Does Time since Fire Explain Plant Biomass Allocation in the Florida, USA, Scrub Ecosystem?

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ABSTRACT

Although belowground biomass patterns are important in understanding aboveground responses, few studies have quantified how belowground biomass changes in response to fire cycles. In this study, we determined if patterns of time-since-fire (TSF; range 3 yr to 25 yr) affect belowground and aboveground biomass in scrubby flatwoods, a type of Florida, USA, scrub ecosystem. We also examined if plant groups (oaks, palmettos and all other species) show variation in biomass partitioning between belowground to aboveground biomass. We found that TSF had a significant positive impact on shoot biomass of oaks and leaf litter but did not affect total aboveground biomass or the aboveground biomass of other species groups. Total belowground biomass was not significantly explained by TSF, although the belowground biomass of oaks showed a significant quadratic relationship with TSF ($r^2 = 0.45$, $P = 0.023$). Mean belowground to aboveground biomass ratios were 3.47 ±0.76 overall, 2.18 ±0.99 for oaks, 7.25 ±1.01 for palmettos, and 4.94 ±0.89 for other species. Management of fire-prone ecosystems can use belowground biomass patterns to avoid too-frequent burns that may reduce belowground biomass and affect the ability of ecosystems to respond to subsequent fires. Management actions should also maintain sufficient belowground biomass to buffer against periodic drought.

Keywords: aboveground, belowground, oaks, palmettos, rhizomes, scrubby flatwoods

INTRODUCTION

Fire regimes play an important role in biomass allocation patterns. For example, in fire-prone ecosystems, total plant biomass, growth rates, and distribution of biomass between roots and shoots is influenced by fire intensity and frequency (Pare and Bergeron 1995, de Vinas and Ayanz 2000, Dijkstra *et al.* 2002, Day *et al.* 2006, Mack *et al*. 2008). Pyrogenic ecosystems often have higher aboveground biomass accumulation shortly after fire, with declining growth rates as time-since-fire (TSF) increases (Hanes 1971, Wirth *et al.* 2002, Mappin *et al.* 2003). A chronosequence approach (holding all variables but time since fire constant; Jenny 1941) is one of the most used methods to examine long-term ecosystem response such as fire in a short time frame (Ewers and Pendall 2008).

Ecosystem-level patterns of plant biomass in relation to TSF, especially for roots and other belowground organs, are poorly understood (Williams *et al.* 2008). Uncertainties in estimation of carbon fluxes are attributed to poor resolution of biomass data, since most data are satellite-derived (Quaife *et al.* 2008). Understanding the patterns in biomass distribution between aboveground and belowground biomass sheds light on ecosystem processes such as carbon sequestration and water table dynamics (Feddes *et al.* 2001, Day *et al.* 2006, Collins and Braas 2007, Rodriguez-Iturbe *et al.* 2007, Sierra *et al.* 2007).

One ecosystem that is shaped by recurrent fire is Florida scrub (Myers 1990, Menges 2007), a shrub-dominated ecosystem on nutrient-poor soils (Myers 1990) harboring several endemic and rare plants (Estill and Cruzan 2001). For scrubby flatwoods, a type of Florida scrub, the optimal fire return interval that maximizes species diversity and yields positive population growth rates of endemic plants is about 8 years to 16 years (Menges *et al.* 2008). Biomass patterns in relation to TSF have been described in a coastal Florida scrub by Schmalzer and Hinkle (1987), and more recently by Day *et al.* (2006). However, these studies do not explicitly consider variation in belowground biomass with TSF, and the number of categories of TSF is limited as well (2, 4, 8, and 25 yr in Schmalzer and Hinkle 1987). Moreover, no estimates of belowground biomass dynamics with TSF exist for interior Florida scrub ecosystems.

A main objective of this study was to describe TSF-related patterns in total belowground biomass (rhizomes and roots), total aboveground biomass (leaves, stems, and reproductive parts), litter, and ratios of belowground to aboveground biomass in interior Florida scrub on the Lake Wales Ridge, Florida, USA. We also tested for differences in biomass allocation among oaks, palmettos, and all other species; as well as described belowground biomass in relation to depth. Based on prior work, we made several predictions. First, based on theoretical predictions of biomass distribution in harsh environments experiencing frequent fires (Chapin 1980, Iwasa and Kubo 1997, Gurvich *et al.* 2005), we predicted that Florida scrub plants will allocate greater biomass to belowground storage organs than aboveground shoots. We also predicted that aboveground biomass will increase with TSF, because plants are top-killed by fires and resprout with greater vigor after fire in similar sclerophyllous shrub-dominated ecosystems (Schmalzer and Hinkle 1987, Dijkstra *et al.* 2002). Though the fine root biomass in recently burned scrub shows an immediate (within 1 yr) increase after fire (Day *et al.* 2006, Schafer and Mack 2009), we posited that belowground biomass will remain steady with TSF due to two opposing mechanisms—carbon removal from storage to support resprouting, and addition of photosynthates to belowground compartments (Langley *et al.* 2002).

METHODS

Site Description

The study was conducted at the ca. 2000 ha Archbold Biological Station (ABS; 22°11'N, 81°21'W), located at the southern boundary of the Lake Wales Ridge in central Florida, USA. The climate includes hot, wet summers from June to September, and mild, dry winters. Typically, temperatures are highest in August and lowest in January (Abrahamson 1984). Average annual rainfall is 1.365 mm (ABS weather data, 77 years), with 60% falling between June and September; the wet season and intermittent rainfall occurs during the eight-month dry season and may account for 40% of total annual rainfall (Chen and Gerber 1990). Depth to water table, measured at the main grounds of ABS, varies from 0.5 m to 1.8 m annually (Saha *et al.* 2008). Soils are coarse-grained, drought-prone, and infertile (Carter *et al.* 1989, Saha *et al.* 2008).

The ABS area is characterized by a mosaic of scrub, flatwoods, and seasonal ponds (Abrahamson 1984, Menges and Hawkes 1998, Menges 1999). Interior Florida scrub vegetation is divided into several major assemblages described in detail by Abrahamson (1984). These include scrubby flatwoods, sand pine scrub, and rosemary scrub. We worked in scrubby flatwoods, a type of Florida scrub, and the most common vegetation type at ABS (covering about 30 % of ABS area). In particular, we chose sites dominated by sandhill oak (*Quercus inopina* Ashe), as mapped by Abrahamson (1984). Scrubby flatwoods dominated by *Q. inopina* are characterized by white sands belonging to the Satellite soil series and consist of hypothermic uncoated Aquic Quartzipsamments (Carter *et al.* 1989). Soils are highly infertile with available N and P ranging from 0.0 µg g^{-1} to 2.5 µg g^{-1} and 0.11 µg g^{-1} to 0.45 µg g^{-1}, respectively (S. Saha, Institute for Regional Conservation, unpublished data; J. Schafer, University of Florida, unpublished data). Periodic fires, mainly prescribed, have occurred in these scrubby flatwoods since 1967, and ABS has maintained spatially explicit records of their fire intensity and spatial extent. The ABS fire management plan calls for a modal fire return interval of 5 yr to 20 yr for most areas of scrubby flatwoods (Main and Menges 1997).

Vegetation in the study area was comprised of sclerophyllous shrubs, dominated by clonal oaks (Chapman oak [*Quercus chapmanii* Sarg.], sand live oak [*Q. geminate* Small], and sandhill oak), shrubby palmettos (saw palmetto [*Serenoa repens* {Bartram} Small] and scrub palmetto [*Sabal etonia* Swingle ex Nash]), and ericaceous shrubs such as fetterbush lyonia (*Lyonia lucida* [Lam.] K. Koch), coastal plain staggerbush (*L. fruticosa* [Michx.] G.S. Torr.), shiny blueberry (*Vaccinium myrsinites* [Lam]), and Darrow's blueberry (*V. darrowi* Camp). These nine dominant species constitute 85 % of total biomass in scrubby flatwoods (Saha *et al.* 2008) and are all post-fire resprouters (Menges and Kohfeldt 1995, Abrahamson 2007). Individual clones of scrub oaks often spread over areas of >4 m^2 (S. Saha, personal observation) and oaks are particularly persistent in long-unburned scrubby flatwoods (Menges *et al.* 1993).

Biomass Sampling

We initially selected 21 20 m by 20 m field sites, all in scrubby flatwoods on flat ground, on Satellite soils dominated by sandhill oak. We discarded one site dominated by sandheath (*Ceratiola ericoides* Mitchx.). All sites experienced complete burns (all ground burned, all shrubs top-killed) during the last fire. Sites varied in fire history; time-since-fire (TSF) was 3, 6, 8, 14, 18, 21 and 25 yr. Thus, our sample size was three sites per TSF (2 sites for TSF = 21 years), totaling 20 sites for 7 TSF categories. We sampled biomass in January 2007, during the early dry season when all species irrespective of their leaf phenology had intact leaves present.

We conducted biomass excavations in conjunction with excavation for drift fences around lizard enclosures. First, we marked the boundary of our sampling plots at the northwestern and southeastern corner of each of the 20 m × 20 m enclosures. We then collected aboveground biomass from within the plot boundary. After the mechanized trenches were excavated, we collected the sand, roots, and rhizomes from within our plot boundary. We had to hand excavate the plots if our plot volume of 2 m × 0.5 m × 0.5 m was not completely excavated. We used the means from two plots per enclosure or site as an independent estimate of biomass (g m^{-2}) per site.

Enclosures were selected to be in typical and uniform scrubby flatwoods patches of the specified TSF. Since our study preceded the enclosure installation, there were no cumulative effects of enclosures (herbivory or lack of) on vegetation structure.

Aboveground Biomass Sampling

We collected aboveground biomass in each of the 21 enclosures (sites). Most plants in our ecosystem were evergreen and had leaves present in January. All living stems rooted within the plot were clipped at the base. If a branch from stems rooted outside the plot contributed to the canopy, we did not include it. We collected the plants into paper bags. We identified all the aboveground material to species, separated leaves and stems of each species, and weighed leaves and stems separately. We pooled all plant species into three categories for analyzing biomass data: oaks (Chapman oak, sand live oak, and sandhill oak), palmettos (saw palmetto and scrub palmetto), and other plant species (including the ericaceous shrubs of genera *Lyonia* and *Vaccinium* as well as all other plant species). We also calculated leaf to stem ratios for oaks and other species; palmetto stems (rhizomes) were near the ground surface and were not considered in leaf to stem ratios.

Belowground Biomass Sampling

We collected living belowground biomass (roots and rhizomes) to a depth of 0.5 m from two 1 m² (2 × 0.5 m) plots in each of the 21 enclosures. We followed Mokany *et al.* (2006) in considering excavations to the depth of 0.5 m critical for shrubland ecosystems. Rhizomes and roots extending beyond the plot volume were clipped at the plot boundary. Sand from the trenches was examined thoroughly for belowground parts. The standard sieve number 4 (opening 4.75 mm) was used to separate sand and fine roots. Although the limit between fine roots and coarse roots is ambiguous, we use the sieve size 4 as a cutoff in accordance with other studies (e.g., 5 mm cutoff used in the global database compiled by Gill and Jackson 2000).

To estimate belowground biomass occurring deeper than 0.5 m, we collected three soil cores of 0.05 m diameter and 2.5 m depth from three enclosure sites representing TSF intervals of 3, 8, and 25 yr. Samples were air dried and sieved (sieve size 4) to separate belowground parts from sand.

After the initial sieving, we oven dried biomass samples for 48 hours at 70 °C. Instead of adjusting for the mass of clinging sand (Janzen *et al.* 2002), dried material was again sieved using the size 4 sieve to remove loose sand sticking to the plant parts.

Further belowground biomass separation into three categories (oaks, palmettos, other) was based on morphology, based in part on excavated samples of known plants. Rhizomes were separated from roots based on morphology only. Palmettos have characteristic reddish-brown roots with white rings along the entire length of the roots and lack root hairs (Fisher and Jayachandran 1999). We distinguished oak rhizomes from rhizomes of other species based on greater robustness, presence of woody tissue, and darker color. We recognized oak roots by the presence of short roots with ectomycorrhizal tissue (Valentine *et al.* 2002). Other ectomycorrhizal woody species (e.g., scrub hickory [*Carya floridana* Sarg.]) did not co-occur in our sites.

We also collected litter biomass (leaves, dead stems, ground lichens) from twelve 0.1 m² subplots per enclosure. Litter was oven dried to constant mass at 58 °C for 60 hours.

Standing dead stems were not considered in this analysis. If a small branch of a live stem appeared dead, we did not isolate it from the live biomass. No explicit efforts were made to separate dead roots from the biomass; only rhizomes that were dead and rotting (common due to inundation of rhizomes in surficial water table during wet season; S. Saha, personal observation) were removed from belowground biomass samples.

Data Analysis

All data are reported as site level means ±95 % CI. Linear regressions were used to determine the relationships between TSF and to-

tal aboveground and belowground biomass, belowground to aboveground biomass ratios (b/a), and litter biomass. Each TSF category was represented by three independent replicates, while the data at each replicate (site) were obtained by averaging two sample plots. We did not calculate b/a ratio from samples for which no aboveground or belowground biomass for a plant category was recorded. We reported such data but did not use the samples for analyzing the relationship between TSF and b/a for the plant category. We utilized a curve estimation procedure to determine if the relationship between the variables was linear. Mean b/a ratios averaged across all categories of TSF were compared among the plant categories with one-way ANOVA using SPSS Version 11.5 (SPSS Inc., Chicago, Illinois, USA).

Bonferroni tests were used to conduct *post hoc* comparisons. We checked for normal distribution of variables and detected outliers using Grubb's test (Barnett and Lewis 1998). We used SPSS (2003) for statistical analyses.

RESULTS

Biomass in Relation to TSF

Biomass and belowground to aboveground (b/a) biomass ratios with time-since-fire (TSF), separated by species groups, had variable patterns (Table 1). While total aboveground biomass did not show a significant increase with TSF ($r^2 = 0.067$, $P = 0.182$), aboveground biomass of oaks significantly increased with TSF ($r^2 = 0.29$, $P < 0.05$; Figure 1). The above-

Table 1. Mean aboveground (a) and belowground (b) biomass (g m^{-2}± SEM), litter (g m^{-2}), and belowground to aboveground (b/a) biomass ratio of oaks, palmettos and other species across categories of TSF (yr). Here we calculated mean belowground to aboveground biomass ratios of palmettos and other species only for sites for which both the aboveground and belowground biomass were observed.

Species measure	Time Since Fire (TSF)							Mean
	3 (*n* = 3)	6 (*n* = 3)	8 (*n* = 3)	14 (*n* = 3)	18 (*n* = 3)	21 (*n* = 2)	25 (*n* = 3)	
Oak below	1000.41±300.5 (*n* = 3)	253.32±98.6 (*n* = 3)	383.51±160.4 (*n* = 3)	590.13±198.7 (*n* = 3)	680.86±200.4 (*n* = 3)	393.13±76.3 (*n* = 2)	817.13±287.6 (*n* = 2)	575.39±56.4
Palm below	207.71±91.9 (*n* = 3)	229.88±78.5 (*n* = 3)	195.58±32.4 (*n* = 3)	216.85±18.6 (*n*= 3)	571.60±108.5 (*n* = 3)	113.06 (*n* = 1)	702.82±190.6 (*n* = 3)	331.34±97.5
Other below	319.79±79.5 (*n* = 3)	55.10±8.6 (*n* = 3)	170.55±56.3 (*n* = 2)	167.72±5.4 (*n* = 3)	106.07±32.3 (*n* = 3)	251.85±89.1 (*n* = 2)	622.51±230.0 (*n* = 3)	224.21±67.5
Oak above	87.73±23.1 (*n* = 3)	206.04±87.3 (*n* = 3)	425.60±62.2 (*n* = 3)	487.50±100.8 (*n* = 3)	460.56±64.4 (*n* = 3)	702.40±108.3 (*n* = 2)	444.02±117.0 (*n* = 3)	375.01±46.6
Palm above	247.53±109.5 (*n* = 3)	83.00±54.1 (*n* = 3)	15.68±14.3 (*n* = 3)	70.40±5.5 (*n* = 3)	16.70±6.0 (*n* = 3)	0.00 (*n* = 2)	113.30±89.2 (*n* = 3)	71.06±28.8
Other above	91.07±67.2 (*n* = 3)	99.05±76.4 (*n* = 3)	104.00±98.3 (*n* = 3)	0.00 (*n* = 3)	80.77±33.6 (*n* = 3)	2.09±2.0 (*n* = 2)	25.40±3.6 (*n* = 3)	68.46±24.3
Oak b/a	4.49±1.6 (*n* = 3)	2.71±1.1 (*n* = 3)	1.51±0.9 (*n* = 3)	1.14±0.1 (*n* = 3)	1.01±0.6 (*n* = 3)	0.60±0.2 (*n* = 2)	9.97±4.3 (*n* = 3)	2.69±0.67
Palm b/a	1.22±0.91 (*n* = 3)	0.79 (*n* = 1)	3.02±1.42 (*n* = 2)	3.19±0.49 (*n* = 2)	1.40±0.27 (*n* = 2)	No data	1.37 (*n* = 1)	1.99±0.45
Other b/a	0.30 (*n* = 1)	0.79 (*n* = 1)	5.16±0.53 (*n* = 3)	No data	0.88 (*n* = 1)	No data	5.40 (*n* = 1)	2.87±1.06
Total b/a	4.14±1.2 (*n* = 3)	1.67±0.8 (*n* = 3)	2.65±1.0 (*n* = 3)	1.82±0.2 (*n* = 3)	3.38±1.2 (*n* = 3)	3.32±2.1 (*n* = 2)	5.61±1.4 (*n* = 3)	3.47±0.48
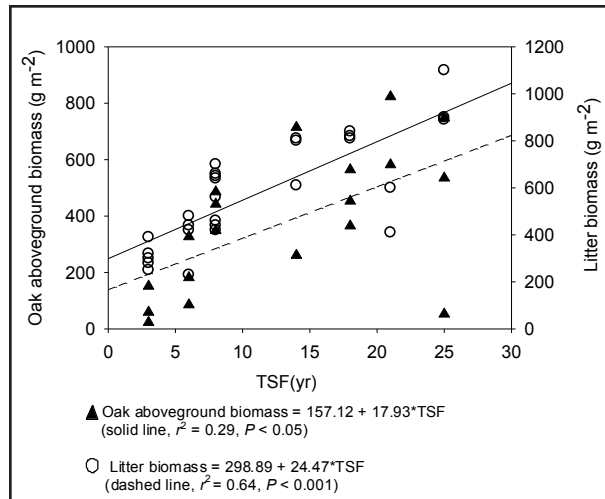
Figure 1. Aboveground biomass of oaks (g m^{-2}) had a significant linear increase with time-since-fire (TSF). Litter biomass (g m^{-2}) also had a significant linear relationship with TSF. Biomass data were collected in Florida scrubby flatwoods ecosystem at Archbold Biological Station (Lake Placid, Florida, USA)..

ground biomass of other species peaked at an intermediate TSF but did not vary significantly with TSF ($r^2 = 0.01$, $P = 0.14$). No significant effect of TSF was observed for aboveground biomass of palmettos ($r^2 = 0.08$, $P = 0.09$).

Total belowground biomass was not significantly related to TSF ($r^2 = 0.03$, $P = 0.16$). After removal of one outlier (3247 g per TSF = 25 years) we did not detect significant effect of TSF on belowground biomass of oaks. The TSF did not explain the belowground biomass of palmettos ($r^2 = 0.01$, $P = 0.09$) or other plant species ($r^2 = 0.01$, $P = 0.15$).

Most belowground biomass was found in the top 0.5 m of soil. Total belowground root biomass averaged 20 % greater when sampling was done to the depth of 2.5 m. Belowground biomass was 1516.34 g m^{-2} to the depth of 0.5 m and 1917.61 g m^{-2} to the depth of 2.5 m in plots with TSF of 3 years. In plots with TSF of 8 years, the biomass was 959.31 g m^{-2} to 0.5 m depth and 1251.18 g m^{-2} to 2.5 m depth. For the greatest TSF of 25 years, belowground biomass was 4528 g m^{-2} and 5233 g m^{-2} to the depths of 0.5 m and 2.5 m, respectively.

Litter biomass strongly increased with TSF ($r^2 = 0.64$, $P < 0.001$; Figure 1). Litter ranged from 254.0 g m^{-2} ±82.2 g m^{-2} for a recently burned (TSF = 3 years) site to 1160.9 g m^{-2} ±178.6 g m^{-2} for a long-unburned (TSF = 25 years) site. Because most of the litter was comprised of oak leaves, the pattern in litter with TSF reflected the pattern in oak aboveground biomass.

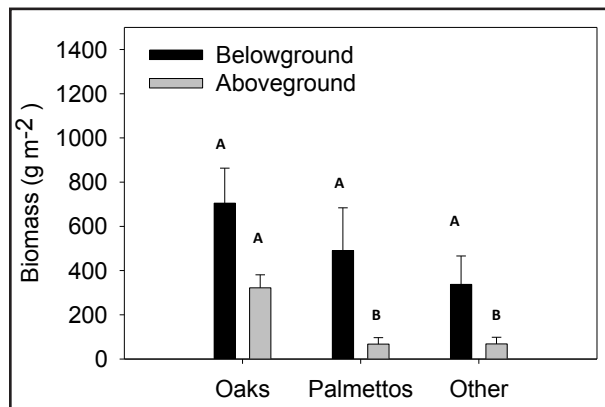### Belowground to Aboveground Biomass (b/a) Ratio in Relation to TSF

The overall b/a biomass ratio was 3.47±0.48 but was lower for oaks (2.69 ±0.47). The total b/a combined across plant categories ratio was not explained by TSF ($r^2 = 0.09$, $P = 0.10$). When analyzed separately, the biomass ratio of oaks ($r^2 = 0.21$, $P = 0.05$) was not explained by TSF either.

We did not analyze effects of TSF on b/a biomass ratio of palmettos and other species because no aboveground biomass was recorded in some sample plots. For example, we did not record any aboveground data for palmettos in TSF category of 21 years (Table 1) and from one or more sites with TSF of 3, 6, 8, 14, 18, and 25 yr. Similarly, no aboveground biomass was recorded for the other species in samples collected from one or more sites with TSF of 3, 6, 8, 18, 21 and 25 years. Other species were absent from all samples from sites with TSF of 14 years (Table 1).

We pooled both aboveground and belowground data across sites to get the mean b/a ratio of palmettos (7.25 ±1.01) and that of the other species (4.94 ±0.89). Rhizomatous stems contributed disproportionately to the belowground biomass, comprising 90 % of belowground palmettos biomass and 70 % of belowground oak biomass. When rhizomes were analyzed separately, the biomass patterns mimicked the trends in belowground biomass. Rhizome biomass of oaks ($r^2 = 0.042$, $P > 0.05$), palmettos ($r^2 = 0.23$, $P > 0.5$), other species ($r^2 = 0.10$, $P > 0.05$) and total ($r^2 = 0.09$, $P > 0.05$) were not explained by TSF.

Biomass Distribution across
Plant Categories

Oaks had the greatest total aboveground biomass (331 ±58.62 g m^{-2}; Figure 2), followed by palmettos (68.72 ±38.15 g m^{-2}) and other species (67.69 ±28.82 g m^{-2}). Aboveground biomass of oaks was an order of magnitude greater than the palm aboveground biomass (Figure 2). One-way ANOVA indicated that aboveground biomass was significantly different among three plant groups ($F_{1, 19}$ = 12.49, P < 0.001). The *post hoc* tests (Bonferroni-adjusted) indicated significant pairwise differences between oaks and palmettos (P < 0.01) and oaks and other species (P < 0.01), while no significant differences were found between palmettos and other species (P > 0.01). Stems (vs. leaves) had most of the aboveground biomass of woody shrubs; mean stem to leaf ratios averaged 3.9 ±0.5 in oaks and 3.9 ±1.2 in

Figure 2. Belowground and aboveground biomass across plant groups (oaks, palmettos, and other species) in a Florida scrubby flatwoods ecosystem. The means are calculated from 20 plots sampled in this study. The bars represent mean biomass (g m^{-2}), while the error bars are 95 % CI. Comparisons of aboveground and belowground biomass between plant categories were made using pairwise Bonferroni tests. Bars topped by different letters are significantly different.

other species. Leaf biomass of palmettos, oaks, and other species averaged 69 g ±18.2, 39 ±6.2 g m^{-2}, and 16 ±6.4 g m^{-2}, respectively.

Stem biomass was 133 ±20.4 g m^{-2} and 49 ±16 g m^{-2} for oak and other species, respectively.

There was no difference in belowground biomass among the three plant categories ($F_{1, 20}$ = 1.294, P = 0.282; Figure 2). Oaks, palmettos, and other species had mean belowground biomass of 704.18 ±98 g m^{-2}, 505 ±102.1 g m^{-2}, and 337.68 ±68.23 g m^{-2}, respectively. Palmetto rhizomes occurred sporadically and weighed from 179 g to 600 g in our study plots.

DISCUSSION

In the Florida scrub ecosystem, patterns in aboveground biomass in relation to time-since-fire varied among plant functional categories, while the total aboveground biomass pooled across all plants was not significantly affected by TSF. Time-since-fire explained significant variation in aboveground biomass of oaks and plant litter as predicted. Because most of the leaf litter was comprised of oak leaves, the pattern in leaf litter with TSF reflected the pattern in oak aboveground biomass. Oak biomass and litter increased linearly with TSF, and did not taper off at TSF of 25 years.

In contrast, we found little effect of TSF on palmettos. Florida scrub palmettos resprout and reach (or exceed) pre-fire leaf numbers within one year of fire (Abrahamson and Abrahamson 2006). Subsequent stability in leaf numbers and aboveground biomass of palmettos probably reflects a balance between greater leaf life span and lower leaf production rates (Abrahamson 2007). Other (non-oak) woody species comprise less than 15 % of total scrub biomass (Saha *et al.* 2008) and did not show any notable trend in relation to TSF, perhaps due to small sample sizes.

Pyrogenic ecosystems vary in biomass trajectories with TSF. For example, plant biomass and productivity stabilized after a TSF of 40 yr to 60 yr in Californian chaparral (Hanes 1971), after 100 years for Siberian Scots pine (*Pinus sylvestris* L.) stands (Wirth *et al.* 2002), after 68 years in Kermes oak-(*Quercus coccifera* L.) dominated shrublands in Spain (de

Vinas and Ayanz 2000), and by 75 years in Canadian boreal forests (Kajimoto *et al*. 2006). Oaks in our study required at least 21 years to attain maximum biomass, but palmettos show a rapid recovery of biomass (TSF of 3 years). The native fire return interval of approximately 8 yr to 16 yr predicted for scrubby flatwoods (Menges 2007) would occur before maximum belowground biomass was achieved.

In scrubby flatwoods, the TSF that supports maximal aboveground biomass does not support maximal diversity, which occurs at intermediate TSF (6 yr to 8 yr; Menges *et al*. 2008). An intermediate TSF may provide optimal conditions for a mixture of dominant and subdominant species, but increases in aboveground biomass of dominant woody shrubs such as oaks, which exhibited maximum biomass at 25 years since fire, probably suppress many species. Other species besides oaks and palmettos exhibit a peak in aboveground biomass at intermediate TSF. Herbaceous plants that occur in fire-created gaps are limited by woody species as the TSF increases and gaps become smaller (Menges *et al.* 2008).

Belowground oak biomass remained stable with TSF, which amounted to comparable oak belowground biomass in recently burned and long-unburned sites. Given that rhizomes constitute 70 % to 90 % of total belowground biomass among dominant species, this pattern is not surprising. Though roots form greater than 50 % of belowground biomass among grasses and non-clonal forbs (Dwire *et al.* 2004), our belowground biomass values of other species might be skewed in favor of rhizomes. Even though the fine root biomass and abundance in coastal scrub increased after fire (Day *et al.* 2006), root biomass remained stable with time-since-fire as shown by Langley *et al.* (2002). The stability in the larger compartment of belowground biomass, especially for dominant species, suggests that allocation to rhizomes might confer advantage in fire-prone systems.

The mean b/a ratio found in this study was 3.47 (range 0.29 to 7.6), similar to the observation that 70 % of total biomass resides in the belowground compartment reported by Johnson *et al.* (1986) for sandhill pine, and to the biomass ratio observed in the Florida's coastal scrub ecosystem (b/a of 5.5 including fine and coarse roots; Rachel E. Schroeder, Old Dominion University, unpublished results). The large belowground allocation of woody species in Florida scrub is similar to the plants found in other fire-prone ecosystems such as Kermes oak in Mediterranean ecosystem (b/a ratio of 3.45; de Vinas and Ayanz 2000), and Scots pine on permafrost stands (b/a ratio of 5.1; Kajimoto *et al.* 2006). A high belowground to aboveground biomass ratio is predicted from optimal allocation models in fire-prone and resource-limited systems (Iwasa and Kubo 1997). Based on empirical tests of optimal allocation models, the root to leaf biomass ratio of 2.5 was considered optimal for annual herbs in low light and low nutrient environments (Osone and Tateno 2005). Perennial plants often devote more biomass belowground than annual or short-lived plants. The high root to leaf biomass ratio of 7.6 ±2.12 among dominant shrubs in this study suggests that the plants in this fire-prone and infertile environment allocate disproportionately more to belowground biomass as an alternative survival strategy, given simultaneous constraints imposed by water availability and nutrient scarcity.

Differential allocation patterns are associated with ecological niche separation along gradients of resource availability (Casper and Jackson 1997). Co-occurring species in Mediterranean ecosystems differ in root morphology and biomass (Silva and Rego 2003, Ackerly 2004). Distinct root morphological patterns confer a differential tolerance to drought as demonstrated by Mediterranean woody plants (Padilla and Pugnaire 2007). Palmettos and oaks in Florida scrub show a differential mechanism of soil water uptake. Palmettos have a dual root system with both shallow (utilizing surficial water table) and deep roots (reaching the groundwater table; Brown *et al.* 1990),

while the oaks take water from shallower depths (up to 80 cm), as shown by analyses of stable isotope data (Saha *et al.* 2008). Palmettos have numerous small-sized roots distributed across soil layers, possibly compensating for the absence of root hairs (Fisher and Jayachandran 1999). In contrast, oak roots span a diversity of size classes but are largely found in the top 0 cm to 50 cm of soil. Palmettos exhibited high b/a ratios due to relatively higher biomass allocation to belowground storage as rhizomes. High belowground biomass in palmettos may be one reason they exhibit extremely low mortality rates during extreme droughts (Abrahamson and Abrahamson 2002). Oaks also allocate a great deal to belowground structures, although not as much as palmettos, and oaks also exhibit low mortality during droughts (Saha *et al.* 2008). Distinct rooting morphologies also confer differential advantages to plants in ecosystems affected by periodic fires (Pate and Bell 1999, Holdo 2006). Scrubby flatwoods investigated in this study showed prevalence of rhizomes in the belowground biomass, consistent with their strong sprouting response after fires (Menges and Kohfeldt 1995).

Our belowground biomass data compare well with estimates of root biomass predicted by Canadell *et al.* (1996) and Jackson *et al.* (1996) for sclerophyllous shrublands. Our measure of mean belowground biomass (1533 ±102.15 g m^{-2}, ranging from 78 g m^{-2} to 5438 g m^{-2} to 0.5 m depth) falls within the range reported by Brown *et al.* (2007) of root biomass data in Florida's coastal scrub ecosystem (mean of 5704 ±368 g m^{-2}; F. Day, Old Dominion University, personal communication). Our data encompass multiple sites with different TSF and thus yield a wider range in biomass values; moreover, they do not account for roots smaller than 5 mm diameter. The measure of total root biomass to the depth of 0.5 and total shoot biomass are comparable to the tundra ecosystem (Jackson *et al.* 1996, Mokany *et al.* 2006).

Our finding that post-fire patterns of belowground biomass differed from aboveground biomass patterns has implications for land managers and restoration ecologists (Pare and Bergeron 1995, Franklin *et al.* 2008). For example, if fires occurred repeatedly before plants attained sufficient belowground biomass (including non-soluble sugars; Olano *et al.* 2006), plants might have reduced reserves during intervals between fires, affecting subsequent post-fire resprouting vigor. Sufficient belowground reserves should also provide resistance to droughts, which may increase with climate change. Thus, we propose that the data on belowground biomass as well as aboveground biomass should be an integral part of understanding native fire return intervals and designing ecologically informed fire regimes.

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