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Growth, Biomass, and Allometry of Resprouting Shrubs after Fire in Scrubby Flatwoods

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ABSTRACT.—Resprouting is advantageous for plants in pyrogenic ecosystems because it allows for quick re-acquisition of space after fire. Resprouting species build multiple stems during their lifetime and have an established root system, which may affect growth and biomass allocation and whether resprouts conform to predicted scaling relationships. We measured height, basal diameter, and biomass of stems of five resprouting shrub species in scrubby flatwoods sites in Florida, varying in time after fire (6 w, 1 y, 8–9 y, 20–21 y). Differences among species in size and allocation ratios tended to be greater in recently burned sites. Six weeks after fire, the dominant species, *Quercus inopina*, had the highest height:diameter and leaf:stem biomass ratios, which may contribute to the ability of this species to persist over fire cycles. The slope of the relationship between stem height and diameter was higher in recently burned sites than 8 to 21 y after fire, whereas the slope of the relationship between stem height and biomass was higher 8 to 21 y after fire than in recently burned sites. Height and biomass of resprouts generally scaled differently with respect to diameter and height than predicted by allometric theory, but biomass of resprouts, on average, scaled with diameter as predicted. Therefore, resprouted stems were taller for a given diameter and accumulated less biomass with height growth. In pyrogenic ecosystems, it may be more advantageous to grow tall, to maximize light capture, than to invest in strength to avoid damage because fire will eventually remove stems. Our results indicated that current allometric theory does not adequately represent scaling of growth and biomass of resprouting shrubs.

INTRODUCTION

Disturbances such as fire often result in the nearly complete removal of aboveground biomass. Woody species in many ecosystems persist after fire by resprouting from surviving belowground organs (Menges and Kohfeldt, 1995; Higgins *et al.*, 2000; Bond and Midgley, 2001; Keeley *et al.*, 2006; Paula and Pausas, 2006). Differences among resprouting species in their ability to occupy space aboveground after fire may be indicative of differences in competitive ability (Kozovits *et al.*, 2005) and contribute to maintenance of species abundances and dominance. Furthermore, changes in fire frequency and severity have the potential to alter allocation to resprouting as a response to disturbance (Bellingham and Sparrow, 2000; Lawes and Clarke, 2011). Thus, variation in growth, biomass allocation, and allometry of resprouts with time after fire, and among species, has important consequences for recovery of ecosystem structure and biomass after fire.

Plant allometry theory predicts how stem height and diameter scale in relation to each other and in relation to stem biomass (Niklas, 1994; West *et al.*, 1999; Niklas and Enquist, 2001). For example the elastic self-similarity model predicts that stem length scales as the 2/3 power of diameter and the geometric self-similarity model, which assumes stems are constructed to resist wind forces with minimal investment in biomass, predicts that stem length is proportional to diameter (Niklas, 1994; Niklas, 1995). Large trees exhibit elastic or

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stress self-similarity (McMahon and Kronauer, 1976; Niklas, 1994; Niklas, 1995), while geometric self-similarity has been documented in young trees (King, 1990; Alvarez-Buylla and Martinez-Ramos, 1992; Niklas, 1995) and shrubs (Whittaker and Woodwell, 1968). Scaling relationships, however, can vary across species and with plant size (Niklas and Spatz, 2004). Allometry research has focused on seed plants (*e.g.,* West *et al.*, 1999; Niklas and Enquist, 2002b), with the implied assumption that stems have grown from a seed. It is not known whether stems of fire-adapted resprouters conform to predicted scaling relationships or if there are different constraints on the growth of resprouted stems that allow for rapid growth after fire.

Many plants build one main stem during their lifetime, but shrub stems consumed by fire are rebuilt multiple times in part from belowground resources. Root biomass comprises approximately 25% of total plant biomass in angiosperm species in general (Niklas and Enquist, 2002a), while belowground biomass may comprise over 80% of total biomass of resprouting shrubs (Saha *et al.*, 2010). Belowground reserves (McPherson and Williams, 1998; Paula and Ojeda, 2009) affect resprouting ability (Moreno and Oechel, 1991) and biomass of resprouts (Lloret and López-Soria, 1993; Cruz *et al.*, 2002), and new stems are usually recruited in clumps (*e.g.,* Silva *et al.*, 2009) around dead stems. Initial stem growth is likely dominated by primary growth because vigorous resprouting after fire is important for re-acquisition of space and continued survival. Higher rates of photosynthesis in resprouts than unburned stems (Fleck *et al.*, 1998; Clemente *et al.*, 2005) may be related to higher allocation to leaf biomass or young green stems. Allometric relationships of recently resprouted shrub stems may depend on resprouting ability and the capacity to reach an aboveground equilibrium that existed prefire, more so than on scaling rules applicable to other woody species.

As stems grow taller, they must increase their mechanical strength by increasing trunk diameter by means of secondary growth (King, 1986) and therefore should have a greater proportion of biomass in stems versus leaves (Givnish, 1982). The fraction of whole plant biomass allocated to leaves is negatively correlated with light availability (Poorter *et al.*, 2012), which should also contribute to a greater proportion of biomass of taller shoots being allocated to stems. Furthermore, the number of resprouted stems per clump is higher in more recently burned sites (Davies and Myerscough, 1991) and differential growth of and resource allocation to aboveground plant parts is affected by competition (Weiner and Thomas, 1992; Kozovits *et al.*, 2005). Because scaling of stem diameter and height is size dependent (Niklas, 1995), increasing stem size and a changing environment with time after fire may lead to changes in allometric relationships and biomass allocation. Variation in biomass scaling in relation to height and diameter with time after fire has implications for the effectiveness of allometric equations in estimating recovery of biomass (Toma *et al.*, 2005) and carbon storage (Williams *et al.*, 2008) after fire.

We examined growth, biomass allocation, and allometric relationships of shrub species after fire in scrubby flatwoods ecosystems of central peninsular Florida. Scrubby flatwoods are a type of Florida scrub where the dominant species are shrubs that resprout after fire (Abrahamson *et al.*, 1984; Menges and Kohfeldt, 1995). Resprouts of dominant scrubby flatwoods species recruit in clumps, and we predicted that the growth ratios and the biomass allocation of these species would change with time after fire, as the stems grow taller and the strength of intra-individual and inter-specific competition decreases. Specifically, we hypothesized that height growth per unit diameter growth would decrease with time after fire as stem crowding decreases and stem age increases (Henry and Aarssen, 1999). In addition we assessed whether height, diameter, and biomass of shrub resprouts scale in relation to each other as predicted by allometric theory. Understanding the scaling of growth and biomass allocation of resprouts is important considering the dominance of resprouting species in pyrogenic ecosystems and, therefore, their contribution to the maintenance of biomass and ecosystem structure after fire.

METHODS

We conducted our study at the Archbold Biological Station (ABS), located near the southern tip of the Lake Wales Ridge in Highlands County, Florida, U.S.A. (27°10′50″N, 81°21′0″W). Mean annual precipitation is 136.5 cm (ABS weather records, 1932–2004), and mean annual temperature is 22.3 C (ABS weather records, 1952–2004), typically with warm wet summers and cool dry winters (Abrahamson *et al.*, 1984). The Station's 2101 ha preserve comprises a mosaic of plant communities and is divided into burn units that have been managed with prescribed fires for $>$ 35 y.

Our research focused on scrub oak (*Quercus inopina* Ashe) dominated scrubby flatwoods, a type of Florida scrub (Abrahamson *et al.*, 1984), which occurs on sandy soils that have no horizon development, little organic matter, and low ion exchange capacity (Brown *et al.*, 1990). Scrubby flatwoods experience fire return intervals of 8 to 16 y (Menges, 2007), and the dominant species resprout after fire. Shrub height varies with resource availability and time after fire but averages 1 to 2 m (Abrahamson *et al.*, 1984). In other types of Florida scrub, shrub heights can reach 4 to 6 m where fire has been suppressed (Schmalzer *et al.*, 2003).

We selected the most abundant scrubby flatwoods shrub species (Abrahamson *et al.*, 1984): the ericaceous shrubs *Lyonia fruticosa* (Michx.) G.S. Torr. and *Lyonia lucida* (Lam.) K. Koch and the oaks *Quercus chapmanii* Sarg., *Quercus geminata* Small, and *Quercus inopina* Ashe (nomenclature follows that of Wunderlin and Hansen, 2003). All species are clonal, multi-stemmed, and resprout after fire (Menges and Kohfeldt, 1995). In our study sites, *L. fruticosa*, *L. lucida*, *Q. chapmanii*, and *Q. geminata* each make up approximately 5% of the total shrub cover, while *Q. inopina* makes up approximately 50% of the total shrub cover; the palmettos *Serenoa repens* and *Sabal etonia* make up approximately 25% and 5% of the total shrub cover, respectively (Schafer, 2010). During the summer of 2007, we measured and harvested aboveground stems of *L. fruticosa*, *L. lucida*, *Q. chapmanii*, *Q. geminata*, and *Q. inopina* from three sites of each of three times after fire: 6 w, 8 y, and 20 y. During the summer of 2008, we measured and harvested aboveground stems of each species from the same nine sites, which were then 1, 9, and 21 y after fire. We randomly selected clumps of stems of each species ($n = 6$ to 25 clumps per species per time after fire) and measured the basal diameter (to the nearest 0.01 mm) within 1 cm of ground level using digital calipers and height (to the nearest cm) of each stem, harvested each stem, and separated stems into leaves and stems. Stems within a clump were likely part of the same clone. All samples were dried at 60 C for a minimum of 48 h and then weighed (to the nearest 0.01 g if $>$ 0.01 g and to the nearest 0.0001 if $<$ 0.01 g). The number of stems harvested varied among years and time after fire, but overall totals were 119, 164, 144, 146, and 327 stems for *L. fruticosa*, *L. lucida*, *Q. chapmanii*, *Q. geminata*, and *Q. inopina*, respectively.

Stems from sites 8 and 9 y after fire were combined for data analysis (hereafter referred to as 8 y after fire), as were stems from sites 20 and 21 y after fire (hereafter referred to as 20 y after fire). To determine if the relationships between stem height and diameter and biomass varied with time after fire, and by species, we used standardized major axis (SMA) regression to fit slopes as is recommended for assessing allometric scaling (Warton *et al.*, 2006). We tested for homogeneity of slopes of diameter vs. height, height vs. shoot biomass, diameter vs. shoot biomass, and stem biomass vs. leaf biomass with time after fire for each species using the SMATR stats package (http://bio.mq.edu.au/ecology/SMATR/). All variables were $\log_{10}$ transformed. The significance of the test for homogeneity of SMA slopes was determined by comparison to a chi-squared distribution. We also tested for homogeneity of slopes of diameter vs. height and stem biomass vs. leaf biomass among species for each time after fire.

We tested SMA slopes to determine if they were equal to the scaling exponents (*i.e.*, slopes) most commonly documented and predicted by allometric theory. Stem length (*i.e.*, height) is predicted to scale as the 2/3 power of diameter or in proportion to diameter according to the elastic and geometric self-similarity models, respectively (Niklas, 1994, 1995). Shoot biomass is predicted to scale as the 4th power of height and the 8/3 power of diameter (Niklas, 1994; West *et al.*, 1999; Niklas and Enquist, 2001), consistent with the elastic self-similarity model. Leaf biomass is predicted to scale as the 3/4 power of stem biomass (Niklas and Enquist, 2001; Niklas and Enquist, 2002a). However, Niklas and Spatz (2004) showed that the slopes predicted by allometric theory do not hold for small stems (*e.g.,* basal diameter < 0.03 m, height < 0.3 m); height and shoot biomass increase with diameter more rapidly in small stems than in large stems.

Testing for differences in elevation (*i.e.*, y-intercepts) among SMA regression lines is only possible when there is a common slope (Warton *et al.*, 2006). Slopes differed significantly in the majority of cases (*see* Results). Therefore, we assessed differences in the ratios of height to diameter and leaf biomass to stem biomass, among time periods after fire for each species and among species for each time after fire, because these ratios are indicative of allocation to sequestration of space and photosynthetic tissue, respectively. Kruskal-Wallis tests were used to analyze differences in height:diameter and leaf:stem biomass ratios of shrub species because these variables could not be transformed to fit normality (SPSS 11.5 for Windows, SPSS, Inc. Chicago, Illinois, U.S.A.).

We also counted the number of stems per individual (*i.e.*, stem density) – defined as all stems growing in a clump within 12 cm of the central stem; we sampled 119, 174, 139, 272, and 355 individuals of *L. fruticosa*, *L. lucida*, *Q. chapmanii*, *Q. geminata*, and *Q. inopina*, respectively. Stem density was assessed at nine sites (three of each time after fire), and the number of individuals of each species varied among times after fire. Kruskal-Wallis tests were used to analyze differences in the number of stems per individual of shrub species (SPSS 11.5 for Windows, SPSS, Inc. Chicago, Illinois, U.S.A.).

RESULTS

Height, basal diameter, and biomass per stem of each species increased from 6 w to 1 y after fire and from 1 y to 8 y after fire but remained similar from 8 to 20 y after fire (Table 1). The slope of the relationship between stem height and basal diameter changed with time after fire for all species (Fig. 1). Slopes tended to be steepest at 6 w and 1 y after fire. The slope of the relationship between stem height and basal diameter differed among species 6 w ($P = 0.007$) and 1 y ($P = 0.021$) after fire but not 8 y ($P = 0.172$) or 20 y ($P = 0.061$) after fire. Across all species and times after fire, height scaled as the 0.8 to 2.7 power of diameter (*see* slopes in Table 2). This is significantly higher than the predicted 2/3 power, but height tended to scale proportionally to diameter in older sites. Only *Q. inopina* had significantly steeper slopes at all times after fire than predicted by self-similarity models.

Height:diameter ratios were affected significantly by species and time after fire (Table 3). For all species, height:diameter ratios were lowest 6 w after fire (Fig. 2). *Quercus chapmanii* and *Q. inopina* had the highest height:diameter ratios 6 w after fire, whereas *L. lucida* had greater height:diameter ratios than *Quercus* species 8 y after fire.

Table 1.—Summary of stem sizes of each species for each time after fire, including the number of stems sampled (N), and the mean (with standard error, se), minimum (Min), and maximum (Max) height, basal diameter, and biomass per stem

			Height (cm)			Basal diameter (mm)			Stem biomass (g)		
Species	Time after fire	N	Mean (se)	Min	Max	Mean (se)	Min	Max	Mean (se)	Min	Max
L. fruticosa	6 w	48	10 (1)	2	31	2.02 (0.09)	1.05	4.45	0.41 (0.07)	0.01	2.29
	1 y	29	28 (3)	2	56	3.33 (0.29)	1.07	6.78	6.53 (1.94)	0.04	54.50
	8–9 y	21	68 (11)	19	176	7.19 (0.85)	2.33	16.25	39.60 (11.18)	1.49	161.81
	20–21 y	21	53 (9)	3	157	6.59 (0.88)	0.69	12.95	24.86 (7.12)	0.03	99.94
L. lucida	6 w	69	7 (1)	1	16	2.04 (0.08)	0.55	4.11	0.20 (0.02)	0.01	1.11
	1 y	43	25 (2)	3	68	3.00 (0.17)	1.03	5.82	3.05 (0.41)	0.06	12.99
	8–9 y	20	48 (5)	17	113	4.83 (0.52)	2.06	11.72	10.25 (2.82)	0.69	58.04
	20–21 y	32	29 (2)	14	53	3.51 (0.33)	1.39	10.06	4.14 (0.95)	0.47	27.50
Q. chapmanii	6 w	66	16 (1)	2	38	2.41 (0.10)	0.94	5.30	1.59 (0.24)	0.03	10.19
	1 y	33	31 (2)	7	63	3.81 (0.27)	1.03	8.04	6.29 (1.39)	0.12	33.62
	8–9 y	21	49 (5)	16	99	6.57 (0.75)	1.77	12.42	29.89 (8.43)	0.96	144.29
	20–21 y	24	50 (6)	5	142	6.33 (0.96)	1.31	19.62	33.95 (13.84)	0.05	314.59
Q. geminata	6 w	60	11 (1)	1	41	1.97 (0.09)	0.83	3.62	0.86 (0.13)	0.01	5.07
	1 y	33	23 (2)	7	47	3.66 (0.26)	1.52	7.52	6.54 (1.27)	0.27	32.16
	8–9 y	27	41 (5)	14	124	6.29 (0.59)	2.30	14.94	22.54 (6.49)	0.57	153.49
	20–21 y	26	39 (4)	11	103	5.47 (0.51)	1.73	11.43	18.61 (5.82)	0.39	122.83
Q. inopina	6 w	149	15 (1)	2	44	2.11 (0.05)	0.69	4.28	1.33 (0.10)	0.04	8.27
	1 y	87	33 (2)	3	92	3.49 (0.18)	0.91	8.77	6.16 (0.91)	0.07	45.34
	8–9 y	43	51 (4)	7	109	6.98 (0.53)	1.79	14.75	32.45 (5.86)	0.14	156.96
	20–21 y	48	51 (5)	6	140	6.59 (0.56)	1.75	17.60	42.45 (10.39)	0.34	323.50

The slope of the relationship between height and shoot biomass differed with time after fire for all species with the exception of *L. fruticosa* (Fig. 3). Slopes tended to be steeper in sites 8 and 20 y after fire than in more recently burned sites (Table 4). For *L. fruticosa*, biomass per unit height was lower at 6 w than for other times after fire (Wald statistic = 130.81, $P < 0.001$). Across all species and times after fire, shoot biomass scaled to the 1.7 to 3.0 power of height, significantly lower than the 4th power predicted by allometric theory (Table 4).

The slope of the relationship between basal diameter and shoot biomass changed with time after fire for all species (Fig. 4). Slopes were steepest 6 w after fire. Across all species and times after fire, shoot biomass scaled as the 2.1 to 4.9 power of diameter; approximately half of the slopes were similar to the 8/3 power predicted by allometric theory (Table 4).

Leaf:stem biomass ratios of *Quercus* species decreased with time after fire, while leaf:stem biomass ratios of *Lyonia* species were more variable (Fig. 5). For each time after fire, there were significant differences among species in leaf:stem biomass ratios (Table 3). *Quercus inopina* had a higher leaf:stem biomass ratio than all other species 6 w after fire, *Lyonia* species tended to have greater leaf:stem biomass ratios than *Quercus* species 1 y after fire, and *L. lucida* had the highest leaf:stem biomass ratios 20 y after fire (Fig. 5).

The slope of the relationship between stem biomass and leaf biomass differed with time after fire for all species with the exception of *L. lucida* (Fig. 6). Slopes were steepest 6 w after fire (Table 5). The slope of the relationship between stem and leaf biomass differed among species 6 w ($P < 0.001$) and 8 y ($P < 0.001$) after fire but not 1 y ($P = 0.116$) or 20 y ($P =$

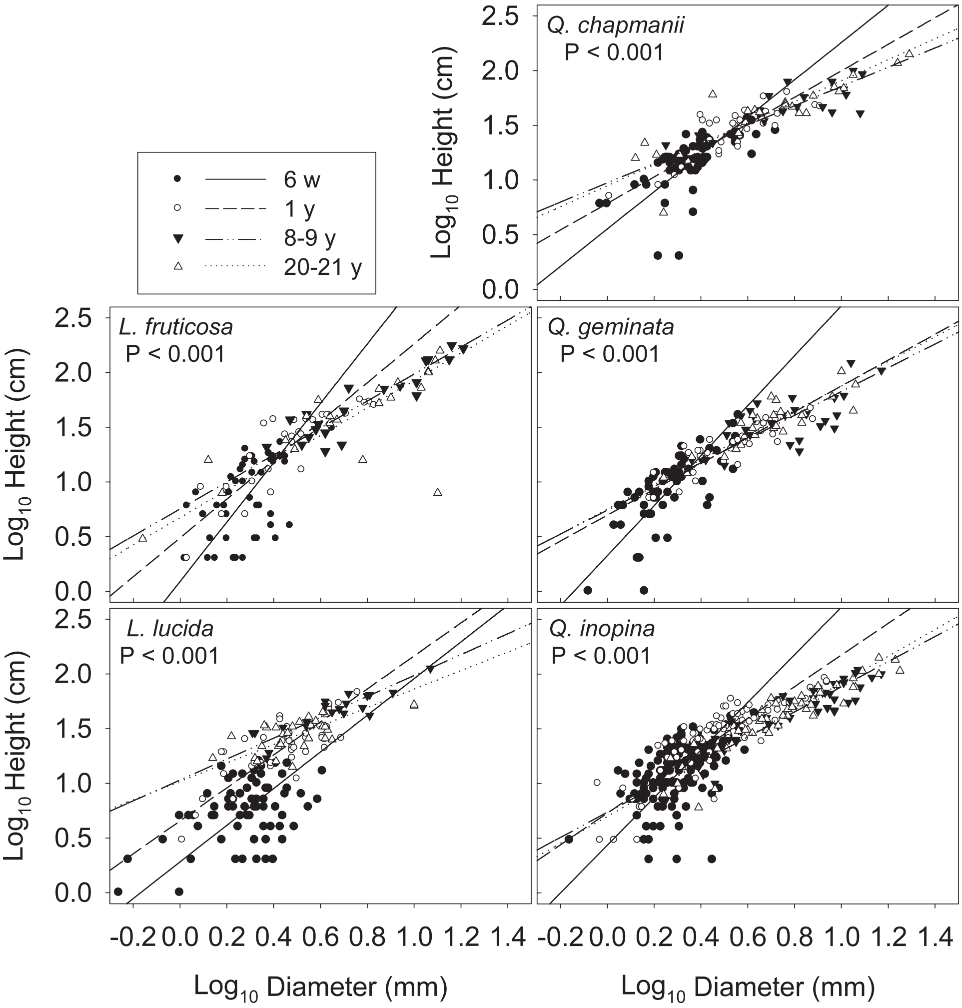

FIG. 1.—Relationship between height and diameter (both $\log_{10}$ transformed) for all shrub species at each time after fire; P values < 0.05 indicate that regression slopes are not homogeneous. SMA regression lines are extended past the data to improve clarity of relationships

0.120) after fire. Across all species and times after fire, leaf biomass scaled to the 0.5 to 1.3 power of stem biomass. Six weeks after fire, slopes were significantly higher than the 3/4 power predicted by allometric theory (Table 5).

The stem density of *Quercus* species declined with time after fire (Fig. 7). Stem density of *L. fruticosa* individuals was generally higher 6 w and 1 y after fire, but *L. lucida* stem density did not change with time after fire (Table 3). *Quercus inopina* had the highest number of resprouts per individual (median = 5 stems), whereas *Q. geminata* had the lowest number of resprouts per individual (median = 2 stems; Fig. 7). Eight and 20 y after fire, there were minimal differences in stem densities among species.

TABLE 2.—Basal diameter vs. height SMA regression equations and R^2 values for scrubby flatwoods shrub species at each time after fire with comparisons (F and P values) between slopes and predicted scaling relationships (slope = 2/3 (elastic self-similarity model) or 1 (geometric self-similarity model)). Log_{10} Height (cm) = y_0 + a * Log_{10} Diameter (mm). N = number of stems; a = slope. For all SMA regressions, $P < 0.001$

					Vs. slope = 2/3		Vs. slope = 1	
Species	Time after fire	y_0	a	R^2	F	P	F	P
L. fruticosa	6 w	0.091	2.714	0.308	242.69	<0.001	91.34	<0.001
	1 y	0.488	1.775	0.743	137.12	<0.001	38.55	<0.001
	8–9 y	0.753	1.234	0.831	48.13	<0.001	5.04	0.037
	20–21 y	0.674	1.253	0.565	19.79	<0.001	2.27	0.149
L. lucida	6 w	0.281	1.676	0.191	92.60	<0.001	24.12	<0.001
	1 y	0.656	1.508	0.637	93.24	<0.001	20.12	<0.001
	8–9 y	1.030	0.955	0.792	11.68	0.003	0.18	0.676
	20–21 y	1.016	0.845	0.454	3.14	0.086	1.56	0.221
Q. chapmanii	6 w	0.552	1.705	0.411	127.32	<0.001	33.98	<0.001
	1 y	0.785	1.213	0.672	37.99	<0.001	3.57	0.068
	8–9 y	0.974	0.881	0.704	5.10	0.002	1.04	0.321
	20–21 y	0.947	0.960	0.767	13.07	0.036	0.16	0.693
Q. geminata	6 w	0.327	2.285	0.551	317.01	<0.001	110.15	<0.001
	1 y	0.696	1.182	0.757	46.53	<0.001	3.59	0.068
	8–9 y	0.741	1.086	0.445	11.58	<0.001	0.31	0.584
	20–21 y	0.751	1.126	0.756	29.48	0.002	1.39	0.250
Q. inopina	6 w	0.435	2.177	0.295	455.95	<0.001	153.81	<0.001
	1 y	0.728	1.446	0.719	220.16	<0.001	42.99	<0.001
	8–9 y	0.736	1.148	0.844	85.57	<0.001	5.06	0.030
	20–21 y	0.697	1.221	0.856	131.88	<0.001	12.92	0.001

DISCUSSION

Stem size and biomass and height:diameter ratios increased from 6 w to 8 y after fire for all scrubby flatwoods shrub species, whereas the effects of time after fire on leaf:stem biomass ratios depended on the individual species. The relationships between height and basal diameter, height and shoot biomass, and basal diameter and shoot biomass were affected by time after fire, indicating that constraints on resprout growth and biomass change over time. Differences among species in height:diameter and leaf:stem biomass ratios were most pronounced 6 w after fire, when *Q. inopina* had the highest height:diameter and leaf:stem biomass ratios; by 20 y after fire, there was little difference among species in size and biomass ratios.

Six weeks after fire, oak (*Quercus* species) resprouts tended to be taller, larger in diameter, and have greater biomass than resprouts of the ericaceous shrub *Lyonia* spp. (Table 1). In general below ground starch and nonstructural carbohydrate reserves (McPherson and Williams, 1998; Olano *et al.*, 2006; Paula and Ojeda, 2009), prefire plant size (Bonfil *et al.*, 2004; Konstantinidis *et al.*, 2006), and the number of active meristems (Bret-Harte *et al.*, 2001) are likely to be the more important factors in contributing to differences in the size and biomass of resprouts among species. Rhizome resprouting potential may be similar for *Q. chapmanii* and *Q. geminata* (Cavender-Bares *et al.*, 2004), but oak species have greater

TABLE 3.—Differences in height:diameter ratios, leaf:stem biomass ratios, and number of stems per individual among species for each time after fire and among times after fire for each shrub species determined from Kruskal-Wallis tests. Degrees of freedom = 3 and 4, respectively, for comparisons among times after fire for each species (top) and comparisons among species for each time after fire (bottom)

		Height:Diameter		Leaf:Stem biomass		Stems per individual	
		χ^2	P	χ^2	P	χ^2	P
Species	*Lyonia fruticosa*	39.09	<0.001	39.84	<0.001	21.50	<0.001
	Lyonia lucida	97.53	<0.001	14.28	0.003	5.38	0.146
	Quercus chapmanii	11.74	0.008	93.63	<0.001	25.41	<0.001
	Quercus geminata	15.13	0.002	77.54	<0.001	27.50	<0.001
	Quercus inopina	43.65	<0.001	209.41	<0.001	110.75	<0.001
Time after fire	6 w	96.42	<0.001	178.12	<0.001	97.25	<0.001
	1 y	33.21	<0.001	43.04	<0.001	19.78	0.001
	8–9 y	26.01	<0.001	10.56	0.032	35.55	<0.001
	20–21 y	11.48	0.022	32.22	<0.001	16.86	0.002

belowground biomass than other Florida scrub species, including *Lyonia* spp. (Saha *et al.*, 2010).

For all of our study species, height growth rate after fire was negatively correlated with conspecific stem density (Maguire and Menges, 2011), indicating each species experiences some degree of intra-specific or intra-individual competition among stems within a clump. Resprouts of *Q. inopina* and *Q. chapmanii* had the largest height:diameter ratios and the highest stem densities, which is consistent with crowded individuals having larger height:diameter ratios than individuals growing in the open (Holbrook and Putz, 1989). Height:diameter ratios of *L. fruticosa*, *L. lucida*, and *Q. inopina* increased from 6 w to 1 y after fire, but the stem density of these species did not change. Shading (Vilà, 1997) and aboveground competition (den Dubbelden and Knops, 1993; Kozovits *et al.*, 2005) can cause a decrease in leaf:stem biomass ratios, and in our study leaf:stem biomass ratios of oaks decreased from 6 w to 1 y after fire. These results indicated that *Q. inopina* experienced the greatest intra-individual competition. The concomitant increase in stem height and basal diameter and decrease in leaf:stem biomass ratios of each species from 1 to 8 y after fire is consistent with results from Givnish (1982), who showed that greater investment in support tissue (*i.e.*, stems) elevates leaves to a greater height, which can reduce leaf biomass investments.

Variation in aboveground allocation patterns among species may be important in determining relative species abundance, as the use of resources to sequester space aboveground may be a quantitative parameter of competitiveness (Kozovits *et al.*, 2005). Six weeks after fire, *Q. inopina*, the most abundant species in the scrubby flatwoods communities studied (Abrahamson *et al.*, 1984; Schafer, 2010), had one of the highest height:diameter ratios and the highest leaf:stem biomass ratio, and by 20 y after fire, *Q. inopina* had the highest (although not significantly higher) mean biomass per stem. The ability of *Q. inopina* to sequester space aboveground after fire by investing in height and leaf biomass, even though this appears to cause greater intra-individual competition, may contribute to the ability of *Q. inopina* to maintain dominance in scrubby flatwoods communities over many fire cycles.

The slopes of the relationship between stem height and diameter tended to decrease with time after fire (Table 2). This relationship may be dependent on light conditions (Coomes

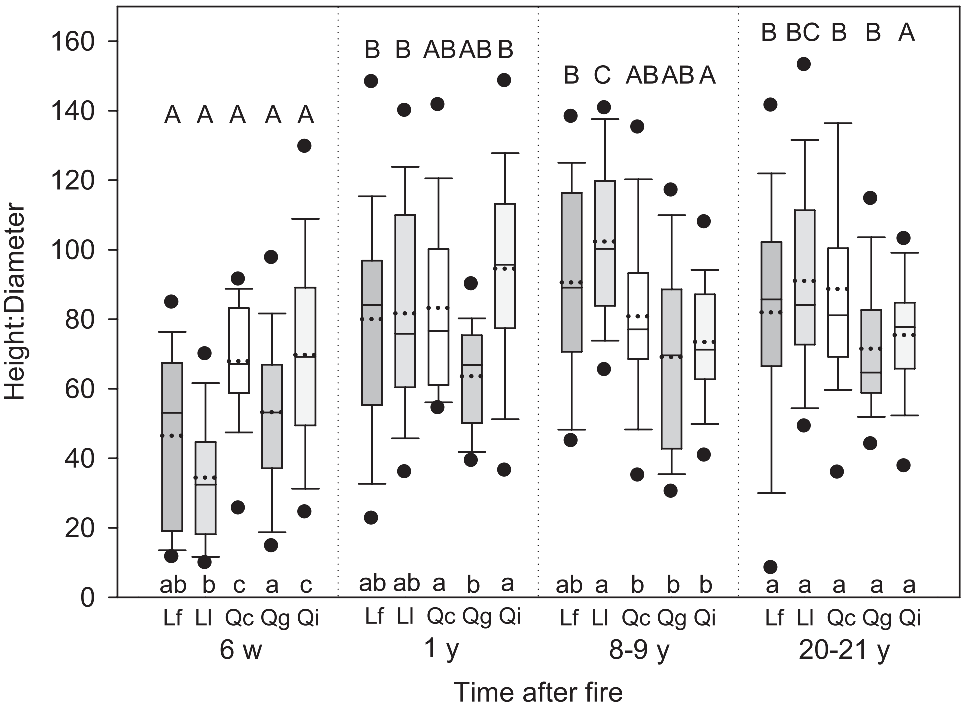

FIG. 2.—Grouped boxplots of height:diameter ratios (both in cm) of shrub species at each time after fire. The lower and upper bars of the boxplot represent the 25th and 75th percentiles, respectively; the solid middle bar represents the median and the dotted bar represents the mean. The lower and upper 'whiskers' show the largest and smallest values that are not outliers. The circles show the 5th and 95th percentiles; outliers are not shown. Lf = *Lyonia fruticosa*, Ll = *Lyonia lucida*, Qc = *Quercus champanii*, Qg = *Quercus geminata*, Qi = *Quercus inopina*. Different lowercase letters below the boxplots indicate significant differences among species within each time after fire. Different uppercase letters above the boxplots indicate significant differences among times after fire within a species

and Grubb, 1998), with height growth per unit diameter being greater in crowded conditions, causing a larger slope in the relationship between height and diameter (Henry and Aarssen, 1999). Our data are consistent with the observation that stems of shrubs tended to be more crowded in recently burned scrubby flatwoods than they were 20 y after a fire (Fig. 7). Variation in scaling of height versus diameter could also be related to stem age (Niklas, 1994) and ontogeny (Silveira *et al.*, 2012). An old stem mechanically supports more biomass than a young stem such that height may scale as a lower power of diameter over time (Niklas, 1994; Henry and Aarssen, 1999). The numerically lower slopes for the relation of height to diameter in longer unburned sites in our study supported this prediction. Changes in allometry with age and ontogeny, however, may be greater for trees than for resprouting species such as those examined here. Within a cluster of stems of *Q. inopina*, stems turnover such that, across sites from 4 to 50 y after fire, median and maximum stem ages were 4 y and approximately 9 y, respectively (Johnson and Abrahamson, 2002); other scrubby flatwoods shrub species likely have similar patterns of stem turnover (Menges *et al.*, 1993), although stems may not turn over in the absence of fire (Schmalzer *et al.*, 2003).

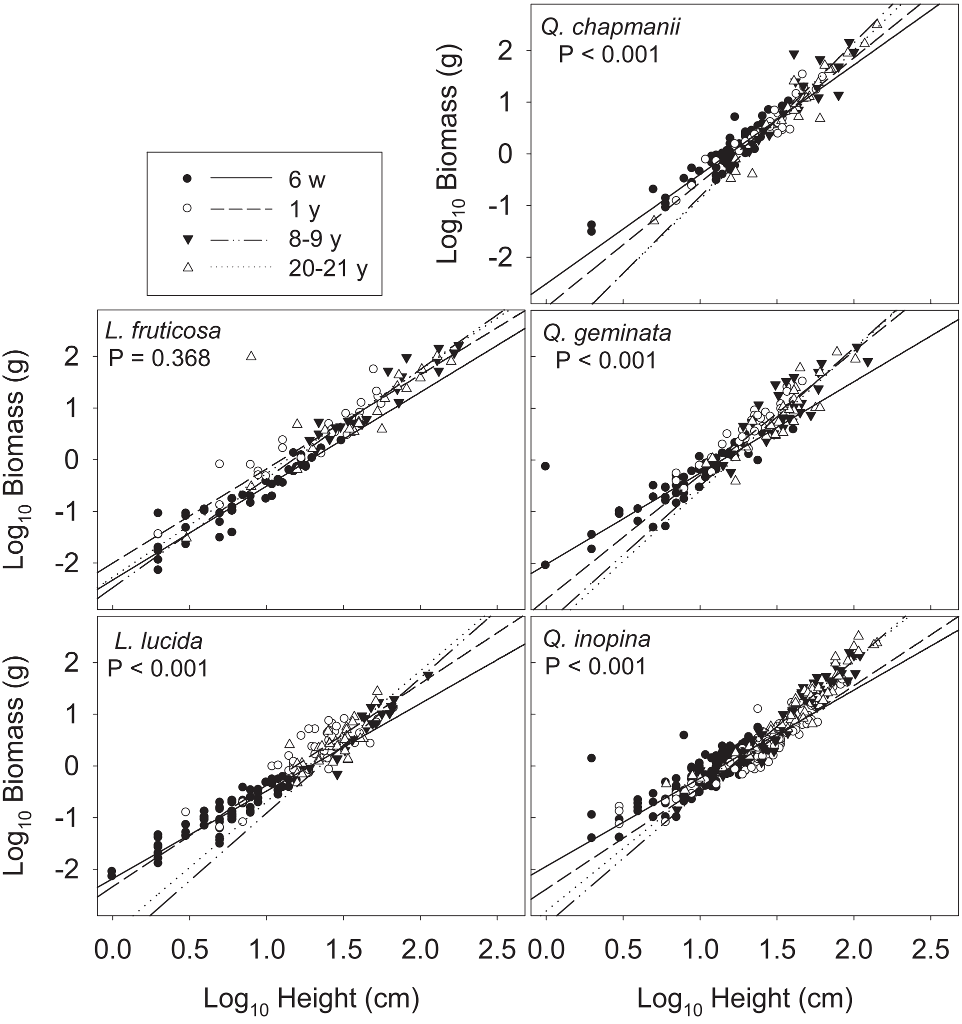

FIG. 3.—Relationships between height and shoot biomass (both $\log_{10}$ transformed) for all shrub species at each time after fire; P values < 0.05 indicate that regression slopes are not homogeneous. SMA regression lines are extended past the data to improve clarity of relationships

Stems harvested from sites 8 to 21 y after fire were likely older than those harvested 6 w and 1 y after fire but younger than the age of the site. Furthermore, increases in size over the lifetime of a stem may be smaller in shrub resprouts than for longer-lived trees.

Height has been found to scale as the 2/3 power of diameter, exhibiting elastic self-similarity, or in one-to-one proportion with diameter, exhibiting geometric self-similarity (Whittaker and Woodwell, 1968; McMahon and Kronauer, 1976; King, 1990; Niklas, 1994; Niklas, 1995). For resprouts in scrubby flatwoods, however, height scaled approximately as the 5/6 to 8/3 power of diameter (Table 2). A well established network of rhizomes that supports multiple stems (Johnson and Abrahamson, 2002), with maximum heights as low as

Table 4.—Height and basal diameter vs. shoot biomass SMA regression equations and R^2 values for scrubby flatwoods shrub species at each time after fire with comparisons (F and P values) between slopes and predicted scaling relationships (slope = 4 for height and 8/3 for diameter, following the elastic self-similarity model). Log_{10} Biomass = $y_0 + a * \text{Log}_{10}$ Height (left side). Log_{10} Biomass = $y_0 + a * \text{Log}_{10}$ Diameter. N = number of stems; a = slope. For all SMA regressions, $P < 0.001$

		Height					Diameter				
Species	Time after fire	y_0	a	R^2	F	P	y_0	a	R^2	F	P
L. fruticosa	6 w	−2.331	1.818	0.888	313.74	<0.001	−2.166	4.934	0.470	37.17	<0.001
	1 y	−2.003	1.824	0.870	156.72	<0.001	−1.113	3.238	0.859	7.28	0.012
	8–9 y	−2.480	2.114	0.897	85.65	<0.001	−0.887	2.610	0.941	0.15	0.701
	20–21 y	−2.276	2.007	0.585	25.40	<0.001	−0.924	2.516	0.946	1.20	0.288
L. lucida	6 w	−2.183	1.695	0.861	452.55	<0.001	−1.707	2.840	0.329	0.40	0.531
	1 y	−2.339	1.966	0.734	91.65	<0.001	−1.049	2.964	0.811	2.43	0.127
	8–9 y	−3.535	2.619	0.873	26.84	<0.001	−0.839	2.503	0.893	0.68	0.420
	20–21 y	−3.236	2.539	0.607	16.87	<0.001	−0.658	2.147	0.748	5.71	0.023
Q. chapmanii	6 w	−2.514	2.118	0.848	194.93	<0.001	−1.344	3.610	0.585	14.57	<0.001
	1 y	−2.967	2.413	0.890	78.63	<0.001	−1.073	2.927	0.850	1.80	0.189
	8–9 y	−3.798	2.974	0.783	7.93	0.011	−0.900	2.620	0.944	0.11	0.744
	20–21 y	−3.760	2.884	0.923	31.56	<0.001	−1.030	2.768	0.917	0.37	0.551
Q. geminata	6 w	−2.024	1.770	0.724	173.42	<0.001	−1.446	4.045	0.616	27.77	<0.001
	1 y	−2.698	2.402	0.899	86.94	<0.001	−0.932	2.838	0.860	0.86	0.362
	8–9 y	−3.173	2.671	0.705	14.60	<0.001	−1.194	2.901	0.875	1.41	0.246
	20–21 y	−3.330	2.732	0.784	16.94	<0.001	−1.279	3.076	0.883	4.20	0.051
Q. inopina	6 w	−1.946	1.707	0.738	515.13	<0.001	−1.204	3.717	0.541	36.58	<0.001
	1 y	−2.387	1.970	0.864	369.99	<0.001	−0.952	2.848	0.835	2.23	0.139
	8–9 y	−3.071	2.557	0.922	112.70	<0.001	−1.190	2.936	0.918	4.62	0.038
	20–21 y	−2.811	2.419	0.921	159.83	<0.001	−1.126	2.953	0.940	8.00	0.007

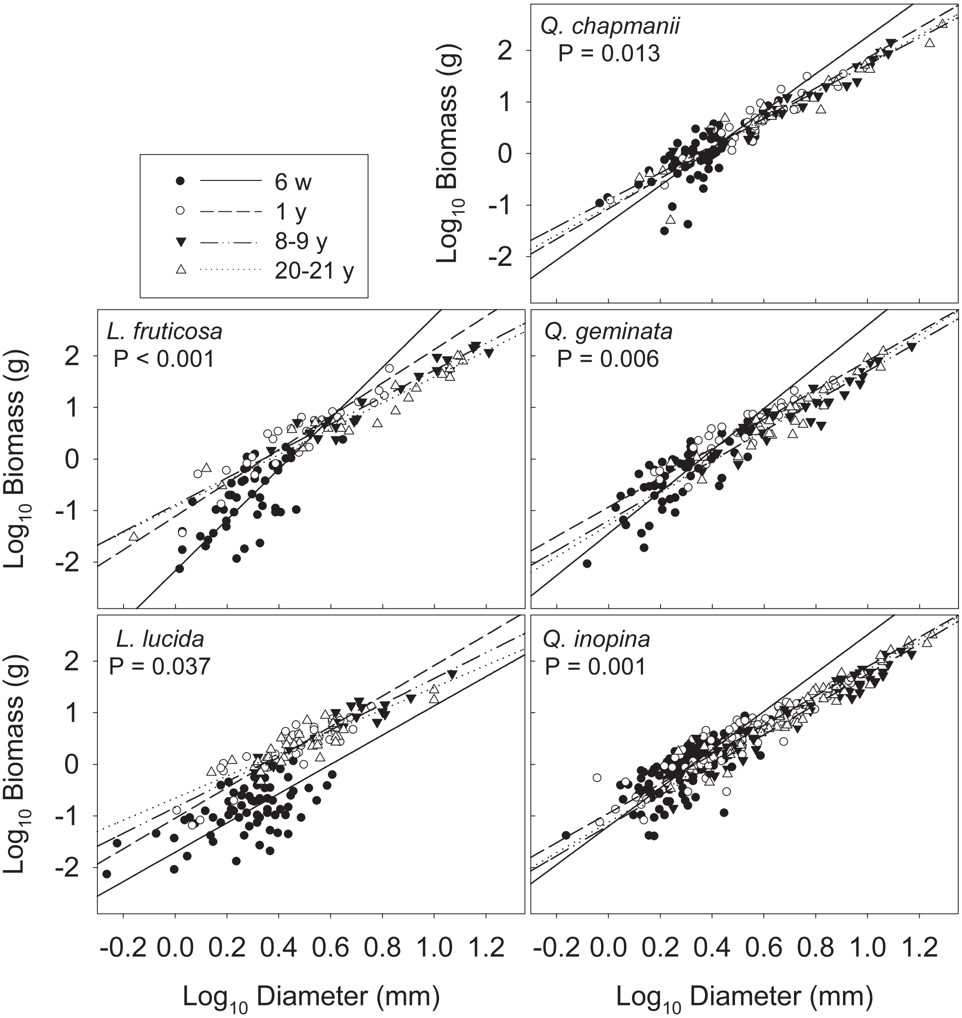

FIG. 4.—Relationships between basal diameter and shoot biomass (both $\log_{10}$ transformed) for all shrub species at each time after fire; P values < 0.05 indicate that regression slopes are not homogeneous. SMA regression lines are extended past the data to improve clarity of relationships

1.5 to 2 m (Abrahamson *et al.*, 1984), may allow stems of scrubby flatwoods resprouting shrubs to increase height with smaller increases in diameter, causing height to scale at a higher power of diameter than predicted. Scrubby flatwoods shrubs may be close enough to the ground and grow in dense enough stands that wind-induced stress is minimal, making it advantageous to build taller rather than stronger stems. In addition Utsumi *et al.* (2010) found resprouts of *Juglans californica* have a higher modulus of elasticity (*i.e.*, stiffness) than unburned stems, which indicates that resprouts would require less cross-sectional area to achieve the same height as unburned stems. Alternatively, investing in height rather than diameter growth may be adaptive for resprouting species in pyrogenic ecosystems.

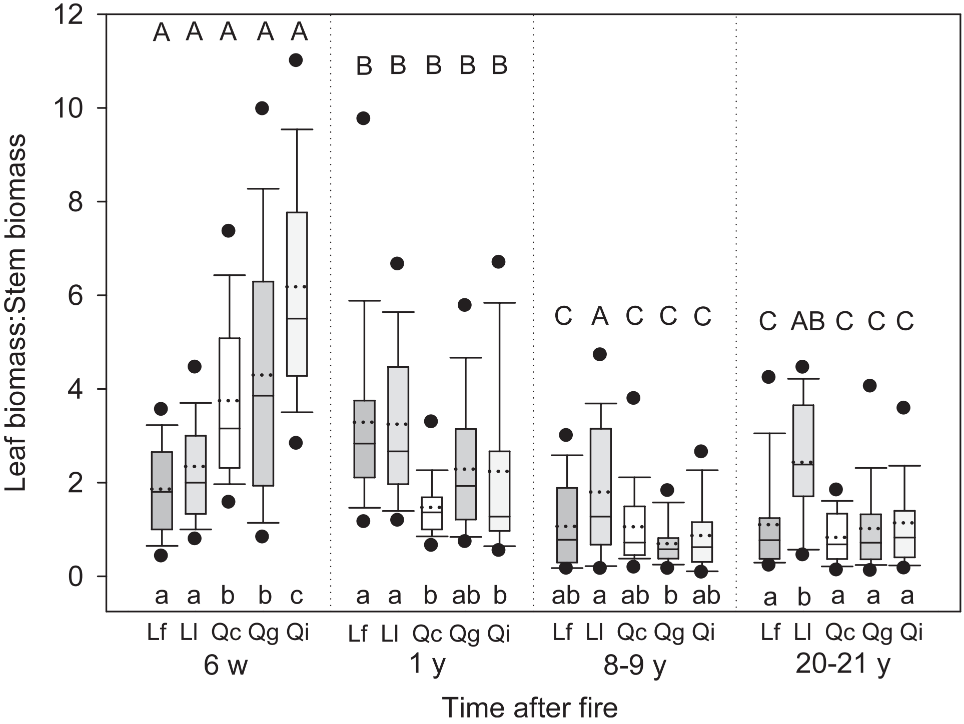

FIG. 5.—Grouped boxplots of leaf biomass:stem biomass ratios of shrub species at each time after fire. Specifics of the boxplots are the same as in Figure 2. Lf = *Lyonia fruticosa*, Ll = *Lyonia lucida*, Qc = *Quercus champanii*, Qg = *Quercus geminata*, Qi = *Quercus inopina*. Different lowercase letters below the boxplots indicate significant differences among species within each time after fire. Different uppercase letters above the boxplots indicate significant differences among times after fire within a species

Increasing height growth should increase light capture, but increasing mechanical strength through diameter growth (King, 1986) may not be an effective strategy because stems would eventually be consumed by an intense fire in scrubby flatwoods.

Biomass scales, on average, as the 4th power of height (West *et al.*, 1999; Niklas and Enquist, 2001), following the elastic self-similarity model (Niklas, 1994). However, for the scrubby flatwoods shrub species examined here, shoot biomass scaled approximately as the 5/3 to 3rd power of height (Table 4). The lower biomass per unit height in resprouting species is likely related to the fact that for a given height, stems are not as thick, and therefore, have a lower biomass. Wood density likely does not contribute to the lower biomass per unit height because the wood density of our study species (species mean = 0.52 to 0.81 $g \cdot cm^{-3}$; J. Schafer, unpubl. data) is similar to the wood density of trees (Chave *et al.*, 2006; Ducey, 2012). In addition the relationship between height and biomass differs for plants growing with and without competition (Weiner and Thomas, 1992; Anten and Hirose, 1998), such that the clumped distribution of resprouting species may affect scaling relationships. In other studies, biomass has been found to scale to the 8/3 power of diameter, following the elastic self-similarity model (West *et al.*, 1999; Niklas, 1994). Biomass of scrubby flatwoods shrub stems scaled as the 2nd to 5th power of diameter (Table 4); 6 wk

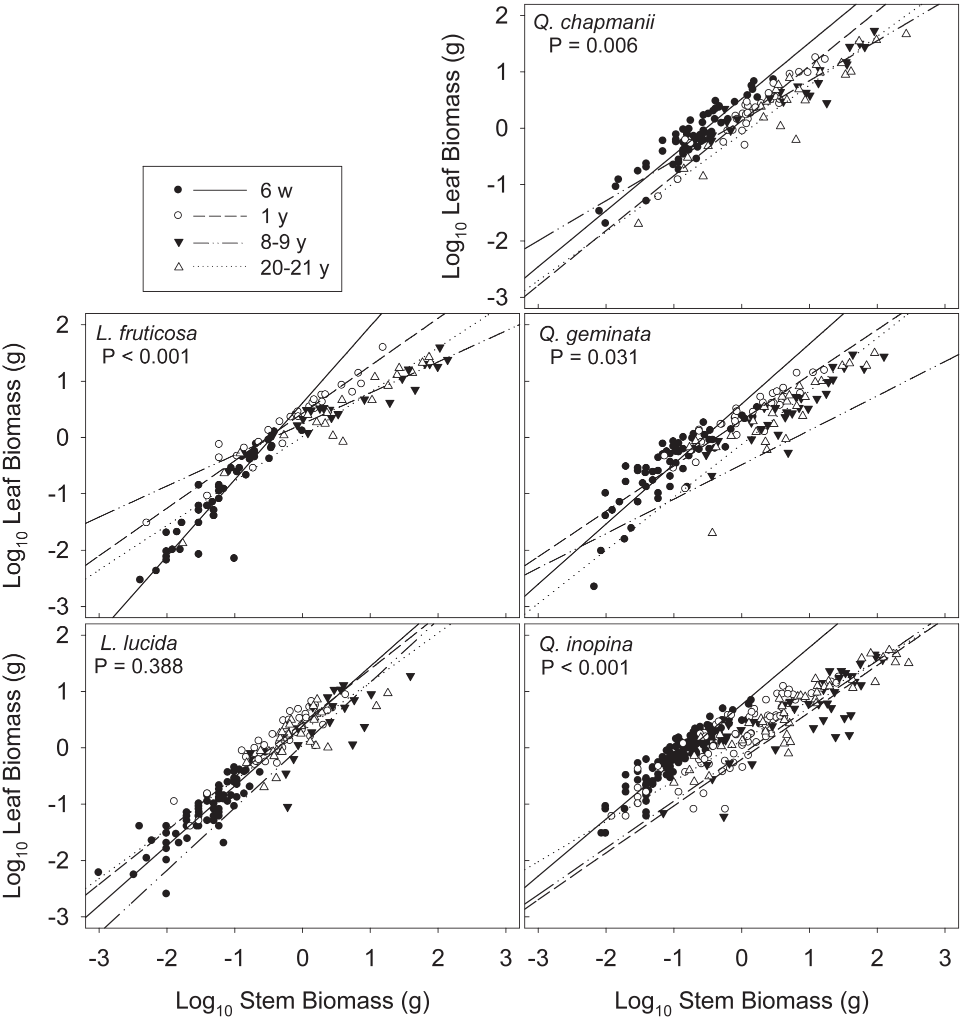

FIG. 6.—Relationships between stem biomass and leaf biomass (both $\log_{10}$ transformed) for all shrub species at each time after fire; P values < 0.05 indicate that regression slopes are not homogeneous. SMA regression lines are extended past the data to improve clarity of relationships

after fire, biomass scaled at a power greater than 8/3 for all species with the exception of *L. lucida*. This pattern may be related to the high investment in leaf rather than stem biomass, indicated by the high scaling power of leaf biomass to stem biomass of shoots in recently burned sites. The biomass of scrubby flatwoods shrub stems, on average, scales to diameter, but not height, as is predicted by allometric theory (Niklas, 1994).

The resprouts of scrubby flatwoods shrubs had a high stem density and a greater allocation to leaf versus stem biomass than predicted (Niklas and Enquist, 2001; Niklas and Enquist, 2002a). Because all stems in a clump are part of the same individual, it may be advantageous to maximize leaf biomass, and therefore, carbon gain, in new stems.

TABLE 5.—Stem biomass vs. leaf biomass SMA regression equations and R^2 values for scrubby flatwoods shrub species at each time after fire with comparisons (F and P values) between slopes and the predicted scaling relationship (slope = 3/4). Log_{10} Leaf Biomass = y_0 + a * Log_{10} Stem Biomass. N = number of stems; a = slope. For all SMA regressions, $P < 0.001$

Species	Time after fire	y_0	a	R^2	F	P
L. fruticosa	6 w	0.612	1.361	0.846	119.30	<0.001
	1 y	0.429	0.843	0.932	5.36	0.028
	8–9 y	0.239	0.551	0.892	17.17	0.001
	20–21 y	0.014	0.789	0.896	0.46	0.506
L. lucida	6 w	0.384	1.061	0.737	31.90	<0.001
	1 y	0.440	0.954	0.827	14.03	0.001
	8–9 y	0.048	1.112	0.504	6.06	0.024
	20–21 y	0.293	0.871	0.538	1.47	0.236
Q. chapmanii	6 w	0.523	0.994	0.848	34.25	<0.001
	1 y	0.132	0.974	0.890	19.60	<0.001
	8–9 y	0.133	0.710	0.881	0.49	0.492
	20–21 y	−0.105	0.867	0.878	3.81	0.064
Q. geminata	6 w	0.594	1.066	0.722	26.90	<0.001
	1 y	0.301	0.806	0.835	0.99	0.328
	8–9 y	−0.111	0.832	0.832	1.60	0.218
	20–21 y	−0.121	0.942	0.695	4.17	0.052
Q. inopina	6 w	0.767	1.015	0.846	89.74	<0.001
	1 y	0.201	0.832	0.757	3.76	0.056
	8–9 y	−0.115	0.831	0.705	1.47	0.232
	20–21 y	0.124	0.715	0.853	0.70	0.406

Investment in leaf tissue, concomitant with high rates of photosynthesis in the first year of resprouting (Fleck *et al.*, 1998; Clemente *et al.*, 2005), allows for rapid growth and replenishment of belowground reserves. This strategy may be beneficial for longer-term resource balance and mechanical support of stems that emerge and become dominant. Nonresprouting species may experience a decrease in stem density over time, similar to resprouting species (Fig. 7), but nonresprouting species should not experience the same intra-individual effects and constraints as their resprouting counterparts.

Taller height per unit diameter and higher leaf to stem biomass ratios are traits that should increase light reception and photosynthetic capacity and are likely to occur in post-fire resprouts in a variety of ecosystems. Whether height scales at a higher power of diameter than predicted with time after fire, however, may be related to maximum stem height. We focused on shrub species, but many tree species resprout after fire (*e.g.,* Hoffmann *et al.*, 2009). Dodonov *et al.* (2011) found that height scaled to diameter at a power greater than one for four out of six of the species examined in their study across shrubs and trees in a Brazilian savanna. Therefore, our results are consistent with species differing in growth form and from different pyrogenic ecosystems.

In summary growth and allocation of resources to aboveground tissues tended to differ with time after fire, but the majority of differences occurred between recently burned (*i.e.*, 6 w and 1 y after fire) and longer unburned (*i.e.*, 8 y and 20 y after fire) sites. The differential ability of scrubby flatwoods resprouting species to acquire space after fire likely contributes to the maintenance of species abundances over time. Resprouting species recruit new

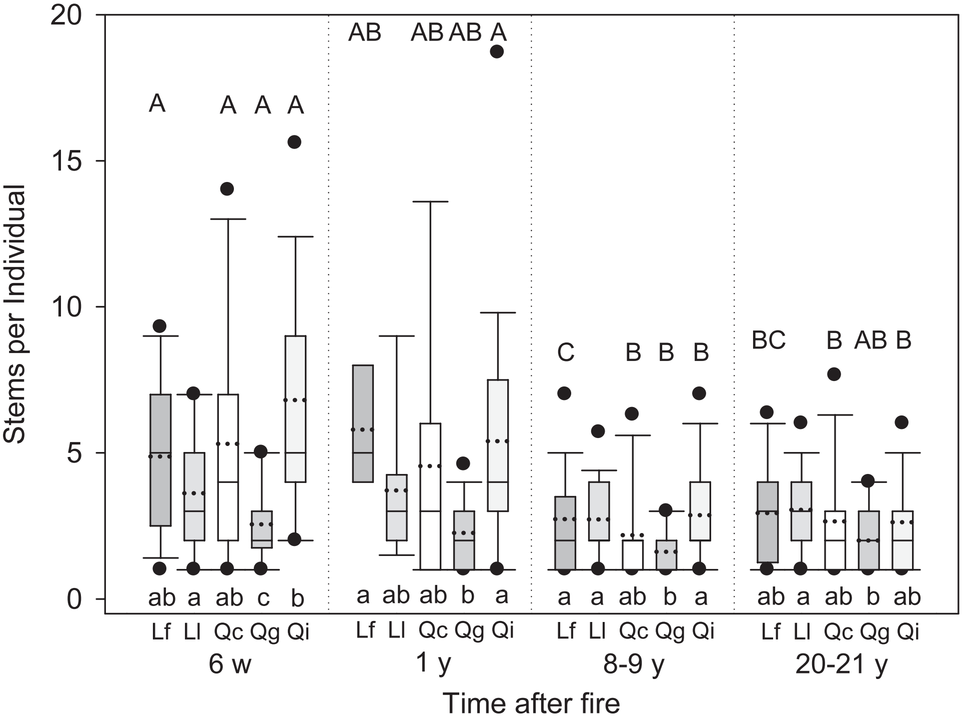

FIG. 7.—Grouped boxplots of the number of stems per individual (*i.e.*, stem density) of shrub species at each time after fire. Specifics of the boxplots are the same as in Figure 2. Lf = *Lyonia fruticosa*, Ll = *Lyonia lucida*, Qc = *Quercus champanii*, Qg = *Quercus geminata*, Qi = *Quercus inopina*. Different lowercase letters below the boxplots indicate significant differences among species within each time after fire. Different uppercase letters above the boxplots indicate significant differences among times after fire within a species

stems in clumps (Silva *et al.*, 2009) and show a tradeoff between height growth and stem density (Maguire and Menges, 2011), indicating that stem density likely plays an important role in allometry and biomass allocation. Stems of resprouting species are able to reach greater heights per unit diameter growth than predicted, but this translates into lower biomass accumulation per unit height than expected based on plant allometric theory. Therefore, the scaling of the growth and the biomass of resprouts in pyrogenic ecosystems is inconsistent with current allometric theory and with the elastic and geometric self-similarity models most often documented in plants (Niklas, 1994, 1995; West *et al.*, 1999; Niklas and Enquist, 2001, 2002a). The ability of resprouting shrubs to create tall stems with large leaf biomass may facilitate the maximization of carbon fixation after fire, which may allow for replenishment of belowground reserves and persistence after future fires.

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