United States
Department of
Agriculture

Forest Service

**Southern
Research Station**

Research Paper
SRS–48

Fertilizer Responses of Volunteer Longleaf Pine Trees within a Loblolly Pine Plantation: Separating Direct Effects from Competition Effects

Peter H. Anderson and Kurt H. Johnsen

Authors:

Peter H. Anderson, Research Biologist, and **Kurt H. Johnsen**, Research Physiologist, U.S. Forest Service, Southern Research Station, Durham, NC 27709.

Cover photo: Longleaf pine seedling Scotland County, NC, 2009. Photo by Peter H. Anderson.

DISCLAIMER

December 2009

Southern Research Station
200 W.T. Weaver Blvd.
Asheville, NC 28804

Fertilizer Responses of Volunteer Longleaf Pine Trees within a Loblolly Pine Plantation: Separating Direct Effects from Competition Effects

Peter H. Anderson and Kurt H. Johnsen

Abstract

Evidence is mixed on how well longleaf pine (*Pinus palustris* Mill.) responds to increased soil nitrogen via fertilization. We examined growth and physiological responses of volunteer longleaf pine trees within an intensive loblolly pine (*P. taeda* L.) fertilization experiment. Fertilizer was applied annually following thinning at age 8 years (late 1992) at rates tailored to maintain a high needle nitrogen concentration. We measured the annual growth of 20 volunteer longleaf pine trees per treatment. We took bimonthly gas exchange measures on 12 longleaf pine trees per treatment from June 1999 through June 2000, after which we estimated carbon isotope discrimination and foliar nitrogen concentration on foliage. The impact of fertilization in both growth and gas exchange was dependent on competition for light with neighboring loblolly pine trees. When fertilized longleaf pine trees were separated into categories with respect to being dominant or suppressed (relative to the loblolly pine trees) dominant-fertilized trees had the lowest carbon isotope discrimination, increased photosynthesis, and decreased stomatal conductance, indicating greater water use efficiency in these trees. Compared to loblolly pine, longleaf pine growth is restricted less by poor soil nutrition. However, early rotation longleaf pine appears to have the potential to increase growth rate via fertilization to almost the same extent as loblolly pine.

Keywords: Carbon isotopes, fertilization, growth, longleaf pine, photosynthesis, stomatal conductance.

Introduction

Longleaf pine (*Pinus palustris* Mill.) is an important conifer of the Southeastern United States Coastal Plain. Due to overexploitation, land use changes, and wildfire suppression, about 95 percent of the longleaf pine ecosystems have been eliminated since Europeans settled in the region (Landers and others 1995). Even so, enough of these pine systems remain to support an important industry for the Southeast in the removal of longleaf pine straw or litter for landscaping mulch. Often this removal is practiced on an annual basis. McLeod and others (1979) found significantly reduced growth of 16-year-old longleaf pine in South Carolina 1 year after litter removal. While they found no decrease in macronutrients in needles formed after removal, it is reasonable to assume that litter removal reduces litter biomass and, thus, removes macronutrients from the soil around trees. It is unclear how continuous annual removals of litter organic matter will impact long-term site fertility and productivity, particularly in the deep sandy and infertile soils where longleaf pine often grow.

Commercial fertilization of southern pine stands has increased steadily over the decades with 1.2 million acres fertilized in 2004 (Fox and others 2006). Research has shown that fertilization increases productivity of loblolly pine (*P. taeda* L.) (Albaugh and others 1998, 2004), the most common southern pine species, but little research on fertilization responses of longleaf pine has been done. Because longleaf pine has adapted to sites with low nutrient availability, there has been a perception that longleaf pine is less responsive to fertilization than loblolly pine. However, longleaf pine straw biomass, foliar nitrogen (N), and phosphorous concentrations increased up to 50 percent 2 years after fertilization, and fertilized trees in the sandhills of North Carolina had large percentage increases in both diameter and basal-area growth compared to controls (North Carolina State Forest Nutrition Cooperative 1998).

We examined growth and physiological responses of volunteer longleaf pine trees within an intensive loblolly pine fertilization experiment. We started fertilization treatments in 1992, when the trees were 8 years old, and continued annually for the 7 years of our study. The experimental loblolly pine planting was established on deep, well-drained sandy soil in 1985 following the harvest of a natural longleaf pine stand. We measured growth, photosynthetic gas exchange, and foliar carbon stable isotope discrimination. The objective of our study was to determine the impact of fertilization on the volunteer longleaf pines as well as the influence of competition of the crop loblolly pine trees on the responses.

Materials and Methods

The study was conducted at the Southeast Tree Research and Education Site (SETRES), in the sandhills of Scotland

County, NC (34°55′ N.; 79°30′ W.). SETRES sits on an infertile, excessively drained site that was once a naturally regenerated longleaf pine stand. The soil is mapped as a Wakulla series, which is highly permeable and well drained. Loblolly pine seedlings (1–0 containerized stock) were hand planted on 2 m × 3 m spacing in 1985 using a mix of 10 open-pollinated families originating from the North Carolina Piedmont. The full SETRES study is a 2 × 2 factorial experiment with fertilization and irrigation treatments and four replicate blocks. Beginning in 1992, plots were thinned to 1,260 stems/ha and fertilizer was applied to achieve "optimum" foliar nutrition on fertilized plots. For the optimum nutrition treatment, N was applied annually in an attempt to achieve an N concentration in leaf dry matter of 1.3 percent with other macro- and micro-nutrients in balance; control foliar N concentration was approximately 0.9 percent. Fertilization treatment goals have been achieved for the crop loblolly pine trees (Albaugh and others 1998). More details on the site, stand, and treatments can be found in Albaugh and others (1998, 2004).

We utilized only the nonirrigated control and fertilized plots where, on average, there were 41.3 (S.E. = 5.93) volunteer longleaf pine trees interspersed among the 1,136.7 (S.E. = 83.5) loblolly pine stems/ha. Five longleaf pines per plot (20 per treatment) have been measured for height and diameter since 1992. A subset of 3 trees per plot (12 per treatment) was measured for gas exchange bimonthly from June 24, 1999, through June 15, 2000. Measurements of net photosynthesis (P_n) and stomatal conductance (g_{wv}) were conducted using a portable photosynthesis system (Model Licor 6400, Li-cor Inc., Lincoln, NE) on detached fascicles within 2 minutes from removal with a pole pruner. Fascicles were placed into the chamber while still attached to the removed shoot segment. On each date, measurements were made in the morning and in the afternoon on foliage collected from the upper and lower third of the crown of each tree. Measurements were conducted on sunny days, and light levels within the leaf chamber were set to ambient conditions.

Foliage samples were collected in October 2000 to estimate foliar N concentration and stable carbon isotope discrimination. First-flush foliage was collected from the upper, middle, and lower thirds of the crown from four trees per sample plot. Foliage from approximately 10 fascicles per sample were ground and analyzed for $\delta^{13}C$. Samples were analyzed for ^{13}C:^{12}C ratio using the Duke University, Phytotron SIRA Seriea II isotope ratio mass spectrometer (Micromass, Manchester, UK) operated in automatic trapping mode after combustion (SUMAS combustion) of samples in an elemental analyzer (NA1500 Series 1, Carla Erba Instrumentation, Milan, Italy). The reference carbon dioxide was standardized against standard Pee Dee belemnite. A system check of the combustion and mass spectrometer measurement was achieved with two interspersed (every 10 samples) working standards of cellulose with a $\delta^{13}C$ of –24.1±0.03 percent and –23.6±0.06 percent. The accuracy of $\delta^{13}C$ with this analysis procedure is ±0.1 percent.

Due to the generally slow growth of the loblolly pine crop trees in the control plots, all volunteer longleaf pine trees in these plots had crowns in the dominant crown class. In the fertilized plots, due to the more rapid growth of the loblolly pine, seven of the longleaf pines trees were classified as dominant (comparable in height and diameter to neighbors) and five trees were classified as intermediate to suppressed (smaller than neighbors). Growth, gas exchange, and carbon isotope discrimination results were first analyzed via ANOVA using a randomized complete block design. Data was then analyzed using repeated measures ANOVA using a randomized split plot design (two treatments, four blocks), wherein this analysis fertilization regime is the whole plot and subplots were the three treatment classifications: control, dominant fertilized, and intermediate fertilized.

Results

Seven years (1992–99) of annual fertilizer applications significantly increased height increment but not d.b.h. increment relative to control trees (table 1). Mean 1999 height and d.b.h. of fertilized trees were not significantly different from controls. However, when fertilized trees were further split into intermediate and dominant crown classes, fertilization significantly increased height increment by 21 percent and d.b.h. increment by 18 percent in dominant trees, but suppressed-fertilized trees grew less than control trees after 7 years of annual fertilization.

Across all dates, P_n and g_{wv} were significantly lower in fertilized compared to control trees in both the upper and lower crown (table 1). When crown classes were separated, these effects appeared stronger in suppressed trees but still generally occurred in dominant trees. Fertilized trees had more positive foliar $\delta^{13}C$ values than control trees, indicating they had lower C isotope discrimination. When crown classes were separated, dominant-fertilized trees had higher $\delta^{13}C$ values than intermediate-fertilized trees, which were higher than estimated from foliage of control trees. Mean $\delta^{13}C$ and the P_n:g_{wv} ratio from upper canopy needles,

Table 1—Volunteer longleaf pine d.b.h. and height in December 1999; 1992–99 d.b.h. and height increment; mean (all measurement dates) net photosynthesis (P_n) (µmol/m^{2}s, g_s) of upper and lower canopy and needle conductance (g_{wv}) (mol/m^2/s); and foliar N concentration and δ^{13}C from upper, middle, and lower canopy on foliage collected in October 1999 at Southeast Tree Research and Education Site, Scotland County, NC

	Treatment			
Trait	Control	Fertilized (all)	Fertilized (suppressed)	Fertilized (dominant)
N for growth measures	20	20	9	11
D.b.h. (cm)	13.72	13.94	12.1	15.04
	(0.60) AB	(0.65)	(0.53) B	(0.81) A
D.b.h. increment (cm)	8.24	9.22	8.03	9.93
	(0.37) B	(0.47)	(0.52) B	(0.61) A
Height (m)	10.05	10.16	9.45	10.69
	(0.18) AB	(0.30)	(0.25) B	(0.66) A
Height increment (cm)	6.17	6.98	6.5	7.27
	(0.13) B *	(0.24)	(0.51) B	(0.23) A
Foliar N (%) upper canopy	0.82	1.11	1.12	1.12
	(0.03) B *	(0.04)	(0.07) A	(0.05) A
Foliar N (%) mid canopy	0.79	1.03	1.06	1
	(0.03) B *	(0.05)	(0.07) A	(0.07) A
Foliar N (%) lower canopy	0.75	1.13	1.26	1.01
	(0.03) C *	(0.12)	(0.20) A	(0.07) B
N for physiology measures	12	12	5	7
P_n, upper canopy	3.67	2.99	2.85	3.1
	(0.15) A*	(0.17)	(0.27) B	(0.21) B
P_n. lower canopy	2.65	2.33	1.86	2.65
	(0.11) A	(0.15)	(0.17) B	(0.22) A
g_{wv}, upper canopy	0.0415	0.0254	0.0254	0.0253
	(0.0025) A*	(0.0019)	(0.0031) B	(0.0023) B
g_{wv}, lower canopy	0.0332	0.0207	0.0173	0.0232
	(0.0022) A*	(0.0017)	(0.0021) B	(0.0025) B
δ^{13}C, upper canopy	−27.65	−27.15	−27.56	−26.80
	(0.20) A	(0.33)	(0.52) A	(0.41) B
δ^{13}C, middle canopy	−28.28	−27.45	−27.78	−27.18
	(0.28) A*	(0.27)	(0.43) AB	(0.35) B
δ^{13}C, lower canopy	−28.69	−27.97	−28.28	−27.72
	(0.19) A*	(0.23)	(0.37) AB	(0.26) B

* = significant difference between control and fertilized.

Letters represent significant differences among control, fertilized (suppressed), and fertilized (dominant) trees.

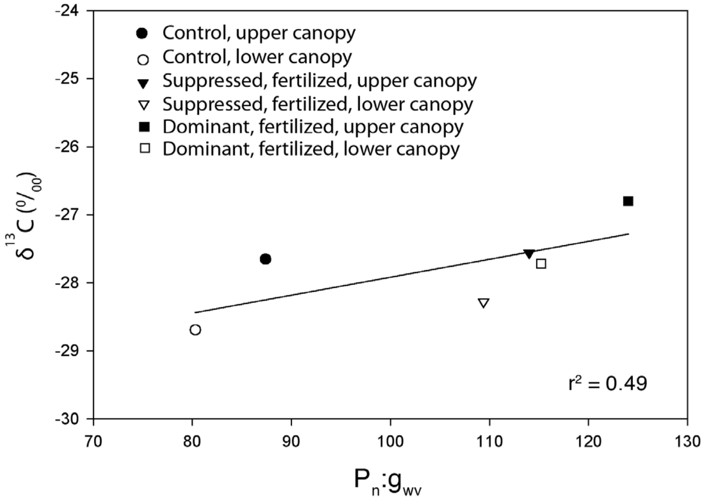

Figure 1— Relationship between the mean (across all measurement dates) ratio of net photosynthesis to needle conductance (P_n:g_{wv}) with $\delta^{13}C$ estimated for needles collected in October 1999 for upper canopy needles from control, suppressed fertilized, and dominant fertilized volunteer longleaf pine interspersed within a loblolly pine plantation.

by treatment/crown class, were positively correlated (fig. 1). Fertilization increased foliar N concentration, although not as much in dominant trees as in intermediate trees.

Discussion

Clearly, SETRES is an extremely nutrient deficient site; by the time this study was completed, nonfertilized 14-year-old loblolly pine winter foliar N concentrations were below 1.05 percent and peak projected leaf areas were below 2 m^2/m^{-2} throughout the year. In the control plots, the volunteer longleaf pines on average grew 6.2 m over the 7-year study period, compared to 4 m for the control loblolly pine crop trees (Albaugh and others 2004). This supports the contention that longleaf pine is better adapted to nutritionally poor sites than loblolly pine (Harrington 1990). Fertilization increased longleaf pine growth, but only when neighboring loblolly pine trees did not suppress the response. However, dominant longleaf pine trees grew an average of 7.3 m, compared to 8 m for the loblolly pine crop trees, over the 7-year study period (Albaugh and others 2004). Thus, it appears that early rotation longleaf pine growth can be increased via fertilization to almost the same extent as loblolly pine.

Fertilization increased foliar N concentration measured in October 2000 (table 1), but not as much in dominant trees as in intermediate trees. Values were lower than loblolly pine trees in both the control and fertilized treatments measured in a concurrent study (Gough and others 2004). Control longleaf pine foliar N was similar to values reported by Boyer and Miller (1994) but lower than what has been estimated as sufficient for commercial production of longleaf pine (Blevins and others 1996).

Across all dates, fertilization generally decreased rates of P_n and g_{wv} in both dominant and intermediate longleaf pine. Although Murthy and others (1996) found that loblolly pine P_n increased the year after the fertilization treatment was initiated, Maier and others (2002) and Gough and others (2004) reported no impact effect or slightly lower rates of P_n due to fertilization after 4 and 6 years, respectively, of annual application, all at SETRES. It is likely that increased leaf area induced by fertilization was driving increased growth of longleaf pine, similar to what occurs in loblolly pine after an initial but brief increase in P_n rates (Gough and others 2004a, 2004b).

The lower g_{wv} of fertilized trees is consistent with both theory (Ewers and others 2000, Gough and others 2004a) and empirical data (Ewers and others 1999, 2000), again tested on loblolly pine at SETRES. Fertilization on excessively drained sandy soil, without irrigation, reduces g_{wv} by reducing the ratio of leaf mass to fine root mass which imposes water stress. This stress induces leaf and root tissue to develop with decreased specific conductivity and then more resistant to hydraulic failure from cell cavitation (Ewers and others 1999).

The larger reduction in g_{wv} than P_n, caused by fertilization, increased the mean ratio of P_n:g_{wv}, based on instantaneous gas exchange measurements. This result was consistent with foliar $\delta^{13}C$ data. However, where light was not limited by competition with neighboring loblolly pine trees, the reduction in g_{wv} due to fertilization did not result in a decrease in growth rate as would be expected if other factors were more or less equivalent (Farquhar and others 1982, 1989).

Conclusions

Longleaf pine grew faster than loblolly pine on an excessively drained soil with low nutrition. In fertilized plots, the impact of fertilization of longleaf pine growth was dependent on competition with the crop loblolly pine trees. If longleaf pine was suppressed by neighboring loblolly pines, then overall growth after 7 years of annual fertilization was slower than control trees. However, nonsuppressed longleaf pine trees increased growth due to fertilization almost to the same extent as the loblolly pine trees. Annual fertilization increased longleaf pine foliar N but decreased P_n and, to larger extent g_{wv}, increasing the P_n:g_{wv} ratio. These analyses indicate that, at the time of the experiment, growth increases due to fertilization were not due to leaf level changes in physiology; they were likely due to increases in leaf area. These results may be partly attributed to competition effects with loblolly pine, which has responded positively (volume growth = 2.5 × controls) to fertilization. This suggests that longleaf pines grown in mixed plantations may have different fertilization requirements than when grown in pure stands.

Acknowledgments

We thank John M. Seiler, Virginia Polytechnic Institute and State University, and S. Reza Pezeshki, University of Memphis, for their review of this article. We also thank Daniel McInnis, Chris Gough, and Luke McCall for help in data collection.

Literature Cited

Albaugh, T.A.; Allen, H.L.; Dougherty, P.M.; Johnsen, K.H. 2004. Long term growth responses of loblolly pine to optimal nutrient and water resource availability. Forest Ecology and Management. 192: 3–19.

Albaugh, T.J.: Allen, H.L.; Dougherty, P.M. [and others]. 1998. Leaf area and above- and below-ground growth responses of loblolly pine to nutrient and water additions. Forest Science. 44: 1–12.

Blevins, D.; Allen, H.L.; Colbert, S.; Gardner, W. 1996. Woodland owner notes - nutrient management for loblolly pine straw. WON 30. Raleigh, NC: North Carolina Cooperative Extension Service, North Carolina State University. 8 p.

Boyer, W.D.; Miller, J.H. 1994. Effect of burning and brush treatments on nutrient and soil physical properties in young longleaf pine stands. Forest Ecology and Management. 70: 311–318.

Ewers, B.E.; Oren, R.; Albaugh, T.J.; Dougherty, P.M. 1999. Carry-over effects of water and nutrient supply on water use of Pinus taeda. Ecological Applications. 9: 513–525.

Ewers, B.E.; Oren, R.; Sperry, J.S. 2000. Influence of nutrient versus water supply on hydraulic architecture and water balance in Pinus taeda. Plant, Cell and Environment. 23: 1055–1066.

Farquhar, G.D.; Ehleringer, J.R.; Hubick, K.T. 1989. Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology. 40: 503–537.

Farquhar, G.D.; O'Leary, M.H.; Berry, J.A. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Australian Journal of Plant Physiology. 9: 121–137.

Fox, T.R.; Allen, H.L.; Albaugh, T.J. [and others]. 2006. Forest fertilization in southern pine plantations. Better Crops. 90(3): 12–15.

Gough, C.M.; Seiler, J.R.; Johnsen, K.H.; Sampson, D.A. 2004a. Seasonal photosynthesis in fertilized and nonfertilized loblolly pine. Forest Science. 50: 1–9.

Gough, C.M.; Seiler, J.R.; Maier, C.A. 2004b. Short-term effects of fertilization on loblolly pine (*Pinus taeda* L.) physiology. Plant, Cell and Environment. 27: 876–886.

Guehl, J-M.; Fort, C.; Ferhi, A. 1995. Differential response of leaf conductance, carbon isotope discrimination and water use efficiency to nitrogen deficiency in maritime pine and pedunculate oak plants. New Phytologist. 131: 149–157.

Harrington, C.A. 1990. PPSITE - a new method of site evaluation for longleaf pine: model development and users guide. Gen.Tech. Rep. SO–80. New Orleans: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 28 p.

Landers, J.L.; Van Lear, D.H.; Boyer, W.D. 1995. Longleaf pine forest of the Southeast: requiem or renaissance? Journal of Forestry. 93(11): 39–44.

Maier, C.A.; Johnsen, K.H.; Butnor, J. [and others]. 2002. Branch growth and gas exchange in 13 year-old loblolly pine (*Pinus taeda* L.) trees in response to elevated CO2 and fertilization. Tree Physiology. 22: 1093–1106.

McLeod, K.W.; Sherrod, C., Jr.; Porch, T.E. 1979. Responses of longleaf pine plantations to litter removal. Forest Ecology and Management. 2: 1–12.

Murthy, R.; Dougherty, P.M.; Zarnoch, S.J.; Allen, H.L. 1996. Effect of carbon dioxide, fertilization and irrigation on photosynthetic capacity of loblolly pine trees. Tree Physiology. 16: 537–546.

North Carolina State Forest Nutrition Cooperative. 1998. Growth and litterfall responses of longleaf pine to fertilization. NCSFNC Res. Note 16. Raleigh, NC: North Carolina State University. 7 p.

Anderson, Peter H; Johnsen, Kurt H. 2009. Fertilizer responses of longleaf pine trees within a loblolly pine plantation: separating direct effects from competition effects. Res. Pap. SRS–48. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 6 p.

Evidence is mixed on how well longleaf pine (*Pinus palustris* Mill.) responds to increased soil nitrogen via fertilization. We examined growth and physiological responses of volunteer longleaf pine trees within an intensive loblolly pine (*Pinus taeda* L.) fertilization experiment. Fertilizer was applied annually following thinning at age 8 years (late 1992) at rates tailored to maintain a high needle nitrogen concentration. We measured the annual growth of 20 volunteer longleaf pine trees per treatment. We took bimonthly gas exchange measures on 12 longleaf pine trees per treatment from June 1999 through June 2000, after which we estimated carbon isotope discrimination and foliar nitrogen concentration on foliage. The impact of fertilization in both growth and gas exchange was dependent on competition for light with neighboring loblolly pine trees. When fertilized longleaf pine trees were separated into categories with respect to being dominant or suppressed (relative to the loblolly pine trees), dominant-fertilized trees had the lowest carbon isotope discrimination increased photosynthesis, and decreased stomatal conductance, indicating greater water use efficiency in these trees. Compared to loblolly pine, longleaf pine growth is restricted less by poor soil nutrition. However, early rotation longleaf pine appears to have the potential to increase growth rate via fertilization to almost the same extent as loblolly pine.

Keywords: Carbon isotopes, fertilization, growth, longleaf pine, photosynthesis, stomatal conductance.

The Forest Service, United States Department of Agriculture (USDA), is dedicated to the principle of multiple use management of the Nation's forest resources for sustained yields of wood, water, forage, wildlife, and recreation. Through forestry research, cooperation with the States and private forest owners, and management of the National Forests and National Grasslands, it strives—as directed by Congress—to provide increasingly greater service to a growing Nation.

The USDA prohibits discrimination in all its programs and activities on the basis of race, color, national origin, age, disability, and where applicable, sex, marital status, familial status, parental status, religion, sexual orientation, genetic information, political beliefs, reprisal, or because all or part of an individual's income is derived from any public assistance program. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternative means for communication of program information (Braille, large print, audiotape, etc.) should contact USDA's TARGET Center at (202) 720-2600 (voice and TDD).

To file a complaint of discrimination, write to USDA, Director, Office of Civil Rights, 1400 Independence Avenue, SW, Washington, D.C. 20250-9410, or call (800) 795-3272 (voice) or (202) 720-6382 (TDD). USDA is an equal opportunity provider and employer.