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Establishment treatments affect the relationships among nutrition,  
productivity and competing vegetation of loblolly pine saplings  
on a Gulf Coastal Plain site

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# Establishment treatments affect the relationships among nutrition, productivity and competing vegetation of loblolly pine saplings on a Gulf Coastal Plain site

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## Abstract

After cultural treatments such as site preparation, release and fertilization, changes in the supply of mineral nutrients relative to each other and shifts in the composition of vegetation may have a delayed effect on the nutrition, carbon partitioning and growth of forest trees. This study was conducted to evaluate the influence of early management options that control vegetation and fertility on the nutrition and productivity of a young loblolly pine (*Pinustaeda* L.) plantation on a phosphorus-deficient site in the Gulf Coastal Plain. Two levels each of herbicide application, fertilization and litter addition were applied in a factorial arrangement to three open-pollinated families of newly planted loblolly pine seedlings. Competing vegetation was evaluated after three growing seasons, loblolly pine nutrition and tannin synthesis were evaluated after four growing seasons and loblolly pine productivity was quantified after five growing seasons. Fertilization and herbicide application increased the growth and decreased the foliar tannin concentration of loblolly pine. Herbicide application also increased the potassium concentration of loblolly pine foliage. A negative correlation between foliar tannin and potassium concentrations was found on plots that were fertilized with nitrogen and phosphorus. On southern pine sites that are fertilized with phosphorus, the accelerated growth of planted pine and invading vegetation may create new nutrient limitations. Where phosphorus is limiting, however, nutrient utilization may not be great enough for new deficiencies to develop. Loblolly pine stand productivity and foliar nutrient concentrations were affected by genetic family and the foliar calcium and magnesium concentrations of loblolly pine families responded differently to the establishment treatments. We also found that the establishment treatments influenced the occurrence of herbaceous and woody competitors. We hypothesize that corresponding treatment effects on exchangeable cation concentrations and pH of the soil were caused by changes in vegetation. ©1998 Elsevier Science B.V.

*Keywords:* Calcium; Fertilization; Genetic family; Herbicide; Litter; Magnesium; Nitrogen; Phosphorus; *Pinustaeda* L.; Potassium; Productivity; Tannin

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## 1. Introduction

The worldwide demand for wood products is increasing as land is withdrawn from timber production necessitating greater productivity on the remaining land base (Apsey and Reed, 1996). Unfortu-

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nately, inadequate regeneration and control of competing vegetation often compromise the early growth of managed forests (Dougherty and Duryea, 1991; USDA Forest Service, 1988). Consequent reductions in forest stand productivities have been observed in the southern United States (Bechtold et al., 1991; Ruark et al., 1991; USDA Forest Service, 1988).

In addition to a general reduction in commercial productivity of forests in the southern United States, a decrease in the growth rate of second rotation, intensively managed plantations has been found on nutrient-poor sites in Louisiana (Haywood, 1994; Tiarks and Haywood, 1996). Haywood (1994) reported 24 and 18% reductions in the height of 7-yr-old second rotation loblolly and slash pine (*Pinus elliottii* Engelm.), respectively. In a 10-yr-old second rotation slash pine plantation, Tiarks and Haywood (1996) reported a 23% reduction in tree volume compared to that achieved in the first rotation. These studies demonstrate that the productivity of second rotation southern pine is affected by silvicultural activities conducted in the first rotation that continue to control the availability and acquisition of essential resources.

Most soils in the southern coastal plain region are deficient in phosphorus and nitrogen and fertilization is often necessary to achieve established productivity goals (Allen, 1987; Shoulders and Tiarks, 1983; Tiarks, 1982). Fertilization also stimulates the growth of competing vegetation and influences the dominance of specific components of a plant community (Haywood and Tiarks, 1990; Huenneke et al., 1990). In a pine plantation, for example, Tiarks and Haywood (1986) reported that woody plants competed more strongly than grass with pines that received phosphorus fertilization; whereas, grass was the dominant competitor in the absence of phosphorus fertilization. In general, as competing vegetation uses more resources, the productivity of planted pine declines (Perry et al., 1993). Mineral nutrients that were not initially identified as limiting may become depleted depending on the initial fertility of the site, the type of plant community that develops and its affinity for specific mineral nutrients.

Alternatively, the cycling of mineral nutrients between soil and plant components may be positively influenced by the dynamics of the vegetation on a site (Duzan, 1994; Mou et al., 1993; Wood et al.,

1992). For example, Wood et al. (1992) suggested that the structure of the plant community that developed after the harvest of a loblolly pine plantation on a coastal plain site in Alabama may have benefitted the long-term nitrogen economy of newly planted loblolly pine.

As resource limitations develop, the balance between photosynthate production and growth is altered (Chapin, 1991; Lorio, 1986). With the accumulation of photosynthate in the absence of growth, carbohydrates are shunted to metabolic pathways that yield starch and secondary products such as lignin, tannin and terpenoids (Lorio, 1986; Tiarks et al., 1989; Waring et al., 1985). Condensed tannins are common secondary plant metabolites and their synthesis is closely related to mineral nutrition and productivity (Bryant et al., 1993; McKee, 1995; Tiarks et al., 1989; Waring et al., 1985).

Early management options affect stand productivity and secondary metabolism in the current rotation and in subsequent rotations if mineral nutrient resources are depleted. This study was conducted to determine the effects of early management options on the mineral nutrition of loblolly pine and to subsequently investigate relationships among pine nutrition and productivity and the profile of competing vegetation in a loblolly pine plantation.

## 2. Materials and methods

The study is located in Rapides Parish, LA, USA at 30°10'N, 92°40'W and at an elevation of 75 m. The soil is a gently sloping Beauregard silt loam (fine-silty, siliceous, thermic, Plinthaquic Paleudult) that is low in fertility (Kerr et al., 1980; Shoulders and Tiarks, 1983; Tiarks, 1982). The climate of central Louisiana is typified by 150 cm mean annual precipitation with 47% in spring and summer and 53% in fall and winter. Mean daily air temperature is 23.6°C in spring and summer and 14.7°C in fall and winter. When this study was installed, the vegetation was dominated by grasses, but included herbaceous plants and hardwood and pine seedlings and saplings that had regenerated naturally from the pine and mixed pine-hardwood forest harvested 22 yrs earlier. Vegetation was rotary mowed and glyphosate (1.8 kg ha<sup>-1</sup>) was broadcast in September 1987 as a

site preparation treatment to reduce the heavy grass cover on the site. Twenty-four 25 X 25 m treatment plots were established. In November 1988, 100 28-week-old container-grown loblolly pine seedlings from three seed sources were planted in randomly assigned locations in each plot at a 2.5 X 2.5 m spacing. Seedlings originated from seed produced by one Texas and two Louisiana open-pollinated loblolly pine genetic families from a first generation seed orchard in central Louisiana. The families were selected for superior growth and form.

Plots were grouped into three blocks based on soil drainage indicated by chroma at 50 cm. In each block, two levels of three establishment treatments were randomly assigned to treatment plots in a 2 X 2 X 2 factorial arrangement. Establishment treatments were fertilization, herbicide application and litter addition. Levels of fertilization were either no amendment or broadcast application of 750 kg ha<sup>-1</sup> diammonium phosphate (135 kg N ha<sup>-1</sup> and 151 kg P) in March 1988 and 93 kg ha<sup>-1</sup> urea (42 kg N ha<sup>-1</sup>) in March 1989. Herbicide treatment was either no chemical treatment after site preparation or single broadcast applications in April 1989 and 1990 of hexazinone (1.12 kg ha<sup>-1</sup>) and sulfomethron (0.21 kg ha<sup>-1</sup>) with spot applications of 1% aqueous glyphosate and single broadcast applications of glyphosate (1.55 kg ha<sup>-1</sup>) and sulfomethron (0.39 kg ha<sup>-1</sup>) in April 1991. Levels of litter treatment were either no litter addition or monthly broadcast applications of loblolly pine needle litter from December 1988 to April 1989 to maintain a 10 to 15 cm layer on the soil surface. A total of 37 Mg ha<sup>-1</sup> litter, on an oven-dried basis, was applied.

Within each treatment plot, a 15 X 15 m measurement plot containing six rows of six trees each was established. In April 1989, four 1.25 X 1.25 m sections of the litter layer in measurement plots were randomly sampled. Samples were oven-dried to equilibrium at 70°C. A subsample of each litter sample was ground in a Wiley mill (20 mesh). After sulfuric acid/cupric sulfate digestion, nitrogen (N) and phosphorus (P) concentrations were determined by ammonia specific probe (Powers et al., 1981) and colorimetry (John, 1970), respectively. Potassium (K), calcium (Ca) and magnesium (Mg) concentrations of the digested foliage were determined by atomic absorption spectrophotometry (Isaac and Kerber, 1971).

Results indicated that the added litter contained 200 kg N, 11 kg P, 13 kg K, 114 kg Ca and 23 kg Mg ha<sup>-1</sup> at the end of the litter application period.

In May 1991, successional vegetation was inventoried by determining the oven-dried weight (70°C) of the herbaceous biomass and the total number of competing woody stems at the ground line on five randomly selected 0.004-ha quadrants per measurement plot. Since hardwood tree and blackberry stems were dominant components of the competing woody vegetation, they were quantified separately.

In March 1992, soil was sampled to a 15 cm depth at 10 randomly selected locations per plot. Soil from each plot was composited and evaluated for pH (1:1, soil:water) and organic carbon (Amacher et al., 1986). Available P was quantified in Melich 3 extracts (Melich, 1984), by colorimetry (John, 1970). Exchangeable bases were measured after extraction with 1 N ammonium acetate (Thomas, 1982) by atomic absorption spectrophotometry (Isaac and Kerber, 1971) and cation exchange capacities (CEC) were determined by the method of Gilman (1979) using 0.1 M BaCl<sub>2</sub> as the displacing cation.

Percent volumetric soil water content at 0-20 and 20-40 cm was measured between July and December 1992 with a time domain reflectometer (Soil Moisture Equipment, Santa Barbara, CA) at 10-day intervals using one set of stationary sensors placed in the center of each plot. Precipitation was recorded in an open field 1.0 km from the study with an electronic weather station (Omnidata International, Logan, UT).

In early March 1992, mature foliage from the last complete flush of 1991 in the upper crown of three dominant or co-dominant trees per genetic family was collected, composited, lyophilized and ground in a Wiley mill (20 mesh). After sulfuric acid/cupric sulfate digestion, foliar concentrations of N, P, K, Ca and Mg were measured by the methods used for the analysis of litter samples.

Foliar tannin concentrations were determined by sequential extraction and quantification of anthocyanidins formed in *n*-butanol-HCl (Tiarks et al., 1992). For this determination ground foliage was sequentially extracted in methanol, acetone-water, *n*-butanol and *n*-butanol-hydrochloric acid-FeSO<sub>4</sub>. Condensed tannin concentrations in each extract were determined spectrophotometrically using a standard

curve generated from condensed tannin that was purified from loblolly pine foliage. The concentration of condensed tannin in each foliage sample was expressed as the sum of the tannin concentrations of the sequential extracts.

In December 1993, tree heights and diameters at breast height were measured. These data were used to calculate the inside-bark volume per tree (Schmitt and Bower, 1970) and the pine productivity ( $\text{m}^3 \text{ha}^{-1}$ ) on each plot.

Analyses of variance were conducted on quantities of herbaceous biomass and woody competitors using a randomized complete block,  $2 \times 2 \times 2$  factorial experimental design with three blocks as replications. With the same experimental design, soil pH, concentrations of soil organic carbon, available P, exchangeable K, Ca and Mg and soil CEC were subjected to analyses of variance. Soil water content data were evaluated by analyses of variance using a repeated-measures randomized complete block design with three blocks as replications. Foliar concentrations of N, P, K, Ca, Mg and condensed tannins

were subjected to an analysis of variance using a  $2 \times 2 \times 2$  factorial split-plot, randomized complete block design with three blocks as replications. Two levels each of fertilization, herbicide application and litter addition were the whole plot effects and genetic family was the sub-plot effect. Using the same experimental design, an analysis of variance was conducted on tree volume  $\text{ha}^{-1}$ . Main and interaction effects were considered significant at  $P \leq 0.05$  unless otherwise noted. Treatment means were compared with the Least Significant Difference test ( $P \leq 0.05$ ).

### 3. Results

After three growing seasons, the total number of competing woody plants, but not herbaceous biomass  $\text{ha}^{-1}$ , was significantly increased by fertilization (Table 1). However, the hardwood tree component of the competing woody vegetation was significantly reduced (56%) by fertilization. An interaction be-

Table 1

Treatment combination means and probabilities of a greater F-value associated with herbaceous and woody plant competition after three growing seasons in response to two levels each of fertilization, herbicide application and litter addition applied to loblolly pine

Treatment combination	Herbaceous biomass ( $\text{kg ha}^{-1}$ )	Number of woody plants ( $\# \text{ha}^{-1}$ )		
		Hardwood trees	Blackberry	Total <sup>b</sup>
Control <sup>c</sup>	207.1	3800	967	12,183
F	1744	950	9000	37,183
L	430	2483	13,167	32,317
FL	492	400	17,817	31,783
H	97	567	183	5017
HF	498	650	183	3383
HL	17	1450	83	5450
HFL	91	1617	1183	7150
Effect (df)	Probability > F-value			
Block (2)	0.0380	0.0575	0.1286	0.3820
F (1)	0.6798	0.0196	0.1411	0.0415
L (1)	0.0001	0.9926	0.0185	0.1053
H (1)	0.0001	0.0804	0.0003	0.0001
F × L (1)	0.9042	0.6398	0.7381	0.0618
F × H (1)	0.1596	0.0113	0.2148	0.0425
L × H (1)	0.0003	0.0552	0.0280	0.3317
F × L × H (1)	0.1747	0.7064	0.5572	0.0194

<sup>a</sup>Number of stems at the ground line.

<sup>b</sup>Total number of hardwood tree, blackberry, shrub and liana stems at the ground line.

<sup>c</sup>Control: no establishment treatment; F: fertilization; H: herbicide application; L: litter addition.

Table 2

Treatment combination means and probabilities of a greater F-value associated with soil pH, organic carbon, available phosphorus (P), exchangeable potassium (K), calcium (Ca) and magnesium (Mg) concentrations and cation exchange capacity (CEC) in the 0 to 15 cm depth of the soil after four growing seasons in response to two levels each of fertilization, herbicide application and litter addition applied to loblolly pine

Treatment combination	pH	Organic carbon (%)	P (mg kg <sup>-1</sup> )	K (cmol. kg <sup>-1</sup> )	Ca (cmol. kg <sup>-1</sup> )	Mg (cmol. kg <sup>-1</sup> )	CEC (cmol. kg <sup>-1</sup> )
Control <sup>a</sup>	5.52	1.47	1.27	0.096	1.50	0.37 I	3.63
F	5.31	1.53	22.63	0.109	1.38	0.429	3.49
L	5.46	1.30	1.30	0.086	1.66	0.442	2.84
FL	5.34	1.60	27.20	0.098	1.58	0.389	3.78
H	5.39	1.30	1.57	0.065	1.51	0.254	2.84
HF	5.19	1.37	26.90	0.109	1.38	0.429	3.49
HL	5.20	1.43	1.80	0.047	1.02	0.244	3.31
HFL	5.08	1.33	39.13	0.052	0.91	0.183	2.73

Effect (df)	Probability > F-value						
Block (2)	0.041 I	0.8645	0.4768	0.7404	0.0884	0.48 I5	0.3553
F (1)	0.0121	0.4804	0.000 I	0.2546	0.3908	0.1274	0.8893
L (1)	0.0870	1.0000	0.0920	0.0742	0.5828	0.88 I I	0.9379
H (1)	0.0015	0.3274	0.093 I	0.0005	0.0586	0.004 I	0.1886
F × L (1)	0.5906	0.8868	0.1016	0.8327	0.708 I	0.4749	0.7827
F × H (1)	0.8169	0.3990	0.1249	0.7783	0.7394	0.691 I	0.3333
LX H (1)	0.3239	0.6702	0.4 184	0.5389	0.1513	0.6595	0.5375
F × L × H (1)	0.8 169	0.3990	0.44 19	0.8664	0.7940	0.7436	0.2260

<sup>a</sup>Control: no establishment treatment; F: fertilization; H: herbicide application; L: litter addition,

Table 3

Probabilities of a greater F-value associated with percent volumetric soil water content at the 0 to 20 cm depth during July through December 1992 in response to two levels each of fertilization, herbicide application and litter addition applied to loblolly pine

Treatment combination	df	Probability > F-value	df	Adjusted probability > F-value <sup>a</sup>
Block	2	0.0998		
F <sup>b</sup>	1	0.0976		
L	1	0.3269		
H	1	0.1245		
F X L	1	0.978 I		
F × H	1	0.8033		
L X H	1	0.5019		
F × L × H	1	0.9307		
Time			13	0.000 I
Time X Block			26	0.0736
Time X F			13	0.0008
Time X L			13	0.0242
Time X H			13	0.5082
Time X F X L			13	0.4378
Time X F X H			13	0.4502
Time X L X H			13	0.9252
Time × F × L × H			13	0.8077

<sup>a</sup>Sphericity test not significant for Time ( $P = 0.0818$ ). Degrees of freedom associated with repeated-measures effects were adjusted by the Greenhouse-Geisser Epsilon (0.4570) (SAS Institute, 1991).

<sup>b</sup>F: fertilization; H: herbicide application; L: litter addition.

tween fertilization and herbicide application indicated that the number of competing woody plants  $ha^{-1}$  was significantly greater in response to fertilization on plots that were not treated with herbicides (no fertilization: 22,250 plants  $ha^{-1}$ ; fertilization: 34,483 plants  $ha^{-1}$ ), but that this response to fertilization was absent on plots that received herbicide application (no fertilization: 5234 plants  $ha^{-1}$ ; fertilization: 5267 plants  $ha^{-1}$ ). In contrast, the same interaction indicated that a reduction in the number of competing hardwood trees  $ha^{-1}$  occurred with fertilization in the absence of herbicide application (no fertilization: 3 142 plants  $ha^{-1}$ ; fertilization: 675 plants  $ha^{-1}$ ), but not when fertilizer and herbicides were applied together (no fertilization: 1009 plants  $ha^{-1}$ ; fertilization: 1134 plants  $ha^{-1}$ ).

Herbicide application significantly reduced herbaceous biomass and the total number of competing

woody plants  $ha^{-1}$  in the understory (Table 1). The number of blackberry plants  $ha^{-1}$  was significantly reduced (96%) but the number of hardwood trees  $ha^{-1}$  in the understory was unaffected by herbicide application. Litter addition significantly reduced herbaceous biomass by 77%, but resulted in a 2.2-fold increase in the number of blackberry plants  $ha^{-1}$ . Interactions between litter addition and herbicide application indicated that although the magnitude of these responses were similar on plots that were and were not treated with herbicides, there were significantly less herbaceous biomass and blackberry plants  $ha^{-1}$  on plots that were treated with herbicides. Application of litter without herbicides resulted in 461 kg of herbaceous biomass and 15,792 blackberry plants  $ha^{-1}$  and the application of both litter and herbicides resulted in 54 kg of herbaceous biomass and 633 blackberry plants  $ha^{-1}$ .

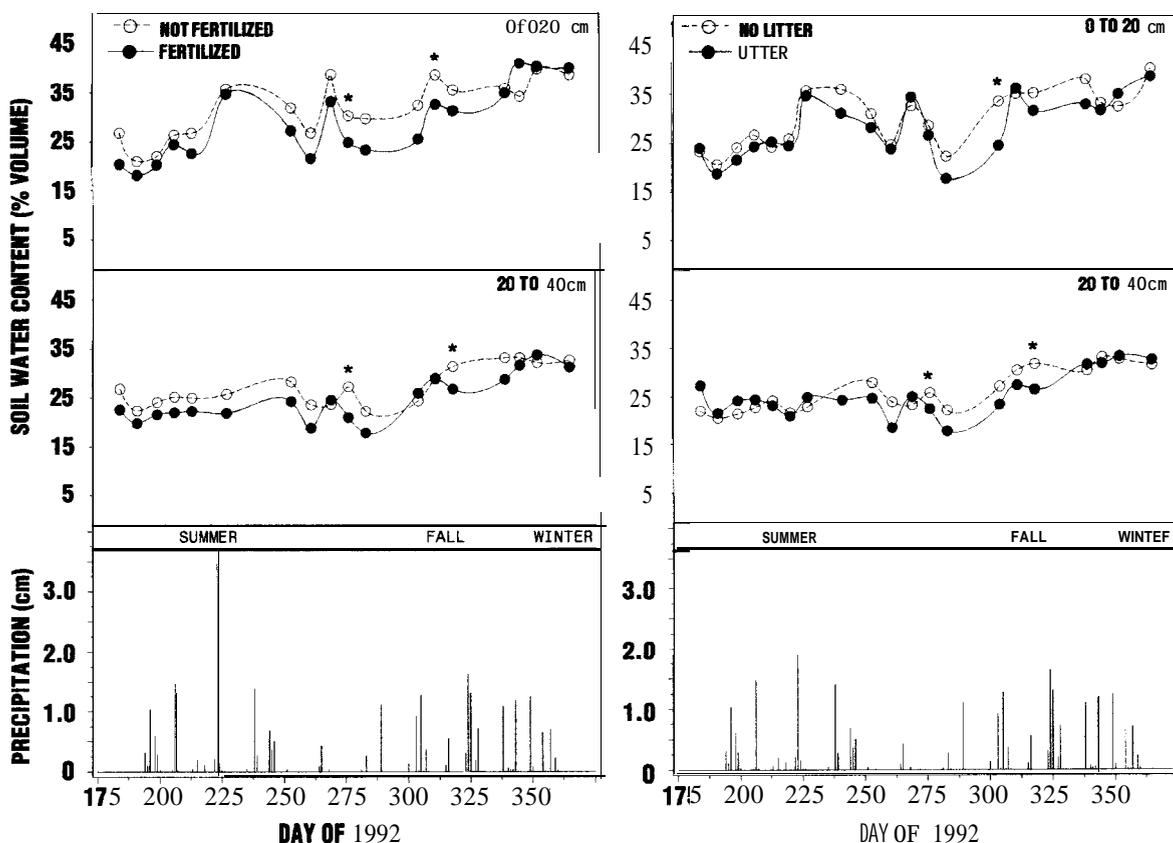


Fig. 1. Seasonal volumetric soil water content (%) at 0 to 20 and 20 to 40 cm depths and precipitation during 1992 in response to fertilization and litter addition applied to loblolly pine. Daily means associated with an asterisk are significantly different ( $P < 0.05$ ).

Four years after fertilization, the concentration of available P in the soil was significantly increased (Table 2). On plots receiving either fertilization or herbicide application the soil pH was significantly reduced. Available K and Mg concentrations in the soil were significantly reduced 30 and 32%, respectively, in response to herbicide application. A similar trend was observed with the concentration of available Ca in the soil ( $P=0.0586$ ). Significant litter addition and interaction effects on soil pH, percent organic carbon, CEC and fertility were not detected.

Volumetric soil water content at 0 to 20 cm was significantly affected by interactions between time and both fertilization and litter addition (Table 3). Analyses of variance by measurement date indicated that fertilization and litter addition each resulted in

decreases in volumetric soil water content in the fall (Fig. 1). Although the presence of missing data prevented a repeated measures analysis of variance of data collected at 20 to 40 cm, analyses by measurement date indicated that trends at 0 to 20 and 20 to 40 cm were similar.

Stand volume and foliar concentrations of N and tannin were significantly affected by an interaction among all three establishment treatments (Table 4). Significant negative relationships were observed among stand volume and foliar N ( $R = -0.572$ ,  $P=0.004$ ) and tannin concentrations ( $R = -0.515$ ,  $P=0.010$ ) (Fig. 2). Linear functions of the relationship between foliar tannin and K concentrations were significantly different on fertilized and non-fertilized plots. On plots not fertilized with N and P, there was

Table 4  
Treatment combination means and probabilities of a greater F-value associated with foliar mineral nutrient and tannin concentrations of loblolly pine after four growing seasons and inside-bark tree volume  $\text{ha}^{-1}$  of loblolly pine after five growing seasons in response to two levels each of fertilization, herbicide application and litter addition

Treatment combination	Nitrogen ( $\text{g kg}^{-1}$ )	Phosphorus ( $\text{g kg}^{-1}$ )	Potassium ( $\text{g kg}^{-1}$ )	Calcium ( $\text{g kg}^{-1}$ )	Magnesium ( $\text{g kg}^{-1}$ )	Tannin ( $\text{g kg}^{-1}$ )	Volume $\text{ha}^{-1}$ ( $\text{m}^3$ )
Control <sup>a</sup>	10.6	0.86	4.40	3.64	0.96	154	7.8
F	11.9	1.33	5.38	2.70	0.71	137	20.0
L	13.8	0.90	4.40	2.34	0.67	154	13.0
F L	10.8	1.33	4.47	2.38	1.07	149	37.9
H	11.9	0.90	5.97	2.57	0.59	151	20.3
H F	9.6	1.41	6.21	1.53	0.55	131	48.1
H L	12.0	0.87	6.06	2.04	0.50	148	20.6
H F L	10.3	1.46	6.24	1.59	0.64	139	40.7
Effect (df)	Probability > F-value						
Block (2)	0.2100	0.8658	0.0011	0.8569	0.0132	0.0001	0.3193
F (1)	0.0036	0.0001	0.3915	0.0291	0.3446	0.0003	0.0001
L (1)	0.1075	0.7016	0.5472	0.0523	0.7581	0.4363	0.0310
H (1)	0.0601	0.1635	0.0033	0.0044	0.0005	0.0327	0.0001
F × L (1)	0.0391	0.8538	0.6139	0.1347	0.0044	0.8652	0.4595
F × H (1)	0.1808	0.1055	0.7084	0.5591	0.8463	0.4625	0.1294
L × H (1)	0.5010	0.8779	0.6407	0.2669	0.7917	0.1392	0.0005
F × L × H (1)	0.0105	0.3876	0.5672	0.6970	0.0742	0.0410	0.0087
G (2)	0.0028	0.0047	0.0031	0.0004	0.0001	0.0763	0.0341
F × G (2)	0.3172	0.3401	0.8452	0.0374	0.0002	0.6427	0.9873
L × G (2)	0.2965	0.9213	0.4327	0.2114	0.0015	0.1148	0.1806
H × G (2)	0.3621	0.3175	0.1322	0.9247	0.4065	0.9961	0.2719
F × L × G (2)	0.7529	0.7202	0.8688	0.6547	0.4275	0.9902	0.2676
F × H × G (2)	0.2479	0.4167	0.2914	0.7152	0.4712	0.3852	0.8369
L × H × G (2)	0.4858	0.5650	0.5960	0.3944	0.9549	0.4250	0.0842
F × L × H × G (2)	0.3487	0.6786	0.5440	0.9192	0.7527	0.4693	0.3274

<sup>a</sup>Control: no establishment treatment; F: fertilization; H: herbicide application; L: litter addition; G: genetic family.

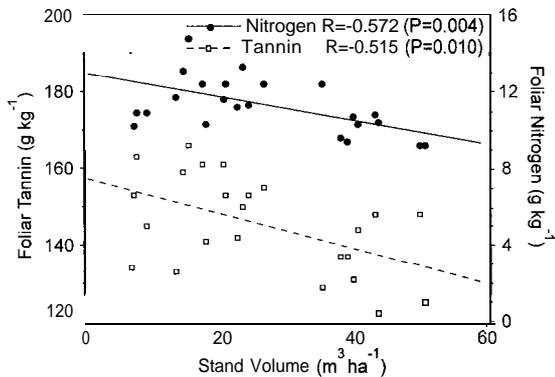


Fig. 2. Correlations among stand volume and foliar tannin and N concentrations of 4-yr-old loblolly pine planted on a Gulf Coastal Plain site in central Louisiana.

no correlation among foliar concentrations of tannin and K ( $P = 0.500$ ) (Fig. 3). However, on the fertilized plots, a significant negative correlation was observed among foliar concentrations of tannin and K ( $R = -0.643$ ,  $P = 0.024$ ).

Fertilization, litter addition and herbicide application, as well as interaction among these three treatments, significantly affected stand volume (Table 4). Thus, the response to each treatment depended on the level of the other two treatments. The stand volume response to litter addition was most affected by the level of the other treatments. Litter addition alone increased pine volume from 7.8 to 13.0  $\text{m}^3 \text{ha}^{-1}$ . Litter addition with fertilization increased stand volume by 17.9  $\text{m}^3 \text{ha}^{-1}$  compared to fertilization alone, but litter addition combined with herbicide application increased stand volume by only 0.3  $\text{m}^3 \text{ha}^{-1}$  compared to herbicide application alone. Litter addition combined with fertilization and herbicide application decreased stand volume by 7.4  $\text{m}^3 \text{ha}^{-1}$ .

Fertilization alone increased loblolly pine volume by 12.2  $\text{m}^3 \text{ha}^{-1}$  (Table 4). This 1.6-fold increase in volume was associated with significant decreases in the concentration of foliar N (12%), Ca (23%) and tannin (8%) and an increase in the concentration of foliar P (57%) (Table 4). Herbicide application significantly reduced foliar N (7%) ( $P = 0.060$ ), Ca (30%), Mg (33%) and tannin (4%) concentrations and increased foliar K (31%) concentration. Litter addition did not significantly affect foliar nutrient or tannin concentrations.

Litter addition and fertilization interacted to significantly affect foliar N concentration with a higher foliar N concentration in response to litter addition on plots that were not fertilized (no litter: 11.3  $\text{g kg}^{-1}$ ; litter: 12.9  $\text{g kg}^{-1}$ ) and no effect of litter addition on foliar N concentration on plots that were fertilized (no litter: 10.8  $\text{g kg}^{-1}$ ; litter: 10.5  $\text{g kg}^{-1}$ ) (Table 4). Foliar Mg concentration was also significantly affected by an interaction between litter addition and fertilization with a lower foliar Mg concentration in response to litter addition on plots that were not fertilized (no litter: 0.78  $\text{g kg}^{-1}$ ; litter: 0.59  $\text{g kg}^{-1}$ ) and a higher foliar Mg concentration in response to litter addition on plots that were fertilized (no litter: 0.63  $\text{g kg}^{-1}$ ; litter: 0.86  $\text{g kg}^{-1}$ ).

Genetic family had small but significant effects on stand volume and foliar mineral nutrient concentrations (Table 4). One of the Louisiana families (family 14) produced more volume  $\text{ha}^{-1}$ , while the Texas family (family 36) produced less volume  $\text{ha}^{-1}$  than the other families (Table 5). The family with an intermediate yield (family 28) had higher foliar N, P, Ca and Mg concentrations and a lower foliar K concentration compared to that of the other families. Family 36 had a higher foliar K concentration compared to the other families. The foliar P concentration of family 14 was lower than that of the other families. Fertilization significantly reduced the concentrations of Ca (40%) and Mg (22%) in the foliage of family 14 but did not affect the concentration of Ca and Mg in the foliage of family 36. The Ca

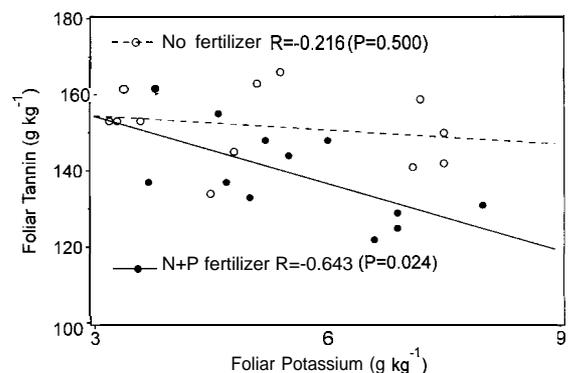


Fig. 3. Effect of N plus P fertilization at planting on the relationship between foliar tannin and K concentrations of 4-yr-old loblolly pine planted on a P-deficient, Gulf Coastal Plain site in central Louisiana.

Table 5  
Stand volume and foliar mineral nutrient and tannin concentrations of three open-pollinated families of loblolly pine

Family	Stand volume <sup>a</sup> (m <sup>3</sup> ha <sup>-1</sup> )	Foliar concentration (gkg <sup>-1</sup> ) <sup>b</sup>					Tannin
		Nitrogen	Phosphorus	Potassium	Calcium	Magnesium	
14	27.7a	11.5b	1.07c	5.76b	2.17b	0.62b	141a
28	26.3b	11.9a	1.21a	4.47c	2.75a	0.85a	148a
36	24.1c	10.8b	1.12b	5.95a	2.12b	0.66b	146a

<sup>a</sup>Measured after five growing seasons.

<sup>b</sup>Measured after three growing seasons.

concentration of foliage of family 28 was unaffected by fertilization but the Mg concentration of foliage of family 28 was significantly increased (38%) by fertilization. Litter addition significantly reduced the foliar Mg concentration of family 14 (20%), increased that of family 28 (29%) and had no effect on that of family 36.

#### 4. Discussion

In southern pine plantations, early cultural practices such as site preparation, release and fertilization are conducted to optimize the availability of light, water and mineral nutrients for the growth of the merchantable trees (Kozlowski et al., 1991, Morris and Campbell, 1991). In our study, main and interaction effects of three establishment treatments strongly influenced stand productivity and it is likely that these responses were caused by effects of the treatment combinations on the availability of key resources.

Water and mineral nutrients are the primary resources that control the productivity of managed southern pine (Morris and Campbell, 1991). In our study, fall soil water content was reduced but stand productivity was increased by fertilization and litter addition. By fall, the observed increases in pine growth and vegetative competition on these plots may have resulted in more transpirational surface area causing soil water loss. However, the small magnitude of these treatment effects and the occurrence of regular precipitation suggest that stand nutrition and productivity were not strongly affected by water availability.

Phosphorus is the most commonly deficient mineral nutrient in southern coastal plain soils (Pritchett and Gooding, 1975). As a result, fertilization with P

is often necessary to achieve southern pine productivity goals (Allen, 1987; Pritchett and Gooding, 1975; Shoulders and Tiarks, 1980). In our study, foliar P concentrations three years after planting indicated that the availability of P on plots that were not fertilized was below the critical level of 1.0 g kg<sup>-1</sup> which represents the boundary between deficiency and sufficiency for loblolly pine (Allen, 1987; Wells et al., 1986). Since the soil in this study is inherently P-deficient and no fertilizer amendments were made on these plots, it is likely that available P was limiting at the time of planting. As expected, fertilization increased P availability throughout the duration of this study.

A shift in the partitioning of carbon from cell wall-forming compounds to secondary metabolites occurs when resource limitations are encountered (Chapin, 1991; Lorio, 1986). A close relationship between P nutrition and the partitioning of carbon to either height growth or tannin synthesis was demonstrated by Tiarks et al. (1989). In their study, 12 levels of P fertilizer were applied at two locations where loblolly pine was regenerated. After three years, a significant relationship existed between the amount of P applied and both seedling height ( $R^2 = 0.87$ ) and foliar tannin concentration ( $R^2 = 0.79$ ). Similarly in our study, P fertilization reduced the partitioning of photosynthate to foliar tannin synthesis and increased the growth of loblolly pine.

Fertilization decreased foliar N and Ca concentrations and herbicide application decreased foliar Ca and Mg concentrations by the fourth year after planting. These decreases in foliar mineral nutrient concentration were associated with increases in stand productivity. Since the dilution of mineral nutrients frequently occurs in response to rapid growth (Jarrell and Beverly, 1981; Kozlowski et al., 1991), reduced

foliar mineral nutrient concentrations in our study may have been caused by their dilution as the trees grew.

Past research has documented the mobility of K within forest ecosystems (Johnson and Todd, 1987; Klemmedson et al., 1985; Mou et al., 1993; Shoulders and Tiarks, 1980). For example, Shoulders and Tiarks (1980) found that after 1 yr, fertilization of slash pine with K increased the concentration of this nutrient in the current year's foliage. At the same time, the concentration of K in the soil declined to pre-treatment levels. After the third year and senescence of foliage that was initially produced after fertilization, the concentrations of K in the foliage and soil were higher again. These authors suggested that the added K was rapidly immobilized in plant biomass or was leached from the soil in the first year. Increases in foliar and soil K after three years were attributed to re-translocation within trees, leaching from live and senescent foliage followed by immediate uptake and mobilization as litter decomposition occurred.

In our study, foliar K concentrations observed on plots that were not and were treated with herbicides were 33 and 75% greater, respectively, than the critical value of  $3.5 \text{ g kg}^{-1}$  reported by Allen (1987). The magnitude of the difference between treatments suggests that although for initial site fertility, N and P availability are of immediate concern, future limitations of other mineral nutrients such as K may arise depending on the rate at which they are retained in, or lost from the ecosystem.

The importance of understanding the K dynamics of southern pine sites is emphasized by the relationships that we observed between foliar K and tannin concentrations on plots that were not and were fertilized with N and P. Without N and P fertilization, a statistically significant relationship between foliar K and tannin concentrations was not detected. However, with N and P fertilization, the concentration of foliar tannin decreased as the concentration of foliar K increased ( $R = -0.643$ ,  $P = 0.024$ ). Similar relationships between the foliar concentration of other mineral nutrients and tannin were not detected.

As previously stated, tannin synthesis is a secondary use of photosynthate that is initially available for tree growth, but because of limited resource availability for growth, is used for secondary

metabolite production (Chapin, 1991; Waring et al., 1985). The negative relationship observed between foliar K and tannin on plots where P was no longer deficient suggests that the availability of K, in addition to P, influenced the growth potential of loblolly pine on this site. Additional research is needed to understand the mechanism by which K nutrition may affect carbon partitioning and tannin synthesis. While the concentration of K in the foliage of the fastest growing plots indicates that K was not deficient, foliar tannin concentrations show that tree growth may have been even greater with K amendment. This information supports the belief that there is a site-specific hierarchy of mineral nutrient limitations that inhibit southern pine productivity and that fertilizer recommendations should be made with consideration of the secondary effects of nutrient amendments on the future nutrition of planted pine.

Once transferred to the soil by litterfall and throughfall, without rapid root uptake, K is readily leached (Johnson and Todd, 1987; Klemmedson et al., 1985). Van Rees and Comerford (1990) reported that in addition to new roots, woody roots were necessary to supply sufficient K to slash pine seedlings. Therefore, on sites where K is not abundant, the amount and distribution of tree roots may be critical for the absorption of K.

Past research has also emphasized the importance of vegetation recovery after the disturbance of forest sites for the extraction, conservation and accretion of mineral nutrients (Duzan, 1994; Mou et al., 1993; Wood et al., 1992). For example, Wood et al. (1992) found a positive relationship between the invasion of competing vegetation and the concentration of soil organic N in a 7-yr-old loblolly pine plantation. They proposed that without the development of a successional plant community, nitrate may have been leached from the soil during stand establishment resulting in a decrease in the concentration of soil organic N at age seven. Perhaps the plant communities that developed in response to the vegetation management regimes in our study influenced the availability of K to planted pine trees.

Herbicide application resulted in a decrease in exchangeable soil K. Since herbicide application increased both stand volume and foliar K concentration, it is likely that the majority of the K lost from the soil was absorbed and immobilized by the planted

pinus. With less competition between the planted pine and invading vegetation, K availability for uptake by loblolly pine roots may have been greater on plots that received herbicide application even though the concentration of exchangeable K in the soil decreased.

Calcium uptake is limited by number of unsubsided root tips and K uptake is limited by root system surface area (Mengel and Kirkby, 1987; Russell and Clarkson, 1976). In our study, both foliar and soil Ca concentrations were reduced by herbicide application. After mineral nutrients became more available with the suppression of competing vegetation by herbicide application, the mechanism of K absorption may have accelerated K uptake: whereas, the mechanism of Ca absorption may have prevented a similar increase in Ca uptake.

The rate of Mg uptake by plant roots is lower than that of K and elevated K nutrition decreases the uptake of Mg (Mengel and Kirkby, 1987). In our study, concentrations of foliar and soil Mg were reduced and the concentration of foliar K was increased by herbicide application. Perhaps, Mg uptake was depressed by K competition on the plots that received herbicide application. Furthermore, the foliar Mg concentration on plots treated with herbicides was  $0.57 \text{ g kg}^{-1}$  which is 19% less than the critical value for loblolly pine foliage reported by Allen (1987). This information suggests that rapid increases in K availability and uptake in loblolly pine plantations could negatively affect the Mg nutrition of the merchantable trees. However, the duration and long term effect of this nutritional shift is unknown.

Herbicide-induced reductions in exchangeable K, Mg and Ca in the soil were associated with a similar reduction in soil pH. With larger loblolly pine trees by the fourth year after planting, greater uptake of K, Mg and Ca on plots treated with herbicides and their corresponding displacement with hydrogen ions would account for the lower soil pH.

Similar to herbicide application, fertilization resulted in a decrease in soil pH. Fertilization also stimulated loblolly pine productivity but did not dramatically affect the abundance of herbaceous and woody competitors. As previously discussed, an increase in the amount of pine biomass and an increase in cation uptake may have acidified the soil.

Litter addition alone or in combination with herbicide application had no effect on foliar tannin concentration. When litter was applied in combination with fertilizer, foliar tannin concentration increased and herbicide application had no effect on this response. In general, the mean stand productivity values of vegetation management regimes that included litter addition were inversely related to their respective foliar tannin concentrations. This information suggests that some aspect of litter addition caused energy to be shunted to tannin production rather than tree growth.

Changes in foliar mineral nutrient concentrations were not proportional to changes in stand productivity and foliar tannin concentrations on plots that received litter addition. Thus, the negative relationship between stand productivity and foliar tannin concentration in response to litter addition was not caused by macronutrient limitations. Furthermore, although litter addition resulted in a reduction in soil water content, it is unlikely that this decrease was large enough to affect tree growth. We did, however, observe a peculiar response to litter addition that may be related to both increased tannin production and decreased soil water content. Specifically, litter addition resulted in a 218% increase in the number of competing blackberry plants on the site. Mou et al. (1995) reported that 71% of the fine root length in a 4-yr-old loblolly pine stand was in the 0 to 10 cm depth of a Gulf Coastal Plain soil. In contrast, we found that litter addition reduced pine root growth in the upper 10 cm of the soil profile (Haywood et al., 1997). Perhaps competition between loblolly pine and blackberry root systems caused the distributions of pine and blackberry roots to be greater in the lower and upper depths of the soil profile, respectively. Vertical displacement of loblolly pine fine roots would reduce the ability of the pines to exploit soil resources near the surface. A similar phenomenon was observed by Van Rees and Comerford (1986) who evaluated the uptake of a strontium spike placed in either the litter or subsoil of a lower coastal plain site supporting 20-yr-old slash pine. Foliar strontium and root distribution analyses indicated that because of root distribution patterns, the understory vegetation was more competitive than pine for strontium placed in the upper portion of the soil profile; whereas, the opposite was true deeper in the

soil profile. Thus, below ground competition for one or more limiting resources other than those measured in our study, may be a possible explanation for tannin synthesis and stand productivity responses to vegetation management regimes that included litter addition.

## 5. Summary

We have presented some of the consequences of establishment treatments that directly affect the natural vegetation and fertility of young loblolly pine plantations on Gulf Coastal Plain sites. An increase in stand growth and a decrease in tannin synthesis were, observed with fertilization and herbicide application. This suggests that the resource demands of loblolly pine were satisfied to a greater extent on plots that received fertilizer and herbicide application. Since our study site was inherently deficient of available P, we expected the observed decrease in tannin synthesis and increase in pine growth in response to fertilization. However, our results also demonstrated that site productivity was closely related to the K nutrition of the planted trees. Where P demands were met with fertilization at the time of planting, pine productivity increased. However, accelerated pine growth was accompanied by a significant negative relationship between foliar K and tannin concentrations. On P-deficient plots, pine growth was suppressed and foliar K and tannin concentrations were unrelated.

We also found that herbicide application increased loblolly pine K uptake, but decreased the concentration of foliar Mg to less than the critical level for loblolly pine. Manipulation of competing vegetation in response to fertilizer and herbicide treatments may have changed the availability of mineral nutrients to the pines. Furthermore, litter addition increased the number of blackberry plants  $\text{ha}^{-1}$  and the concentration of foliar tannin in the planted pine. This relationship may have been caused by competition in the 0 to 1.5 cm depth for soil resources other than those measured in our study.

Generalizations about the emergence of K and Mg limitations with the development of intensively managed southern pine plantations are premature. However, our results suggest that the accelerated growth

of planted pine and invading vegetation caused by early cultural treatments may create new nutrient limitations on moderately infertile coastal plain sites. In particular, our study indicated that the availability of K and Mg were of primary concern. Recently reported decreases in southern forest productivity (Bechtold et al., 1991; Ruark et al., 1991) and the occurrence of this phenomenon in second rotation stands of loblolly and slash pine (Haywood, 1994; Tiarks and Haywood, 1996), together with our results, suggest that further research is needed to understand the dynamics of K, Mg and other mineral nutrients in response to common cultural treatments and throughout consecutive rotations of intensively managed southern pine.

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# Forest Ecology and Management

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