1. Agron. Monogr. 9. American Society of Agronomy, Madison, WI, pp 552–562

Foil R, Ralston C (1967) The establishment and growth of loblolly pine seedlings on compacted soils. Soil Sci Soc Am J 31:565–568

Frost C (2006) History and future of the longleaf pine ecosystem. In: Jose S, Jokela E, Miller D (eds) The longleaf pine ecosystem, ecology, silviculture, and restoration. Springer, New York, pp 9–42

Gower ST, Vogt KA, Grier CC (1992) Carbon dynamics of Rocky Mountain Douglas-Fir: influence of water and nutrient availability. Ecol Monogr 62:43–65

Greacen E, Sands R (1980) Compaction of forest soils. A review. Aust J Soil Res 18:163–189. doi:10.1071/SR9800163

Green TH, Mitchell RJ, Gjerstad DH (1994) Effects of nitrogen on the response of loblolly pine to drought II. Biomass allocation and C:N balance. New Phytol 128:145–152. doi:10.1111/j.1469-8137.1994.tb03997.x

Grossman RB, Reinsch TG (2002) Bulk density and linear extensibility. In: Dane JH, Topp GC (eds) Methods of soil analysis, part 4. Physical methods. Soil science society of america book series no. 5. Soil Science Society of America, Madison, pp 221–228

Haywood JD, Grelen HE (2000) Twenty years of prescribed burning influence the development of direct-seeded longleaf pine on a wet pine site in Louisiana. South J Appl For 24:86–92

Jackson DP, Dumroese RK, Barnett JP (2012) Nursery response of container *Pinus palustris* seedlings to nitrogen supply and subsequent effects on outplanting performance. For Ecol Manag 265:1–12. doi:10.1016/j.foreco.2011.10.018

Johnsen KH, Butnor JR, Kush JS et al (2009) Hurricane Katrina winds damaged longleaf pine less than loblolly pine. South J Appl For 33:178–181

Ludovici KH (2008) Compacting coastal plain soils changes midrotation loblolly pine allometry by reducing root biomass. Can J For Res 38:2169–2176. doi:10.1139/X08-060

Maron J, Jefferies R (2001) Restoring enriched grasslands: effects of mowing on species richness, productivity, and nitrogen retention. Ecol Appl 11:1088–1100

Mitchell ML, Hassan AE, Davey CB, Gregory JD (1982) Loblolly pine growth in compacted greenhouse soils. Trans ASAE 25:304–312

Miwa M, Aust WM, Burger JA, Patterson SC, Carter EA (2004) Wet-weather timber harvesting and site preparation effects on coastal plain sites : a review. South J Appl For 28:137–151

Moehring DM, Grano CX, Bassett JR (1966) Properties of forested loess soils after repeated prescribed burns. Research Note SO-40, U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, LA 4pp

Moore WH (1985) Geologic map of Mississippi. Mercury Maps Inc., Jackson

Olson S, Dean L (1965) Phosphorus. In: Black C (ed) Methods of soil analysis, part 2. American Society of Agronomy, Madison, pp 1035–1050

Richards LA (1949) Methods of measuring soil moisture tension. Soil Sci 68:95–112

Scott DA, Dean TJ (2006) Energy trade-offs between intensive biomass utilization, site productivity loss, and ameliorative treatments in loblolly pine plantations. Biomass Bioenergy 30:1001–1010. doi:10.1016/j.biombioe.2005.12.014

Siegel-Issem CM, Burger JA, Powers RF et al (2005) Seedling root growth as a function of soil density and water content. Soil Sci Soc Am J 69:215–226

Stagg RH, Scott DA (2006) Understory growth and composition resulting from soil disturbances on the long-term soil productivity study sites in Mississippi. In: Connor KF (ed) Proceedings of the 13th biennial southern silvicultural research conference. Gen. Tech. Rep. SRS-92. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp 52–56

Stainback GA, Alavalapati JRR (2004) Restoring longleaf pine through silvopasture practices: an economic analysis. For Policy Econ 6:371–378. doi:10.1016/j.forpol.2004.03.012

Sword Sayer MA (2007) Repeated fire effects on soil physical properties in two young longleaf pine stands on the West Gulf Coastal Plain. In: Kush JS (ed) Longleaf Alliance Report No. 10. Proc. of the Sixth Longleaf Alliance Regional Conference, 2006 November 13-16, Tifton, GA. Auburn University, Auburn, AL, pp 134–136

Sword Sayer MA, Brissette JC, Barnett JP (2005) Root growth and hydraulic conductivity of southern pine seedlings in response to soil temperature and water availability after planting. New For 30:253–272. doi:10.1007/s11056-005-7481-x

Sword Sayer MA, Haywood JD (2009) Fire and longleaf pine physiology–Does timing affect response? Proc. of the 2009 Society of American Foresters National Convention, 2009 September 30-October 4, Orlando, FL. Washington DC: Society of American Foresters. pp 1–11

Sword Sayer MA, Kuehler EA (2010) Influence of repeated prescribed fire and herbicide application on the fine root biomass of young longleaf pine. In: Stanturf JA (ed) Proceedings of the 14th biennial southern silvicultural research conference. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, pp 267–273

USDA Soil Survey Staff (1992) Soil survey methods. Soil Survey Investigations Report No 42, National Soil Survey Center, Lincoln, NE 400 pp

Worrell R, Hampson A (1997) The influence of some forest operations on the sustainable management of forest soils - a review. Forestry 70:61–85