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Loblolly pine needle decomposition and nutrient dynamics as affected by irrigation, fertilization, and substrate quality

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Abstract

This study examined the effects of initial litter quality and irrigation and fertilization treatments on litter decomposition rates and nutrient dynamics (N, Ca, K, Mg, and P) of loblolly (*Pinus taeda* L.) pine needles in the North Carolina Sand Hills over 3 years. Litter quality was based on the initial C/N ratios, with the high-quality litter having a significantly ($P < 0.001$) lower C/N ratio (143 ± 2.5) compared with the low quality litter (172 ± 1.3). Initial litter quality and the irrigation treatment did not significantly affect decomposition rates but the fertilization treatment effects were significant. Low quality needles on fertilized plots had higher decomposition rates ($k = 0.36 \pm 0.01$ year^{-1} for the fertilized and irrigated + fertilized plots) than on unfertilized plots ($k = 0.26 \pm 0.01$ and 0.28 ± 0.01 year^{-1} for the control and irrigated plots, respectively). The decomposing litter was a net sink for P and N and a net source of Mg, Ca, and especially K. Whereas initial substrate quality did not affect decomposition rates, it did affect the rate of release. Compared to the low quality litter, the high quality litter released K at a higher rate, released Mg at a lower rate, and accumulated N at a higher rate. Fertilization decreased the rate of release of Mg and K in high-quality litter and Mg and Ca in low quality litter. In addition, fertilization increased the rate of accumulation of P in both.

Keywords: Litter decomposition; Nutrient dynamics; Litter quality

1. Introduction

The availability of essential nutrients, especially nitrogen (N) and phosphorus (P), commonly limits growth of pine forests in the southern United States (Allen, 1987). The availability of these nutrients can be influenced by litter decomposition that, in turn, is influenced by factors such as climate, nutrient level, and litter quality (Melillo et al., 1982). Generally, the course of nutrient dynamics during decomposition follows three phases: (1) initial nutrient release through leaching, (2) net immobilization when decomposer microorganisms retain or import nutrients, followed by, (3) nutrient release when nutrients are released from the litter at a rate paralleling mass loss (Prescott et al., 1993). However, this general pattern can vary depending on litter type, species, and ecosystem. For example, in conifers the leaching phase is typically short or absent (depending on the nutrient). This may be particularly true of conifers in the southern United States, where a warm climate, an annual wet–dry cycle, active insect and decomposer micro-organisms and infertile soils can affect the rate and mechanisms of litter decomposition.

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Accumulation of nutrients in forest litter has been attributed to exogenous sources such as fertilization, throughfall, and nutrient importation from lower in the forest floor (Griffin, 1972; Berg, 1988). During the immobilization phase, large amounts of nutrients, especially N and P, can be sequestered in the litter layer during stand development (Gholz and Fisher, 1982). Nevertheless, decomposing litter can be a major nutrient source for forest soils (Raison et al., 1987; Stump and Binkley, 1993) and external factors that increase nutrient release from decomposing litter may accelerate stand growth. An exogenous nutrient supply, whether from the forest floor, throughfall, or applied through fertilization, might influence the rate of decomposition and the litter's nutrient release pattern. Prescott et al. (1993) found that the availability of N and P in the forest floor did not influence the rate of N and P release. However, fertilization has been found to increase litter decomposition rates (Prescott et al., 1992; White et al., 1988) and N accumulation in decomposing litter (Titus and Malcolm, 1987).

Initial nutrient concentrations in litter, the endogenous nutrient supply, may also influence decomposition and nutrient dynamics. Berg et al. (1987) found that needles with higher initial N concentrations released N more rapidly, but maintained higher N concentrations than needles with lower initial N concentrations. In the Pacific Northwest, conifer needles with higher initial N concentrations showed a net release of N during the first year, while needles with lower initial N concentrations showed net immobilization (Prescott et al., 1992). In north-central Florida, Polglase et al. (1992) found that loblolly pine (*Pinus taeda* L.) needles with higher P initial concentrations, released P at a higher rate than needles with lower initial P concentrations.

Temperature and moisture, as well as nutrients, play a significant role in litter decomposition and nutrient dynamics. In an old-growth temperate rain forest, higher temperatures during the first year greatly accelerated the decomposition of western hemlock (*Tsuga heterophylla* Sarg.) and Pacific silver fir (*Abies amabilis* Forb.) litter, and resulted in a corresponding loss of litter mass (Edmonds, 1991; Edmonds and Thomas, 1995). The substrate chemistry became more important to litter decomposition in subsequent years (Edmonds and Thomas, 1995). In loblolly pine stands, higher temperatures increased decomposition rates (Hornsby et al., 1995) and net nutrient mineralization from litter (Vitousek and Matson, 1985). Increased N deposition in southern forest ecosystems, resulting from accelerated economic development, coupled with the effects of increased precipitation anticipated under Global Change scenarios (Houghton et al., 1996), stresses the need to quantify the impact of these phenomena on the decomposition process.

This study investigated factors affecting loblolly pine needle decomposition rates and nutrient-release dynamics in a southern forest ecosystem. The objectives of this study were to quantify the effects of increased nutrient and water availability on loblolly pine needle decomposition rates and nutrient dynamics. It compares decomposition rates affected by endogenous nutrient supply (substrate quality) with exogenous sources (fertilization). Biological influences (i.e. microbial and faunal populations and activity) on decomposition rates and nutrient release patterns were not addressed in this study.

2. Site Description

The study site is the Southeast Tree Research and Education Site (SETRES) in the Sand Hills region of North Carolina. The mean annual temperature and precipitation for the site are 17°C and 1210 mm, respectively. The soil is classified in the Wakulla Series (sandy, siliceous, thermic Psammentic Hapludult), has a low water holding capacity, and is nutrient deficient for loblolly pine growth. In 1984, longleaf pine (*Pinus palustris* Mill.) was harvested from the site, and in 1985 a contractor planted loblolly pine. Glyphosate (1.5 vol.%) was applied to control understory vegetation. The study is a 2×2 factorial with treatments replicated on four blocks. Treatments were: (1) control (no irrigation or fertilization), (2) irrigation, (3) fertilization, and (4) irrigation and fertilization. A complete description of the site and experimental design is provided elsewhere (Albaugh et al., 1998).

3. Materials and methods

In 1993, loblolly pine needles from SETRES were collected from the control and fertilized plots at the time of senescence each month from September to December. The needles were collected in eight 1 m × 1 m litter traps randomly placed within each measurement (control and fertilized) plot in each block. Subsamples of the needles were analyzed for total C and N on a NA 1500 Carlo Erba C/N/S analyzer (Fisons Instruments, Danvers, MA).[1] Needles from trees on the fertilized plots had a significantly ($P < 0.001$) lower C/N ratio (143 ± 2.5) than those obtained from the control plots (172 ± 1.3). Litter quality was based on C/N ratios with the litter with the lower C/N ratio representing high-quality litter. Both high and low quality litter were air dried and approximately 55 g of litter was placed in each of 30.5 cm × 20 cm litterbags made from 18 mesh × 16 mesh fiberglass screen. On April 28 and 29, 1994, bags containing the high and low-quality litter were paired (nine pairs, or 18 bags) and placed in three locations on each treatment in each block. The Oi horizon was cleared at each location and the litterbags were placed on top of the Oe horizon. After placement in the study site, any additional litter fall was allowed to remain on top of the litterbags. To estimate total annual litter fall, eight 1 m × 1 m litter traps were placed in each block and treatment combination. For the duration of the study, the litter was collected monthly. The loblolly pine needles were separated from other debris, placed in plastic bags, and weighed.

Soil moisture was monitored with time domain reflectometry (TDR) probes installed 2 cm below the litterbags in the mineral soil. One 15 cm probe was installed at each of the three locations for each treatment plot and replicate and the TDR measurements were taken biweekly. Soil temperature was monitored with a Barnant 100 model 600–2820 thermocouple thermometer equipped with a J-type probe (Barnant Corporation, Barrington, IL). Measurements were taken at 2 cm below the litterbags in the mineral soil at the same time as the TDR measurements. Irrigated plots were watered with a head sprinkler system beginning in May 1993. Irrigation was done as needed to maintain available soil moisture in the upper 50 cm of the soil profile between field capacity and 60% available soil moisture. During each irrigation event, 2.5 cm of water was added per plot, and the irrigated plots received, on average, 19 and 61% more water than the non-irrigated plots in 1994 and 1995, respectively (Albaugh et al., 1998). In March 1992, and continuing to the present, fertilization was aimed at maintaining 1.3 g kg^{-1} leaf N on a dry weight basis (Allen, 1987; Albaugh et al., 1998). Table 1 shows the fertilization history at SETRES from 1992 to 1996. Similar fertilization protocols have been used since 1996.

During the first year, one pair of litterbags (one high and one low quality) was collected from each of the three locations at 3-month intervals. In the second year, the collections were at 6-month intervals. The remaining litterbags were collected from each location yearly. A total of 96 litterbags (48 high quality litter and 48 low quality litter) were collected each time and each was sealed in a plastic bag to prevent moisture loss.

All litter samples were oven-dried at 65°C and ground in a Wiley mill to pass a 20 mesh screen

Table 1
Fertilization history (kg ha^{-1}) at SETRES from 1992 to 1996 (King et al., 1997)

Date[a]	N	P	K	Ca	Mg	S	B
26/3/92	225	56	112	–	–	–	–
12/4/92	–	–	–	135	56	–	–
18/6/92	–	–	–	–	–	–	1.7
30/3/93	–	28	–	–	–	–	–
20/4/93	26	22	21	–	0.2	–	–
10/6/93	–	–	92	–	56	120	
31/8/93	56	–	–	–	–	–	–
24/3/94	112	–	–	–	–	–	–
2/3/95	56[b]	28	56	24	34	74	–
25/5/95	–	–	–	–	–	–	1.1
25/3/96	112	12	56	10	–	15	–
10/4/96	–	–	–	–	–	–	1.1
Total	587	146	337	169	146.2	209	3.9

[a] Solid fertilizer was applied to the soil surface except on 20/4/93 which was liquid fertilizer applied to foliage.
[b] Applied to two plots only.

[1] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

before laboratory processing. Subsamples were placed in a 450°C muffle furnace for 8 h to determine loss-on-ignition. Other subsamples were ashed for 6 h and then digested with 0.3 M HNO_3. The digests were analyzed for P, potassium (K), calcium (Ca), and magnesium (Mg). For the initial and first three collection dates, K was analyzed by atomic absorption spectrometry on a Laboratory Instrumentation AA 457 (Wilmington, MA). During this period, P, Ca, and Mg were analyzed by inductively coupled plasma (ICP) spectrometry on a Perkin-Elmer 6500 ICP (Perkin-Elmer Corp., Norwalk, CT). On all remaining sampling dates, P, K, Ca, and Mg were analyzed by ICP spectrometry on a Jobin Yvon 2000 ICP (Instruments S.A. Inc., Edison, NJ). The methods were determined to be comparable after analysis of standards from the National Institute of Standards and Technology (Galthersburg, MD). Finally, subsamples were analyzed for total C and N on a NA 1500 Carlo Erba C/N/S analyzer. All results are reported on an ash-free basis.

Decomposition was determined by the percent of the original sample mass remaining at different times and by calculating the decay rate constant (k). The decay rate constant for a given time was determined by solving the exponential decay model, $(X/X_0) = e^{-kt}$, where X is the sample mass at a given time, X_0 the original sample mass, and t the time measured in years (Olson, 1963). Decomposition rates were calculated by solving the exponential decay model for k after each sample date following the procedure described by King et al. (1997). Using this method k correlated well with values obtained by fitting the exponential decay model to data at the end of the study, and it afforded an opportunity to generate continuous fractional loss rates anytime during the study. The proportion of sample nutrient content remaining over time was calculated by multiplying the sample mass by the respective nutrient concentration (Schlesinger and Hasey, 1981). Treatment and litter quality effects on percent mass remaining, the proportion of nutrient content remaining over time and k were tested for statistical significance using the PROC GLM procedure on the SAS statistical program (SAS Institute, Cary NC). Data were analyzed as a split-plot design, where the irrigation and fertilization treatments were the main effects and litter quality was the split-plot effect.

4. Results

4.1. Soil microclimate

Figs. 1 and 2 show the monthly mean averages for soil moisture and soil temperature over the duration of the study. The irrigated plots (irrigated and irrigated + fertilized) generally maintained a higher soil moisture level compared with the non-irrigated plots (control and fertilized). Additionally, the non-irrigated plots had large fluxes in soil moisture corresponding to periods of low rainfall (Fig. 1). For the duration of the study, the irrigated plots had significantly ($P < 0.0001$) higher soil moisture levels ($\mu = 0.082$ cm cm^{-1}) than the non-irrigated plots ($\mu = 0.069$ cm cm^{-1}). Annual litter production was considerably higher on the fertilized plots compared with the unfertilized plots (Fig. 3) and it might be anticipated that the higher litter layer on the fertilized plots would better moderate soil temperature compared with the unfertilized plots. However, there was no significant difference in soil temperature between the treatments over the duration of the study or for any individual monthly measure. Soil temperature for all the plots followed a seasonal pattern (Fig. 2) ranging from approximately 6 to 27°C

5. Decomposition

There were no significant differences in percent mass remaining among the treatments during the first year. However, in the second and third years, the fertilized plots had less mass remaining (Fig. 4A and B). Because quality did not significantly affect decomposition, only one litter quality is shown in Fig. 4. By the second year of the study, litter on the unfertilized plots had lost approximately 40% of their mass, while litter on the fertilized plots had lost approximately 50%. By the end of the third year, the unfertilized plots had lost approximately 45% of their mass while the fertilized plots had lost approximately 60%. Mean decay rates calculated at the end of the study for each treatment and litter quality are shown in Table 2. Fertilization had a significant effect on both the percent mass remaining ($P = 0.004$) and the decay rate ($P = 0.009$). However, irrigation, litter quality, and their interactions did not significantly

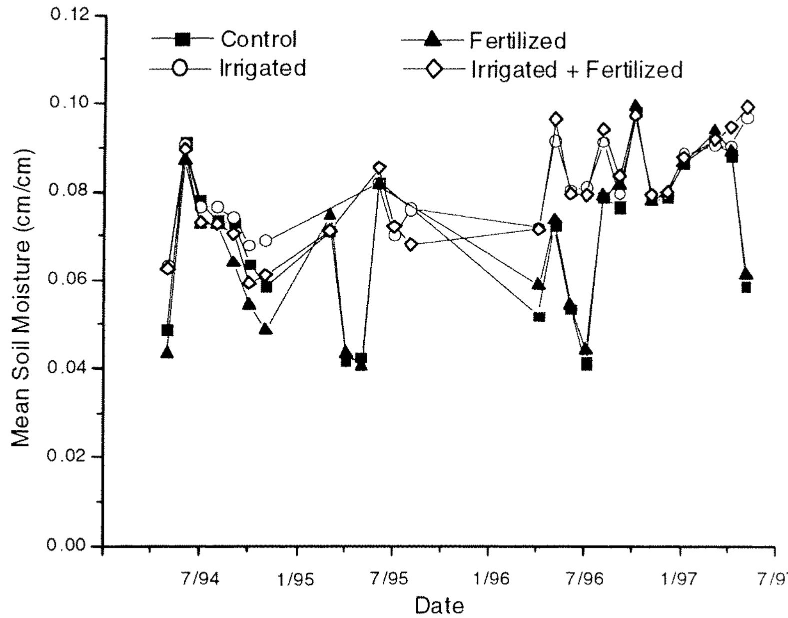

Fig. 1. Mean monthly soil moisture in the upper 2 cm of mineral soil for the control, irrigated, fertilized, and irrigated and fertilized treatment plots at SETRES.

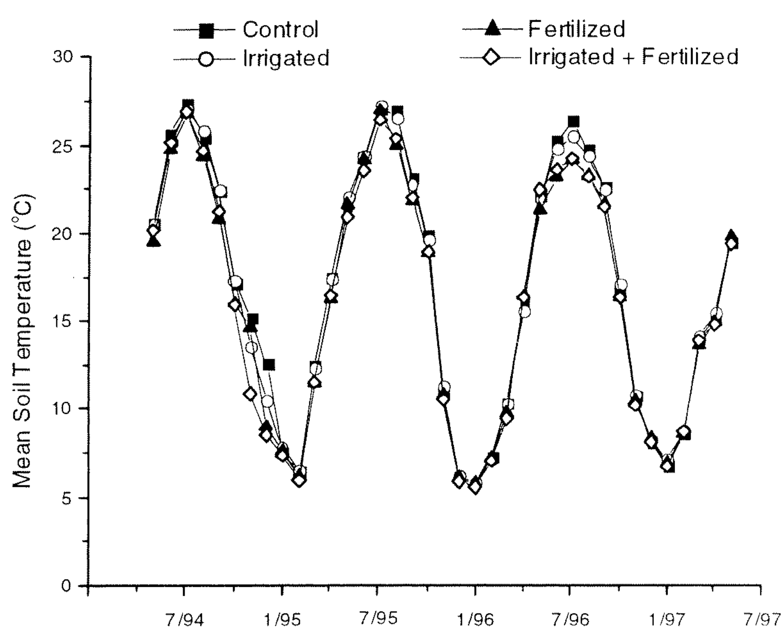

Fig. 2. Mean monthly soil temperature in the upper 2 cm of mineral soil for the control, irrigated, fertilized, and irrigated and fertilized treatment plots at SETRES.

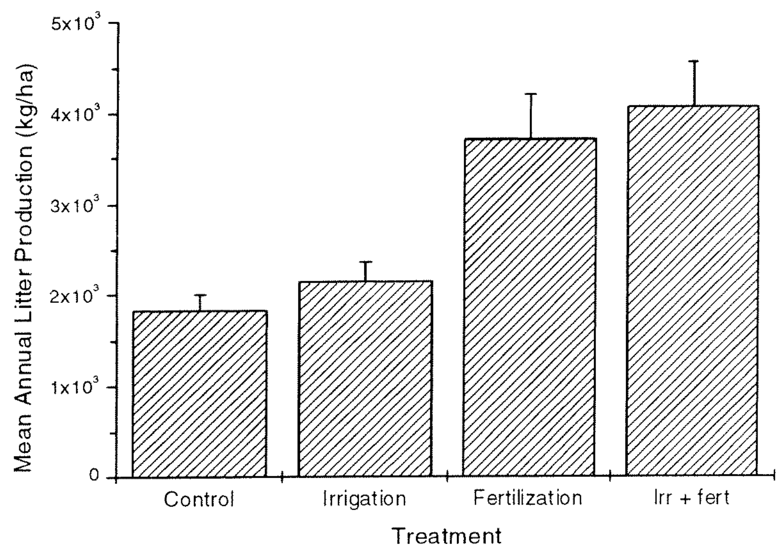

Fig. 3. Mean annual litter production for the control, irrigated, fertilized, and irrigated and fertilized treatment plots at SETRES.

affect either measure of decomposition. The November 1994 sampling point is a deviation from the exponential decay model. Reexamination of the data did not reveal any obvious sampling error. This observation has been previously noted in the literature and has been attributed to a variety of factors including an increase in biomass of invading hetrotrophs, contamination by new litterfall, and dust accumulation (Tamm and Troedsson, 1955; Bocock et al., 1960; Gosz et al., 1973; Klemmedson et al., 1985).

Table 3 shows the initial nutrient levels in the two litter qualities. The low quality litter had significantly ($P < 0.0001$) higher concentrations of Mg and Ca and lower concentrations of K and N compared with the high quality litter. Initial P and C concentrations were not significantly different ($P = 0.53$ and $P = 0.11$, respectively) for the two litter qualities. Over the duration of the study, fertilization significantly ($P < 0.05$) affected all nutrient concentrations except Ca. For Mg, the interaction between block, irrigation, and fertilization was significant ($P = 0.005$). Litter quality significantly affected N ($P = 0.005$), K ($P = 0.02$), Ca ($P = 0.008$), and Mg ($P = 0.005$) concentrations. Irrigation did not significantly affect any nutrient concentration over the study duration. Carbon concentrations were not significantly affected by any main or split-plot effect.

Table 2
Mean decay rates (k), after 3 years, for high and low quality on the control, irrigated, fertilized, and irrigated and fertilized treatment plots at SETRES

Treatment	n	Mean k for high quality (yearr^{-1})[a]	Mean k for low quality (year^{-1})
Control	69	0.33 (0.04) A[b]	0.34 (0.06) A
Irrigation	69	0.35 (0.03) A	0.35 (0.05) AB
Fertilization	69	0.43 (0.04) B	0.41 (0.05) AB
Irrigation + Fertilization	69	0.45 (0.05) B	0.43 (0.05) B

[a] Standard errors are shown in parenthesis.
[b] Within a column, means with the same letter are not significantly different at the $P = 0.05$ level.

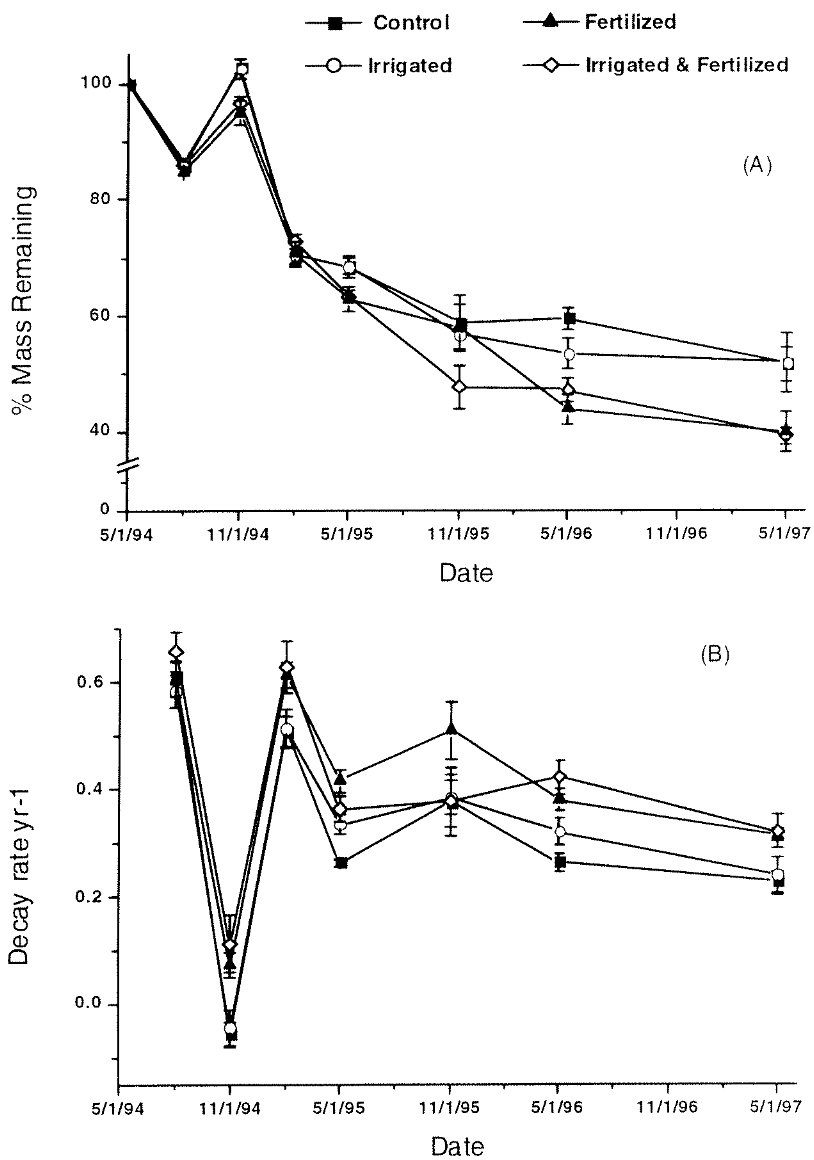

Fig. 4. Low quality litter decomposition, as expressed as percent mass remaining and decay rates, on the control, irrigated, fertilized, and irrigated and fertilized treatments plots.

Table 3
Initial nutrient levels for high and low quality litter (g kg^{-1}) collected from the control and fertilized plots, respectively ($n = 8$)[a]

Quality	Ca	Mg	K	N	P
High	3.46 (0.05) A[b]	0.52 (0.01) A	0.86 (0.03) A	0.37 (0.02) A	0.25 (0.01) A
Low	4.27 (0.02) B	0.77 (0.01) B	0.45 (0.05) B	0.31 (< 0.01) B	0.24 (0.03) A

[a] Standard errors are shown in parenthesis.

[b] For each column, means with the same letter are not significantly different at the $P = 0.05$ level.

6. C/nutrient ratios

The C/N and the C/P ratios declined during the study, and fertilized plots declined more rapidly after the first year (Fig. 5A and B). The decline in C/N and C/P indicates the relative immobilization of these nutrients compared with C. Both the C/N and C/P ratios remained above levels at which mineralization is thought to occur, 30:1 for N (Broadbent, 1957) and 200:1 for P (Schlesinger, 1991). Ratios of C/Ca declined for the first 2 years of the study, then increased in the third year (Fig. 5C). The C/K ratios

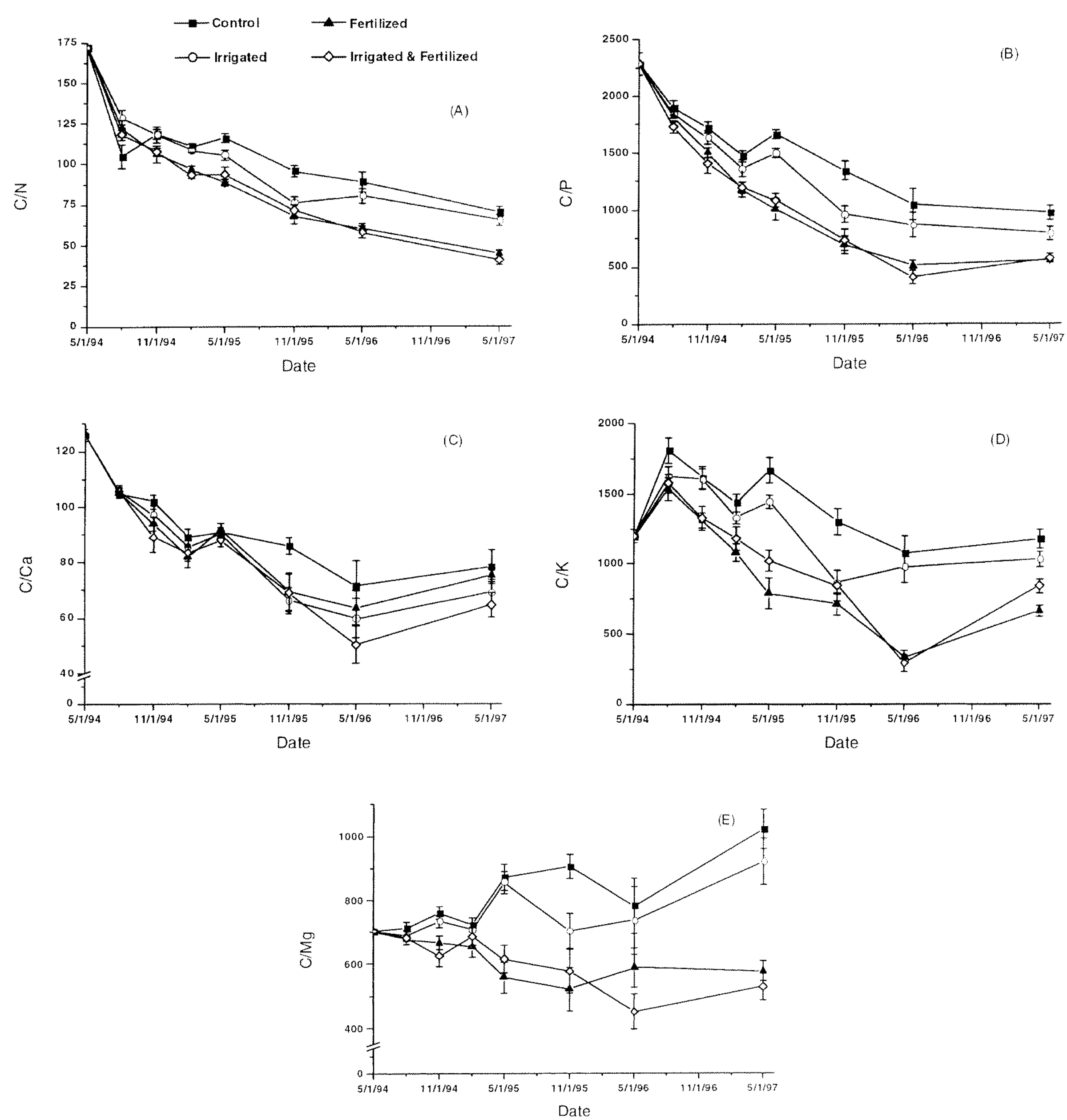

Fig. 5. C/nutrient ratio dynamics over 3 years for the control, irrigated, fertilized, and irrigated and fertilized treatments.

rapidly increased then dropped until the final year of the study, when it increased again (Fig. 5D). Initial increases in C/K ratios were sustained longer in the high-quality needles (1 year) than in the low-quality litter (3 months). Fertilization effects became significant as the C/K ratio dropped. The C/Mg ratio on unfertilized plots remained essentially constant for the first 2 years, but increased during the third year (Fig. 5E). On fertilized plots, the C/Mg ratio gradually declined for the duration of the study.

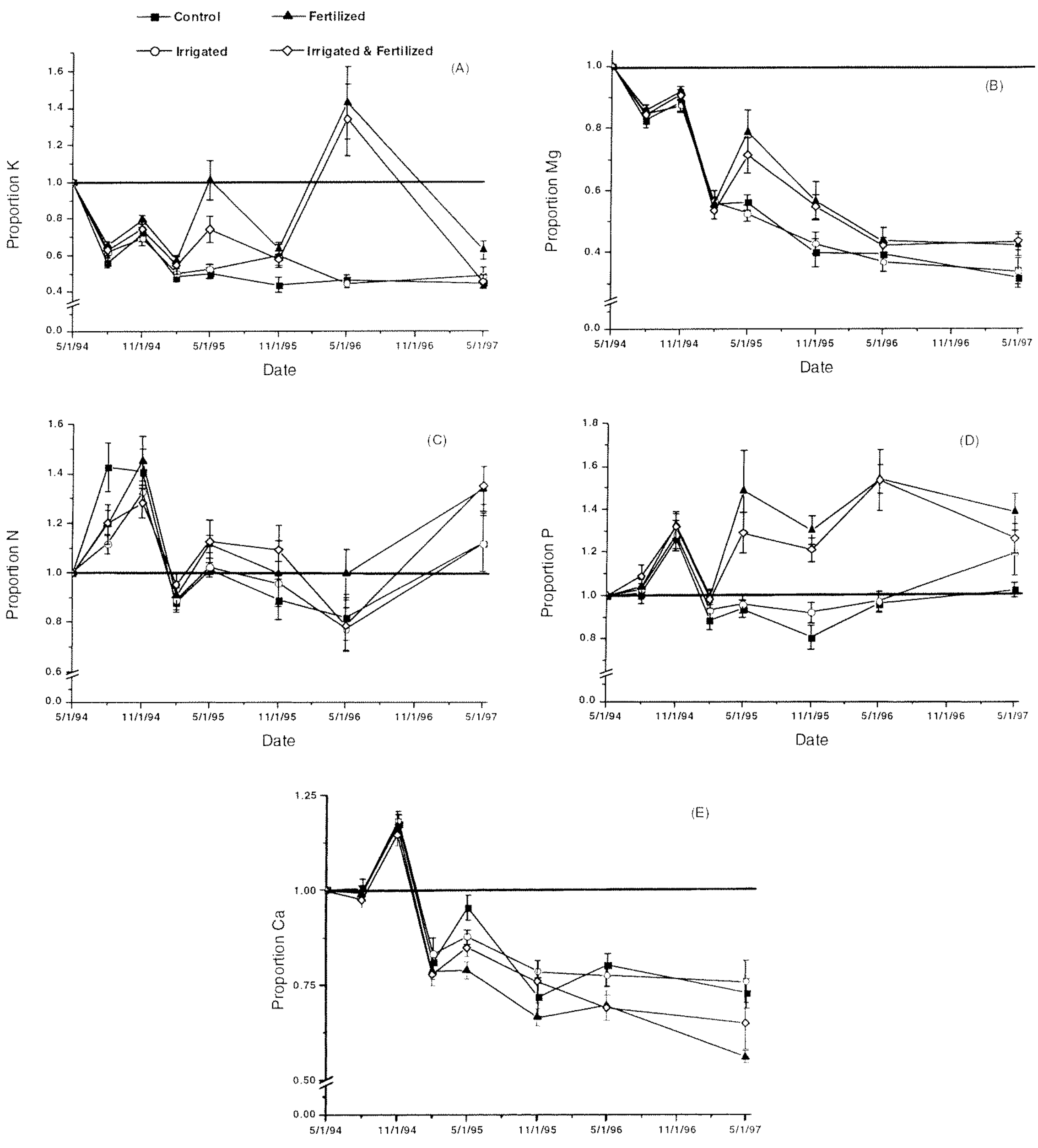

Fig. 6. Proportion of nutrients remaining in the pine litter over 3 years for the control, irrigated, fertilized, and irrigated and fertilized treatments plots.

7. Nutrient dynamics

Potassium was released for the first 9 months of the study then stabilized, except where immobilization occurred on the fertilized plots at the end of the first and second years (Fig. 6A). Magnesium dynamics were similar to K dynamics, except that Mg immobilization occurred only after the first year on the fertilized plots whereas K had two periods of immobilization, after the first and second years (Fig. 6A and B). Nitrogen was immobilized during the first 6 months followed by a gradual release until the end of the second year. Immobilization of N occurred again in the third year (Fig. 6C). Treatment effects on N dynamics were significant only in the third year and greater N immobilization occurred on fertilized plots. For all treatments and in both litter qualities, P was immobilized during the first 6 months of the study and released during the next 3 months (Fig. 6D). Treatment effects became significant for the remainder of the study, with P on the fertilized plots remaining essentially constant until a gradual immobilization occurred during the last year of the study. By contrast, P was strongly immobilized on the unfertilized plots for the remainder of the study. For all the treatments and litter qualities, there was a net accumulation of N and P. This was also demonstrated in the decline of the C/N and C/P ratios (Fig. 5A and B). Calcium was immobilized during the first 6 months, followed by release for the remainder of the study (Fig. 6E). Treatment effects became significant after the first year, when Ca was released at a higher rate on the fertilized than on unfertilized plots.

Phosphorus and N accumulations indicated that decomposing litter was a net sink for these nutrients, and a net source of Mg, Ca, and especially K. The relative nutrient mobilities across all treatments and litter qualities were K > Mg > Ca > N > P. Whereas initial litter quality did not affect the relative mobility of nutrients, it did affect their rate of release and/or accumulation. The high quality litter had higher rates of release for K, lower rates of release for Mg, and lower rates of N accumulation. Litter quality did not significantly affect the rates of Ca release or P accumulation. Fertilization decreased the rate of release of Mg and K in high-quality litter and Mg and Ca in low-quality litter. In addition, fertilization increased the rate of accumulation of P in both litter qualities. Although large spikes in the nutrient concentrations for the litter on the fertilized plots are evident (Fig. 6A–E) and correspond to the fertilization schedule, they quickly return to the general trend exhibited for the specific nutrient.

8. Discussion

At SETRES, the prevailing factor affecting loblolly pine needle decomposition and nutrient dynamics is the exogenous nutrient supply, or fertilization treatment. The endogenous nutrient supply (initial substrate quality) did not affect the decomposition rate, but affected nutrient immobilization and release. Irrigation was not a significant factor in either litter decomposition or nutrient dynamics. This is expected since the soil's sandy texture results in excessive drainage at the site. Drainage resulted in greater water use and loss on the irrigated plots as compared with the non-irrigated plots (Abrahamson et al., 1998). At SETRES, the lack of a significant difference in soil temperature for all the treatments coupled with the excessive drainage at the site may lessen the potential impact of microclimate on litter decomposition and nutrient dynamics. Irrigation may be considered a viable management option on well-drained forest soils in order to minimize the potential for water deficiencies. However, this study indicates that no additional benefit will be realized from the decomposition of the forest floor due to the irrigation of well-drained soils. Irrigation may become a significant factor on litter decomposition and nutrient dynamics on soils with poorer drainage. The objectives (i.e. C sequestration, biomass production) of forest managers should determine whether or not to use irrigation as a management option.

Although loblolly pine litter immobilizes N and P, it is a good source of Ca, Mg, and K. For initial site fertility, N and P are of immediate concern, however, in latter years other nutrients could significantly affect productivity (Sword et al., 1998). Sword et al. (1998) found a negative relationship between foliar K and tannin concentration on plots, where P was no longer deficient. Since the synthesis of secondary metabolites (i.e. tannins) is correlated to mineral nutrition and productivity (Bryant et al., 1993; McKee, 1995), this observation implies that the availability of K and P could influence productivity. Sword et al. (1998)

found no significant relationship for any other nutrient and tannin concentration, but did find an inverse relationship between K availability and Mg uptake. It is not clear if the interaction between the nutrients would significantly affect forest productivity.

Over a rotation, the buildup of litter and associated nutrients can be substantial, especially on the fertilized plots. On a well-drained upland site that had been converted from agriculture to a loblolly pine plantation, it was found that the forest floor built up from nothing to 34.9 Mg/ha by age 34 (Richter et al., 1995). More importantly, on this dry site it was estimated that almost the entire N that was deposited on to the forest floor over the 34-year rotation was still present in the forest floor at age 34. Harvest and site preparation options that incorporate the forest floor into the soil can benefit from these C and nutrient resources (Buford and Stokes, 2000). Conversely, management options that remove or decrease the forest floor, such as litter raking or burning, could result in a negative effect on productivity (Haywood et al., 1996). With the increasing trend to go to shorter rotations, the effects of removing litter may not be observed until later rotations. Decreases in forest productivity in second rotation loblolly and slash pine stands have been reported (Haywood, 1994; Tiarks and Haywood, 1996) and nutrient availability may be a significant contributor to this phenomenon. Properly managing our forests, including the forest floor, will be the key in achieving and maintaining optimal productivity. Additionally, proper management of the forest floor can be important when the goal of land managers is to sequester C in the soil, forest floor, and in above ground biomass.

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