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Nitrogen supply and demand in short-rotation sweetgum plantations

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Abstract

Intensive management is crucial for optimizing hardwood plantation success, and nitrogen (N) nutrition management is one of the most important practices in intensive management. Because management of short-rotation woody crop plantations is a mixture of row-crop agriculture and plantation forestry, we tested the usefulness of an agronomic budget modified for deciduous perennial trees for estimating N fertilizer recommendations. We studied the foliar N demand, resorption, and uptake response of two sweetgum (*Liquidambar styraciflua* L.) plantations on a converted agricultural field and a pine cutover site to biannual applications of three nitrogen (N) fertilizer rates: 0, 56 and 112 kg N ha^{-1}. We also estimated soil N supply, foliar N uptake efficiency, and apparent fertilizer N uptake efficiency. Fertilization increased foliar demand (defined as total foliar N content), resorption, and uptake at both sites, but to a greater degree on the cutover site, which had lower soil N supply. Resorption efficiency did not increase with fertilization, but resorption proficiency, the N concentration of senesced leaves, was reduced (N concentrations higher) at the drier agricultural field site and in the fertilized trees. Based on our budget analysis, we recommend fertilizing sweetgum plantations with 50 kg N ha^{-1} for each 2000 kg ha^{-1} of foliage biomass, assuming they have 45–65 kg ha^{-1} of soil N supply.

Keywords: Short-rotation forestry; Nitrogen fertilization; Sweetgum

1. Introduction

Nitrogen (N) fertilizer applications to forest systems are generally limited to the correction of diagnosed tree deficiencies, and then only in intensively managed plantation systems. Plantation forest systems have been structured around relatively nutrient efficient species, e.g., *Pinus* spp., that achieve acceptable production with relatively little input (Bowen and Nambiar, 1984). Because N demand reaches a maximum when stands fully occupy sites, plantations become N-limited during or shortly after canopy closure. A combination of thinning and fertilization is generally sufficient to synchronize N supply with plant N demand (Allen, 1987). Short-rotation woody crop (SRWC) systems are the most intensively managed forest systems, and are usually grown in 5–20-year cycles for rapid production of wood that is used for pulp or fuel. The tree species

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used for SRWC in North America and Europe are generally deciduous hardwoods that are less N efficient compared to pines due to greater N concentrations required by the trees and a complete renewal of foliage each year. The high N demand of these intensively managed hardwoods often creates an asynchrony between soil N supply and tree N demand before canopy closure (van Miegroet et al., 1994). Repeated applications of fertilizer are needed to minimize N deficiencies, but we do not know the optimal N fertilizer rate and timing that will maximize plantation productivity and minimize N export from the system, especially on a species- and site-specific basis.

Because SRWC systems are analogous to cropping systems, an agronomic model may be useful for determining fertilizer recommendations. Current diagnostic techniques are effective at determining when stands are already deficient; a more proactive approach is to forecast N supply and demand and fertilize accordingly.

The N fertilizer (N_f) required by an annual crop depends on the dry matter yield (Y_{dry}), the N concentration in the biomass (N_y), and the soil N supply during the growing season (N_s) (Stanford, 1973; Neeteson, 1990) (Eq. (1)):

$$N_f = (Y_{dry}N_y) - e_sN_s \tag{1}$$

The crop will not recover all the fertilizer N (N_f) or soil N (N_s); N uptake efficiency of from soil (e_s) and fertilizer (e_f) will be less than 100%. These uptake efficiencies will influence the quantity of N needed to achieve a certain yield and can be represented as a modification of Eq. (1) (Eq. (2)):

$$N_f = \frac{(Y_{dry}N_y) - e_sN_s}{e_f} \tag{2}$$

Trees can internally transfer N, known as resorption (Killingbeck, 1986), from the foliage prior to senescing. Nitrogen resorption can be expressed as a modification of Eq. (2), where e_y is the N resorption efficiency, or the proportion of N recovered before leaf fall the previous year, and e_yN_y the total amount recovered the previous year. The N fertilizer required is then a function of the plant N demand adjusted for soil supply and its efficiency of uptake, resorption efficiency, and the efficiency of fertilizer use (Eq. (3)):

$$N_f = \frac{(Y_{dry}N_y) - e_sN_s - e_yN_y}{e_f} \tag{3}$$

In perennial tree crop systems, a complete N demand budget would entail measurements of the biomass and N concentration of all the various plant components (i), e.g., foliage ($Y_{dry_{foliar}}N_{y_{foliar}}$), branches ($Y_{dry_{branch}}N_{y_{branch}}$), bole ($Y_{dry_{bole}}N_{y_{bole}}$), and roots ($Y_{dry_{roots}}N_{y_{roots}}$) (Eq. (4)):

$$\sum_{1}^{i} Y_{dry_i}N_{y_i} \tag{4}$$

Whereas bole, branch, and roots may contain a substantial quantity of N, the foliage and fine root structures are the most dynamic and responsive to N availability. Foliar N demand is the most useful for diagnostic and prescriptive purposes, especially since foliage is relatively easily measured compared to fine roots.

Similarly, a complete N supply budget would include measurements of all sources of N supply and potential N losses (i); deposition (atmospheric and overland flow), throughfall, stemflow, litter N release, and soil supply. However, of these, soil N supply is the most significant and estimable natural source of N, and may be measured directly (Eno, 1960) or estimated with models (Molina and Smith, 1988). Although the budget accuracy is limited by the exclusion of other forms of uptake and supply, especially fine root uptake and litter N release, the primary goal of this budget technique is a relatively simple, straightforward estimation of fertilizer needs that can be applied over a wide range of sites.

Accordingly, the objective of our study was to determine the N fertilizer needed for two sweetgum (*Liquidambar styraciflua* L.) plantations in the southeastern US by determining the foliage component of Y_{dry} and N_y, the soil N supply, e_s, e_y, and e_f, and solving Eq. (3). This was done on two contrasting soils to determine the usefulness of this approach for diagnosing N needs and prescribing N fertilizer and to discuss site influences on the component responses to N fertilizer.

2. Materials and methods

2.1. Site descriptions

Two sites of contrasting soil type and land use history were selected to study the effect of site and soil type on soil N supply, plant N demand, and fertilizer need. One was a well-drained agricultural field, while the other was a poorly drained harvested loblolly pine (*Pinus taeda* L.) plantation site, hereafter referred to as the "ag field" and "cutover" sites, respectively. Compared to forest sites, converted agricultural fields in the middle Atlantic coastal plain tend to have higher soil pH due to liming and the removal of acid-producing forest litter, and they have higher levels of phosphorus and nutrient cations due to repeated fertilization. Herbaceous weed communities dominate ag fields due to past cultivation and weed control, and equipment access and soil trafficability is excellent due to the nature of the past land use. Harvested forest sites, or cutovers, are generally less eroded and tend to have higher quantities of soil organic matter and nitrogen (Richter et al., 2000). However, they have not been repeatedly fertilized and have not had annual weed control, so soil nutrients and weeds must be managed when converting to SRWC. Within these two land use groupings, wide differences in soil types and herbaceous and competing woody vegetation cloud our understanding of site-specific plantation responses to various fertilization treatments. These two sites were selected to represent the range of site types currently considered for operational plantations by forest industry in the southeastern US.

The ag field study site was located on International Paper's Trice Research Forest in Sumter County, South Carolina (33°58′N, 80°12′W) on the middle Atlantic coastal plain. The soil is a well-drained Norfolk sandy loam (loamy, kaolinitic, thermic Typic Kandiudult). Nine 0.2 ha treatment plots with 0.04 ha measurement plots were established in February 1996 with 280 1–0 bare-root sweetgum seedlings (3 m × 2.4 m spacing, $\sim$1400 ha^{-1}). The sites had been regularly managed for dry land crops, e.g., corn (*Zea mays* L) and soybeans (*Glycine max* (L.) Merr), for more than 20 years, and soybeans, a N_2 fixing legume, were the primary crop for the 5 years previous to plantation establishment. All plots were treated with an initial fertilizer application of 280 kg ha^{-1} diammonium phosphate (DAP), which supplied 50 kg N ha^{-1} and 56 kg P ha^{-1} in November 1995, and 100 kg ha^{-1} urea, which supplied 46 kg N ha^{-1}, in August 1996. Non-crop vegetation was restricted to herbaceous vegetation, mostly broomsedge (*Andropogon virginicus* L.) and dogfennel (*Eupatorium capillifolium* Lam.), due to the agricultural legacy and early rotation chemical weed control. The site was also mowed intermittently throughout the study to reduce the herbaceous competition for water and nutrients.

The cutover pine site was on MeadWestvaco Corporation land, located in Colleton County, South Carolina (32°8′N, 80°7′W) on the lower Atlantic coastal plain, and was established in February 1995. The soil is a somewhat poorly to poorly drained Argent sandy loam (clayey, mixed, active, Typic Endoaqualfs) developed from marine deposits. The site undergoes wide fluctuations in soil water contents, from saturated soils with standing water in the dormant season to dry soils during the growing season. The heavy clay subsoil restricts water percolation through the solum, and the low elevational gradient (<2%) restricts lateral flow. These mechanisms induce short-term saturation after heavy rain events throughout the growing season. Nine 0.2 ha treatment plots with 0.04 ha measurement plots were established with 280 1–0 bare-root sweetgum seedlings (3 m × 2.4 m spacing, $\sim$1400 ha^{-1}) of the same genetic source as the ag field site following loblolly pine harvest and site preparation, which consisted of bedding, fertilization and non-crop vegetation control. All plots received 50 kg N ha^{-1} and 56 kg P ha^{-1} as DAP and 3.9 Mg ha^{-1} dolomitic lime in March 1995. The lime application raised pH from approximately 4.75–5.5. Non-crop vegetation control consisted of pre-emergent herbicide applications in February and March 1995, 1996 and 1997. Herbicides were also applied by directed spray in 1995 and 1996 during the growing season. Although this aggressive chemical weed control program was used for the first three years, woody and herbaceous plants were present when competition control measures ceased. No data were taken of understory biomass.

2.2. Experimental design

At each site, three biannual N fertilizer rates were initiated at age 2 (1996 on the cutover site and 1997 on the ag field site) and replicated three times. Every 2 years, i.e., ages 2, 4, 6, ammonium nitrate (NH_4NO_3) was applied at the following rates: 0 (control), 168 and 336 kg ha^{-1}, which provided 0, 56 and 112 kg N ha^{-1}, respectively. At the cutover site, 56 kg P ha^{-1} was added as triple superphospate at age 6 because fertilization with N alone at age 4 induced P deficiencies. The error control design at the cutover site was a completely randomized design, while the design at the ag field site was a randomized complete block design (Steel and Torrie, 1980), where the blocking factor was the depth to redoximorphic features. The wide separation of the sites in space, the different establishment years (1996 at the ag field site and 1995 at the cutover site), and slightly different cultural management approaches between the two sites precluded a quantitative comparison of the two sites. The similarity in fertilizer application rates and data collection procedures, however, allows qualitative comparisons of site-to-site differences in plant responses.

Treatment effects within a site and age class were determined using analysis of variance at $\alpha = 0.10$. If the model was significant, Duncan's multiple range test was used to separate the means (SAS Institute, 2000).

2.3. Soil characterization

Soil samples were collected from each treatment plot in 1999 and 2000. Nine 1.5 cm diameter subsamples were collected per treatment plot in April and November of each year from the 0 to 20 cm depth. The subsamples were air-dried, sieved to pass a 2 mm sieve and bulked by treatment plot and year. The samples were then analyzed for total carbon (C), N, phosphorus (P), and pH. Carbon and N were determined with a vario MAX CNS analyzer (Elementar, Hanau, Germany), and C was converted to organic matter by multiplying by 1.7 (Nelson and Sommers, 1996). Available phosphorus was determined by extracting the soils with Mehlich I extractant (Kuo, 1996) and analyzing the extract via inductively coupled plasma-atomic emission spectroscopy (SpectroFlame Modula Tabletop ICP, Spectro Analytical Instruments, Fitchburg, MA) (Soltanpour et al., 1996). Bulk density (Grossman and Reinsch, 2002) was determined on five 5 cm diameter $\times$ 5 cm tall cores taken from random depths within the surface 20 cm at each site by oven drying at 105 °C to a constant weight.

2.4. Foliage sampling

In September 1998–2000, which corresponded to ages 3–5 at the ag field site and ages 4–6 at the cutover site, respectively, three foliage samples were taken of the canopy from five trees in each treatment plot. The samples were comprised of six leaves of all stages of development from single branches and were collected within the upper, middle, and lower crown positions on the south side of each tree (Kuers and Steinbeck, 1998). The samples were chilled on-site, transported to the laboratory in a cooler, and processed within 24 h. The leaves were oven-dried at 65 °C to a constant weight. We determined the foliage mass for each crown position by multiplying the total litterfall, measured from five randomly located litter traps (approximately 1 m^2 per trap) per plot by the relative weighting factors of Kuers and Steinbeck (1998), who showed that fertilization increases young sweetgum foliage mass disproportionately among crown positions. Foliar N was determined on each sample with a N analyzer (LECO FP-528, St. Joseph, MI). Total foliar nutrient content on an area basis was determined by multiplying the foliar N concentration by the foliage mass for each crown position. Litter N concentrations and contents were determined similarly.

2.5. In situ nitrogen production

Annual soil N supply was estimated for 1999 and 2000, which corresponded to ages 4 and 5 at the ag field and ages 5 and 6 at the cutover site. Our original design called for measuring N mineralization for two growing seasons. Therefore, net N mineralization was measured from April 1999 to September 2000 with the buried bag method (Eno, 1960). To provide an estimate of soil N supply for the 2 calendar years, data from January to March 2000 was used to complete the annual production rate estimate for 1999, and data from October to December 1999 was used to complete the annual production rate estimate for 2000. Although the assumption that the winter N supply rates were the same for both years may be erroneous, this supply represented only about 20% of the total estimate for both years and sites. Thus, the error introduced was assumed to be small.

Two soil samples (bags) were collected for each sampling date for the buried bag procedure. One was incubated in situ and the other returned to the laboratory for analysis. For each experimental unit, three subsamples were taken of the top 20 cm, each consisting of three composited 1.5 cm soil core samples.

Each soil sample was air-dried, sieved to pass a 2 mm sieve, and the NH_4^+ and NO_3^--N extracted with 2 M KCl in a 10:1 solution:soil ratio. The NH_4^+ and NO_3^- concentration in each extract was determined via automatic colorimetric spectrophotometry on a TRAACS 2000 autoanalyzer (Bran and Luebbe Corporation, Oak Park, IL). Nitrogen supply was calculated as the difference between the N intensity in the soils incubated for approximately 30 days and the samples taken at the time of incubation. If negative values occurred, which represent immobilization or denitrification, the soil N supply was set to 0 for that sample.

3. Results

The soils on the two sites were quite different (Table 1). Soil organic matter at the cutover site (5.49%) was more than six times greater than that at the ag field site (0.88%). The C:N ratio, a measure of substrate quality, was only 15:1 at the ag field site but twice that at the cutover site.

Foliar N demand $Y_{\text{dry}_{\text{foliar}}} N_{\text{y}_{\text{foliar}}}$ was 7.95, 30.3 and 18.7 kg ha^{-1} on the control plots at ages 3, 4 and 5, respectively, at the ag field site (Fig. 1). At ages 3 and 5, when no fertilizer was applied, the foliar N demand did not respond to fertilizer treatment at $P = 0.10$, although the 112 kg N ha^{-1} treatment had 66% more foliar N than the control at age 5. At age 4, the application of 112 kg N ha^{-1} increased the total foliar N 73% over the control. At the cutover site, the unfertilized trees had 15.0, 24.4 and 18.8 kg N ha^{-1} at ages 4, 5 and 6, respectively. The trees treated with 112 kg N ha^{-1} had 193, 91 and 223% greater foliar N at ages 4, 5 and 6, respectively, while the 56 kg N ha^{-1} treatment was consistently higher than the control, but these differences were not statistically significant at the 10% level.

The midsummer foliar N content that was not returned in the leaf litter was considered to be resorbed (Eq. (5)):

$$\text{Resorbed N} = (Y_{\text{dry}_{\text{foliar}}})(N_{\text{y}_{\text{foliar}}} - N_{\text{y}_{\text{littter}}}) \tag{5}$$

About 4, 13 and 10 kg N ha^{-1} was resorbed at ages 3, 4 and 5, respectively, at the ag field site, and was not significantly affected by fertilization at any age, although the amount returned at age 4 varied from 6.8 to 17.8 kg N ha^{-1} (Fig. 1). At the cutover site, the unfertilized trees resorbed 6.4, 10.7 and 6.2 kg N ha^{-1} at ages 4, 5 and 6, respectively. The trees fertilized with 112 kg N ha^{-1} resorbed 248 and 313% more N at ages 4 and 6, respectively. At age 5, the trees of the 112 kg N ha^{-1} treatment resorbed 95% more N, but the difference was not significant at $P = 0.10$. The efficiency of N resorption, calculated as the proportion of total foliar N resorbed, ranged from 24 to 45% at the ag field site and 31–51% at the cutover site. At the cutover site, fertilization did not affect N resorption rates. At the ag field site, N resorption in the 112 kg N ha^{-1} treatment was significantly greater than the control or 56 kg N ha^{-1} treatment at age 5, but did not differ among rates at ages 3 or 4.

Mineralized N in the top 0.20 m of the unamended treatment plots, or soil N supply (N_s), was about 69 kg ha^{-1} at the ag field site and about 47 kg ha^{-1} at the cutover site (Fig. 2). On the ag field at age 4 and the cutover at age 6, soil N supply was about 37% greater in the plots fertilized with 112 kg N ha^{-1} than the other plots. Soil N supply was similar across treatments at age 5, when no fertilizer was added at either site.

Foliar N uptake was calculated as the foliar N content of the current year less the N resorbed the previous year (Eq. (6)):

$$\text{Foliar N uptake} = (Y_{\text{dry}_{\text{foliar}}} N_{\text{y}_{\text{foliar}}})_{\text{T1}} - ((Y_{\text{dry}_{\text{foliar}}})(N_{\text{y}_{\text{foliar}}} - N_{\text{y}_{\text{littter}}}))_{\text{T0}} \tag{6}$$

N uptake at the ag field site ranged from 27.1 to 47.9 kg ha^{-1} at age 4 and 11.9–16.3 at age 5 (Fig. 2). Foliar N uptake of the 56 and 112 kg N ha^{-1} treatment plots was 11.2 and 20.8 kg ha^{-1} greater, respectively, than the unfertilized treatment plots at age 4. The fertilizer treatments at age 4 had no residual

Table 1
Soil properties of the top 0.2 m at two sweetgum plantations in South Carolina, USA

Site	Organic matter (%)	Total N (kg ha^{-1})	C:N	Available P (kg ha^{-1})	Bulk density (g cm^{-3})
Converted agricultural field	0.88	834	15.2	104.3	1.39
Cutover pine site	5.49	1958	29.6	10.7	0.89

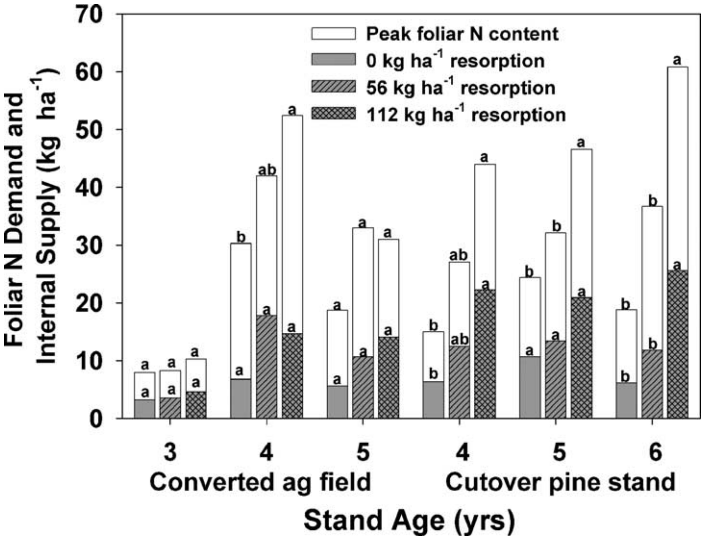

Fig. 1. Foliar N demand and resorption in two young sweetgum stands in South Carolina, USA. Fertilizer treatments, denoted by shaded patterns, were applied at ages 4 and 6, but not at age 5. Foliar N demand and N resorption means within a site and age followed by the same letter are not different at $\alpha = 0.10$.

effect on uptake at age 5. The uptake at age 4 was greater than at age 5 due to a drought-induced foliage re-flush and generally higher foliar N concentrations. At the cutover site, foliar N uptake ranged from 18.0 to 24.3 kg N ha^{-1} at age 5 and 8.1–39.8 kg N ha^{-1} at age 6. Uptake did not differ among treatments at age 5, when no fertilizer was applied. At age 6, uptake was 15.3 and 31.7 kg ha^{-1} greater for the 56 and 112 kg N ha^{-1}, respectively, treatment plots compared to the control plots.

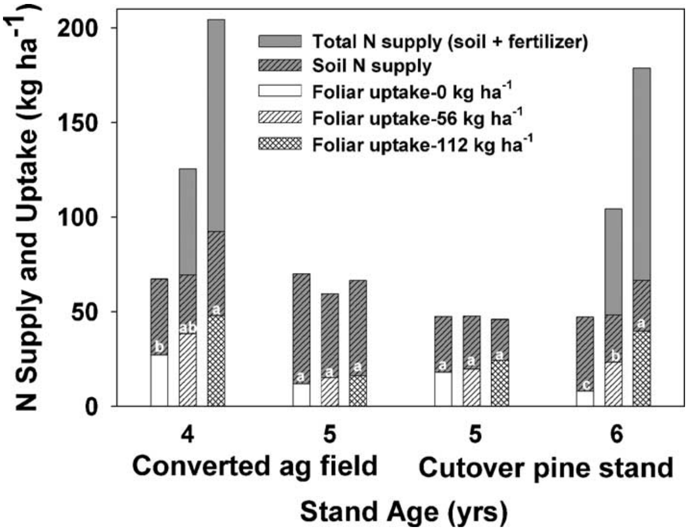

Fig. 2. Foliar N uptake (demand less resorption from previous year), soil N supply, and fertilizer applied in two sweetgum stands in South Carolina, USA. Fertilizer treatments, denoted by shaded patterns, were applied at ages 4 and 6, but not at age 5. Foliar uptake means within a site and age followed by the same letter are not different at $\alpha = 0.10$.

Foliar N uptake efficiency (Eq. (7)) was calculated as foliar N uptake (Eq. (6)) divided by the total N supply (soil + fertilizer):

$$\text{Foliar N uptake efficiency} = \frac{\text{foliar N uptake}}{N_f + N_s} \quad (7)$$

Soil N uptake efficiency (e_s) is the foliar N uptake efficiency for the unfertilized plots. At the ag field site, foliar uptake of the unfertilized trees at age 4 was 43% of the total N supply (Fig. 2). Foliar uptake of the trees fertilized with 56 and 112 kg N ha^{-1} at age 4 was 31 and 24%, respectively, of total N supply. At age 5, when no fertilizer was applied, the foliar N uptake efficiency of the fertilized trees, regardless of treatment, was about 28%, while the foliar N uptake efficiency of the unfertilized trees was only 18%. However, this difference was not significant at $P = 0.10$.

At the cutover site, foliar N uptake efficiencies ranged from 17 to 51% of the total N supply. At age 6, unlike the ag field site, fertilization had no effect on foliar N uptake efficiency. In fact, the trees fertilized with 112 kg N ha^{-1} had the highest foliar N uptake efficiency (23%) at age 6. At age 5, which was a non-fertilized year, the fertilized trees were not significantly more efficient than the unfertilized trees.

The apparent fertilizer uptake efficiency (e_f) was estimated as the proportion of fertilizer applied that could be attributed to increased canopy N uptake (Eq. (8)). It does not account for uptake by aboveground perennial plant components, roots, or competing vegetation:

$$\text{Fertilizer uptake efficiency} = \frac{\text{foliar N uptake}_{\text{fertilized plots}} - \text{foliar N uptake}_{\text{unfertilized plots}}}{N_f} \quad (8)$$

For example, at the ag field site at age 4, the foliar uptake of the trees fertilized with 56 kg N ha^{-1} was 38.3 kg ha^{-1}, while uptake of the unfertilized trees was 27.1 kg ha^{-1}, which indicates that about 11.2 kg of foliar uptake was met by the 56 kg N ha^{-1} applied, or 20%. The fertilizer uptake efficiencies calculated for the two sites varied little. At the ag field site, fertilizer uptake was 11.2 and 20.8 kg ha^{-1} for the 56 and 112 kg N ha^{-1} treatments, respectively, which was about 20% of the fertilizer applied for both treatments. At the cutover site, the fertilizer uptake was 15.3 and 31.7 kg ha^{-1} for the 56 and 112 kg N ha^{-1} treatments, respectively, which was about 28% of the fertilizer applied for both treatments. The similarity in fertilizer efficiency among treatments within each site and across sites was remarkable given the number of inputs to the calculation and the differences between the two sites.

4. Discussion

Studies have shown that shortly after site preparation and planting, soil N supply is elevated due to high soil temperature and water availability caused by the absence of site cover and evapotranspiration as well as soil perturbations inherent in site preparation operations (Burger and Pritchett, 1984; Vitousek and Matson, 1985). Near canopy closure, however, tree N demand reaches a maximum. The increase in canopy cover and evapotranspiration with stand age reduces soil temperature and moisture, which reduces soil microbial activity and soil N supply. Because soil N supply is quite variable across soils and sites and tree N demand is influenced by a host of factors other than N availability, plantations reach N deficiency at different times and to different degrees. In general, the greatest asynchrony occurs at or near canopy closure, and in operational plantations a single application of N fertilizer at or near that time is usually all that is done to correct the asynchrony (Allen, 1987). Even in the most intensive operational plantations, fertilization generally only occurs in response to a N deficiency diagnosed by, for example, foliar N concentrations.

In young SRWC plantations, foliar demand is high, which creates an asynchrony between supply and demand at an early age (van Miegroet et al., 1994). A conservative fertilizer approach promotes fertilization only in response to a diagnosed deficiency (Dickmann and Stuart, 1983). However, N demand constrained by low supply, i.e., N deficiency, is difficult to diagnose and detect in SRWC plantations due to a lack of well-developed indicators for each species or clone. Potential yield losses arising from undiagnosed N deficiencies, e.g., "hidden hunger" (Dow and Roberts, 1982), can be high (Heilman and Fu-Guang, 1993). In this study, N demand (foliar N content) ranged from 8 to 61 kg ha^{-1} from age 3 to 6. Applying 112 kg ha^{-1} of fertilizer N more than doubled demand

(133%) at age 4 across both sites. At age 6, the trees on the cutover site fertilized with 112 kg N ha^{-1} had over three times the demand as the unfertilized trees. At age 5, when neither site received fertilizer, the demand remained 80% greater in the trees fertilized with 112 kg N ha^{-1} compared to the unfertilized trees. Obviously, the potential demand of these young plantations was greater than the amount they were able to take up from the soil and from resorption.

Foliar demand is met in tree plantations from three sources: soil N (which includes forest floor, fine root, and soil organic matter turnover), fertilizer N, and internal N stores arising from resorption of N from senescing leaves. In most forest systems, about 50% of foliar N is resorbed prior to leaf fall (Aerts and Chapin, 2000). However, because the foliage biomass in young, pre-canopy closure plantations is rapidly aggrading, the amount resorbed in one year will generally be less than 50% of the demand in the following year. Only when foliar demand reaches a semi-steady state will 50% of the annual demand be met by resorption.

The range of resorption efficiencies, defined as the proportion of green leaf nutrient content resorbed prior to leaf fall in the current year, observed in this study (24–51%) is low for sweetgum plantations. Nelson et al. (1995) found that 9-year-old sweetgum resorbed about 50% of foliar N, while Kuers and Steinbeck (1998) found that 43–62% of foliar N was resorbed by 4-year-old sweetgum. In this study, the average resorption efficiency for the ag field at age 3 and the cutover at ages 4 and 5 was 44%, which, although still low, is more similar to the findings of Nelson et al. (1995) and Kuers and Steinbeck (1998). The lowest resorption efficiencies, which occurred at the ag field at ages 4 and 5 and the cutover at age 6, were caused by higher litter N concentrations in those years.

The relationship between plant nutrient status and resorption efficiency has been debated for some time. The classic theory holds that plants growing on nutrient-poor sites have greater resorption efficiency than those growing on nutrient-rich sites (Del Arco et al. (1991)). However, this theory has been questioned by Chapin (1980) and Aerts (1996), who showed that evidence from the literature does not support the theory. In this study, except for the trees on the 112 kg N ha^{-1} treatment plots at the ag field at age 5, which were 50% more efficient than the unfertilized trees, fertilization had no effect on N resorption efficiency at either site at any age. These findings are in general agreement with Nelson et al. (1995), who found no influence of fertilization on resorption efficiencies in sweetgum, but in contrast to Kuers and Steinbeck (1998), who found that fertilization increased resorption efficiency. Because N fertilization generally increases foliar N concentrations, the lack of a fertilization effect on resorption efficiency means that resorption proficiency (Killingbeck, 1996) must be less (litter N concentrations higher) when fertilized. In fact, this pattern can be seen at age 4 on the ag field and ages 4 and 6 on the cutover site. Foliar N concentrations were greater when fertilized, but resorption efficiency was not increased because resorption proficiency was reduced.

Potential plant N demand in excess of internal N stores from the previous year's resorption is met, to the extent possible, by root uptake of soil or fertilizer N. Uptake clearly responded to fertilizer application at both sites when applied. Foliar N uptake was 77 and 391% greater on the ag field and cutover sites, respectively, in the trees fertilized with 112 kg N ha^{-1} compared to the unfertilized trees. On the ag field at age 4, the foliar N demand was almost exclusively (91%) met by uptake (Fig. 2), since resorption at age 3 was minimal (Fig. 1). On the cutover site, about 43% of the demand at age 6 was met by resorption (Fig. 1), and the remaining 57% met by uptake. These results indicate that resorption was not an effective N source until age 4, and even then uptake was limited by soil N supply and its uptake efficiency.

Differences in plant uptake between sites occur due to differences in either soil N availability or uptake efficiency. The ag field site had about 40% more soil N supply than the cutover site (Fig. 2), which was somewhat unexpected given the nature of the two soils. The cutover site had more than twice the total N as the ag field site, but the cutover SOM had a higher C:N ratio than the ag field SOM and was probably more recalcitrant due to the difference in plant origin (loblolly pine vs. soybeans) between the two sites (Table 1). Nitrogen immobilization within the microbial biomass can represent a very significant process controlling the intensity of available N (Jansson, 1958), and in many situations where labile C is readily available and the C:N ratio is above about 30:1

(Tate, 1995), immobilization may exceed mineralization, causing net N supply to be zero. Because the cutover site had an average C:N ratio of 30:1, a greater proportion of the gross N mineralization was probably immobilized by the microbial biomass than at the ag field site. At both sites, soil N supply was about 22 kg more on the plots fertilized with 112 kg N than the unfertilized plots in the year fertilizer was applied, i.e., 1999 at the ag field and 2000 at the cutover site. The effect was not apparent in the years fertilizer was not applied. These results indicate that the application of fertilizer increased net N mineralization, probably by reducing immobilization. This effect, called "priming" (Jenkinson et al., 1985; Kuzyakov et al., 2000), is important, because it effectively increased the fertilization rate from 112 to about 135 kg N ha^{-1} at both sites. Because our objective was not to study "priming" effects, these results are not definitive, and further work needs to be done in these soils and plantations to determine if native soil N supply is affected by fertilizer applications, especially repeated applications (Whynot and Weetman, 1991; Binkley and Reid, 1985). Johnson et al. (1980) showed that soil C is an important regulator of urea-N dynamics and microbial immobilization, so differences in soil C, such as those between the ag field and cutover sites in this study, may cause the "priming" response to vary across site types.

Soil uptake efficiency (e_s) was calculated as the foliar N uptake efficiency for the unfertilized plots. Uptake efficiency is a function of both plant root architecture and function and soil characteristics. The rooting habits were not studied at either site, but proportional biomass allocation to roots is greater on dry, infertile sites compared to moist, fertile ones (Keyes and Grier, 1981). The soil uptake efficiency was surprisingly similar between the two sites. The ag field, which averaged 11% volumetric soil water content in the surface 20 cm (data not shown), was 35% drier than the cutover site, which averaged 17% volumetric soil water content. Both sites could be considered fertile (Table 1). The drier soil conditions would suggest that the ag field site might have a lower shoot:root ratio compared to the cutover site. Even so, foliage on the ag field site was able to take up about the same proportion of soil N as on the cutover site.

Hydrology and plant competition influence uptake efficiency partly by controlling the fate of soil N. Losses of N occur when NO_3^- is removed in runoff, leached, or denitrified. Runoff and erosional losses were minimal on both sites since neither site had slope gradients greater than 2% and both had little bare soil (Dissmeyer and Foster, 1980). Leaching, however, was probably much different on the two sites. The cutover site was poorly drained, while the ag field was well drained. Therefore, the potential for nitrate leaching was probably much higher at the ag field site. This site was similar in soil and site characteristics to a study on intensively managed loblolly pine and sweetgum on a converted peanut (*Arachis hypogaea* L.), which is a N-fixing legume, farm (Williams and Gresham, 2000), in which significant nitrate leaching was observed in both fertilized and unfertilized treatments after 4 years of tree growth.

Denitrification potential was greater at the cutover site, since it remained saturated longer after rainfall events and had relatively high levels of soil carbon that act as an energy source for denitrifying microorganisms (Davidson and Swank, 1987). Competition from herbaceous and woody plants was greater on the cutover site. Because soil N uptake efficiency was, on average, only 28% of annual soil N supply, these plant and soil factors were important in determining the uptake efficiency. However, given the similarity in soil uptake efficiency between the two sites, the difference in these factors between the two sites was either small, or, more likely, many of the differences counteracted each other. The ag field probably lost more available N via leaching, but the cutover probably lost more through denitrification or weed competition.

By assuming that the fertilized trees absorbed the same amount of N from the soil as the unfertilized trees and that any additional uptake was met by fertilizer N, we were able to estimate the proportion of fertilizer that was absorbed in the year fertilizer was applied. This estimate does not take into account fertilizer-induced changes in overall N uptake efficiency, e.g., through differential fine root growth patterns. Sweetgum fine root growth is plastic in response to N-rich microsites (Ludovici and Morris, 1996; Mou et al., 1995), so roots may respond to localized increases in soil N rapidly after fertilization and improve fertilizer N uptake efficiency. However, if N-rich microsites homogenize once the fertilizer N diffuses throughout the soil profile, then the roots may not have an ideal architecture for capturing N arising from mineralization, thus reducing the soil N uptake efficiency. It also does not account for increased soil N availability due to fertilization, i.e., priming, which was evident at both sites in the 112 kg treatment. Even so, estimating fertilizer uptake separate from soil N in this manner gives us a general idea of the relationship between fertilizer N, soil N, and foliar N uptake in sweetgum plantations. From a practical standpoint, it does not matter if tree N uptake is met from actual fertilizer N, soil N made available by fertilizer ''priming'', or N captured through altered rooting patterns.

Fertilizer uptake efficiency was similar and unexpectedly consistent within and across sites. It is also remarkable that the average fertilizer uptake efficiency (24%) was quite similar to soil uptake efficiency (28%). The discrepancy between the cutover site and ag field site was probably related to fertilizer timing. Fertilization at the ag field at age 4 did not occur until early August due to operational constraints, while fertilization at the cutover site at ages 4 and 6 occurred in March. Fertilizer uptake efficiency would likely have been even less at the ag field site, but in the year fertilization occurred about 70% of the foliage fell in July and re-flushed in September due to summer-long droughts. The re-flushing probably was responsible for most of the fertilizer uptake.

One factor not specifically addressed with our proposed fertilizer estimate model is fertilizer carry-over to the following year. About 50% of fertilizer N remains on-site after fertilization in operational forest stands (Johnson, 1992); about half in tree biomass and half in the soil, regardless of N input rate. In these intensively managed plantations, the potential for loss is much greater due to the repeated inputs and reduced weed nutrient uptake and storage. Studies have shown that smaller, more frequent doses of fertilizer increase nitrification and leaching losses (Johnson and Todd, 1988; Tschaplinski et al., 1991). In our study, we expected to see an improvement in overall uptake efficiency in the fertilized trees during the unfertilized year, which would reflect fertilizer carry-over. At age 5, when no fertilizer was applied, foliar N uptake was about 4.4 and 6.3 kg greater in the trees that were fertilized at age 4 with 112 kg N ha^{-1} than in the unfertilized trees on the ag field and cutover sites, respectively. If soil N uptake efficiency was 28% (the overall average), about 16 and 23 kg of fertilizer N were available at the ag field and cutover sites, respectively, at age 5. The fertilizer N remaining at age 5 from the 56 kg N ha^{-1} treatment at age 4 was about 12 and 6 kg at the ag field and cutover sites, respectively. Overall, these data suggest that only about 15% of the fertilizer N remained available in the year following application.

From these results, the fertilizer needed for young sweetgum plantations was estimated by solving Eq. (3) for N_f given a level of Y_{dry}. Since Y_{dry}, N_y, e_s, e_f, and e_y varied between sites, among treatments, and across years, we estimated parameters for each site given our results. We estimated that the whole-crown foliar N concentration (N_y) would be 1.70%, because this is approximately the highest concentration reached at both sites (data not shown). The uptake efficiency of mineralized soil N (e_s), was taken as the foliage uptake efficiency on the unfertilized plots, which averaged 30 and 28% at the ag field and cutover sites, respectively. Soil N supply was estimated as the average supply on the unfertilized plots at each site, and set at 68.7 kg ha^{-1} for the ag field site and 47.4 kg N ha^{-1} for the cutover site. Because we calculated uptake as the foliar N content less the resorption from the previous year, we calculated the resorption efficiency for Eq. (3) as the proportion of the current year's foliar N that was met by the previous year's resorption. Because resorption at age 3 at the ag field was much lower than at other ages, we used only age 4, 5 and 6 data. At the ag field site, about 46% of the age 5 foliar N was met by the resorption at age 4. At the cutover site, about 40% of the foliar N at ages 5 and 6 was met by resorption at ages 4 and 5. The fertilizer uptake efficiency was estimated as the average efficiency at each site, which was 20% at the ag field and 28% at the cutover site.

Using these parameters, the final equations for the two sites are

Agricultural field:

$$N_f = \frac{(Y_{dry} \times 0.0175) - (0.30 \times 68.7) - (0.38 Y_{dry} \times 0.0175)}{0.20} \tag{9}$$

Cutover site:

$$N_f = \frac{(Y_{dry} \times 0.0175) - (0.28 \times 47.4) - (0.39 \times Y_{dry} \times 0.0175)}{0.28} \tag{10}$$

Because the foliar N concentrations are not independent of fertilizer rate, we estimated that about 60 and 110 kg N ha^{-1} was necessary to reach a foliar N concentration of 1.70% at the ag field and cutover sites, respectively. Solving these equations for an estimated foliage biomass of 3500 kg results in fertilizer N recommendations of 87 and 86 kg N ha^{-1} per year for the ag field and cutover sites, respectively, which translates into a fertilizer recommendation of 50 kg N ha^{-1} 2000 kg^{-1} of foliage biomass. While our recommendations for these two sites are similar, each arose from quite different circumstances. The ag field site had 40% more soil N supply than the cutover site, but had a 20% fertilizer uptake efficiency compared to the 28% of the cutover site. While this approach appears to work well for these two sites, more detailed investigations of soil N supply and N uptake efficiency (both soil and fertilizer N) are needed to extend this approach to varied site types.

With a minimum estimated soil N supply of 45 kg N ha^{-1}, and a soil uptake efficiency of 28%, foliar N demand will probably not respond until the potential uptake is greater than 13 kg N ha^{-1}, which, in our study, did not occur until age 4, and we suggest caution in fertilizing stands before age 4. Using general estimates based on these results from ages 3 to 6, we projected foliage biomass and recommended fertilizer rates for young, intensively managed sweetgum plantations based on optimum foliar N biomass (Fig. 3). Although this approach resulted in a calculated fertilizer rate of 15 kg N ha^{-1} at age 3, this low amount is not practical and is not recommended. These recommendations do not address tree growth explicitly, but Kuers and Steinbeck (1998), and Nelson et al. (1995) showed that tree growth is well correlated with foliage biomass production and nutrition. Linking fertilizer rates to plant uptake by increasing the fertilizer rate as the stand matures has been shown by several researchers (van Miegroet et al., 1994; Ingestad, 1988; Landsberg, 1986) to improve N fertilizer use efficiency, defined as total biomass growth per unit N applied.

The discrepancies among these predicted optimum rates and the actual results at age 4 on the ag field and age 6 on the cutover site are due to year-specific conditions. At age 4 on the ag field site, soil uptake efficiency was 43%, compared to the average of 30.5% across ages 4 and 5. The actual N available from resorption was also very low, because the foliage biomass and N demand at age 3 was low. At the cutover site at age 6, soil uptake efficiency was 17% compared to the average of 27.5% across ages 5 and 6. Given the limited ranges of N rates and fertilization frequencies tested, our general fertilizer recommendation for sweetgum plantations is 90 kg N ha^{-1} per year beginning at age 4 until canopy closure, which should occur between ages 5 and 7 on fertilized sites. Fertilization before age 4 (this study was fertilized at planting and

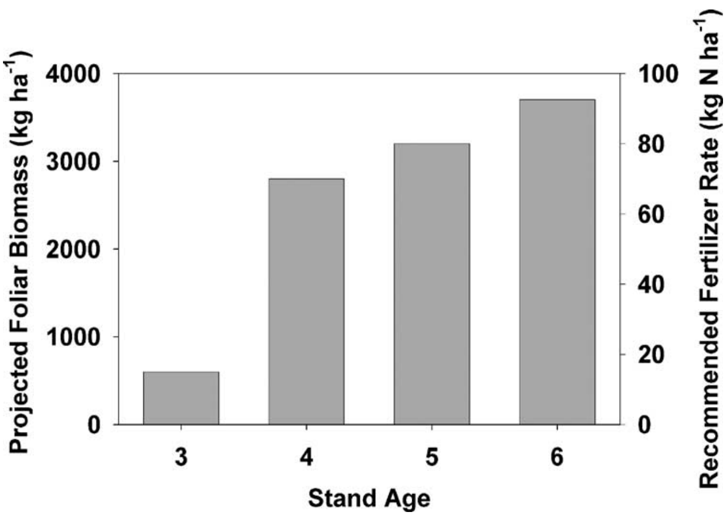

Fig. 3. Projected foliage biomass and recommended fertilizer rates for young sweetgum plantations.

at age 2) is unnecessary. Instead of fertilizing at stand establishment and age 2, these two fertilization events could be moved to ages 5 and 7 to avoid over-fertilization early in the rotation, when potential loss would be high.

5. Conclusions

Forest management, especially for wood fiber, is intensifying in order to meet an increasing demand. Efficient fertilization is key to maintain high productivity while avoiding deleterious environmental and economic effects. Using an agronomic approach, modified for perennial plants, we were able to budget soil N supply and foliage demand, determine uptake efficiency of soil and fertilizer N, and prescribe N fertilizer rates for young sweetgum plantations in the southeastern US. We found that foliar N demand responded to fertilizer applications as early as age 4, when the foliage biomass was greater than 1000 kg ha^{-1}. The increase in foliar N demand was met by both increases in total resorption and increased uptake. Foliar N resorption efficiency was not changed by fertilization. About 28% of the N supplied from soil N mineralization was taken up, and about 25% of fertilizer N applied was taken up by the foliage. Our recommendations for repeated fertilization of young sweetgum using this budget approach, support the concept and findings of Ingestad (1988), and suggest fertilizing at a rate of 50 kg N for each 2000 kg of expected foliage biomass after age 4. Further work needs to be done to (1) quantify the influence of water availability on foliage dynamics and growth in young sweetgum and other important SRWC species, (2) better understand the site controls on soil N supply, and (3) characterize and quantify root production and nutrient uptake on different soils and under different levels of water and nutrient availability.

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