POST-FIRE GROWTH STRATEGIES OF RESPROUTING FLORIDA SCRUB VEGETATION

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ABSTRACT

Although resprouting is recognized as a key post-disturbance response for plants, few studies have closely examined post-fire growth responses of resprouting species. Following a prescribed burn in Florida scrub, we compared intraspecific and interspecific growth patterns of 16 resprouting shrub species. We then examined how resprouting growth is related to species life history strategies to understand how the resprouting response could contribute to niche differentiation and species coexistence. We defined growth by calculating relative growth rates based on height, crown area, and crown volume of resprouts. In addition, we measured the number, diameter, and height of all resprouting stems. The number and diameter of all stems present before fire were also estimated. The number of resprouting stems after the fire was higher than the number of stems present before the fire for all species. As expected, species varied significantly in their post-fire growth rates, especially between those with differing recovery modes. Resprouting shrubs that are also post-fire seeders had the lowest growth rates compared to those that resprout and grow clonally, those that only resprout, and palmettos. We also found differences in post-fire growth among species with different growth forms, with palmettos having the fastest growth, followed by shrubs, and then by sub-shrubs. Within species, tradeoffs were found between height and the density of new stems, but not between height and diameter of resprouting stems. Overall, Florida scrub species exhibit a continuum of post-fire growth rates, suggesting the coexistence of a number of successful strategies for post-fire resprouting rather than a single optimal recovery strategy.

INTRODUCTION

The capacity of woody plants to persist after fire in many of the world's ecosystems is remarkable (Bond and Midgley 2001, Del Tredici 2001, Pausas *et al*. 2004). In Florida scrub, most plants are adapted to fire and there is minimal vegetation change with periodic fire

(Abrahamson 1984*a*). Many species, including rare plants, can survive and respond positively to fire (Slapcinsky *et al*. 2010). Species can resprout, spread clonally, and recruit seedlings from persistent soil or aerial seed banks (Menges and Kohfeldt 1995).

Resprouting is a widespread adaptation allowing persistence in disturbed ecosystems (Bond and Midgley 2001), and is an ancestral trait in angiosperms (Lloret *et al*. 1999, Bond and Midgley 2003). Resprouting plants are able to respond to many types of disturbances by quickly regaining aboveground biomass after a disturbance event such as fire (Bond and Midgley 2003). The same genotype can continue to occupy a site throughout disturbance cycles, lending long-term stability to many pyrogenic ecosystems (Clarke *et al*. 2010). Nonetheless, variation in the vigor of resprouting in response to disturbances of various intensities and frequencies will be important to ecosystem responses to disturbance regimes.

In systems with intense fire disturbance, percentages of resprouting species are generally bimodal, with few species having resprouting proportions in the 30 % to 70 % range (Vesk and Westoby 2004). This bimodal distribution does not hold for lower fire intensities and other types of disturbances (Vesk and Westoby 2004). The resprouting response can vary within species depending on fire frequency; intensity; and season (Schmalzer and Hinkle 1992, Bellingham and Sparrow 2000, Weekley and Menges 2003, Konstantinidis *et al*. 2005); and environmental factors such as habitat type, climate, and nutrient availability (Cruz *et al*. 2002, Lloret *et al*. 2004, Clarke *et al*. 2005). In reality, there is a continuum of recovery strategies across disturbance regimes (Bellingham and Sparrow 2000).

Much of the work on resprouting plants has contrasted the life-history strategies of resprouters and non-resprouters. Resprouters live longer, have later maturation, and produce fewer seeds than non-resprouters (Bond and Midgley 2001, Pausas *et al*. 2004, Knox and

Clarke 2005, Pausas and Verdú 2005). In contrast, since obligate seeders are killed by fire or other disturbances, they necessarily recover by seedling recruitment (Keeley 1986, Vesk and Westoby 2004). Resprouting plants invest more resources in persistence, while seeders use their resources for recruitment (Pausas and Verdú 2005). Obligate seeders also produce seeds that have higher germination in response to heat (Paula and Pausas 2008). Although these two modes of recovery are often treated as distinct, there is not a clear dichotomy between resprouters and non-resprouters. Some species regenerate by both resprouting and seedling recruitment (Menges and Kohfeldt 1995). When this is the case, species that resprout vigorously as adults tend to have lower seedling recruitment than less vigorous resprouters, indicating a tradeoff even among species with mixed recovery modes (Bond and Midgley 2001).

Resprouting vigor should be affected by competition for resources, and species that are specialized to resprout should have stronger resprouting vigor than species that combine resprouting with other recovery modes. For example, species that recover from fire by seedling recruitment and also resprout would be predicted to have lower resprouting vigor than resprouting specialists (Bellingham and Sparrow 2000). In addition, if a species allocates resources to recovering through clonal spread, it will have lower resprouting vigor due to competition among ramets for genet resources (Chapin *et al*. 1990, Matlack 1997). Within one recovery mode, the vigor of resprouting can vary among species (Hodgkinson 1998, Bond and Midgley 2001, Weekley and Menges 2003), due to the tradeoffs among intrinsic growth rate, resource storage, and resprouting vigor (Gurvich *et al*. 2005). Post-fire growth rates should also vary among species with different growth forms due to inherent differences in allocation. For example, shrubs tend to have larger root systems than sub-shrubs, which would make more resources available

for post-fire recovery. Resprouting patterns can also vary among individuals of the same species (Bond and Midgley 2001, Gurvich *et al.* 2005, Vivian *et al.* 2010). Resprouting vigor is influenced both by plant size before fire and by concentrations of nonstructural carbohydrates stored belowground (Malanson and Trabaud 1988, Bowen and Pate 1993, Lloret and Lopez-Soria 1993, Olano *et al.* 2006, Quevedo *et al.* 2007). Resprouting vigor can be measured in different ways, and there are likely tradeoffs among different aspects of post-fire growth. Within a species, an individual that allocates more to height gain should produce fewer stems (Falster and Westoby 2005). Stem diameter should increase with stem height, but the growth in height relative to the growth in diameter will differ among species (Schafer 2010).

We conducted our research in scrubby flatwoods, a type of Florida scrub. Scrubby flatwoods are dominated by evergreen shrubs such as oaks, palmettos, and ericads (Abrahamson 1984*a, b;* Schmalzer and Hinkle 1992; Menges and Kohfeldt 1995). Most dominant species have high root:shoot ratios that allow them to quickly regenerate aboveground structures after fires (Johnson *et al.* 1986, Saha *et al.* 2010). Scrubby flatwoods were once burned by lightning-ignited fires (Myers 1990, Duncan and Schmalzer 2004), probably at intervals of 8 to 16 years (Menges 2007). Protected areas of scrubby flatwoods are currently managed by prescribed fire, but the majority of extant scrubby flatwoods is fire-suppressed. This can cause deleterious structural and functional changes, including the reduction of biodiversity, especially in the herbaceous layer (Menges *et al.* 1993, Abrahamson and Abrahamson 1996). Resprouting is relatively more important in Florida scrub (Menges and Kohfeldt 1995, Weekley and Menges 2003) than many other pyrogenic ecosystems where both resprouting and post-fire seeding are widespread (Lloret *et al.* 1999). With most Florida scrub species recovering from fire by resprouting,

differences in the resprouting vigor may be important in structuring communities and maintaining diversity in Florida scrub. Previous studies in Florida scrub have documented differences in resprouting vigor, but only by quantifying differences in cover or individual resprouting probabilities (Abrahamson 1984*b,* Weekley and Menges 2003, Vesk and Westoby 2004). The aim of this study was to examine the post-fire growth strategies of resprouting Florida scrub plants and compare intraspecific and interspecific growth patterns. We examined how resprouting growth is related to species life history strategies in order to understand how the resprouting response could contribute to niche differentiation and species coexistence. We also examined tradeoffs in the type of resprouting growth to identify possible constraints in resprouting strategies. Based largely on prior studies, we hypothesized that:

1. Individuals with greater pre-fire size would have higher post-fire growth rates of resprouting stems.
2. Post-fire growth rates would vary among growth forms (shrub, sub-shrub, and palmetto). Sub-shrubs would have the slowest post-fire growth rates, palmettos the highest growth rates, and shrubs intermediate (Schmalzer and Hinkle 1992, Abrahamson and Abrahamson 2006).
3. Post-fire growth rates would vary among post-fire recovery modes (resprout only, resprout and seed, resprout and clonal, and palmetto). Species that grow both clonally and by resprouting would have the lowest post-fire growth rates, followed by species that are both post-fire seeders and resprouters, then by obligate resprouters.
4. There would be tradeoffs between stem density and height as well as between stem diameter and height.

METHODS

Study Site

We conducted this study at Archbold Biological Station (ABS) (27°11' N, 81°21' W, Highlands County, Lake Placid, Florida, USA), an inland Florida scrub site located at the southern tip of the Lake Wales Ridge (Weekley *et al*. 2008) in south-central Florida. Among the multiple vegetation types identified by Abrahamson *et al*. (1984), we confined this study to scrubby flatwoods, the most common vegetation type at ABS. This habitat was dominated by resprouting shrubs including oaks (Archbold oak [*Quercus inopina* Ashe], sand live oak [*Q. geminata* Small], Chapman oak [*Q. chapmanii* Sarg.]), ericaceous shrubs (fetterbush lyonia [*Lyonia lucida* {Lam.} K. Koch], coastal plain staggerbush [*L. fruticosa* {Michx.} G.S. Torr], shiny blueberry [*Vaccinium myrsinites* Lam.]), and palmettos (saw palmetto [*Serenoa repens* {Bartram} Small] and scrub palmetto [*Sabal etonia* Swingle ex Nash]) (Menges and Kohfeldt 1995). There are little data on natural fire regimes, but the estimated fire return interval used for management of scrubby flatwoods is about 8 yr to 16 yr (Menges 2007).

Prescribed fires are used at ABS to maintain the structure and function of native ecosystems and to test research questions. The property is divided into burn units with documented fire histories. We collected all data from a 97.1 ha burn unit 61B, located in the south end of ABS, just after its most recent fire (22 October 2008). This fire was prescribed and ignited using drip torches, with a combination of backing, flanking, and head fires. Fire weather included a maximum temperature of 29 °C, minimum relative humidity about 45 %, maximum wind speed of about 5 m s⁻¹, winds from NE to ENE, and clear skies. Flame lengths were not reported. The fire burned a mosaic of vegetation, primarily flatwoods, scrubby flatwoods, seasonal ponds, and rose-

mary scrub. Most of this vegetation had last been burned in 1986. The 1986 fire occurred on 7 to 8 June, and was ignited by lightning. It was extinguished by a combination of backing fires and rain. The 1986 fire had flame lengths of 2 m to 4 m and was driven by gusty, shifting winds.

Species

We collected size data from 16 of the most common woody (shrub) resprouting species exhibiting a range of post-fire recovery modes and growth forms: bigflower pawpaw (*Asimina obovata* [Willd. Nash]), tarflower (*Bejaria racemosa* Vent.), dwarf huckleberry (*Gaylussacia dumosa* [Andrews] Torr. & A. Gray), gopher apple (*Licania michauxii* Prance), coastal plain staggerbush, fetterbush lyonia, Feay's palafox (*Palafoxia feayi* A. Gray), silk bay (*Persea humilis* Nash), Chapman oak, sand live oak, Archbold oak, scrub palmetto, saw palmetto, Darrow's vaccinium (*Vaccinium darrowii* Camp), shiny blueberry, and tallow wood (*Ximenia americana* L.) (Table 1). Being monocots, the two palmettos lack secondary growth and they also appear demographically unique (Abrahamson and Abrahamson 2009); therefore, we classified them as an additional growth form (Table 1).

Sampling

We collected data in February and March 2009 during the winter dry season, after four to five months of post-fire recovery. We randomly established three 60 m transects in the recently burned scrubby flatwoods using GIS with the criteria that they were at least 10 m from the edge of sand roads and from other habitat types. Along each transect, we randomly chose two points within each 10 m segment, then measured the nearest plant of each species within 1 m of each point until we had sampled 12 individuals per species per transect. We sampled in this way to ensure ade-

Table 1. Study species, family, sample size, growth form (shrub, sub-shrub, or palmetto), and post-fire recovery mode (resprouter, clonal, seeder) classification for resprouting species in Florida, USA, in 2009.

Species	Common name	Family	*n*	Growth form[a]	Post-fire recovery[b]
Asimina obovata	bigflower pawpaw	Annonaceae	35	shrub	R
Bejaria racemosa	tarflower	Ericaceae	36	shrub	R
Gaylussacia dumosa	dwarf huckleberry	Ericaceae	36	sub-shrub	R, C
Licania michauxii	gopher apple	Chrysobalanaceae	37	sub-shrub	R, C
Lyonia fruticosa	coastal plain staggerbush	Ericaceae	36	shrub	R, C
Lyonia lucida	fetterbush lyonia	Ericaceae	38	shrub	R, C
Palafoxia feayi	Feay's palafox	Asteraceae	38	sub-shrub	R, S
Persea humilis	silk bay	Lauraceae	34	shrub	R
Quercus chapmanii	Chapman oak	Fagaceae	39	shrub	R, C
Quercus geminata	sand live oak	Fagaceae	36	shrub	R, C
Quercus inopina	sandhill oak	Fagaceae	39	shrub	R, C
Sabal etonia	scrub palmetto	Arecaceae	36	palmetto	P
Serenoa repens	saw palmetto	Arecaceae	46	palmetto	P
Vaccinium darowii	Darrow's vaccinium	Ericaceae	36	sub-shrub	R, C
Vaccinium myrsinites	shiny blueberry	Ericaceae	38	sub-shrub	R, C
Ximenia americana	tallow wood	Olacaceae	36	shrub	R, S

[a] Weekley *et al.* (2006).
[b] R = resprouter, C = clonal, S = seeder, P = palmetto (which is both a resprouter and a seeder, but put in its own category) (Menges and Kohfeldt 1995).

quate sample sizes for the less common species. If fewer than 12 individuals were present along the transect, we searched the area around the transect until at least 12 individuals per transect were sampled.

We defined an individual plant as clumps of stems that included all stems within 15 cm of each other. Most of the species studied here form distinct clumps (e.g., Johnson and Abrahamson 2002), and we recorded measurements only for well-defined clumps. We recognized that these "individuals" could be clones connected underground, but determining connectivity was impractical for this study. For each plant, we took measurements on burnt remains of stems present before the burn as well as on stems that resprouted after the burn. We measured stem number and basal stem diameter at the soil surface on each skeletal stem of the burnt remains to estimate the pre-fire size of

the plant. We assumed that the majority of stems present before fire left behind intact charred stems because of the absence of stubs at the base, and that they retained similar diameters. In some cases, this may have underestimated the size and number of stems present before the fire, but this would be rare (as in Gurvich *et al.* 2005). To quantify the resprouting response, we measured stem number, basal diameter, and height of each resprouting stem, as well as the maximum crown diameter length and the perpendicular crown width of the resprouts. To estimate pre-fire size for palmettos (scrub palmetto and saw palmetto), whose stems are often belowground, we recorded only the stem diameter of the aboveground portion of the stem where it emerged from the ground. Resprouting in palmettos was measured in terms of numbers of leaves and the height of each leaf.

Analysis

We calculated relative growth rates based on height, area, and volume, each defined as the natural logarithm of the growth measure divided by the number of days after the fire that the plant was measured. Crown area was estimated as the area of the ellipse calculated from the length of the maximum crown diameter and the perpendicular crown width. Volume growth was calculated as the product of the area of the ellipse and mean stem height:

$$\pi \; (l \times 2^{-1})(w \times 2^{-1})h^{-1} \qquad (1)$$

We analyzed intraspecific relationships between growth rates and estimated pre-fire size using linear regressions. To estimate pre-fire size of each plant (as defined above), we used the summed basal stem diameter of burnt remains. We compared volume growth rates among species, growth forms, and post-fire recovery modes with one-way ANCOVAs with pre-fire size as a covariate. We then compared pairwise differences in relative growth rates between species pairs using Bonferroni post-hoc tests. We used relative growth rates based on height to examine tradeoffs between different types of stem growth using Pearson correlations. Before analysis, we natural log transformed pre-fire size estimates and stem densities to meet statistical assumptions. We used IBM® SPSS® Statistics18 (SPSS Inc., Chicago, Illinois, USA) for all analyses.

RESULTS

Influence of Pre-Fire Size on Post-Fire Size

In general, post-fire size (volume) increased with estimated pre-fire size (summed stem diameter) ($n = 596$, $r^2 = 0.508$, $P \leq 0.001$) (Figure 1). The strength and direction of this relationship varied among species. Of the 12 species in which significant relationships were found, all were positive. Silk bay had the
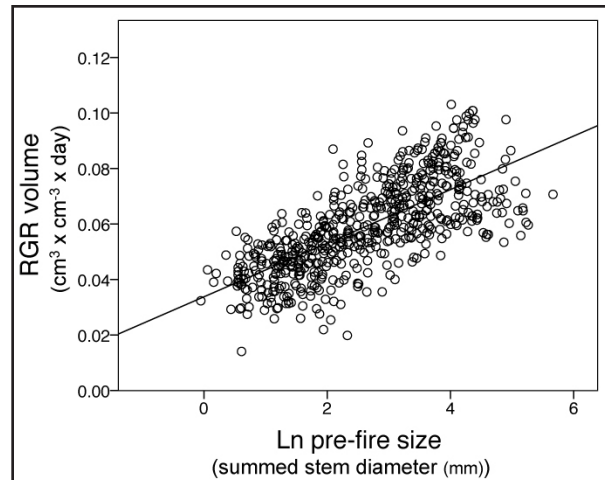
Figure 1. Relative growth rate (RGR) based on volume (cm³ × cm⁻³ × day) as a function of pre-fire size defined as the summed stem diameter (mm) across sixteen shrub species ($n = 596$, $r^2 = 0.508$, $P \leq 0.001$). Each point represents an individual plant. Data were collected in February and March 2009 following an October 2008 prescribed burn in Florida scrubby flatwoods habitat at Archbold Biological Station (Lake Placid, Florida, USA).

strongest and dwarf huckleberry the weakest relationships (Table 2). No significant relationship was found for Feay's palafox, tallow wood, and shiny blueberry (Table 2).

All species responded to fire by generating more stems after fire than the estimated number of stems before fire (with saw palmetto and scrub palmetto excluded from the analysis). The ratio of the number of new stems to the number of old stems was highest for tarflower and silk bay (Appendix 1).

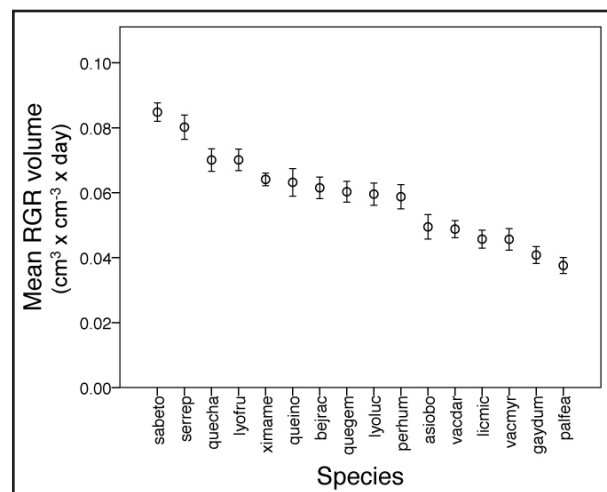## *Species Differences in Post-Fire Relative Growth Rates*

Post-fire relative volume growth rates varied among species ($n = 594$, $F_{15, 577} = 38.115$, $P \leq 0.001$), with estimated pre-fire size as a covariate ($F_{1, 577} = 227.31$, $P \leq 0.001$). The 16 species fell along a continuum with scrub palmetto having the highest relative growth rates, about double that of Feay's palafox, the lowest relative growth rates (Figure 2). Pairwise

Table 2. Results from regressions of volume of resprouting stems and estimated pre-fire size (summed diameter of burnt stems), and correlations of mean height growth with mean stem density and mean stem diameter for clumps of resprouting stems for resprouting species in Florida, USA, in 2009. Stem density and stem diameters were not measured for palmettos, which have belowground stems.

Species	Abbreviation	Pre-fire size vs post-fire size		Height growth vs stem density		Height growth vs stem diameter	
		r^2	P	r	P	r	P
bigflower pawpaw	asiobo	0.512	≤0.001	−0.800	≤0.001	0.559	≤0.001
tarflower	bejrac	0.360	≤0.001	−0.570	≤0.001	0.619	≤0.001
dwarf huckleberry	gaydum	0.110	0.048	−0.546	0.023	0.588	0.012
gopher apple	licmic	0.180	0.009	−0.433	0.007	0.357	0.036
coastal plain staggerbush	lyofru	0.293	0.001	−0.675	≤0.001	0.818	≤0.001
fetterbush lyonia	lyoluc	0.214	0.003	−0.749	≤0.001	0.557	≤0.001
Feay's palafox	palfea	0.018	0.417	−0.455	0.004	0.073	0.729
silk bay	perhum	0.678	≤0.001	−0.596	≤0.001	0.739	≤0.001
Chapman oak	quecha	0.230	0.002	−0.606	≤0.001	0.655	≤0.001
sand live oak	quegem	0.595	≤0.001	−0.643	≤0.001	0.586	0.001
sandhill oak	queino	0.344	≤0.001	−0.785	≤0.001	0.627	≤0.001
scrub palmetto	sabeto	0.229	0.003	--	--	--	--
saw palmetto	serrep	0.440	≤0.001	--	--	--	--
Darrow's vaccinium	vacdar	0.150	0.018	−0.442	0.007	0.620	≤0.001
shiny blueberry	vacmyr	0.080	0.096	−0.700	≤0.001	0.342	0.047
tallow wood	ximame	0.510	0.242	−0.505	0.002	0.464	0.004

comparisons separated palmettos from all other species ($P < 0.05$); the other 14 species fell into six overlapping groups. Species also varied in relative height and area growth rates as well as post-fire stem number, diameter, and density (Appendix 1).

Relative growth rates varied among groups of species with different growth forms: shrubs, sub-shrubs, and palmettos ($n = 594$, $F_{2, 590} = 128.52$, $P \leq 0.001$), with estimated pre-fire size as a covariate ($F_{1, 590} = 160.31$, $P \leq 0.001$) (Figure 3). As expected, palmettos had the fastest growth, which was 32 % higher than shrubs ($P \leq 0.001$) and 88 % higher than sub-shrubs ($P \leq 0.001$). There were also significant differences in relative growth rates among species grouped by different recovery modes: resprouting only, resprouting and seeding, resprouting and clon-


Figure 2. Species differences in relative volume growth rate (RGR, $cm^3 \times cm^{-3} \times day$) ordered from fastest growing to slowest growing. Error bars indicate 95 % confidence intervals. Species abbreviations are defined in Table 2.
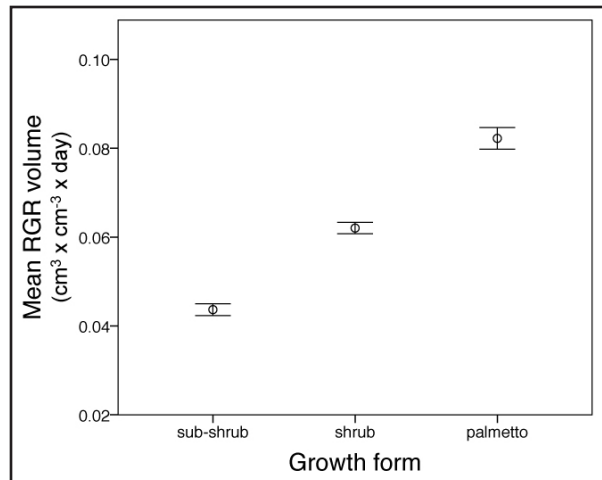
Figure 3. Relative volume growth (RGR, cm^3 × cm^{-3} × day) differences among different growth forms: shrubs, sub-shrubs, and palmettos. Error bars indicate 95 % confidence intervals.

al growth, and palmetto (n = 594, $F_{3, 589}$ = 141.43, $P \leq 0.001$), with estimated pre-fire size as a covariate ($F_{1, 589}$ = 791.41, $P \leq 0.001$) (Figure 4). Species that regenerate only from resprouting had relative growth rates 31 % lower that palmettos ($P \leq 0.001$); species that resprout and grow clonally had relative growth rates 2 % lower than resprouters ($P \leq 0.001$), and 33 % lower than palmettos ($P \leq 0.001$).
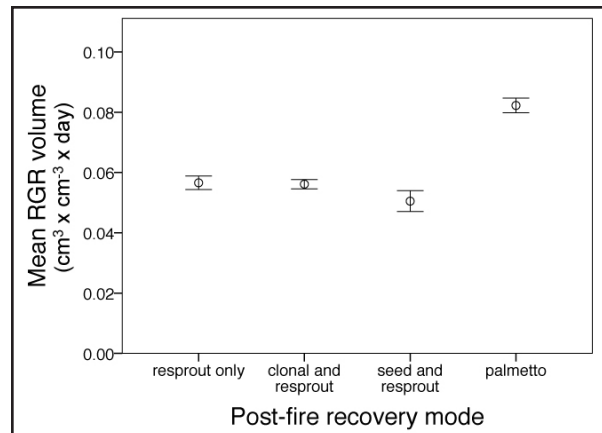
Figure 4. Relative volume growth (RGR, cm^3 × cm^{-3} × day) differences among different post-fire recovery mechanisms: resprouting only, resprouting and seeding, both resprouting and clonal growth, and palmetto. Error bars indicate 95 % confidence intervals.

Species that combined resprouting and post-fire seeding had the lowest relative growth rates ($P \leq 0.001$).

Growth Tradeoffs

A tradeoff between height growth and stem production was apparent across and within species. There was a negative correlation between the relative height growth rate and stem density (n = 512, r = −0.647, $P \leq 0.001$) (Figure 5), indicating a tradeoff between these types of growth (palmettos were not included in the analyses because stem density was not measured). There were also significant negative correlations between the relative height growth rate and stem density within each of the 14 species included in the analysis (Table 2). The opposite was true for relative height growth rate and stem diameter, which showed a positive correlation overall (n = 512, r = 0.654, $P \leq 0.001$) and for each species considered separately (Table 2).
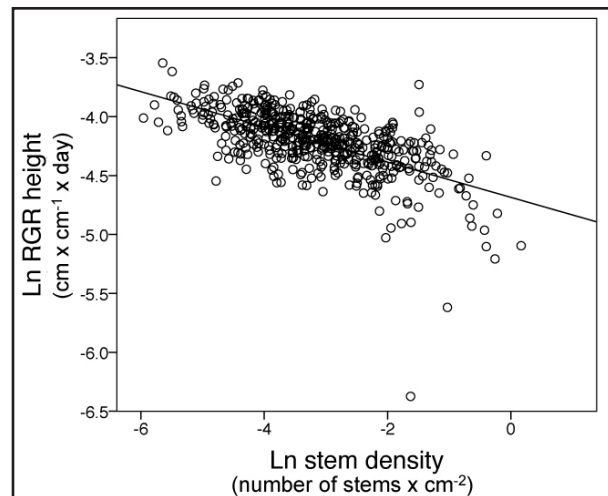
Figure 5. The relationship between the relative height growth rate (RGR, cm × cm^{-1} × day) and stem density (number of stems × cm^{-2}) for all species except saw palmetto and scrub palmetto. Each point represents an individual plant (n = 147, r = −0.504, $P \leq 0.001$).

DISCUSSION

Resprouting vigor, measured by relative growth rate, varied widely among Florida scrub species. While species fell along a continuum of post-fire resprouting vigor, the two palmetto species had markedly faster rates of initial re-growth. Excluding palmettos, species recovering from fire only by resprouting had the fastest growth, while species with mixed recovery modes exhibited slower growth rates.

Palmettos had the strongest resprouting response even though they also have substantial post-fire seedling recruitment. This is consistent with other studies that highlight palmettos' adaptation to fire (Schmalzer and Hinkle 1992, Menges and Kohfeldt 1995, Abrahamson and Abrahamson 2006). Palmettos have extremely high ratios of belowground to aboveground biomass and up to 90 % of belowground biomass allocated to storage organs (Saha *et al.* 2010). Although palmettos recruit by seed post-fire, growth from seedlings is remarkably slow (Abrahamson and Abrahamson 2009). Palmettos also have very high survival rates even as small plants (Abrahamson and Abrahamson 2002, 2009) and saw palmetto clones are tens of thousands of years old (Takahashi *et al.* 2011). This unique combination of traits, including stress tolerance and strong response to disturbance (Grime 1977), makes palmettos exceptionally successful in pyrogenic ecosystems in Florida.

In contrast, initial post-fire responses of oaks were slower than palmettos. This is consistent with the visual appearance of scrubby flatwoods, which appears palmetto dominated for several months, but oak dominated after a year or so. Oaks are more persistent than palmettos in long unburned sites (Menges *et al.* 1993). Scrub oaks are known to double in number of shoots after fire, and then thin out as shoot size increases (Abrahamson 1984*b*, Johnson and Abrahamson 2002). Our results show that all three oaks more than double in

the number of shoots shortly after fire. Sand live oak had a slightly higher proportion of post-fire stems to pre-fire stems than Archbold oak, which is consistent with previous findings of an increased abundance of sand live oak after fire (Abrahamson 1984*b*). These initial responses could have an impact on relative abundance of stems over time despite thinning.

While tradeoffs exist among different post-fire recovery modes such as post-fire seeders and post-fire resprouters (Bond and Midgley 2001, Pausas and Verdú 2005), this study is one of the first to show tradeoffs among resprouting species. These tradeoffs could be important in maintaining species diversity in this system. Species that combined resprouting with seeding had lower post-fire growth than species with other recovery modes, possibly because they have significant resources tied up in sexual reproduction, relative to resprouting specialists. These patterns were consistent with hypotheses made prior to the study.

We hypothesized that clonal resprouting species would have slower post-fire growth than resprouters due to competition between allocation to clonal spread and resprouting *per se* (Matlack 1997). While this hypothesis was supported, the difference was small. Species that can both resprout and spread clonally (with little tradeoff) can take advantage of the temporary availability of post-fire space. For example, other studies indicate that shiny blueberry increases clonal growth after fire, and its density and height peak around one year after fire before decreasing (Abrahamson 1984*b*, Menges and Kohfeldt 1995). There is a similar pattern in dwarf huckleberry, which peaks around 6 months post-fire (Abrahamson 1984*b*). By increasing allocation to clonal shoots, these subordinate shrubs can quickly exploit open space before larger shrubs recover.

For most species in the present study, resprouting vigor increased with estimated pre-fire plant size, and stem number increased after fire, which is consistent with previous studies

(Lloret and Lopez-Soria 1993, Quevedo *et al*. 2007). Within individuals, we found a negative correlation between plant height and stem density, which suggests a tradeoff among these types of growth, as hypothesized. This indicates that there is high competition among stems of the same plant and that there are constraints on the number and size of resprouting stems. We did not find evidence for a tradeoff in stem height and diameter at the individual level, but height scaled with stem diameter differently among species. This is consistent with patterns found in Schafer (2010) for scrub oaks and ericaceous shrubs.

The growth responses we found from this single fire may not be indicative of all fires. Growth rates in this study were measured after 22 years of fire exclusion, slightly longer than the proposed fire rotation for scrubby flatwoods (8 yr to 16 yr; Menges 2007). We expect that most species had large reserves of carbohydrates and that the observed resprouting response might be greater than resprouting in frequently burned sites (E. Menges, Archbold Biological Station, unpublished data). However, there is also a possibility that the effects of infrequent fire had negative effects on resprouting vigor. Depletion of carbohydrate reserves due to competition and decreased bud viability may lead to lower vigor (Drewa *et al*. 2002). The resprouting response may have also been affected by seasonality. The season for lightning-ignited fires in Florida peaks in late spring and early summer (Robbins and Myers 1992). The fall burn in this study was at the end of the growing season when seasonal carbohydrate levels are predicted to be lowest (Drewa *et al*. 2002).

Resprouting vigor is affected by storage organ size and morphology (Del Tredici 2001). Specialized storage organs may allow for rapid post-fire growth and quick flowering, and subsequently high seedling recruitment after fire (Olano *et al*. 2006). Genet age and size, not known for these species, could influence differences in resprouting vigor. Clones of scrub oaks have been shown to occupy areas from 30 m² to 1000 m² (Guerin 1993). Saw palmetto clones can be very large and very old; nevertheless, clonal diversity exists within small areas (Takahashi *et al*. 2011). Finally, a better understanding of clonal structure could help us further understand growth tradeoffs in resprouting shrubs.

Our study highlights the diversity of ways co-occurring resprouting plants recover after fire, and shows that some of this variation can be predicted by growth form and the presence of other post-fire recovery modes. The size of an individual also affects its resprouting vigor and additional factors such as past fire regime, carbohydrate dynamics, and clonal structure undoubtedly play a role in resprouting. In Florida scrub, resprouters dominate and the range of resprouting strategies may allow these species coexistence and the maintenance of species diversity. Resprouting has been increasingly recognized as a key functional trait that is important to understanding the resilience of ecosystems undergoing human-caused disturbances; therefore, individual- and species-level differences in resprouting responses can be important for informing management.

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