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Flammability of native understory species in pine flatwood and hardwood hammock ecosystems and implications for the wildland–urban interface

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Abstract. Six understory species from five pine flatwood sites and six understory species from five hardwood hammock sites were harvested for biomass analyses to compare potential flammability between two ecosystems in the south-eastern coastal plain of the United States. Plant components were separated into live and dead foliage, accumulated litter on and under the plant, and small and large stems. Foliar biomass was further analysed for moisture content, volatile solid content, and energy content. Statistical analyses revealed differences among species and between ecosystems. *Serenoa repens* plants present a wildfire hazard because they contain greater biomass than other species studied. *Ilex glabra* and *Lyonia ferruginea* are also hazardous to wildland–urban interface (WUI) structures because they have greater foliar energy content than other species studied. *Callicarpa americana* plants present the least wildfire hazard to WUI structures. We conclude that differences in flammability among species exist, but the causes of flammability are different among species. In addition, species in the same genus do not always have the same flammability. Based on measured characteristics, understory plants in pine flatwoods have greater ignitability, sustainability and combustibility than understory plants in hardwood hammocks. However, the measurements for consumability were similar between ecosystems.

Additional keywords: Callicarpa americana; energy content; firewise landscaping; *Gaylussacia dumosa*; *Ilex glabra*; *Ilex opaca*; *Lyonia ferruginea*; *Myrica cerifera*; *Quercus nigra*; *Serenoa repens*; *Vaccinium arboreum*; *Vaccinium myrsinites*; wildland–urban interface.

Introduction

Two dominant forest ecosystems in the south-eastern coastal plain of the United States are pine flatwoods and hardwood hammocks. Due to the lightning frequency in the South, both ecosystems are routinely exposed to potential ignition sources (Abrahamson and Hartnett 1990). Pine flatwoods are fire-prone ecosystems with a fire frequency of 1–8 years with wildfires generally being carried by the dense understory (Abrahamson and Hartnett 1990; FNAI 1990). Hardwood hammocks, on the other hand, are not fire-prone, but are affected by fire at intervals of 30–50 years or more through generally isolated and patchy wildfires (FNAI 1990; Platt and Schwartz 1990). The fire ecology of these two ecosystems is different although several understory species are associated with both.

With rapid human population expansion, both pine flatwood and hardwood hammock ecosystems are being developed for urban land use. Development affects ecosystem processes and functions (Hermansen and Macie 2002) and exposes more residents to catastrophic disturbances, especially fire (Monroe *et al.* 2003). From a natural resource management perspective, the interaction between natural areas and urban development is called the wildland–urban interface (WUI). Wildfire preparedness and mitigation programs educate and assist WUI homeowners and communities in becoming 'firewise'. Firewise refers to an understanding of and preparedness for wildfire, including entry and access, building materials, and landscaping. Firewise landscaping around homes allows firefighting equipment and personnel access and reduces the risk of wildfire damage if

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firefighting agencies are unable to defend each home. This is accomplished with vertical and horizontal separation of vegetation; less flammable plant species are also strongly desired (Monroe *et al.* 2003). There is not a standard methodology for testing the flammability of plants, therefore determining the relative flammability of plants is complex. As a result, many suggested lists of firewise plant species in the southern United States have unknown origins or are taken from lists originating from the western United States where a few research studies on flammability have been completed. More regionally specific flammability studies would improve the accuracy of firewise plant lists in the southern United States.

Flammability has been defined as having four components: ignitability, sustainability, combustibility, and consumability (Anderson 1970; Martin *et al.* 1994). Ignitability is the amount of time until ignition once a material is exposed to a known ignition source (Anderson 1970). Sustainability is the amount of time that a material will combust with or without a constant ignition source (Anderson 1970). Combustibility refers to how rapidly or intensely a material burns (Anderson 1970). Consumability is the quantity of material that is consumed (Martin *et al.* 1994).

Characteristics shown to influence the components of plant flammability include moisture content (Gill *et al.* 1978); percentage carbon compounds (cellulose, hemicellulose and lignin) (Philpot 1970; Susott 1982); volatile compounds (Shafizadeh *et al.* 1977; Susott 1982; Wang and Huffman 1982; Van Wilgen *et al.* 1990; Owens *et al.* 1998); silica-free mineral content (Mutch and Philpot 1970); leaf thickness (Montgomery and Cheo 1971); surface area-to-volume ratio (Rundel 1981; Papió and Trabaud 1990); and particle density (Brown 1970; Papió and Trabaud 1990). However, these characteristics have been studied to different extents by various methods and are not equally important to plant flammability, nor are they all independent of one another (Shafizadeh *et al.* 1977; Etlinger 2000; Francis 2000).

Few studies have compared the comprehensive flammability of plants among multiple species. In a study of six shrub species found in the western United States, Etlinger (2000) found that the amount of dry mass consumed determined the total heat released. Etlinger (2000) also concluded that foliar biomass and foliar moisture content contribute more to the peak heat release rate of plants than many other characteristics.

Gallberry (*Ilex glabra* (L.) A. Gray) and saw palmetto (*Serenoa repens* (Bartr.) Small) are species common in southern pine ecosystems; they have been shown to have foliar characteristics that make them extremely flammable (Hough and Albini 1978). Unfortunately, little is known about the flammability of other species composing these ecosystems. Due to the nature of the WUI, native plant species naturally exist near urban development and around homes. In addition, native plant species are popular with residents wishing to promote local wildlife and natural surroundings. To improve our understanding of pine flatwood and hardwood hammock flammability and to enhance the effectiveness of firewise planning, we conducted a study to test the following null hypotheses:

(1) Based on representative understory species, pine flatwood and hardwood hammock ecosystems have similar plant flammability characteristics.
(2) Species within the same genus have similar flammability characteristics.

Materials and methods

Study sites

Five sites of each ecosystem (pine flatwood and hardwood hammock) were located throughout north central Florida. Each site had experienced no fires for at least 3 years and contained a suite of understory species characterizing the respective ecosystem types. Pine flatwood study sites included property managed by the USDA Forest Service (Osceola National Forest), Florida Division of Forestry (Jennings State Forest, Withlacoochee State Forest, and Welaka State Forest) and the University of Florida (Austin Cary Memorial Forest). Hardwood hammock study sites included property managed by the USDA Forest Service (Osceola National Forest), Florida Division of Forestry (Jennings State Forest, Twin Rivers State Forest), and the Suwannee River Water Management District (Little River Springs and Steinhatchee).

Vegetation was characterized at each site by randomly selecting and measuring four circular tree plots (400 m^2) and eight circular shrub plots (12.56 m^2). Within the tree plots, diameter at 1.37 m (dbh) and height to the lowest branch were recorded for tree species (>3 m in height and >6.4 cm dbh). Height to the lowest branch was measured using a hypsometer (Haglöf, Vertex III). Stems of midstory trees (>3 m in height but <6.4 cm dbh) were also recorded. Canopy closure was measured from the center of each tree plot by averaging four readings from a concave spherical densiometer (Model-C, Forestry Supply, Inc.). Within the understory plots, the total number of stems was recorded for understory plants (0.4–3 m in height and <6.4 cm dbh).

Species selection and sampling

Understory species for this study were chosen based on their abundance in the two ecosystems and availability as native landscape plants at local nurseries. Species studied within pine flatwoods were dwarf huckleberry (*Gaylussacia dumosa* (Andr.) A. Gray), *I. glabra*, rusty lyonia (*Lyonia ferruginea* (Walt.) Nutt.) and evergreen blueberry (*Vaccinium myrsinites* Lam.). American beautyberry (*Callicarpa americana* L.), American holly (*Ilex opaca* Ait. var. *opaca*), water oak (*Quercus nigra* L.), and sparkleberry (*Vaccinium arboreum* Marsh.) were studied within hardwood hammocks. Wax

myrtle (*Myrica cerifera* L.) and *S. repens* were studied in both ecosystems.

At each study site, three plants of each species were randomly selected and harvested between May and July 2002. Sites were sampled alternately between flatwood and hardwood sites. Plants between 1 m and 3 m in total length were considered appropriate for this study. However, *G. dumosa* and *V. myrsinites* were accepted into the random sample if above 0.6 m and 0.4 m in length respectively. These two species are common within pine flatwoods but do not reach 1 m in height. Fifteen plants (three individuals at five sites) were sampled of *G. dumosa*, *I. glabra*, *L. ferruginea*, *V. myrsinites*, *C. americana*, *I. opaca*, *Q. nigra* and *V. arboreum*. A total of thirty plants (three individuals at five sites in both ecosystems) were sampled of *M. cerifera* and *S. repens*. In total, 180 plants were harvested from the sites. Because many of the species studied are clonal (*G. dumosa*, *L. ferruginea*, *V. myrsinites*, *M. cerifera*, *S. repens* and *V. arboreum*), only the above-ground biomass of one sprout was harvested.

Biomass measurements

To determine the litter layer beneath each sampled plant, three measurements of litter depth were taken within a 625 cm^2 equilateral quadrat. The litter was cut along the inside edge of the quadrat, removed, placed into a paper bag, and weighed. Before harvesting, total height and height to lowest branch were measured for each plant. The plant was not disturbed nor physically extended to take these measurements. The lowest branch measurement was made from the bottom of the litter layer to the point of the lowest vegetation on a branch, whether it was at the stem junction or at the terminal end. If multiple stems from the same individual emerged from beneath the litter layer, then the height to lowest branch was recorded as zero. Two measurements of crown width were taken at the widest point in perpendicular directions. The plant was then harvested at the soil line for above-ground biomass measurements. Fuel bed bulk density was calculated by dividing the total dry biomass by the gross plant volume (equation 1).

$$\text{Fuel bed bulk density (mg cm}^{-3}) = \frac{\text{plant biomass (mg)}}{\text{height} \times \text{width 1} \times \text{width 2 (cm)}}. \quad (1)$$

The above-ground biomass was separated into components: live foliage, dead foliage, litter accumulated on plant (referred to as debris), small stems (<6 mm diameter), and coarse fuel (≥6 mm diameter) for biomass analyses (Van Wilgen *et al.* 1990). Live foliage, dead foliage, debris, and small stems were considered the fine fuel component of biomass. If the amount of dead foliage was ≤0.1 g, it was included in the measurement of debris. For foliar biomass samples, a small sample was removed for volatile solid analysis and the resulting sub-sample was reweighed. All fresh weights were measured at the sites with an Ohaus® Scout II balance with a maximum of 600 g and accuracy to 0.1 g.

Litter, foliar, debris and small stem samples were dried at 70°C for 72 h. Large stem samples were dried at 70°C to a constant weight. Total dry foliar biomass for each plant was calculated based on the moisture content of the subsample dried in the oven. Dry weights were measured with the same balance used to measure fresh weight.

Foliar analyses

Moisture content of each sample was calculated based on dry weight (Van Wilgen *et al.* 1990; Eriksson *et al.* 2003) (equation 2).

$$\text{Moisture content (\%)} = \frac{\text{fresh weight} - \text{dry weight}}{\text{dry weight}} \times 100. \quad (2)$$

Live foliar samples were collected from each plant to be tested for volatile solids content. This sample was placed in a sealed plastic bag and transported in a cooler with ice to prevent decomposition. Samples were processed within 48 h by Advanced Environmental Laboratories located in Tampa, FL, by EPA standard 160.4. In this procedure, foliar samples were dried and then combusted at 550°C in a muffle furnace to determine the quantity of sample that was combustible. Data were originally reported in mg volatile solids per kg dry weight (mg kg^{-1}), which was converted to percentage volatile solids by dry weight.

Live foliar samples were used to determine the energy content for each individual using standard isoperibol oxygen vessel calorimetry (Parr® Model 1261 calorimeter). Dried foliar samples were ground in an electric coffee grinder and ~300 mg of sample was placed in dried and weighed crucibles. Crucibles and sample were dried for 24 h at 70°C, cooled, and weighed before processing. Samples were processed in random order so that each site had equal opportunity to be processed on a given day. Samples were placed in a desiccator until analysed with the calorimeter. Each ground foliar sample was processed in two runs completed on separate days. If the replicate run was greater than 2.5% (Dickinson and Kirkpatrick 1985) different from the first run, the samples were rejected and re-run twice at a later time. Acceptable runs were averaged to give a single foliar energy content value per plant.

The calorimeter was calibrated using benzoic acid, 10 ignitions per vessel. A fixed acid correction of 10 and a fixed fuse correction of 15 (25 calories total) were automatically subtracted from the total energy released in combustion. This accounts for energy released from the production of nitric acid from atmospheric N_2 gas in the vessel and the combustion of the NiChrome fuse wire. The sealed vessel was purged with 30 atm O_2 gas and submerged in 2 L of deionized water. Energy content was calculated based on sample dry weight

and expressed in kilojoules per gram (kJ g^{-1}). Total potential foliar energy content per plant was calculated by multiplying the energy content per gram by the total dry weight of foliage per plant (kJ $plant^{-1}$).

Statistical analyses

Site characterization data (in stems per hectare), tree basal area, height to lowest branch, and canopy closure were analysed for overall ecosystem and site differences. Sites were considered fixed and nested within ecosystems and analysed in a general linear model (GLM) procedure in Statistical Analysis Software (SAS). Pairwise comparisons of fixed means were performed using Tukey's test within each ecosystem ($\alpha = 0.05$).

Species data were analysed for ecosystem, species, and site effects using the GLM procedure in SAS. Species and site effects were nested within ecosystem type. Site effects were considered random in these analyses. When interaction variables were not significant ($P > 0.1$), they were removed from the model. All other tests were performed at $\alpha = 0.05$. Pairwise comparisons of fixed means were performed using Tukey's test; pairwise comparisons among species were performed within each ecosystem ($\alpha = 0.05$).

Because *M. cerifera* and *S. repens* were sampled in both ecosystems, data from these two species were also analysed in a separate general linear model to determine if flammability characteristics differed between ecosystems. In this model species were not nested within ecosystem. Additional analyses of the flammability characteristics for species within the genus *Ilex* (*I. glabra* and *I. opaca*) and *Vaccinium* (*V. myrsinites* and *V. arboreum*) were completed to determine if species within the same genus have similar flammability characteristics.

Results

Site characteristics

Collectively, the pine flatwood sites contained greater understory density, less midstory density, and less overstory density than hardwood hammock sites (Table 1). Further analyses of the overstory reveal that the pine flatwood sites contained less basal area per hectare than hardwood hammock sites. The trees in hardwood hammock sites had less height to the lowest branch and greater percentage of canopy closure than trees in flatwood sites (Table 1). Although sites within ecosystems were generally similar, there were some small differences especially among flatwood sites. Austin Cary Memorial Forest and Osceola National Forest sites contained fewer but larger overstory trees than several other flatwood sites. On the other hand, Jennings State Forest and Withlacoochee State Forest sites contained more overstory trees and the Withlacoochee State Forest site had greater canopy closure than all other flatwood sites.

Species differences

Biomass measurements

In pine flatwoods, litter depth was greatest under *S. repens* (10.1 cm) (Table 2). The other species in pine flatwoods had

Table 1. Study site characterization

Understory, midstory, and overstory stems per hectare ± standard error ($n = 8$ for understory and $n = 4$ for midstory and overstory site means; $n = 40$ for understory and $n = 20$ for midstory and overstory ecosystem means). Basal area, height to lowest branch, and canopy closure also given for each site ± s.e. ($n = 4$ for site means and $n = 20$ for ecosystem means). Within a column, sites followed by the same lowercase letters are not significantly different ($P > 0.05$) in Tukey's pairwise comparison within an ecosystem. * Indicates significant ($P < 0.05$) difference in Tukey's pairwise comparison between ecosystems. BA, basal area; MF, Memorial Forest; NF, National Forest; SF, State Forest

Ecosystem	Site	Understory (stems ha^{-1})	Midstory (stems ha^{-1})	Overstory (stems ha^{-1})	BA (m^2 ha^{-1})	Lowest branch (m)	Canopy closure (%)[A]
Flatwood	Austin Cary MF	$135\,600 \pm 32\,000^{a}$	0 ± 0	169 ± 33^{c}	1.4 ± 0.3	17.2 ± 1.0^{a}	52 ± 5^{b}
	Jennings SF	$79\,100 \pm 37\,600^{b}$	118 ± 64	650 ± 110^{a}	3.0 ± 0.4	7.1 ± 0.1^{c}	62 ± 6^{b}
	Osceola NF	$135\,200 \pm 13\,400^{a}$	0 ± 0	206 ± 30^{c}	1.8 ± 0.3	$16.4 \pm 1.0^{a,b}$	60 ± 1^{b}
	Welaka SF	$177\,200 \pm 15\,700^{a}$	68 ± 32	$275 \pm 25^{b,c}$	2.0 ± 0.2	12.1 ± 2.0^{b}	59 ± 6^{b}
	Withlacoochee SF	$85\,400 \pm 16\,200^{b}$	175 ± 69	$563 \pm 156^{a,b}$	3.1 ± 0.4	$15.4 \pm 1.9^{a,b}$	84 ± 4^{a}
Mean		$122\,500 \pm 12\,100$	72 ± 23	380 ± 60	2.3 ± 0.2	13.6 ± 1.0	63 ± 3
Hardwood	Jennings SF	$17\,100 \pm 1800$	1137 ± 241	606 ± 104	3.0 ± 0.5	$5.9 \pm 0.7^{a,b}$	87 ± 2^{b}
	Little River	8000 ± 1800	1381 ± 344	681 ± 75	3.7 ± 0.5	$5.9 \pm 0.2^{a,b}$	$94 \pm 1^{a,b}$
	Osceola NF	5800 ± 800	500 ± 245	365 ± 91	2.7 ± 0.6	10.3 ± 1.6^{a}	85 ± 5^{b}
	Steinhatchee	$13\,900 \pm 2300$	1000 ± 193	600 ± 78	4.3 ± 0.5	$7.2 \pm 0.2^{a,b}$	88 ± 3^{b}
	Twin Rivers SF	2200 ± 400	881 ± 160	619 ± 65	3.3 ± 0.5	4.9 ± 0.4^{c}	98 ± 1^{a}
Mean		$9400 \pm 1100^{*}$	$980 \pm 118^{*}$	$572.5 \pm 42.0^{*}$	$3.4 \pm 0.2^{*}$	$6.8 \pm 0.5^{*}$	$90 \pm 2^{*}$

[A] Statistical analysis on canopy closure was performed using an arcsin transformation.

similar litter depths. In hardwood hammocks, *S. repens* had the greatest depth (4.6 cm) but it was not significantly different from the other species. Litter under *S. repens* and *M. cerifera* was twice as deep in the pine flatwoods as under the same two species in the hardwood hammocks. Site effects were significant for all litter measurements for all species studied.

Serenoa repens had shorter height to the lowest branch than most other species (Table 2). *Vaccinium myrsinites* and *G. dumosa* averaged 51.9 cm and 71.0 cm in height, respectively, significantly shorter than other flatwood species (Table 2). At 182.9 cm, *V. arboreum* was taller than all hardwood hammock species except *I. opaca*. *Myrica cerifera* had the greatest variation in height in both pine flatwoods and hardwood hammocks. The total height of *L. ferruginea* and *V. myrsinites* was different among sites, resulting in a significant site × species interaction. There was no difference between plant widths among pine flatwood species (Table 2). However, *S. repens* had greater plant width than *Q. nigra* or *M. cerifera* in hardwood hammocks. *Myrica cerifera* and *S. repens* were significantly wider in hardwood hammocks than they were in pine flatwoods, but there were no other structural differences between ecosystems for these two species.

In pine flatwoods, *V. myrsinites* and *G. dumosa* had greater fuel bed bulk density than *I. glabra*. In hardwood hammocks, *C. americana* had less fuel bed bulk density than *V. arboreum* or *S. repens*. There were no significant differences in fuel bed bulk density between ecosystems for *M. cerifera* or *S. repens* (Table 2). However, there was a significant site × species interaction for fuel bed bulk density because the fuel bed bulk density of *I. glabra*, *V. myrsinites*, and *M. cerifera* were different among pine flatwood sites.

Total fine fuel biomass, coarse fuel biomass, and total biomass per individual were greatest for *S. repens* in pine flatwoods and hardwood hammocks (Table 3). In either ecosystem, *S. repens* contained the greatest live foliage and dead foliage biomass (Table 3). All other species retained negligible dead foliage biomass. In addition, *S. repens* in either ecosystem had greater accumulated debris than all other species. In pine flatwoods, *M. cerifera* contained greater small stem biomass than all other species except *L. ferruginea*. *Ilex opaca* and *V. arboreum* had greater small stem biomass than all other species in hardwood hammocks. There were no significant differences between ecosystems for any biomass components of *M. cerifera* or *S. repens*.

Species × site interaction was significant for live foliage biomass, small stem biomass, large stem biomass, and total biomass. Further analyses showed that site was significant for *V. myrsinites* (small stem biomass), *S. repens* in pine flatwoods (live foliage biomass and total biomass), and *M. cerifera* in hardwood hammocks (large stem biomass and total biomass).

Foliar analyses

Within pine flatwoods, there was no difference in foliar moisture content among species. *Callicarpa americana* had greater foliar moisture content during the sampling period (460%) than any other species studied in hardwood hammocks (Fig. 1). By comparison, *S. repens* in the hardwood hammocks had foliar moisture content of 113%. Although

Table 2. Litter and phenotypic data

Litter depth, litter volume, height to lowest branch, total height, and fuel bed bulk density measurements per individual plant ± s.e. ($n = 15$ for species and $n = 90$ for ecosystem). Within a column, species followed by the same lowercase letters are not significantly different ($P > 0.05$) in Tukey's pairwise comparison within an ecosystem. * Indicates significant ($P \leq 0.05$) difference in Tukey's pairwise comparison between ecosystems

Ecosystem	Species	Litter depth (cm)	Litter bulk density (mg cm^{-3})	Lowest branch (cm)	Total height (cm)	Width (cm)	Fuel bed bulk density (mg cm^{-3})
Flatwood	*G. dumosa*	5.4 ± 0.6^{b}	$17.6 \pm 2.4^{a,b}$	$27.4 \pm 4.9^{a,b}$	71.0 ± 2.3^{b}	27.0 ± 2.7	0.28 ± 0.05^{b}
	I. glabra	4.9 ± 0.4^{b}	20.5 ± 1.4^{a}	39.9 ± 6.6^{a}	129.2 ± 4.4^{a}	46.5 ± 2.4	0.17 ± 0.02^{c}
	L. ferruginea	6.3 ± 0.5^{b}	$13.4 \pm 1.2^{b,c}$	$27.5 \pm 5.0^{a,b}$	126.1 ± 8.4^{a}	48.7 ± 3.7	$0.23 \pm 0.02^{b,c}$
	V. myrsinites	4.5 ± 0.5^{b}	$19.0 \pm 3.5^{a,b}$	$4.1 \pm 1.8^{b,c}$	51.9 ± 3.4^{b}	27.1 ± 1.6	0.39 ± 0.03^{a}
	M. cerifera	6.2 ± 1.0^{b}	$17.0 \pm 1.6^{a,b}$	37.1 ± 6.0^{a}	141.3 ± 9.3^{a}	63.5 ± 5.6	$0.24 \pm 0.02^{b,c}$
	S. repens	10.1 ± 0.9^{a}	9.5 ± 1.6^{c}	0.0 ± 0.0^{c}	131.2 ± 6.5^{a}	158.8 ± 8.4	$0.25 \pm 0.03^{b,c}$
Mean		6.2 ± 0.3	16.2 ± 0.9	22.7 ± 2.5	108.5 ± 4.4	61.9 ± 5.2	0.26 ± 0.01
Hardwood	*C. americana*	3.6 ± 0.4	16.0 ± 1.4	$15.9 \pm 7.5^{a,b}$	121.8 ± 9.9^{c}	$86.5 \pm 9.0^{a,b}$	0.04 ± 0.01^{b}
	I. opaca	3.7 ± 0.4	16.8 ± 2.1	35.1 ± 8.1^{a}	$162.9 \pm 10.1^{a,b}$	$121.2 \pm 10.2^{a,b}$	$0.12 \pm 0.01^{a,b}$
	Q. nigra	3.2 ± 0.1	19.5 ± 2.9	32.5 ± 6.2^{a}	$144.6 \pm 10.4^{b,c}$	64.1 ± 5.9^{b}	$0.11 \pm 0.01^{a,b}$
	V. arboreum	3.8 ± 0.3	14.5 ± 1.7	32.8 ± 6.2^{a}	182.9 ± 12.5^{a}	$100.4 \pm 7.8^{a,b}$	0.14 ± 0.02^{a}
	M. cerifera	3.1 ± 0.2	19.4 ± 2.5	39.5 ± 7.4^{a}	$142.3 \pm 9.6^{b,c}$	83.5 ± 5.9^{b}	$0.10 \pm 0.02^{a,b}$
	S. repens	4.6 ± 0.5	15.0 ± 1.5	2.9 ± 2.9^{b}	$139.7 \pm 7.5^{b,c}$	218.4 ± 12.5^{a}	0.16 ± 0.02^{a}
Mean		$3.7 \pm 0.2^{*}$	16.9 ± 0.9	26.4 ± 3.0	$149.0 \pm 4.5^{*}$	$112.4 \pm 6.4^{*}$	$0.11 \pm 0.01^{*}$

Table 3. Biomass components

Dry weight of fine fuel biomass components (live foliage, dead foliage, debris, and small stems), coarse fuel biomass, and total biomass per individual plant ± s.e. ($n = 15$ for species and $n = 90$ for ecosystem). Within a column, species followed by the same lowercase letters are not significantly different ($P > 0.05$) in Tukey's pairwise comparison within an ecosystem. * Indicates significant ($P \leq 0.05$) difference in Tukey's pairwise comparison between ecosystems

Ecosystem	Species	Fine fuels (g)					Coarse fuels (g)	Total biomass (g)
		Live foliage	Dead foliage	Debris	Small stems	Total fine fuels		
Flatwood	*G. dumosa*	3.9 ± 0.5^{b}	0.0 ± 0.0^{b}	1.0 ± 0.2^{b}	6.5 ± 1.0^{b}	11.4 ± 1.5^{b}	0.1 ± 0.1^{b}	11.6 ± 1.6^{b}
	I. glabra	10.1 ± 2.2^{b}	0.0 ± 0.0^{b}	1.8 ± 0.5^{b}	20.0 ± 3.4^{b}	31.9 ± 5.3^{b}	16.3 ± 2.6^{b}	48.2 ± 7.5^{b}
	L. ferruginea	15.5 ± 2.4^{b}	0.0 ± 0.0^{b}	2.9 ± 0.6^{b}	$22.7 \pm 3.0^{a,b}$	41.2 ± 5.5^{b}	23.5 ± 5.2^{b}	64.6 ± 10.0^{b}
	V. myrsinites	3.6 ± 0.7^{b}	0.0 ± 0.0^{b}	2.7 ± 0.9^{b}	9.9 ± 2.4^{b}	16.1 ± 3.5^{b}	0.0 ± 0.0^{b}	16.1 ± 3.5^{b}
	M. cerifera	40.3 ± 6.8^{b}	0.0 ± 0.0^{b}	4.8 ± 1.0^{b}	45.4 ± 7.9^{a}	90.5 ± 14.8^{b}	50.2 ± 8.7^{b}	140.7 ± 22.4^{b}
	S. repens	242.2 ± 45.3^{a}	192.1 ± 40.5^{a}	38.4 ± 8.9^{a}	0.0 ± 0.0^{b}	472.8 ± 91.4^{a}	309.8 ± 45.1^{a}	782.5 ± 122.3^{a}
Mean		52.6 ± 11.7	32.0 ± 10.0	8.7 ± 2.1	17.4 ± 2.2	110.6 ± 23.0	66.7 ± 13.9	177.3 ± 35.4
Hardwood	*C. americana*	4.9 ± 0.9^{c}	0.0 ± 0.0^{b}	0.3 ± 0.2^{b}	15.5 ± 2.6^{c}	20.7 ± 3.3^{c}	10.4 ± 3.7^{c}	31.1 ± 6.5^{c}
	I. opaca	84.6 ± 15.9^{b}	0.0 ± 0.0^{b}	8.0 ± 4.2^{b}	69.0 ± 12.3^{a}	161.6 ± 29.7^{b}	147.1 ± 28.4^{b}	308.7 ± 57.6^{b}
	Q. nigra	14.8 ± 4.9^{c}	0.1 ± 0.1^{b}	0.8 ± 0.4^{b}	$20.1 \pm 3.6^{b,c}$	$35.8 \pm 8.3^{b,c}$	$48.2 \pm 15.5^{b,c}$	$84.0 \pm 22.8^{b,c}$
	V. arboreum	$34.0 \pm 8.4^{b,c}$	0.0 ± 0.0^{b}	6.3 ± 1.9^{b}	60.6 ± 11.6^{a}	$100.9 \pm 20.2^{b,c}$	151.7 ± 28.6^{b}	$252.6 \pm 45.5^{b,c}$
	M. cerifera	$28.4 \pm 9.4^{b,c}$	0.0 ± 0.0^{b}	1.8 ± 0.6^{b}	38.1 ± 10.9^{b}	$68.3 \pm 20.5^{b,c}$	$54.4 \pm 18.2^{b,c}$	$122.7 \pm 38.5^{b,c}$
	S. repens	324.5 ± 48.1^{a}	192.4 ± 44.0^{a}	40.4 ± 9.6^{a}	0.0 ± 0.0^{c}	557.2 ± 93.7^{a}	455.8 ± 103.0^{a}	1013.0 ± 195.3^{a}
Mean		81.9 ± 14.5	32.1 ± 10.4	9.6 ± 2.3	$33.9 \pm 4.2^{*}$	157.4 ± 25.7	$144.6 \pm 24.2^{*}$	$302.0 \pm 49.3^{*}$

not statistically significant ($P = 0.0771$), *M. cerifera* and *S. repens* had slightly greater foliar moisture content in hardwood hammocks than pine flatwoods.

Vaccinium myrsinites and *G. dumosa* had greater foliar volatile solid content than *I. glabra*, *M. cerifera* and *S. repens* in pine flatwoods (Fig. 1). *Serenoa repens* had less foliar volatile solid content than all other species in hardwood hammocks. There was no significant difference between the volatile solids of either *M. cerifera* or *S. repens* between ecosystems.

Foliar energy content per gram ranged from 19.42 kJ g^{-1} to 21.48 kJ g^{-1} among all species (Fig. 2). *Ilex glabra* and *L. ferruginea* had greater total energy content per gram than all other species in pine flatwoods. *Serenoa repens* had the least foliar energy content. In hardwood hammocks, *I. opaca* had the greatest foliar energy content and *C. americana*, *Q. nigra*, and *S. repens* had the least foliar energy content. There was no difference in the foliar energy content for *M. cerifera* and *S. repens* between ecosystems.

Serenoa repens had greater total energy content than any other species in both ecosystems (Fig. 2). *Ilex opaca* had greater foliar energy per plant than *C. americana* or *Q. nigra* in hardwood hammocks. There was no significant difference between ecosystems for *M. cerifera* or *S. repens* for total energy content per plant, although there was a slight increase in the energy content per plant for *S. repens* in hardwood hammocks as a result of greater plant biomass in that ecosystem (Table 3).

Both energy content measurements had significant interaction between site and species. By analysing data individually for each species, the effect of site was significant for the total energy content per gram of *M. cerifera* and *S. repens*. Site was significant for the foliar energy content per plant of *S. repens*.

In this study we found significant differences between *I. glabra* and *I. opaca*. *Ilex opaca* had significantly greater overall height, width, total biomass, and foliar energy content per plant than *I. glabra*. Live foliage biomass, small stem biomass, and coarse fuel biomass was greater for *I. opaca* than *I. glabra*. *Ilex glabra* had greater fuel bed bulk density than *I. opaca*. In addition, differences between *V. myrsinites* and *V. arboreum* existed. *Vaccinium arboreum* had significantly greater height to the lowest branch, overall height, width, total biomass, live foliage biomass, small stem biomass, coarse fuel biomass, foliar moisture content, and total energy content per plant than *V. myrsinites*. *Vaccinium myrsinites* had greater fuel bed bulk density, volatile solid content, and foliar energy content per gram than *V. arboreum*.

Ecosystem differences

Biomass measurements

Litter depth in the pine flatwoods (6.2 cm) was almost twice that in the hardwood hammocks (3.7 cm) (Table 2). Litter volume, however, was similar between ecosystems. Based on all understory species studied, there was no difference between the average height to the lowest branch between flatwood and hardwood sites (Table 2). Understory species sampled were taller and wider in hardwood hammocks than pine flatwoods (Table 2). Fuel bed bulk density was greater for understory species in pine flatwoods than in hardwood hammocks (Table 2).

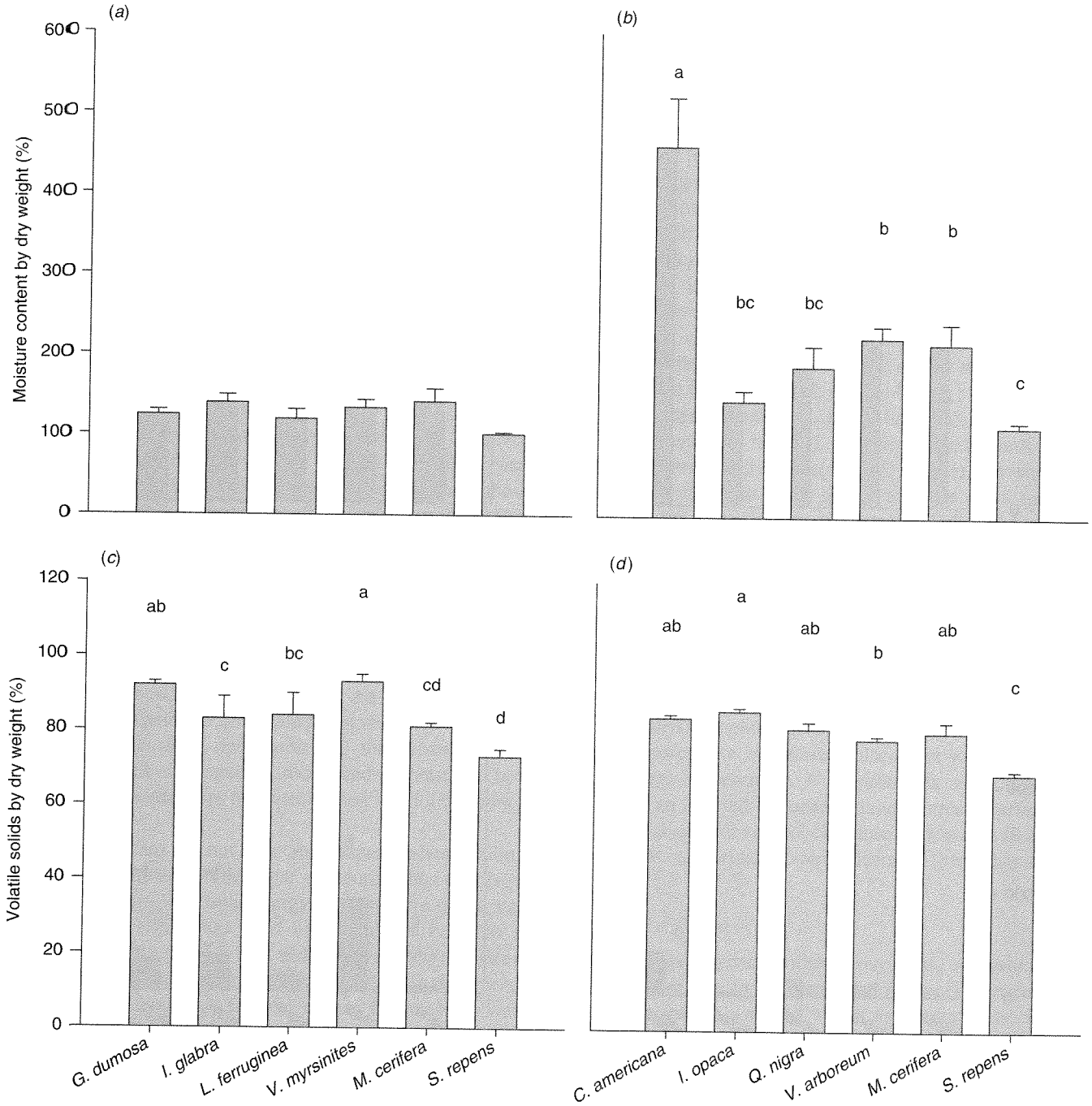

Fig. 1. Foliar moisture content (% dry weight) and volatile solid content (% dry weight) for species within pine flatwood (*a*,*c*) and hardwood hammock (*b*,*d*) ecosystems. Standard error is shown in error bars ($n = 15$). Within an ecosystem, species with the same letter were not significantly different in Tukey's pairwise comparison ($\alpha = 0.05$).

Total (per plant) fine fuel biomass and the fine fuel components—live foliage, dead foliage and debris—were not different between pine flatwood and hardwood hammock ecosystems (Table 3). However, small stem biomass per plant was greater in hardwood hammocks than pine flatwoods. There was more coarse fuel per individual plant in hardwood hammocks than in pine flatwoods. Similarly, total biomass per individual plant was greater in hardwood hammocks than in pine flatwoods.

Foliar analyses

Hardwood hammocks had greater foliar moisture content during the sampling period than pine flatwoods (224%

fire-prone ecosystems typically contain less foliar moisture content than species from other ecosystems (Dickinson and Kirkpatrick 1985; Van Wilgen *et al.* 1990; Eriksson *et al.* 2003).

Sustainability is best represented in this study with the measurement of fuel bed bulk density. Although the chemical components of the biomass may play a role in the fire sustainability of a plant, the continuity of that fuel is also important. More continuous fuel within individual understory plants in pine flatwoods may increase the sustainability of fire once the plant is ignited.

Combustibility, measured in energy content, was also greater for understory species within pine flatwoods. These results are similar to the results of Dickinson and Kirkpatrick (1985) and Van Wilgen *et al.* (1990), who reported greater energy content per gram in foliage from more fire-prone ecosystems (*Eucalyptus–Casuarina* dry sclerophyll and fynbos, respectively) than less fire-prone ecosystems (woodlands and forest patches, respectively).

In contrast with similar studies, the amount of fine fuels was the same between pine flatwood and hardwood hammock ecosystems. Less fire-prone ecosystems in South Africa and Ethiopia were found to contain greater fine fuel biomass in the understory than more fire-prone ecosystems (Van Wilgen *et al.* 1990; Eriksson *et al.* 2003). Foliar volatile solids were also similar between ecosystems in this study. Therefore, the amount of volatile, combustible material in leaves is not different between ecosystems. We conclude that, although the ignitability, sustainability, and combustibility were greater for understory species in pine flatwoods, the consumability was similar between ecosystems.

The possible natural selection of flammability characteristics or traits in fire-prone environments has been a topic of scientific debate since a published hypothesis by Mutch (1970). On a more individualistic approach, Bond and Midgley (1995) concluded that a flammability trait might evolve in a species only in certain circumstances, dependent on the fire survival mechanisms of the species and the density of the surrounding plant community. The evolution of a flammability trait is more likely to occur when the trait also provides additional benefits to the plant (Bond and Midgley 1995). Schwilk and Kerr (2002) demonstrate that a flammability trait can evolve and increase in frequency in a population even when the trait has the direct effect of reducing plant fitness due to a process the authors refer to as 'genetic niche-hiking'. From these arguments, natural selection seems to be a possible, but not absolute, explanation for the greater flammability of understory species in pine flatwoods; the interactions are complex.

Although wildfires can occur in both ecosystems, urban development in pine flatwoods are more prone to fire than those built in hardwood hammocks. This was evident in our site data; pine flatwoods contained greater litter depth and much greater understory density than hardwood hammocks. The increased understory density is likely due to the increase in light penetration to the understory, as observed in the canopy closure. The dense understory and, as our study indicates, the potential high flammability of pine flatwood understory species makes firewise planning critical for WUI homes associated with pine flatwood ecosystems. Plant lists containing recommended species for firewise landscaping should be based on multiple characteristics. The lists should not assume that species from the same genus have the same flammability. Extension publications should also include horticultural methods that can reduce the flammability of landscape plants in addition to stressing the need to select a landscape species based on a variety of desired characteristics, one of them being less flammable.

Conclusions

This study focuses on biomass and foliar characteristics likely to influence the components of flammability—ignitability, sustainability, combustibility, and consumability. More research is needed on the different components of flammability and how the flammability components of landscape plants affect home survival in the WUI during wildfire. From this study, we conclude that differences in flammability between species exist, but that species differ in flammability for different reasons. Also, species within the same genus do not always have similar flammability characteristics. Understory species in pine flatwoods are more flammable than understory species in hardwood hammocks. In addition, the dense understory in pine flatwoods facilitates wildfire, making wildfire preparedness planning in pine flatwoods necessary.

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References

Abrahamson WG, Hartnett DC (1990) Pine flatwoods and dry prairies. In 'Ecosystems of Florida'. (Eds RL Myers, JJ Ewel) pp. 103–149. (University of Central Florida Press: Orlando)

Anderson HE (1970) Forest fuel ignitibility. *Fire Technology* **6**, 312–319.

Bond WJ, Midgley JJ (1995) Kill thy neighbor: an individualistic argument for the evolution of flammability. *Oikos* **73**, 79–85.

Bond WJ, Van Wilgen BW (1996) 'Fire and plants.' (Chapman & Hall: London)

Brown JK (1970) Ratios of surface area to volume for common fine fuels. *Forest Science* **16**, 101–105.

Burgan RE, Susott RA (1991) Influence of sample processing techniques and seasonal variation on quantities of volatile compounds of gallberry, saw-palmetto, and wax myrtle. *International Journal of Wildland Fire* **101**, 57–62.

Dickinson KJM, Kirkpatrick JB (1985) The flammability and energy content of some important plant species and fuel components in the forests of southeastern Tasmania. *Journal of Biogeography* **12**, 121–134.

Eriksson I, Teketay D, Granström A (2003) Response of plant communities to fire in an *Acacia* woodland and a dry Afromontane forest, southern Ethiopia. *Forest Ecology and Management* **177**, 39–50. doi:10.1016/S0378-1127(02)00325-0

Etlinger MG (2000) Fire performance of landscape plants. MS Thesis, University of California, Berkeley.

FNAI (1990) 'Guide to the natural communities of Florida.' (Florida Natural Areas Inventory and Florida Department of Natural Resources: Tallahassee)

Foote LE, Jones SB, Jr (1989) 'Native shrubs and woody vines of the southeast: Landscape uses and identification.' (Timber Press: Portland, OR)

Francis JK (2000) Comparison of hurricane damage to several species of urban trees in San Juan, Puerto Rico. *Journal of Arboriculture* **26**, 189–197.

Gill AM, Trollope WSW, MacArthur DA (1978) Role of moisture in the flammability of natural fuels in the laboratory. *Australian Forest Research* **8**, 199–208.

Hermansen LA, Macie EA (2002) Introduction. In 'Human influences on forest ecosystems: The southern wildland–urban interface assessment'. pp. 1–7. USDA Forest Service, General Technical Report GTR-SRS-55. (Asheville, NC)

Hough WA, Albini FA (1978) 'Predicting fire behavior in palmetto–gallberry fuel complexes.' USDA Forest Service Research Paper SE-184. (Asheville, NC)

Lippi C, Kuypers M (1998) 'Flagler horticulture: making your landscape more resistant to wildfires.' Flagler County Extension, Florida Cooperative Extension Service. (Institute of Food and Agricultural Sciences, University of Florida: Gainesville, FL)

MacCubbin T, Mudge D (2002) 'Fire wise landscaping: making sensible choices.' Orange County Extension, FL Cooperative Extension Service. (Institute of Food and Agricultural Sciences, University of Florida: Gainesville, FL)

Martin RE, Gordon DA, Gutierrez MA (1994) Assessing the flammability of domestic and wildland vegetation. In 'Proceedings 12th conference on fire and forest meteorology, 26–28 October 1993, Jekyll Island, GA'. p. 796. (Society of American Foresters: Bethesda, MD)

Monroe MC, Long AJ (2001) 'Landscaping in Florida with fire in mind.' Florida Cooperative Extension Service. FOR 71. (Institute of Food and Agricultural Sciences, University of Florida: Gainesville, FL)

Monroe MC, Long AJ, Marynowski S (2003) Wildland fire in the Southeast: Negotiating guidelines for defensible space. *Journal of Forestry* **101**, 14–19.

Montgomery KR, Cheo PC (1971) Effect of leaf thickness on ignitibility. *Forest Science* **17**, 475–478.

Mutch RW (1970) Wildland fires and ecosystems—a hypothesis. *Ecology* **51**, 1046–1051.

Mutch RW, Philpot CW (1970) Relation of silica content to flammability in grasses. *Forest Science* **16**, 64–65.

Narog MG, Paysen TE, Koonce AL, Burke GM (1991) Burning irrigated and unirrigated chamise. In 'Proceedings 11th conference on fire and forest meteorology, 16–19 April 1991, Missoula, MT.' pp. 352–356. (Society of American Foresters: Bethesda, MD)

Owens MK, Lin CD, Taylor CA, Jr, Whisenant SG (1998) Seasonal patterns of plant flammability and monoterpenoid content in *Juniperus ashei*. *Journal of Chemical Ecology* **24**, 2115–2129.

Papió C, Trabaud L (1990) Structural characteristics of fuel components of five Mediterranean shrubs. *Forest Ecology and Management* **35**, 249–259. doi:10.1016/0378-1127(90)90006-W

Philpot CW (1970) Influence of mineral content on the pyrolysis of plant materials. *Forest Science* **16**, 461–471.

Platt WJ, Schwartz MW (1990) Temperate hardwood forests. In 'Ecosystems of Florida'. (Eds RL Myers, JJ Ewel) pp. 194–229. (University of Central Florida Press: Orlando)

Pyne SJ, Andrews PL, Laven RD (1996) 'Introduction to wildland fire.' 2nd edn. (John Wiley & Sons: New York)

Rundel PW (1981) Structural and chemical components of flammability. In 'Fire regimes and ecosystem properties.' pp. 183–207. USDA Forest Service General Technical Report GTR-WO-26. (Washington, DC)

Schwilk DW (2003) Flammability is a niche construction trait: canopy architecture affects fire intensity. *American Naturalist* **162**, 725–733. doi:10.1086/379351

Schwilk DW, Kerr B (2002) Genetic niche-hiking: an alternative explanation for the evolution of flammability. *Oikos* **99**, 431–442.

Shafizadeh F, Chin PPS, DeGroot WF (1977) Effective heat content of green forest fuels. *Forest Science* **23**, 81–89.

Susott RA (1982) Characterization of the thermal properties of forest fuels by combustible gas analysis. *Forest Science* **28**, 404–420.

Van Wilgen BW, Higgins KB, Bellstedt DU (1990) The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* **78**, 210–222.

Wang S, Huffman JB (1982) Effect of extractives on heat content of melaleuca and eucalyptus. *Wood Science* **15**, 33–38.