Interactions of biological and herbicidal management of *Melaleuca quinquenervia* with fire: Consequences for ecosystem services

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ABSTRACT

Exotic plant species invasion can alter ecosystem nutrient dynamics and natural disturbance patterns. The Australian tree *Melaleuca quinquenervia* has extensively invaded the Florida Everglades and is currently being suppressed using mechanical, herbicidal, and biological control management strategies. While these methods have been evaluated based on reductions in density and abundance of the target weed, other factors should be considered including consequences for ecosystem nutrient storages and interactions with natural disturbances such as fire. We hypothesized that the choice of management tactics, namely herbicidal or biological control, would differentially influence the quantity and availability of soil nutrients before and after a seasonal fire. The management of *M. quinquenervia* with a herbicide reduced the above- and belowground storage of nutrients both before and after a fire compared to a non-invaded area, while biological control increased storage. There were no differences in nitrogen availability between sites (non-invaded, herbicide, biological control) in the 0–5 cm or 5–15 cm soil depths before or after the fire. Pre-fire phosphorus availability was highest in the non-invaded site in the 0–5 cm soil depth and in the biological control site in the 5–15 cm soil depth. However, phosphorus availability was highest at both depths in the herbicide site post-fire. Biological control of *M. quinquenervia* using insect herbivores has proven to be effective at controlling plant growth and reproduction. The results of this study suggest that this method may have less of an impact on nutrient storage and cycling than herbicides.

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1. Introduction

Ecosystems invaded by exotic plants are often managed to maximize the delivery of services such as space for recreational activities, wildlife habitat, and maintenance of biological diversity. However, few evaluations have been done on the effects of management programs on less obvious, but no less important, ecosystem services such as nutrient storage and cycling. Tipping et al. (2008a) found that biological control of *Salvinia molesta* not only reduced the biomass and density of infestations in several Texas and Louisiana lakes, but also increased dissolved oxygen needed to support organic matter decomposition and aquatic life. Malcom et al. (2008) reported that lower, pre-invasion levels of soil nitrogen (N) were restored after the mechanical removal of the invasive

tree *Robinia pseudoacaia* in a pine-oak system. This is biologically significant because plant induced increases in the level of available nutrients in the soil may promote fast-growing, invasive species (Huenneke et al., 1990; Davis et al., 2000; Ehrenfeld, 2003; Blumenthal, 2005).

Not all control programs are successful in restoring ecosystem services and any fundamental changes in the cycling and storage of nutrients may complicate the management of invasive plants. For example, despite the significant suppression of the invasive plant *Lupinus arboreus* by herbicides, soil available N was not restored to the lower pre-invasion levels in a California coastal dune (Pickart et al., 1998). Ogden and Rajmanek (2005) found that although the use of fire and herbicides did significantly decrease the cover of the invasive fennel *Foeniculum vulgare*, it was replaced by non-native Mediterranean annual grasses.

Longer-term management of invasive plants may have a cumulative effect on nutrient dynamics. This might include continuous and regular applications of herbicides to suppress aquatic vegetation in semi-tropical areas where plant growth occurs year round. For example, an average of 2461 ha of floating aquatic vegetation was treated each year with herbicides from 1975 to 1998 on Lake

Okeechobee in central Florida (Grimshaw, 2002). These treatments were responsible for up to 17% and 49% of the external annual N and phosphorus (P) loads, respectively, for that lake which serves as a source of water for the Florida Everglades. Fundamental alterations in the timing and quantity of nutrient pulses may disrupt downstream native plant communities and allow invasive plants to maintain ecosystem dominance. In the northern Florida Everglades, a combination of disturbance and P loading has resulted in the large-scale replacement of the low-nutrient adapted species *Cladium jamaicense* with *Typha domingensis* (Newman et al., 1998).

Natural environmental perturbations can further complicate or exacerbate management efforts. Many natural areas depend on fire to maintain community structure and function by opening canopies, promoting seed release and germination, and providing temporary pulses of soluble nutrients (Wade et al., 1980; Neary et al., 1999). However, fire-adapted invasive species may benefit disproportionally from any increases in space and resource availability after fires (Hobbs and Huenneke, 1992; D'Antonio and Vitousek, 1992; Keeley, 2006). Once established, invasive species may also change the basic pattern and influence of fire in natural communities (Mack and D'Antonio, 1998; Brookes et al., 2004). For example, the invasive plant *Bromus tectorum* both increases the frequency of fires and permanently alters soil N dynamics thereby promoting its own persistence and dominance (Evans et al., 2001).

The Australian tree *Melaleuca quinquenervia* (Cav.) Blake, has successfully colonized and invaded natural areas within Florida including the fire-regulated *Pinus elliottii* Englem-*Taxodium distichum* (L.) L.C. Rich var. nutans (Ait.) Sweet eco-tone forest (Myers, 1984). High concentrations of essential oils found in *M. quinquenervia* have promoted destructive canopy fires which are more likely to kill native vegetation than the cooler ground fires that normally occur in the natural systems. These same fires trigger the release of massive amounts of *M. quinquenervia* seed which have resulted in the establishment of widespread monotypic stands of *M. quinquenervia* (Serbesoff-King, 2003). This sequence was repeated for decades allowing *M. quinquenervia* to colonize most freshwater ecosystems in South Florida until an integrated, interagency control program was created to suppress the weed in the 1980s (Van Driesche et al., 2010). Although these programs have been evaluated based on the quantity of plant biomass removed, changes in density, or reduction in rates of population spread, other evaluation factors need to be considered including their impact on non-target vegetation, alteration of nutrient cycles, and interactions with natural disturbances such as fire (D'Antonio and Meyerson, 2002; Denslow and D'Antonio, 2005).

The objective of this research was to elucidate the above- and belowground changes to a *P. elliottii-T. distichum* eco-tone forest after the invasion by and subsequent management of *M. quinquenervia*. In particular, emphasis was given to the management consequences for nutrient storage and availability before and after a fire. We hypothesized that the choice of management tactics, namely herbicidal or biological control, will differentially influence the quantity and availability of nutrients both before and after a fire.

2. Methods

2.1. The target weed

Melaleuca quinquenervia, otherwise known as the paper-bark tree, is a member of the Myrtaceae family, sub-family Leptospermoidae (Serbesoff-King, 2003). This tall evergreen tree historically occupies tropical wetland sites throughout its native range along the eastern coast of Australia (Kauffman 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 (Dray et al., 2006). A 1998 study estimated that *M. quinquenervia* had invaded approximately 400,000 ha in the State of Florida (LaRoche, 1998). Studies have shown that *M. quinquenervia* infestations can alter the abundance of native plant species, wildlife habitats, and ecosystem nutrient storages (Serbesoff-King, 2003; Martin et al., 2009).

2.2. Biological control agents

Currently the growth and reproductive capacities of *M. quinquenervia* are being suppressed by two intentionally introduced, specialized insect herbivores, *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae) and *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae) (Tipping et al., 2008b). Two other species have only recently been released so information on their impact is unavailable. *Oxyops vitiosa* larvae and adults feed on buds and newly flushing leaves (Balciunas et al., 1994). The feeding activity of the larvae is the most damaging to the plant and causes long, window-like scars on leaves (Purcell and Balciunas, 1994). Larvae are covered in a thick viscous coating consisting of essential oils sequestered from *M. quinquenervia* which provides an effective anti-predator defense (Wheeler et al., 2002). *Boreioglycaspis melaleucae* adults and nymphs feed on plant phloem (Purcell et al., 1997; Wineriter et al., 2003). Both *O. vitiosa* and *B. melaleucae* have established and spread throughout South Florida (Center et al., 2006; Tipping et al., 2008b).

2.3. Site description

The study site 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 which are loamy, siliceous, hyperthermic Arenic Glossoqualfs. The soil series is Pineda-Boca-Hallandale which is characterized by moderately to poorly drained sands which overlie limestone bedrock to a depth of approximately 1.4 m (USDA, 1998). The water table fluctuates annually between greater than 15 cm below the soil surface to approximately 25 cm above. The area has a distinct wet season from about July to December and a dry season from January to June. Average annual rainfall in this region is approximately 1.36 m (SERC, 2007). Historically, the vegetation in this area was a mixed *T. distichum–P. elliottii* forest with a hardwood under-story. Over the past several decades, many areas in this landscape have been invaded by *M. quinquenervia* and are now comprised of sparse populations of mature trees with dense understories of saplings that can exceed densities of 100 plants per square meter.

2.4. Experimental design

In order to assure the proper assignment of treatment causality in experiments several fundamental assumptions must be met including the random assignment of treatments across experimental units and treatment replication (Beyers, 1998). The most rigorous field studies have randomly assigned, replicated experimental treatments. Often, however, land managers manipulate natural areas to restore function, provide habitat, or mitigate anthropogenic disturbance without regard for experimental design. As a result, large tracts of land are treated as needed or as resources allow. The resulting landscapes are complex and provide a statistical challenge to empirical studies. Despite this, evaluating large-scale field treatments can provide unique opportunities and should be pursued to gain insight on the outcomes of adaptive management of ecosystems.

The current study evaluated the results of a multi-agency, integrated management strategy that has taken place over the course of several decades. As large tracts of the native forest became in-

fested with *M. quinquenervia* populations, the two biological control agents mentioned above were released: *O. vitiosa* in 1998 and *B. melaleucae* in 2002. These two agents quickly spread and became common throughout the entire landscape. Later, in 2003, a limited amount of state funding became available to aerially treat a single tract of reproductive *M. quinquenervia* with the herbicide Velpar® (Hexazinone, 3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3, 5-triazine-2,4(1H,3H)-dione). The end result of these two management strategies is a complex landscape of large, contiguous, unreplicated blocks of native, invaded, and managed vegetation.

This study began in March 2007, with the establishment of 25, 1 m^2 plots (replicates) arranged five per transect with five transects in each of three contiguous study sites (15 transects and 75 plots in total). The sites (treatment) sampled were: site #1) reproductive *M. quinquenervia* managed with a herbicide application in the summer of 2003 (hereafter referred to as "herbicide site"), site #2) reproductive *M. quinquenervia* managed with the two biological control agents (hereafter referred to as "biological control site"), and site #3) native forest with no history of *M. quinquenervia* invasion (hereafter referred to as "non-invaded site"). Sites were re-visited and all parameters re-sampled after a fire (sub-treatment) in 2007. In early May of 2007 the Great Balsa fire burned approximately 8000 ha in southwest Florida and all of the sites. The fire was unplanned so no direct measurements were taken of fire intensity.

2.5. Litter and soil sampling

The litter on the surface of the soil was sampled in every m^2 plot (*n* = 25 in each study site) by placing a 0.1 m^2 frame on the surface of the soil and collecting all of the organic material therein. Pre-fire litter samples were separated into undecomposed Oi (intact litter), moderately decomposed Oe (fragmented litter), humified Oa (highly decomposed litter), and woody biomass layers. Post-fire litter samples were separated into an additional "after" layer which sampled leaves that fell from the trees after the fire. Litter samples were air dried to a constant weight and reported on a dry weight basis. Fire intensity was estimated by calculating the percentage of the total litter that was lost after the fire. One 5 cm diameter soil core was taken in each plot and separated into 0–5 cm and 5–15 cm depths. Soil samples were returned to the laboratory, sieved to remove roots and large plant debris, homogenized, and kept at 4 °C for a maximum of 10 days for microbial analysis.

2.6. Soil characteristics

Percent moisture and bulk density of soils were determined by drying 20–30 g sub-samples of field-moist, sieved, and homogenized soil at 70 °C for three days. Bulk density and percent moisture were determined on a wet soil weight basis. Soil organic matter was measured by loss on ignition from 0.2 to 0.5 g samples of dried and ground soils, 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.

2.7. Nutrient and microbial biomass analyses

Dried and ground soil and plant material were analyzed for total carbon (C) and N on a Thermo-Electron, 1112 Series elemental analyzer (Martin et al., 2009). Total P was determined by a two-phase acid extraction after loss on ignition (Andersen, 1976; Martin et al., 2009). Microbial biomass carbon (MBC) was measured by a modified chloroform-fumigation extraction method (Vance et al., 1987; Martin et al., 2009). Two replicates of 1 g field-moist soil samples

were weighed into 50 mL centrifuge tubes. One of the replicates was immediately extracted and the second replicate of soil underwent chloroform-fumigation. All extracts were stored at 4 °C until analysis for MBC. This was calculated as the difference between the total C in the fumigated and un-fumigated soil extracts as measured on a Shimadzu TOC 5050C, total organic C analyzer. An extraction coefficient was not applied to the calculation for MBC.

2.8. Nutrient availability

Potentially mineralizable nitrogen (PMN) was measured with a modified incubation-extraction method (White and Reddy, 2000) that calculates a mineralization potential based on the net production of ammonium during a 10 day anaerobic incubation. In order to determine the initial amount of ammonium in the soil, a replicate of 1 g field-moist soil samples were weighed into 50 mL centrifuge tubes. The tubes received 25 mL of 0.5 M K$_2$SO$_4$, shaken on a longitudinal shaker for one hour, and extracts were filtered through a #41 Whatman filter. A second replicate of 1 g field-moist soil samples was weighed into 50 mL serum bottles with 5 mL of deionized water. These bottles were seal-ed with butyl rubber stoppers and aluminum crimps and their head-space was purged with oxygen (O$_2$)–free nitrogen (N$_2$) gas for 2–5 min. Bottles were incubated in the dark at 35 °C for 10 days then extracted as described above with 25 mL of 0.5 M K$_2$SO$_4$ to determine final ammonium concentration. Total ammonium was determined with an automated colorimetric method on a Bran and Luebbe Auto Analyzer 3, Digital Colorimeter (Method 353.2; USEPA, 1993). Specifically mineralizable nitrogen (SMN) was determined by dividing PMN by the concentration of N in the soil (SMN = PMN $*$ TN^{-1}).

Potentially mineralizable phosphorus (PMP) was measured with a modified incubation-extraction method under aerobic conditions (Grierson et al., 1999). Soils were incubated at a temperature of 35 °C for a period of 10 days in capped 125 mL polyethylene bottles that contained 5 g of soil held under optimal percent moisture conditions (4–7%). Soils were aerated every three days and moisture content was adjusted if necessary. Soil sub-samples were collected after 10 days from each incubation bottle, extracted with 0.1 M potassium chloride (KCl) at a ratio of 10:1, shaken for one hour, and then filtered with 0.45 μm membrane filters. Available P was measured with an ascorbic acid method on a Shimadzu Spectrophotometer UV-160 (Method 365.4; USEPA, 1993). Specifically mineralizable phosphorus (SMP) was determined by dividing PMP by the concentration of P in the soil (SMP = PMP $*$ TP^{-1}).

2.9. Statistical analyses

Values of measured soil and vegetation characteristics, as well as microbial population size, were calculated as a mean for each site. ANOVA and Tukey means separation tests were used to detect any differences among the measured parameters. Differences are reported as significant for tests with *p* values $\leqslant 0.05$ unless otherwise stated. Data that varied from normal distributions were transformed with square root(x), log(x), or log(x + 1) functions. The datasets that were transformed with the square root(x) function were pre- and post-fire soil moisture (0–5 and 5–15 cm), pre- and post-fire litter biomass, pre- and post-fire soil N concentration (0–5 and 5–15 cm), and pre- and post-fire soil P concentration (0–5 and 5–15 cm). The datasets that were transformed with the log(x + 1) function were pre- and post-fire soil organic matter (0–5 and 5–15 cm) and pre- and post-fire soil C concentration (0–5 and 5–15 cm). The datasets that were transformed with the log(x) function were pre- and post-fire soil MBC (0–5 and 5–15 cm). All statistical analyses were preformed using JMP 7.0.1 software (SAS Institute, North Carolina, USA).

3. Results

Full models were run for the main experiment effects and all interactions. The main effects of management strategy/site (treatment), fire (sub-treatment), and depth were the most important influences on the response variables. There were no consistent transect effects for any of the measured variables.

Litter moisture was affected primarily by fire ($F_{1,128} = 430$, $p < 0.0001$) and secondarily by site ($F_{2,128} = 36.6$, $p < 0.0001$). The litter in the non-invaded site had the highest percent moisture pre- and post-fire (Table 1). There was a significant interaction between fire and site ($F_{2,128} = 25.1$, $p < 0.0001$) that was caused by the greater loss of litter moisture in the herbicide site after the fire.

Litter biomass (excluding the "after" litter component) was influenced by fire ($F_{1,139} = 255$, $p < 0.0001$) and site ($F_{2,139} = 26.5$, $p < 0.0001$). The non-invaded site had the greatest amount of litter biomass, both before and after the fire (Table 1). The litter in the herbicide site consisted of 66% wood material compared to only 15% in the non-invaded and 26% in the biological control sites (Fig. 1, $F_{2,70} = 6.8$, $p < 0.001$). Percent biomass loss or fire intensity was greatest in the herbicide site ($F_{2,64} = 4.68$, $p = 0.013$) (Table 1).

For many of the measured soil variables there was a significant interaction of fire and depth that was caused by the proximately of the 0–5 cm soil depth to the fire. Pre- and post-fire values for soil moisture, bulk density, and organic matter are reported in Table 2. Soil moisture was affected more by fire ($F_{1,271} = 464$, $p < 0.0001$) than by site ($F_{2,271} = 16.5$, $p < 0.0001$) or depth ($F_{1,271} = 11.4$, $p = 0.0009$). There was a significant interaction between fire and depth ($F_{1,271} = 109$, $p < 0.0001$) and site and depth ($F_{2,271} = 4.6$, $p = 0.01$). The site and depth interaction was caused by the similarity of moisture levels in the pre-fire herbicide soil depths.

Soil bulk density was affected primarily by depth ($F_{1,281} = 271$, $p < 0.0001$) and secondarily by site ($F_{2,281} = 25.9$, $p < 0.0001$) and fire ($F_{1,281} = 12.3$, $p = 0.0005$). There was a significant interaction between fire and depth ($F_{1,281} = 12.2$, $p = 0.0005$) and site and depth ($F_{2,281} = 12.6$, $p < 0.0001$). Soil organic matter was affected primarily by depth ($F_{1,262} = 175$, $p < 0.0001$) and secondarily by site ($F_{2,262} = 35.4$, $p < 0.0001$). There were significant interactions between fire and depth ($F_{1,262} = 4.37$, $p = 0.04$) and site and depth ($F_{2,262} = 14.8$, $p < 0.0001$). The site and depth interactions for bulk density and organic matter were caused by the low bulk density level in the 0–5 cm soil layer of the biological control site resulting from its higher organic matter content.

The concentration of C in the litter was affected by fire ($F_{1,128} = 135$, $p < 0.0001$). The litter in the non-invaded site had the highest concentration of C before the fire and the biological control site had the highest concentration of C after the fire (Table 3). There was a significant interaction between fire and site ($F_{2,128} = 5.6$, $p = 0.005$) that was caused by the proportionally greater reduction in the C concentration of the litter in the herbicide site after the fire. The concentration of N in the litter was influenced primarily by site ($F_{2,128} = 14$, $p < 0.0001$) and secondarily by fire ($F_{1,128} = 12.3$, $p = 0.0006$) with no interactions. The concentration
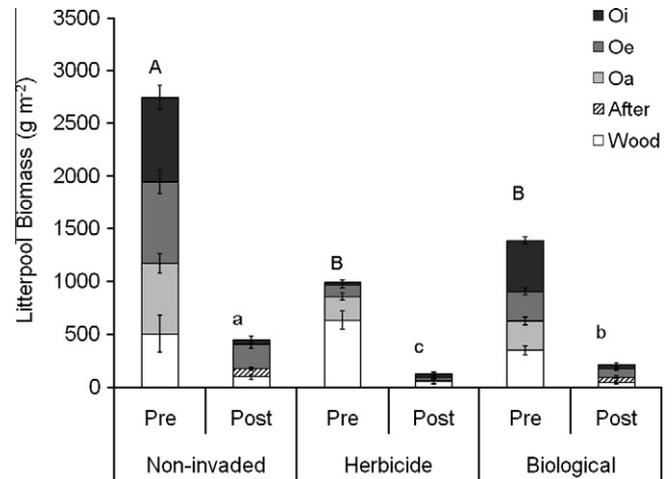
Fig. 1. Mean (±SE) of pre- and post-fire biomass of all litter components (Oi, Oe, Oa, after, and wood) measured in the non-invaded, herbicide, and biological control sites (Different capital and lower case letters indicate significant differences for pre- and post-fire means, respectively).

of P in the litter was affected primarily by fire ($F_{1,130} = 120$, $p < 0.0001$) and secondarily by site ($F_{2,130} = 16.6$, $p < 0.0001$) with no interactions. Carbon, N, and P concentrations are reported in Table 3.

The soil in the herbicide site had the lowest concentration of C, N, and P at both depths before and after the fire compared to the non-invaded and biological control sites (Table 3). Conversely, in the 0–5 cm soil depth the biological control site had the highest concentration of N and P both before and after the fire compared to the other two sites (Table 3). Soil C concentration was affected primarily by depth ($F_{1,252} = 234$, $p < 0.0001$) and secondarily by site ($F_{2,252} = 18.8$, $p < 0.0001$). There were significant interactions between fire and depth ($F_{1,252} = 6.39$, $p = 0.01$) and site and depth ($F_{2,252} = 7.05$, $p = 0.001$). Soil N concentration was affected primarily by depth ($F_{1,273} = 107$, $p < 0.0001$) and secondarily by site ($F_{2,273} = 22.3$, $p < 0.0001$). There was a significant interaction between site and depth ($F_{2,273} = 6.16$, $p = 0.002$). Soil P concentration was affected primarily by depth ($F_{1,273} = 85.2$, $p < 0.0001$) and secondarily by site ($F_{2,273} = 19$, $p < 0.0001$) and fire ($F_{1,273} = 5.3$, $p = 0.02$). There was a significant interaction between site and depth for P ($F_{2,273} = 4.92$, $p = 0.008$).

Specifically mineralizable nitrogen was affected more by depth ($F_{1,276} = 18.9$, $p < 0.0001$) than by fire ($F_{1,276} = 8.52$, $p = 0.004$). Although there were no differences in SMN among sites in the 0–5 cm or 5–15 cm soil depths before or after the fire (Table 4), there was a significant interaction between fire and depth ($F_{1,276} = 5.58$, $p = 0.02$). Specifically mineralizable phosphorus was affected by site ($F_{2,48} = 3.2$, $p = 0.0495$) with an interaction between site and depth ($F_{2,48} = 5.19$, $p = 0.009$). In addition, depth ($F_{1,48} = 3.64$, $p = 0.06$) and the interaction of fire and site ($F_{2,48} = 3.2$, $p = 0.05$)

Table 1
Mean (±SE) of pre- and post-fire litter moisture and biomass (excluding the "after" litter component) and post-fire litter loss (fire intensity) in the non-invaded, herbicide, and biological control sites (different lower case letters within rows indicate significant differences).

Variable	Fire[b]	Non-invaded[a]	Herbicide[a]	Biological[a]	P
Moisture (%)	Pre-fire	38.7 ± 1.79 a	25.8 ± 2.33 b	17.1 ± 1.39 c	<0.0001
	Post-fire	3.33 ± 0.40 a	1.15 ± 0.15 b	1.42 ± 0.15 b	<0.0001
Biomass (kg m^{-2})	Pre-fire	2.75 ± 0.37 a	1.06 ± 0.13 b	1.39 ± 0.15 b	<0.0001
	Post-fire	0.36 ± 0.06 a	0.12 ± 0.04 b	0.16 ± 0.03 b	<0.0001
Litter loss (%)		85 ± 2.24 a	94.3 ± 2.04 b	88.3 ± 2.12 ab	0.013

[a] Treatment.
[b] Sub-treatment.

Table 2
Mean (±SE) of pre- and post-fire soil moisture, bulk density (BD), and organic matter (OM) in the non-invaded, herbicide, and biological control sites (different lower case letters within rows indicate significant differences).

Variable	Fire[b]	Depth	Non-invaded[a]	Herbicide[a]	Biological[a]	P
Moisture (%)	Pre-fire	0–5	11.2 ± 1.17 a	7.05 ± 0.65 b	11.3 ± 1.64 a	0.048
		5–15	7.86 ± 0.46 a	6.07 ± 0.17 b	5.48 ± 0.37 b	<0.0001
	Post-fire	0–5	1.37 ± 0.25 a	0.29 ± 0.06 b	1.17 ± 0.20 a	<0.0001
		5–15	3.96 ± 0.25 a	2.54 ± 0.13 b	3.17 ± 0.21 b	<0.0001
BD (g cm^{-3})	Pre-fire	0–5	1.11 ± 0.06 a	1.20 ± 0.05 a	0.89 ± 0.05 b	0.0004
		5–15	1.30 ± 0.05 b	1.43 ± 0.02 a	1.35 ± 0.03 ab	0.017
	Post-fire	0–5	1.13 ± 0.60 a	1.19 ± 0.03 a	0.88 ± 0.03 b	<0.0001
		5–15	1.49 ± 0.03 a	1.60 ± 0.02 b	1.49 ± 0.03 a	0.004
OM (%)	Pre-fire	0–5	1.87 ± 0.22 b	1.70 ± 0.17 b	3.71 ± 0.49 a	0.0001
		5–15	0.95 ± 0.09 a	0.52 ± 0.04 b	0.82 ± 0.07 a	0.0001
	Post-fire	0–5	2.46 ± 0.32 b	1.07 ± 0.04 c	3.49 ± 0.37 a	<0.0001
		5–15	1.38 ± 0.14 a	0.68 ± 0.05 b	1.05 ± 0.10 a	<0.0001

[a] Treatment.
[b] Sub-treatment.

Table 3
Mean (±SE) of pre- and post-fire carbon (C), nitrogen (N), and phosphorus (P) concentrations in non-invaded, herbicide, and biological control sites (different lower case letters within rows indicate significant differences).

Variable	Fire[b]	Depth	Non-invaded[a]	Herbicide[a]	Biological[a]	P
C (mg g^{-1})	Pre-fire	Litter	470 ± 9.79 a	461 ± 8.82 a	421 ± 8.45 b	0.008
		0–5	12.9 ± 1.80	8.45 ± 1.06	16.8 ± 2.82	0.08
		5–15	3.77 ± 0.61 a	1.74 ± 0.21 b	1.92 ± 0.24 b	0.003
	Post-fire	Litter	273 ± 29.6	203 ± 26.7	300 ± 26.8	0.07
		0–5	10.3 ± 1.56 a	3.78 ± 0.33 b	14.1 ± 1.79 a	<0.001
		5–15	3.73 ± 0.55 a	1.70 ± 0.16 b	2.59 ± 0.34 ab	0.008
N (mg g^{-1})	Pre-fire	Litter	9.45 ± 0.29 b	7.98 ± 0.40 c	11.1 ± 0.28 a	<0.001
		0–5	0.93 ± 0.14 a	0.43 ± 0.07 b	0.96 ± 0.18 a	0.01
		5–15	0.33 ± 0.05 a	0.15 ± 0.02 b	0.19 ± 0.03 b	0.002
	Post-fire	Litter	12.3 ± 0.75 a	8.94 ± 1.19 b	13.2 ± 0.96 ab	0.01
		0–5	0.78 ± 0.13 a	0.30 ± 0.04 b	0.93 ± 0.13 a	<0.001
		5–15	0.38 ± 0.06 a	0.13 ± 0.01 b	0.20 ± 0.02 b	<0.001
P (mg kg^{-1})	Pre-fire	Litter	135 ± 6.33 b	142 ± 8.83 b	198 ± 6.66 a	<0.001
		0–5	15.8 ± 1.98 ab	10.3 ± 0.98 b	23.5 ± 3.1 a	0.004
		5–15	9.03 ± 0.83	7.26 ± 0.52	8.64 ± 0.65	0.21
	Post-fire	Litter	274 ± 14.3 b	281 ± 37.1 b	388 ± 24.3 a	0.015
		0–5	20.1 ± 2.64 ab	13.4 ± 1.55 b	23.9 ± 2.49 a	0.006
		5–15	10.5 ± 1.03 ab	7.18 ± 0.50 b	11.7 ± 1.36 a	0.01

[a] Treatment.
[b] Sub-treatment.

Table 4
Mean (±SE) of pre- and post-fire specifically mineralizable nitrogen (SMN) and specifically mineralizable phosphorus (SMP) measured in the non-invaded, herbicide, and biological control sites (different lower case letters within rows indicate significant differences).

Variable	Fire[b]	Depth	Non-invaded[a]	Herbicide[a]	Biological[a]	P
SMN (µg PMN mg^{-1} N soil)	Pre-fire	0–5	18.7 ± 3.35	14.8 ± 1.67	18.1 ± 4.01	0.66
		5–15	12.4 ± 2.47	12.6 ± 2.76	16.0 ± 2.41	0.55
	Post-fire	0–5	22.5 ± 3.53	29.8 ± 4.01	27.6 ± 3.04	0.33
		5–15	15.2 ± 3.11	11.9 ± 2.24	16.9 ± 3.07	0.45
SMP (µg PMN mg^{-1} P soil)	Pre-fire	0–5	16.3 ± 2.14 a	8.38 ± 4.31 ab	4.49 ± 1.01 b	0.03
		5–15	3.41 ± 0.99	8.69 ± 2.89	12.5 ± 5.88	0.28
	Post-fire	0–5	16.1 ± 4.81	17.3 ± 3.5	6.54 ± 0.82	0.09
		5–15	4.82 ± 2.14 ab	15.3 ± 4.56 a	2.73 ± 0.69 b	0.02

[a] Treatment.
[b] Sub-treatment.

were significant at the $p = 0.065$ level. Pre-fire SMP was highest in the non-invaded site in the 0–5 cm soil depth and in the biological control site in the 5–15 cm soil depth (Table 4). However, post-fire there were no differences among sites in the 0–5 cm soil depth with the herbicide site containing the highest availability of P at both depths.

The pool of total C (litter, 0–5 cm, and 5–15 cm, combined) was affected more by fire ($F_{1,124} = 43.5$, $p < 0.0001$) than by site ($F_{2,124} = 15$, $p < 0.0001$). Before the fire, the non-invaded site con-tained a larger pool of total C compared to the herbicide and bio-logical control sites (Fig. 2). However, after the fire, the biological control and non-invaded sites contained a larger pool of total C compared to the herbicide site (Fig. 2). There was a significant interaction between fire and site ($F_{1,124} = 5.07$, $p = 0.008$) caused by the greater loss of aboveground C in the herbicide site. The pool of total N was influenced by site ($F_{1,133} = 17$, $p < 0.0001$) with no interactions. The pool of total N was largest in the non-invaded site compared to the herbicide and biological control sites before the
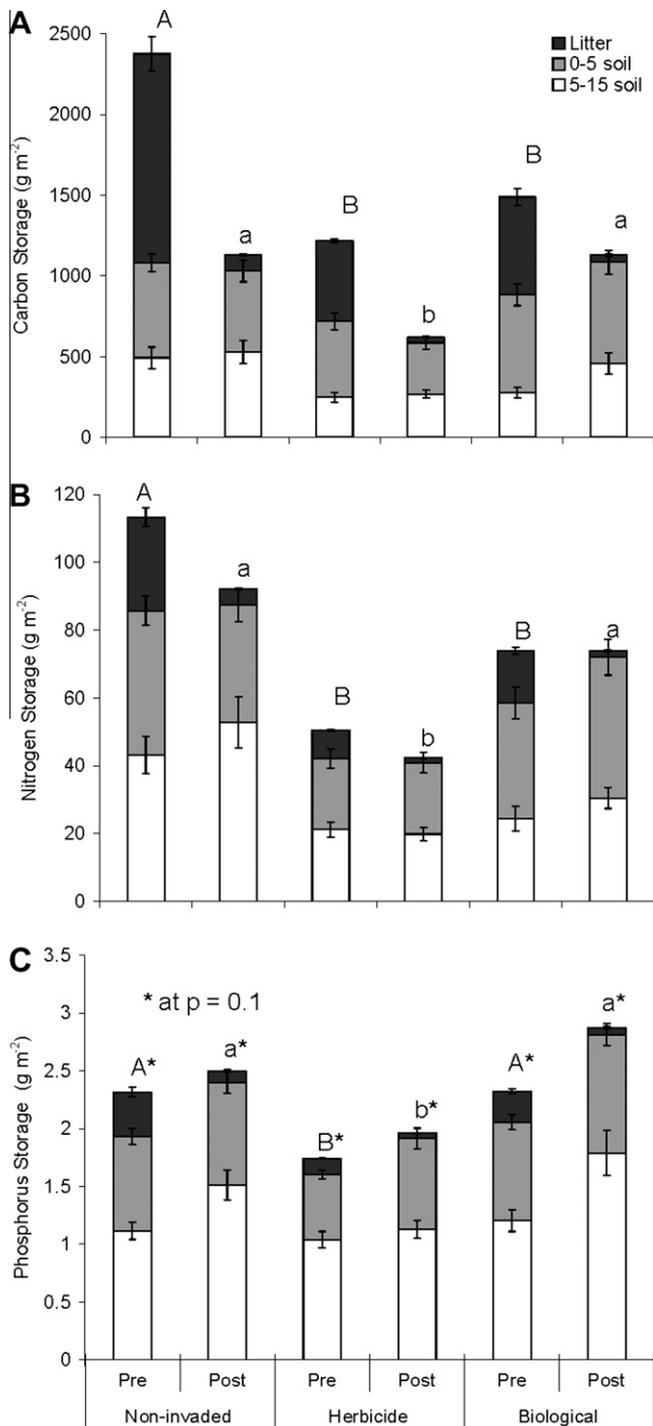
Fig. 2. Mean (±SE) of pre- and post-fire total storages of (A) carbon, (B) nitrogen, and (C) phosphorus measured in the non-invaded, herbicide, and biological control sites (Different capital and lower case letters indicate significant differences for pre- and post-fire means, respectively).

fire (Fig. 2). However, after the fire, the herbicide site contained the smallest pool of total N compared to the non-invaded and biological control sites (Fig. 2). The pool of total P was affected by site ($F_{1,129} = 4.88$, $p = 0.009$) with no interactions. The non-invaded and biological sites contained the largest pool of total P, before and after the fire (Fig. 2).

Microbial biomass carbon was affected more by fire ($F_{1,268} = 86.9$, $p < 0.0001$) than by depth ($F_{1,268} = 27.3$, $p < 0.0001$) or site ($F_{2,268} = 6.69$, $p = 0.002$). Microbial biomass carbon was low-

er in the 0–5 cm soil depth in the herbicide site compared to the non-invaded and biological control sites, both before and after the fire (Table 5). There were significant interactions between fire and site ($F_{1,268} = 5.37$, $p = 0.005$), site and depth ($F_{2,268} = 4.60$, $p = 0.01$), and fire, site, and depth ($F_{1,268} = 3.65$, $p = 0.03$). Interactions between fire and site were caused by the greater reduction in MBC levels in the non-invaded and biological control sites after the fire. The site and depth interaction was caused by the similarity of MBC levels in the pre-fire herbicide soil depths. The fire, site, and depth interaction was caused by the greater reduction in MBC levels in the 5–15 cm soil level of the non-invaded after the fire. The pre-fire MBC was strongly correlated with soil moisture in the non-invaded ($R^2 = 0.89$, $p < 0.0001$) (Fig. 3A), herbicide ($R^2 = 0.52$, $p = 0.0005$) (Fig. 3B), and biological control sites ($R^2 = 0.82$, $p < 0.0001$) (Fig. 3C).

4. Discussion

4.1. Alteration of aboveground components

The invasion and management of *M. quinquenervia* caused significant and persistent changes in the aboveground litter storage of a sub-tropical wetland forest. Litter will accumulate on the forest floor when organic matter inputs exceed outputs. The main source of the organic matter input to the litter in these forests was from litterfall. Before the release of the two biological control agents, Van et al. (2002) measured litterfall in a mature *M. quinquenervia* forest as 750–930 g dry weight m^{-2} year^{-1}. In Australia, where *M. quinquenervia* is attacked by many insect herbivores, litterfall ranged from 675 to 809 g dry weight m^{-2} year^{-1} in seasonally inundated sites (Greenway, 1994). Litterfall from *M. quinquenervia* was not measured in this study although rates in the biological control site were presumed to be lower than reported by the previous studies because of the smaller sized trees. Martin et al. (2009) reported native litterfall rates of 257.5 g dry weight m^{-2} year^{-1} in a *T. distichum* forest adjacent to the non-invaded study area. The herbicide site had no new litterfall inputs, as all the trees were killed with this management strategy and had not re-grown.

The main source of the organic matter output from the litter in these forests is from litter decomposition. Previous studies have suggested that *M. quinquenervia* has a lower rate of litter decay compared to *T. distichum* because leaves of *M. quinquenervia* contain antibacterial phenolics which hinder microbial decomposition (Greenway, 1994; Gordon, 1998; Ehrenfeld, 2003). Although no direct measurements of *M. quinquenervia* decomposition have been published, litterfall and litter accumulation data from Greenway (1994) have been re-analyzed to obtain an estimate of 4.3 years for the turnover time of *M. quinquenervia* litter. Nessel and Bayley (1984) estimated 3 years for the turnover time of *T. distichum* litter, the dominant litterfall component in the non-invaded site. The estimates of litterfall and decomposition rates would logically predict that greater amounts of litter would accumulate in the biological and non-invaded sites compared to the herbicide site.

Although four years had passed since the herbicide application, there was a reduction in both litter biomass and nutrient storage in the herbicide site compared to the non-invaded site (Figs. 1 and 2). This is most likely due to differences in the relative compositions of the litter among sites where the herbicide site contained a greater proportion of relatively low-nutrient wood material compared to the non-invaded and biological control sites (Fig. 1). The biological control site also contained less litter biomass and stored less nutrients compared to the non-invaded site (Figs. 1 and 2). There are two possible explanations for these observed differences: (1) the biological control agents may be altering the quality of nutrient in-

Table 5
Mean (±SE) of pre- and post-fire microbial biomass carbon (MBC) measured in the non-invaded, herbicide, and biological control sites (different lower case letters within rows indicate significant differences).

Variable	Fire[b]	Depth	Non-invaded[a]	Herbicide[a]	Biological[a]	P
MBC (mg C kg^{-1})	Pre-fire	0–5	785 ± 116	330 ± 46.4	791 ± 150	0.08
		5–15	408 ± 45.4 a	295 ± 29.5 a	181 ± 34.3 b	0.0001
	Post-fire	0–5	186 ± 20.4 a	105 ± 9.75 b	174 ± 19.5 a	0.002
		5–15	99.3 ± 10.7	109 ± 18.5	144 ± 24.9	0.5

[a] Treatment.
[b] Sub-treatment.
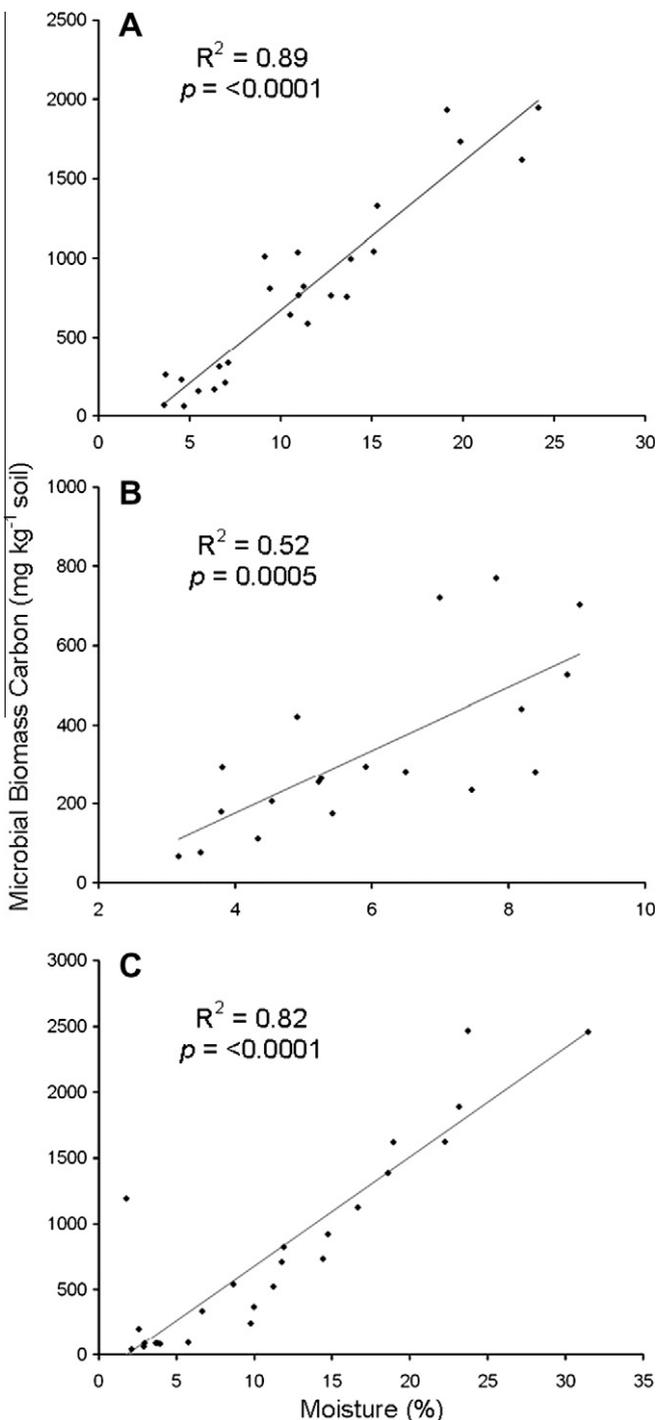
Fig. 3. Relationship between microbial biomass carbon concentration and percent soil moisture in the pre-fire, 0–5 cm soil depth of the (A) non-invaded, (B) herbicide, and (C) biological control sites.

puts thereby accelerating the decomposition of the *M. quinquenervia* litter in the biological control site and/or (2) a low quality litter-fall component is slowing litter decomposition rates in the non-invaded site.

With regard to the first explanation, Franks et al. (2006) found that higher densities of the biological control agent *B. melaleucae* caused *M. quinquenervia* seedlings to drop leaves prematurely, which could interrupt the natural cycle of nutrient resorption during senescence and result in higher quality leaf litter inputs. In addition, the frass produced by both biological agents may be rich in N and P thereby short-circuiting ecosystem nutrient limitations and accelerating litter decomposition (Frost and Hunter, 2007). The second explanation involves the accumulation of *P. elliottii* needles on the forest floor in the non-invaded site. Martin et al. (2009) found that 7% of the litterfall in plots adjacent to the non-invaded site was *P. elliottii* needles, which are known to decompose at a much slower rate than *T. distichum* and may accumulate on the forest floor (Gholz et al., 1985). This could increase total biomass inputs while slowing the decomposition rate of the *T. distichum* litter, resulting in greater litter accumulation than expected.

All of the sites lost a significant amount of litter biomass and aboveground nutrient storage after the fire (Table 1, Fig. 2). However, the herbicide site lost more of the total biomass compared to the non-invaded site. This may indicate that the intensity of the fire was greatest in the herbicide site. Unfortunately, as this fire was not planned, there were no intensity measurements taken during the burn. The herbicide site also lost significantly more of the litter storage of C (96%, $p = 0.05$), N (90%, $p = 0.04$), and P (90%, $p = 0.005$) compared to the non-invaded site (Fig. 2). Other studies have reported similar losses of aboveground N after fires (Kauffman et al., 1993; Hughes et al., 2000; Wan et al., 2001; Wanthongchai et al., 2008).

Phosphorus losses from the herbicide site were higher than previously reported (Kauffman et al., 1993; Hughes et al., 2000; Wanthongchai et al., 2008). Nutrient losses from aboveground storages after fire can be caused by volatilization and particulate transport, transformation of organic to inorganic forms, and transport by wind and water (Neary et al., 1999; Certini, 2005). Before the fire, the landscape in the herbicide site consisted of sparsely distributed herbaceous plants and large amounts of dry woody debris on the soil surface. The fire reduced woody debris by 94% and killed most of the standing vegetation, leaving bare mineral soil that was vulnerable to wind transport. While some of the litter P was incorporated into the mineral soil after the fire, it is possible that some was blown off-site by wind (Neary et al., 1999; Certini 2005).

4.2. Alteration of belowground components

The invasion and management of *M. quinquenervia* significantly altered the biotic and abiotic components of the surface soils both before and after the fire. Before the fire, the herbicide site had significantly less moisture at 0–5 cm compared to the biological and non-invaded sites (Table 2). This may be explained by the litter composition in the herbicide site which, unlike the mostly unde-

composed and moderately decomposed leaves in the non-invaded and biological control sites, consisted primarily of coarse woody material that left large portions of the mineral soil exposed to wind and solar radiation (Fig. 1). Post-fire the herbicide site had lower levels of soil moisture at 0–5 cm compared to the non-native and biological control sites. This may be the result of lower initial soil moisture and increased fire intensity in the herbicide site.

The herbicide site had consistently lower storages of C, N, and P both pre- and post-fire at both soil depths, although not all measured differences were significant (Fig. 2). Findlay et al. (2003) noted a similar pattern with the invasive reed *Phragmites australis* whose removal from a marsh by herbicides and cutting disrupted the system's ability to process and store N. In addition, the herbicidal treatment and cutting of the invasive plant *Pteridium aquilinum* led to a loss of ecosystem C storage in an European moorland (Marrs et al., 2007). In this study, despite increased P storage in the 0–5 cm soil depth in every site, the only significant increase was found in the herbicide site ($p = 0.03$). As discussed above the higher intensity of the fire in this site probably caused the significantly higher loss of the litter P. It is likely that some of the P rich ash produced from the combustion of the litter was incorporated into the 0–5 cm soil depth by wind events and microbial communities (Neary et al., 1999; Carter and Foster, 2004; Certini, 2005).

Nitrogen availability in the 0–5 cm soil depth increased in biological control ($p = 0.06$) and herbicide ($p = 0.002$) sites after the fire (Table 5). Several studies have found similar results with increasing N availability after fire (Giardina and Rhoades, 2001; Carter and Foster, 2004; Wanthongchai et al., 2008). In contrast, although the availability of P was consistently lower at 0–5 cm in the biological control site, the fire did not alter its availability in any site or soil depth. These changes in the storage and availability of nutrients may have unpredictable effects on ecosystem structure and function in the future. For example, minimum levels of N and P availability are needed for maintenance of soil microbial communities and to support regrowth by native plants after disturbances such as fire. However, any N or P produced in excess of these needs may be vulnerable to loss by leaching and erosion. Further study is required to determine the current baseline requirements of the plant and microbial communities in these sites in order to ensure that invasive species management strategies do not promote nutrient leaching with negative consequences for downstream ecosystems.

In addition to alterations in nutrient cycling and storage caused by the management of invasive species, microbial communities may also exhibit changes that may ultimately influence future ecosystem services. Wardle et al. (2004) detailed how plant community structure drove changes in soil microbial community size and composition via a series of above- and belowground feedback loops. In this study, MBC was lower at 0–5 cm in the herbicide site both before and after the fire (Table 5). Nutrient availability did not explain the differences between sites suggesting that environmental factors such as soil moisture and temperature controlled levels of MBC. Although pre-fire levels of MBC were highly correlated with soil moisture, no relationship existed post-fire (Fig. 3). This lack of a relationship post-fire may reflect higher soil temperatures normally found right after a fire that would reduce MBC (Neary et al., 1999; Certini, 2005). Prieto-Fernandez et al. (1998) found a significant decrease in the size of the soil microbial biomass after a fire in a pine forest. Changes in microbial community structure may significantly affect the ability of these systems to recover after the fire.

Determining the best management practices for invasive species requires consideration of a broad array of factors and their potential interactions, including future interactions with natural events such as fires. Most efforts to date have emphasized aboveground factors such as plant and animal diversity and richness, with little to no consideration of belowground factors such as nutrient storage, nutrient cycling, and microbial community biomass. Although this study clearly demonstrates how foundational ecosystem components were affected by the management of invasive plants in the backdrop of a natural fire event, the challenges involved in the statistical analysis of large-scale treatment designs should limit the extrapolation of these results without further experimentation.

Biological control of *M. quinquenervia* using insect herbivores has proven to be effective at controlling plant growth and reproduction (Tipping et al., 2008b, Tipping et al., 2009; Van Driesche et al., 2010). The results of this study suggest that this method may have less of an impact on nutrient storage and cycling than herbicides. Although herbicides remain a valuable tool in the management of invasive species, their potential consequences on ecosystem structure and function should be evaluated. Clearly, alterations to foundational communities including microbes are occurring because of management practices. If the belowground side effects of invasive plant management in context of natural disturbance regimes remains poorly understood, then our ability to restore entire ecosystems such as the Florida Everglades remains an open question.

Acknowledgments

References

Andersen, J.M., 1976. Ignition method for determination of total phosphorus in lake sediments. Water Research 10, 329–331.

Balciunas, J.K., Burrows, D.W., Purcell, M.F., 1994. Field and laboratory host ranges of the Australian weevil, *Oxyops vitiosa* (Coleoptera, Curculionidae), a potential biological control agent for the paperbark tree, *Melaleuca quinquenervia*. Biological Control 4, 351–360.

Beyers, D.W., 1998. Causal inference in environmental impact studies. Journal of the North American Benthological Society 17, 367–373.

Blumenthal, D., 2005. Interrelated causes of plant invasion. Science 310, 243–244.

Brookes, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. BioScience 53, 677–688.

Carter, M.C., Foster, C.D., 2004. Prescribed burning and productivity in southern pine forests: a review. Forest Ecology and Management 191, 93–109.

Center, T.D., Pratt, P.D., Tipping, P.W., Rayamajhi, M.B., Van, T.K., Wineriter, S.A., Dray, F.A., Purcell, M., 2006. Field colonization, population growth, and dispersal of *Boreioglycaspis melaleucae* Moore, A biological control agent of the invasive tree *Melaleuca quinquenervia* (Cav.) Blake. Biological Control 39, 363–374.

Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143, 1–10.

D'Antonio, C., Meyerson, L.A., 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restoration Ecology 10, 703–713.

D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23, 63–87.

Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invisibility. Journal of Ecology 88, 528–534.

Denslow, J.S., D'Antonio, C.M., 2005. After biocontrol: assessing indirect effects of insect releases. Biological Control 35, 307–318.

Dray, F.A., Bennett, B.C., Center, T.D., 2006. Invasion history of *Melaleuca quinquenervia* (Cav.) S.T. Blake in Florida. Castanea 71, 210–225.

Ehrenfeld, J.G., 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6, 503–523.

Evans, R.D., Rimer, R., Belnap, S.T., 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. Ecological Application 11, 1301–1310.

Findlay, S., Groffman, P., Dye, S., 2003. Effects of *Phragmites australis* removal on marsh nutrient cycling. Wetlands Ecology and Management 11, 157–165.

Franks, S.J., Kral, A.M., Pratt, P.D., 2006. Herbivory by introduced insects reduces growth and survival of *Melaleuca quinquenervia* seedlings. Environmental Entomology 35, 366–372.

Frost, C.J., Hunter, M.D., 2007. Recycling of nitrogen in herbivore feces: plant recovery, herbivore assimilation, soil retention, and leaching losses. Oecologia 151, 42–53.

Gholz, H.L., Perry, C.S., Cropper, W.P., Hendry, L.C., 1985. Litterfall, decomposition, and nitrogen and phosphorus dynamics in a chronosequence of slash pine (*Pinus elliottii*) plantations. Forest Science 31, 463–478.

Giardina, C.P., Rhoades, C.C., 2001. Clear cutting and burning affect nitrogen supply, phosphorus fractions and seedling growth in soils from a Wyoming lodgepole pine forest. Forest Ecology and Management 140, 19–28.

Gordon, D.R., 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecological Applications 8, 975–989.

Greenway, M., 1994. Litter accession and accumulation in a *Melaleuca quinquenervia* (Cav) Blake. S.T. wetland in southeastern Queensland. Australian Journal of Marine and Freshwater Research 45, 1509–1519.

Grierson, P.F., Comerford, N.B., Jokela, E.J., 1999. Phosphorus mineralization and microbial biomass in a Florida Spodosol: effects of water potential, temperature and fertilizer application. Biology and Fertility of Soils 28, 244–252.

Grimshaw, H.J., 2002. Nutrient release and detritus production by herbicide-treated freely floating aquatic vegetation in a large, shallow subtropical lake and river. Archives fur Hydrobiologie 153, 469–490.

Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6, 324–337.

Huenneke, L.F., Hamberg, S.P., Koide, R., Mooney, H.A., Vitousek, P.M., 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology 71, 478–491.

Hughes, R.F., Kauffman, J.B., Cummings, D.L., 2000. Fire in the Brazilian Amazon 3: dynamics of biomass, C, and nutrient pools in regenerating forests. Oecologia 124, 574–588.

Kauffman, J.B., Sanford, R.L., Cummings, D.L., Salcedo, I.H., Sampaio, E., 1993. Biomass and nutrient dynamics associated with slash fires in neotropical dry forests. Ecology 74, 140–151.

Kauffman, S.R., Smouse, P.E., 2001. Comparing indigenous and introduced populations of *Melaleuca quinquenervia* (Cav.) Blake: response of seedlings to water and pH levels. Oecologia 127, 487–494.

Keeley, J.E., 2006. Fire management impacts on invasive plants in the western United States. Conservation Biology 20, 375–384.

LaRoche, F.B., 1998. Managing melaleuca (*Melaleuca quinquenervia*) in the Everglades. Weed Technology 12, 726–732.

Luczak, C., Janquin, M.A., Kupka, A., 1997. Simple standard procedure for the routine determination of organic matter in marine sediment. Hydrobiologia 345, 87–94.

Mack, M.C., D'Antonio, C.M., 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution 13, 195–198.

Malcom, G.M., Bush, D.S., Rice, S.K., 2008. Soil nitrogen conditions approach pre-invasion levels following restoration of nitrogen-fixing black locust (*Robinia pseudoacacia*) stands in a pine-oak ecosystem. Restoration Ecology 16, 70–78.

Marrs, R.H., Galtress, K., Tong, C., Cox, E.S., Blackbird, S.J., Heyes, T.J., Pakeman, R.J., Le Duc, M.G., 2007. Competing conservation goals, biodiversity or ecosystem services: element losses and species recruitment in a managed moorland-bracken model system. Journal of Environmental Management 85, 1034–1047.

Martin, M.R., Tipping, P.W., Sickman, J.O., 2009. Invasion by an exotic tree alters above and belowground ecosystem components. Biological Invasions 11 (8), 1883–1894.

Myers, R.L., 1984. Ecological compression of *Taxodium distichum* var. nutans by *Melaleuca quinquenervia* in Southern Florida. In: Ewel, K.C., Odum, H.T. (Eds.), Cypress Swamps. University Presses of Florida, Gainesville, FL, pp. 358–364.

Neary, D.G., Klopatek, C.C., DeBano, L.F., Folliott, P.F., 1999. Fire effects on belowground sustainability: a review and synthesis. Forest Ecology and Management 122, 51–71.

Nessel, J.K., Bayley, E., 1984. Distribution and dynamics of organic matter and phosphorus in a sewage-enriched cypress swamp. In: Ewel, K.C., Odum, H.T. (Eds.), Cypress Swamps. University Presses of Florida, Gainesville, Florida, pp. 262–278.

Newman, S., Schuette, J., Grace, J.B., Rutchey, K., Fontaine, T., Reddy, K.R., Poetrucha, M., 1998. Factors influencing cattail abundance in the northern Everglades. Aquatic Botany 60, 265–280.

Ogden, J.A.E., Rajmanek, M., 2005. Recovery of native plant communities after the control of a dominant invasive plant species, *Foeniculum vulgare*: implications for management. Biological Conservation 125, 427–439.

Pickart, A.J., Miller, L.M., Duebendorfer, T.E., 1998. Yellow bush lupine invasion in northern California coastal dunes: I. Ecological impacts and manual restoration techniques. Restoration Ecology 6, 59–68.

Prieto-Fernandez, A., Acea, M.J., Carballas, T., 1998. Soil microbial and extractable C and N after wildfire. Biology and Fertility of Soils 27, 132–142.

Purcell, M.F., Balciunas, J.K., 1994. Life history and distribution of the Australian weevil *Oxyops vitiosa* (Coleoptera, Curculionidae), a potential biological control agent for *Melaleuca quinquenervia* (Myrtaceae). Annals of the Entomological Society of America 87, 867–873.

Purcell, M.F., Balciunas, J.K., Jones, P., 1997. Biology and host-range of *Boreioglycaspis melaleucae* (Hemiptera: Psyllidae), potential biological control agent for *Melaleuca quinquenervia* (Myrtaceae). Environmental Entomology 26, 366–372.

Serbesoff-King, K., 2003. Melaleuca in Florida: a literature review on the taxonomy, distribution, biology, ecology, economic importance, and control measures. Journal of Aquatic Plant Management 41, 98–112.

SERC, SRCC, 2007. Naples, Florida (086078) Period of Record Monthly Climate Summary.

Tipping, P.W., Martin, M.R., Center, T.D., Davern, T.M., 2008a. Suppression of *Salvinia molesta* Mitchell in Texas and Louisiana by *Cyrtobagous salviniae* Calder and Sands. Aquatic Botany 88, 196–202.

Tipping, P.W., Martin, M.R., Pratt, P.D., Center, T.D., Rayamajhi, M.B., 2008b. Suppression of growth and reproduction of an exotic invasive tree by two introduced insects. Biological Control 44, 235–241.

Tipping, P.W., Martin, M.R., Nimmo, K.R., Pierce, R.M., Smart, M.D., White, E., Madeira, P.T., Center, T.D., 2009. Invasion of a West Everglades wetland by *Melaleuca quinquenervia* countered by classical biological control. Biological Control 48, 73–78.

USDA, NRCS, 1998. Soil Survey of Collier County Area, Florida. United State Department of Agriculture, Natural Resource Conservation Service.

Van, T.K., Rayachhetry, M.B., Center, T.D., Pratt, P.D., 2002. Litter dynamics and phenology of *Melaleuca quinquenervia* in South Florida. Journal of Aquatic Plant Management 40, 22–27.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass-C. Soil Biology & Biochemistry 19, 703–707.

Van Driesche, R.G., Carruthers, R.I., Center, T.D., Hoddle, M.S., Hough-Goldstein, J., Morin, L., Smith, L., Wagner, D.L., Blossey, B., Brancatini, V., Casagrande, R., Causton, C.E., Coetzee, J.A., Cuda, J., Ding, J., Fowler, S.V., Frank, J.H., Fuester, R., Goolsby, J., Grodowitz, M., Heard, T.A., Hill, M.P., Hoffmann, J.H., Huber, J., Julien, M., Kairo, M.T.K., Kenis, M., Mason, P., Medal, J., Messing, R., Miller, R., Moore, A., Neuenschwander, P., Newman, R., Norambuena, H., Palmer, W.A., Pemberton, R., Perez Panduro, A., Pratt, P.D., Rayamajhi, M., Salom, S., Sands, D., Schooler, S., Sheppard, A., Shaw, R., Schwarzländer, M., Tipping, P.W., van Klinken, R.D., 2010. Classical biological control for the protection of natural ecosystems. Biological Control 54, S2–S33.

Wade, D., Ewel, J., Hofstetter, R., 1980. Fire in south Florida ecosystems. Southeastern Florida Experimental Station.

Wan, S.Q., Hui, D.F., Luo, Y.Q., 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecological Applications 11, 1349–1365.

Wanthongchai, K., Bauhus, J., Goldammer, J.G., 2008. Nutrient losses through prescribed burning of aboveground litter and understorey in dry dipterocarp forests of different fire history. Catena 74, 321–332.

Wardle, D.A., Yeates, G.W., Williamson, W.M., Bonner, K.I., Barker, G.M., 2004. Linking aboveground and belowground communities: the indirect influence of aphid species identity and diversity on a three trophic level soil food web. Oikos 107, 283–294.

Wineriter, S.A., Buckingham, G.R., Frank, J.H., 2003. Host range of *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae). A potential biocontrol agent of *Melaleuca quinquenervia* (Cav.) S.T. Blake (Myrtaceae), under quarantine. Biological Control 27, 273–292.

Wheeler, G.S., Massey, L.M., Southwell, I.A., 2002. Antipredator defense of biological control agent *Oxyops vitiosa* is mediated by plant volatiles sequestered from the host plant *Melaleuca quinquenervia*. Journal of Chemical Ecology 28, 297–315.

White, J.R., Reddy, K.R., 2000. Influence of phosphorus loading on organic nitrogen mineralization of everglades soils. Soil Science Society of America Journal 64, 1525–1534.