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Influence of Hydroperiod on Litter Conversion to Soil Organic Matter in a Floodplain Forest

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ABSTRACT

Lignin and cellulose dynamics were followed for 23 mo during degradation of foliar litter in an oligotrophic floodplain forest located in south Georgia. Litter was placed in microcosms, which were subjected to hydroperiod variation in terms of duration and nutrient inflow. Treatments were compared in terms of rates of lignin and cellulose loss and the degree to which a theoretical asymptotic value of the ratio of lignin to lignin plus cellulose (LCI) was approached. Flooding strongly stimulated loss rates of lignin and cellulose, and results suggest that a single, relatively brief flooding event promoted loss rates to the greatest extent. The elevation of N inflow reduced lignin degradation rates compared with other flooding treatments. Observed temporal patterns of LCI ratios did not follow theorized patterns and may suggest that, in warm climates such as south Georgia, lignin loss is greater than in boreal forest systems where theoretical LCI relationships were developed.

A FOCAL POINT for many processes within forest ecosystems is the SOM pool and, consequently, its importance is well recognized. In addition to representing a critical interface for energy flow and nutrient circulation within forests (Swift et al., 1979; Kimmins, 1987), the maintenance of the SOM pool has, in recent years, attracted attention in regard to its direct relationship to vegetation productivity. In the latter context, SOM represents one of the primary keys to maintenance of forest ecosystem sustainability (Powers et al., 1990). Also, in wetland systems that are subject to high geochemical inputs of N and P from anthropogenic sources, initial element retention may be associated with organic matter dynamics as litter is converted to SOM (Richardson, 1985).

Although numerous investigations in upland forests have examined factors that control Phase I decomposition dynamics (Berg, 1986; Melillo et al., 1989; Swift et al., 1979; Vitousek et al., 1994; Rustad, 1994; and many others), fewer studies of that nature have occurred in forested floodplains where the nature of the decomposition environment can be quite different. While wetting–drying cycles (i.e., alternating periods of adequate vs. deficient water) frequently drive decomposition dynamics in uplands, moisture availability to decomposer organisms usually ranges between adequate to excessive in many floodplain systems (Lockaby et al., 1996). As is the case with all ecological processes in wetlands, hydroperiod is the dominant influence on decomposition although confusion exists with regard to the nature of that influence (Lugo et al., 1990). The confusion stems from the highly variable nature of hydroperiod both within and among individual forested wetlands. The high degree of variation causes this important influence to be difficult to study in a cause–effect manner.

One approach that has been advocated for examining the transition of organic matter from litter to SOM focuses on changes in lignin/lignin + cellulose (LCI) ratios during that process (Melillo et al., 1989). According to those authors, the LCI ratio increases rapidly in accordance with mass loss during Phase I and then approaches 0.7 as Phase II is achieved. The second Phase is controlled by degradation of recalcitrant materials such as lignin (Berg, 1986) and is, consequently, more stable than its predecessor. While the time required to achieve a LCI = 0.7 may vary significantly among systems (as a function of initial litter quality and the nature of the decomposition environment), reports from upland hardwood systems of the northeast USA indicate that as long as 60 mo may be necessary (Melillo et al., 1989).

One aspect of lignin dynamics that is particularly unclear is the influence of elevated N (and to a lesser extent, P) on decomposition. Reports conflict in terms of the direction of influence (i.e., decrease, no change, increase) that may occur in mass loss following elevation of N (Fog, 1988) or P (Peterson et al., 1993). While some investigations of this influence have taken place in aquatic or wetland habitats (Peterson et al., 1993; Deghi et al., 1980), additional research seems warranted in view of contradictory findings.

Given that hydroperiod is the dominant factor in controlling conversion of litter to SOM in floodplain forests, the primary objective of the following study was to investigate the role of hydroperiod variation (i.e., duration and frequency) on the SOM formation process. In addition, a secondary objective was to examine the effects of elevated N and P on the same process.

METHODS

Study Site

The study utilized the eastern floodplain of the Ogeechee River near Savannah, GA. The flood plain is occupied by a mature, uneven-aged stand of mixed (primarily deciduous) species composed of laurel oak (*Quercus laurifolia*), sweetgum (*Liquidambar styraciflua* L.), water oak (*Q. nigra* L.), black gum (*Nyssa sylvatica* Marshall), and swamp tupelo [*Nyssa sylvatica biflora* (Walter) Sarg.]. Ground vegetation consists primarily of switch cane [*Arundinaria gigantea* (Walter) McClure]. Flooding in that system occurs predominantly from winter through spring on an intermittent basis. Soils are classified as inceptisols. Daytime river temperatures near the study site ranged from 22 to 32°C during the study period (Georgia Department of Natural Resources).

The Ogeechee River is a low-gradient, blackwater system

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Abbreviations: LCI, lignin to lignin plus cellulose; SOM, soil organic matter; ANOVA, analysis of variance; NF, no flooding; F6, flooded for 6 mo; F3, flooded for 3 mo; F2/2, flooded for 2 mo, nonflooded for 1 mo, reflooded for 2 mo; FP, flooded for 3 mo with elevated P; FN, flooded for 3 mo with elevated N.

and consequently carries low sediment and nutrient loads. In general, concentrations of total P and N in river waters average 0.1 and 1.0 mg L^{-1}, respectively. Extractable P in surface soils of the eastern floodplain average 7 mg kg^{-1} (Bray 2 extraction), which is near the deficiency level for many hardwoods in the southeastern USA (Harvey Kennedy, USDA Forest Service, Southern Hardwoods Laboratory, Stoneville, MS, 1992, personal communication).

Approach

Many of the previous efforts related to examining linkages between hydroperiod and decomposition have taken a gradient or correlative approach. This might be typified by characterization of spatial variation (in some cases, combined with temporal) in litter mass and nutrient pools across a wetness gradient within a floodplain forest (Bell and Sipp, 1975; Brinson, 1977; Bell et al., 1978; Peterson and Rolfe, 1982; Shure et al., 1986). However, since multiple factors such as litter quality and quantity as well as the nature of the decomposition environment change along those gradients, these studies were limited in terms of their ability to elucidate causal mechanisms.

The need for greater emphasis on ecological studies of a manipulative nature has been stressed (Eberhardt and Thomas, 1991). There have been efforts to accomplish that by developing experimental approaches that lend themselves more to a cause–effect interpretation, and these have frequently utilized microcosm designs (Yarbro, 1979; Day, 1983; Cuffney and Wallace, 1987; Taylor and Parkinson, 1988). In some cases, these took place in laboratory environments and, as noted by Day (1983) and Hagvar (1988), may have suffered from excessive departure from realistic conditions.

Consequently, we developed an experimental approach that would function in a field environment. We designed a simple microcosm that allowed considerable manipulation of hydroperiod characteristics primarily for the purpose of studying surface litter decomposition. Within this design, we are minimizing variation in litter quality (albeit with native materials) and focus on studying the effect of manipulations of the decomposition environment.

Microcosm chambers consist of plastic cylinders that are 0.45 m in diameter and 1.0 m in height. To ensure a reasonable degree of mixing (and oxygenation) in water within chambers, the inflow spout was placed 35 cm above the 30-cm water level, the latter being controlled by the height of the outflow line. Flooding was accomplished using water from the nearby Ogeechee River. Levels of dissolved oxygen within flooded microcosms averaged 5 to 6 mg L^{-1} and were uniform among individual microcosms. Those levels were also very similar to those occurring simultaneously in the Ogeechee River. Cylinders remained open on the upper end so that litter could be exposed to throughfall precipitation as would be the case under natural conditions.

The lower end, buried to a depth of 45 cm, also remained open and was inserted over a minimally disturbed soil core of the same diameter. The soil core had surrounding soil removed for that purpose. After the cylinder was inserted over the central soil core, displaced soil was back-filled around the cylinder's exterior. A narrow band of chemically nonreactive silicon caulk was used to help seal the interface between the interior cylinder wall and the soil core.

Twenty-four microcosms of this design were installed on the Ogeechee floodplain underneath the forest canopy. The microcosms were installed in a randomized complete-block design with four replications and six treatments. Blocking was based on spatial patterns of homogenous soil properties (i.e., pH, extractable P, and organic matter in the surface 7.6 cm).

Table 1. Percentage of original cellulose, lignin, and LCI indices compared among treatments at Month 23.

Treatments†	Cellulose*	Lignin*	LCI**
NF	54.3a	70.0a	0.46ab
F6	24.1b	31.7bc	0.49ab
F3	18.3b	16.3c	0.41b
F2/2	27.2b	39.2bc	0.51ab
FP	30.1b	37.7bc	0.41b
FN	29.4b	48.4ab	0.53a

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† NF = no flooding; F6 = flooded for 6 mo; F3 = flooded for 3 mo; F2/2 = flooded for 2 mo, nonflooded for 1 mo, reflooded for 2 mo; FP = flooded for 3 mo with elevated P; FN = flooded for 3 mo with elevated N.

Treatments were initiated in May 1992 and consisted of the following: (1) no flooding (NF), (2) flooded continuously for 6 mo (F6), (3) flooded continuously for 3 mo (F3), (4) flooded for 2 mo, nonflooded for 1 mo, reflooded for 2 mo (F2/2), (5) flooded continuously for 3 mo with elevation of P (FP), and (6) flooded continuously for 3 mo with elevation of N (FN).

Elevation of N and P inflow was accomplished by drip application of a concentrated nutrient solution near the inflow. The concentrations of drip solutions were determined by flow rates within particular microcosms. Flow rates were checked each time drip solutions were replaced, and drip rates were adjusted accordingly. Once adjusted, constant drip rates were maintained with the use of peristaltic pumps. Target concentrations within microcosms associated with elevated nutrient treatments reflected 10-fold increases over those observed in the river (i.e., targets were 1 and 10 mg L^{-1} for P and N, respectively). Nitrogen and phosphorus were elevated using ammonium chloride and potassium phosphate sources, respectively.

Seven litterbags, each filled with ≈10 g of a common species mix of air-dried abscised foliage, were utilized per chamber. Abscised foliage was collected in littertraps and was comprised of laurel oak, sweetgum, water oak, black gum, and swamp tupelo leaves. The foliage of the species was mixed within bags in proportion to the frequency of occurrence within litterfall. Bags were 12.7 by 12.7 cm in size and were constructed of nylon mesh with 6-mm openings on the upper side and 2-mm openings on the underside. Litterbag collection schedules were 0, 0.25, 11.0, 14.0, 17.0, 20.0, and 23.0 mo.

The initial litter N/P ratio and LCI were 8.1 and 0.34, respectively. The N/P ratios of this nature (i.e., <10) have been suggested to indicate that P is probably not limiting to the decomposition process (Vogt et al., 1986). The LCI values near 0.40 are indicative of moderate litter quality (Melillo et al., 1989). Lignin and cellulose were determined using forage fiber analyses (Van Soest and Wine, 1968), which have been reported to be superior to forest product techniques (Technical Association of the Pulp and Paper Industry, 1969, 1975) for

Table 2. Comparison of rates of change in cellulose and lignin concentrations during 23-mo decomposition period.

Treatment†	Cellulose*	Lignin*
NF	−0.62b	−0.31b
F6	−0.87a	−0.39ab
F3	−0.92a	−0.49a
F2/2	−0.85a	−0.34b
FP	−0.78ab	−0.35ab
FN	−0.79ab	−0.33b

* Significant at the 0.05 probability level.
† NF = no flooding; F6 = flooded for 6 mo; F3 = flooded for 3 mo; F2/2 = flooded for 2 mo, nonflooded for 1 mo, reflooded for 2 mo; FP = flooded for 3 mo with elevated P; FN = flooded for 3 mo with elevated N.

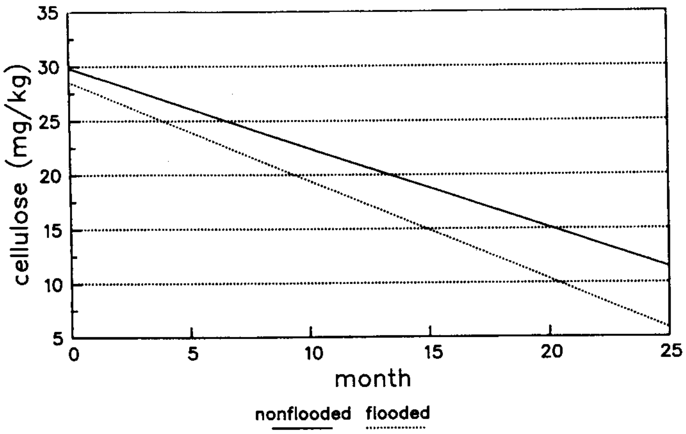

Fig. 1. Generalized patterns of cellulose loss under flooded vs. nonflooded conditions.

those analyses of foliar litter in decomposition studies (Ryan et al., 1990).

Statistical analysis consisted of ANOVA at Month 23 comparing LCI, percentage lignin, and percentage cellulose remaining as response variables. In addition, lignin and cellulose loss rates were determined for each treatment by regressing lignin and cellulose concentrations against time and the absolute values of the resulting *k* values were also compared via ANOVA. Means were separated using Duncan's New Multiple Range Test, and probabilities of a greater *F* of 10% or less are reported.

RESULTS AND DISCUSSION

Cellulose and Lignin Relationships

Comparisons of the proportion of original cellulose remaining at Month 23 indicated that flooding stimulated cellulose loss (Table 1). All flooding treatments exhibited greater cellulose losses at Month 23 than nonflooded. Treatments F3 and F6 retained only approximately one-third the quantity of cellulose as did the NF. Those treatments, in conjunction with F2/2, also displayed the most rapid rates of cellulose loss (Table 2).

Lignin degradation was similarly stimulated by flooding (Table 1). Seventy percent of the original lignin remained in NF treatments while residual lignin associated with flooding treatments ranged between 16 and 48%. As was the case with cellulose, the F3 and F6 treatments reduced lignin quantities to the greatest extent (Tables 1 and 2). Compared with other flooding treatments, the FN treatment had the highest amount of lignin remaining, was not statistically different from the NF, and had the slowest loss rate (Table 2) numerically. Thus, the largest losses of cellulose and lignin occurred in Treatment F3, which was associated with a single, relatively brief inundation period. Comparisons of F3 vs. F6 indicate that additions of N in the same inundation scenario significantly reduced lignin loss (Tables 1 and 2).

Although Dierberg and Ewel (1984) found that N elevation (in terms of both litter quality and the decomposition environment) as sewage sludge stimulated mass loss in baldcypress [*Taxodium distichum* (L.) Rich.] domes, Deghi et al. (1980) reported no measurable effect on mass loss due to effluent application. Hunt et al.

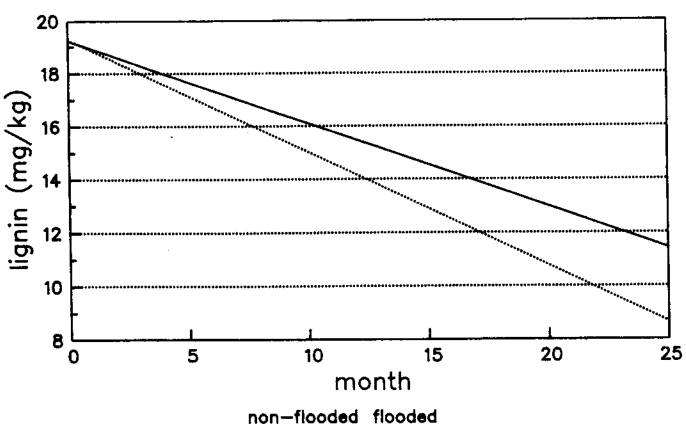

Fig. 2. Generalized patterns of lignin loss under flooded vs. nonflooded conditions.

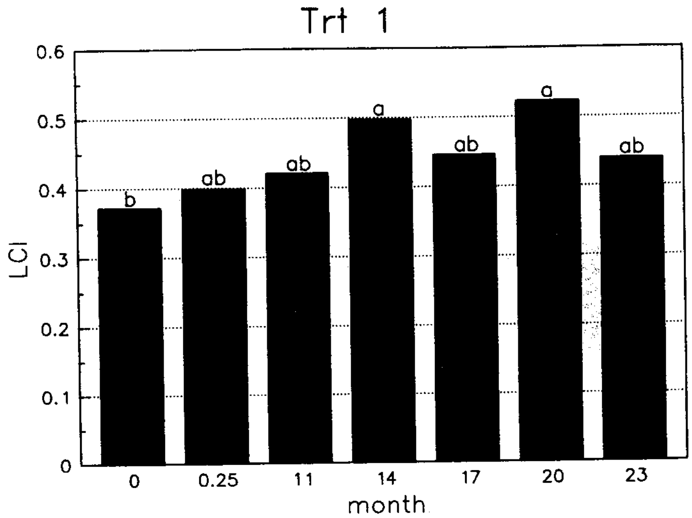

Fig. 3. Changes in lignin to lignin plus cellulose (LCI) values in litterbags subjected to nonflooded conditions.

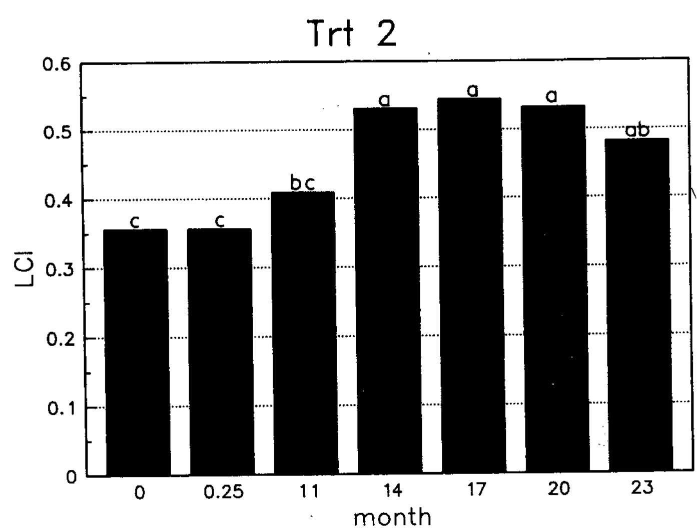

Fig. 4. Changes in lignin to lignin plus cellulose (LCI) values in litterbags subjected to 6-mo flooding regime.

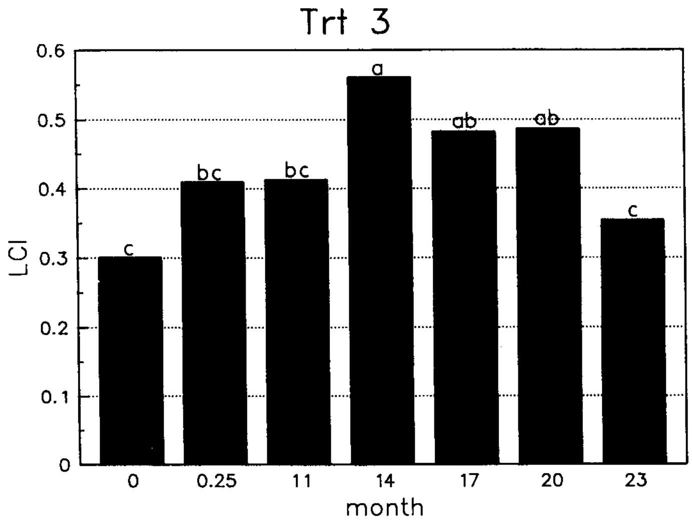

Fig. 5. Changes in lignin to lignin plus cellulose (LCI) values in litterbags subjected to 3-mo flooding regime.

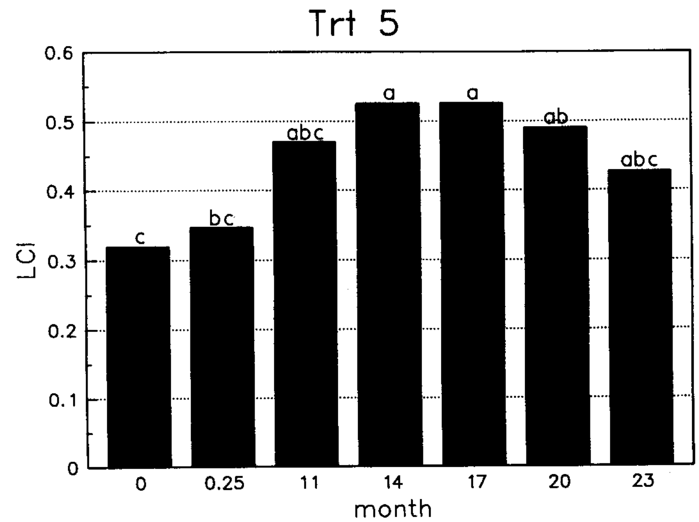

Fig. 7. Changes in lignin to lignin plus cellulose (LCI) values in litterbags subjected to 3-mo flooding plus elevated P.

(1988) found decomposition of grasses to be positively influenced when NH_4NO_3 was applied. Howarth and Fisher (1976) reported increased mass loss following enrichment of stream microcosms with NO_3 but no effect when phosphate solutions were added. Similarly, Aumen et al. (1985) and Peterson et al. (1993) reported little effect of P enrichment on lignocellulose and mass loss, respectively. However, both lignin and cellulose degradation were stimulated when phosphate and NO_3 solutions were added simultaneously (Aumen et al., 1985). In his review, Fog (1988) cites numerous reports that indicate that N has the potential to suppress decomposition rates and, in particular, lignin degradation. An exception to the reports of P non-effects is the work of Elwood et al. (1981) where P additions promoted mass loss in red oak (*Q. rubra* L.) litter within streams.

Generalized effects of flooding vs. nonflooding on cellulose and lignin loss are provided in Fig. 1 and 2. In both cases, flooding accelerates reductions in concentrations. This is probably due primarily to enhanced microbial activity following flooding and, secondarily, to greater disintegration and subsequent export during contact with floodwaters (Boulton and Boon, 1991).

Lignocellulose Indices

Lignocellulose ratios (Table 1) indicated that Treatments F3 and FP had approached SOM formation to the least extent. In the case of F3, this was because both lignin and cellulose were lost rapidly, while in the case of FP, a high residual cellulose value generated a low LCI. Treatment FN, where cellulose loss was moderate but lignin loss was relatively low, most closely resembled SOM and exhibited LCI values associated with the transition from Phase I to Phase II dynamics by Melillo et al. (1989). Statistical separation between FN vs. FP and F3 treatments provided a clear indication of the acceleration of SOM formation provided by elevated N.

Temporal patterns of LCI ratios show increases until

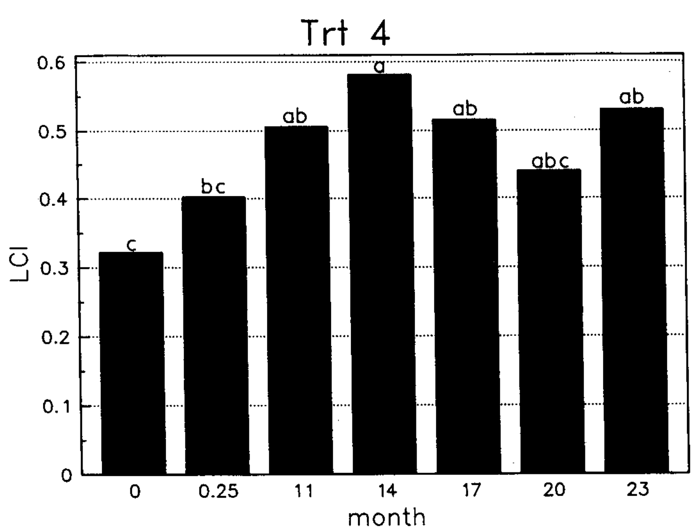

Fig. 6. Changes in lignin to lignin plus cellulose (LCI) values in litterbags subjected to discontinuous 2 + 2-mo flooding regime.

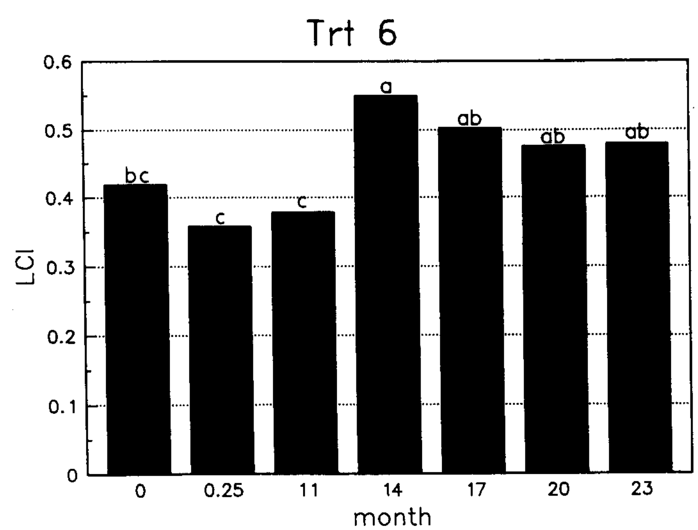

Fig. 8. Changes in lignin to lignin plus cellulose (LCI) values in litterbags subjected to 3-mo flooding plus elevated N.

approximately Month 17 for all treatments (Fig. 3–8). Thereafter, further increases in LCI were not apparent. In treatments NF and F3, LCI values declined significantly in Month 23 and numerical decreases were observed in some of the other treatments. The failure of LCI to increase as well as, in some cases, to decrease during the latter stages of the 23-mo period suggests that lignocellulose dynamics associated with sites where inundation is a dominant influence and temperatures are warm may differ from those of less dynamic, upland forest soils at higher latitudes. Alternatively, as described by Melillo et al. (1989), the rate of LCI increase declines as the asymptotic value of 0.7 is approached so that, if later analyses were available in this study, higher values might be observed.

Although both lignin and cellulose loss seemed to be stimulated by flooding, there was no differentiation between flooding vs. nonflooding in terms of LCI values. These data indicate that rapid decomposition such as that reflected by Treatment F3 (i.e., high cellulose and lignin losses) may not correspond to rapid SOM formation. Alternatively, the data suggest that N contamination of streamwater has the potential to reduce lignin degradation and thereby hasten the formation of SOM in riparian areas subject to flooding. Elevated P (FP) did not produce a readily definable effect on either cellulose or lignin losses.

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