Fall nitrogen fertilization and the biology of **Pinus taeda** seedling development

S.S. Sung, C.C. Black, T.L. Kormanik, S.J. Zarnoch, P.P. Konnanik, and P.A. Counce

Abstract: In mid-September when stems and roots of nursery-grown loblolly pine (*Pinus taeda* L.) seedlings are actively accumulating dry weight (DW), an extra 10, 20, or 40 kg $NH_4NO_3 \cdot ha^{-1}(10N, 20N, 40N)$ was applied. Seedlings receiving no extra N(ON) were the controls. The temporal patterns of seedling growth, nutrient concentrations, and sugar-metabolizing enzyme activities were determined during that fall and winter to assess the dynamics of seedling vigor. The 40N-treated seedlings had significantly fewer culls and greater first-order lateral root numbers, root collar diameter, DW of needle, stem, and root, and N concentration (percentage of DW) and content (milligrams per seedling) than controls and the 10N-treated seedlings. However, the temporal patterns of DW allocation, sugar metabolism, or the concentrations of P, K, Mg, and Ca were not affected by fall N fertilization. These results fit the hypothesis that basic plant morphological and biochemical processes, e.g., periodicity in stem and root DW growth or in stem and root sucrolysis and glycolysis, were not altered by human-made changes such as fall N fertilization. Fall N fertilization near 40 kg N·ha⁻¹ is a beneficial treatment because it decreased the number of culls and increased seedling N concentrations and DW without causing nutrient imbalance or detectably disturbing seedling development.

Résumé: À la mi-septembre, lorsque la tige et les racines des semis de pin à encens (Pinus taeda L.) cultivés en pépinières accumulent activement du poids sec, une application additionnelle de 10, 20 ou 40 kg NH₄NO₃·ha⁻¹(10N, 20N, 40N) a été effectuée. Les semis ne recevant pas de N additionnel (ON) ont servi de temoins. Les patrons temporels de croissance des semis, les concentrations en nutriments et l'activité enzymatique reliée au métabolisme des sucres ont été determines durant l'automne et l'hiver afin d'évaluer la dynamique de la vigueur des semis. Les semis traités avec 40N avaient significativement moins de rejets et un plus grand nombre de racines latérales de premier ordre, un diamètre au collet plus élevé, une masse anhydre des aiguilles, de la tige et des racines plus élevée et une concentration (pourcentage du poids sec) et un contenu foliaire (milligrammes par semis) en N plus élevés que les témoins ainsi que ceux traités à 10N. Toutefois, les patrons temporels d'allocation de biomasse, le métabolisme des sucres ou les concentrations de P, K, Mg et Ca n'étaient pas affectés par la fertilisation azotée d'automne. Ces résultats concordent avec l'hypothèse que les processus morphologiques et biochimiques de base des plants, par. ex., périodicité dans l'accroissement en masse sèche de la tige et des racines ou de la sucrolyse et de la glycolyse dans la tige et les racines, ne sont pas altérés par les changements apportés par les humains, tels une fertilisation automnale azotée. La fertilisation automnale azotée de l'ordre de 40 kg N·ha⁻¹ est un traitement bénéfique car elle diminue le nombre de rejets et accroit la concentration en N du semis ainsi que le poids sec sans causer de déséquilibre nutritionnel ou perturber le développement des semis de façon perceptible. [Traduit par la Redaction]

Introduction

The success of artificial forest regeneration commonly is assessed by seedling survival rate on a natural forest site and by stem growth after the first few growing seasons (Grossnickle and Folk 1993). At lifting, attempts have been made to identify key characteristics of nursery seedlings that are responsible for their field performance. Longleaf pine (*Pinus palustris* Mill.) seedlings with greater first-order lateral root numbers at lifting survived better and added more height after two growing

seasons (Hatchell and Muse 1990). Seedling needle N concentrations at lifting were reported to be positively correlated with height and volume growth of loblolly pine (*Pinus taeda* L.) 3 years after transplanting (Switzer and Nelson 1963; Larsen et al. 1988). In seedling production of several coniferous species, a fall N application has been reported to increase needle N contents and enhance field performance of transplanted seedlings (Hinsley and Maki 1980; van den Driessche 1985; Margolis and Waring 1986b). Based on several morphological, physiological, and biochemical traits of loblolly pine

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grown in the southeastern United States, we predicted that an added fall N supply should produce more vigorous seedlings to withstand transplanting stress. For example, fall N fertilization did not change bud dormancy and only caused a temporary increase in the apical meristem mitotic index for nursery-grown loblolly pine seedlings (Williams and South 1992). Loblolly pine maintains a net photosynthesis even in January in the southeastern United States (Kuhns and Gjerstad 1991; Murthy et al. 1996). In early winter, the strong stem sink strength is diminishing while, concurrently, the roots become strong sinks (Drew and Ledig 1980; Kuhns and Gjerstad 1991; Sung et al. 1993, 1995). Thus, fall N fertilized seedlings might grow large root systems as a result of higher needle N concentrations that are usually associated with increased photosynthesis (Green and Mitchell 1992). In addition to root morphology and nutrient concentrations, the vigor of nursery seedling stock may be assessed by measuring other growth parameters and sugar-metabolizing enzyme activities. It has been reported that several sucrolytic and glycolytic enzymes are indicators of tissue physiological status in loblolly pine seedlings and trees (Sung et al. 1993, 1996).

Throughout the literature, it has been noted that basic plant morphological, physiological, and biochemical processes, e.g., seasonal growth, photosynthesis, carbohydrate metabolic pathways, and N assimilation and metabolism, remain the same qualitatively regardless of natural or human-made environmental stresses. Still, quantitatively, these biological processes are under the strong influences of both environment and plant ontogeny. We tested the hypothesis that fall N fertilization will not change the periodicity in top and root growth or the seasonal patterns of sugar metabolism. We also tested the hypothesis that positive effects would result from a fall N fertilization in growing vigorous loblolly pine seedlings for bareroot transplanting.

Materials and methods

Nursery protocol

In early April of 1991, stratified loblolly pine seeds of mixed seedlots were sown into nursery beds (250 x 1.2 m) at a density of $260-280 \cdot m^{-2}$ in the Georgia Forest Commission's Flint River Nursery, Montezuma, Georgia, U.S.A. Nursery protocol used followed that described by Kormanik et al. (1993). Soil fertility before sowing was adjusted to 80 ppm extractable P (Bray II), 80-90 ppm extractable K, 40–50 ppm Mg, 350–400 ppm Ca, 0.3-3 ppm Cu, 3-8 ppm Zn, and 0.5-1.2 ppm B with soil pH ranging between 5.1 and 5.9. Prior to fall N fertilization, all beds had received a total of 108 kg N·ha⁻¹ between mid-May and late August. The four fall N treatments, namely 0, 10, 20, and 40 kg N·ha⁻¹ (ON, 10N, 20N, 40N), were randomly assigned to each of the four segments (75 x 1.2 m) within each bed. On September 18, 1991, the actual application rates were 0, 33, 66, and 132 kg NH₄NO₃·ha⁻¹ or 0, 11.5, 23.1, and 46.2 kg N·ha⁻¹.

Seedling sampling and processing

Loblolly pine seedlings were sampled twice in September, October, and November and once in December and February. Ten seedlings were randomly selected and carefully lifted from each bed and three beds were sampled for each of the four treatments. Seedling height (HT), root collar diameter (RCD), and oven dry weight (DW) of needles, stems including branches, and roots were recorded for each seedling. Organs of 10 seedlings from each bed were composited, ground with a Wiley mill, and stored at -20°C for nutrient analysis.

In February, an additional 100 seedlings were lifted from each of

the three beds for all treatments and graded for the number of first-order lateral roots (FOLR). Only those suberized FOLR with diameter greater than 1 mm were counted (Kormanik et al. 1990). Seedlings with fewer than three FOLR or damaged seedlings were culled (Kormanik et al. 1993).

Enzyme analysis was conducted from a different sample of seedlings than those used for growth measurement and nutrient analysis. Seedlings were lifted from each of the three beds for all treatments and transported on ice to the laboratory for enzyme analysis within 12 h.

Nutrient analysis

Total N was determined by the combustion method (Nelson and Sommers 1982). Analyses for P, K, Ca, and Mg were made after a perchloric – nitric acid digest (Jones and Case 1990). One-gram samples were used for digestion. P was determined by the molybdate blue colorimetric method with OD_{882 nm} (Olsen and Sommers 1982). Standard atomic absorption spectroscopy methods were used to determine K, Ca, and Mg. Results were expressed on a percentage of DW basis. Total nutrient content (milligrams per seedling) was calculated from nutrient concentration (percentage of DW) and the composite DW of 10 seedlings.

Enzyme extraction and analysis

Xylem-side cambial tissues were scraped off the debarked seedling stems and taproots. In the beginning of the study, nearly 100 seedlings were used to obtain a sample of cambial tissue of approximately 3 g fresh weight (FW). Fewer seedlings were required for a sample as seedlings increased in size and 20 seedlings were used for the last sampling in late February. Samples were extracted and desalted for soluble proteins as described by Sung et al. (1993). Sucrose synthase (SS) (EC 2.4.1.13), acid invertase (AI) (EC 3.2.1.26), neutral invertase (NI) (EC 3.2.1.26), pyrophosphate-dependent phosphofructokinase (PPi-PFK) (EC 2.7.1.90), and ATP-dependent phosphofructokinase (ATP-PFK) (EC 2.7.1.11) were assayed at 25°C (Sung et al. 1993). Changes in $OD_{340 \text{ nm}}$ were monitored with a Beckman DU-70 spectrophotometer. Soluble protein content was determined at $OD_{595\,nm}$ with Bradford reagent using bovine serum albumin (BSA) as standard. Enzyme specific activity was expressed on a grams FW or a milligrams of protein basis. Enzyme activities in seedlings from each of the three replicates were within 15% of each other and average values of three replicates are presented.

Statistical analysis

The statistical design consisted of a split-plot with fall N treatment as the main factor and sampling date as the split-plot factor. Replication was by means of three beds and each variate was the mean of 10 seedlings per treatment per bed. PROC GLM (SAS Institute Inc. 1987) was used to carry out the analysis for the growth and nutrient variables. Significant differences (P = 0.05) between the fall N treatments within a specific date were determined with a least significant difference (LSD) value based on a synthesized error term (Milliken and Johnson 1984). The Bonferroni approach was used to maintain the experimentwise error rate for all six possible tests within a date by using the P = 0.05/6 = 0.0083 level for each LSD comparison. Response relationships over time for each fall N treatment were fitted to linear regression models and compared by means of the test of conditional error (Milliken and Johnson 1984) using the Bonferroni approach where each pair of regression lines was tested at the 0.0083 level. Since the FOLR data were collected only in February, a one-way analysis of variance (ANOVA) was performed based on a randomized block design where the variate was the mean of 100 seedlings per treatment per bed. Treatment differences were detected with Tukey's test.

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Fig. 1. Effects of fall N fertilization on growth of loblolly pine seedlings harvested on different dates from a commercial nursery in Georgia. All seedlings received a total of 108 kg $N \cdot ha^{-1}$ until September 18 when seedlings of treatments ON, 10N, 20N, and 40N received an additional level of 0, 10, 20, and 40 kg $N \cdot ha^{-1}$, respectively. Treatments with the same letter do not have significantly different regression lines at the 0.05 level. LSD values used to compare treatment differences within individual sampling dates are (a) 5.59 for height, (b) 0.69 for root collar diameter (RCD), (c) 0.59 for needle DW, (d) 0.29 for stem and branch DW, (e) 0.24 for total root DW, and (f) 1.03 for total seedling DW.

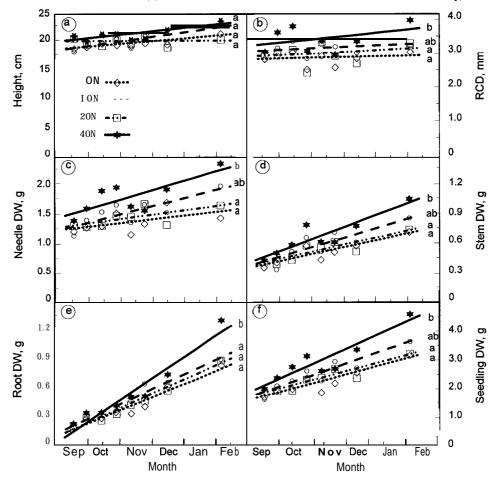
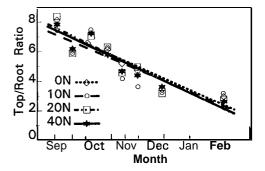


Fig. 2. Temporal trends of top to root ratio of loblolly pine seedlings. Values are calculated from Fig. 1.



Results

Seedling growth

At the time of fall N application in mid-September, loblolly pine seedlings from all treatments exhibited no significant differences in all growth parameters (Fig. 1). However, regressions over all sampling dates showed that seedlings receiving the 40N treatment had significantly greater RCD and DW in all organs than controls and 20N seedlings (Fig. 1). This level of fall N did not affect HT growth (Fig. la) or the presence of tight terminal buds (data not shown). Neither was the temporal trend of seedling development changed by fall N treatments. For example, minimum increases in HT, RCD, or needle DW were observed from mid-September through mid-February for all seedlings (Figs. la-lc), but total seedling DW increased during this period. This increase was attributed to a nearly fivefold increase in root DW and a twofold increase in stem DW (Figs. 1d-1f). The developmental patterns of DW allocation within a seedling were nearly the same among all treatments. Root DW allocation increased from 10% in September to 25% in February, needle DW allocation steadily decreased from 70% in September to 50% in February, and stem DW allocation remained between 20 and 25% throughout the fall and winter. The top to root (T/R) ratio decreased from nearly 8: 1 in September to 3: 1 in February for all treatments (Fig. 2).

By February, 40N seedlings had 5.31 FOLR, which was significantly greater than the other treatment means of 4.07, 4.09, and 4.40 for controls, 10N, and 20N seedlings, respectively.

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Table 1. Results (P-values) from the ANOVA based on a split-plot design for N concentration and content	į
in loblolly pine seedlings.	

	N concentration, % DW				N content, mg			
Source	Needle	Stem	Root	Seedling	Needle	Stem	Root	Seedling
Treatment	0.01*	0.02*	0.06	0.02*	0.00*	0.00"	0.00*	0.00*
Date	0.00*	0.00*	0.00*	0.00*	0.01*	0.00*	0.00*	0.00"
Treatment x date	0.10	0.08	0.03*	0.01*	0.82	0.10	0.64	0.75

^{*}Significant at the 0.05 level.

Fig. 3. Effects of fall N fertilization on (a) N concentration and (b) N content of loblolly pine seedlings harvested on different dates. The same seedlings used for growth analysis in Figs. 1 and 2 were analyzed for nutrients in Figs. 3, 4, and 5. Treatments with the same letter do not have significantly different regression lines at the 0.05 level. An LSD value of 0.286 and 12.97 for N concentration and content, respectively, can be used to compare treatment differences within individual sampling date.

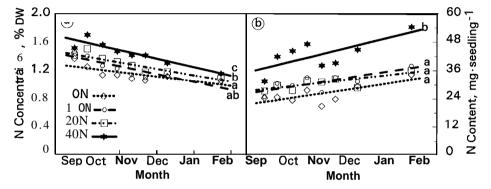
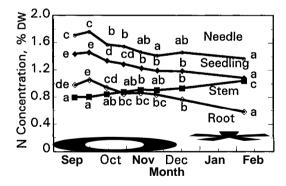


Fig. 4. Composite temporal and spatial patterns of N concentration for all loblolly pine seedlings, regardless of fall N treatments. Within each seedling component, different letters indicate significance at the 0.05 level.



Seedlings receiving 40N had 15% culls whereas controls, 10N, and 20N treatments had 33, 34, and 28% culls, respectively.

Nutrient concentrations

Results of the ANOVA indicated that N concentrations (percentage of DW) and contents (milligrams) in all seedling organs were, in general, significantly affected by treatments and by sampling dates (Table 1). But the concentrations or contents of other major nutrients, e.g., P, K, Mg, and Ca, were only affected by sampling dates and not by treatments or treatment x sampling date interaction (data not shown).

Regressions over all sampling dates indicated that seedling N concentrations in 40N seedlings were significantly higher

than those of the other treatments and that 20N seedlings have significantly higher N concentrations than controls (Fig. 3a). But, only 40N-treated seedlings had higher total N contents than controls (Fig. 3b). The regression slopes, positive and significantly different from zero, of 2.15, 2.10, 1.51, and 3.36 for ON, 10N, 20N, and 40N treatments, respectively, indicated that all seedlings significantly increased N contents from September through February. However, there were significant decreases in seedling N concentrations with regression slopes of -0.053, -0.093, -0.083, and -0.101, respectively, and each was significantly different from zero. Independent of treatments, both needle and root N concentrations tracked the temporal pattern of seedling N concentration (Fig. 4). However, the stem N concentration increased steadily over the study period, indicating that the stem is a N sink in the winter, although needles contain much more N.

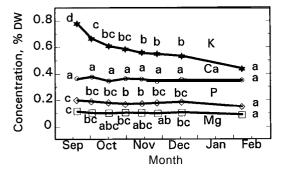
Since no treatment effects were observed for the concentrations or contents of P, K, Mg, and Ca in all organs, seed-ling nutrient data were combined for all treatments (Fig. 5). Similar to N, seedling concentrations of P, K, and Mg decreased over time (Fig. 5). There were no seasonal changes in Ca concentration (Fig. 5). Generally, the seasonal trends for the concentrations of P, K, Mg, and Ca in all organs were similar to those of the whole seedling (data not shown).

Sucrolytic enzyme activities

Among the three alternative sucrose breakdown enzymes, namely SS, AI, and NI, SS was the major catalyzing activity in stems and roots of loblolly pine seedlings (data not shown). Neither invertases exhibited much influence by season or N treatment. In this study, ranges of AI and NI activities

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Fig. 5. Composite temporal patterns of seedling K, Ca, P, and Mg concentration for all loblolly pine seedlings, regardless of fall N treatments. For each nutrient, different letters indicate significance at the 0.05 level.



were between 30 and 55 nmol·mg protein⁻¹·min⁻¹ and 5 and 15 nmol·mg protein⁻¹·min⁻¹, respectively. Generally, there were no fall N treatment differences in SS specific activity level in either stem or taproot cambial tissues throughout this study (Fig. 6). However, a strong seasonal influence on SS specific activity was exhibited by stem and root cambial tissues. Root SS activity lagged behind stem SS activity until near mid-November when stem SS began to decrease rapidly. But root SS peaked in November and remained relatively high through the winter. During the winter, the taproot maintained its SS activity at 40% of the peaked level whereas very little winter SS activity was found in the stem. In late February, both stem and taproot SS activity increased (Fig. 6).

No fall N fertilization effects were observed with PPi-PFK (Fig. 7) or ATP-PFK specific activity (data not shown). And after October, the temporal and spatial patterns of PPi-PFK specific activity tracked those of SS activity, with roots exhibiting more activity through the winter than stems (cf. Figs. 6 and 7). The levels of ATP-PFK activity ranged between 150 and 200 nmol·mg protein⁻¹·min⁻¹ for stem and 125 and 175 nmol·mg protein⁻¹·min⁻¹ for root throughout the study without a strong seasonal periodicity.

Discussion

Growth and seedling vigor

The fall and winter seedling growth trends shown in Figs. 1 and 2 are similar to those reported with loblolly pine seedlings grown under a variety of conditions (Drew and Ledig 1980; Kuhns and Gjerstad 1991; Sung et al. 1995), including transplanted seedlings (Sung et al. 1993). The amounts of fall N fertilization in conjunction the fertility regime used (Kormanik et al. 1993) did not change the general temporal or spatial trends of DW growth, allocation, or T/R ratio (Figs. 1 and 2). In an earlier nursery study by Switzer and Nelson (1963), fertility or seedling density did not cause any change in DW allocation in loblolly pine seedlings, and their seedlings had similar percentages of DW allocated to each organ as our seedlings (Figs. 1 and 2). Studies on other coniferous species also indicated that levels of CO,, water, and nutrients changed the amount of DW production but not the general seasonal growth patterns (McMillin and Wagner 1995; Townend 1995).

Seedlings receiving the 40N treatment had significantly greater DW and RCD growth than controls (Fig. 1). These

N-related DW increases in all loblolly pine seedling organs, especially roots, are similar to the loblolly pine study by Switzer and Nelson (1963). In a greenhouse study, it was found that N stress favored root DW allocation at the expense of needles and stems of loblolly pine seedlings (Li et al. 1991). Throughout the 6-month sampling period in this study, even ON seedlings were not under N stress, as indicated by their N concentrations (Fig. 3) and by their DW allocation pattern being similar to 40N-treated seedlings (Figs. 1 and 2).

There is a linear relationship between photosynthesis and foliar N concentration for loblolly pine grown under the same conditions (Green and Mitchell 1992). Even during the coldest month in the southern United States, net photosynthesis was quite active in loblolly pine needles (Murthy et al. 1996). In our study, the slight increase in needle DW and significantly higher N concentration for 40N seedlings might have contributed to higher levels of photosynthate production per seedling over time. Moreover, since root systems are the major growing sinks in winter, they will benefit most from these probable fall N-related increases in photosynthesis.

Compared with ON controls, 40N seedlings have fewer culls, greater FOLR number, larger RCD, and greater DW in all seedling components (Fig. 1). Any one or combination of these morphological attributes has been correlated with field performance of transplanted seedlings in various studies with some success (Hatchell and Muse 1990; Rose et al. 1992; Grossnickle and Folk 1993; Sulzer et al. 1993). Although we did not conduct a field performance study with these seedlings in this study, it is probable that these morphologically more vigorous 40N seedlings will survive and grow better than controls.

Nutrient concentrations and seedling vigor

Several studies on coniferous species showed that Mg, K, or S deficiency is caused by excessive levels of N (Brockley 1995; van den Driessche and Ponsford 1995). The 40N treatment did not have this effect on other major nutrient levels in loblolly pine seedlings (Fig. 5). In fact, regardless of fall N treatments, seedlings had all major nutrients in ranges similar to reportedvalues for loblolly pine seedlings and trees (Switzer and Nelson 1963; Larsen et al. 1988; Rathfon et al. 1993).

In the literature, only a few studies have reported seasonal temporal and spatial distribution of major nutrients in loblolly pine seedlings or trees. It is important to follow nutrient dynamics over time, instead of a single point sampling, to assess nursery seedling vigor. In this study, N concentrations in needle and root steadily decreased whereas stem N concentrations increased over time (Fig. 4). Seedling K concentrations decreased significantly whereas Ca concentrations remained constant from September through February (Fig. 5). In plantation loblolly pine trees, concentrations of N, P, K, and Mg increased in current-year needles between September and December following earlier decreases in summer (Rathfon et al. 1993). But Murthy et al. (1996) observed no change in N concentrations for current-year loblolly pine tree needles from July through March. Nevertheless, no fall N fertilization effects on temporal and spatial distribution of nutrients were observed here. Also, fertilization did not change the temporal patterns of N concentrations in previous- or current-year needles of loblolly pine trees (Murthy et al. 1996) or of Monterey pine (Pinus radiata D.Don) trees (Thomas and Mead 1992).

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Fig. 6. Effects of fall N fertilization on the temporal patterns of sucrose synthase (SS) specific activity in xylem-side cambial tissues of loblolly pine seedling (a) stems and **(b)** taproots. The same plant extracts were used for all enzyme analysis and these extracts were from different seedlings than those used for growth and nutrient analysis.

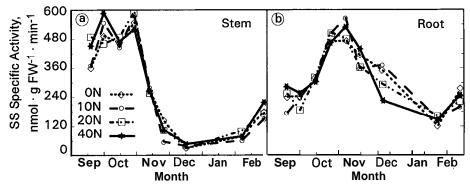
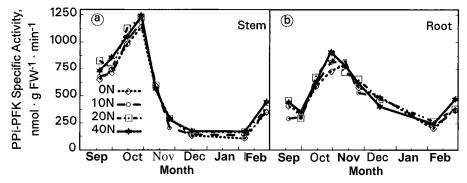


Fig. 7. Effects of fall N fertilization on the temporal patterns of pyrophosphate-dependent phosphofmctokinase (PPi-PFK) specific activity in xylem-side cambial tissues of loblolly pine seedling (a) stems and (b) taproots.



A study by Larsen et al. (1988) showed a positive correlation between loblolly pine needle N concentrations at lifting and seedling field performance after 3 years. Munson and Bemier (1993) reported retranslocation of N, P, and K from older needles of transplanted black spruce (Picea mariana (Mill.) B.S.P.) seedlings. A study of internal cycling of N in Sitka spruce (Picea sitchensis (Bong.) Carr.) seedlings showed that the majority of N was remobilized from N stored in previous years' needles (Millard and Proe 1993). Timmer and Munson (1991) used a steady-state fertilization process to grow containerized black spruce. They reported that these "nutrient loaded" seedlings had higher foliar N concentrations at planting and grew more roots and shoots than regularly fertilized seedlings after 1 year. The buildup of preplant N served as a source for internal retranslocation to new growth (Timmer and Munson 1991). It is also possible that loblolly pine seedlings with 40N treatment can mobilize their stored N for new growth after transplanted into forest sites of generally low N fertility. Hence, the beneficial effect of fall 40N fertilization on seedling morphological vigor (i.e., more root growth) and physiological vigor (i.e., higher N concentration) can be further enhanced after transplanting.

Sucrose metabolism and seedling vigor

No differences in SS and PPi-PFK activities were observed among treatments (Figs. 6 and 7). These results further indicated that seedlings of all treatments in this study are not under any stress while growing in the nursery. Margolis and Waring

(1986a) also showed that fall fertilization did not change sugar and starch levels in needles, stems, or fine roots of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings whereas it increased free amino acids and total N levels. Similar to its lack of influence on growth periodicity in loblolly pine seedlings, fall N fertilization did not change the temporal or spatial patterns of sucrose-metabolizing or glycolytic enzyme activities (Figs. 6 and 7). SS still showed major sucrose cleavage activity in seedlings of all treatments, as reported in several tree and crop species (Sung et al. 1993, 1994).

SS activity has been associated with plant sink strength in various growing, storing, or stressed tissues (Sung et al. 1993, 1994). In this study, increased DW allocation to loblolly pine seedling roots during winter coincided with high levels of root SS and PPi-PFK specific activity (Figs. 1, 6, and 7). Likewise, stems were still active in DW allocation and had high of SS and PPi-PFK activities before November. Theses basic traits of sucrose metabolism, glycolysis, and growth in loblolly pine (Figs. 6 and 7) are well preserved qualitatively in young seedlings (Sung et al. 1993) as well as in more mature trees (Sung et al. 1996). Moreover, these traits are maintained in transplanted seedlings (Sung et al. 1993) and in seedlings receiving different levels of fall N fertilization (Figs. 6 and 7).

Conclusions

Loblolly pine seedlings grown with current nursery protocol and with or without fall N fertilization did not show any signs

of morphological, physiological, or biochemical abnormality or any signs of stress from September through February. We concluded that a fall N application near 40 kg N·ha⁻¹ will produce more vigorous loblolly pine seedlings in nurseries because (i) it increases seedling root and stem DW, seedling N concentrations and contents, and the number of FOLR, (ii) it decreases the number of culls at lifting, and (iii) it does not change seasonal patterns of DW allocation, sucrose metabolism, T/R ratio, or bud formation.

Acknowledgments

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