MORPHOLOGICAL AND NUTRITIONAL DEVELOPMENT OF THREE SPECIES OF NURSERY-GROWN HARDWOOD SEEDLINGS IN TENNESSEE

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MORPHOLOGICAL AND NUTRITIONAL DEVELOPMENT OF THREE SPECIES OF NURSERY-GROWN HARDWOOD SEEDLINGS IN TENNESSEE

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MORPHOLOGICAL AND NUTRITIONAL DEVELOPMENT OF THREE SPECIES OF NURSERY-GROWN HARDWOOD SEEDLINGS IN TENNESSEE

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Humberto Zeraib dos Santos, son of Norival dos Santos and Ivone Calixto Zeraib dos Santos, was born April 11, 1974 in Sao Paulo, Sao Paulo-Brazil. He attended the Escola Superior de Agricultura “Luiz de Queiroz” at the University of Sao Paulo and graduated with a Bachelor of Science degree in Forestry in December, 2003. He served as Visiting Scientist in the Southern Forest Nursery Management Cooperative at Auburn University for one year. After working as a Visiting Scientist he entered Graduate School at Auburn University in January 2004 and accepted a research assistantship under Kenneth L. McNabb.

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THESIS ABSTRACT

MORPHOLOGICAL AND NUTRITIONAL DEVELOPMENT OF THREE SPECIES OF NURSERY-GROWN HARDWOOD SEEDLINGS IN TENNESSEE

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We followed the morphological and nutritional development of three common hardwood species growing under typical cultural practices in a southern hardwood nursery. Yellow poplar was by far the largest seedling at the end of the season, followed by Nuttall oak and green ash. Seasonal periodicity of morphological development varied by species, although large increases in lateral root weight occurred in late fall for all three species. Coefficients of variation for the morphological components over time were high for all three species and most parameters. All three species had strong correlations between root collar diameter (RCD) and many other morphological parameters including number of first order lateral roots.

The seasonal periodicity of nutrient concentrations, translocation and allocation were documented. No changes in soil carbon and organic matter content were found, probably as a result of the addition of mulch and leaf litterfall. In spite of similar fertilization regimes, foliar nutrient concentrations varied by species. Yellow poplar appeared to be the most efficient at withdrawing nutrients from senescent leaves while Nuttall oak had higher nutrient translocation efficiencies. Large amounts of fertilizer elements were removed by harvesting, but overall nitrogen and phosphorous balance (applied fertilizer minus removed) was positive. Nitrogen use efficiency was relatively high for all species. Yellow poplar had the highest nitrogen removal efficiency and biomass productivity, indicating higher use of fertilizer materials.

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I. MORPHOLOGICAL AND NUTRITIONAL DEVELOPMENT OF THREE SPECIES OF NURSERY-GROWN HARDWOOD SEEDLINGS IN TENNESSEE

INTRODUCTION

Hardwood seedlings grown in forest tree nurseries account for only 3.6% of the total southern seedling production and are grown in less than half of all tree nurseries in the region (McNabb and Santos, 2004). However, hardwoods are an important source of nursery revenue as hardwood seedlings cost around five times more than pine and, on an area basis, are more valuable (South and Carey, 2004). As a result, hardwood seedling establishment costs more than pine and good seedling survival is critical to protect this investment (Grebner et al., 2004).

Despite the higher investment required for hardwood planting, the demand for hardwood seedlings has held steady over the past several years and may have actually increased (Barnett, 2002). This increase in seedling demand is likely related to federal cost share programs, particularly those related to wetland restoration (Matherne, 2002; Smith, 1999). The demand also resulted in hardwood seedling shortages in the central hardwood region (Jacobs, 2003). It was estimated that demand outpaced supply in 1999 by 25 to 50 million seedlings with demand expected to rise 20% annually (Jacobs et al., 2004). This increasing demand caused some nurseries to begin producing hardwood planting stock (Jacobs et al., 2004a) which generated concerns regarding seedling quality. Nursery managers, who devoted their career to the production of pine seedlings, suddenly needed to produce hardwoods and they faced a totally different world (Davey, 1994). Concerns were heightened by poor survival and growth observed in reforestation programs in the Lower Mississippi River Alluvial Valley (LMRAV) region (Lockhart et al., 2003). The interest in hardwood seedling establishment increased the need for hardwood seedling production research (Vanderveer, 2004).

Unfortunately, compared to conifers, there is a limited amount of peer-reviewed scientific literature for hardwood nursery culture. Most forest tree research has focused primarily on issues related to conifers. Research on hardwoods is further complicated by the large number of species produced. Conifers grown in southern nurseries are mostly from the *Pinaceae* family, while the common hardwood species are from many families such as: Aceraceae (*Acer*), Fagaceae (*Castanea and Quercus*), Hamamelidaceae (*Liquidambar*), Juglandaceae (*Carya and Juglans*), Magnoliaceae (*Liriodendron*), Oleaceae (*Fraxinus*), Platanaceae (*Platanus*), and Rosaceae (*Prunus*)., with each species having individual cultural requirements (Boyer, 2003).

Although there is much debate among nursery managers and scientists as to the best methods for growing hardwood seedlings, most nurseries follow general practices for hardwood seedling nursery production (Jacobs, 2003). Guidelines describing typical hardwood seedling development have not been published (Gardiner et al., 2002). An understanding about morphological and nutritional characteristics may lead to the development of management practices based on rate and periodicity of growth, which may conduct to higher quality seedling production (Thompson, 1985; Vanderveer, 2004). Morphological targets for the individual species to be grown, as well as guidelines for different stages of seedling development, need to be better defined.

A fundamental step in documenting "normal" seedling development is the periodicity of absorption and translocation of each specific nutrient. This characterization is needed to identify nutrient requirements and deficiencies as well as avoid negative environmental effects caused by over-fertilization (Stanturf et al., 2002). Soil nutrient depletion through crop harvesting and the relationship between plant nutrient concentration and productivity are needed to manage soil fertility more efficiently (Boyer and South, 1985).

Hardwood Seedling Culture

In 2003, nurseries in 12 southern states (excluding Kentucky) produced around 39 million hardwood seedlings (McNabb and Santos, 2004). *Quercus* was the most important genera accounting for 60% of all hardwood production. A commonly produced oak species is Nuttall oak (*Quercus nuttallii* Palmer). It was not distinguished as a species until 1927 and it has been called red oak, Red River oak, and pin oak (Filer, 1990). Nuttall oak is a commercially important species that produces heavy annual mast. It grows well on poorly drained, alluvial clay soils in the first bottoms of the Mississippi Delta region, performing best on soils with a pH of 4.5 to 5.5. It is common on clay ridges but is not found in permanent swamps or on well-drained loams. Typically, it grows on clay flats that are normally covered with 8 to 20 cm of water throughout the winter (Filer, 1990).

The second most common genera produced in southern hardwood nurseries was *Fraxinus*, particularly *F. pennsylvanica (*Marsh), which was 4.7% of all regional hardwood production. It is also called red ash, swamp ash, and water ash, and is the most widely distributed of all the American ashes. It grows best on fertile, moist, well-drained soils, but is probably the most adaptable of all the ashes, growing naturally on a range of sites (Kennedy, 1990).

The third most commonly produced hardwood species in the South is yellow poplar (*Liriodendron tulipifera* L.). A commercially valuable species, it grows on a wide variety of soil types, avoiding only very wet or very dry sites. Although it will grow on those sites, it does so poorly. "The best growth usually occurs on north and east aspects, on lower slopes, in sheltered coves, and on gentle, concave slopes" (Beck, 1990).

Nursery production of hardwood seedlings is different than the production of pine seedlings in several important ways. Most hardwoods are broadleaved and deciduous, while most conifers have needlelike leaves and are evergreen. Hardwoods tend to show more branching, have thicker roots, require higher fertility, and are more susceptible to pests and diseases when compared to conifers (Tinus, 1978). When compared to pine, hardwood seedlings need approximately twice the water and significantly more essential elements and should be grown at lower seedbed densities than pines (Davey, 1994). For instance, recommended nursery bed densities for oaks are 86-107 (high) and 64-85 (low) per square meter (Formy-Duval, 1976). Stoeckeler, (1967) found that green ash produced the highest number of good-quality trees at a density of 134 trees per square meter. Each nursery has its own method for grading, counting, and bundling seedlings, though most are somewhat similar (Williams and Hanks, 1994). Normally, hardwood nurseries count individual seedlings for grading (Grieve and Barton, 1960). Bareroot seedlings are grown in a nursery bed, lifted by undercutting at 20 to 25 centimeters below the soil surface which mechanically loosens the soil around the roots. They are then graded, and packed into bags at the nursery to keep the roots moist (Pijut, 2003). Top-pruning may reduce the costs involved with lifting, bundling, packing, storing, shipping, and planting hardwoods (South, 1996) and is recommended for species like northern red oak (Johnson et al., 1986), sycamore (Briscoe, 1969), and for some tropical species (Djapilus, 1990).

Hardwood Seedling Nutrition

Very little is known about the nutrient requirements of relatively important hardwood species, especially information on optimum nutrient levels, critical ranges for essential elements, and the physiological effects of nutrient deficiencies (Erdmann et al., 1979). Most hardwoods develop a pattern of nutrient utilization different from conifers. Conifers have less than half the annual nutrient requirement of most hardwoods (Lassoie et al., 1985) because they retain numerous foliage age classes and thus have lower demand for foliage replacement (Elliot and White, 1993). Hardwood seedlings need 50% more nitrogen (N) than most pines (Davey, 1994). Knowledge about hardwood micronutrient nutrition (Stone, 1968) is much less than the macronutrients (Davey, 1994).

Average N uptake for mature hardwood trees is approximately 10 times higher than P and 3 times that of K. Ca uptake may be higher than N for most hardwoods (Pritchett and Fisher, 1987) and the ability of a species to respond to a resource level availability should be related somehow to nutrient use efficiency (Elliott and White, 1993) as nutrient use efficiency generally decreases as the amount of cellulose per seedling increases (Gray and Schlesinger, 1983; Shaver and Melillo, 1984; Birk and Vitousek, 1986; Lajtha and Klein, 1988).

Fertilizer prescriptions are unique to each nursery, and, to continually grow high quality seedlings on one nursery site, nutrients must be added to replace those lost when seedlings are harvested (South and Boyer, 1985). A deficiency occurs when plant concentrations are so low they limit plant development (Landis et al., 2004). Effective monitoring and nutrient application prevents the “hidden hunger” that occurs when plant nutrients are deficient, yet show no symptoms. Fertilizer application should be based on soil nutrient analysis, tissue analysis, and stock performance (Triebwasser, 2003). Many factors impact the effectiveness of nutrient application on hardwood seedling growth. These factors include when and where fertilizer is applied and availability of nutrients to the seedling. Before maximum growth response to fertilization can be obtained, the elements that limit productivity in a given species on a given site must be correctly diagnosed (Brown, 1999). In particular, the quantities of mineral nutrients required for maximum growth may differ among hardwoods.

Hardwood Seedling Quality

Many studies have shown that field survival and productivity are related to planting stock quality (Jaenicke, 1999). Defining the characteristics of a high quality seedling for each species is important. Another important characteristic of seedling quality is root collar diameter (Davey, 2005). Bareroot hardwood seedlings should have a minimum shoot height of 46 centimeters with 61 centimeters preferred (Allen et al., 2001) and a root collar diameter of at least 7 mm. According to Pijut (2003), some seedlings of oak can be considered optimum when height is 25 to 30 centimeters tall, if they have good diameter. Initial root collar diameters are good indicators of field performance of northern red oak (*Quercus rubra* L.) seedlings (Dey and Parker 1997).

Most seedling grading have concentrated on shoot characteristics with little attention to root systems. Taproots should be healthy looking, well-developed, have several lateral roots, and have a minimum root length of 20 to 25 centimeters (Pijut, 2003). Shoot to root ratios are usually based on the mass of roots without consideration for root morphology. Seedlings should have a low shoot to root ratio. A low ratio — one which predicts better survival — is 1:1 to 1:2 shoot to root ratio (Jaenicke, 1999). Hardwood seedlings with too much shoot to root volume may die back (Pijut, 2003); therefore, pruning is an important way of restoring the balance between shoots and roots. South (1998) stated that for hardwood seedlings less than 50 centimeters tall, there was no relationship between survival of pruned and non-pruned seedlings.

Height and stem diameter provide the best estimate of seedling performance after outplanting. For example, diameter in conifers is the best predictor of survival, while height seems to best predict height growth (Mexal and Landis, 1990). Parameters such as root mass or number of lateral roots are also useful in assessing potential performance (Aphalo and Rikala, 2003). Typically generic hardwood seedling quality standards are a problem. Species-specific standards do not exist, yet it is apparent that each species presents unique morphological characteristics and considerable morphological variability between individuals (Jacobs, 2003). Even less is known about species-specific nutritional demand.

This research will attempt to characterize the development of three commonly grown hardwood species. The temporal morphological growth patterns for several plant parts will be reported. Nutritional analysis will document nutrient concentration. Content over time for the various seedlings' morphological parameters, litterfall, mulch inputs, nutrient uptake, periodicity of absorption, allocation, and translocation will be followed over the season and used to calculate seedling nutrient use efficiency. This research should help growers to set parameters for both morphological and nutritional crop development.

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II. MORPHOLOGICAL DEVELOPMENT OF THREE SPECIES OF NURSERY-GROWN HARDWOOD SEEDLINGS IN TENNESSEE

ABSTRACT

We followed the morphological development of three common hardwood species growing under typical cultural practices in a southern hardwood nursery. The seasonal development of morphological parameters were compared. Yellow poplar was by far the largest seedling at the end of the season, followed by Nuttall oak and green ash. Seasonal periodicity of morphological development varied by species, indicating that similar nursery practices may affect species differently. Several parameters, such as the development of first order lateral roots, occurred at the same time. Large increases in lateral root weight occurred in late fall. Coefficients of variations for the morphological components over time were high for all three species and most parameters. All three hardwood species had strong correlations between root collar diameter (RCD) and many other morphological parameters, including number of first order lateral roots.

INTRODUCTION

Hardwood seedlings grown in southern tree nurseries correspond to 3.6% of the total seedling production and are grown in less than half of tree nurseries in the region (McNabb and Santos, 2004). However, hardwood crops are an important source of nursery revenue since on an area basis they are more valuable than a pine crop (South and Carey, 2004). In fact, the demand for nursery production of hardwood species has held steady over the past several years and may have actually increased (Barnett, 2002) due to federal cost share programs, particularly those related to wetland restoration (Smith, 1999; Matherne, 2002).

Morphological measurements are commonly used as a predictor for the field performance of hardwood seedlings (Wilson and Jacobs, 2004). Parameters such as shoot height, root collar diameter (RCD), root volume, and number of first order lateral roots have been used with moderate success (Thompson and Schultz, 1995; Ward et al., 2000; Jacobs and Seifert, 2004). For example, hardwood seedlings with a greater quantity of first order lateral roots (>1mm) were found to survive better (Jacobs and Seifert, 2004) and seedlings with large root collar diameters and tall shoots exhibited improved field performance (Dey and Parker, 1997). Unfortunately, compared to conifers, there is a limited amount of peer-reviewed scientific literature for hardwood nursery culture (Gardiner et al., 2002) and the literature is generally deficient in hardwood seedling quality research (Wilson and Jacobs, 2004).

Each hardwood species possess unique morphological characteristics. Several quality assessment approaches are likely needed to understand variability in hardwood seedling morphology. For example, a poor quality black walnut (*Juglans nigra* L.) seedling may have more large lateral roots than a good quality white oak (*Quercus alba* L.) seedling. In addition, nursery related morphological variability may persist in the field many years after planting (Wightman, 1999). Thus, it is helpful to understand the general morphological character of each species of interest (Jacobs, 2003).

This study was conducted at the Tennessee Division of Forestry (TDF), East Tennessee Nursery in Delano, Tennessee. The TDF produces approximately ten million seedlings annually, with hardwood production close to two million seedlings. Currently, 28 hardwood species are grown at this nursery with yellow poplar, green ash, and various oaks produced in the largest numbers. Winter-sown Nuttall oak (*Quercus nuttallii* Palmer), spring-sown green ash (*Fraxinus pennsylvanica* Marsh), and yellow poplar (*Liriodendron tulipifera* L.) were selected for this study as they are routinely grown by the TDF and are commonly produced in southern hardwood nurseries (McNabb & Santos, 2004). The objective of this research was to describe the morphological development of three common hardwood species when grown under typical cultural practices in a southern hardwood nursery. There are three hypotheses to test:

1: Seedling morphology and development are distinct and unique for the three species measured

2: Morphological variability is affected by species

3: RCD is the best single morphological parameter to predict overall seedling morphology for the three species

MATERIALS AND METHODS

Nursery location and Culture

This study was conducted at the Tennessee Division of Forestry (TDF), nursery in Delano, Tennessee. A mixed lot of Nuttall oak (209 seeds/kg, 100% germination, 60% expected seed efficiency) was sown on March 1st using a NB-2 sower and a 107 seeds/m^2 sowing density. A total of 3,316 linear bed meters was sown. A mixed lot of yellow poplar (43% germination, 100% purity, 80% expected seed efficiency) was sown on April 18th using a NB-2 sower at a target spacing of 247 seeds/m^2. Seeds were stratified for 90 days prior to sowing. A total of 3,332 linear bed meters were sown. A mixed lot of green ash (76% germination, 100% purity, 60% expected feed efficiency) was sown on April 18th using a NB-2 sower at a target sowing density of 141 seeds/m^2. Seeds were stratified for 90 days prior to sowing. A total of 2,182 linear bed meters was sown.

Cultural practices

A total of 287 kg/ha elemental nitrogen (N) was applied as top dressing for Nuttall oak between May 6 and September 23 in eight applications (Table 1). Elemental phosphorus was applied at 50 kg/ha in two applications. A directed spray of 2 ml/L glyphosate was applied on May 11 to control weeds. Oxyfluorfen (Goal 4F®) was applied at 280 grams/ha on July 29. The insecticide diazinon was applied at 2.3 kg/ha as a directed spray on August 19.

A total of 234 kg/ha elemental N was applied as top dressing for yellow poplar between May 6 and August 4 in seven applications (Table 1). Elemental phosphorus was applied at 87 kg/ha in three applications. A directed spray of 20 ml/L glyphosate was applied on May 5 and June 28 to control weeds. The selective herbicide napropamide (Devrinol®) was applied at 2.25 kg/ha as a directed spray on August 16.

A total of 217 kg/ha elemental N was applied as top dressing to green ash between May 6 and August 4 in six applications (Table 1). Elemental phosphorus was applied at 25 kg/ha in a single application. A directed spray of 20 ml/L glyphosate was applied on May 11 and June 29 to control weeds. The herbicide sethoxydim (Poast®) was applied at 413 g/ha on May 25.The insecticide diazinon was applied at 2.3 kg/ha as a directed spray on August 19.

Sampling Design

All three species were periodically sampled from 6 blocks in three separate beds. Each block was one bed wide and 4.87 m long, for a total length of 29.2 m. Seedlings were sampled within blocks in the months of May, July, September, and November using a 0.3 m x 1.22 m counting frame. Sample plots were randomly distributed within the block, with 0.91 m buffers between them. To carefully harvest as much of the root system as possible, seedlings were sampled using a shovel except on the last sampling time when a tractor drawn undercutting blade lowered to around 33 cm deep lifted the seedlings and then loosened the soil from around the roots. All seedlings were taken to laboratory facilities in Auburn for analysis.

Table 1. Elemental fertilizer application for three hardwood species grown at the Tennessee Division of Forestry, East Tennessee Nursery.

Species	Date	N kg/ha	P kg/ha	Product
Nuttall oak	May6	39	-	Ammonium nitrate
	June 2	39	-	Ammonium nitrate
	June 21	22	25	Diammonium phosphate
	July 20	39	-	Ammonium nitrate
	July 29	39	-	Ammonium nitrate
	August 4	22	25	Diammonium phosphate
	August 4	39	-	Ammonium nitrate
	September 23	48	-	Ammonium nitrate
	Total	*287*	*50*	
Yellow poplar	May 6	39	-	Ammonium nitrate
	June 2	39	-	Ammonium nitrate
	June 21	22	25	Diammonium phosphate
	July 20	34	37	Ammonium nitrate
	July 29	39	-	Ammonium nitrate
	August 4	22	25	Diammonium phosphate
	August 4	39	-	Ammonium nitrate
	Total	*234*	*87*	
Green ash	May 6	39	-	Ammonium nitrate
	June 2	39	-	Ammonium nitrate
	June 21	22	25	Diammonium phosphate
	July 20	39	-	Ammonium nitrate
	July 29	39	-	Ammonium nitrate
	August 4	39	-	Ammonium nitrate
	Total	*217*	*25*	

Measurements

Seedling height, root collar diameter (RCD), number of first order branches (FOB), number of first order lateral roots (FOLR) (>1 mm) and number of leaves were tallied. Fresh and dry weights were obtained for stem, taproot, FOLR, FOB, and leaves on a plot basis. Average seedling values for these variables were calculated by dividing plot values by the number of seedlings sampled. The root/shoot ratio was based on average seedling dry weights.

Average seedling foliar area was estimated by first measuring approximately 30 randomly selected leaves from each plot using a LICOR 3100C Leaf Area Meter. The average area per leaf was multiplied by the average number of leaves per seedling to calculate an average seedling leaf area by plot.

Analysis

Statistical analyses were performed using SAS version 9.1 (SAS Institute, Cary, NC). Individual seedling values were used to calculate averages for height, RCD, number of FOB and FOLR, and number of leaves. Average values were obtained for each seedling component at each sampling time. Linear regressions were employed to explore the relationship between the morphological parameters from July, September, and November data. Analyses involving dry weight data were based on average plot values per seedling.

RESULTS

Nuttall Oak

Nuttall oak grew to an average RCD of 9.9 mm and 57.7 cm height, with 9.3 first order lateral roots, and 6.8 first order branches by November, eight months after sowing (Table 2). Seedlings sampled in September, prior to the beginning of autumn leaf fall, averaged 64 leaves and 1,385 cm^2 leaf surface area. The periodicity of morphological development was not uniform across all components. The largest increases in RCD and FOLR occurred from September to November with 36% and 71%, of total RCD and FOLR growth occurring in this period, respectively. Interestingly, RCD showed its lowest growth from July to September, at a time when many seedling parameters are growing fastest. Leaf area and height, for example, grew 65% and 34%, respectively, of their total growth from July to September. From July to September the average number of leaves per seedling increased from 41.5 to 64, an increase of 54%. At the same time average leaf area per seedling increased from 494 to 1,385 cm^2, an increase of 192%. Interestingly, average Nuttall oak height increased 17% from September to November.

Average seedling dry weight increased throughout the season, including 101% and 112% increases in stem and tap root dry weights, respectively, from September to November. The dry weight of FOLR increased nearly 400% from September to November. This increase in root mass impacted the root/shoot ratio which increased from 0.07 to 0.82 during this period. Extended and unexpected warm temperatures in October and November may have delayed leaf fall, resulting in a drop of only 34% of leaf dry weight in the November sample.

Seedling Morphological Variability

Variability between seedlings was high for all parameters, with Coefficients of Variation (CV) ranging from 21% to 46% for RCD and 29% to 44% for shoot height. The number of first order lateral roots was particularly highly variable. Seedling variability may have increased, decreased or remained the same over the sample period. It appeared there was little change for several variables such as RCD, height, first order branch weight, and root/shoot ratio. The number of leaves, however, was the only variable showing a strong tendency to increase in variability over time. The CV's for NFOLR, leaf area, and the variables related to the dry weights all decreased through the fall. On the other hand, CV's were highest for these variables in July, then declined through the rest of the growing season.

Correlations between Seedling Morphological Parameters

RCD is one of the easiest morphological parameters to measure and is widely used as an indicator of morphological development. The RCD of Nuttall oak is highly correlated (R^2>0.70) with 3 out of 13 other morphological variables (Table 3). RCD was a good predictor of height, NFOLR, and leaf area. Interestingly, height appears to correlate better than RCD with weight variables. Height is highly correlated (R^2>0.70) with 11 out of 13 other morphological variables with a very good prediction for stem weight and total shoot weight. The number of leaves correlated well with height but not (0.47) with RCD. Leaf area correlated strongly with RCD and with all weight variables except lateral root weight. One of the highest R^2 values (0.78) for morphological variables was found between the number of first order lateral roots and RCD, however, that was the only strongly correlated variable for lateral roots. All weight variables related well to height but very poorly with number of first order branches which appears to be the variable with the smaller potential for correlation. The total stem weight of Nuttall oak is strongly correlated (R^2>0.70) with 8 out of 13 other morphological variables. STEM was a good predictor of RCD, NL, and NFOB.

Table 2. Average value for morphological parameters of Nuttall oak seedlings sampled on specific dates at the Tennessee Division of Forestry Nursery (Coefficient of variation in parenthesis).

	May	July	September	November
N	*67*	*162*	*226*	*176*
RCD (mm)	2.8	4.9	6.3	9.9
	(21%)	*(35%)*	*(46%)*	*(40%)*
Shoot Height (cm)	13.4	27.8	47.4	57.7
	(29%)	*(34%)*	*(42%)*	*(44%)*
N^o of Leaves	7.9	41.5	64	0
	(37%)	*(73%)*	*(84%)*	-
N^o of First Order Lateral Roots	0	*1.2*	2.7	9.33
	-	*(175%)*	*(148%)*	*(86%)*
N^o of First Order Branches	4.8	5.1	6.7	6.8
	(48%)	*(80%)*	*(99%)*	*(75%)*
Leaf Area (cm^2)	94.5	473.7	1385.0	-
	(28%)	*(32%)*	*(17%)*	-
	Dry Weight (g/seedling)			
Leaves	0.275	1.67	4.22	2.76
	(32%)	*(34%)*	*(14%)*	*(14%)*
First Order Branches	0.0033	0.3	0.96	1.72
	(158%)	*(51%)*	*(23%)*	*(22%)*
Stem	0.175	1.12	5.28	10.62
	(16%)	*(44)*	*(35%)*	*(17%)*
Tap Root	0.3383	1.41	5.14	10.92
	(14%)	*(30%)*	*(22%)*	*(20%)*
First Order Lateral Roots	0	0.05	0.31	1.55
	-	*(102%)*	*(51%)*	*(18%)*
Total Shoot	0.4517	3.08	10.46	15.09
	(24%)	*(39%)*	*(23%)*	*(13%)*
Total root	0.3383	1.46	5.45	12.47
	(14%)	*(30%)*	*(20%)*	*(19%)*
Total dry mass	0.7933	4.54	15.91	27.55
	(15%)	*(34%)*	*(21%)*	*(14%)*
Root/Shoot ratio	0.7	0.49	0.52	0.82
	(37%)	*(22%)*	*(13%)*	*(16%)*

Table 3. R^2 values for regressions between bareroot Nuttall Oak seedling morphological variables sampled from July to November at the East Tennessee Nursery at Delano, TN *(n=564)*.

	(Code)	HT	RCD	NL	NLR	LA	NFOB	LV	FOB	ST	TAP	FOLR	STEM	ROOT	TOT
Height	HT	–	0.71	0.70	0.61	0.84	0.57	0.93	0.83	0.88	0.80	0.71	0.94	0.82	0.91
Pr > F			*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
RCD	RCD	0.71	–	0.47	0.78	0.62	0.69	0.70	0.64	0.55	0.60	0.64	0.64	0.62	0.64
Pr > F		*<.01*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
No. of Leaves	NL	0.70	0.47	–	0.39	0.65	0.65	0.80	0.82	0.48	0.57	0.23	0.64	0.57	0.62
Pr > F		*<.01*	<.01		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
No. of FOLR[1]	NLR	0.61	0.78	0.39	–	0.54	0.41	0.64	0.58	0.48	0.58	0.67	0.57	0.61	0.59
Pr > F		*<.01*	<.01	*<.01*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*0.05*	*<.01*	*0.03*
Leaf Area	LA	0.84	0.62	0.65	0.54	–	0.48	0.91	0.89	0.83	0.91	0.50	0.91	0.92	0.92
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
No. of FOB[2]	NFOB	0.57	0.69	0.65	0.41	0.48	–	0.61	0.66	0.40	0.40	0.24	0.52	0.41	0.48
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
Dry Weight *(n=90)*															
Leaves	LV	0.93	0.70	0.80	0.64	0.91	0.61	–	*0.95*	*0.83*	*0.90*	*0.56*	*0.95*	*0.91*	*0.95*
Pr > F		<.01	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
FOB	FOB	0.83	0.64	0.82	0.58	0.89	0.66	0.95	–	0.73	0.87	0.40	0.87	0.86	0.88
Pr > F		<.01	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*		*<.01*	*<.01*	*0.02*	*<.01*	*<.01*	*<.01*
Stem	ST	0.88	0.55	0.48	0.48	0.83	0.40	0.83	0.73	–	0.86	0.71	0.96	0.88	0.95
Pr > F		<.01	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
Taproot	TAP	0.80	0.60	0.57	0.58	0.91	0.40	0.90	0.87	0.86	–	0.53	0.92	0.99	0.96
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*		*<.01*	*<.01*	*<.01*	*<.01*
FOLR	FOLR	0.71	0.64	0.23	0.67	0.50	0.24	0.56	0.40	0.71	0.53	–	0.71	0.53	0.66
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*0.02*	*<.01*	*<.01*		*<.01*	*<.01*	*<.01*

TABLE 3. *Continued.*

Total	(Code)	HT	RCD	NL	NLR	LA	NFOB	LV	FOB	ST	TAP	FOLR	STEM	ROOT	TOT
Stem	STEM	0.94	0.64	0.64	0.57	0.91	0.52	0.95	0.87	0.96	0.92	0.71	–	0.93	0.99
Pr > F		*<.01*	*<.01*	*<.01*	*0.05*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*		*<.01*	*<.01*
Root	ROOT	0.82	0.62	0.57	0.61	0.92	0.41	0.91	0.86	0.88	0.99	0.53	0.93	–	0.93
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*		*<.01*
Seedling	TOT	0.91	0.64	0.62	0.59	0.92	0.48	0.95	0.88	0.95	0.96	0.66	0.99	0.93	–
Pr > F		*<.01*	*<.01*	*<.01*	*0.03*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	

† All variables were positively correlated

[1] First Order Lateral Roots

[2] First Order Branches

Yellow Poplar

Yellow poplar seedlings grew to an average of 12.0 mm RCD and 97.2 cm height by November, seven months after sowing in April (Table 4). While most RCD and Shoot height (63% of final growth) development occurred from July through September, the highest production of leaves occurred from May through July. Fewer leaves were produced after July yet foliar area increased by a large amount, indicating that leaf expansion was occurring as opposed to the addition of new leaves. The highest accumulation of leaf biomass occurred during the months of July and September when 93% of total leaf dry weight was added. During the same period FOB weight also added 93% of its maximum dry weight. Stem dry weight and tap root dry weight increased similarly with significant increases during the growing season with little or no gain from September to November. Interestingly, FOLR dry weight increased by nearly 400% during September to November. This increase in root mass impacted the root/shoot ratio which increased from 0.2 to 1.0 during this period.

Seedling Morphological Variability

As indicated by the coefficient of variation, seedling morphological variability may have increased, decreased or remained the same over the nursery season. It appeared there was little change for several variables such as RCD, height, first order branch weight, first order lateral root weight, total shoot weight, and root/shoot ratio. Variables related to leaves, however, showed a strong tendency to increase in variability over time. The CV for the number of leaves, leaf area, and leaf weight all increased during the growing season. On the other hand, the CV's for variables, such as the number of first order lateral roots, dropped over the growing season.

Correlations between Morphological Parameters

All variables seem to correlate strongly between each other with few exceptions. The RCD of yellow poplar is strongly correlated ($R^2>0.70$) with 12 out of 13 other morphological variables (Table 5). RCD was a good predictor for all variables including total seedling weights. RCD was very strongly correlated to FOLR ($R^2 = 0.90$ *prob. F<0.01*). The only variable not well correlated with RCD was leaf area which correlated poorly with all variables. Height followed the same pattern and correlated well with 12 out of 13 morphological variables.

Table 4. Average value for morphological parameters of yellow poplar seedlings sampled on specific dates at the Tennessee Division of Forestry Nursery (Coefficient of variation in parenthesis).

	May	**July**	**September**	**November**
N	*196*	*158*	*152*	*147*
RCD (mm)	1.1	4.1	9	12
	(18%)	*(39%)*	*(41%)*	*(37%)*
Shoot Height (cm)	1.8	33.1	89.3	92.2
	(28%)	*(37%)*	*(35%)*	*(32%)*
N° of Leaves	3.3	10.3	16.2	0
	(21%)	*(43%)*	*(75%)*	-
N° of First Order Lateral Roots	0	2.4	9.6	23.1
	-	*(129%)*	*(71%)*	*(52%)*
N° of First Order Branches	0	7.1	11.5	2.8
	-	*(37%)*	*(57%)*	*(96%)*
Leaf Area (cm^2)	2.4	597.3	2794	0
	(20%)	*(21%)*	*(29%)*	-
	Dry Weight (g/seedling)			
Leaves	0.0098	1.44	20.36	0
	(16%)	*(21%)*	*(24%)*	-
First Order Branches	0	0.15	2.24	1.13
	-	*(35%)*	*(27%)*	*(30%)*
Stem	0.0017	0.99	19.96	18.98
	(29%)	*(38%)*	*(24%)*	*(20%)*
Tap Root	0.0042	0.44	8.14	8.72
	(52%)	*(23%)*	*(35%)*	*(26%)*
First Order Lateral Roots	0	0.12	2.4	11.55
	-	*(30%)*	*(38%)*	*(30%)*
Total Shoot	0.0112	2.59	42.55	20.11
	(17%)	*(27%)*	*(20%)*	*(18%)*
Total root	0.0042	0.56	10.54	20.27
	(52%)	*(23%)*	*(32%)*	*(21%)*
Total dry mass	0.0153	3.14	53.09	40.38
	(25%)	*(25%)*	*(21%)*	*(18%)*
Root/Shoot ratio	0.33	0.22	0.24	1.01
	(52%)	*(14%)*	*(21%)*	*(17%)*

Table 5. R^2 values for regressions between bareroot yellow poplar seedling morphological variables sampled from July to November at the East Tennessee Nursery at Delano, TN *(n=457)*.

	(Code)	HT	RCD	NL	NLR	LA	NFOB	LV	FOB	ST	TAP	FOLR	STEM	ROOT	TOT
Height	HT	–	0.94	0.85	0.78	0.39	0.88	0.88	0.96	0.90	0.85	0.65	0.92	0.83	0.91
Pr > F			*<.01*	*<.01*	*<.01*	*0.02*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
RCD	RCD	0.94	–	0.88	0.90	0.50	0.96	0.89	0.94	0.98	0.94	0.75	0.97	0.93	0.97
Pr > F		*<.01*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
No. of Leaves	NL	0.85	0.88	–	0.73	0.31	0.89	0.77	0.85	0.82	0.82	0.57	0.83	0.79	0.83
Pr > F		*<.01*	<.01		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
No. of FOLR[1]	NLR	0.78	0.90	0.73	–	0.60	0.87	0.82	0.82	0.93	0.88	0.84	0.90	0.90	0.91
Pr > F		*<.01*	<.01	*<.01*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
Leaf Area	LA	0.39	0.50	0.31	0.60	–	0.47	0.32	0.39	0.54	0.51	0.29	0.43	0.47	0.44
Pr > F		*0.02*	*<.01*	*<.01*	*<.01*		*0.01*	*0.05*	*0.02*	*<.01*	*<.01*	*0.07*	*0.10*	*<.01*	*<.01*
No. of FOB[2]	NFOB	0.88	0.96	0.89	0.87	0.47	–	0.87	0.90	0.94	0.93	0.74	0.93	0.92	0.94
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*0.01*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
Dry Weight *(n=84)*															
Leaves	LV	0.88	0.89	0.77	0.82	0.32	0.87	–	0.87	0.88	0.81	0.80	0.96	0.84	0.95
Pr > F		<.01	*<.01*	*<.01*	*<.01*	*0.05*	*<.01*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
FOB	FOB	0.96	0.94	0.85	0.82	0.39	0.90	0.87	–	0.93	0.91	0.73	0.94	0.90	0.94
Pr > F		<.01	*<.01*	*<.01*	*<.01*	*0.02*	*<.01*	*<.01*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
Stem	ST	0.90	0.98	0.82	0.93	0.54	0.94	0.88	0.93	–	0.97	0.82	0.97	0.97	0.98
Pr > F		<.01	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*		*0.01*	*<.01*	*<.01*	*<.01*	*<.01*
Taproot	TAP	0.85	0.94	0.82	0.88	0.51	0.93	0.81	0.91	0.97	–	0.79	0.92	0.98	0.94
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*0.01*		*<.01*	*<.01*	*<.01*	*<.01*
FOLR	FOLR	0.65	0.75	0.57	0.84	0.29	0.74	0.80	0.73	0.82	0.79	–	0.82	0.79	0.83
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*0.07*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*		*<.01*	*<.01*	*<.01*

TABLE 5. *Continued.*

Total	(Code)	HT	RCD	NL	NLR	LA	NFOB	LV	FOB	ST	TAP	FOLR	STEM	ROOT	TOT
Stem	STEM	0.92	0.97	0.83	0.90	0.43	0.93	0.96	0.94	0.97	0.92	0.82	–	0.94	0.99
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*0.10*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*		*<.01*	*<.01*
Root	ROOT	0.83	0.93	0.79	0.90	0.47	0.92	0.84	0.90	0.97	0.98	0.79	0.94	–	0.96
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*		*<.01*
Seedling	TOT	0.91	0.97	0.83	0.91	0.44	0.94	0.95	0.94	0.98	0.94	0.83	0.99	0.96	–
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	

[†] All variables were positively correlated
[1] First Order Lateral Roots
[2] First Order Branches

Green Ash

Green ash averaged 7.4 mm RCD and 40.7 cm height at the November sampling, seven months after sowing in April. The largest increases in root collar diameter (RCD) and leaf area occurred from July to September with 38% and 65% respectively, of seedling growth occurring in this period. First order lateral roots (FOLR), on the other hand, had its largest development (58%) from September to November. Interestingly, the largest increases in first order branches (FOB), number of leaves, and shoot height occurred from May to July with around 55% of their maximum development. FOB actually declined 97% from September to November, yet the remaining branches accounted for 20% of maximum FOB weight.

Fewer leaves and branches were produced after July and shoot height growth slowed, yet there was an increase in foliar area by 100%. Sixty six percent of total leaf dry weight was added from July to September. Stem dry weight and tap root dry weight increased similarly during the period with 70% and 57%, respectively, of its maximum dry weight. Interestingly, stem dry weight, tap root weight, and FOLR weight increased significantly from September to November with FOLR dry weight increasing by nearly 300% from September to November. This increase in root mass impacted the root/shoot ratio which increased from 0.5 to 1.3 during this period.

Seedling Morphological Variability

Dependent upon the morphological parameter measured, seedling variability may have increased, decreased or remained the same over the season. Apparent patterns are difficult to determine although the CV for average number of leaves greatly increased from May through September while the CV first order lateral roots decreased from July through September (Table 6).

Correlations between Seedlings Morphological Parameters

Correlations between either height or RCD and other morphological variables were generally strong (>0.70). RCD was strongly correlated to first order lateral roots ($R^2 = 0.92$, *prob. F<0 .01*). Leaf area correlated well with only 4 out of 13 variables (Table 7). The number of first order branches showed weak correlation with all parameters tested. Total stem and root weight correlated well with most of the variables except to the number of first order lateral roots; however, FOLR does correlate with the total seedling weight.

Table 6. Average value for morphological parameters of green ash seedlings sampled on specific dates at the Tennessee Division of Forestry Nursery (Coefficient of variation in parenthesis).

	May	**July**	**September**	**November**
N	*187*	*195*	*261*	*190*
RCD (mm)	1.2	3.6	6.4	7.4
	(33%)	*(36%)*	*(38%)*	*(36%)*
Shoot Height (cm)	4.2	28.2	43.1	40.7
	(38%)	*(38%)*	*(39%)*	*(41%)*
N^o of Leaves	5.7	24.6	38.6	0
	(23%)	*(50%)*	*(96%)*	-
N^o of First Order Lateral Roots	0	1.2	5.3	12.7
	-	*(133%)*	*(91%)*	*(65%)*
N^o of First Order Branches	2	8.5	12.3	0.3
	(80%)	*(79%)*	*(63%)*	*(233%)*
Leaf Area (cm^2)	5.9	243.9	702.9	0
	(20%)	*(42%)*	*(35%)*	-
	Dry Weight (g/seedling)			
Leaves	0.0257	0.68	2.01	0
	(23%)	*(42%)*	*(46%)*	-
First Order Branches	0.0005	0.05	0.3	0.06
	(100%)	*(59%)*	*(31%)*	*(44%)*
Stem	0.0107	0.67	4.58	5.6
	(19%)	*(45%)*	*(31%)*	*(44%)*
Tap Root	0.0125	0.33	2.57	3.92
	(13%)	*(38%)*	*(20%)*	*(48%)*
First Order Lateral Roots	0	0.06	1.01	3.53
	-	*(75%)*	*(32%)*	*(52%)*
Total Shoot	0.0367	1.41	6.83	5.65
	(20%)	*(44%)*	*(35%)*	*(44%)*
Total root	0.0125	0.39	3.58	7.45
	(13%)	*(42%)*	*(20%)*	*(50%)*
Total dry mass	0.049	1.79	10.41	13.1
	(16%)	*(44%)*	*(28%)*	*(47%)*
Root/Shoot ratio	0.35	0.27	0.55	1.29
	(26%)	*(7%)*	*(18%)*	*(7%)*

Table 7. R^2 values for regressions between bareroot green Ash seedling morphological variables sampled from July to November at the East Tennessee Nursery at Delano, TN *(n=646)*.

	(Code)	HT	RCD	NL	NLR	LA	NFOB	LV	FOB	ST	TAP	FOLR	STEM	ROOT	TOT
Height	HT	–	0.88	0.83	0.84	0.72	0.45	0.68	0.79	0.75	0.87	0.70	0.76	0.83	0.81
Pr > F			*<.01*	*<.01*	*<.01*	*<.01*	*0.02*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
RCD	RCD	0.88	–	0.69	0.92	0.73	0.42	0.53	0.77	0.76	0.90	0.82	0.71	0.90	0.80
Pr > F		*<.01*		*<.01*	*<.01*	*<.01*	*0.02*	*0.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
No. of Leaves	NL	0.83	0.69	–	0.77	0.65	0.50	0.83	0.85	0.81	0.80	0.69	0.84	0.78	0.85
Pr > F		*<.01*	<.01		*<.01*	*<.01*	*0.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
No. of FOLR[1]	NLR	0.84	0.92	0.77	–	0.67	0.32	0.58	0.84	0.82	0.98	0.92	0.78	0.98	0.87
Pr > F		*<.01*	<.01	*<.01*		*<.01*	*0.06*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
Leaf Area	LA	0.72	0.73	0.65	0.67	–	0.27	0.60	0.61	0.67	0.73	0.51	0.67	0.67	0.70
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*		*0.19*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
No. of FOB[2]	NFOB	0.45	0.42	0.50	0.32	0.27	–	0.29	0.33	0.24	0.28	0.24	0.27	0.27	0.28
Pr > F		*0.02*	*0.02*	*0.01*	*0.06*	*0.19*		*0.08*	*0.63*	*0.11*	*0.09*	*0.12*	*0.09*	*0.09*	*0.09*
Dry Weight *(n=84)*															
Leaves	LV	0.68	0.53	0.83	0.58	0.60	0.29	–	*0.86*	*0.84*	*0.67*	*0.55*	*0.91*	*0.65*	*0.85*
Pr > F		<.01	*0.01*	*<.01*	*<.01*	*<.01*	*0.08*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
FOB	FOB	0.79	0.77	0.85	0.84	0.61	0.33	0.86	–	0.93	0.89	0.83	0.94	0.89	0.96
Pr > F		<.01	*<.01*	*<.01*	*<.01*	*<.01*	*0.63*	*<.01*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
Stem	ST	0.75	0.76	0.81	0.82	0.67	0.24	0.84	0.93	–	0.88	0.87	0.98	0.90	0.98
Pr > F		<.01	*<.01*	*<.01*	*<.01*	*<.01*	*0.11*	*<.01*	*<.01*		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*
Taproot	TAP	0.87	0.90	0.80	0.98	0.73	0.28	0.67	0.89	0.88	–	0.90	0.85	0.99	0.93
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*0.09*	*<.01*	*<.01*	*<.01*		*<.01*	*<.01*	*<.01*	*<.01*
FOLR	FOLR	0.70	0.82	0.69	0.92	0.51	0.24	0.55	0.83	0.87	0.90	–	0.80	0.95	0.88
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*0.12*	*<.01*	*<.01*	*<.01*	*<.01*		*<.01*	*<.01*	*<.01*

TABLE 7. *Continued.*

Total	(Code)	HT	RCD	NL	NLR	LA	NFOB	LV	FOB	ST	TAP	FOLR	STEM	ROOT	TOT
Stem	STEM	0.76	0.71	0.84	0.78	0.67	0.27	0.91	0.94	0.98	0.85	0.80	–	0.85	0.98
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*0.09*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*		*<.01*	*<.01*
Root	ROOT	0.83	0.90	0.78	0.98	0.67	0.27	0.65	0.89	0.90	0.99	0.95	0.85	–	0.93
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*0.09*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*		*<.01*
Seedling	TOT	0.81	0.80	0.85	0.87	0.70	0.28	0.85	0.96	0.98	0.93	0.88	0.98	0.93	–
Pr > F		*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*0.09*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	*<.01*	

[†] All variables were positively correlated
[1] First Order Lateral Roots
[2] First Order Branches

DISCUSSION

Seedling Size

A minimum RCD of 9.5 mm and 45 cm height for hardwood seedlings is recommended by the Alabama Forestry Commission (AFC, 1997). Wann and Rakestraw (1998) recommended a minimum of 10 mm RCD for hardwood planting stock. Of the three species produced in this study, only yellow poplar can be said to meet this criteria. Green ash was the smallest species observed with an average height of only 42 cm. This is difficult to explain as site, fertilization, and sowing times are comparable with the other two species, and others (Kennedy, 1990) have found green ash capable of growing 0.8 – 1.0 m in height during the nursery season. The influence of seed source cannot be discounted in this case. Typical of most hardwood sources, this seed was part of a mixed lot and the exact origin is unknown. Shorter green ash height may be advantageous for nursery managers as the species is not top pruned as it typically results in severe forking (South, 1996). Although pruning has not been performed during the season, all species had root/shoot weight ratio <1.4, which is considered well balanced (Miller, 1996).

Yellow poplar was the tallest species and was much taller than a typically marketable seedling. The seedlings were 20% taller than yellow poplar seedling grown under standard nursery cultural practices at the Indiana Department of Natural Resources (Jacobs et al., 2005). With an average height of 92 cm, yellow poplar was more than twice as tall as green ash and 60% taller than Nuttall oak. With 57 cm of height Nuttall oak was 40% taller than the average Nuttall oak seedlings commonly planted in the lower Mississippi Alluvial Valley (Schweitzer et al., 1997). Yellow poplar was consistently the largest species but did not have the highest November root/shoot ratio which was highest for green ash, followed by yellow poplar and Nuttall oak. Even tough Nuttall oak seedlings were generally larger than green ash seedlings, and the latter had more than twice as much mass in first order lateral roots. First order lateral roots were only 12% of the total root mass of Nuttall oak at the November sample date, yet 47% of the root mass of green ash and 57% of the root mass of yellow poplar. It appears that Nuttall oak may tend to put root development primarily into the taproot.

Another factor that can greatly impact seedling development is bed spacing. The average bed spacing for Nuttall oak, yellow poplar, and green ash was 52.1, 43.5, and 56.2 per m^2 of bed surface. While the largest species also had the widest spacing (yellow poplar), there was still a very large difference in seedling size between Nuttall oak and green ash, and only a small change in spacing. Obviously the difference in size between species cannot be safely attributed to bed spacing.

Growth Periodicity

The three species demonstrated distinct and unique periodicity of major plant organ development over the nursery season. In terms of aboveground development, yellow poplar increased height 61% from July to September while the larger share of height growth for green ash occurred from May to July (Table 8). Little, if any, aboveground growth of these two species occurred in September to November, yet the aboveground component of Nuttall oak increased by 18% during this period. Nuttall oak was the last to drop its leaves in the fall. There was significant root growth of Nuttall oak from September through November when this species produced 56% of its final root mass. Harris et al. (1995) observed a similar pattern with root growth beginning after shoot growth in green ash and in some oak species. Green ash and yellow poplar also increased root mass by large amounts during the fall period. The development of first order lateral roots in yellow poplar and green ash from September to November was substantial. FOLR increased by 140% in number and 381% in mass in the case of yellow poplar. An increase of 139% in number and 249% in mass of green ash occurred during the same two month period. It is not known how much root mass increased before leaf fall as opposed to after.

Table 8. Growth of RCD, height, and root mass for yellow poplar, Nuttall oak, and green ash during three periods of the nursery growing season expressed as of percentage of the November sample value

		May→ July	July→ Septmeber	September→ November
RCD			%	
	N. oak	21	14	36
	Y. poplar	25	41	25
	G. ash	32	38	14
Height				
	N. oak	25	41	18
	Y. poplar	34	61	3
	G. ash	59	37	0
Root				
	N. oak	9	32	56
	Y. poplar	3	49	48
	G. ash	5	43	52

Intra-Specific variability

It is generally accepted that hardwood seedlings are highly variable in terms of morphological development (Wilson and Jacobs, 2004). All three species in this study showed this characteristic with high coefficients of variation in the November sample for virtually all morphological parameters measured. The CVs for November RCD, for example, ranged from 36% to 40% and those for height ranged from 32% to 44%. Comparatively, smaller variation has been observed in four southern nurseries for loblolly pine with average CVs ranging from 17% to 22% for RCD and from 7% to 21% for heights (unpublished data, 2006). In a study with english oak (*Quercus robur* L.) and white oak (*Quercus alba* L.), Clausen (1983) reported seedlings graded as medium with slightly higher CVs of 49% and 46%, respectively. The variability of first order lateral roots and branches was very high, ranging from 52% to 86% for the former, and 75% to 233% for the latter. One cause for this variability may be spacing irregularities since target densities are rarely attained uniformly across a nursery, resulting in a large variation in seedling size (Jacobs, 2003). Average spacing for Nuttall oak, for example, varied from 101 seedlings/m^2 in the September sample to 73 seedlings/m^2 for the July samples. These averages were comparable with typical growing densities on different species of hardwood seedlings in the Central Hardwood Region ranging from 43 to 129 seedlings/m^2 (Jacobs, 2003). Sowing irregularities, variable germination, or even mulch depth might influence seedling size variability. Particular attention to sowing and mulch techniques may improve germination uniformity. Karrfalt (2005) found that small differences in acorn size can result in substantial seedling size differences. Seedling variability is important from a practical standpoint, as uniformity can attract and retain customers, especially if there is a regional seedling surplus (South, 1998). Seedling morphological variability is still visible in the field many years after planting (Jaenicke, 1999).

Correlations of Morphological Parameters

There were a large number of strong correlations between morphological parameters for all three hardwood species of this study. Of particular importance are the strong correlations between RCD and other parameters. The number of first order lateral roots has been linked to outplanting performance by Kormanik (1986) and Schultz and Thompson (1997). The three species studied here have strong correlations between RCD and the number of first order lateral roots and to a slightly lesser extent their mass. These data indicate that RCD may be used as a surrogate for first order lateral roots as an indicator of seedling quality. Similar RCD correlations were reported for sweetgum by McNabb (2001) with accurate prediction for both the number and biomass of first order lateral roots as well as for other several parameters with R^2 above 0.90. In the current study, height also had reasonably good correlations with the number of first order laterals, but not as strong as with RCD.

Implications for seedling production

Hardwood seedling culture may involve a number of different cultural practices, including weed control, fertilization, top pruning, and mechanical lifting. It seems apparent there are distinct characteristics of morphological development of yellow poplar, Nuttall oak and green ash. Whether there might be an interaction between morphological development and the timing and nature of cultural treatments is difficult to interpret. It is possible, for example, that earlier and larger applications of nitrogen fertilizer may have changed the timing of seedling morphological development. In the case of green ash, most of the foliar expansion occurred from May to July. Latter applications of nitrogen may not have been as effective in promoting growth as would have been earlier applications in May and June.

It's apparent that all three species showed considerable intra-specific variability in morphological development. Because uniformity is a desired seedling crop characteristic, development of strategies to increase uniformity should be a high priority to hardwood nursery managers. The relatively high variability in seedling spacing undoubtedly contributes to morphological variability. A high priority should be given to the development of management techniques that improve uniform germination. These might include improved seed quality, better matching of seed source to nursery location, more uniform stratification techniques, more uniform sowing and mulching depth, and better sowing equipment. Shoot pruning can be used to improve uniformity and facilitate handling (Sterling and Lane, 1975).

CONCLUSION

Yellow poplar, Nuttall oak, and green ash produce seedlings of different size even when grown under similar soil fertility and climatic conditions. Yellow poplar grew the fastest over the nursery season, followed by Nuttall oak, and green ash. The size difference between species was substantial with yellow poplar having 46% more total seedling dry mass in November than did Nuttall oak and 208% more than Green ash.

There were distinct periodicities to the morphological development of each species. Yellow poplar increased aboveground dry weight most significantly in the July to September period, whereas green ash added more dry weight in May through July period. Nuttall oak continued to add aboveground dry weight through the September to November period, increasing aboveground dry weight by 30%. All three species showed considerable root dry weight gains from September to November.

All three species showed extensive intra-specific variability in seedling morphology with high coefficients of variation for virtually all parameters. Because environmental conditions, soil type, and cultural treatments were similar between all three species, this high degree of variability is probably due to factors related to seed vigor, seed source, and other as yet undefined factors.

All three species showed strong correlations between numbers of seedling morphological parameters. Both height and RCD correlated well with several parameters including first order lateral roots. The strength of these correlations indicated that both, particularly RCD, might be used as an accurate determinant of overall morphological development, and therefore seedling quality.

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III. NUTRITIONAL DEVELOPMENT OF THREE SPECIES OF NURSERY-GROWN HARDWOOD SEEDLINGS IN TENNESSEE

ABSTRACT

The nutritional development of three hardwood species grown under southern hardwood nursery cultural practices were compared and their seasonal periodicity of nutrient concentrations, translocation, and allocation were documented. Yellow poplar (*Liriodendron tulipifera* L), Nuttall oak (*Quercus nuttallii* Palmer), and green ash (*Fraxinus pennsylvanica* Marsh) production resulted in small shifts in soil nutrient levels from May to November. However, there were no changes in soil carbon and organic matter content, probably as a result of the addition of mulch and leaf litterfall. In spite of similar fertilization regimes, foliar nutrient concentrations varied by species (when averaged across the growing season). Yellow poplar appeared to be the most efficient at withdrawing nutrients from senescent leaves while Nuttall oak had higher nutrient translocation efficiencies. Significant amounts of fertilizer elements were removed by harvesting, but overall removal of nitrogen and phosphorous was lower than the total fertilizer application. Nitrogen use efficiency was relatively high for all species. Yellow poplar had highest nitrogen removal efficiency and biomass productivity, followed by Nuttall oak and green ash.

INTRODUCTION

The demand for hardwood planting stock has held steady over the past several years and may have increased (Barnett, 2002) due to federal cost share programs including wetland restoration programs (Smith, 1999; Matherne, 2002). Hardwood seedlings are 3.6% of the total southern nursery production and are grown in less than half of all southern tree nurseries (McNabb and Santos, 2004). Nevertheless, the hardwood crop is an important source of nursery revenue since on an area basis it is more valuable than a pine crop (South and Carey, 2004).

Most nursery research has focused on issues related to conifers due to their larger production numbers. As a result there is relatively little literature for hardwood seedling culture (Wilson and Jacobs, 2004). Very little is known about the nutrient requirements of relatively important hardwood species. Information on optimum nutrient levels, critical ranges for essential elements, and physiological effects of nutrient deficiencies is limited (Erdmann et al., 1979). Conifers have less than half the annual nutrient requirement of most hardwoods (Lassoie et al., 1985). Pines retain numerous age classes of foliage and thus have lower demand for foliage replacement (Elliot and White, 1993). Nutrient requirements are generally higher for hardwood seedlings, especially nitrogen (N), with hardwood seedlings requiring 50% more N than pines (Davey, 1994) as well as higher amounts of phosphorus (P), calcium (Ca), and magnesium (Mg). Available literature about hardwood micronutrient nutrition (Stone, 1968) is more limited than for macronutrients (Davey, 1994).

Fertilization recommendations are based on soil analysis (Triebwasser, 2003). Most hardwood nursery standards were set nearly 30 years ago with little input from hardwood fertility research (McNabb, 2004). The main concern of nursery managers is with nitrogen (Dumroese, 2003). It is the most commonly deficient nutrient, especially when high carbon-nitrogen ratio mulch is applied on the seedbed (Williams and Hanks, 1976). Fertility standards described by Davey (1973) as cited by Stone (1980) recommend available phosphorous at 56-168 kg/ha, potassium at 168-336 kg/ha, calcium at 672-1,344 kg/ha, and organic matter greater than 10 g/kg. Nitrogen fertilizer top dressings are usually applied every two weeks beginning in late spring and extending through the summer; a typical operational nitrogen application for hardwoods is reported to be around 204 kg/ha (McNabb, 2004).

Fertilizer prescriptions are unique to each nursery, and to continually grow high quality seedlings on a nursery site, nutrients must be added to replace those that are lost when seedlings are harvested (South and Boyer, 1985). Nutrient content can be determined for a whole seedling or even particular seedling parts although foliar N concentration is the most commonly used value for nursery stock (Dumroese, 2003). The elements that limit productivity (for a given species on a given site) must be correctly diagnosed before maximum growth responses to fertilization can be obtained (Brown, 1999). The quantities and application timing of nutrients required for maximum growth may differ among hardwood species.

The objective of this research was to describe the nutritional development of three commonly produced hardwood species under nursery conditions. This study was conducted at the Tennessee Division of Forestry (TDF), East Tennessee Nursery in

Delano, Tennessee. The TDF produces approximately ten million seedlings annually, with hardwood production close to two million seedlings. Currently, 28 hardwood species are grown at this nursery with yellow poplar, green ash, and various oaks produced in the largest numbers. Winter-sown Nuttall oak (*Quercus nuttallii* Palmer), spring-sown green ash (*Fraxinus pennsylvanica* Marsh), and yellow poplar (*Liriodendron tulipifera* L.) were selected for this study as they are routinely grown by the TDF and are commonly produced in southern hardwood nurseries (McNabb & Santos, 2004).

These results should help determine seedling development parameters for the three species and may be useful in the determination of grade criterion based on nutrient content. Two hypotheses will be tested:

1: Hardwood seedling species from different botanical families, grown with similar nursery practices do not affect nutrient concentrations in the soil.

2: Nutrient cycling through litterfall does not vary by month.

MATERIALS AND METHODS

Nursery location and Culture

This study was conducted at the Tennessee Division of Forestry (TDF), East Tennessee Nursery in Delano, Tennessee. Soil in the study area was a sandy loam of the Toccoa series. They are typic udifluvent soils, commonly fine-textured with stratified layers of mineral and organic matter throughout (USDA, 1996).

A mixed lot of Nuttall oak (*Quercus nuttallii* Palmer) (209 seeds/kg, 100% germination, 60% expected seed efficiency) was sown on March 1st using a NB-2 sower and a 107 seeds/m^2 sowing density. A total of 3,316 linear bed meters was sown. A mixed lot of yellow poplar (*Liriodendron tulipifera* L.) (43% germination, 100% purity, 80% expected seed efficiency) was sown on April 18th using a NB-2 sower at a target spacing of 247 seeds/m^2. Seeds were stratified for 90 days prior to sowing. A total of 3,332 linear bed meters were sown. A mixed lot of green ash (*Fraxinus pennsylvanica* Marsh) (76% germination, 100% purity, 60% expected feed efficiency) was sown on April 18th using a NB-2 sower at a target density of 141 seeds/m^2. Seeds were stratified for 90 days prior to sowing. A total of 2,182 linear bed meters was sown.

Cultural practices

A total of 287 kg/ha elemental nitrogen (N) was applied as top dressing for Nuttall oak between May 6 and September 23 in eight applications (Table 9). Elemental phosphorus was applied at 50 kg/ha in two applications. A directed spray of 2 ml/L glyphosate was applied on May 11 to control weeds. Oxyfluorfen (Goal 4F®) was applied at 280 grams/ha on July 29. The insecticide diazinon was applied at 2.3 kg/ha as a directed spray on August 19.

A total of 234 kg/ha elemental N was applied as top dressing for yellow poplar between May 6 and August 4 in seven applications (Table 9). Elemental phosphorus was applied at 87 kg/ha in three applications. A directed spray of 20 ml/L glyphosate was applied on May 5 and June 28 to control weeds. The selective herbicide napropamide (Devrinol®) was applied at 2.25 kg/ha as a directed spray on August 16.

A total of 217 kg/ha elemental N was applied as top dressing to green ash between May 6 and August 4 in six applications (Table 9). Elemental phosphorus was applied at 25 kg/ha in a single application. A directed spray of 20 ml/L glyphosate was applied on May 11 and June 29 to control weeds. The herbicide sethoxydim (Poast®) was applied at 413 grams/ha on May 25.The insecticide diazinon was applied at 2.3 kg/ha as a directed spray on August 19.

Table 9. Elemental fertilizer application for three hardwood species grown at the Tennessee Division of Forestry, East Tennessee Nursery.

Species	Date	N kg/ha	P kg/ha	Product
Nuttall oak	May6	39	-	Ammonium nitrate
	June 2	39	-	Ammonium nitrate
	June 21	22	25	Diammonium phosphate
	July 20	39	-	Ammonium nitrate
	July 29	39	-	Ammonium nitrate
	August 4	22	25	Diammonium phosphate
	August 4	39	-	Ammonium nitrate
	September 23	48	-	Ammonium nitrate
	Total	*287*	*50*	
Yellow poplar	May 6	39	-	Ammonium nitrate
	June 2	39	-	Ammonium nitrate
	June 21	22	25	Diammonium phosphate
	July 20	34	37	Ammonium nitrate
	July 29	39	-	Ammonium nitrate
	August 4	22	25	Diammonium phosphate
	August 4	39	-	Ammonium nitrate
	Total	*234*	*87*	
Green ash	May 6	39	-	Ammonium nitrate
	June 2	39	-	Ammonium nitrate
	June 21	22	25	Diammonium phosphate
	July 20	39	-	Ammonium nitrate
	July 29	39	-	Ammonium nitrate
	August 4	39	-	Ammonium nitrate
	Total	*217*	*25*	

After sowing in April, yellow poplar and green ash beds were covered with hardwood planer mill waste (Table 10). No mulch was added to beds used to grow Nuttall oak.

Table 10. Nutrient levels applied through a mulch application to green ash and yellow poplar nursery beds

	Species	
	Green ash	Yellow poplar
Element	- - - - - - - - - - - - - - *kg/ha*- - - - - - - - - --- - -	
N	22.42	16.90
P	1.30	1.30
K	4.87	5.85
Ca	16.57	15.60
Mg	4.87	6.50
Al	27.46	42.60
B	0.07	0.08
Cu	0.17	0.16
Fe	17.91	29.76
Mn	1.16	1.68
Na	1.55	1.19
Zn	0.09	0.10
C	3,715.37	3,596.44

Sampling Design

All three species were sampled from 6 blocks in three separate beds. Each block is one bed wide and 4.87 m long, for a total length of 29.2 m. Seedlings were sampled within blocks in the months of May, July, September, and November using a 0.3 m x 1.22 m counting frame. Sample plots were randomly distributed within the block, with 0.91 m buffers between them. To carefully harvest as much of the root system as possible, seedlings were sampled using a shovel except during the last sampling procedure when a tractor drawn undercutting blade lowered to 33 cm deep lifted the seedlings and then loosened the soil from around the roots. Litterfall was collected in 0.1 m^2 traps (20 cm x 50 cm) placed in each sample plot two months prior to sampling in July, September, and November. To determine the amount of nutrients being added to the site through mulching, sample plots of 17 cm x 16 cm were randomly established within each block in May. All seedlings and mulch material were taken to laboratory facilities in Auburn for analysis.

Soil analysis

Composite soil samples were taken to a depth of 25 cm from each block for each species in May, prior to N fertilization and in subsequent sampling times in July, September and November. Soil samples were analyzed by the AU Soil Testing and Plant Analysis Laboratory. Routine elemental analyses were applied to determine phosphorus, potassium, calcium, and magnesium using the Mehlich I solution. Phenoldisulfonic acid method was used to determine nitrates. Micro-nutrients were determined with Inductively Coupled Plasma (ICP) Emission Spectroscopy and organic matter determined by dry combustion method with a LECO carbon analyzer.

Measurements

Seedling height, root collar diameter (RCD), number of first order branches (FOB), number of first order lateral roots (FOLR) (>1mm) and number of leaves were tallied. Fresh and dry weights were obtained for stem, taproot, FOLR, FOB, and leaves on a plot basis. The root/shoot ratio was based on root and shoot dry weights.

Dried samples of at least 5 grams were sent to the Auburn diagnostics laboratory for grinding and nutrient analysis. Total nitrogen and carbon were determined by combustion. The P, K, Ca, Mg, Mn, Fe, Al, B, Cu, and Zn were determined by ICP. Samples were taken for taproot, FOLR, FOB, and leaves by first combining each into a single block and then randomly selecting sufficient material for analysis. Stem tissue sections were taken from the lower, middle, and upper part of the stem and used for the block combination and random selection. Litterfall collections from traps were bagged, weighed (dry) and analyzed for nutrient content. The total number of seedling tissue samples to be chemically analyzed was 165. Blocks 1 and 2, 3 and 4, and 5 and 6 were combined for all nutrients' analysis.

Analysis

Total plot (block) dry weight was divided by the number of seedlings in the plot to obtain an average seedling value for each component (at each sampling time). Nutrient concentration and content were reported over time by species for the various seedling morphological components. The following seedling nutrient utilization factors were calculated:

1) Nitrogen removal efficiency (Bruulsema, 2005).

The crop nitrogen removal efficiency (NRE) was calculated at the November sample date for (belowground, aboveground, and litterfall) seedling components of each species.

$$\textit{Nitrogen Removal Efficiency (\%)} = \frac{\textit{Nitrogen harvested } (kg.ha^{-1})}{\textit{Nitrogen applied}(kg.ha^{-1})} \times 100$$

2) Partial Factor of Productivity (Cassman et al., 2002).

Partial Factor of Productivity (PFP), the ratio of crop biomass per unit of applied N fertilizer, was calculated for each species for (belowground, aboveground, litterfall) seedling components at the November sample.

$$\textit{Partial Factor of Productivity} = \frac{\textit{Biomass produced } (kg.ha^{-1})}{\textit{Nitrogen applied } (kg.ha^{-1})}$$

3) Nutrient translocation efficiency (Ntanos and Koutroubas, 2002).

Nutrient translocation efficiency for N and P was calculated using foliage nutrient content at the July sample date against nutrient content in litterfall sampled at November.

$$\textit{Translocation efficiency} = \frac{\textit{nutrient foliage } (g.m^{-2}) - \textit{nutrient litterfall } (g.m^{-2})}{\textit{nutrient foliage } (g.m^{-2})} \times 100$$

4) Resorption efficiency (Van Heerwarden et al., 2003).

This parameter describes the relative amount of nutrient pool translocated back into the seedling before leaf abscission. It was calculated for each species using the foliage in September and litterfall sampled from September to November for N and P as denoted:

$$\textit{Resorption efficiency} = 1 - \left(\frac{\textit{Litterfall Nutrient concentration } (g.g^{-1})}{\textit{Foliage Nutrient concentration } (g.g^{-1})} \right) \times 100$$

5) Nutrient use efficiency (U.S. EPA, 2002).

Seedling nutrient use efficiency (NUE) of each species was estimated for (belowground, aboveground, litterfall) seedling components using 8 to 9 month old seedlings to estimate the efficiency of biomass production per unit of absorbed nitrogen.

$$NUE = \frac{\textit{Net Primary Productivity } (g.m^{-2})}{\textit{Total Nitrogen Uptake } (g.m^{-2})}$$

For purposes of this study, net primary productivity (NPP) is considered seedling dry weight plus litterfall. Total nitrogen uptake includes nutrients accumulated in aboveground and belowground biomass, and litterfall. An analysis of variance with orthogonal contrasts was used to compare soil nutrient concentrations between sample dates for each species with SAS® 9.1. To compare litterfall differences between sampling times within species, t-tests were performed with Bonferroni correction with SPSS® 11.5.

RESULTS

Soil Chemical Analysis

The results of periodic soil sampling found there were some shifts in soil nutrient levels from May to November (Tables 11 to 13). It was expected that the addition of nitrogen fertilizers and organic matter would decrease pH and this may, in fact, have occurred as average pH fell from 5.3 to 4.9 from May to the July sample for the three species. An average pH of 4.9 to 5.3 is generally considered acidic for hardwood seedling culture (Pritchett and Fisher, 1987). In spite of 246 to 289 kg N/ha added in the form of mineral nitrogen fertilizer, soil nitrogen content remained constant. On the other hand, inorganic fertilizer additions of 44 kg of P per hectare in the cultivation of Nuttall oak and yellow poplar and 22 kg/ha in the cultivation of green ash significantly increased soil P levels for all species. Average soil P content across the three species increased from 23.2 kg/ha in May to 28.5 kg/ha in September and November, an increase of 23%. With one exception (Mg), soil K, Ca and Mg significantly decreased from May to November for all three species. For example, soil Ca levels in May across all three species averaged 632 mg/kg, but had decreased to 417 mg/kg in November.

Table 11. Soil chemical analysis for Nuttall oak seedlings at the Tennessee Division of Forestry during the 2004 crop season

Month	*Species*	pH	O.M.	C	N	P	K	Mg	Ca	Al	B	Cu	Fe	Mn	Na	Zn
			g/kg			*mg/kg*										
Nuttall oak																
May		5.2	17.0	9.7	0.7	22.8	90.5	54.3	602.1	303.7	0.1	3.5	47.5	41.1	27.4	1.6
July		4.7	17.0	10.0	0.8	24.9	98.6	45.8	499.0	321.6	0.2	1.9	59.6	50.5	25.2	1.6
September		4.7	16.5	9.7	0.8	32.3	87.9	53.4	483.4	342.6	0.2	3.1	50.1	56.1	30.8	1.6
November		4.9	19.0	11.0	0.8	27.7	71.4	26.8	372.2	334.8	0.2	1.9	62.3	50.5	25.0	1.9
ANOVA																
Linear		0.03	0.83	0.85	0.91	<.01	0.03	0.86	0.08	<.01	0.13	0.55	0.33	0.01	0.50	0.64
Quadratic		<.01	0.71	0.22	0.80	0.03	0.02	0.15	0.90	0.04	0.46	0.79	<.01	0.00	0.70	0.31
Lack of fit		<.01	0.04	0.04	0.24	0.22	0.04	0.01	<.01	0.01	0.13	0.11	<.01	0.02	0.60	0.19

Table 12. Soil chemical analysis for yellow poplar seedlings at the Tennessee Division of Forestry during the 2004 crop season

Month	*Species*	pH	O.M.	C	N	P	K	Mg	Ca	Al	B	Cu	Fe	Mn	Na	Zn
			– – – – *g/kg* – – – –			– – – – – – – – – – – *mg/kg* – – – – – – – – – – –										
Yellow poplar																
May		5.4	17.0	10.0	0.7	28.4	111.5	72.8	627.4	349.3	0.1	4.3	35.4	39.9	29.7	1.8
July		5.1	19.4	11.4	0.8	32.5	117.3	72.9	509.3	342.4	0.1	3.5	40.1	48.1	27.9	1.7
September		5.0	18.2	10.7	0.8	29.7	86.5	43.4	412.3	337.2	0.2	1.7	53.3	52.8	24.3	1.8
November		5.1	18.0	10.6	0.8	33.7	96.5	66.7	424.7	339.0	0.6	2.0	48.6	57.4	27.0	1.6
ANOVA																
Linear		0.27	0.49	0.48	0.79	0.72	<.01	0.01	0.02	0.37	0.02	0.02	0.05	<.01	<.01	0.79
Quadratic		0.06	0.16	0.17	0.31	0.99	0.60	0.11	0.13	0.48	0.02	0.39	0.38	0.12	<.01	0.34
Lack of fit		0.06	0.32	0.32	0.23	0.06	0.44	0.70	0.02	0.37	<.01	0.08	0.29	<.01	0.05	0.03

Table 13. Soil chemical analysis for green ash seedlings at the Tennessee Division of Forestry during the 2004 crop season

Month	*Species*	pH	O.M.	C	N	P	K	Mg	Ca	Al	B	Cu	Fe	Mn	Na	Zn
			g/kg			*mg/kg*										
Green ash																
May		5.4	17.0	10.0	0.7	18.5	90.7	66.1	667.2	307.4	0.1	3.1	46.6	54.0	28.9	1.5
July		5.1	18.0	10.6	0.7	23.8	99.4	54.7	485.2	307.6	0.2	1.6	72.9	85.6	24.2	1.3
September		5.1	18.7	11.1	0.8	24.2	83.7	47.6	444.2	301.4	0.3	1.8	63.8	59.4	25.4	1.1
November		5.1	19.0	10.8	0.8	24.2	84.3	48.8	455.6	311.7	0.2	3.2	60.8	55.5	25.8	1.9
ANOVA																
Linear		*0.25*	0.29	0.28	0.24	0.07	<.01	<.01	<.01	0.29	<.01	0.81	0.48	<.01	0.90	0.80
Quadratic		*0.03*	0.36	0.36	0.44	0.01	0.06	<.01	<.01	0.12	<.01	0.10	0.01	<.01	0.07	0.02
Lack of fit		*0.01*	0.45	0.45	0.58	<.01	0.67	<.01	<.01	0.17	0.02	0.96	0.02	0.01	0.09	0.06

There were no significant trends in soil carbon and organic matter content (Tables 11 to 13) over the growing season (Table 10). Around 3.5 tons of carbon per hectare were added to the soil through mulch application to green ash and yellow poplar growing areas. What soil carbon content might have been without these additions is difficult to ascertain. What is apparent, however, is that soil organic matter did not decline from May to November. This may indicate the importance of litterfall and mulch in the maintenance of soil organic matter in hardwood nurseries. From September to November, Nuttall oak, yellow poplar, and green ash deposited 828, 3270, and 810 kg/ha, respectively, of dry matter to the soil surface through litterfall (Table 20). Current seedling cultural practices at the Tennessee Division of Forestry Nursery appears to be maintaining soil chemical components, including soil organic matter levels, with the exception of soil Ca, Mg, and K.

Litterfall is an important source of nutrients (Table 14). From July, when the litterfall traps were first collected, to lifting time, the amount of nitrogen deposited by litterfall was 21.9, 73.2, and 29.8 kg/ha for Nuttall oak, yellow poplar, and green ash, respectively. This was equivalent to 8, 31, and 14 percent of the nitrogen applied as fertilizer to Nuttall oak, yellow poplar, and green ash, respectively. Considering that Nuttall oak had dropped only 34% of its leaves at the sample time in November, the expected amount of nitrogen deposited on the nursery soil could be as much as 64 kg/ha. Nitrogen and magnesium concentrations in the litterfall significantly decreased from September to November for Nuttall oak and yellow poplar. Phosphorous concentration decreased for yellow poplar while potassium increased for Nuttall oak. No macro-nutrient changed from September to November for green ash.

Table 14. Macro and micronutrient concentrations and deposition through hardwood seedling litterfall for the 2004 crop season

Species	*Month*	N	P	K	Ca	Mg	Al	B	Cu	Fe	Mn	Na	Zn
		g/kg					*mg/kg*						
Nuttall oak	*September*	**24.6***	0.6	**4.2**	9.6	**2.0***	**1320.6***	**27.8***	**35.7***	**775.6***	459.1	220.4	69.5
		(1.2)	*(0.0)*	*(0.2)*	*(1.6)*	*(0.1)*	*(474.6)*	*(1.2)*	*(5.0)*	*(267.2)*	*(148.4)*	*(54.8)*	*(1.7)*
	November	**12.7**	0.6	**4.8***	8.4	**1.5**	**390.0**	**18.0**	**19.5**	**234.9**	332.1	199.5	76.0
		(2.0)	*(0.1)*	*(0.3)*	*(1.2)*	*(0.1)*	*(35.9)*	*(0.9)*	*(1.1)*	*(43.8)*	*(141.7)*	*(34.2)*	*(16.3)*
Yellow poplar	*September*	**17.2***	**0.6***	8.5	18.5	**3.6***	505.1	19.8	30.0	297.4	336.4	217.7	15.8
		(0.8)	*(0.0)*	*(1.9)*	*(1.3)*	*(0.5)*	*(139.2)*	*(0.4)*	*(14.2)*	*(47.4)*	*(38.1)*	*(23.1)*	*(5.5)*
	November	**10.2**	**0.4**	5.1	15.1	**2.6**	426.9	16.0	21.5	222.9	302.4	195.0	12.3
		(0.9)	*(0.1)*	*(1.6)*	*(1.8)*	*0.2*	*(136.5)*	*(0.8)*	*(0.7)*	*(81.5)*	*(11.6)*	*(29.6)*	*(1.1)*
Green ash	*September*	26.4	0.7	3.2	8.6	1.9	**3637.3***	**23.5**	99.5	**2428.2***	**357.7***	316.2	**29.7***
		(5.3)	*(0.1)*	*(0.9)*	*(1.4)*	*(0.2)*	*(868.6)*	*(5.0)*	*(46.2)*	*(539.6)*	*(87.0)*	*(142.8)*	*(8.0)*
	November	17.8	0.8	3.0	10.1	1.9	**441.3**	**23.6***	46.7	**427.0**	**215.2**	147.6	**12.1**
		(1.9)	*(0.1)*	*(0.3)*	*(0.4)*	*(0.2)*	*(274.3)*	*(3.8)*	*(23.3)*	*(120.9)*	*(13.9)*	*(23.9)*	*(4.6)*
		kg/ha											
Nuttall oak	*September*	5.5	0.1	0.9	2.2	0.5	0.3	<.1	<.1	0.2	0.1	0.1	<.1
	November	16.4	0.8	6.2	10.9	2	0.5	<.1	<.1	0.3	0.4	0.3	0.1
Yellow poplar	*September*	15.6	0.5	7.7	16.9	3.2	0.5	<.1	<.1	0.3	0.3	0.2	<.1
	November	57.6	2.3	28.7	84.8	14.5	2.4	0.1	0.1	1.3	1.7	1.1	0.1
Green ash	*September*	5.9	0.2	0.7	1.9	0.4	0.8	<.1	<.1	0.5	0.1	0.1	<.1
	November	23.9	1.1	4.1	13.6	2.6	0.6	<.1	0.1	0.6	0.3	0.2	<.1

* Column means are significantly different within species at the 0.05 level using t-tests with Bonferroni correction.
[1] Standard error of mean in parenthesis

Foliar nutrient concentrations averaged across the nursery growing season are presented in Table 15. Values are similar across species, but not identical. There was a strong trend for yellow poplar to have higher nutrient concentrations. In fact, average yellow poplar nutrient concentrations were higher than both Nuttall oak and green ash for N, P, K, Ca, and Mg. Average green ash nutrient concentrations were higher than Nuttall oak for N, P, K, and Mg.

Table 15. Average foliar seedling nutrient concentrations of three hardwood species sampled periodically from May through November at the Tennessee Division of Forestry Nursery.

	C	N	P	K	Ca	Mg	AL	B	Cu	Fe	Mn	Na	Zn
Species	*g/kg*						*mg/kg*						
N. Oak	449.2	18.8	1.5	8.4	6.8	1.7	417.0	23.0	20.2	282.2	361.8	219.2	53.9
	(8.3)	*(1.4)*	*(0.2)*	*(2.2)*	*(1.3)*	*(0.4)*	*(133.3)*	*(5.2)*	*(12.1)*	*(105.2)*	*(108.6)*	*(86.7)*	*(19.5)*
Y. poplar	429.3	30.4	2.4	14.4	12.2	3.5	554.7	20.3	21.7	396.3	264.4	284.9	25.0
	(7.0)	*(4.1)*	*(0.5)*	*(3.5)*	*(2.6)*	*(0.5)*	*(541.9)*	*(6.1)*	*(4.0)*	*(360.9)*	*(59.7)*	*(137.8)*	*(11.8)*
G. ash	444.9	26.4	2.1	14.7	6.0	1.9	330.1	21.8	24.2	323.6	147.6	193.1	21.6
	(13.3)	*(3.3)*	*(0.4)*	*(3.9)*	*(0.3)*	*(0.2)*	*(390.6)*	*(3.4)*	*(6.8)*	*(227.4)*	*(32.9)*	*(48.1)*	*(6.3)*

† Standard error of the mean in parenthesis

NPK concentrations and contents in the seedling tissues

Average nitrogen, phosphorous, and potassium contents increased in the leaves for the three species, primarily as a consequence of morphological growth (Figure 4). However, nutrient concentration in the leaves of yellow poplar and green ash decreased from May to September (Figure 1). This was probably due to translocation of nitrogen and phosphorous from the leaves during the process of senescence in the fall, indicated also by the decrease in nitrogen concentrations from September to November litterfall samples (Table 14). The decrease in potassium for all species was evident but it may not be completely linked to translocations since it is easily confounded with leaching. Leaching of potassium greatly increases when the leaves turn yellow and cell turgor decreases, resulting in considerable leaching before leaf fall (Witkamp, 1971). Nuttall oak did not follow the same trend, possibly related to the warmer temperatures at the end of the season, delaying leaf fall.

Average nitrogen concentrations in both stem and branches decreased from July to September, probably due to tissue maturation during seedling development. There were large increases in average stem nitrogen concentrations in the November sample (Figure 2). This was probably due to translocation of nitrogen from the leaves during the process of senescence in the fall. Seasonal variation in stem phosphorous concentrations appeared to change by species. Potassium, on the other hand, showed declining stem concentrations over the nursery season, which appeared to affect greatly yellow poplar with a sharp decrease in the potassium content in the stems and branches (Figure 5).

Although roots had major biomass increases from September to November, average root nitrogen increased for all three species (Figure 6), indicating no dilution effect regarding their concentrations (Figure 3). In similar fashion to the aboveground components, root phosphorous concentration seasonal changes varied by species. On the other hand, root potassium concentrations did not seem to follow the same seasonal changes as the aboveground components.

Figure1. Nitrogen, phosphorous, and potassium in the leaves of three hardwood species grown at the Tennessee Division of Forestry Nursery (NO=Nuttall oak, YP=yellow poplar, GA=green ash) (Bars reported with standard error).

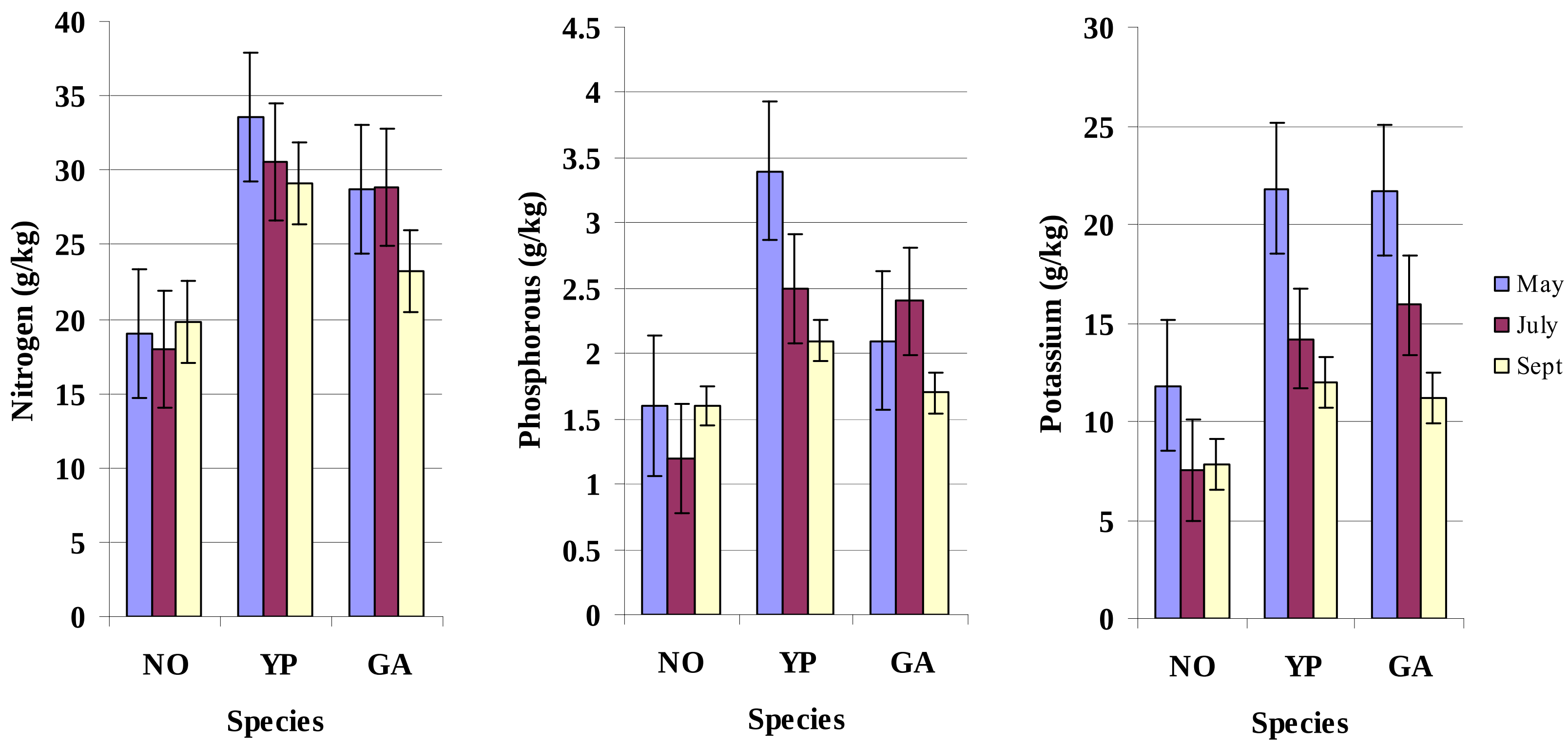


Figure2. Nitrogen, phosphorous, and potassium in the stems and branches of three hardwood species grown at the Tennessee Division of Forestry Nursery (NO=Nuttall oak, YP=yellow poplar, GA=green ash) (Bars reported with standard error).

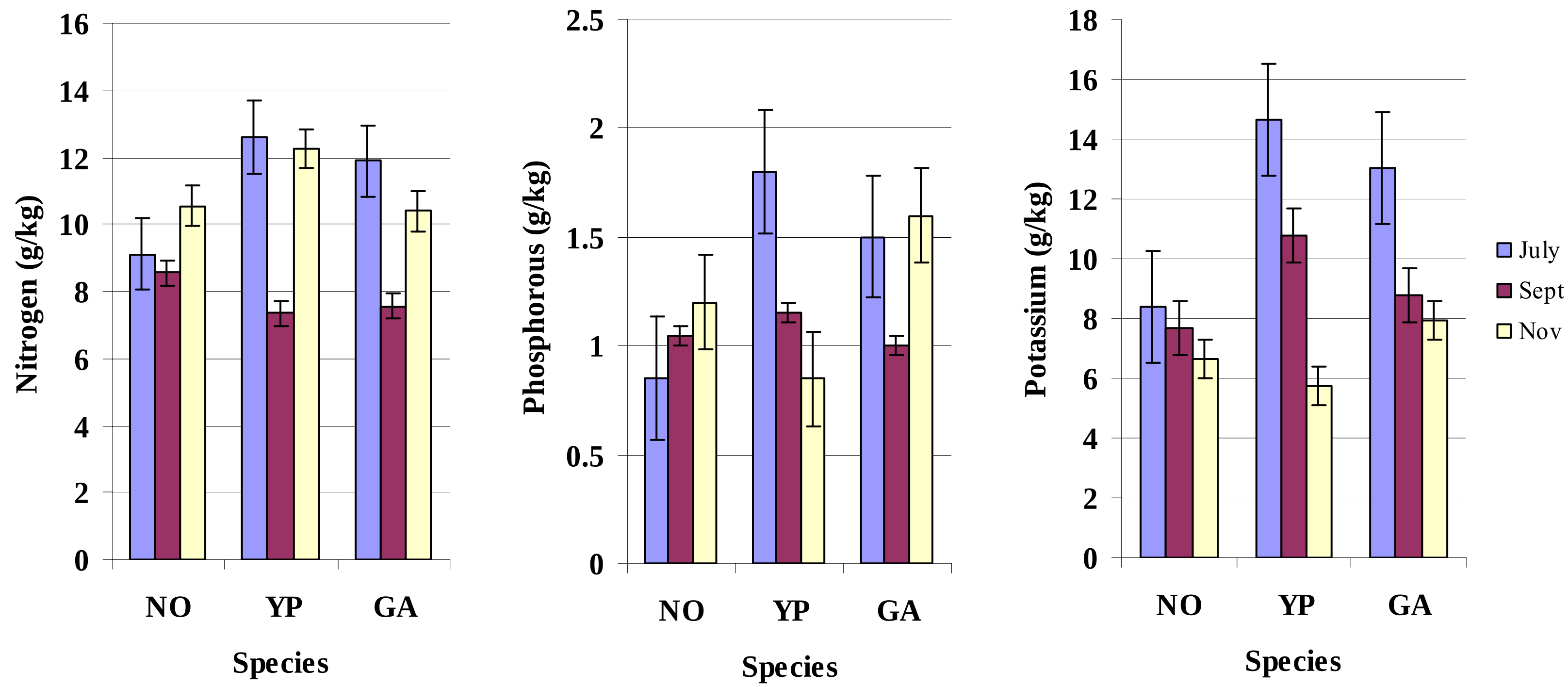


Figure3. Nitrogen, phosphorous, and potassium in the taproot component of three hardwood species grown at the Tennessee Division of Forestry Nursery (NO=Nuttall oak, YP=yellow poplar, GA=green ash) (Bars reported with standard error).

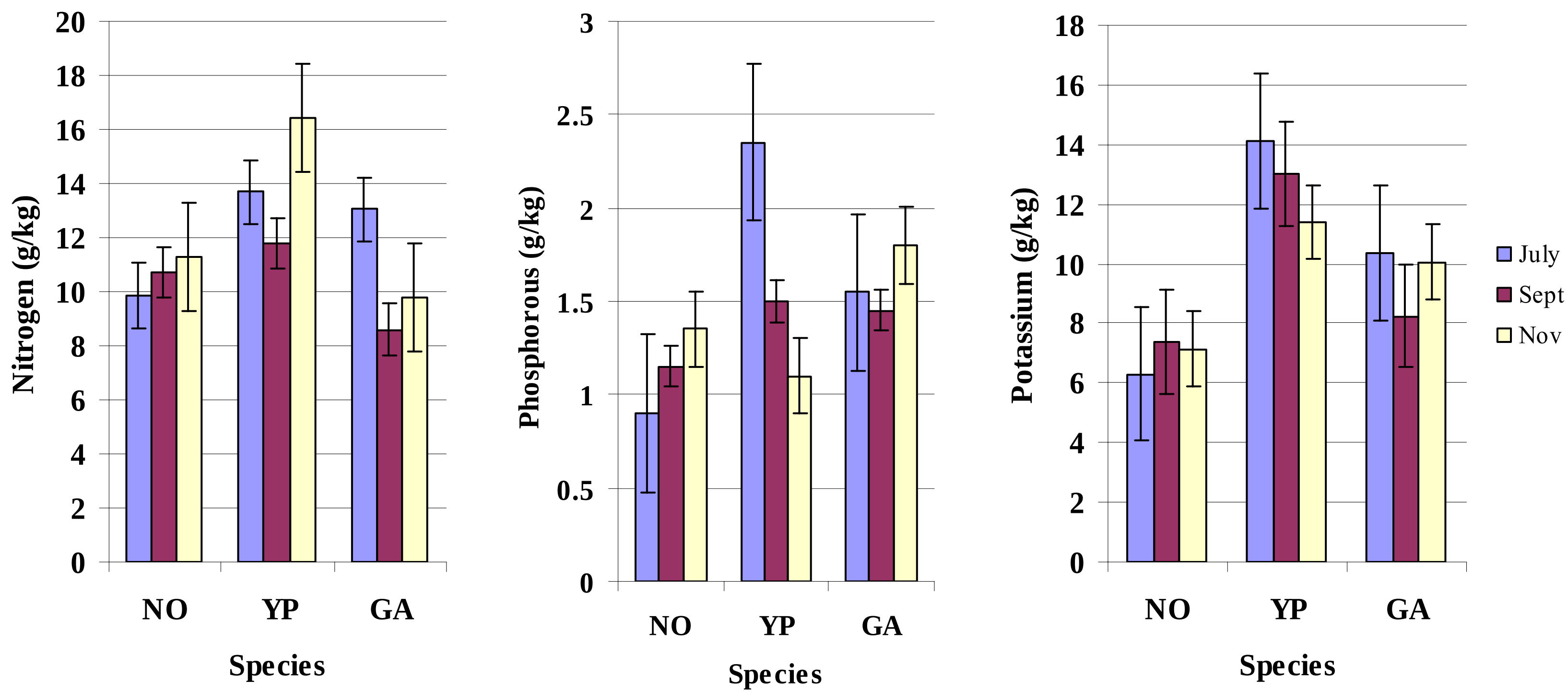
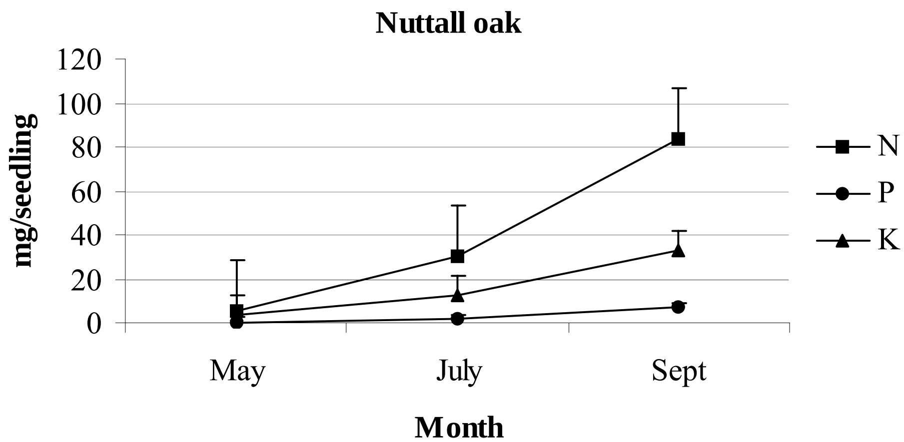
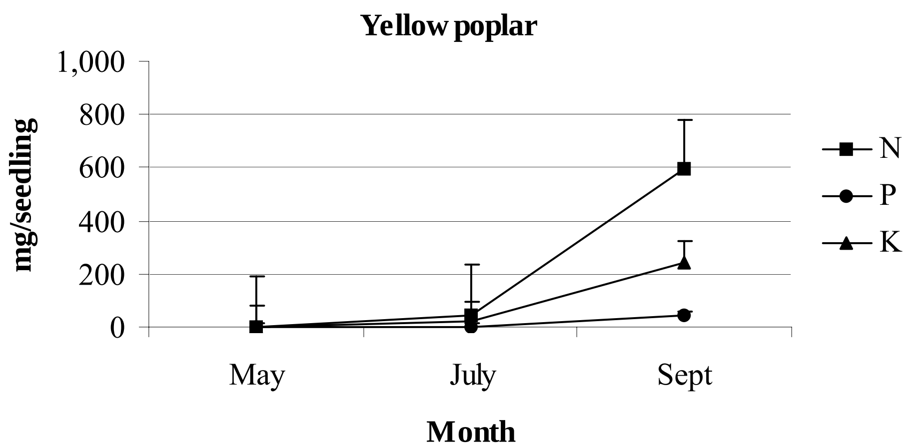


Figure 4. Nitrogen, phosphorous, and potassium contents over time in the leaves of three hardwood species grown at the Tennessee Division of Forestry Nursery (Data series reported with standard error).





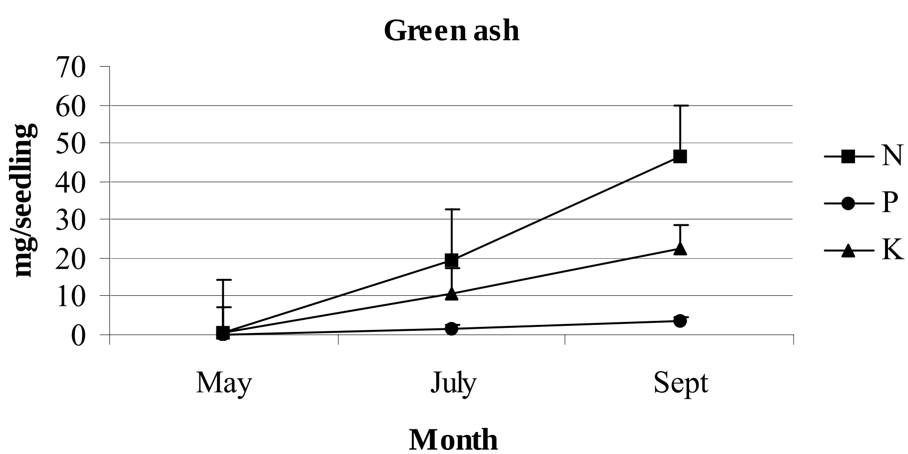
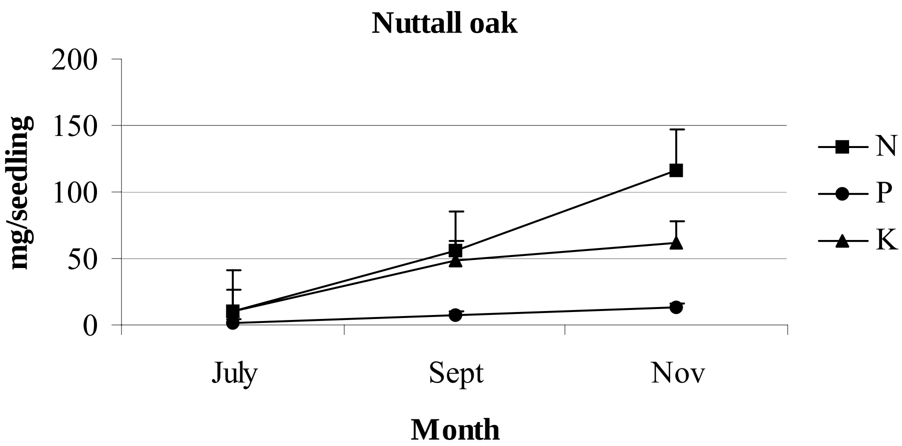
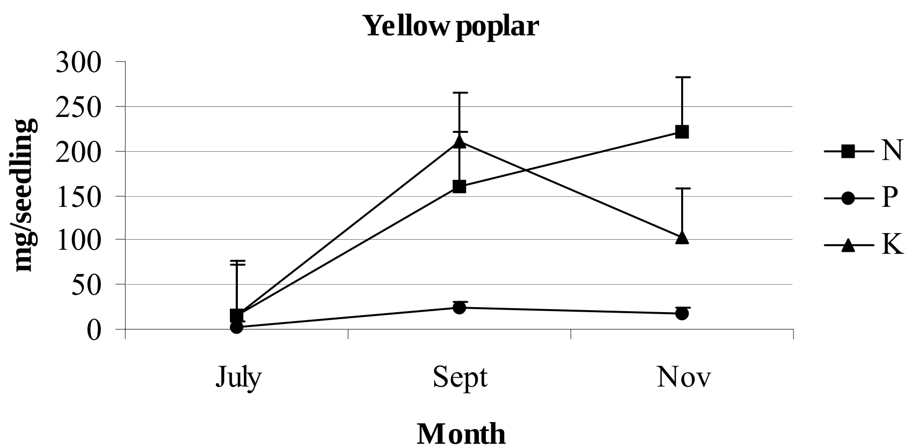


Figure 5. Nitrogen, phosphorous, and potassium contents over time in the branches and stems of three hardwood species grown at the Tennessee Division of Forestry Nursery) (Data series reported with standard error).





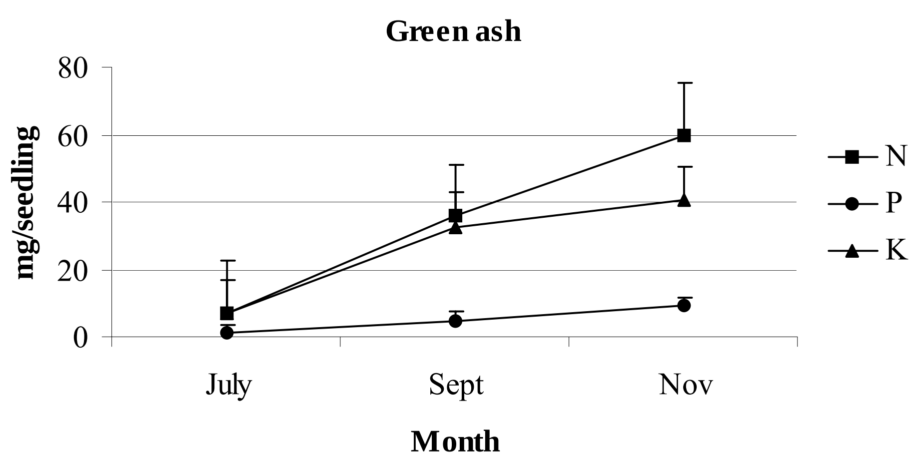
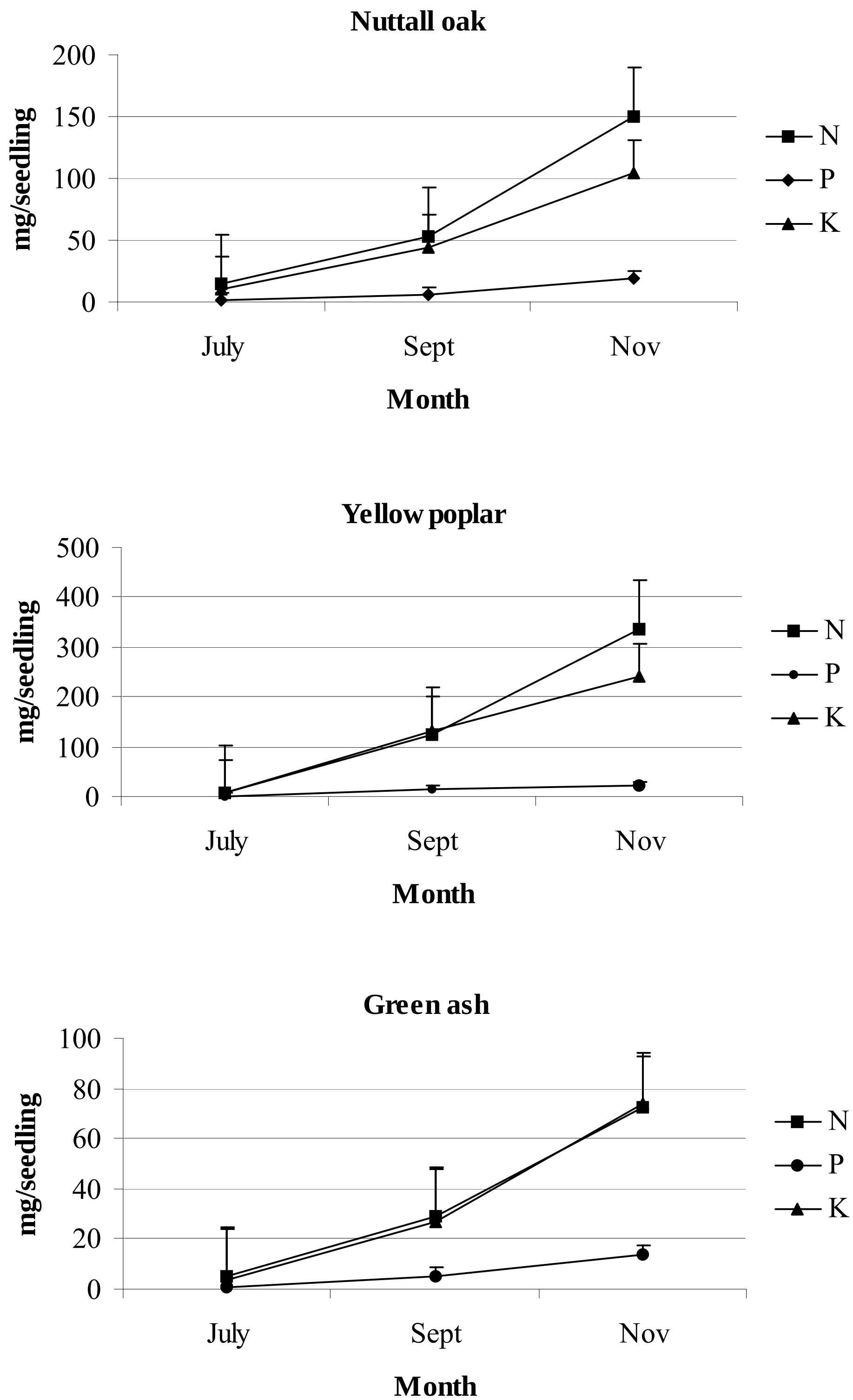


Figure 6. Nitrogen, phosphorous, and potassium contents over time in the roots of three hardwood species grown at the Tennessee Division of Forestry Nursery (Data series reported with standard error).



Translocation Efficiencies

The ability of a species to move nutrients from aging leaves so they can be used in growing tissues is estimated by the resorption efficiency (RE). Calculations indicated that yellow poplar had higher RE values for nitrogen and potassium when compared to both green ash and Nuttall oak (Table 16). Yellow poplar appeared, therefore, to be the most efficient at withdrawing nutrients from senescent leaves before abscission. Nutrients withdrawn will normally be used for new growth or storage in the vegetative tissue until the next growing season.

Table 16. Seedling resorption efficiency (RE) for three hardwood species produced in the Tennessee Division of Forestry Nursery.

Species	*N*	*P*
	––––––––– %	–––––––––
Nuttall oak	36.2	62.5
Yellow poplar	64.8	80.8
Green ash	23.1	53.0

Seedling translocation efficiency (TE) differs from RE in that it calculates the amount of nutrient moved from senescent leaves in July into other plant organs. Nutrient translocation in forest trees is an efficient strategy which makes the plants less dependent on soil nutrient reserves, by optimizing the consumption of available nutrients within the biogeochemical cycle (Colin-Belgrand, 1996). Yellow poplar, in this case, averaged lower efficiencies when compared to the other two species. Nuttall oak had very high TE values of 69 and 77 for nitrogen and phosphorous. Green ash translocation for both N and P was relatively high.

Table 17. Seedling translocation efficiency (TE) for three hardwood species produced in the Tennessee Division of Forestry Nursery.

Species	*N*	*P*
	––––––––%	––––––––
Nuttall oak	69.3	77.5
Yellow poplar	22.9	61.8
Green ash	43.4	69.3

Seedling Nutrient Exports

Nutrient export occurs when seedlings are harvested during the lifting season and their nutrient content removed from the nursery. The amount of nutrient export is a function of both nutrient concentration and seedling size. Yellow poplar showed the greatest level of export, primarily a function of its large size (Table 18), removing 233.6, 14.8, and 136.1 kg/ha of N, P, and K, respectively. Nuttall oak was second in the amount of nutrients exported and green ash the third. The amount of nitrogen carried from the site in green ash seedlings is only 36% of that removed by yellow poplar.

Even though there are significant amounts of fertilizer elements removed by harvesting, the overall nitrogen and phosphorous balance is positive for all three species (Table 19). There were 107, 18, and 153 kg/ha more nitrogen applied to Nuttall oak, yellow poplar, and green ash, respectively, than removed through harvesting. Around 62% of all nitrogen applied to green ash was not exported from the nursery, indicating an inefficient use of fertilizer materials when compared to the other two species. On the other hand, yellow poplar nitrogen balance was slightly positive and phosphorous was much higher than the other two species. Around 93% of all nitrogen applied to the species was removed through harvesting while phosphorous removed was only 17%.

Table 18. Macro and micronutrients removed through harvesting three hardwood seedling crop grown at the Tennessee Division of Forestry Nursery.

Species		C	N	P	K	Ca	Mg	Al	B	Cu	Fe	Mn	Na	Zn
		kg/ha												
N. oak	Mean	6429.5	180.1	17.1	93.8	88.5	17.1	6.6	0.2	0.2	3.7	3.3	3.1	0.6
	Min	6025.9	126.9	7.3	57.2	36.8	11.1	0.5	0.1	0.1	0.7	1.5	2.3	0.1
	Max	6705.1	288.7	28.7	156.6	142.3	28.2	24.3	0.4	0.5	11.3	6.9	5.4	1.3
Y. poplar	Mean	7452.8	233.6	14.8	136.1	115.0	32.8	8.0	0.2	0.3	4.9	2.5	3.7	0.2
	Min	6915.2	159.8	7.0	69.7	54.7	21.3	1.0	0.1	0.2	0.9	0.8	2.8	<.1
	Max	7787.0	320.0	23.4	280.8	285.0	46.5	28.2	0.3	0.7	16.8	5.4	5.7	0.5
G. ash	Mean	3241.6	86.2	11.0	55.3	40.1	10.5	4.1	0.1	0.2	4.3	1.2	1.5	0.1
	Min	3137.1	63.7	5.0	19.8	16.2	8.1	0.5	0.1	0.1	0.6	0.4	0.9	<.1
	Max	3375.1	146.2	15.6	112.8	77.6	15.3	9.5	0.2	0.5	12.5	2.2	2.6	0.2

Table 19. Nitrogen and phosphorous balance for fertilizer application and removal through the harvest of three hardwood species grown at the Tennessee Division of Forestry Nursery

	Nuttall oak		Yellow poplar		Green ash	
	------*kg/ha*-----		------*kg/ha*-----		------*kg/ha*-----	
	N	P	N	P	N	P
Additions						
Fertilizer	287	50	234	87	217	25
Mulch	0	0	17	1	22	1
Removal by harvesting	180	29	233	15	86	11
Balance	**+107**	**+21**	**+18**	**+73**	**+153**	**+15**

Nutrient Use Efficiencies

Yellow poplar had the lowest seedling density, and the highest aboveground and belowground biomass, followed by Nuttall oak and green ash. Green ash produced only 39% of the biomass that Nuttall oak produced (Table 20). Phosphorous application amounts varied by species, following the same pattern as that of biomass production. Interestingly, species receiving higher phosphorous applications appeared to have more growth.

Table 20. Nitrogen and phosphorus fertilization and seedling above and below ground biomass for the three hardwood species produced at the Tennessee Division of Forestry Nursery.

Species	Seedlings	N	P	Biomass Produced			
	N°/ha[1]	*kg/ha*[2]		– – – – – – – – – – *kg/ha* – – – – – – – – – –			
				Above	Below	Litterfall	Total
N. oak	520,968	287	50	7,952.6	6,560.6	828.9	15,342.1
Y. poplar	435,127	251	88	8,598.6	8,663.7	3269.3	20,531.6
G. ash	562,409	239	26	3,177.6	4,189.9	810.8	8,178.3

[1]Considering 66% in seedling bed area; [2]Includes mulch application

Yellow poplar had the highest amount of biomass produced per unit of fertilizer and organic nitrogen added to the soil (Table 21). For each kilogram of nitrogen added per hectare in the form of fertilizer and mulch, yellow poplar produced 82 kg of biomass per hectare (i.e. Partial Factor of Productivity), which included aboveground and belowground seedling components as well as total seasonal litterfall. Nuttall oak produced 53.5 kg of biomass for every kilogram of additional nitrogen, but green ash only 34.5 kg (40 % of what yellow poplar produced). Interestingly, the NUE of Nuttall oak was higher than that of yellow poplar. The crop NRE followed the same order as PFP; however, with yellow poplar removal efficiency was very high. Green ash had the lowest efficiencies ratings for PFP and NRE but relative high NUE.

Table 21. Seedling nitrogen partial factor of productivity (PFP), nitrogen use efficiency (NUE), and crop nitrogen removal efficiency (NRE) for the three hardwood nursery cultures samples in November

Species	PFP	NUE	NRE (%)
Nuttall oak	53.5	75.9	62.8
Yellow poplar	81.8	66.9	93.0
Green ash	34.2	70.5	36.0

DISCUSSION

Soil Chemistry

There is little evidence to indicate that hardwood seedling culture modified the nursery soil in any significant fashion over the course of the growing season. In fact, organic matter, nitrogen, and carbon levels remained unchanged, indicating that fertilization, litterfall, and the use of mulch all contribute to maintaining soil health. Inorganic fertilization appeared to have maintained nutrient concentrations at satisfactory levels throughout the season. However, soil Ca and Mg levels decreased and may be related to inadequate fertilization. Nuttall oak and green ash exported 4 to 6 times more Ca than 8 month old slash pine seedlings (Pritchett and Fisher, 1987). Litterfall is a major component of hardwood nursery soil management. This study found an average litterfall of 1,636 kg/ha (163.6 g/m^2), returning 42, 2, and 16 kg of N, P, and K to the soil, respectively, over the nursery season. A typical temperate deciduous forest will average 5400 kg/ha/yr of litterfall and return 61 and 42 kg of N and P, respectively (Cole and Rapp, 1981). The annual litterfall rate for the fertilized nursery was around 30% that of a mature deciduous forest and deposited around 70% as much as nitrogen.

The right amount of soil O.M. depends upon soil texture, drainage and climatic factors. Generally, it should be 15 to 20 g/kg for sandy soils and 20 to 30 g/kg for heavier soils (May, 1964). Maintenance of 40 g/kg to 50 g/kg organic matter in Oregon nursery soils may be less difficult than maintaining 10 g/kg to 20 g/kg in southern Coastal Plain soils (Pritchett and Fisher, 1987). There is a necessity of O.M. replacement on a regular schedule for hardwood nurseries (Davey, 1984) and in this study may have been fulfilled through litterfall deposition, which may have contributed to maintain O.M. levels at the end of the season. Litterfall was an important source of soil carbon and organic matter, and may have helped retain fertilizer elements from leaching, and buffered the soil against rapid changes in acidity (Pritchett and Fisher, 1987). Without the nitrogen deposited by litterfall, the total nitrogen removed by yellow poplar would be higher than total fertilization.

Seedling Nutrition

All species were grown with similar nursery soil fertility protocols and nitrogen application levels ranging close to the operational fertilization procedures described by Stone (1980) with 280 kg/ha of N. The seedling bed density between 65-85/m^2 (Table 20) was close to the density reported by Kormanick et al. (1997) for oaks but far behind that recommended for yellow poplar by Williams and Hanks (1976), with bed densities of 110 seedlings/m^2. Green ash bed density was slightly above the target of 57 seedling/m^2 reported by Kormanick et al. (1999). The apparent differences between the growth of green ash and the other two species may be related to several factors. There is the potential for an improper seed source, given the unknown origin of most hardwood seed (Bonner, 1987). Relative low P levels in the soil for green ash (24 mg/kg P) may be another reason for the lower growth. Lamar and Davey (1988) described that green ash, isolated from low-P soils (5-7 mg/kg), grown in high fertility (148 mg/kg P) nursery soil with VAM fungi significantly increased seedling height, RCD, and dry matter accumulation. Moreover, phosphorus applied as a fertilizer for green ash was much lower than the other two species and the lower translocation efficiency showed that this species is more dependent on soil nutrients than the other two. Sometimes there are no symptoms of P deficiency besides severe reduction in growth (Edwards, 1985). P levels increased in the soil from May to November for all species, but its availability depends on pH. Acid soil may result in fixation or precipitation of P as insoluble phosphates. Soil pH of 6.0 - 7.0 is preferable for hardwoods regarding P availability (Edwards, 1985). Some authors consider the optimum range for many hardwood seedlings between 5.2 and 6.2 (Pritchett and Fisher, 1987) and the pH of around 5 in this study might be considered low for most hardwoods (Miller, 1999). However, given the adequate levels of available soil nutrients, it is likely that pH did not have much affect on seedling growth.

Average foliar nitrogen concentrations in yellow poplar seedlings and green ash seedlings decreased around 50% from May to late November. The reduction of N applications after July while the seedlings were still growing may have resulted in a "dilution" of N within the plant. Xue (2003) described that from the time of full leaf expansion to the end of the growing season there is a decrease in N and P contents in the leaves of most deciduous tree species. The N translocation efficiency for several species ranged from 43-75% (Xue, 2003), which was slightly higher than the results of this study, whereas their P translocation efficiency ranged from 62-84%, which was close for all species in this study.

Kennedy (1988) found that one year old Nuttall oak and green ash seedlings had N concentrations of 9.5 g/kg for shoots and 14.0 g/kg for roots, similar to the average of 12.0 g/kg found in this study for both species. Average green ash leaf nitrogen concentration levels were similar to Villarrubia (1980), where foliar N varied from 24.0 g/kg to 29.0 g/kg.

This study indicates that hardwood seedlings export a much larger amount of nutrients from the nursery than pine. Typical loblolly pine seedlings export 32 mg N per seedling (South and Boyer, 1985), which at a typical spacing of 200 seedlings/m^2 is 6.4 g/m^2 of bed space. The current study found a nitrogen removal rate of 18, 23, and 9 g N/m^2 for Nuttall oak, yellow poplar, and green ash, respectively. According to Pritchett and Fisher (1987), slash pine seedlings from a Florida nursery, harvested at eight months of age removed 5.3 g N/m^2. This amount is half of that removed from the nursery by green ash seedlings but four times less than yellow poplar. The high variability between hardwood species nutrient requirements was noted by Davey (2005), who stated that generally hardwoods require more nutrient that pine – but not all hardwoods.

Resorption of nitrogen and phosphorous from senesced leaves were not highly proficient in this study according to Killingbeck (1996), which considered resorption in non-fertilized sites as highly proficient in plants when N and P in senescing leaves fell to concentrations below 7.0 g/kg and 0.5 g/kg respectively. In this study, N concentration in the senescing leaves was much higher for all species, especially for green ash, suggesting that resorption may be a function of soil fertility with higher efficiency in infertile sites. Green ash seems to be more dependent on current nutrient uptake from the soil than the other two species. According to Singh (2004), fertilization decreases N and P resorption efficiencies in all tree species.

It is notable that green ash may have a different nutrient use strategy than the other two species of this study. The nutrient translocation efficiency value for green ash fell between both Nuttall oak and yellow poplar, indicating this species utilized considerable amounts of fertilizer elements without the need of higher resorption from the leaves. Whether typical or a result of the growing conditions, the green ash sampled in this study tended to recycle the major fertilizer elements within the seedling. Nuttall oak growth strategies appeared to be based less on internal recycling than on soil uptake. The translocation of nutrients in this study, in effect, combines the ideas that growth potential and nutrient supply determine nutrient translocation (Munson et al., 1995).

Nutrient Use Efficiencies

Nutrient use efficiency values were comparable to the forest and agronomic crop values gathered by Jørgensen and Schelde (2001) (Table 22). The NUE for Nuttall oak, yellow poplar and green ash fell within the typical range for other species grown in fertilized systems. Yellow poplar indicated lower nitrogen use efficiency under the conditions of this study when compared to the other two species.

As the availability of a limiting nutrient increases, the mechanisms used by plants to conserve that nutrient may become less efficient, resulting in lower NUE (Gray and Schlesinger, 1983; Singh et al., 2005). Nutrient use efficiency calculations indicated a higher utilization of the absorbed nitrogen for Nuttall oak, followed by green ash and yellow poplar. The nitrogen concentration for yellow poplar was at normal levels according to Villarrubia (1980). Thus, the higher yellow poplar nitrogen removal efficiency and NUE may indicate the species has been adequately fertilized. The NUE for Nuttall oak was quite high at 75.9%, yet the NRE of 62.8% and a PFP of 53.5, would indicate that perhaps this species is being over-fertilized relative to its nitrogen use efficiency and PFP. Yellow poplar had the highest NRE and smallest NUE. Although the effects of nitrogen fertilization on nitrogen use strategies is not completely understood

(Aerts and Chapin, 2000), over fertilization may result in an increase in the growth of the aboveground plant components relative to belowground.

Table 22. Nutrient use efficiencies for nitrogen of some forest trees and conventional agricultural crops (Calculated for the aboveground material at harvest).

	NUE	Source
Poplar (*Populus*)	143-1000	(Jug et al., 1999)
Pine (*Pinus*) 100y	129	(Lodhiyal and Lodhiyal, 1997)
Wheat (*Triticum*) whole crop	83-87	(Jorgensen, 2000)
Potatoes *(spp)*	73	(Beale and Long, 1997)
Ryegrass (*Lolium*)	63	(Beale and Long, 1997)
Maize (*Zea*)	66-111	(Beale and Long, 1997)
Reed Canary grass (*Phalaris*)	43-78	(Geber, 2000)

NUE = Dry matter production/nitrogen content (g/g)
Source: adapted from Jørgensen and Schelde (2001)

Implications for Nursery Management

The results of this study indicate the high degree of complexity required of hardwood seedling nutrition management. Hardwood species evolved under highly variable environment and edaphic conditions. Nursery production systems may or may not optimally address the needs of each species (or genera). This study found apparent differences between species regarding fertilizer use efficiencies as well as strong indications that the timing and amounts of fertilizers applications may need to vary by species. How these nutritional characteristics may interact with other nursery cultural practices such as seed source, sowing date, mulching, top-pruning, and undercutting, needs to be further evaluated.

CONCLUSIONS

Yellow poplar, Nuttall oak and green ash cultivation resulted in small shifts in soil nutrient levels from May to November. However, there were no changes in nitrogen, soil carbon and organic matter content, probably as a result of mulch and leaf litterfall which appeared to be very important in the maintenance of soil organic matter. In spite of similar fertilization, some foliar nutrient concentrations averaged across the nursery growing season varied by species.

Resorption of nitrogen and phosphorous from senesced leaves was not highly efficient for all three species. Yellow poplar had higher resorption efficiency values for nitrogen and phosphorous when compared to both green ash and Nuttall oak. On the other hand, yellow poplar had much lower translocation efficiencies when compared to the other two species, while green ash showed very high TE values. It's notable that green ash may have a different use strategy than the other two species, indicating this species inefficiently removed nitrogen from the soil but efficiently utilized absorbed fertilizer nitrogen; however, green ash seems to be the least efficient at withdrawing nutrients from senescent leaves before abscission.

Yellow poplar showed the greatest level of nutrient export, primarily a function of its large size. Nuttall oak was second in the amount of nutrients exported and green ash third. Significant amounts of fertilizer elements were removed by harvesting. Nitrogen and phosphorous balance (applied minus removed) was positive for all three species. Yellow poplar had lowest amount of N left in the soil after harvesting, however, the species had highest PFP and NRE.

Most Nuttall oak growth occurs in the fall, and fertilizer applications during this period may improve its productivity. Green ash removed less nitrogen, and had relatively high nitrogen use efficiency, but produced less biomass.

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APPENDIX

Table A. Average aboveground nutrient concentrations of Nuttall oak seedling components grown at the Tennessee Division of Forestry Nursery.

	N	C	Ca	K	Mg	P	Al	B	Cu	Fe	Mn	Na	Zn
	g/kg						mg/kg						
Leaves													
May	1.90	43.99	0.83	1.18	0.23	0.16	530.40	27.51	31.61	409.71	457.49	320.86	29.86
July	1.80	44.48	0.66	0.75	0.18	0.12	458.20	25.54	15.03	236.27	244.98	169.08	56.99
Sept	1.98	45.40	0.56	0.78	0.16	0.16	283.81	17.30	15.16	202.58	393.17	200.83	50.46
Nov	1.81	45.82	0.69	0.64	0.12	0.15	395.77	21.51	19.06	280.10	351.55	186.00	78.40
FOB[1]													
May[2]	1.04	42.21	0.71	1.17	0.17	0.13	211.80	16.61	19.00	162.54	161.66	300.32	14.92
July	1.16	44.13	0.55	1.03	0.14	0.11	94.11	16.79	14.13	104.74	162.73	199.53	45.56
Sept	0.81	44.32	0.58	0.77	0.09	0.10	165.69	14.89	18.43	120.78	353.46	191.57	25.72
Nov	1.21	43.35	0.29	0.89	0.15	0.14	1,492.73	24.43	20.93	724.02	162.40	291.71	26.81
Stem													
May[2]	1.04	42.21	0.71	1.17	0.17	0.13	211.80	16.61	19.00	162.54	161.66	300.32	14.92
July	0.66	44.19	0.79	0.65	0.10	0.06	95.72	12.17	16.53	103.98	135.15	193.33	26.54
Sept	0.90	43.96	0.79	0.77	0.09	0.11	119.82	12.78	14.59	87.93	299.54	225.95	18.69
Nov	0.90	44.19	0.74	0.44	0.09	0.10	66.34	10.85	11.86	64.98	292.13	185.69	25.71

[1] First order branches
[2] First order branches and stem combined

Table B. Average belowground nutrient concentrations of Nuttall oak seedling components grown at the Tennessee Division of Forestry Nursery.

	N	C	Ca	K	Mg	P	Al	B	Cu	Fe	Mn	Na	Zn
	g/kg						mg/kg						
FOLR[1]													
May	–	–	–	–	–	–	–	–	–	–	–	–	–
July	0.97	44.10	0.36	0.60	0.11	0.07	2,795.04	22.26	38.05	1,423.62	157.31	313.63	43.62
Sept	1.18	43.01	0.29	0.67	0.12	0.11	2,380.66	15.54	27.76	1,170.22	172.33	332.76	40.03
Nov	1.04	44.91	0.71	0.56	0.09	0.11	82.41	15.53	14.17	59.67	111.62	184.64	26.46
Taproot													
May	1.08	40.76	0.26	0.83	0.11	0.15	2,722.65	15.58	187.55	1,739.21	126.90	342.73	34.28
July	1.00	42.87	0.45	0.66	0.10	0.11	1,712.85	11.67	23.38	1,108.88	115.11	300.67	26.63
Sept	0.96	43.07	0.61	0.81	0.12	0.12	872.74	11.08	13.93	440.71	158.16	412.63	13.44
Nov	1.22	41.85	0.39	0.87	0.11	0.16	296.41	10.61	13.69	170.34	126.33	243.49	13.19

[1] First order lateral roots

Table C. Average aboveground nutrient concentrations of yellow poplar seedling components grown at the Tennessee Division of Forestry Nursery.

	N	C	Ca	K	Mg	P	Al	B	Cu	Fe	Mn	Na	Zn
	g/kg						*mg/kg*						
Leaves													
May	3.36	42.31	0.82	2.18	0.44	0.34	1,733.08	30.42	25.28	1,181.41	226.31	569.18	32.36
July	3.06	43.46	1.15	1.42	0.33	0.25	456.78	22.63	23.32	343.61	238.75	222.08	33.93
Sept	2.91	42.61	1.42	1.20	0.34	0.21	259.82	14.60	18.92	187.30	302.69	252.94	13.63
Nov	–	–	–	–	–	–	–	–	–	–	–	–	–
FOB[1]													
May	–	–	–	–	–	–	–	–	–	–	–	–	–
July	1.05	43.05	0.49	1.54	0.18	0.17	141.47	18.96	16.05	137.19	99.34	226.83	22.61
Sept	0.75	42.55	0.57	1.25	0.14	0.12	88.94	13.69	15.78	64.35	150.63	316.85	9.21
Nov	1.36	44.85	0.60	0.65	0.17	0.08	112.17	15.65	12.56	83.64	151.13	207.44	6.98
Stem													
May[2]	2.48	33.83	0.64	3.17	0.51	0.58	6,775.65	29.42	50.44	4,748.76	346.29	986.38	68.63
July	1.47	42.90	0.49	1.39	0.20	0.19	194.05	14.95	17.13	172.34	74.35	229.77	33.88
Sept	0.72	43.31	0.49	0.91	0.11	0.11	86.79	11.88	13.91	46.41	85.93	237.12	7.39
Nov	1.09	44.57	0.49	0.50	0.13	0.09	106.73	11.98	16.66	77.94	131.30	204.13	9.54

[1] First order branches
[2] Stem and taproot combined

Table D. Average belowground nutrient concentrations of yellow poplar seedling components grown at the Tennessee Division of Forestry Nursery.

	N	C	Ca	K	Mg	P	Al	B	Cu	Fe	Mn	Na	Zn
	g/kg						mg/kg						
FOLR[1]													
May	–	–	–	–	–	–	–	–	–	–	–	–	–
July	1.62	42.97	0.44	1.62	0.31	0.28	3,800.00	18.00	112.24	2,528.76	175.66	424.78	60.63
Sept	1.21	42.04	0.48	1.39	0.29	0.15	1,761.43	12.47	43.50	1,089.73	133.89	499.67	27.66
Nov	1.76	40.60	0.38	1.47	0.23	0.11	1,335.13	11.27	28.65	794.00	97.80	278.33	17.98
Taproot													
May[2]	2.48	33.83	0.64	3.17	0.51	0.58	6,775.65	29.42	50.44	4,748.76	346.29	986.38	68.63
July	1.12	42.35	0.38	1.20	0.24	0.19	2,301.00	13.17	50.06	1,589.78	123.30	365.78	34.44
Sept	1.15	42.06	0.54	1.21	0.27	0.15	1,091.10	12.24	28.37	727.66	98.03	442.33	17.02
Nov	1.53	42.45	0.35	0.81	0.17	0.11	339.81	6.89	14.50	246.93	54.05	184.28	12.95

[1] First order lateral roots
[2] Stem and taproot combined

Table E. Average aboveground nutrient concentrations of green ash seedling components grown at the Tennessee Division of Forestry Nursery

	N	C	Ca	K	Mg	P	Al	B	Cu	Fe	Mn	Na	Zn
	g/kg						mg/kg						
Leaves													
May	2.87	44.09	0.63	2.17	0.24	0.21	1,209.25	24.09	24.7	835.77	127.19	254.77	20.72
July	2.88	43.24	0.6	1.59	0.19	0.24	221.87	24.47	29.13	261.54	174.04	217.17	26.79
Sept	2.32	45.86	0.59	1.12	0.18	0.17	145.36	18.29	19.06	214.93	127.88	148.47	16.8
Nov	–	–	–	–	–	–	–	–	–	–	–	–	–
FOB[1]													
May	–	–	–	–	–	–	–	–	–	–	–	–	–
July	1.43	42.88	0.53	1.71	0.16	0.16	146.24	20.62	23.89	167.66	115.99	196.79	33.67
Sept	0.78	40.43	0.64	1.12	0.16	0.1	3,567.19	36.5	100.16	10,294.96	172.74	213.96	279.43
Nov	1.13	43.51	0.48	0.97	0.15	0.17	416.87	15.29	25.28	368.64	132.61	179.21	19.3
Stem													
May[2]	1.7	38.75	0.5	2.94	0.24	0.17	3,150.40	23.25	33.34	1,944.55	228.02	670.87	37.12
July	0.95	43.42	0.34	0.9	0.13	0.14	66.81	8.06	20.85	83.11	77.41	267.69	31.65
Sept	0.73	42.78	0.45	0.64	0.12	0.1	20.13	10.02	20.98	75.65	56.93	188.64	16.57
Nov	0.95	44.61	0.55	0.62	0.12	0.15	74.72	13.74	23.58	91.13	75.64	197.81	8.76

[1] First order branches
[2] Stem and taproot combined

Table F. Average belowground nutrient concentrations of green ash seedling components grown at the Tennessee Division of Forestry Nursery.

	N	C	Ca	K	Mg	P	Al	B	Cu	Fe	Mn	Na	Zn
	g/kg						mg/kg						
FOLR[1]													
May	–	–	–	–	–	–	–	–	–	–	–	–	–
July	1.43	42.44	0.25	1.14	0.17	0.16	3,235.10	19.82	49.02	2,573.42	398.92	382.77	38.83
Sept	0.99	41.92	0.31	0.98	0.18	0.16	2,186.49	15.75	39.93	2,254.18	303.41	429.97	23.49
Nov	1.05	43.32	0.27	1.34	0.14	0.17	1,278.16	15.34	37.85	1,348.86	201.71	301.47	19.48
Taproot													
May[2]	1.7	38.75	0.5	2.94	0.24	0.17	3,150.40	23.25	33.34	1,944.55	228.02	670.87	37.12
July	1.18	41.84	0.26	0.93	0.15	0.15	2,416.09	16.97	40.29	2,131.10	377.94	328.89	26.91
Sept	0.73	41.99	0.27	0.67	0.12	0.13	926.04	11.14	27.52	1,123.88	165.95	311.81	17.49
Nov	0.91	42.86	0.36	0.67	0.12	0.19	503.39	11.68	30.14	554.83	186.63	200.28	11.63

[1] First order lateral roots
[2] Stem and taproot combined