

Comparing Native and Exotic Litter Decomposition and Nutrient Dynamics

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ABSTRACT

Melaleuca (*Melaleuca quinquenervia* [Cav.] Blake) has been one of the most problematic invasive species in the Florida Everglades' ecosystem. This exotic tree has colonized and thrived in most natural areas of South Florida, including the pine-cypress ecotone forest. Mechanical and chemical control programs have contained the spread, and biological agents have largely eliminated the invasive potential of existing melaleuca populations. However, live trees remain a part of the vegetative landscape and are targets for future management. Treatment of these populations has been justified in part by hypothesized changes in the rate of organic matter decomposition and nutrient release from exotic litter. We investigated these questions with the primary hypothesis that melaleuca litter will have the slowest rate of decomposition and the slowest rate of carbon, nitrogen, and phosphorus turnover compared to cypress and pine litter. As hypothesized, the residence time of melaleuca litter was significantly longer than cypress litter. However, the residence time of the melaleuca litter was significantly shorter compared to pine litter. In addition, melaleuca litter did not alter nitrogen or phosphorus release rates compared to the native species. Treating remnant melaleuca populations with chemical or mechanical methods may cause significant collateral damage to native plant communities and may negatively influence ecosystem function. Research is needed to determine if the benefits outweigh the costs to plant communities from the continued treatment of this exotic, but now less invasive plant.

Key words: decomposition, invasion, *Melaleuca quinquenervia*, nutrient.

INTRODUCTION

The invasion of exotic plants into natural areas may cause significant alterations to plant community structure and ecosystem function (Martin et al. 2009, Mack and D'Antonio 2003, Rothstein et al. 2004, Standish et al. 2004). As a result, invaded ecosystems may provide fewer critical services such as wildlife habitat and nutrient storage and cycling (Ehren-

feld 2003, Martin et al. 2009). The aforementioned studies and others have provided justification for the management of invasive plant populations; however, not all ecosystems undergo functional changes after invasion and, in certain cases, continual management of exotic plants may endanger critical processes. We investigated the consequences of the invasion of the Australian tree *Melaleuca quinquenervia* (Cav.) Blake on organic matter decomposition and nutrient turnover to evaluate the need for continued management of this species beyond that provided by classical biological control.

Melaleuca quinquenervia, otherwise known as the paperbark tree, is a member of the Myrtaceae family, subfamily Leptospermoidae. This tall evergreen tree historically occupies tropical wetland sites throughout its native range along the eastern coast of Australia (Kaufman and Smouse 2001). It was introduced into South Florida in 1886 originally for sale as an ornamental, but later was used for erosion control, as a forestry crop, and as an agricultural windrow plant (Meskimen 1962, Stocker and Sanders 1981, Dray et al. 2006). Although this exotic tree colonized and thrived in most natural areas of South Florida, one ecosystem that has been extensively invaded is the *Pinus elliotii* Englem—*Taxodium distichum* (L.) L.C. Rich var. *nutans* (Ait.) Sweet ecotone forest (Myers 1984). This is the transition zone between upland *P. elliotii*-dominated sites and depressional *T. distichum*-dominated swamps, where both trees codominate but neither grows to its full potential (Myers 1983). Invasion in these systems is managed using a combination of chemical, mechanical, and biological methods. Classical biological control has radically reduced seed production while increasing the mortality of existing populations (Tipping et al. 2008, 2009). Overall, the highly successful integrated program has contained the spread and largely eliminated the invasive potential of existing *M. quinquenervia* populations (Tipping et al. 2008, 2009, Van Driesche et al. 2010).

Despite these changes in the invasive status of this plant, chemical and mechanical management continues in many of Florida's natural areas, justified in part by assumed differences in functional traits between *M. quinquenervia* and the replaced natives, *P. elliotii* and *T. distichum*. One of these proposed differences is the rate of organic matter decomposition (Gordon 1998, Ehrenfeld 1999). *Melaleuca alternifolia*, a close relative of *M. quinquenervia*, is known to produce volatile essential oils with antimicrobial properties (Carson et al. 2006). DiStefano and Fisher (1983) found that extracts of *M. quinquenervia* leaves reduced fungal infections of plant embryos. A 1999 report suggested that *M. quinquenervia* can alter rates of decomposition and increase the storage of organic material (FL Exotic Pest Plant Council 1999); however, no research has directly measured the rate of *M. quinquen-*

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eria litter decomposition and its effect on nutrient storage and cycling in South Florida ecosystems. The primary hypothesis tested in this study was that *M. quinquenervia* litter will have the slowest rate of decomposition and the slowest rate of carbon, nitrogen, and phosphorus turnover compared to *T. distichum* and *P. elliotii* litter.

MATERIALS AND METHODS

Site Description

The study was located in the Belle Meade Tract of the Picayune Strand State Forest in Collier County, Florida. This area consists of nearly level, poorly drained, low fertility soils that are loamy, siliceous, hyperthermic Arenic Glossoqualls. The soil series is Pineda-Boca-Hallandale, which is characterized by moderately to poorly drained sands that overlie limestone bedrock to a depth of approximately 1.4 m (USDA 1998). The water table fluctuates annually between >15 cm below the soil surface to approximately 25 cm above. The area has a wet season from approximately July to December and a dry season from January to June. Average annual rainfall is approximately 1.36 m (SERC 2007). Historically, the vegetation in this area was a mixed *T. distichum*—*P. elliotii* forest with a hardwood under-story. Over the past several decades, many areas have been invaded by *M. quinquenervia* and are now composed of sparse populations of mature trees with dense understories of saplings that can exceed 100 plants per square meter.

In early April 2007, twenty-five 1 m² plots were established along five transects in two contiguous study areas (10 transects total): area #1, a forest of reproductive *M. quinquenervia* with an under-story of saplings and area #2, a mixed *T. distichum*—*P. elliotii* forest with a hardwood under-story and no *M. quinquenervia*. Each transect was 100 m long and spaced a distance of 25 m from the nearest transect. Leaves or needles that were senescent but still attached were collected from trees in every plot (n = 25 in each study site) for *M. quinquenervia* (area #1), *T. distichum* (area #2), and *P. elliotii* (area #2). Samples were air dried to a constant weight and analyzed for initial chemical composition and nutrient concentration. Because there were no significant differences between transects for any of the measured variables, the leaves or needles collected from each plot were combined to create a pooled sample for each plant species.

Experimental Approach

Litter bags were constructed using 1 mm mesh fiberglass screen. Samples of 2 g dry weight of litter (leaves or needles) from each species were placed into separate 15 by 15 cm, fiberglass mesh litter bags deployed at three locations within a noninvaded, mixed *T. distichum*—*P. elliotii* forest adjacent to area #2. Litterbags of each species were replicated three times within a location and held in place on the ground using staples. Samples were deployed in the field in late August of 2007 and collected from each location at 6 week and 3, 6, and 12 month intervals. Decay rate was calculated as the percentage mass lost after 1 year. Decomposition rate constants (k_d) were calculated using a single exponential model that

assumed a constant fraction of litter mass was lost per unit time: $k_d = -\ln(M_t/M_0) t^{-1}$ (Olson 1963), where M_t is the mass at time t and M_0 is the original mass of litter. The mean residence time, or time required for the litter to decompose under steady state, was calculated as $1/k$ (Chapin et al. 2002).

Litter Component Analyses

Organic matter was measured by loss on ignition from 0.2 to 0.5 g samples of dried and ground plant material, which were first measured into 50 mL beakers (Luczak et al. 1997). The beakers were placed in a muffle furnace and brought to 250 C for 30 min. The furnace temperature was then increased to 550 C for 4 h. Organic matter content was calculated as the mass loss on ignition on a dry weight basis.

Chemical composition was measured with a sequential extraction using an Ankom A200 Fiber Analyzer (Rowland and Roberts 1994). One-half gram of coarsely ground litter material was weighed and sealed into Ankom filter bags. The bags were extracted with a neutral detergent to remove soluble cellular contents (sugars, carbohydrates, lipids, etc.) followed by an acid detergent to remove hemi-cellulose. Cellulose was removed by soaking the bags in 72% sulfuric acid (H₂SO₄) for 3 h. The residual (lignin and ash) was combusted at 550 C for 4 h to determine ash content. Chemical composition was calculated on a dry mass basis. The lingo-cellulose index (LCI) is defined as the ratio of lignin (L) to lignin and cellulose (C) in the litter material: $LCI = L * (L + C)^{-1}$ (DeBusk and Reddy 1998, Melillo et al. 1989).

Dried and ground plant material was analyzed for carbon and nitrogen on a Thermo-Electron, 1112 Series elemental analyzer. Total phosphorus was determined by a two-phase acid extraction after loss on ignition (Andersen 1976, Martin et al. 2009). Total phosphorus was measured with an automated ascorbic acid method on a Bran and Luebbe Auto Analyzer 3, Digital Colorimeter (Method 365.4; USEPA 1993). Storages are defined as the mass of dry weight litter remaining multiplied by the concentration of carbon, nitrogen, and phosphorus, at each sample interval. Percent change in pools is defined as the percent change in the storage of carbon, nitrogen, and phosphorus at each sample interval compared to the initial storage. Nutrient ratios were all calculated on a mass basis. Relationships between nutrient concentrations and ratios and the residence time of litter were compared with linear regressions for each individual species and all species combined.

Statistical Analyses

Mean values of measured vegetation characteristics and decomposition rates were calculated for each sample date. ANOVA and Tukey means separation tests were used to evaluate any differences among the measured parameters. Differences were reported as significant for tests with p values ≤ 0.05 . All statistical analyses were performed using JMP 7.0.1 software (SAS Institute, North Carolina, USA).

Full models were run including the main effects (species and sample interval), block effects, and all interactions. Based on the magnitude of the results, species and sample interval were the most important factors influencing the re-

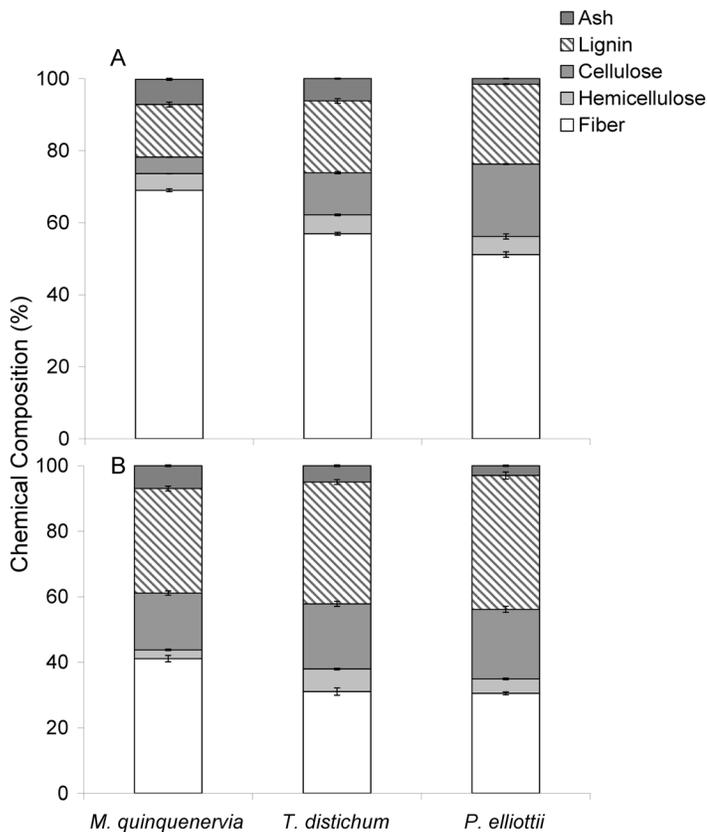


Figure 1. Mean (\pm S.E.) percent chemical composition of each plant species during the (A) initial and (B) final sample intervals.

sponse variables. Although there were consistent block effects for many of the measured variables, this effect did not change the pattern among the three plant species over time.

RESULTS AND DISCUSSION

Organic Matter Turnover

Organic matter decomposition and the subsequent release of plant available nutrients is a vital ecosystem process. The decomposition of plant-derived organic matter occurs in three phases: (1) initial losses due to the leaching of soluble chemical compounds, (2) microbial colonization and degradation, and (3) physical and biological fragmentation (Chapin et al. 2002). All three phases of decomposition are controlled by both biotic and abiotic factors (Berg 2000). For example, plant residues with higher concentrations of nitro-

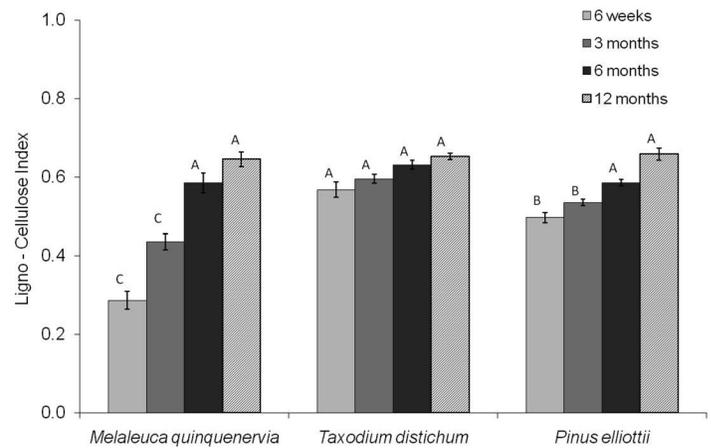


Figure 2. Mean (\pm S.E.) ligno-cellulose index values of each plant species during the (A) initial and (B) final sample intervals. Letters indicate significant differences for each sample interval only.

gen and phosphorus and lower ratios of resistant materials (e.g., lignin) to soluble fibers (e.g., sugars and carbohydrates) often have faster decomposition rates (Berg 2000, Chapin et al. 2002, Mack and D'Antonio 2003). In addition, environmental factors such as temperature, moisture, and pH can alter the structure and function of microbial communities that process organic matter (Couteaux et al. 1995, Katterer et al. 1998, Chapin et al. 2002).

Several studies have shown that ecosystem invasion by exotic plants can significantly alter the rates of organic matter decomposition and nutrient turnover (Pidgeon and Cairns 1981, Baruch and Goldstein 1999, Ehrenfeld 2003, Rothstein et al. 2004, Standish et al. 2004). These changes can be in part the result of differences in the chemical composition (e.g., concentration of soluble fiber vs. lignin) of native and exotic plants (Baruch and Goldstein 1999, Ehrenfeld 2003). Contrary to our hypothesis that *M. quinquenervia* litter would contain the highest concentrations of lignin, *M. quinquenervia* had the highest concentration of soluble materials and the lowest concentration of lignin, both initially and at the 12 month sample interval (Figure 1). The percentage of soluble fiber in the litter was affected primarily by species ($F_{2,95} = 429.4$, $p < 0.0001$) and secondarily by sample interval ($F_{3,95} = 79.1$, $p < 0.0001$). There was a significant interaction between species and sample interval ($F_{6,95} = 9.5$, $p < 0.0001$) caused by the greater initial loss of soluble fiber in the *M. quinquenervia* litter. The *P. elliotii* litter had the highest percentage of lignin both initially and in the last sampling date, followed by the *T. distichum* litter, and then *M. quinquenervia*

TABLE 1. MEAN (\pm S.E.) DECOMPOSITION CONSTANTS AND RESIDENCE TIMES OF LITTER OF EACH PLANT SPECIES (LOWER CASE LETTERS INDICATE SIGNIFICANT DIFFERENCES FOR EACH ANALYSIS).

Species	Decay rate (% mass lost yr ⁻¹)	Decomposition constant, k (yr ⁻¹)	Residence time, 1/k (yr)
<i>Taxodium distichum</i>	53.1 \pm 1.9 a	0.76 \pm 0.04 a	1.34 \pm 0.07 a
<i>Melaleuca quinquenervia</i>	37.0 \pm 1.8 b	0.47 \pm 0.03 b	2.19 \pm 0.13 b
<i>Pinus elliotii</i>	30.9 \pm 1.3 c	0.37 \pm 0.02 b	2.75 \pm 0.13 c
P	<0.0001	<0.0001	<0.0001

($p = 0.0001$; Figure 1). The percentage of lignin was influenced by both species ($F_{2,95} = 203.3$, $p < 0.0001$) and sample interval ($F_{3,95} = 136.1$, $p < 0.0001$). There was a significant interaction between species and sample interval ($F_{6,95} = 9.2$, $p < 0.0001$) caused by the greater initial gain of lignin in the *T. distichum* litter.

In addition, the LCI was lowest in the *M. quinquenervia* litter at the 6 week sample interval indicating a greater substrate quality or carbon availability. The LCI was affected by sample interval ($F_{3,95} = 88.5$, $p < 0.0001$) and species ($F_{2,95} = 59.3$, $p < 0.0001$; Figure 2). There was a significant interaction between species and sample interval ($F_{6,95} = 16.2$, $p < 0.0001$) caused by the greater initial increase in the LCI ratio of *M. quinquenervia* litter. Both the lignin concentration and the LCI increased in all three plant species by end of 12 months, presumably as a result of the preferential degradation of soluble carbon compounds and cellulose during organic matter decomposition (Chapin et al. 2002).

As hypothesized, the *T. distichum* litter had the fastest rate of decay ($F_{2,23} = 43.1$, $p < 0.0001$; Table 1; Figure 3). However, contrary to our hypotheses, the decay rate of the *M. quinquenervia* litter was significantly shorter than *P. elliotii* litter (Table 1), indicating that *M. quinquenervia* invasion into a *P. elliotii*—*T. distichum* ecotone forest may not significantly increase rates of organic matter turnover. At the end of the year, the *T. distichum* litter lost 53% of its weight, the *M. quinquenervia* litter lost 37%, and the *P. elliotii* litter lost 31% (Table 1; Figure 3). Further study is needed to investigate the effects of mixed litter decomposition in areas dominated by exotic plants. Mixed litter analyses conducted under variable environmental conditions could provide additional insights to help predict the rate of decomposition on an ecosystem level.

The decay rate of all three species (Table 1) was somewhat faster than reported in the literature. Estimates of annual

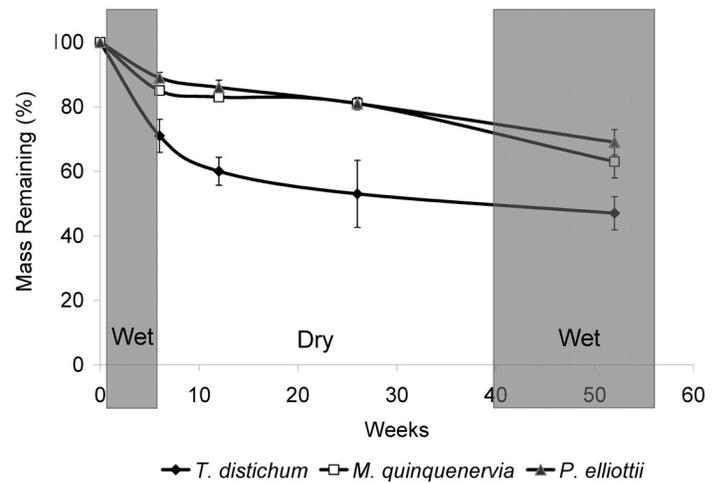


Figure 3. Mean (\pm S.E.) percent litter mass remaining of each plant species during the sample intervals.

mass loss of *T. distichum* litter range from 28% (Day 1982) to 77% (Battle and Golladay 2001) and 53% in this study. Although no direct measurements of *M. quinquenervia* decomposition have been published, we reanalyzed litterfall and litter accumulation data from Greenway (1994) and calculated a residence time of 4.3 yr, compared to the 2.19 yr in this study. Wienand and Stock (1995) found that the decomposition of *P. elliotii* needles can be relatively slow compared to coexisting native species. For example, Gholz et al. (1985) reported that *P. elliotii* litter lost only 13 to 17% of the dry litter in 1 yr. However, decomposition of *P. elliotii* litter was faster in this study, as 31% of the litter had decomposed after 12 months. This faster rate may have been caused by the season-

TABLE 2. MEAN (\pm S.E.) NUTRIENT CONCENTRATIONS OF LITTER OF EACH PLANT SPECIES AT THE DIFFERENT SAMPLE INTERVALS (LOWER CASE LETTERS INDICATE SIGNIFICANT DIFFERENCES FOR EACH ANALYSIS).

Sample interval	<i>M. quinquenervia</i>	<i>T. distichum</i>	<i>P. elliotii</i>	<i>P</i>
Carbon				
	----- mg g ⁻¹ -----			
initial	479 \pm 12.3	523 \pm 28.4	475 \pm 10.80	0.22
6 w	484 \pm 2.92 a	464 \pm 1.81 b	470 \pm 5.39 b	0.0035
3 m	483 \pm 3.50 a	459 \pm 2.07 b	470 \pm 4.00 b	<0.0001
6 m	472 \pm 2.41 a	457 \pm 2.03 b	469 \pm 1.63 a	<0.0001
12 m	494 \pm 3.10 a	461 \pm 3.26 b	463 \pm 4.89 b	<0.0001
Nitrogen				
Initial	7.44 \pm 0.18 a	9.06 \pm 0.68 a	5.38 \pm 0.11 b	0.002
6 w	8.44 \pm 0.20 b	12.1 \pm 0.21 a	6.62 \pm 0.03 c	<0.0001
3 m	9.20 \pm 0.40 b	13.8 \pm 0.34	6.75 \pm 0.22 c	<0.0001
6 m	9.70 \pm 0.31 b	14.5 \pm 0.42 a	8.44 \pm 0.41 b	<0.0001
12 m	11.4 \pm 0.71 b	15.6 \pm 0.34 a	7.03 \pm 0.26 c	<0.0001
Phosphorus				
	----- mg kg ⁻¹ -----			
Initial	103 \pm 1.56 b	127 \pm 3.10 a	106 \pm 1.73 b	0.0006
6 w	188 \pm 11.0 c	526 \pm 19.8 a	266 \pm 18.3 b	<0.0001
3 m	284 \pm 14.4 b	650 \pm 50.7 a	321 \pm 35.7 b	<0.0001
6 m	289 \pm 15.2 b	623 \pm 38.7 a	322 \pm 23.7 b	<0.0001
12 m 4	10 \pm 48.8 b	660 \pm 42.0 a	338 \pm 16.8 b	<0.0001

al hydro-period of the study area. The largest losses of organic material occurred during or immediately after inundation (Figure 3). These fluctuations in the water table may have increased the leaching of soluble compounds and provided moisture for the microbial communities.

Nutrient Turnover

Microbes are responsible for the decomposition of organic matter and cycling of nutrients critical to plant growth (Chapin et al. 2002); however, before a nutrient is released into the ecosystem, internal needs of microbial communities must be met (Davet 2004). For example, it is estimated that microbial communities will immobilize nitrogen to meet internal needs if the C:N molar ratio of the substrate is greater than 25:1 to 30:1. This figure is based on two assumptions: (1) a microbial substrate use efficiency of 40% and (2) a C:N microbial biomass ratio of 10:1 (Chapin et al. 2002). Changes in the soil microbial community structure caused by disturbances like exotic species invasion can alter the rate of nutrient storage and cycling. For example, if fungal biomass were to become more prevalent in the invaded soils, then substrate use efficiency could be greater, thereby increasing the availability of carbon substrates (Davet 2004). In addition, microbial communities with higher C:N biomass ratios have lower requirements for nitrogen and will therefore mineralize nitrogen at lower concentrations (Eviner and Chapin 2003).

The plant tissue concentrations of carbon, nitrogen, and phosphorus (Table 2) show that plant tissue carbon was affected primarily by species ($F_{2,94} = 50.7, p < 0.0001$) and secondarily by sample interval ($F_{3,94} = 2.6, p = 0.05$). There was a significant interaction between species and sample interval ($F_{6,94} = 3.2, p = 0.007$) caused by the greater initial loss of plant tissue carbon in the *T. distichum* litter. Although there was no difference in the initial concentration of carbon among the three species, there was more initial nitrogen in the *T. distichum* and *M. quinquenervia* litter compared to the *P. elliotii* litter (Table 2). Plant tissue nitrogen was influenced more by species ($F_{2,94} = 360.5, p < 0.0001$) than by sample interval ($F_{3,94} = 24.1, p < 0.0001$). There was a significant interaction between species and sample interval ($F_{6,94} = 5.1, p = 0.0001$) caused by the greater initial increase in plant tissue nitrogen in the *T. distichum* litter. The phosphorus concentration was highest in the *T. distichum* litter. Plant tissue phosphorus was affected by species ($F_{2,95} = 139.1, p < 0.0001$) and sample interval ($F_{3,95} = 11.1, p < 0.0001$) with no interactions. Overall, the concentration of nitrogen and phosphorus in the decomposing litter increased over time for each plant species.

Rothstein et al. 2004 found that the invasion of the exotic tree *Fraxinus uhdei* into the Hawaiian rainforest doubled the release of nitrogen of the litter compared to a native forest. Martin et al. (2009) found that *M. quinquenervia* altered the soil microbial community composition, which in turn may change rates of ecosystem nutrient cycling. However, the presence of *M. quinquenervia* litter did not significantly alter the storage and cycling of carbon, nitrogen, or phosphorus in this study. Throughout the study, each plant species lost carbon, resulting in a negative change in total carbon pool at

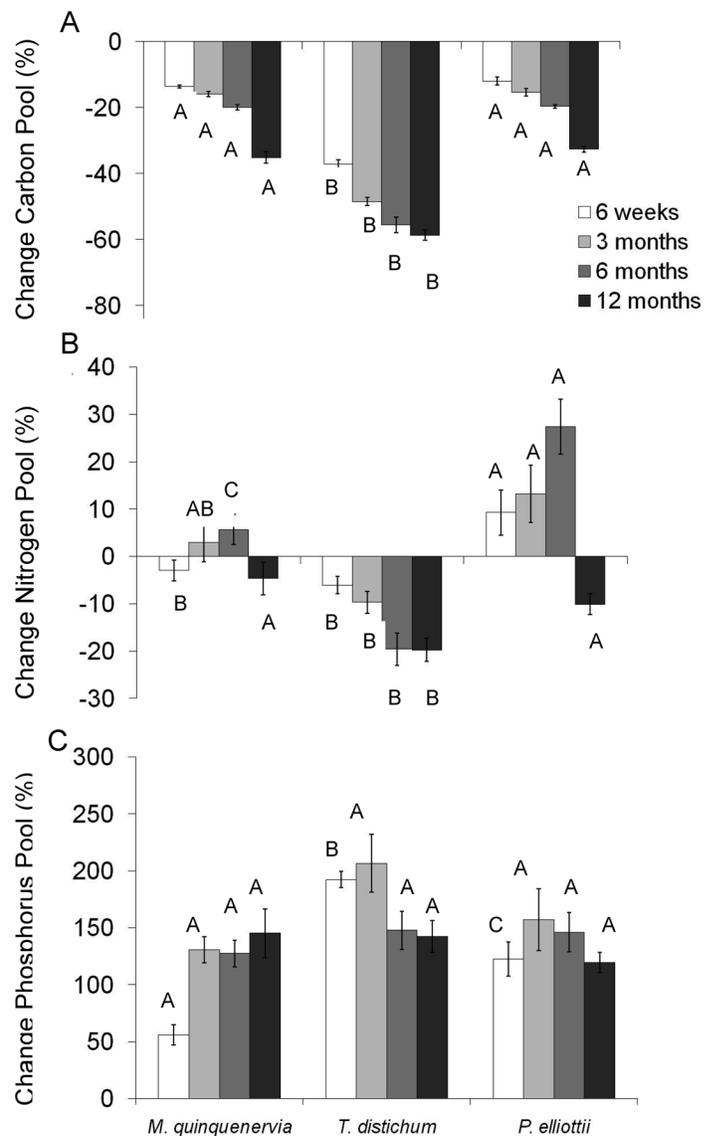


Figure 4. Mean (\pm S.E.) percent change in pools of (A) carbon, (B) nitrogen, and (C) phosphorus of each plant species during the sample intervals. Letters indicate significant differences for each sample interval only.

each sample interval (Figure 4A). The percentage change in the carbon storage was influenced primarily by species ($F_{2,95} = 713.8, p < 0.0001$) and secondarily by sample interval ($F_{3,95} = 147.5, p < 0.0001$). There was a significant interaction between species and sample interval ($F_{6,95} = 6.9, p < 0.0001$) caused by the greater initial decrease in carbon storage in the *T. distichum* litter.

The percentage change in the nitrogen pool was affected by species ($F_{2,95} = 40.4, p < 0.0001$) and sample interval ($F_{3,95} = 10.4, p < 0.0001$). After 6 weeks and 1 yr, the *M. quinquenervia* litter lost nitrogen compared to the initial pool (Figure 4B). However, *M. quinquenervia* litter gained nitrogen at 3 and 6 months. In contrast, *T. distichum* litter lost nitrogen at each sample interval. *Pinus elliotii* litter gained nitrogen at 6 weeks, 3 months, and 6 months compared to the initial pool

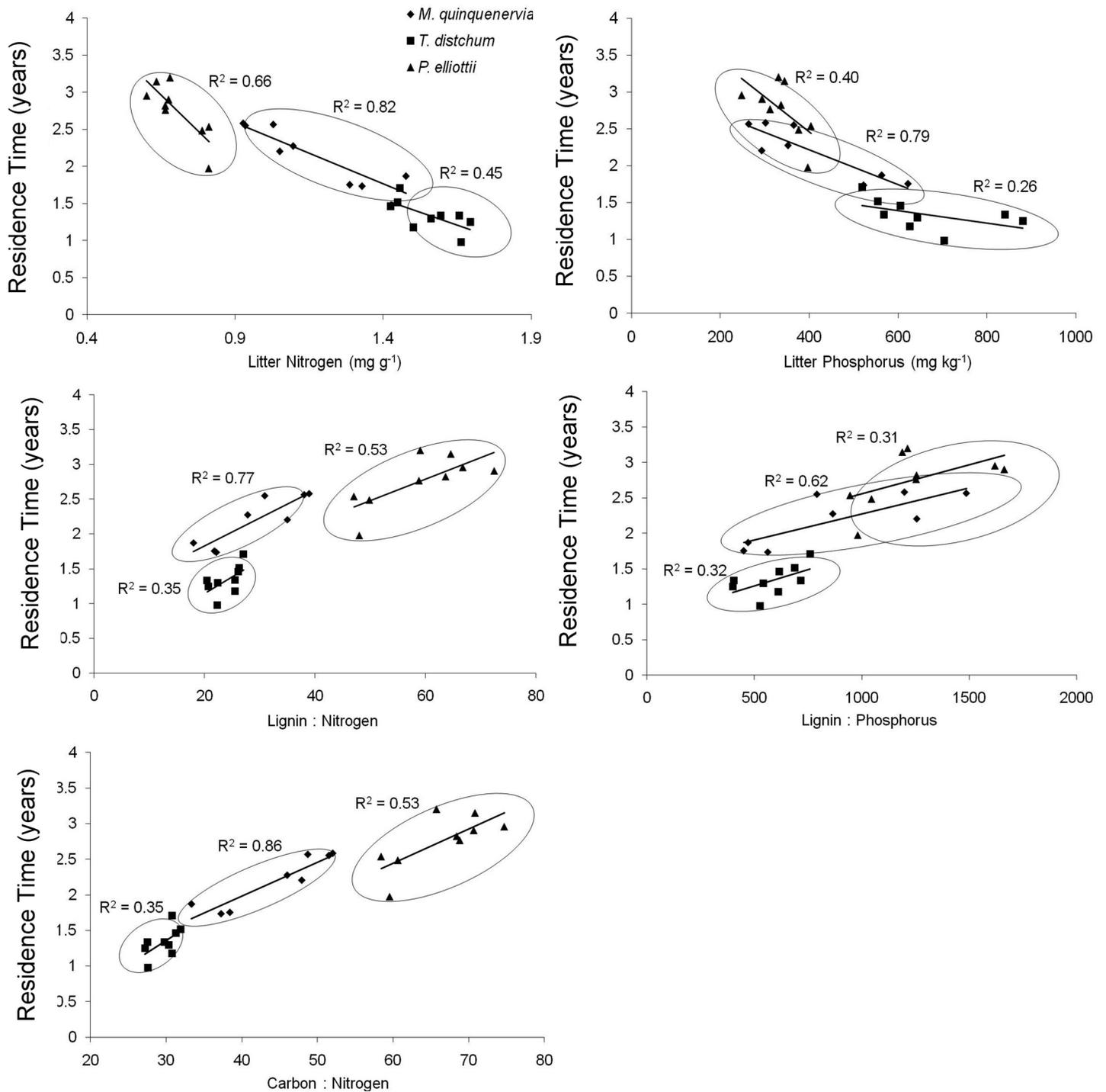


Figure 5. Relationships between litter residence time and final nutrient concentrations of each plant species. Relationship between residence time and (A) litter nitrogen, (B) litter phosphorus concentration, (C) lignin to nitrogen ratio, (D) lignin to phosphorus ratio, and (E) carbon to nitrogen ratio at the final sample interval (ovals encompass individual plant species).

but lost nitrogen at 1 yr. There was a significant interaction between species and sample interval ($F_{6,95} = 5.6, p < 0.0001$) caused by the greater initial increase in nitrogen storage in the *P. Elliottii* litter. Although the litter of all three plant species experienced a net increase in the concentration of nitrogen at the end of 12 months, the overall differences in

nutrient concentration offset mass loss and led to the greater total nitrogen storage in the *T. distichum* and *M. quinquenervia* litter compared to the *P. Elliottii* litter ($p < 0.0001$).

Similarly, all three plant species immobilized phosphorus at every sample interval, resulting in a net increase in phosphorus concentration that was offset by the total mass loss

(Table 2; Figure 5c). The percentage change in the phosphorus storage was influenced by species ($F_{2,95} = 12.1$, $p < 0.0001$) and sample interval ($F_{3,95} = 3.3$, $p = 0.02$). There was a significant interaction between species and sample interval ($F_{6,95} = 3.7$, $p = 0.003$) caused by the greater initial increase in phosphorus storage in the *T. distichum* litter. The total storage of phosphorus was highest in the *T. distichum* followed by *M. quinquenervia* and then *P. elliotii* litter at the end of 12 months ($p = 0.012$). These data suggest that the rate of nutrient release from *M. quinquenervia* litter would not significantly alter ecosystem function.

The final nitrogen concentration, phosphorus concentration, and the final nutrient ratios of the litter material were highly correlated with the differences in the residence time (Figure 5A-E). The strongest relationships existed between the native plant species and nitrogen concentration and *M. quinquenervia* and the carbon to nitrogen ratio (Figure 5A and 5E). When the data for all of the species are combined into one regression, the relationships between residence time and the final nutrient concentrations are: litter nitrogen ($R^2 = 0.9$, $p < 0.001$), litter phosphorus concentration ($R^2 = 0.76$, $p < 0.001$), lignin to nitrogen ratio ($R^2 = 0.74$, $p < 0.001$), lignin to phosphorus ratio ($R^2 = 0.71$, $p < 0.001$), and carbon to nitrogen ratio ($R^2 = 0.88$, $p < 0.001$). These relationships suggest that both nitrogen and phosphorus limitations may be controlling the decomposition of the litter material of all three species and, as the concentration of nitrogen and phosphorus in plant tissues increases, the residence time of the litter decreases.

In addition, in no case did the pattern of nutrient concentration and residency time differ between the litter of native plants and *M. quinquenervia*. This provides another line of evidence that the presence of *M. quinquenervia* in *P. elliotii*–*T. distichum* ecotone forests may not significantly alter litter decomposition or nutrient turnover. In contrast, Standish et al. (2004) found that a higher concentration of nitrogen and lower ratio of carbon to nitrogen in the litter of the invasive plant *Tradescantia fluminensis* contributed to a faster rate of organic matter decomposition compared to several native plant species. Future work should investigate other native South Florida ecosystems to determine if functional changes occur in the presence of remnant *M. quinquenervia* populations. Natural areas dominated by nonwoody native species such as *Cladium jamaicense* may have experienced changes in plant functional traits and environmental factors (e.g., increased shading from tall trees) that could significantly alter decomposition rates.

Past invasions of *M. quinquenervia* have been shown to alter ecosystem structure and function (DiStefano and Fisher 1983, Martin et al. 2009). Although *M. quinquenervia* has colonized and thrived in most natural areas of South Florida, this research presents one line of evidence that *M. quinquenervia* in its current suppressed state may not significantly alter the basic ecosystem processes of organic matter decomposition and nutrient turnover in invaded *P. elliotii*–*T. distichum* ecotone forests. Currently a need remains to manage large monotypic *M. quinquenervia* stands to restore plant community diversity, improve wildlife habitat, and reduce fire hazards, especially in areas that are not ideal for the biological agents. However, smaller remnant *M. quinquenervia* popula-

tions remain part of vegetative landscape and are targets for future management despite the risks of collateral damage to native plant communities posed by chemical and mechanical methods. We submit that additional research is needed to determine if the benefits outweigh the costs to plant communities from the continued conventional management of this exotic, but now less invasive plant.

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