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Nutrient use and uptake in *Pinus taeda*†

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Summary We quantified nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) content, use (nutrient amount for one growth year), retranslocation (nutrients recycled before foliage senescence), uptake (use minus retranslocation), volume production per unit of uptake and fertilizer-uptake efficiency (percent applied taken up) in a 2 × 2 (nutrient and water) factorial experiment replicated four times in an 8-year-old loblolly pine (*Pinus taeda* L.) stand growing on a nutrient-poor sandy soil in Scotland County, North Carolina, USA. Over 14 years, we applied 1140, 168, 393, 168 and 146 kg ha^{-1} of elemental N, P, K, Ca and Mg fertilizer, respectively, and an average of 710 mm year^{-1} of irrigation. All plots received complete vegetation control. Fertilization about doubled tissue N, P, K and Mg contents at age 21, whereas irrigation resulted in smaller increases in nutrient contents. Maximum annual uptake was 101, 9.3, 44, 37 and 13 kg ha^{-1} year^{-1} and volume production per unit of nutrient uptake was 0.35, 3.5, 0.66, 1.1 and 3.1 m^3 kg^{-1}, for N, P, K, Ca and Mg, respectively. Irrigated plots had greater volume production per unit of N, P, K and Mg uptake than control plots, likely because irrigation allowed photosynthesis to continue during dry periods. Fertilized plus irrigated plots had less volume production per unit of these elements than the fertilized plots either because nutrient uptake exceeded the requirement for optimum growth or because available water (rainfall plus irrigation) was insufficient for the leaf area achieved with fertilization. At age 19, fertilizer-uptake efficiencies for N, P, K, Ca and Mg were 53, 24, 62, 57 and 39%, respectively, and increased with irrigation to 68, 36, 78, 116 and 55%, respectively. The scale of fertilizer uptake was likely a result of low native site nutrient availability, study longevity, measurement of all tissue components on site, a comprehensive assessment of coarse roots, and the 3-m rooting depth. Ecosystem nitrogen retention (applied nitrogen found in living plant material, litter fall and soil to 150-cm depth) was estimated at 79% at age 17, a value that would likely be greater when including soil nitrogen to rooting depth and calculating retention at age 21 when the study ended. The ecosystem retention value provides evidence that intensive site resource management can be accomplished with low likelihood of applied materials moving offsite.

Keywords: fertilizer efficiency, leaf area index, volume production.

Introduction

The application of nutrients thought to limit loblolly pine (*Pinus taeda* L.) growth in the southeast United States is increasingly common (Albaugh et al. 2007). The increase in application of limiting nutrients is based on research that has elucidated the mechanism of response (nutrients typically limit foliage development (Vose and Allen 1988, Albaugh et al. 1998)), quantified the long-term biological response to these additional nutrients (Albaugh et al. 2004, Borders et al. 2004, Hennessey et al. 2004, Samuelson et al. 2004) and provided economic information relative to nutrient application in an operational setting (Borders and Bailey 2001, Fox et al. 2007). Consequently, recommendations on the amount of limiting nutrients to apply are based on amounts that have demonstrated biological and economic responses; however, these amounts may exceed tree uptake. The next research objective is thus to quantify the nutrients taken up by trees to produce a given amount of wood.

Many reports of nutrient content, use or uptake are limited to examinations of young stands observed over short periods (Bekele et al. 2003, Hangs et al. 2003, Adegbidi et al. 2005, Dumroese et al. 2005, Blazier et al. 2006). However, short-term studies on young trees may be inappropriate for determining nutrient uptake of a stand over time because young trees may not achieve growth and uptake rates comparable with those of more mature stands (Bekele et al. 2003). Also, some elements may not be limiting early in the rotation but may become limiting in the long term (Fox et al. 2007). For example, calcium was not identified as a limiting nutrient at age 21 but was found important at age 33 in determining growth responses to nitrogen and phosphorus applications (Kyle et al. 2005).

Previous studies on mature loblolly pine stands in this area are limited to short-term assessments (1–2 years) (Switzer et al. 1966, Wells and Jorgensen 1975, Piatek and Allen 2000,

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Will et al. 2006). Wells and Jorgensen (1975) estimated nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) use for one stand, but completed their assessment before mid-rotation fertilization was broadly practiced and consequently did not include application of limiting nutrients. Piatek and Allen (2000) reported only N and P use in the foliage in their two-year study of fertilized and unfertilized stands. Will et al. (2006) examined two stands, one of which had been fertilized annually with N for 13 years; however, their study was also limited to N and P assessments. The two studies (Wells and Jorgensen 1975, Will et al. 2006) reporting belowground estimates are limited because they were based on data from the literature rather than measurement of study site trees. None of these studies on mature loblolly pine stands related nutrient use or uptake estimates to the amount of wood produced.

In the study by Will et al. (2006), the fertilized stand received applications of N, P and K in the first two years followed by the annual addition of N and one P application in year ten. This regime successfully created large treatment differences but it may not be optimal for estimating maximum nutrient use and uptake, which set the upper limit on system potential. Whenever one nutrient limitation is met, the next most limiting nutrient needs to be supplemented to maintain optimum growth (Marschner 1986, Fox et al. 2007). For example, the application of N and P alone had little effect on growth in young and mid-rotation loblolly pine stands because other elements were limiting (Hynynen et al. 1998, Bekele et al. 2003). Additionally, nutrient limitations develop with time (Kyle et al. 2005). Consequently, monitoring the response to the application of a suite of potentially limiting nutrients is required to assess potential uptake.

Besides enhancing our understanding of the system, quantifying nutrient content, use and uptake has practical application for forest managers. Fertilizer applications in excess of what is required to produce a given amount of wood reduce economic benefit and may lead to offsite nutrient movement (Ducey and Allen 2001). Our objectives were to quantify content, use, uptake and volume growth per unit of uptake for nutrients likely to limit loblolly pine growth (N, P, K, Ca and Mg) under different regimes of nutrient and water availability. Additionally, we examined changes in fertilizer-uptake efficiency over time.

Materials and methods

Study site

The study was established in Scotland County, North Carolina, USA (35° N, 79° W) on a flat, infertile, well-drained, sandy, siliceous, thermic Psammentic Hapludult soil (Wakulla series) (Albaugh et al. 1998). Sixteen 50 × 50 m (0.25 ha) treatment plots with 30 × 30 m measurement plots centered in the treatment plot were installed in January 1992 in an 8-year-old loblolly pine stand. Treatments were a 2 × 2 factorial combination of nutrition and water additions replicated four times. The nutrition treatments, which began in March 1992, were (1) optimum nutrition or (2) no addition. Optimum nutrition was defined as maintaining an N concentration of 1.3% in upper-canopy foliage of co-dominant and dominant trees with other nutrients (P, K, Ca and Mg) balanced with N. Also, foliar boron (B) concentrations were maintained at greater than 12 mg kg^{-1}. Foliar nutrient status was monitored and fertilizer was applied annually to meet the stated target (Table 1). Materials applied included urea, boron-coated urea, ammonium sulfate, diammonium phosphate, triple super phosphate, potassium chloride, dolomitic lime, Epsom salts, calcium sulfate and borax. Water treatments, which began in April 1993, were (1) natural precipitation and (2) natural precipitation plus irriga-

Table 1. Nutrient applications (kg elemental nutrient ha^{-1} $year^{-1}$), and precipitation and irrigation (mm $year^{-1}$) during the study. Precipitation and irrigation reported in the summer season (March 1 to October 31). Winter precipitation was from the end of the previous-year summer season to the beginning of the current-year summer season. No irrigation in 1992.

Year	Age (years)	Nutrient applications							Precipitation		Irrigation Summer
		N	P	K	Ca	Mg	S	B	Winter	Summer	
1992	8	224	56	112	134	56	0	2	236	872	0
1993	9	82	50	113	0	56	120	0	443	735	668
1994	10	112	0	0	0	0	0	0	324	723	167
1995	11	0	28	56	24	34	74	1	496	958	601
1996	12	112	11	56	10	0	15	1	247	922	447
1997	13	134	0	0	0	0	0	0	400	758	571
1998	14	56	6	0	0	0	0	0	496	989	1126
1999	15	56	0	0	0	0	0	0	369	987	2143
2000	16	56	6	0	0	0	0	1	380	813	505
2001	17	56	6	0	0	0	0	1	235	580	638
2002	18	56	6	56	0	0	0	1	196	593	501
2003	19	56	0	0	0	0	0	0	323	957	476
2004	20	56	0	0	0	0	64	0	235	626	687
2005	21	84	0	0	0	0	0	1	253	980	700
Total		1140	168	393	168	146	273	6			

tion providing about 650 mm year^{-1} during the growing season (March 1 to October 31) (Table 1). Competing vegetation in all treatment plots was eliminated by a combination of mechanical and chemical (glyphosate) methods.

Stand measurements

From 1991 to 2005, annual winter (December) measurements of height (H), diameter at breast height (1.4 m) (D), height to live crown and assessments of mortality were made on all trees (~100 trees per plot) in each measurement plot. Stem volume (total outside bark (V)) was estimated as: $V = 0.00748 + (0.0000353D^2H)$ (Shelton et al. 1984), where units for volume, diameter at breast height and height were m^3 tree^{-1}, cm and m, respectively. Stem volume and basal area were calculated for each live tree, summed to the plot level and scaled to the hectare level. Volume growth was the difference between stem volume at the end and at the beginning of the selected time period. Live crown length was the difference between height and height to live crown.

Nutrient content

Stand-scale estimates of N, P, K, Ca and Mg contents for branch, foliage, stem, coarse roots (≥ 2 mm diameter) and fine roots (< 2 mm diameter) were derived from destructive aboveground sampling (in 1992, 1994, 1996, 1998 and 2003), root excavations (in 1994, 1996, 1998 and 2003) and soil coring (annually 1992 to 1996). Stand-scale branch, foliage, stem, coarse root and fine root biomass estimates from the destructive harvests have been reported previously (Albaugh et al. 1998, 2004). In general, individual tree component dry mass and nutrient concentrations were determined. Tree component nutrient content was the product of dry mass and nutrient concentration. When nutrient concentration was not measured for a given component × year combination, the treatment mean from the same component from available sample years was substituted for the missing nutrient concentration. Regression equations were derived to predict component nutrient content from tree measurements. Individual tree estimates of nutrient content were summed within a plot and then scaled to an area basis. Sixty-eight trees were sampled for aboveground components (one from each of the sixteen plots in each year in 1992, 1994, 1996, 1998 and four in 2003). Except for 2003 when only large trees were selected, sampled trees represented the range in height and diameter at the time of sampling. Coarse roots were excavated in the square meter surrounding 43 of the sampled trees and in 48 additional meter square pits in the area between trees. All samples were dried at 65 °C to constant mass. Samples for nutrient concentrations were ground and analyzed for nitrogen with a CHN analyzer and a nitric acid digest analyzed by inductively coupled plasma spectrometry for other elements.

Branch wood and foliage nutrient contents were determined on 387 branches selected to represent the range in branch size and crown position found on the destructively harvested trees. Branch-level regressions were developed to predict branch wood and foliage nutrient contents based on treatment, branch basal diameter and distance from the top of the tree. The branch-scale regressions were applied to each branch on the 68 destructively harvested trees and to each branch on an additional 80 trees nondestructively measured every year from 1991 to 2003. Individual tree branch-wood and foliage nutrient contents were the sum of the individual branch-wood and foliage nutrient contents either measured or estimated from the branch-scale regressions. Tree-scale regression equations with treatment and live crown length as independent variables were developed and applied to the annual stand measurements to estimate plot-scale branch-wood and foliage nutrient contents.

Stem nutrient contents were determined from the 68 harvested stems. Total stem dry mass was measured. Nutrient concentrations for each stem were the mean nutrient concentrations derived from two stem cross-sectional disks about 10 cm in length. One disk was from breast height and the second was from half way between the first disk and the base of the current-year growth. For the 1992 samples, nutrient concentrations for each harvested tree were determined from a composite of the stem disks that included all bark and stem wood material. In 1994, 1996 and 2003, nutrient concentrations and dry mass were determined for bark and wood portions of the sample disks. No significant differences between years were found, so treatment mean nutrient concentrations averaged across years for 1994, 1996 and 2003 were used for the 1998 samples. Stem nutrient contents were the sum of the products of the nutrient concentrations and dry masses of the bark and stem wood components. Tree-scale regression equations with treatment, diameter at breast height and height as independent variables were developed and applied to the annual stand measurements to estimate plot-scale stem nutrient contents.

Coarse root nutrient contents were determined from 43 (7 in 1994, 16 in 1996 and 1998, 4 in 2003) of the harvested trees. For these trees, the entire taproot and all coarse roots in a square meter centered on the tree to a depth of 50 cm were excavated and dry mass was determined. Nutrient concentrations for the taproot were available from the 1998 harvest when five 1-cm-long disks equally spaced along the length of the taproot were combined for nutrient concentration determination. Treatment means from the 1998 samples were applied to the taproot samples from other years. Coarse root nutrient concentrations were available from the 1996 harvest and treatment means from these data were applied to samples from the other years. Additional meter square coarse root excavations were completed in the area between trees in 1996 (16 pits to 50 cm) and 2003 (24 pits to 90 cm, 8 pits to 290 cm). Coarse roots from the 2003 excavations were combined for nutrient concentration analysis, and treatment nutrient concentration means from 2003 were applied to the 1996 samples when calculating nutrient content. Coarse root nutrient contents in the meter square excavations were the product of the nutrient concentration and the dry mass from the excavations completed in 1996 and 2003 and scaled to a depth of 290 cm (Albaugh et al. 2006). Plot-scale regression equations with treatment and plot basal area as independent variables were developed and applied to the annual stand measurements to estimate coarse root

nutrient contents between the trees. Overall coarse root nutrient contents were the sum of the nutrient contents for tap root and coarse root in the square meter at the tree base, and coarse root in the area between trees scaled to an area basis.

Fine root nutrient contents were determined from soil cores collected in each plot at year end from 1992 to 1995. Fine roots were removed, and dry mass and nutrient concentrations determined from the twenty 6.6-cm diameter by 10-cm deep cores collected in 1992, 1993 and 1994 (Mignano 1995) and from the four 15-cm diameter by 15-cm deep cores collected in 1995 and 1996. Fine root nutrient contents were the product of the nutrient concentrations (Crook 1995) and the dry mass of the fine root component. These results were scaled to a 50-cm depth based on a root distribution study of Mignano (1995) and then scaled to an area basis. No pretreatment (year end 1991) fine root assessments were completed. We assumed the nutrient pretreatment pool sizes were the same as those found at year end 1992. The block plot estimates from 1996 were carried forward for all remaining years in this analysis (1997 to 2005) because Mignano's (1995) study indicated that the fine root component would be relatively constant and small (compared with other plant components) through time.

Nutrient use

Annual nutrient use was defined as the nutrients measured in one year of tree growth. Perennial tissue (stem and coarse root) nutrient use was the difference between current-year and previous-year nutrient content. Foliar nutrient use was the same as content for a given year because loblolly pine produces a new foliage cohort and drops the previous-year cohort each year (Kinerson et al. 1974). Fine root nutrient use was estimated as the product of the annual fine root production (Albaugh et al. 1998) and the corresponding nutrient concentrations (Crook 1995). Branch nutrient use was estimated from a separate tree-scale regression equation that included only newly produced material and the appropriate nutrient concentration. This branch use estimate was not net of the total branch nutrient content because it did not incorporate branches that may have died during the year. Use of net branch nutrient content was inappropriate because it included losses from previous-year branch mortality that were not part of the nutrients used in the current growth year.

Retranslocation

Retranslocated nutrients are nutrients that were moved out of senescing foliage and back into the plant before the foliage abscised. In 1992, 1993 and 1994, green foliage was collected monthly; and once in the fall, dead brown but still attached foliage was collected from five trees in each plot. The samples were combined for each plot and nutrient analyses were completed. Percent retranslocation was the quotient of dead brown foliage nutrient concentration and the maximum monthly green foliage concentration for each plot. For years where no dead foliage was collected, treatment means of the 1992, 1993 and 1994 estimates averaged across years were used (Table 2). Nutrient retranslocation content was the product of percent retranslocation and the foliar nutrient content for that year. No evidence of retranslocation was found for fine roots (Crook 1995).

Table 2. Mean percent retranslocation (± standard deviation) of nutrients before foliage senescense.

Treatment	N	P	K	Ca	Mg
Control	64 ± 9	68 ± 9	84 ± 10	7 ± 10	19 ± 13
Irrigated	66 ± 10	68 ± 9	86 ± 7	5 ± 7	16 ± 10
Fertilized	67 ± 14	73 ± 9	77 ± 14	9 ± 16	24 ± 17
Fert+irri[1]	71 ± 2	73 ± 8	79 ± 15	14 ± 20	28 ± 18

[1] Fert+irri = fertilized plus irrigated.

Nutrient uptake

Annual nutrient uptake was defined as the portion of total annual nutrient use originating external to the tree and was calculated as nutrient use minus retranslocation. Nutrient uptake attributable to treatment (irrigated, fertilizated and fertilized plus irrigated) was calculated as nutrient uptake in the treated plot minus nutrient uptake in the control plots. Nutrient uptake with irrigation was calculated as nutrient uptake in the fertilized plus irrigated plot minus nutrient uptake in the irrigated plots. Stem volume increment per unit nutrient uptake was the quotient of volume increment and nutrient uptake for each year for N, P, K, Ca and Mg.

Uptake efficiency

Fertilizer-uptake efficiency was the proportion of applied nutrients that was taken up by the plant. It was calculated as the quotient of nutrient uptake plus litter fall nutrient content and the applied nutrient amount at a given time for the fertilized treatments. This calculation was made for the fertilized and fertilized plus irrigated plots relative to the control plots and for the fertilized plus irrigated plots relative to the irrigated plots. For the irrigated treatment where no nutrients were added, the denominator was the control treatment uptake. Litter fall was included in this calculation because all the nutrients in the litter had passed through the plant and other research has shown that nutrients remain in the litter fall until the stand is harvested (Piatek and Allen 2001). Litter fall was collected monthly from 1992 to 2003 (ages 8 to 19) from eight meter square traps in each plot. Samples were dried at 65 °C to constant mass, summed for the year, scaled to an area basis and nutrient concentrations determined on a composite sample for each year by the same methods described for the other tissue types. Litter fall content was the product of litter mass and litter nutrient concentration.

Ecosystem retention of added nutrients included an estimate of soil nutrient content in the calculation, where ecosystem retention was nutrient uptake plus litter fall plus soil nutrient content in the fertilized plots relative to the control. This estimate was available only for N at age 17 and was based on soil assessments from the study of Lee (2002).

Statistical analyses

Regression analysis was used to develop the predictive equations for component (branch, foliage, stem, coarse root and fine root) nutrient (N, P, K, Ca and Mg) content and use. When residuals analysis indicated heterogeneous variance, data were log transformed. In these cases the Baskerville (1972) adjustment was applied when converting back to nominal scale. Standard deviations were reported when presenting data distribution (nutrient concentrations) and standard errors were reported when comparing treatment means (nutrient content and use by component, basal area, total content, use and uptake). Comparisons over time were analyzed as repeated measures using mixed models with an autoregressive structure (Littell et al. 1998) for volume increment per unit of nutrient uptake. Linear regression was used to quantify the relationship between volume increment and nutrient uptake. The relationship examined was in the form of: Dependent variable = Nutrient uptake, where the dependent variable was stem volume increment (m^{-3} ha^{-1} $year^{-1}$) and nutrient uptake was either N, P, K, Ca and Mg uptake (kg of nutrient ha^{-1} $year^{-1}$). All statistical tests were evaluated with alpha equal to 0.05.

Results

In 1991, before the start of the treatments, basal area was 2.2 m^2 ha^{-1}. By the end of the study in 2005, basal area on the control plots had increased about tenfold to 23.4 m^2 ha^{-1} (Figure 1A). In 2005, the applied treatments resulted in 16, 68 and 75% increases in basal area over the control for the irrigated, fertilized and fertilized plus irrigated plots, respectively. Annual volume increment increased 110 and 250% in the non-fertilized and fertilized plots, respectively, during the first 4 years of the study (through age 11) (Figure 1B). Since that time, volume increment in the non-fertilized and fertilized plots averaged 11.7 and 24.2 m^3 ha^{-1} $year^{-1}$, respectively. For a given fertilization regime, the irrigated plots typically had greater annual volume increments than the corresponding non-irrigated plots. Little mortality was observed in any treatment plots during the study.

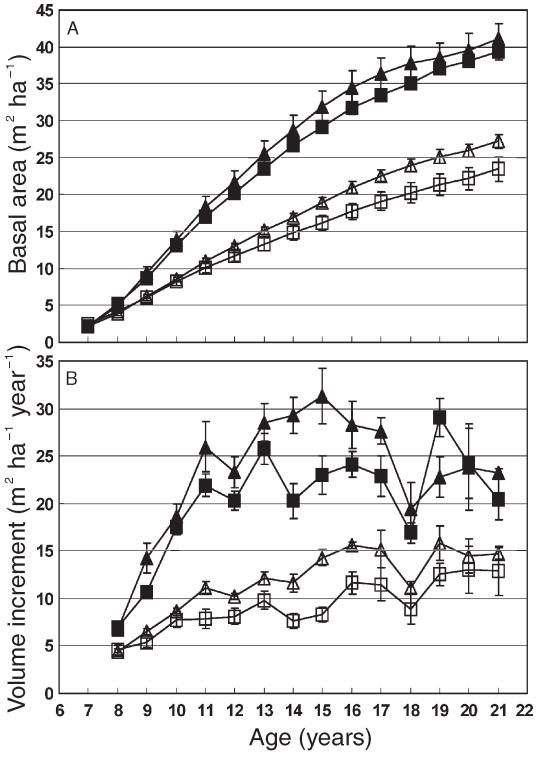

Figure 1. Basal area (A) and volume increment (B) for control (□), irrigated (△), fertilized (■) and fertilized plus irrigated (▲) plots from age 8 to 21 (1992 to 2005). Error bars represent one standard error.

Tissue nutrient concentration

Tissue nutrient concentrations were highest in the foliage for N, P, K and Mg (Tables 3 and 4). Calcium concentrations were typically highest in the branch and coarse roots at some distance from the tree base. When examining only belowground components, fine roots had the highest N and P concentrations. Fine roots also had relatively high K, Ca and Mg concentrations, and coarse roots at a distance from the tree base had similar concentrations of these elements. For all tissues, N concentrations typically increased with fertilization; however, there was an overlap across treatments in the distribution of nitrogen concentrations at one standard deviation for a given tissue. Phosphorus and Mg concentrations were similar among treatments for a given tissue. Calcium concentrations were typically higher in the control and irrigated treatments for most tissues when compared with the fertilized and fertilized plus irrigated treatments, although there was still overlap in the concentrations between treatments at one standard deviation. Potassium concentrations were higher in the plots receiving fertilizer for all tissue types, and for foliage and taproot there was no overlap in the data at one standard deviation. Litter fall N concentrations were higher in the fertilized plots and there was separation of the fertilized and non-fertilized treatments at one standard deviation. Litter fall mean concentrations for P, K and Mg were typically higher in fertilized plots than in non-fertilized plots with overlap in the distributions. Calcium litter fall concentrations in the non-fertilized treatments had higher mean concentrations than in the fertilized treatments.

Nutrient content

Total stand N, P, K and Mg contents followed similar patterns of development through time during the study where, by age 21, the nutrient content of the fertilized plot was about double that of the non-fertilized plot for a given irrigation regime and the difference in nutrient contents between the fertilized and non-fertilized plots continued to increase over time (Figures 2A, 3A, 4A and 5A). For Ca, the irrigated plots achieved similar contents as the fertilized plots (Figure 6A) by age 21. Treatment differences in stand nutrient contents were a function of both mass- and nutrient-concentration-related changes in all elements except the change in Mg concentration which was

Table 3. Mean nutrient concentrations (%; ± standard deviation) for aboveground plant components used to estimate plant-level nutrient content.

Treatment	N	P	K	Ca	Mg
Branch					
Control	0.38 ± 0.069	0.05 ± 0.012	0.18 ± 0.051	0.21 ± 0.035	0.06 ± 0.007
Irrigated	0.35 ± 0.031	0.04 ± 0.008	0.18 ± 0.040	0.22 ± 0.053	0.05 ± 0.007
Fertilized	0.44 ± 0.080	0.06 ± 0.015	0.24 ± 0.051	0.16 ± 0.030	0.07 ± 0.007
Fert+irri[1]	0.47 ± 0.090	0.07 ± 0.021	0.29 ± 0.115	0.16 ± 0.042	0.06 ± 0.015
Foliage					
Control	1.08 ± 0.110	0.11 ± 0.012	0.32 ± 0.033	0.17 ± 0.045	0.09 ± 0.019
Irrigated	1.06 ± 0.122	0.09 ± 0.011	0.33 ± 0.036	0.19 ± 0.054	0.09 ± 0.013
Fertilized	1.33 ± 0.179	0.12 ± 0.013	0.49 ± 0.098	0.15 ± 0.024	0.09 ± 0.017
Fert+irri	1.26 ± 0.178	0.12 ± 0.015	0.48 ± 0.058	0.17 ± 0.046	0.10 ± 0.021
Bark					
Control	0.29 ± 0.062	0.03 ± 0.012	0.08 ± 0.038	0.19 ± 0.033	0.04 ± 0.019
Irrigated	0.29 ± 0.046	0.03 ± 0.010	0.07 ± 0.031	0.19 ± 0.059	0.04 ± 0.020
Fertilized	0.36 ± 0.102	0.03 ± 0.016	0.09 ± 0.036	0.10 ± 0.034	0.04 ± 0.020
Fert+irri	0.32 ± 0.055	0.03 ± 0.010	0.07 ± 0.030	0.10 ± 0.026	0.03 ± 0.014
Stem					
Control	0.09 ± 0.013	0.01 ± 0.003	0.08 ± 0.020	0.07 ± 0.010	0.03 ± 0.004
Irrigated	0.10 ± 0.042	0.01 ± 0.005	0.07 ± 0.012	0.08 ± 0.039	0.02 ± 0.008
Fertilized	0.13 ± 0.020	0.01 ± 0.004	0.09 ± 0.017	0.06 ± 0.010	0.03 ± 0.005
Fert+irri	0.12 ± 0.017	0.01 ± 0.003	0.08 ± 0.014	0.06 ± 0.007	0.02 ± 0.004

[1] Fert+irri = fertilized plus irrigated.

Table 4. Mean nutrient concentrations (%; ± standard deviation) for belowground plant components used to estimate plant-level nutrient content and litterfall used to calculate litter nutrient content. Fine root data from Crook (1995).

Treatment	N	P	K	Ca	Mg
Coarse root in square meter at tree base					
Control	0.17 ± 0.037	0.04 ± 0.022	0.19 ± 0.021	0.12 ± 0.019	0.05 ± 0.011
Irrigated	0.19 ± 0.021	0.02 ± 0.005	0.18 ± 0.027	0.12 ± 0.023	0.04 ± 0.012
Fertilized	0.32 ± 0.035	0.03 ± 0.004	0.23 ± 0.027	0.10 ± 0.050	0.05 ± 0.007
Fert+irri[1]	0.25 ± 0.055	0.04 ± 0.011	0.22 ± 0.053	0.09 ± 0.016	0.04 ± 0.013
Taproot					
Control	0.17 ± 0.037	0.02 ± 0.003	0.15 ± 0.061	0.05 ± 0.023	0.01 ± 0.004
Irrigated	0.19 ± 0.021	0.01 ± 0.001	0.18 ± 0.100	0.06 ± 0.004	0.01 ± 0.004
Fertilized	0.32 ± 0.035	0.03 ± 0.003	0.26 ± 0.039	0.05 ± 0.008	0.00 ± 0.003
Fert+irri	0.25 ± 0.055	0.02 ± 0.006	0.26 ± 0.059	0.04 ± 0.011	0.01 ± 0.002
Coarse root not in square meter at tree base					
Control	0.11 ± 0.071	0.03 ± 0.003	0.18 ± 0.015	0.25 ± 0.020	0.06 ± 0.007
Irrigated	0.10 ± 0.047	0.02 ± 0.003	0.14 ± 0.036	0.21 ± 0.037	0.06 ± 0.012
Fertilized	0.27 ± 0.095	0.04 ± 0.008	0.21 ± 0.055	0.20 ± 0.044	0.06 ± 0.016
Fert+irri	0.21 ± 0.057	0.04 ± 0.008	0.19 ± 0.006	0.19 ± 0.038	0.06 ± 0.007
Fine root					
Control	0.67 ± 0.143	0.07 ± 0.013	0.24 ± 0.039	0.16 ± 0.056	0.06 ± 0.009
Irrigated	0.68 ± 0.185	0.07 ± 0.019	0.23 ± 0.057	0.16 ± 0.041	0.06 ± 0.009
Fertilized	0.95 ± 0.243	0.10 ± 0.026	0.34 ± 0.048	0.18 ± 0.043	0.09 ± 0.020
Fert+Irri	0.99 ± 0.257	0.11 ± 0.024	0.33 ± 0.066	0.18 ± 0.049	0.09 ± 0.019
Litterfall					
Control	0.44 ± 0.084	0.03 ± 0.010	0.07 ± 0.030	0.32 ± 0.054	0.08 ± 0.007
Irrigated	0.45 ± 0.084	0.03 ± 0.009	0.07 ± 0.026	0.37 ± 0.066	0.09 ± 0.011
Fertilized	0.59 ± 0.137	0.04 ± 0.013	0.14 ± 0.043	0.28 ± 0.074	0.09 ± 0.015
Fert+irri	0.60 ± 0.139	0.05 ± 0.013	0.13 ± 0.053	0.28 ± 0.060	0.09 ± 0.015

[1] Fert+irri = fertilized plus irrigated.

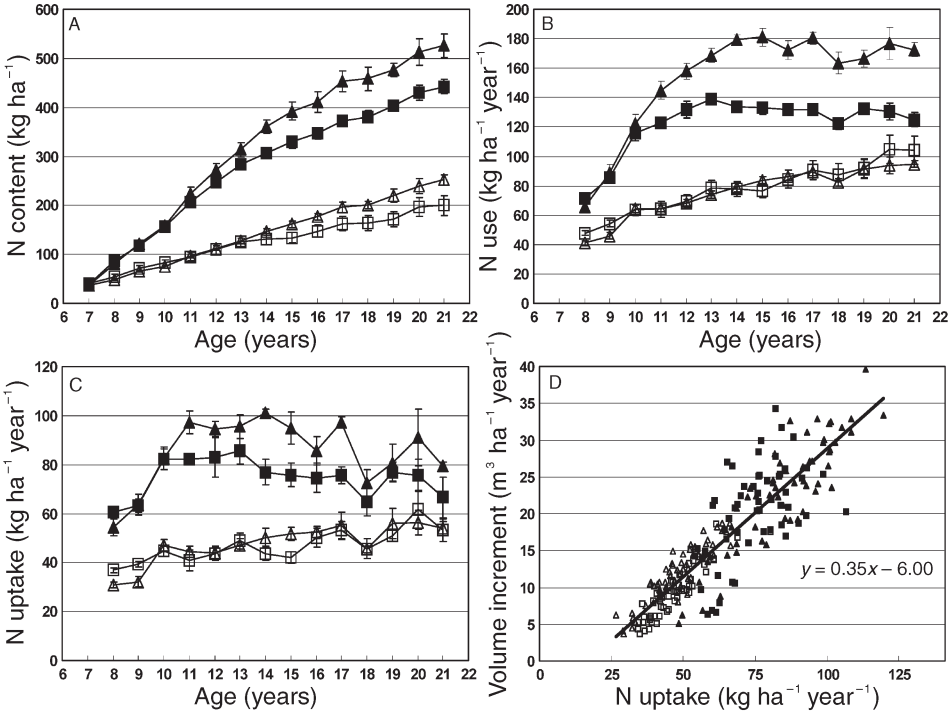

Figure 2. Nitrogen content (A), use (B), uptake (C) and volume growth per unit of uptake (D) for control (□), irrigated (△), fertilized (■) and fertilized plus irrigated (▲) treatments from age 8 to age 21 (1992 to 2005). Error bars represent one standard error.

primarily driven by mass differences (Tables 3, 4 and 5).

Among tissues, foliage and coarse roots represented the highest and lowest contents, respectively, for N, P, K and Mg at age 7 (Table 5). By age 21, stems usually had the highest contents of these elements, whereas fine roots were always the component with the lowest contents of these elements. Stem Ca content was greatest at ages 7 and 21, whereas fine root Ca content was the lowest in all treatments at age 21.

Nutrient use

Nitrogen, P, K and Mg use followed similar patterns through time, with rate of use of the applied fertilizer increasing rap-

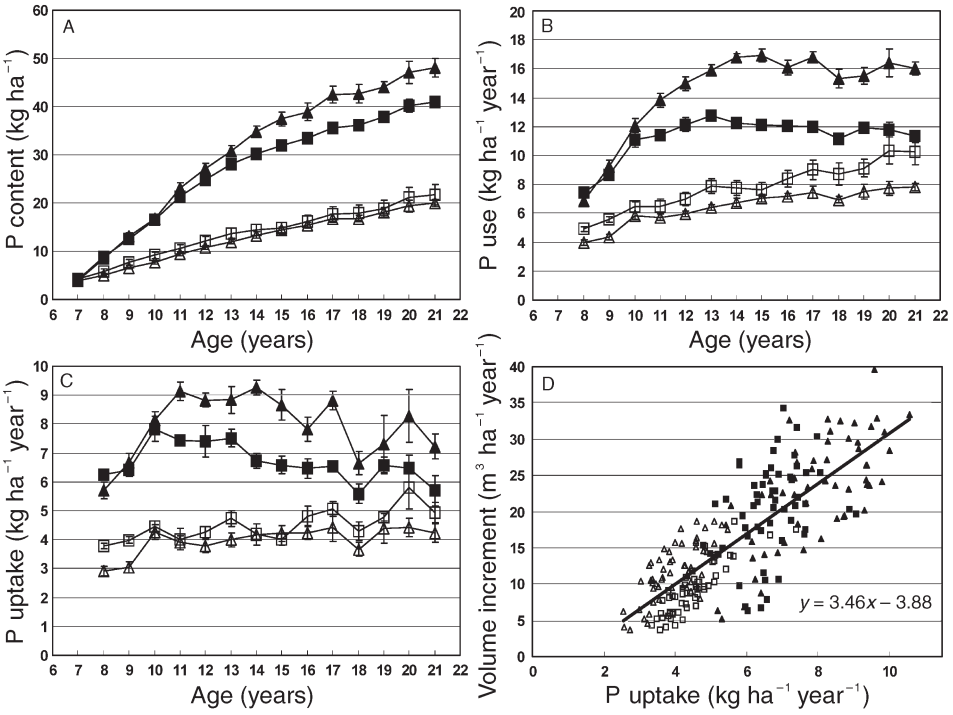

Figure 3. Phosphorus content (A), use (B), uptake (C) and volume growth per unit of uptake (D) for control (□), irrigated (△), fertilized (■) and fertilized plus irrigated (▲) treatments from age 8 to age 21 (1992 to 2005). Error bars represent one standard error.

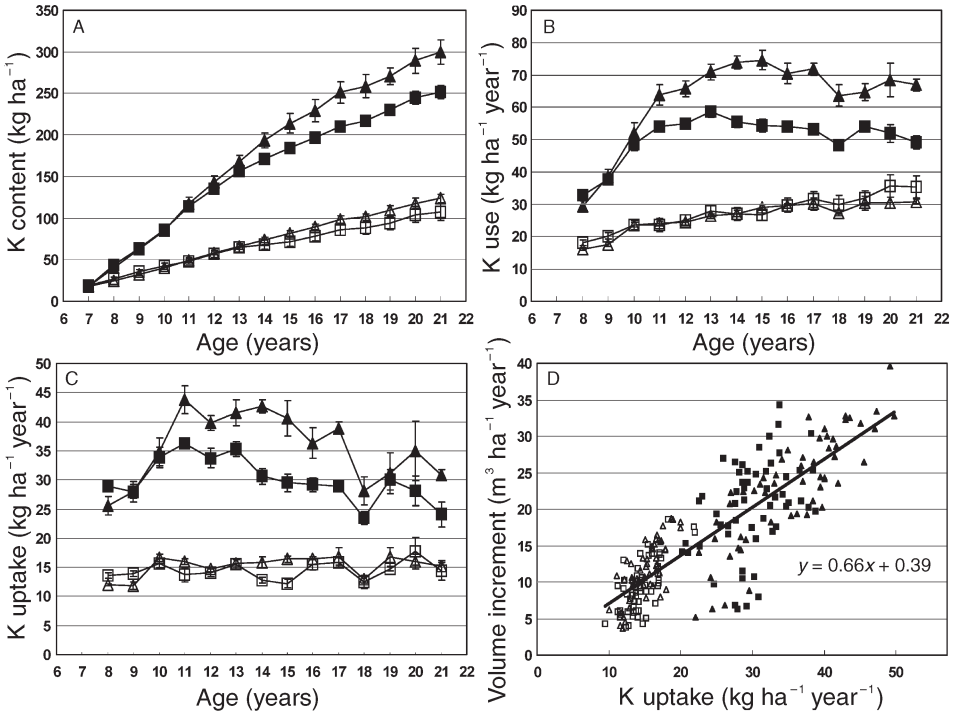

Figure 4. Potassium content (A), use (B), uptake (C) and volume growth per unit of uptake (D) for control (□), irrigated (△), fertilized (■) and fertilized plus irrigated (▲) treatments from age 8 to age 21 (1992 to 2005). Error bars represent one standard error.

idly with the peak use occurring at ages 13 and 15 for the fertilized and fertilized plus irrigated plots, respectively (Figures 2B, 3B, 4B and 5B). After the peak, nutrient-use rate was maintained or decreased slightly until age 21. Rates of use for these elements on non-fertilized plots increased slowly with the peak typically achieved in the last years of the study. For these elements, the use rate was highest in the fertilized plus irrigated plots and lowest in either the control or irrigated plots. By the end of the study, the separation between fertilized plots and the control and irrigated plots was diminished. Rate of Ca use differed little between the fertilized plots and the control and irrigated plots relative to that for the other elements (Figure 6B).

The highest rate of nutrient use was in foliage across all ele-

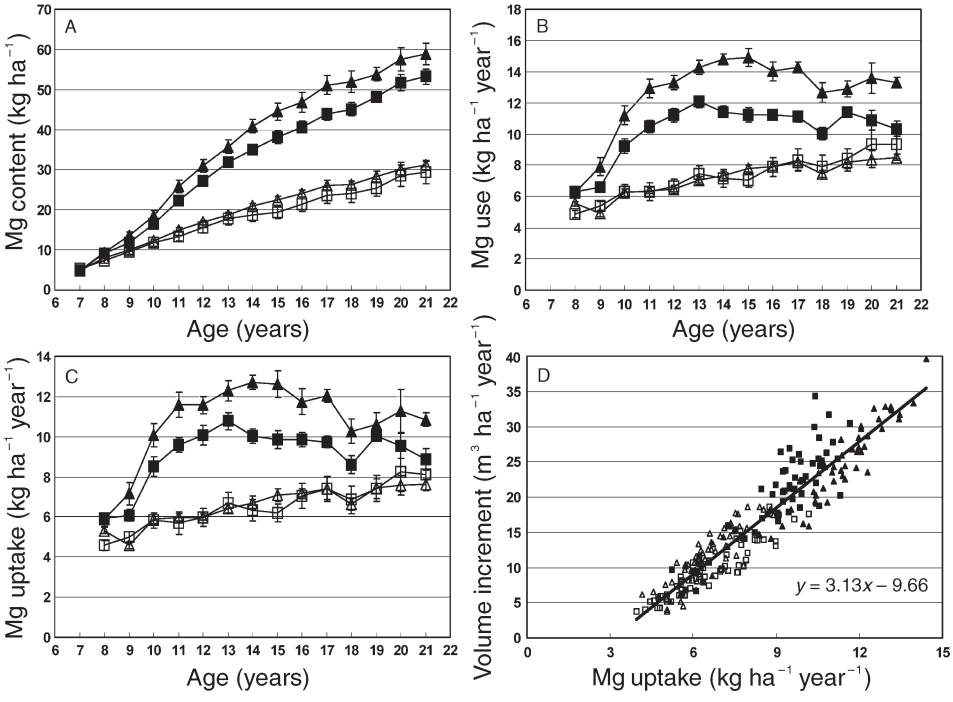

Figure 5. Magnesium content (A), use (B), uptake (C) and volume growth per unit of uptake (D) for control (□), irrigated (△), fertilized (■) and fertilized plus irrigated (▲) treatments from age 8 to age 21 (1992 to 2005). Error bars represent one standard error.

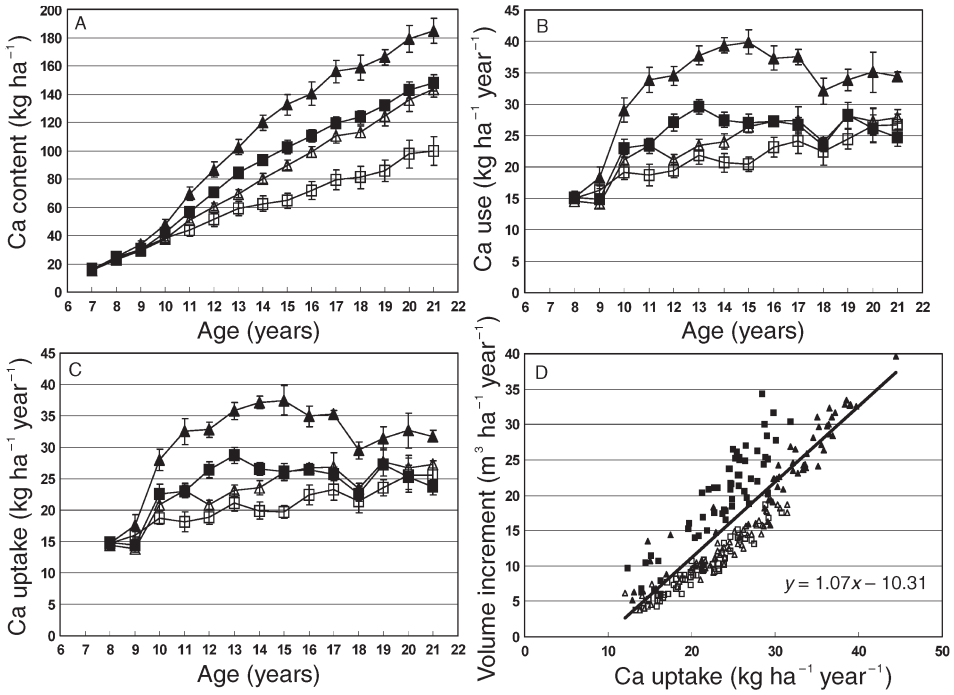

Figure 6. Calcium content (A), use (B), uptake (C) and volume growth per unit of uptake (D) for control (□), irrigated (△), fertilized (■) and fertilized plus irrigated (▲) treatments from age 8 to age 21 (1992 to 2005). Error bars represent one standard error.

Table 5. Mean component nutrient contents (kg ha^{-1}; ± standard error) at pretreatment (age 7) and after 14 years of treatment.

Age	Treatment	Branch	Foliage	Stem	Coarse root	Fine root
Nitrogen						
7	Pretreatment	5.6 ± 0.20	16.1 ± 0.50	5.9 ± 0.18	2.0 ± 0.07	6.6 ± 0.40
21	Control	37.7 ± 4.91	79.2 ± 9.27	42.1 ± 3.32	25.2 ± 2.28	7.7 ± 0.71
21	Irrigated	37.3 ± 1.40	62.9 ± 2.29	91.6 ± 4.50	42.7 ± 2.05	8.8 ± 0.78
21	Fertilized	50.1 ± 2.04	84.3 ± 2.24	143.5 ± 6.05	113.5 ± 3.91	7.9 ± 0.65
21	Fert+irri[1]	64.9 ± 2.55	127.3 ± 4.52	161.6 ± 9.65	117.2 ± 7.13	9.9 ± 1.02
Phosphorus						
7	Pretreatment	0.7 ± 0.02	1.6 ± 0.05	0.7 ± 0.02	0.3 ± 0.01	0.6 ± 0.03
21	Control	3.7 ± 0.45	7.8 ± 0.90	4.4 ± 0.34	3.0 ± 0.27	0.8 ± 0.07
21	Irrigated	3.7 ± 0.14	5.4 ± 0.19	4.6 ± 0.21	3.2 ± 0.15	0.9 ± 0.11
21	Fertilized	5.7 ± 0.22	7.6 ± 0.20	11.5 ± 0.39	10.2 ± 0.34	0.9 ± 0.07
21	Fert+irri	6.6 ± 0.24	11.7 ± 0.41	12.2 ± 0.70	10.8 ± 0.63	1.2 ± 0.19
Potassium						
7	Pretreatment	2.6 ± 0.09	5.1 ± 0.16	3.4 ± 0.11	1.8 ± 0.06	2.2 ± 0.11
21	Control	16.6 ± 2.13	24.8 ± 2.88	30.5 ± 2.54	21.6 ± 1.94	2.8 ± 0.27
21	Irrigated	14.6 ± 0.54	18.3 ± 0.66	32.8 ± 1.52	42.4 ± 2.03	2.9 ± 0.26
21	Fertilized	25.2 ± 0.99	31.7 ± 0.82	69.9 ± 2.56	89.7 ± 3.03	2.9 ± 0.21
21	Fert+irri	28.1 ± 1.04	44.5 ± 1.52	75.3 ± 4.37	114.5 ± 6.86	3.4 ± 0.54
Calcium						
7	Pretreatment	3.4 ± 0.13	3.1 ± 0.09	3.4 ± 0.11	0.8 ± 0.03	1.9 ± 0.14
21	Control	31.1 ± 4.43	14.7 ± 1.71	28.3 ± 2.32	9.1 ± 0.80	1.8 ± 0.09
21	Irrigated	32.7 ± 1.28	11.3 ± 0.41	60.9 ± 2.96	15.2 ± 0.72	2.1 ± 0.19
21	Fertilized	23.2 ± 1.13	10.5 ± 0.37	65.0 ± 2.99	18.7 ± 0.61	1.5 ± 0.10
21	Fert+irri	33.4 ± 1.44	17.4 ± 0.63	77.4 ± 4.79	20.0 ± 1.15	1.9 ± 0.30
Magnesium						
7	Pretreatment	0.9 ± 0.03	1.4 ± 0.04	1.1 ± 0.04	0.2 ± 0.01	0.6 ± 0.04
21	Control	5.8 ± 0.76	6.4 ± 0.72	10.5 ± 0.89	2.4 ± 0.21	0.7 ± 0.04
21	Irrigated	5.9 ± 0.22	5.6 ± 0.21	10.9 ± 0.50	2.8 ± 0.13	0.8 ± 0.07
21	Fertilized	7.9 ± 0.34	5.7 ± 0.18	26.2 ± 1.11	4.0 ± 0.13	0.7 ± 0.04
21	Fert+irri	9.4 ± 0.36	8.5 ± 0.29	25.7 ± 1.49	4.2 ± 0.21	0.9 ± 0.15

[1] Fert+irri = fertilized plus irrigated.

Table 6. Mean component nutrient use (kg ha^{-1} year^{-1}; ± standard error) in the first year after treatment (age 8) and after 14 years of treatment (age 21).

Age	Treatment	Branch	Foliage	Stem	Coarse root	Fine root
Nitrogen						
8	Control	3.2 ± 0.20	23.3 ± 2.03	3.2 ± 0.22	2.1 ± 0.15	16.0 ± 1.36
21		5.2 ± 0.60	79.2 ± 9.27	2.2 ± 0.36	2.1 ± 0.32	15.3 ± 0.87
8	Irrigated	3.4 ± 0.18	21.3 ± 1.13	1.3 ± 0.33	2.1 ± 0.15	13.0 ± 1.10
21		5.8 ± 0.15	62.9 ± 2.29	8.0 ± 0.40	3.6 ± 0.20	14.5 ± 0.70
8	Fertilized	7.2 ± 0.13	33.3 ± 0.73	6.1 ± 0.49	10.0 ± 0.37	14.9 ± 1.03
21		9.4 ± 0.27	84.3 ± 2.24	8.1 ± 0.97	7.0 ± 0.93	16.1 ± 1.06
8	Fert+irri[1]	5.6 ± 0.42	35.8 ± 1.62	5.7 ± 0.67	6.0 ± 0.51	12.4 ± 1.37
21		10.8 ± 0.36	127.3 ± 4.52	9.9 ± 0.32	9.4 ± 0.48	15.2 ± 0.70
Phosphorus						
8	Control	0.4 ± 0.02	2.3 ± 0.20	0.4 ± 0.02	0.3 ± 0.02	1.6 ± 0.16
21		0.5 ± 0.05	7.8 ± 0.90	0.2 ± 0.03	0.3 ± 0.04	1.5 ± 0.11
8	Irrigated	0.4 ± 0.02	1.9 ± 0.10	0.2 ± 0.02	0.3 ± 0.02	1.2 ± 0.14
21		0.6 ± 0.02	5.4 ± 0.19	0.2 ± 0.02	0.3 ± 0.02	1.3 ± 0.11
8	Fertilized	0.9 ± 0.01	3.1 ± 0.07	0.6 ± 0.04	1.3 ± 0.04	1.4 ± 0.12
21		1.1 ± 0.03	7.6 ± 0.20	0.5 ± 0.07	0.6 ± 0.09	1.5 ± 0.11
8	Fert+irri	0.7 ± 0.05	3.4 ± 0.15	0.4 ± 0.05	1.0 ± 0.10	1.3 ± 0.15
21		1.2 ± 0.04	11.7 ± 0.41	0.7 ± 0.03	0.8 ± 0.05	1.6 ± 0.13
Potassium						
8	Control	1.5 ± 0.09	7.4 ± 0.64	2.2 ± 0.15	2.0 ± 0.14	5.0 ± 0.56
21		2.2 ± 0.21	24.8 ± 2.88	1.8 ± 0.29	1.9 ± 0.29	4.8 ± 0.36
8	Irrigated	1.7 ± 0.09	6.7 ± 0.35	1.4 ± 0.11	2.5 ± 0.15	3.9 ± 0.48
21		2.6 ± 0.07	18.3 ± 0.66	1.9 ± 0.12	3.7 ± 0.20	4.3 ± 0.33
8	Fertilized	4.1 ± 0.05	12.3 ± 0.26	3.8 ± 0.22	8.9 ± 0.29	3.9 ± 0.41
21		4.6 ± 0.12	31.7 ± 0.82	3.5 ± 0.43	5.3 ± 0.71	4.2 ± 0.40
8	Fert+irri	3.3 ± 0.22	13.4 ± 0.57	2.7 ± 0.31	6.9 ± 0.53	3.2 ± 0.32
21		5.7 ± 0.18	44.5 ± 1.52	4.4 ± 0.16	8.4 ± 0.40	3.9 ± 0.23
Calcium						
8	Control	2.1 ± 0.15	4.4 ± 0.38	2.0 ± 0.14	1.6 ± 0.10	4.8 ± 0.28
21		4.4 ± 0.66	14.7 ± 1.71	1.6 ± 0.26	1.3 ± 0.16	4.6 ± 0.21
8	Irrigated	2.1 ± 0.13	3.8 ± 0.20	1.5 ± 0.20	3.3 ± 0.25	3.9 ± 0.28
21		5.3 ± 0.14	11.3 ± 0.41	5.1 ± 0.26	1.8 ± 0.11	4.4 ± 0.12
8	Fertilized	2.5 ± 0.07	4.0 ± 0.12	1.9 ± 0.22	3.5 ± 0.13	3.4 ± 0.26
21		4.5 ± 0.17	10.5 ± 0.37	4.0 ± 0.47	2.0 ± 0.29	3.7 ± 0.28
8	Fert+irri	2.1 ± 0.21	5.1 ± 0.23	2.0 ± 0.27	3.0 ± 0.17	3.0 ± 0.34
21		5.8 ± 0.23	17.4 ± 0.63	5.0 ± 0.14	2.5 ± 0.24	3.7 ± 0.16
Magnesium						
8	Control	0.5 ± 0.03	2.0 ± 0.17	0.7 ± 0.05	0.4 ± 0.02	1.3 ± 0.07
21		0.8 ± 0.09	6.4 ± 0.72	0.6 ± 0.11	0.3 ± 0.04	1.2 ± 0.04
8	Irrigated	0.5 ± 0.03	1.8 ± 0.10	0.7 ± 0.04	1.5 ± 0.02	1.0 ± 0.10
21		0.9 ± 0.02	5.6 ± 0.21	0.6 ± 0.04	0.3 ± 0.02	1.1 ± 0.06
8	Fertilized	1.1 ± 0.02	2.2 ± 0.06	1.1 ± 0.09	0.8 ± 0.03	1.1 ± 0.11
21		1.4 ± 0.04	5.7 ± 0.18	1.5 ± 0.18	0.5 ± 0.08	1.2 ± 0.09
8	Fert+irri	0.8 ± 0.06	2.7 ± 0.12	1.0 ± 0.11	0.8 ± 0.04	0.9 ± 0.10
21		1.6 ± 0.05	8.5 ± 0.29	1.5 ± 0.06	0.6 ± 0.07	1.1 ± 0.05

[1] Fert+irri = fertilized plus irrigated.

ments, treatments and age combinations (Table 6). The second highest use rate for N and P was in fine roots for all treatments and age combinations.

Nutrient uptake

Uptake of N, P and K followed similar patterns through time, with uptake increasing rapidly and peak uptake occurring at ages 10 and 11 for the fertilized and fertilized plus irrigated plots, respectively (Figures 2C, 3C and 4C). After the peak, uptake was maintained or decreased slightly until age 18 when a sharp decline followed by a recovery in the following year (age 19) was observed. Mean uptake during this relatively stable period (age 10 for fertilized and age 11 for fertilized plus irrigated until age 17) was 80, 7 and 32 kg ha^{-1} year^{-1} and 95,

Table 7. Summary of mean volume increment per unit nutrient uptake ($m^3\ kg^{-1}$) and the statistical significance ($P > F$) of inter-annual differences for nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg). For a given record, the mean value is for the first age listed in the comparison column.

Comparison	N		P		K		Ca		Mg	
	Mean	$P > F$	Mean	$P > F$	Mean	$P > F$	Mean	$P > F$	Mean	$P > F$
Control										
Age 8 vs. age 9	0.13	0.54	1.23	0.55	0.34	0.26	0.31	0.67	1.01	0.71
Age 9 vs. age 10	0.14	0.02	1.34	0.04	0.38	0.00	0.33	0.06	1.06	0.05
Age 10 vs. age 11	0.17	0.25	1.73	0.27	0.49	0.04	0.41	0.69	1.32	0.77
Age 11 vs. age 12	0.19	0.70	1.94	0.84	0.57	0.82	0.43	1.00	1.36	0.93
Age 12 vs. age 13	0.19	0.37	1.90	0.38	0.58	0.15	0.43	0.43	1.35	0.42
Age 13 vs. age 14	0.20	0.11	2.06	0.19	0.63	0.32	0.46	0.06	1.46	0.06
Age 14 vs. age 15	0.17	0.17	1.82	0.18	0.59	0.01	0.38	0.35	1.20	0.33
Age 15 vs. age 16	0.20	0.03	2.07	0.07	0.68	0.09	0.42	0.02	1.33	0.02
Age 16 vs. age 17	0.23	0.24	2.41	0.35	0.75	0.38	0.52	0.44	1.65	0.37
Age 17 vs. age 18	0.21	0.16	2.23	0.26	0.71	0.63	0.48	0.05	1.53	0.05
Age 18 vs. age 19	0.19	0.00	2.03	0.00	0.70	< 0.001	0.40	0.00	1.27	0.00
Age 19 vs. age 20	0.24	0.02	2.61	0.03	0.85	< 0.001	0.53	0.41	1.70	0.23
Age 20 vs. age 21	0.21	0.08	2.19	0.07	0.72	< 0.001	0.50	0.84	1.54	0.96
Age 21	0.23		2.53		0.88		0.49		1.55	
Irrigated										
Age 8 vs. age 9	0.14	< 0.001	1.50	0.00	0.37	< 0.001	0.30	< 0.001	0.82	< 0.001
Age 9 vs. age 10	0.20	0.23	2.14	0.57	0.55	0.45	0.47	0.19	1.41	0.66
Age 10 vs. age 11	0.18	< 0.001	2.04	< 0.001	0.52	< 0.001	0.41	0.10	1.47	0.00
Age 11 vs. age 12	0.25	0.26	2.85	0.49	0.70	0.94	0.48	0.85	1.87	0.24
Age 12 vs. age 13	0.23	0.15	2.73	0.10	0.70	0.04	0.49	0.43	1.71	0.22
Age 13 vs. age 14	0.26	0.13	3.03	0.21	0.77	0.29	0.52	0.44	1.87	0.28
Age 14 vs. age 15	0.23	0.01	2.80	0.00	0.73	< 0.001	0.49	0.15	1.73	0.03
Age 15 vs. age 16	0.28	0.19	3.40	0.10	0.87	0.04	0.55	0.44	2.02	0.25
Age 16 vs. age 17	0.30	0.11	3.71	0.11	0.94	0.16	0.58	0.54	2.17	0.25
Age 17 vs. age 18	0.27	0.09	3.41	0.06	0.89	0.44	0.56	0.05	2.02	0.01
Age 18 vs. age 19	0.25	0.02	3.06	0.00	0.87	0.04	0.47	0.03	1.68	0.00
Age 19 vs. age 20	0.28	0.10	3.63	0.07	0.94	0.21	0.57	0.46	2.12	0.13
Age 20 vs. age 21	0.26	0.30	3.29	0.21	0.89	0.03	0.54	0.94	1.91	0.82
Age 21	0.27		3.53		0.97		0.54		1.94	
Fertilized										
Age 8 vs. age 9	0.11	0.00	1.11	0.00	0.24	< 0.001	0.47	< 0.001	1.17	< 0.001
Age 9 vs. age 10	0.17	0.00	1.66	0.00	0.38	< 0.001	0.74	0.30	1.76	0.02
Age 10 vs. age 11	0.21	0.00	2.24	< 0.001	0.52	0.02	0.78	< 0.001	2.07	0.11
Age 11 vs. age 12	0.27	0.29	2.94	0.38	0.60	0.98	0.95	< 0.001	2.28	0.05
Age 12 vs. age 13	0.25	0.00	2.78	0.00	0.60	0.00	0.77	0.00	2.02	0.01
Age 13 vs. age 14	0.30	0.02	3.42	0.02	0.73	0.06	0.89	0.00	2.38	0.01
Age 14 vs. age 15	0.27	0.02	3.00	0.01	0.66	0.00	0.76	0.00	2.01	0.02
Age 15 vs. age 16	0.30	0.15	3.48	0.14	0.78	0.16	0.88	0.38	2.33	0.35
Age 16 vs. age 17	0.33	0.16	3.76	0.16	0.83	0.27	0.92	0.43	2.45	0.40
Age 17 vs. age 18	0.30	0.01	3.50	0.01	0.79	0.06	0.88	0.00	2.34	0.00
Age 18 vs. age 19	0.26	< 0.001	3.03	< 0.001	0.72	< 0.001	0.75	< 0.001	1.96	< 0.001
Age 19 vs. age 20	0.38	< 0.001	4.43	< 0.001	0.97	0.00	1.06	0.01	2.89	0.00
Age 20 vs. age 21	0.32	0.77	3.68	0.68	0.85	0.91	0.94	0.04	2.49	0.12
Age 21	0.31		3.60		0.85		0.86		2.29	
Fertilized plus irrigated										
Age 8 vs. age 9	0.12	< 0.001	1.18	< 0.001	0.26	< 0.001	0.46	< 0.001	1.14	< 0.001
Age 9 vs. age 10	0.22	0.87	2.11	0.35	0.50	0.42	0.81	< 0.001	1.97	0.32
Age 10 vs. age 11	0.22	0.01	2.29	0.00	0.53	0.12	0.66	0.00	1.84	0.00
Age 11 vs. age 12	0.27	0.24	2.84	0.31	0.59	0.89	0.79	0.04	2.22	0.11
Age 12 vs. age 13	0.25	0.00	2.65	0.00	0.58	0.01	0.71	0.04	2.01	0.02
Age 13 vs. age 14	0.30	0.54	3.25	0.67	0.69	0.96	0.79	0.83	2.31	0.91
Age 14 vs. age 15	0.29	0.01	3.18	0.02	0.68	0.02	0.79	0.26	2.30	0.19

Continued overleaf.

Table 7 cont'd. Summary of mean volume increment per unit nutrient uptake ($m^3\ kg^{-1}$) and the statistical significance ($P > F$) of inter-annual differences for nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg). For a given record, the mean value is for the first age listed in the comparison column.

Comparison	N		P		K		Ca		Mg	
	Mean	$P > F$	Mean	$P > F$	Mean	$P > F$	Mean	$P > F$	Mean	$P > F$
Age 15 vs. age 16	0.33	0.97	3.62	0.99	0.77	0.83	0.83	0.50	2.47	0.56
Age 16 vs. age 17	0.33	0.00	3.62	0.01	0.78	0.07	0.80	0.62	2.39	0.44
Age 17 vs. age 18	0.28	0.25	3.15	0.25	0.71	0.46	0.78	0.00	2.29	0.00
Age 18 vs. age 19	0.27	0.28	2.94	0.21	0.68	0.12	0.65	0.08	1.86	0.04
Age 19 vs. age 20	0.28	0.09	3.17	0.07	0.74	0.05	0.72	0.78	2.14	0.52
Age 20 vs. age 21	0.26	0.03	2.83	0.03	0.67	0.02	0.71	0.61	2.05	0.50
Age 21	0.29		3.24		0.75		0.73		2.14	

9 and 40 kg ha^{-1} $year^{-1}$ for the fertilized and fertilized plus irrigated plots for N, P and K, respectively. These uptake rates were between 1.5 and 2.5 times greater than the corresponding rates observed in the control and irrigated plots. In non-fertilized plots, uptake rates for these elements increased slowly with the peak typically achieved in the last years of the study. Calcium and Mg uptake patterns through time were similar for the fertilized plus irrigated plot; there was a rapid increase in uptake from the study installation but the peak in uptake was not achieved until age 15, 4 years later than the peaks in uptake for N, P and K (Figures 5C and 6C). Magnesium uptake for the non-fertilized plots increased slowly throughout the study. Calcium uptake in the irrigated plots was similar to that in the fertilized plots for most years.

Volume growth per unit of nutrient uptake

Slopes for N and P volume growth per unit of nutrient uptake were 0.35 and 3.5 $m^3\ kg^{-1}$, respectively (Figures 2D and 3D). Treatment differences in slope and intercept for these relationships were apparent; for example, irrigated plot data were typically found above the overall regression line, whereas control plot data fell below that line for N and P. Volume growth per unit of nutrient uptake varied within a treatment from year to year and control, irrigated, fertilized and fertilized plus irrigated plots achieved maximum volume growth per unit N and P uptake rates of 0.24 and 2.6; 0.30 and 3.7; 0.38 and 4.4; and 0.33 and 3.6 $m^3\ kg^{-1}$, respectively (Table 7). Across treatments, nutrient uptake for a given volume increment varied considerably, for example, at 10 $m^3\ ha^{-1}\ year^{-1}$ volume increment N and P uptake ranged from 38 to 68 and from 3.0 to 6.9 kg ha^{-1} $year^{-1}$, respectively (Figures 2D and 3D). When compared with the N and P volume growth per unit of nutrient uptake relationships, K showed less difference among treatments (Table 7 and Figure 4D), Ca showed a fertilizer effect (most fertilized data were above the regression line and most non-fertilized data below it) (Figure 5D), whereas Mg had a

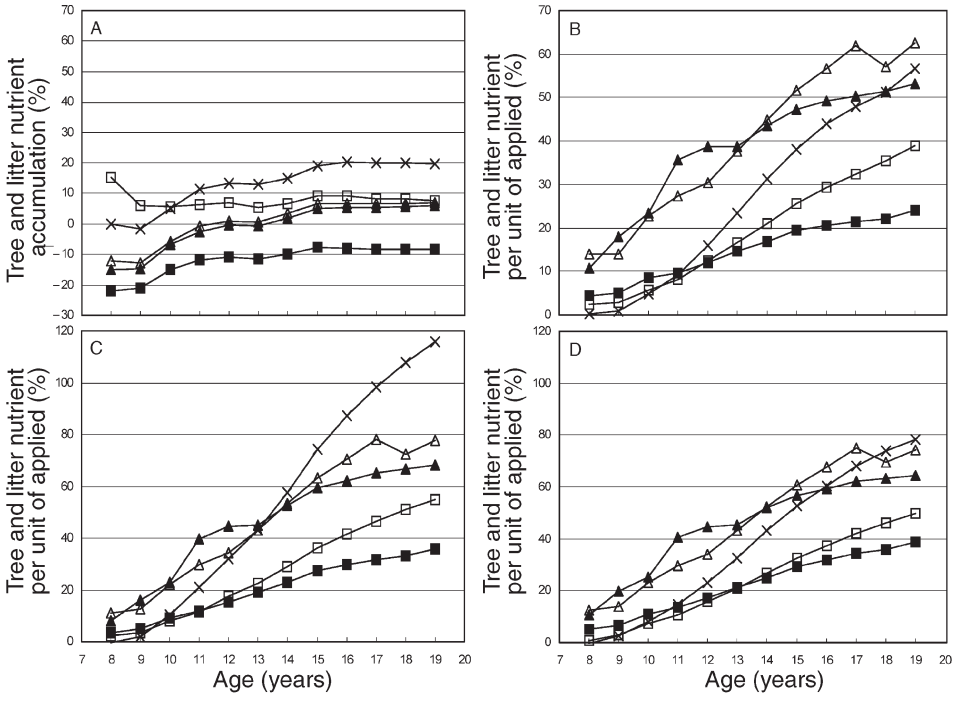

Figure 7. Comparisons of uptake efficiency of applied nutrients, nitrogen (▲), phosphorus (■), potassium (△), calcium (×) and magnesium (□), between irrigated and control (A), fertilized and control (B), fertilized plus irrigated and control (C) and fertilized plus irrigated and irrigated (D) treatments from age 8 to age 19 (1992 to 2003).

slope and range in nutrient uptake for a given volume increment similar to P (Figure 6D).

Nutrient-uptake efficiency

Nitrogen-, K- and Mg-uptake efficiencies in the irrigated plot were between 6 and 8% higher than in the control by age 19 (Figure 7A). At that time, P- and Ca-uptake efficiencies were 8% less and 20% more than in the control, respectively. All nutrients reported on here appeared to have reached asymptotic values in the irrigated versus control treatment comparison with little change in nutrient-uptake efficiency after age 15.

In contrast, uptake efficiency was still increasing at age 19 for all five nutrients in the comparisons of fertilized and fertilized plus irrigated versus the control treatment and of fertilized plus irrigated versus the irrigated treatment (Figures 7B–D). At age 19, the uptake efficiency ranking for the fertilized versus control treatment comparison was K (62%), Ca (57%), N (53%), Mg (39%) and P (24%). When comparing the fertilized plus irrigated treatment with the control treatment at age 19, the ranking of nutrients was different and the efficiencies were greater with Ca (116%), K (78%), N (68%), Mg (55%) and P (36%). Irrigation increased fertilizer-uptake efficiency 15, 12, 15, 59 and 16% for N, P, K, Ca and Mg, respectively (Figures 7B and 7C). In the comparison of fertilized plus irrigated and the irrigated treatments, the ranking of nutrients was the same as for fertilized plus irrigated and the control treatment comparison but the magnitude of uptake efficiency was less for Ca (78%), K (74%), N (64%), Mg (50%) and P (39%). At age 17, we estimated ecosystem N retention at 79%.

Discussion

The ranges in volume growth per unit nutrient uptake for N, P, K, Ca and Mg were 0.11 to 0.38, 1.11 to 4.43, 0.24 to 0.97, 0.30 to 1.06 and 0.82 to 2.89 $m^3 kg^{-1}$, respectively, and demonstrated loblolly pine plasticity. Our volume growth rates bracket those found across a range of southeastern USA sites (Baker and Langdon 1990, Borders and Bailey 2001, Rojas 2005) so the nutrient-uptake efficiencies presented here likely represent typical values for native loblolly pine. However, loblolly pine volume growth rates may exceed the maximum that we observed when this species is grown as an exotic (Harms et al. 2000). Heritable genetic differences in growth per unit applied N were found in loblolly seedlings (Li et al. 1991). When planting these Piedmont families as exotics (Harms et al. 2000) or when examining more productive Atlantic Coastal Plain families (Bongarten and Teskey 1987), volume growth per unit of nutrient uptake might differ from the rates we observed. We calculated nutrient-uptake efficiency when no nutrients were limiting based on current knowledge of the critical thresholds of foliar nutrients. Nevertheless, some elements could have been taken up in amounts exceeding that needed for the growth rate observed.

We observed treatment effects on the slope and intercept of the volume growth per unit nutrient relationship for all nutrients; however, we presented only one slope across all treatments. Some of the observed differences were related to treatment application in an 8-year-old stand rather than at planting and would have provided misleading slopes and intercepts. This artifact was observed in the anomalous combination of relatively low volume growth with relatively high uptake for N, P and K in the fertilized and fertilized plus irrigated plots (Figures 2D, 3D and 4D) for the first years after treatment initiation. Nevertheless, the irrigated and the fertilized plots typically had greater volume growth per unit of N, P, K and Mg uptake than the control and fertilized plus irrigated plots, respectively. For Ca, the fertilized and fertilized plus irrigated plots had greater volume growth per unit of uptake than the control and irrigated plots. Volume production was a function of peak leaf area index, which was about doubled by nutrient additions (Albaugh et al. 1998). The increase in irrigated over control volume growth per unit nutrient uptake may be due to the leaf area in irrigated plots producing more photosynthate than the leaf area in control plots because the added water allowed the stomata to remain open during dry ambient conditions. Conversely, in the fertilized and fertilized plus irrigated plots, the added water may have been insufficient for the leaf area produced in the fertilized plus irrigated treatment and may have prevented this treatment from altering cell morphology to increase water-use efficiency as was observed in the fertilized treatment by Ewers et al. (1999).

These arguments may also explain the wide range in measured nutrient uptake for a given amount of volume production. Inter-annual environmental differences that limited photosynthesis (e.g., timing of the dry period and cold weather onset) would influence the volume growth achieved for a given leaf area and consequently nutrient uptake. For example, we hypothesize that the low uptake of all elements at age 18 was related to low winter precipitation before the age 18 growing season (Table 1). Previous work (Sampson et al. 2001, Ludovici et al. 2002) demonstrated the importance of winter photosynthesis and consequent carbon storage to summer productivity. During the winter preceding the age 18 irrigation season, precipitation may have been low enough to reduce photosynthesis ultimately reducing overall volume production and nutrient uptake. This effect was observed in all treatments because the irrigation system was turned off during the winter when temperatures were below freezing. Additionally, this range may be related to family differences among individual plots in a given treatment. Ten Piedmont families were planted with no effort to distribute the families evenly across the site or to identify families within a plot. If genetic differences in growth per unit of nutrient uptake existed among these families similar to those found by Li et al. (1991), it would be possible, although unlikely, that the grouping of high uptake efficiency families among the replications could add to variation in growth per unit nutrient uptake within a treatment. Another factor to be taken into account when considering the fertilized versus fertilized plus irrigated responses is that there may have been nutrient uptake in excess of that required for the observed growth. Although the same nutrient amounts were applied to all fertilized plots, the fertilized plus irrigated treatment had greater nutrient-uptake efficiency than the fertilized plots for all elements examined (Figures 7B and 7C). Foliar N concentrations in all fertilized plots exceeded the 1.2% critical value,

and from ages 12 to 16 the foliar N concentrations in fertilized plus irrigated plots were about 0.1% greater than in the fertilized plots (Albaugh et al. 2004). This was not the case for the non-fertilized treatments because they were typically well below the established guidelines for sufficiency for N and K (Allen 1987, Colbert and Allen 1996).

Wells and Jorgensen (1975) reported total N, P, K, Ca and Mg use in a 16-year-old stand at 117, 21, 64, 58 and 17 kg ha^{-1} $year^{-1}$, respectively. These values were similar to or higher than the values for our fertilized plots. However, when examining tissue nutrient use, the two studies varied considerably with Wells and Jorgensen (1975) reporting more fine root and less coarse root and foliage use than we observed, probably because they used calculations from the literature for belowground component estimates and they did not fertilize, which would likely have increased the foliage contribution. Of the tissue types we examined, foliage had the highest use for all nutrients in all years, highlighting the importance of foliage development to tree growth regardless of treatment. In contrast, nutrient contents among the tissue types changed over time with foliage having the greatest content in young trees, whereas the perennial tissues of stem and coarse roots had greater nutrient contents in older trees.

In 13-year-old stands, Will et al. (2006) found aboveground N and P contents of 160 and 12 kg ha^{-1} for non-fertilized plots and 410 and 27 kg ha^{-1} for fertilized plots, respectively. The non-fertilized data were similar to our estimates for control plots at age 21, and although their P estimate for the fertilized stand was similar to our value for fertilized plus irrigated plots at age 17, none of our plots achieved aboveground nitrogen content greater than 354 kg ha^{-1}. Nitrogen and P uptake estimates for non-fertilized and fertilized stands studied by Will et al. (2006) were 60 and 100, and 7.5 and 10.0 kg ha^{-1} $year^{-1}$, respectively, similar to our maximum N uptake estimates but higher than our corresponding P estimates. We added 277 and 14 kg ha^{-1} more elemental N and P, respectively, to our fertilized plots than Will et al. (2006) added. Adegbidi et al. (2005) reported total nutrient contents in a 4-year-old fertilized stand at 195, 22, 86, 72 and 28 kg ha^{-1} for N, P, K, Ca and Mg. These values correspond to our fertilized and non-fertilized contents at ages 11 and 20 for N, P and Mg, ages 10 and 17 for K, and ages 11 and 16 for Ca, respectively. Nitrogen and P foliage use (53.2 and 4.5 kg ha^{-1} $year^{-1}$, respectively) and retranslocation (64 and 70%, respectively) estimates from Piatek and Allen (2000) were similar to our values. Zhang and Allen's (1996) retranslocation estimates for N, P, K, Ca and Mg (75, 73, 83, 5 and 28%, respectively) were in the same range as our estimates. These high retranslocation rates for mobile nutrients indicated how important these resources are for plant growth and survival, and that nutrients are largely retained by trees once acquired.

Our fertilizer-uptake efficiencies were similar for P and less for N at 24 and 68%, respectively, compared with the estimates reported by Will et al. (2006) but within the range of Ducey and Allen's (2001) modeled estimates of 23–100 and 0–8% for N and P, respectively. The magnitudes of all our elemental uptake efficiencies increased with time and likely were higher at age 21 than at age 19. Relatively low (7–23%) N-uptake efficiencies have been reported for seedlings and small trees (Blazier et al. 2006); however, other studies on small trees that examined increasing nutrient application rates over time (Dumroese et al. 2005), controlled release fertilizer use (Hangs et al. 2003), and competing vegetation removal (Hangs et al. 2003, Blazier et al. 2006) have reported higher N-uptake efficiencies. The magnitude of N-uptake efficiency that we observed was likely related to the long assessment period (11 years), low application rate after the initial application (typically 56 kg ha^{-1} $year^{-1}$ and less than measured annual uptake), measurement of all plant tissue types on site, and complete removal of competing vegetation. No literature reports of K, Ca or Mg loblolly pine uptake efficiencies were found.

The irrigation-induced increase in fertilizer-uptake efficiency ranged from 12 to 16% for N, P, K and Mg, respectively, but reached 59% for Ca. Similarly, in the irrigated and control plots without fertilizer additions, irrigated plots accumulated 8% more N, K and Mg, 20% more Ca and 9% less P than the control plots. Some increase in fertilizer-uptake efficiency and accumulation was expected with irrigation because of increased mass flow from transpiration during dry periods and increased diffusion in the soil (Marschner 1986). However, the Ca increases were unexpectedly large relative to other nutrients. Calcium in the well water used for irrigation was below detectable levels (< 0.5 mg l^{-1}) when tested at ages 8 and 14 making it unlikely that the higher uptake efficiency and accumulation in the irrigated plots was due to Ca in irrigation water. There were relatively minor differences in tissue Ca concentrations for a given fertilization regime (Tables 3 and 4). However, in both fertilization regimes, irrigation resulted in slightly increased annual peak leaf area index (Albaugh et al. 2004) and greater foliage mass, whereas Ca retranslocation from foliage was low (< 15%). Consequently, increases in Ca content of foliage and subsequent litter fall accounted for part of the higher uptake efficiency and accumulation observed in the irrigated plots relative to non-irrigated plots. In the fertilized plus irrigated plots, fertilizer-uptake efficiency exceeded 100% by age 18. Calcium foliar nutrient concentrations were considered sufficient in both irrigated and non-irrigated plots through age 21 (Allen 1987, Colbert and Allen 1996); however, Ca was identified as a limiting nutrient in stands carried through age 33 (Kyle et al. 2005) and calcium may become limiting at this site with time.

The other elements (N, P, K and Mg) reached asymptotic values below 100% uptake efficiency by age 19 indicating that application amounts for these elements were sufficient in the short term. Compared with published critical foliar concentrations of 1.10, 0.10, 0.35, 0.12 and 0.07% for N, P, K, Ca and Mg, respectively, (Allen 1987) only N and K were considered limiting. Although there is no established critical foliar concentration for loblolly pine, boron was considered a limiting nutrient (Albaugh et al. 1998) because pretreatment concentrations of 7 mg kg^{-1} were less than critical values for other pines (12 mg kg^{-1}) (Will 1978, Smith et al. 2000). Phosphorus use and uptake were consistently less in the irrigated plots than in the control plots, indicating that irrigation increased P-use

efficiency (Figure 3D). The increase in volume growth per unit P uptake in response to irrigation was greater than that observed for the other elements, indicating adequate P nutrition in irrigated trees.

Better nutrient management at this site would begin at the time of planting by selecting appropriate nutrient additions based on desired productivity (McKeand et al. 2000), assuming vegetation control was in place to avoid the 8-year delay required to maximize productivity (Figure 1B) when beginning nutrient applications in mid-rotation. At the end of the study, the differential between the fertilized and control uptake for N, P, K and Mg was smaller than in any previous year. One possible cause for this phenomenon is that nutrient applications after age 12 were less than measured uptake creating a situation where the fertilized plots received less than needed even though foliar nutrient monitoring indicated adequate nutrients. Simultaneously, the removal of all competing vegetation may have increased growth and, consequently, nutrient uptake in the non-fertilized plots for up to 11 years after initial removal (Miller et al. 2003). Even with the continued increase in uptake, the control plots still had lower volume increment than the fertilized plots. Alternatively the control trees may have accessed resources in the fertilized plots. This is unlikely because maximum measured surface lateral root distribution was 5.8 m (Johnsen et al. 2005) whereas the measurement plots had a treated buffer zone of 10 m and were separated by an additional 10 m of untreated buffer zone; in addition a 1.5 m deep trench lined with plastic was maintained between plots. However, with a known rooting depth to 290 cm (Albaugh et al. 2006) and the potential for clay lenses at depth, cross feeding by the non-fertilized trees into the fertilized plots remained a possibility.

Our ecosystem N retention was less than that observed by Will et al. (2006) (79 versus 90%). The soil N estimate was based on soil sampled to 150-cm depth and was collected at age 17 (Lee 2002). An ecosystem N retention calculation that included the additional accumulation in trees and litter fall through age 21 and soil assessments to rooting depth would likely result in a larger N retention estimate. From an operational perspective, fertilization with less total applied N and other elements would still provide dramatic increases in productivity on similar sites (Fox et al. 2007). The high site retention of added nutrients provides further evidence that intensive nutritional management is possible with low risk of offsite effects (Will et al. 2006).

We quantified the N, P, K, Ca and Mg uptake needed to produce a given volume. However, required application amounts may differ from the amounts the trees take up. Our results were based on applications designed to eliminate nutrient limitations including those not presented here (e.g., sulfur (S) and B) and where competing vegetation was eliminated. Our initial high nitrogen application rate was based on knowledge that low rates of N application had not produced biologic responses in previous work (Fox et al. 2007) as well as the poor initial stand nutrient status. Because volatilization losses are known to reduce the effective N application rate (Kissel et al. 2004), we applied boron-coated urea fertilizer designed to reduce volatilization (Whitehurst and Whitehurst 2004) under conditions favorable for low volatilization (cool with rain imminent). Consideration of these conditions should be factored into decisions about using this information in an operational setting. Quantification of nutrient-uptake efficiency provides a basis for determining the appropriate amount of each nutrient for a desired growth rate while limiting off-site effects and improving economic viability of intensive forest management. The next step is to build on available information to improve nutrient addition delivery systems for insuring the materials applied are taken up by the tree (Blazier et al. 2006, Elliot 2006).

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