EARLY LOBLOLLY PINE GROWTH RESPONSE TO CHANGES IN THE SOIL ENVIRONMENT*

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ABSTRACT

Identifying the critical soil- and site-based determinants of pine productivity is a crucial part of developing management practices that facilitate maintenance and enhancement of long-term site productivity. The objectives of this analysis were to: (i) determine the relationships between soil and site properties controlling early loblolly pine (*Pinus taeda* L.) productivity, and (ii) determine the effects of site preparation on these relationships. Fifty-four loblolly pine bioassay plots were established across a gradient of soil disturbance, organic debris removal, and site preparation methods. These mini-stands were designed to simulate the growth response of commercially spaced trees to the disturbance/site preparation gradient at stand closure. Several soil and site properties were selected as indicators of the three dominant soil attributes controlling tree productivity—(i) promotion of root growth, (ii) air/water balance, and (iii) soil fertility—and they were measured at each of the 54 bioassay plots. A multilinear regression analysis showed that soil oxidation depth (air/water balance), the Least Limiting Water Range (LLWR) (promotion of root growth), and net nitrogen mineralisation (soil fertility) were the most important soil indicator variables explaining pine productivity. A multiple interaction model with dummy variables included for the site preparation methods showed that oxidation depth interacted strongly with the LLWR and net nitrogen mineralisation, with the model explaining 87% of the variation in 2-year-old tree height. The model showed that oxidation depth was the most important soil variable affecting early tree growth, having large positive effects on tree height even for soils with very poor

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physical quality (low LLWR). Bedding increased 2-year-old tree height compared to that in non-bedded plots. The bedding response was attributed to a doubling in oxidation depth, and secondarily to improved net nitrogen mineralisation. There was an optimum oxidation depth above and below which tree growth declined, showing that these sites experienced both aeration and available water-limiting conditions. The optimum oxidation depth was 30 cm, which corresponded to an average water table depth in winter of 43 cm. High net nitrogen mineralisation offset the negative effects of high oxidation depths; trees growing on well-drained locations with high nitrogen availability and oxidation depths in excess of 30 cm outgrew trees growing on well-drained locations with similar oxidation depths and low nitrogen availability. These results suggest that with taller beds, and especially with internal drainage treatments such as the mole-plough, soil fertility may have to be increased with fertiliser application if the inherent levels of fertility are low and the goal is to maximise pine production.

Keywords: site productivity; soil indicators; *Pinus taeda*.

INTRODUCTION

The forest industry understands that its economic survival and prosperity are partly tied to its ability to maintain and enhance site productivity. Success in this endeavour depends on understanding how different management practices affect sites, and an ability to employ management strategies to correct both inherent problems and those induced by management. Thus, we need to know what site factors control productivity (i.e., critical factors), and how to correct them when they are found deficient through either neglect or inherent limitations.

In the pine plantations of the Lower Coastal Plain of the south-eastern United States, productivity concerns are centred around site hydrology, which plays a major role in regulating both management access and productivity (Morris & Campbell 1991). A combination of nearly-level topography, poor internal drainage, and high rainfall results in a perched water table which inundates the soil surface several times each year; when timber is harvested under these wet conditions, severe soil disturbances including compaction, displacement, and waterlogging can occur (Hatchell *et al.* 1970; Gent *et al.* 1983; Aust *et al.* 1993, 1995). The potentially negative impacts of these soil disturbances are at least partially mitigated through a combination of drum chopping, disking, and/or bedding (McKee & Shoulders 1974; Haines *et al.* 1975; Gent *et al.* 1983; Morris & Campbell 1991).

Because it takes a rotation-length study to determine if tree growth has been affected by management practices, the benefits or deleterious effects of cultural practices on long-term site productivity are largely unknown (Morris & Miller 1994). In a synthesis of studies conducted across the globe, Powers *et al.* (1990) hypothesised that tree productivity declines were most likely explained by soil compaction and removal of organic debris. Based on this hypothesis, the USDA Forest Service began a series of rotation-length studies to investigate the effects of soil disturbance and organic matter removal on long-term site productivity (Powers 1991).

Soil disturbance and organic matter removal affect long-term site productivity by disrupting the soil air/water balance and/or depleting soil fertility (Burger & Kelting 1998). The extent to which site productivity will be degraded, if at all, depends on the soils' ability to either resist or recover from damage. These abilities are soil-/site-specific, requiring an understanding of the effects of organic matter removal and soil disturbance on soil fertility and air/water balance for all major soil/site types under forest management.

We began a study in 1991 to determine the effects of organic matter removal, soil disturbance, and mitigative practices on the long-term productivity of a site for loblolly pine production located on the Lower Coastal Plain. Within this study, soil properties hypothesised to be key determinants of tree productivity were monitored across a range of management scenarios. This paper reports the relationships found between the soil properties and early loblolly pine growth, and the effects of site preparation on these relationships.

MATERIALS AND METHODS

Location and Description of Study Site

The study sites are located on the Lower Coastal Plain in Colleton County, South Carolina, approximately 65 km west of Charleston (approx. 32°85′ N latitude and 80°45′ W longitude). Precipitation averages 132 cm annually, with the majority of rainfall occurring during the summer months (May-Sept). The average growing season is between 240 and 280 days, with precipitation during this period averaging between 86 and 94 cm. Average summer and winter temperatures are 31° and 18°C, respectively (Stuck 1982). The region is nearly level, being dissected by many broad valleys containing wide meandering streams which terminate in estuaries along the coast. Natural drainage systems are poorly defined, and water moves slowly via lateral drainage through the upper soil horizons (Runge 1977). Soils are developed from beds of unconsolidated sands, clays, and soft limestone. The study area is dominated by two soil series, Argent loam and Santee loam, in the Ochraqualfs and Argiaquolls great groups (Stuck 1982), respectively. Sandy loam-textured A and E horizons are present and average 40 cm deep, combined. A deep (>140 cm) sandy clay to clay loam Bt horizon underlies the surface horizons (Burger 1994). Saturated hydraulic conductivity of the Bt horizon is very slow (0.10 cm/h—Burger 1994), resulting in a perched water table on top of the Bt horizon after heavy rainfall. The Argent and Santee soils are among the highest quality soils in the region for pine production (site index = 24 m at base age 25 years) and receive no fertiliser inputs.

The pre-treatment stand was a 21-year-old second-rotation loblolly pine plantation that had been established in the early 1970s using conventional mechanical site preparation methods (shear-rake, windrow, burn, bed). An intensive pre-harvest timber inventory showed that the plantation had exhibited above-average growth for loblolly pine in the south-eastern United States (475 m^3/ha at age 21 — Preston 1996). A more complete description of other pre-harvest characterisation work done on the study site has been given by Burger (1994) and Preston (1996).

Layout of Harvesting and Site Preparation Treatments

In 1991 three study blocks were selected based on similarity of drainage patterns and soil type (Burger 1994). Each block was subdivided into six 3-ha plots, and two operational harvesting treatments were randomly assigned to five plots per block: (i) two dry harvests and (ii) three wet harvests. Three levels of site preparation, (i) none, (ii) bedded, and (iii) mole ploughed and bedded, were randomly assigned to the wet harvested plots. Two levels of site preparation were randomly assigned to the dry harvested plots: (i) none and (ii) bedded. The plots were harvested in September 1993 (dry harvest) and March 1994 (wet harvest). Dry and wet harvests were defined as surface (0 to 30 cm deep) volumetric soil moisture contents of less than 15% and greater than 30%, respectively. The site preparation treatments were installed in November 1995, and the plots were hand-planted with genetically improved loblolly pine seedlings (Westvaco Corporation, Georgia) in early February 1996. Detailed descriptions of equipment manufacturers and configuration, and treatment installation, have been given by Kelting *et al.* (1999).

Selection of Measurement Subplots

Measurement subplots were selected within each treatment plot across the gradient in surface organic debris and soil disturbance that resulted from harvesting. Five levels of organic debris—(1) bare soil, (2) litter layer, (3) light slash, (4) heavy slash, and (5) slash piles—and five levels of soil disturbance—(1) undisturbed, (2) compacted, (3) shallow ruts (<20 cm), (4) deep ruts (>20 cm), and (5) churned soil—were defined (*see* Kelting *et al.* 1999) and mapped spatially on each wet- and dry-harvested treatment plot prior to site preparation (Preston 1996). The mapping was done using 1/125-ha circular subplots that were established on a 20 × 20-m grid that had been put in place in each treatment plot for measuring shallow water table depth. The 1/125-ha circular subplots were divided into quadrants, and the percentage area covered by each organic debris and soil disturbance class was estimated to the nearest 10% in each quadrant. The soil disturbance and organic debris classes were mapped spatially using the weighted averages from each subplot.

Measurement subplots were selected in each treatment plot that represented the average condition with respect to each level of organic debris and soil disturbance that occurred in the treatment plot (Kelting *et al.* 1999).

Soil Productivity Indicators

Maintaining productivity is one function of forest soils (Burger & Kelting 1998). For productivity to be maintained the soil must be able to promote root growth, maintain air/water balance, and maintain soil fertility. These general attributes of soils are qualitative descriptors that help us focus in on specific measurable soil properties that relate to each attribute. The soil properties that we measure are called soil productivity indicators, as they indicate the direction of movement of the attributes in response to forest practices. The soil productivity indicators shown in Table 1 are the best variables, in our estimation, to represent the attributes, and were selected for measurement based on: (i) their known or hypothesised close relationship to the attribute, (ii) documented relationships with plant growth, and (iii) relative ease of measurement.

At each measurement subplot, perched water table depth (0 to 90 cm) was measured from 5 cm i.d. by 90-cm-deep PVC observation tubes, volumetric soil moisture content in the surface 0- to 30-cm soil layer was measured using Time Domain Reflectometry (TDR; TRASE system, Soil Moisture Equipment Corp, Goleta, CA), and oxidation depth was measured on steel rods (McKee 1978) on a monthly basis from May 1996 through June 1997.

During June 1997, two 5 cm i.d. by 10-cm-long intact soil cores were collected from the 10- to 20-cm depth adjacent to the TDR rods using a hammer-driven core sampler. The cores were used to determine bulk density (Blake & Hartge 1986), total porosity, and macroporosity (Danielson & Sutherland 1986). Also at this time, a composite loose soil sample consisting of 10 subsamples was collected at each location using a 2.5 cm i.d. by 30-cm-long push tube soil sampler. This sample was air-dried and passed through a 2-mm sieve and used to determine available phosphorus and exchangeable base cations.

The Least Limiting Water Range (LLWR) and "the percentage of time the soil water content falls within the LLWR" (Pin) were calculated from the soil physical properties and monthly measurements of soil water content. The operational definition of LLWR is "the range in soil water contents in which limitations for plant growth associated with available water, aeration, and soil strength are minimal" (da Silva *et al.* 1994). As the LLWR increases, the likelihood of plant growth limitations from soil physical restrictions decreases. The Pin is an *in situ* application of the LLWR that recognises that under a given soil physical condition (i.e., LLWR), the field soil water content will determine if soil physical problems limit productivity (*see* da Silva *et al.* (1994) for a complete description of the derivation and application of the Least Limiting Water Range).

An index of available phosphorus was determined by double-acid (0.05 N HCl + 0.025 $N\,H_2SO_4$) extraction in a 1:4 soil-to-solution extract (Watanabe & Olsen 1962) followed by colorimetric analysis (Spectronic 20D$^+$, Spectronic Instruments, Inc., Rochester, NY). Exchangeable base cations (calcium, magnesium, and potassium) were determined by extraction with 1 $M\,NH_4OAc$ (pH 7) in a 1:10 soil-to-solution extract (Thomas 1982) which had been extracted for 1 h on a reciprocating shaker. Concentrations of base cations were determined using inductively coupled plasma (ICP) spectroscopy (Jarrell-Ash Corp., Franklin, MA).

Net nitrogen-mineralisation was determined using the buried bag method (Eno 1960) on an approximate monthly basis from June 1996 through August 1997. Ten soil samples were collected monthly using a 2.5 cm i.d. by 30-cm-long push tube soil sampler. The subsamples were combined in the field, and one-half of the composite sample was incubated in a polyethylene bag buried vertically in the A horizon. The initial inorganic nitrogen was determined from the remaining non-incubated sample. Monthly net nitrogen-mineralisation was calculated as the difference in inorganic nitrogen concentration between the incubated and initial samples. The inorganic nitrogen was extracted from all soil samples with 2 M KCl and analysed for nitrate-nitrogen and ammonium-nitrogen colorimetrically.

The chemical data were corrected for soil moisture content and converted to kilograms per hectare based on the bulk density measurements and a sampling depth of 30 cm.

For all of the field work described above, samples were collected from between wheel tracks for the wet and dry harvest / none site prepared treatments and on the tops of the beds for the bedded treatments. This was done for three reasons: (i) it was generally not possible to collect samples from the ruts due to the high water table, (ii) changes in soil properties in the ruts were previously documented (Preston 1996), and (iii) the trees were planted between the ruts and on the tops of the beds, and we wanted to sample the soil environment in which the trees were growing.

Tree Growth Response

It is often difficult to establish quantitative relationships between soil properties and tree productivity, as the tree productivity we measure is the final expression of complex interactions between genotype and environment (Kozlowski *et al.* 1991). Because young loblolly pine trees planted at commercial spacing have low demand for site resources (e.g., only needing about 5 kg N/ha·year for the first few years — Dougherty 1996), soil resource limitations on tree growth may not be apparent until after stand closure when the trees are under intense competition with each other for soil resources. Thus, we cannot rely solely on the short-term response of the commercially-planted trees to tell us how soil disturbance, organic debris removal, or site preparation may have affected a soil's ability to provide the resources adequate for tree growth. It is likely that the lack of competition for soil resources would result in poor correlations between soil properties and the commercially-planted trees, since these resources would not be limiting tree growth at this time.

To overcome these problems, relationships between loblolly pine productivity and soil properties were determined from "bioassay" plots co-located with a subset of soil process measurement subplots. Fifty-four identically spaced loblolly pine bioassay plots were planted concurrently with the operational planting (i.e., February 1996). The bioassay plots were 2.1 × 6.3 m, and seedlings were planted at 30 × 30-cm spacing (147 seedlings per plot) by the same two-person crew. Only seedlings of similar size and vigour were planted. The exact spacing eliminated the effects of variation in stand density on tree growth, and use of one crew ensured uniformity in tree growth response to planting technique. The bioassay plot size was chosen so as to span an entire soil disturbance class (a disturbance class is the width of a skid trail, which averaged 6 m). The close spacing was chosen to ensure stand closure during the first growing season. Competing vegetation was controlled within each plot by a combination of chemical and manual herbaceous vegetation control.

The theory behind the bioassay plots is that the close spacing of the seedlings will encourage early competition for soil resources, in effect simulating how the trees planted at commercial spacing would respond to limited soil resources after stand closure. Thus, if soil resources are limiting, then good relationships should be found between soil resources and tree growth; tree growth response on the bioassay plots should also give us some foresight on the likely response of the commercially-planted trees to soil resources after stand closure.

The total heights of the trees in the internal rows (external row was left as a buffer) were measured in March 1998, 2 years after planting. Each tree was classified in one of four microsite types on the bedded plots: (i) top of bed, (ii) side of bed, (iii) furrow, and (iv) interbed; and into one of two microsites on the non-bedded plots: (i) in rut and (ii) not in rut. The "top of bed" and "not in rut" microsites corresponded with the locations where the soil productivity indicator data were collected.

Statistical Analysis

Simple and multilinear regression analyses were used to investigate relationships between the average height of trees growing on the "top of bed" and "not in rut" microsites and the soil productivity indicator data collected at those microsites. A major objective of the multilinear regression analysis was to investigate the relative importance of each of the three soil attributes in explaining early tree growth. To meet this objective, an a priori decision was made to restrict the model such that the final model would include at least one soil property from each of the three attributes (Table 1) if possible, *versus* simply identifying the model that explained the most variation in tree growth regardless of the variables included. The first step in the process was to remove variables with high multicolinearity using standard multicolinearity diagnostic techniques (Montgomery & Peck 1992). Then the most

TABLE 1–Soil attributes for the forest soil function of maintaining site productivity, and the soil indicator variables used to measure them*.

Soil attribute	Soil indicator variable	Measurement unit
1. Promote root growth		
	Bulk density	g/cm^3
	Aeration porosity	% by volume (cm^3/cm^3)
	Least limiting water range (LLWR)†	% by volume (cm^3/cm^3)
	% of time within the LLWR	%
	Pin‡	%
2. Maintain air / water balance		
	Surface soil depth	cm
	Water table depth	cm
	Oxidation depth	cm
3. Maintain soil fertility		
	Net nitrogen mineralisation	kg N/ha·year
	Exchangeable calcium	cmol/kg
	Exchangeable magnesium	cmol/kg
	Exchangeable potassium	cmol/kg
	Double-acid extractable phosphorus	kg/ha

* Adapted from Burger & Kelting (1998).
† Least Limiting Water Range (from da Silva *et al.* 1994).
‡ Pin = percentage of time the soil water content is within the LLWR.

discriminating variables were determined using the All Possible Regressions procedure (Montgomery & Peck 1992), wherein a "best" model was selected based on the criteria of maximising the Adjusted R-square and minimising the Mean Square Error (MSE). Residual plots were used in each step in the model development process to qualitatively evaluate the validity of the model. Multilinear regression on standardised (normal 0, 1) data was used to ascertain the relative importance of the variables included in the best model. A primary assumption underlying the modelling was that the soil productivity indicators measured would capture most of the variation in tree growth associated with harvesting disturbance and site preparation. Thus, there should be no additional blocking, disturbance, or site preparation effects on tree growth when these factors are added to the model. This assumption was tested by adding block, disturbance, and site preparation treatment to the final model as dummy variables.

RESULTS AND DISCUSSION

Simple Linear and Quadratic Effects

Individual relationships among the indicators of soil productivity and tree growth were explored with simple linear and quadratic regression models.

There was a weak negative relationship between tree height and bulk density (Table 2). The bulk density ranged from 0.36 to 1.63 g/cm^3. The surface soil texture was relatively uniform across the study site, falling in the sandy loam textural class. In this textural class, bulk density begins to limit tree growth at around 1.5 g/cm^3 (Pierce *et al.* 1983), a level which was exceeded in 13% of the samples. Other studies have reported quadratic effects for bulk

TABLE 2–Linear and quadratic relationships between soil productivity indicators and the height of 2-year-old loblolly pine trees*. The soil productivity indicators are grouped by attribute.

Soil productivity indicator	R^2	Adj. R^2	Linear effects Direction†	Linear effects P-value	Quadratic effects Direction	Quadratic effects P-value
Promote root growth						
Bulk density	0.12	0.11	–	0.009		n.s.‡
Aeration porosity	0.16	0.13	+	0.022	–	0.063
LLWR	0.36	0.35	+	0.000		n.s.
Pin LLWR	0.57	0.54	+	0.000		n.s.
Air / Water balance						
Depth to Bt horizon	0.11	0.10	+	0.013		n.s.
Water table depth	0.54	0.52	+	0.002	–	0.070
Oxidation depth	0.72	0.71	+	0.000	–	0.020
Soil fertility						
Net nitrogen mineralisation	0.11	0.09	+	0.015		n.s.
Exch. calcium				n.s.		n.s.
Exch. magnesium				n.s.		n.s.
Exch. potassium				n.s.		n.s.
Extractable phosphorus				n.s.		n.s.

* General model was: Tree height = $b_0 + b_1$ Property + b_2 (Property)^2; n = 54.
† Direction is the sign of the slope estimate for the soil productivity indicator.
‡ Not significant if the overall model P-value was greater than 0.10.

density for coarse-textured soils, where higher bulk densities can increase water-holding capacity and nutrient diffusion rates (Greacen & Sands 1980). There was a quadratic effect of aeration porosity on tree growth, with tree growth decreasing on either side of 21% aeration porosity. The decrease above 21% aeration porosity probably reflects lower available water from a commensurate reduction in field capacity. The LLWR had a strong positive relationship with tree growth, explaining 36% of the variation in 2-year-old tree height. This relationship improved when the LLWR was used to calculate the Pin, with Pin explaining 57% of the variation in tree height. The strong relationships among the LLWR, Pin, and tree growth illustrate the importance of maintaining or creating the proper soil physical conditions for root growth. Though this is the first attempt at relating tree growth to the LLWR, others have been successful in relating the LLWR to the growth of agricultural crops (da Silva & Kay 1996).

The indicators of air/water balance all had positive relationships with 2-year-old tree height (Table 2). Surface soil depth (depth to Bt) has often been found to have a positive effect on tree growth (Carmean 1975), as surface soil depth is an indicator of effective rooting volume and has been found to correlate well with indicators of soil air/water balance: soil texture, soil colour, available water, and soil pH (Rhoton & Lindbo 1997). The weak relationship between depth to Bt and tree growth reflects the probability that the quantity of rooting volume is not as important as the quality of the rooting volume on these sites. This interpretation is supported by the strong relationships found between water table depth and tree growth, and oxidation depth and tree growth, with these variables explaining 54% and 72% of the variation in tree height, respectively. The strong positive linear relationship between these variables and tree height reflects the importance of soil aeration in determining the quality of the rooting environment for tree growth on wet sites (McKee 1994). The significant negative quadratic effect shows that there is a maximum aeration depth above which tree growth decreases from inadequate water availability; thus, water table depth and oxidation depth are good indicators of air/water balance. The quadratic effect was demonstrated in a bedding study that showed that pine growth decreased on high beds from drought conditions (Mann & McGilvery 1974). Oxidation depth shows the same effect as water table depth because these variables are strongly correlated, as first demonstrated by McKee (1978). Oxidation depth is a more direct measure of soil aeration than water table depth. This, combined with the integrative nature of the rusty rod measurement, probably explains the stronger relationship between tree growth and oxidation depth.

Net nitrogen mineralisation was the only indicator of soil fertility related to tree growth (Table 2), with net nitrogen mineralisation showing a weak positive relationship with tree height. The positive relationship reflects the obvious importance of nitrogen availability, as has been found in many studies (e.g., Nadelhoffer *et al.* 1984; Birk & Vitousek 1986; Zak *et al.* 1989), but the low correlation suggests that soil fertility did not limit tree growth on these sites as much as the quality of the soil physical environment early in the rotation. The lowest net nitrogen mineralisation measured was 40 kg N/ha·year, which is well above the estimated requirements for 2-year-old loblolly pine trees.

No relationships were found between tree growth and exchangeable base cations. This result is consistent with the Alfisols and Mollisols soil orders, which have inherently high levels of exchangeable base cations. Double-acid extractable phosphorus exceeded the 4 mg/kg critical level for loblolly pine growth response to phosphorus (Wells *et al.* 1973) for 90% of the samples, illustrating that phosphorus availability did not limit early productivity on this site. McKee & Shoulders (1974) also found no relationship among exchangeable base cations, phosphorus, and tree growth in pine plantations on similar soils. Their conclusion was that the quality of the physical rooting environment was more important for tree growth than soil chemical properties early in the rotation. Their conclusion, along with the results from this study, illustrate the important role the physical rooting environment plays in soil nutrient availability—i.e., nutrient availability is a function not only of the quantity of nutrients, but also of the ability of the roots to access nutrients.

Multilinear Effects

The multilinear regression analysis started with a full model containing all of the variables listed in Table 1. This model explained 83% of the variation in tree height and had an MSE of 588. The residual plot shows that the full model did a poor job describing the relationship between the soil properties and tree growth, showing a strong quadratic effect in the residuals (Fig. 1A). The multicolinearity diagnostics identified a strong correlation between oxidation depth and water table depth. Through an iterative process of including and removing each of these variables from the full model, water table depth was found to have weaker explanatory ability and was discarded.

The best model selected based on the criteria described in the Methods was a three-variable model with LLWR, oxidation depth, and net nitrogen mineralisation, representing the "promote root growth", "air/water balance," and "soil fertility" attributes, respectively (Table 3). The criterion of having at least one variable from each attribute in the final model resulted in a weaker model based on a reduced R-square and increased MSE, but the residual

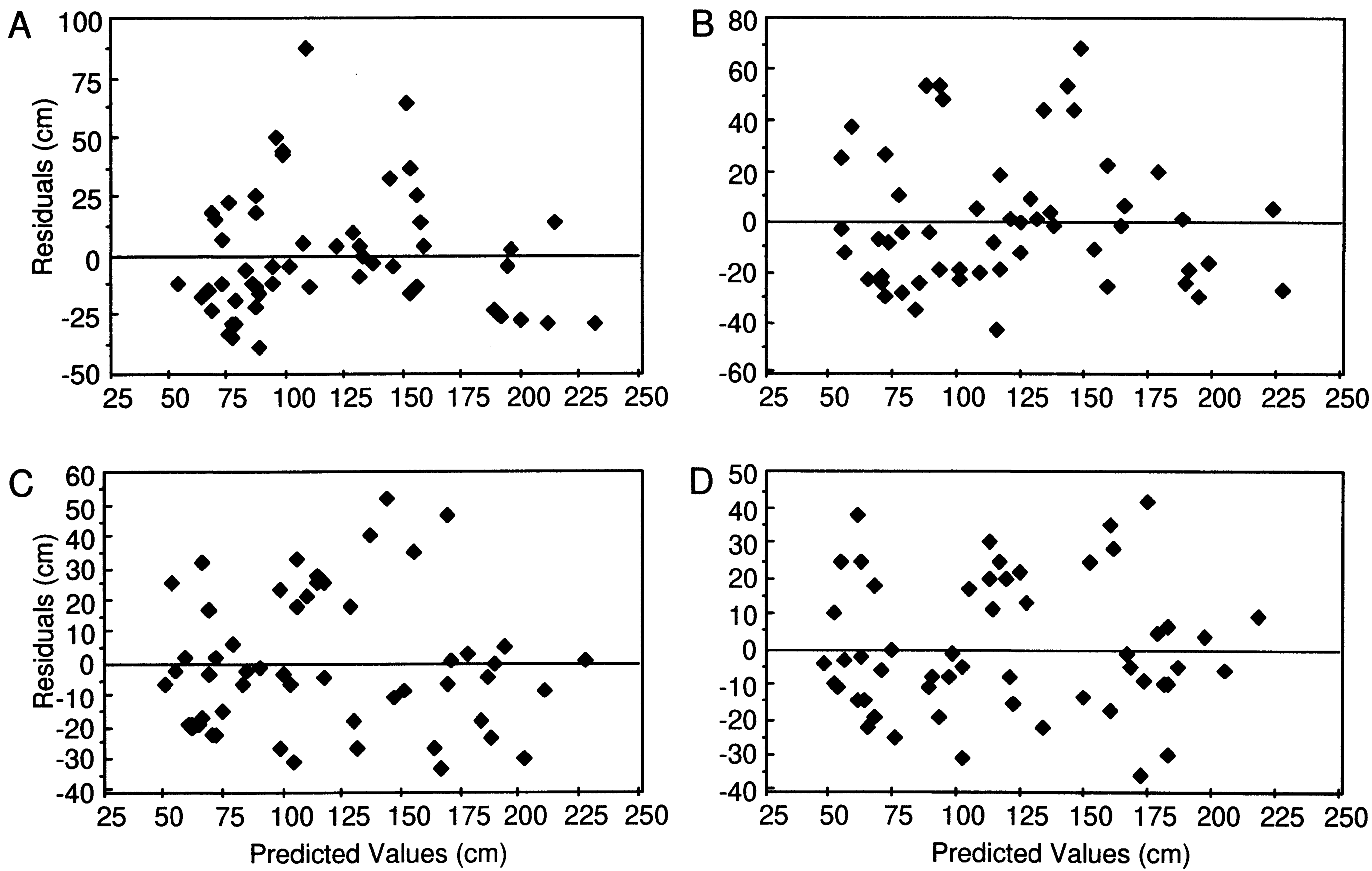

FIG. 1–Residual plots for the full model (A), the best 3-variable model (B), the best 3-variable model with intercept terms for site preparation (C), and the final model with interactions and intercept terms for site preparation (D).

TABLE 3–Final multilinear regression model for relating 2-year-old tree height to soil productivity indicators*

Parameter	Parameter estimate	Standardised estimate	P-value
Promote root growth			
LLWR (cm^3/cm^3)	127.193	0.302	0.000
Air / Water balance			
Oxidation depth (cm)	3.681	0.629	0.000
Soil fertility			
Net nitrogen mineralisation (kg N/ha·year)	0.094	0.123	0.124

* Model: Tree height (cm) = –19.319 + 127.193 LLWR + 3.681 Oxidation depth + 0.094 Net N mineralisation; *R-square* = 0.74; *MSE* = 752; *N* = 54.

plot shows a more even distribution of residuals and a much-reduced quadratic effect (Fig. 1B). Inclusion of net nitrogen mineralisation in the model can be questioned given the p-value; however, we felt justified in taking a conservative approach given the highly variable nature of this measurement and the known relationship between nitrogen availability and tree growth.

Oxidation depth and the LLWR are significantly more important than net nitrogen mineralisation in explaining the variation in 2-year-old tree height (Table 3). The standardised estimates show the relative importance of each of the variables in the model, with oxidation depth, LLWR, and net nitrogen mineralisation weighted at 0.6, 0.3, and 0.1, respectively. So, about 90% of the explanatory power of the model can be attributed to the effects of the soil physical environment on tree growth. This relationship may reverse with time. As the new plantation grows, evapotranspiration rates will increase and the trees and other vegetation will begin to exert greater control over the water table. Also, net nitrogen mineralisation will decrease with time (Dougherty 1996) and may reach a point where nitrogen availability becomes the growth-limiting factor.

Site Preparation Treatment Effects

Blocking and soil disturbance class had no effect on the model (results not shown), but inclusion of the site preparation treatment effect improved the model (Table 4). With site preparation treatment included, the model explains 84% of the variation in tree height, with a large reduction in the MSE. The residual plot also indicates a better model, with a more random distribution of residuals about the predicted line (Fig. 1C).

The intercept term for the dry-harvest/no-preparation treatment was not significantly different from the wet-harvest/no-preparation treatment (Table 4). Oxidation depth was shown to be the primary soil property affecting 2-year-old tree height (Table 3). As was discussed previously, oxidation depth is positively correlated with water table depth. Water table depth is determined by site hydrology and within-site differences in elevation. In this study, site hydrology basically overwhelmed any potential smaller scale wet-harvest disturbance effects on the water table, and thus oxidation depth. The lack of a wet-harvest effect on tree height should be viewed with caution, as the effects of soil disturbance on water table depth are probably related to the percentage of the site disturbed in addition to the intensity of disturbance.

TABLE 4–Site preparation treatment effects on the relationship between 2-year-old tree height and the soil productivity indicators*

Parameter	df	Parameter estimate	T	P > |T|
Treatment effects				
Intercept (Wet / None)	1	–1.729	–0.15	0.879
Intercept terms†				
X1 (Dry / None)	1	–4.089	–0.43	0.672
X2 (Wet / Bed)	1	23.622	2.11	0.040
X3 (Dry / Bed)	1	34.376	3.01	0.004
X4 (Mole / Bed)	1	46.096	4.26	0.000
LLWR (cm^3/cm^3)	1	91.435	2.96	0.005
Oxidation depth (cm)	1	2.802	5.86	0.000
Net nitrogen mineralisation (kg N/ha·year)	1	0.076	1.47	0.149

* Model: Tree height = $b_0 + b_1$ X1 + b_2 X2 + b_3 X3 + b_4 X4 + b_5 LLWR + b_6 Oxidation depth + b_7 Net N mineralisation

where

Treatment	X1	X2	X3	X4
Wet / None	0	0	0	0
Dry / None	1	0	0	0
Wet / Bed	0	1	0	0
Dry / Bed	0	0	1	0
Wet / Mole / Bed	0	0	0	1

R-square = 0.84; *MSE* = 533; *N* = 54.

† Site preparation treatment effects tested with dummy variables.

The site preparation treatments had a significant effect on the intercept (Table 4). The parameter estimates for the intercept terms are the changes in mean tree height resulting from the site preparation treatments. The dry-harvest / bedding treatment increased mean tree height by 34 cm over the wet- and dry-harvest / no-preparation treatments. The wet-harvest / mole-plough / bedding treatment and wet-harvest / bedding treatment had mean tree height responses of 46 and 24 cm, respectively.

The general increase in mean tree height with site preparation is related to the large increases in oxidation depth with bedding (Table 5). Oxidation depth was approximately doubled with bedding. The separation in mean tree height seen between the site preparation treatments is partly due to site preparation effects on the soil productivity indicators, as well as interactions between these variables (interactions discussed in the next section).

The wet-harvest / mole-plough / bedding treatment had the highest oxidation depth (41 cm), and a high net nitrogen mineralisation rate (107 kg/ha·year) compared to the no-preparation treatments. The high oxidation depth with mole-ploughing indicates that the channels created in the subsoil clay horizon with the mole-plough were successful in draining some surface water. The higher net nitrogen mineralisation rate with mole-ploughing is probably due to increased microbial activity from the additional tillage with this treatment and improved soil aeration, as indexed by oxidation depth. Based on the standardised parameter estimates (Table 3) the increased tree height with wet-harvest / mole-plough / bedding is due mainly to enhanced soil aeration, and secondarily to enhanced

TABLE 5–Site preparation effects on the average values of the soil properties used as indicators of soil productivity.

Site preparation treatment	Soil productivity indicators		
	Oxidation depth (cm)	Net nitrogen mineralisation (kg/ha·year)	LLWR (cm^3/cm^3)
None*	16 c†	82 b	0.24 c
Dry / Bed	29 b	119 a	0.41 a
Wet / Bed	32 b	70 b	0.34 b
Wet / Mole / Bed	41 a	107 a	0.32 b

* Average of wet and dry-harvest / none site-prepared treatments.
† Values within columns followed by different letters are significantly different at alpha = 0.10.

nitrogen availability. The increased tree height response to the mole-plough will probably decrease with time as the mole channels fill in, which usually takes from 3 to 5 years (Spoor 1986).

The dry-harvest / bedding treatment resulted in an intermediate mean tree height response compared with the other two bedding treatments (Table 4). The dry-harvest / bedding treatment had the highest LLWR (Table 5), indicating that this treatment resulted in the best soil physical conditions for promoting root growth. The intermediate growth response to the dry-harvest / bedding treatment is partly attributed to the increased LLWR, as the LLWR is the second most important soil productivity indicator for explaining the variation in tree height (Table 3).

The higher LLWR with dry-harvest / bedding relates back to harvesting disturbance effects on soil physical properties. Harvesting disturbance increased the surface soil bulk density and reduced macroporosity (Aust *et al.* 1998), which reduced the LLWR. The wet-harvest treatments had an average of 87% of the harvested area disturbed, compared to about 26% of the harvested area disturbed for the dry-harvest treatments. Bedding following wet-harvesting did not result in an LLWR equal to dry-harvest / bedding, suggesting that the modest tillage effect from bedding was not enough to mitigate the harvesting disturbance. The practical implications of this result are uncertain, since oxidation depth is the most important property affecting tree growth at this time. The soil physical properties represented by the LLWR should improve with time through the natural recovery actions of water table fluctuation, root proliferation, and shrink / swell from 2 to 1 clays.

Interactions Between Soil Properties

The model was further developed by exploring nonlinear effects and interactions between the regressors (Table 6). This analysis resulted in an improved final model with a well-balanced residual plot (Fig. 1D) and significantly reduced MSE. The site preparation treatments and soil productivity indicators explain 87% of the variation in tree height. Oxidation depth interacts significantly with the LLWR and net nitrogen mineralisation, reflecting the overall importance of soil aeration, as previously shown by the standardised estimates (Table 3) and the simple linear effects (Table 2). Oxidation depth and net nitrogen mineralisation were also shown to have significant quadratic effects. The interactive effects

TABLE 6–Best regression model for explaining the effects of site preparation and the soil productivity indicators on the height of 2-year-old loblolly pine trees*.

Parameter	df	Parameter estimate	T	P > |T|
Treatment effects				
Intercept (wet + dry / none)†	1	33.312	2.24	0.030
Intercept terms‡				
X1 (wet / bed)	1	26.538	2.64	0.011
X2 (dry / bed)	1	33.326	3.31	0.002
X3 (wet / mole / bed)	1	40.466	4.00	0.000
LLWR	1	–234.347	–2.19	0.034
LLWR × Oxidation depth	1	24.862	3.87	0.000
Oxidation depth^2	1	0.047	1.92	0.061
LLWR × Oxidation depth^2	1	–0.447	–3.69	0.001
Net N mineralisation^2	1	–0.001	–1.64	0.109
Oxidation depth × Net N mineralisation	1	0.010	2.11	0.041

* Model: Tree height = $b_0 + b_1$ X1 + b_2 X2 + b_3 X3 + b_4 LLWR + b_5 LLWR × Oxidation depth + b_6 Oxidation depth^2 + b_7 LLWR × Oxidation depth^2 + b_8 Net N mineralisation^2 + b_9 Oxidation depth × Net N mineralisation

where,

Treatment	X1	X2	X3
Wet + Dry / None	0	0	0
Wet / Bed	1	0	0
Dry / Bed	0	1	0
Wet / Mole / Bed	0	0	1

R-square = 0.87; *MSE* = 460; *N* = 54.

† Wet and dry harvest / none pooled into one treatment as previous analysis showed they did not have significantly different effects on the intercept (Table 4).

‡ Site preparation treatment effects tested with dummy variables.

of oxidation depth and LLWR, and net nitrogen mineralisation and oxidation depth, on tree height were explored visually (Fig. 2).

The interactive effects of increasing the LLWR and oxidation depth on tree height were calculated using the regression model at a constant net nitrogen mineralisation rate of 60 kg N/ha·year (Fig. 2A). The slight positive slope for tree height *versus* increasing LLWR at 15 cm of oxidation shows that oxidation depth is controlling tree growth at low aeration. Increasing the oxidation depth to 25 cm increases the slope of the relationship between tree growth and the LLWR, showing a positive interactive effect of aeration and LLWR on tree growth at 25 cm of oxidation depth. However, when the oxidation depth is increased to 35 cm, the slope of the relationship between tree height and LLWR decreases, becoming negative somewhere between 35 and 45 cm of oxidation depth. The gradual transition from a strong positive relationship to a negative relationship shows the gradual change from a soil environment in which aeration is limiting tree growth (low oxidation depth) to a soil environment in which water availability is limiting tree growth (high oxidation depth). The slope change occurs at 30 cm oxidation depth, which corresponds with a 43-cm water table depth. The 43-cm water table depth agrees remarkably well with McKee & Shoulders' (1970, 1974) 45-cm optimum water table depth determined for maximum productivity in 6-

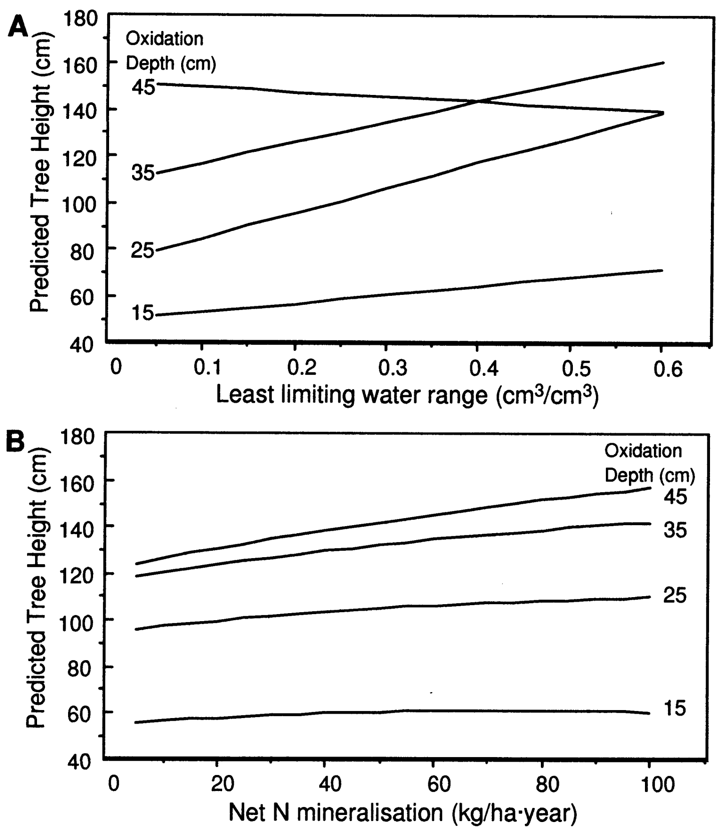

FIG. 2–Predicted tree height at age 2 years as a function of increasing LLWR at constant net nitrogen mineralisation (60 kg N/ha·year) (A), and to increasing net nitrogen mineralisation at constant LLWR (0.3 cm^3/cm^3) (B), at 15, 25, 35, and 45 cm oxidation depth, respectively. Predictions made using equation at bottom of Table 6.

to 8-year-old slash pine (*Pinus elliottii* Engelm. var.elliottii) plantations. The fact that we see the same relationship in 2-year-old trees suggests that the concept of using bioassay plots to simulate the tree growth response to the soil environment in later years has merit.

The functional relationship between water table depth and productivity has also been observed with sugarcane in Florida, where the optimum water table depth was also around 45 cm, decreasing on either side of this level (Obreza *et al.* 1998). The 45-cm optimum water table depth is probably not a magic number, but rather, the optimum will depend on the upward water-flux / water-table-depth relationship (Obreza *et al.* 1998), and this depends on soil texture, density, and hydraulic head (Jury *et al.*1991). A general relationship would be: the higher the percentage silt + clay fraction, the deeper the optimum water table depth. Thus, soil texture should probably be used as a criterion for deciding on the appropriate bed height needed to achieve the maximum productivity response to bedding.

The interactive effects of net nitrogen mineralisation and oxidation depth on tree height were examined using the regression model at a constant LLWR of 0.3 cm^3/cm^3 (Fig. 2B).

Net nitrogen mineralisation does not have any substantial effects on tree height until the effects of inadequate aeration are overcome, at between 25 and 35 cm of oxidation depth. Even after overcoming the effects of poor aeration, tree height increases only about 15 cm at 2 years over the entire range of net nitrogen mineralisation. The previously stated explanation for this was that nitrogen availability was not limiting tree growth at this time, but we may expect the relationship between nitrogen availability and tree growth to become stronger as net nitrogen mineralisation decreases while potential plant utilisation increases.

The slope of the relationship between net nitrogen mineralisation and tree height is in contrast with the relationship between the LLWR and tree height, wherein the height growth response to improving soil physical conditions (i.e., higher LLWR) is much stronger after the limiting effects of aeration are removed: the height growth response at 25 cm oxidation depth to increasing LLWR is about 40 cm. The importance of oxidation depth on its own is clearly demonstrated by the large increase in tree height with increasing oxidation depth for soils with very poor physical conditions for root growth (LLWR = 0.05 cm^3/cm^3). It is clear from this relationship that even if bedding did not improve the soil physical condition (increase the LLWR), the improved oxidation depth from elevating the soil would still result in increased tree growth.

Though the relationship between the LLWR and oxidation depth indicates a negative interactive effect on tree height at high oxidation depths (Fig. 2A), a decrease in tree height at high oxidation depths was not observed. A horizontal asymptote was approached at about 40 cm oxidation depth. The lack of a decrease in tree height at higher oxidation depths may be explained by high nitrogen availability. Nitrogen fertiliser studies have demonstrated that higher nutrient availability decreases carbon allocation below-ground for fine-root production (Haynes & Gower 1995; Albaugh *et al.* 1998), with a resultant increase in above-ground production (Albaugh *et al.* 1998). This relationship seems to hold true for droughty and well-watered soils (Albaugh *et al.* 1998), and partly explains why nitrogen fertiliser studies have reported large increases in above-ground production even on dry-sites (Dougherty 1996).

Unlike the dry-harvest / bedded and wet-harvest / mole plough / bedded treatments, the wet-harvest / bedded treatment did not increase net nitrogen mineralisation (Table 5). This could have resulted in greater carbon allocation to roots compared with the other two treatments. Since the three bedding treatments improved oxidation depth, the lack of a change in nitrogen availability may therefore explain the lower intercept term (height growth) for the wet-harvest / bedded treatment (Table 4). It appears that higher growth rates occur where nitrogen availability is increased along with improvements in soil physical properties (dry-harvest and wet-harvest / mole plough / bedded) compared with treatments that only improve soil physical properties (wet-harvest / bedded).

CONCLUSIONS

The height of 2-year-old trees was found to have significant and meaningful relationships with several indicators of soil productivity. The three most important soil indicators affecting tree growth at this age were oxidation depth, the LLWR, and net nitrogen mineralisation, in decreasing order of importance. Oxidation depth and the LLWR describe the quality of the soil environment for root growth in terms of air/water balance (oxidation depth) and the soil physical condition (LLWR). The strong interaction between oxidation depth and the LLWR showed that these soils can be aeration or available-water limiting. The critical oxidation depth for minimising the limiting effects of aeration and available water on tree growth was 30 cm. This finding has important implications for optimising bed height for maximum productivity, and suggests that the growth of trees planted on beds with oxidation depths in excess of 30 cm may decline after stand closure. However, it is important to understand that this relationship will change depending on soil physical properties. The extent to which tree growth will be affected by droughty conditions depends largely on nutrient availability, with high nutrient availability potentially buffering the effects of low available water on tree growth. This may mean that with taller beds and internal drainage treatments such as the mole-plough, nutrient availability may have to be increased with fertiliser application on sites with low inherent fertility.

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