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Allometry of the pyrophytic *Aristida* in fire-maintained longleaf pine–wiregrass ecosystems

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PREMISE OF THE STUDY: Aboveground biomass (AGB) of herbaceous vegetation is a primary source of fuel in frequent surface fires that maintain grasslands, savannas, and woodlands. Methods for nondestructively estimating AGB are required to understand the mechanisms by which fuels affect fire behavior and the effects of time since the last burn. We developed allometric equations to estimate AGB in wiregrass (*Aristida beyrichiana*/*A. stricta*), a dominant bunchgrass in *Pinus palustris* ecosystems and a key species for ecological restoration.

METHODS: We collected wiregrass from North Carolina to Florida, across a range of time-since-last burn and site types. We tested 32 mixed effect models to see which predictors were best at predicting live, dead, and total AGB. We also examined how time since burn (TSB) affected the live-to-dead ratio (LDR) using regression.

KEY RESULTS: Wiregrass AGB was found to increase with increasing latitude (relative to tussock volume), possibly due to an increase in precipitation, and was greater on more fertile clay soils and flatwoods than on sandy soils. The LDR decreased as a power function with TSB, resulting in rapid accumulation of dead, highly flammable, biomass in the fire-free period.

CONCLUSIONS: Greater biomass will support fires of higher intensity. Our models can be useful in the parameterization of future physics-based models to predict fire behavior. Understanding the environmental variables that influence the allometry of wiregrass should help increase the precision of AGB estimates and the subsequent effects on fire behavior and effects on neighboring vegetation.

KEY WORDS aboveground biomass; *Aristida beyrichiana*; *Aristida stricta*; grasslands; herbaceous fuels; *Pinus palustris*; savannas; wiregrass; woodlands.

Frequent surface fires maintain the structure and composition of grasslands, woodlands, and savannas through complex feedbacks between fire and the vegetation that serves as the fuel source for fire (Beckage et al., 2009, 2011; Mitchell et al., 2009). Plant species that inhabit frequently burned ecosystems have traits that allow them to persist despite recurring consumption of aboveground biomass (Keeley et al., 2011; Varner et al., 2016), including highly flammable leaves that facilitate fire frequency and potentially exclude competing species (Mutch, 1970; Bond and Midgley, 1995). In grass species that dominate the herbaceous layer of grasslands, savannas, and woodlands, the magnitude of aboveground biomass (AGB) has been found to be a significant driver of flammability (Engber et al., 2011; Fill et al., 2016; Simpson et al., 2016).

Aristida stricta Michx. and *A. beyrichiana* Trin. & Rupr. are the dominant bunchgrass species of many longleaf pine (*Pinus palustris* Mill.) savannas and woodlands in the southeastern United States, with a combined range from North Carolina south to Florida and west to Mississippi (Fig. 1; Peet, 2007). Although they were traditionally considered one species (*Aristida stricta*), Peet (1993) proposed that the taxon be split into two species based on morphological differences. Under this new taxonomy, *A. stricta* is the species present in North Carolina and northern South Carolina, while *A. beyrichiana* is the southern species extending from South Carolina to Florida and westward (Peet, 1993; Weakley, 2015). Other researchers have disputed the split, noting that the morphological differences do not hold in all cases (Kesler et al., 2003) and citing genetic studies that suggest the northern and southern

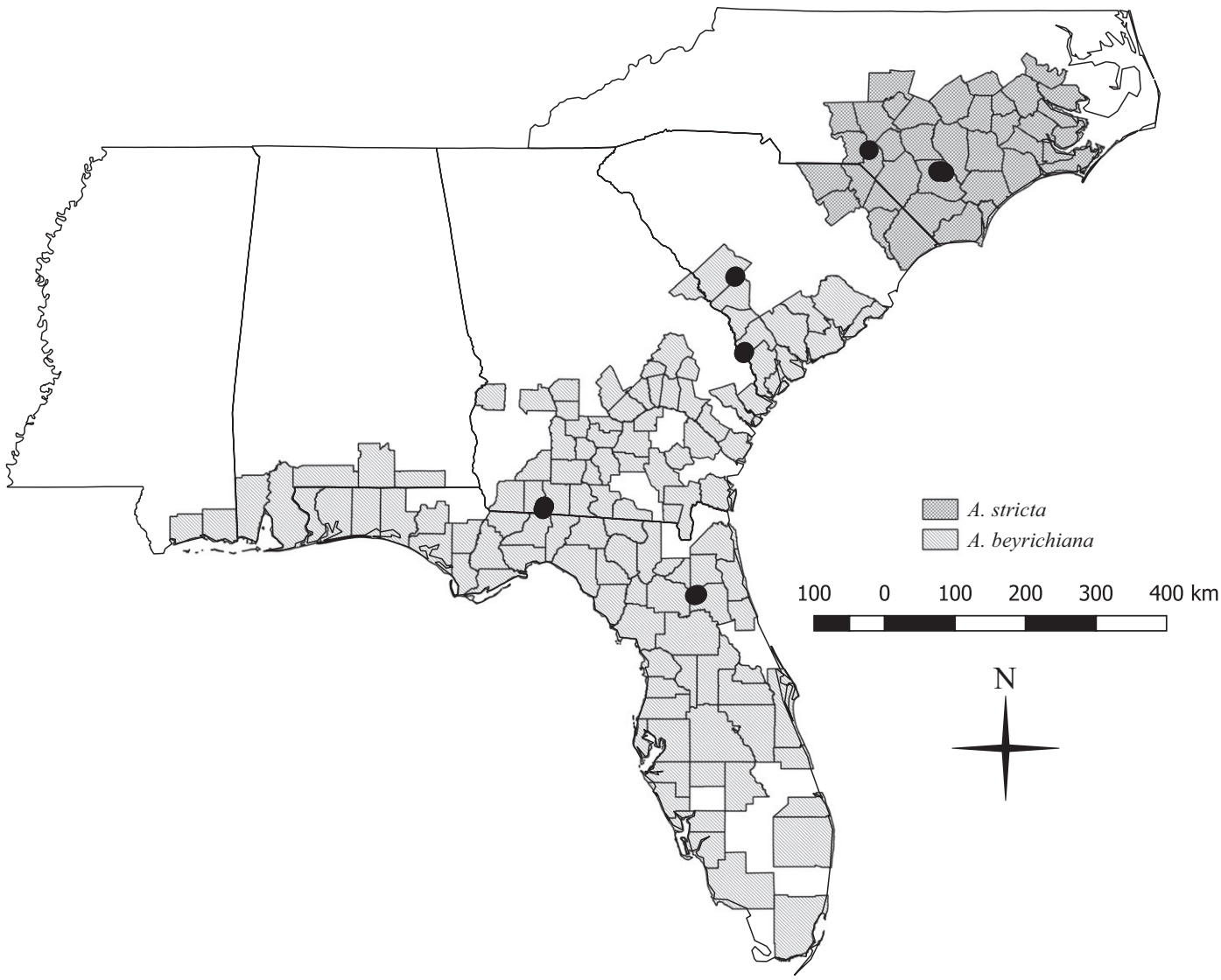

FIGURE 1. County distribution of *Aristida stricta* and *A. beyrichiana* in the southeastern United States based on Peet (1993). Points indicate locations used for wiregrass collection and subsequent development of allometric equations.

populations are more closely related than eastern or western populations (Walters et al., 1994). The two species are referred to collectively as "wiregrass" in this study unless specified by their scientific name.

Wiregrass is a perennial cespitose bunchgrass that occurs in a broad range of plant communities from xeric sandhills to seasonally wet, mesic flatwoods and clayhills (Christensen, 1977; Clewell, 1989; Noss, 1989; Peet, 2007). Wiregrass utilizes the C_4 photosynthetic pathway, which limits photorespiration and provides an advantage over C_3 plants in warm, high light environments (Ehleringer and Monson, 1993). C_4 grasses are thus highly productive in humid grasslands, savannas, and woodlands, which along with lower decomposition rates and fast curing, are conducive to frequent fires (Bond, 2008). The majority of wiregrass leaves (approximately 85%) senesce within the first year of growth but remain on the plant and can accumulate over time (Parrott, 1967). As a result, tussocks have low live-to-dead ratios (LDR) and are highly flammable (Clewell, 1989; Landers, 1991; Outcalt et al., 1999; Fill et al., 2016). Their long fibrous leaves can overlap other individuals' to form a relatively uniform density of tussocks, which may prevent woody encroachment during fire-free periods (Kirkman et al., 2016; Fill et al., 2017) and facilitate fire spread throughout the stand when an ignition occurs (Clewell, 1989; Landers, 1991; Outcalt et al., 1999). Once ignited, the AGB of individual wiregrass tussocks strongly influences flame length, a rough correlate of fireline intensity (Fill et al., 2016). Fill et al. (2016) found that flame lengths in burning wiregrass tussocks were over 3-fold longer than those published in the literature for co-occurring longleaf pine litter (Fonda, 2001) and oak litter (Kane et al., 2008). The highly flammable wiregrass AGB may also increase fire spread rate (Wenk et al., 2011; Fill et al., 2016; Simpson et al., 2016).

Wiregrass AGB is a critical contribution to stand-level productivity in fire-dependent longleaf pine ecosystems (Mitchell et al., 1999; Kirkman et al., 2016). Its contribution to understory productivity has been shown to be a major driver in savanna and woodland recovery from fire (Starr et al., 2015). Wiregrass begins to recover

within days after a fire, with an initial growth rate up to 2.54 cm/day (Parrott, 1967). This rapid rate of recovery allows for a frequent fire regime, with a historical interval of mean fire return of 2.2 years (Stambaugh et al., 2011), that maintains herb dominance. With increased time since burn (TSB) due to fire exclusion, dead wiregrass AGB accumulates (Parrot, 1967; Clewell, 1989), while live AGB decreases (K. Robertson, unpublished data). In long-unburned stands (>25 years), wiregrass frequency decreases (Maliakal et al., 2000), suggesting a decrease in total wiregrass AGB. Similar effects of TSB have been observed in other bunchgrass species. For example, Morgan and Lunt (1999) found that TSB reduced the total number of individuals and the number of tillers per tussock of *Themeda triandra* (R.Br.) Stapf in Australian grasslands.

Wiregrass tussocks interact with other fuels by intercepting litter from overstory trees such as longleaf pine and turkey oak (*Quercus laevis* Walter) that alter the overall fire behavior (Hiers et al., 2009; Wenk et al., 2011; Fill et al., 2016). The high species diversity documented in fire-maintained longleaf pine understories (Walker and Peet, 1984; Kirkman et al., 2004a) depends on the small-scale heterogeneity in fuel and subsequent variations in fire behavior (Mitchell et al., 2006; Thaxton and Platt, 2006; Dell et al., 2017). This pattern is also seen in other frequently burned ecosystems (Rice, 1993; Williams et al., 1994; Collins and Smith, 2006), but wiregrass tussock distribution through its overdispersed patterning provides critical continuity of fuels (Hovanes et al., 2018).

Given the significance of wiregrass AGB, methods for estimating AGB nondestructively are important to better understand and predict fire behavior and fire effects (Seielstad et al., 2011; Rowell et al., 2016). Measuring AGB can be accomplished by destructive sampling (i.e., harvesting the sample and drying it in an oven to remove water mass), but such sampling is not useful for studies involving flammability and fire effects, as the sample cannot be both harvested and burned in situ. As a result, all studies on wiregrass flammability thus far have had to pair the experimental unit, whether on the plot level or on the individual tussock level, with an unburned analogous comparison (Wenk et al., 2011; Fill et al., 2016). Allometric models require an initial destructive sample, but the identified relationships between plant size and AGB can then be used with new measurements, either through field surveys or through LiDAR, to estimate wiregrass AGB (Rowell et al., 2016). Understanding the allometry of wiregrass will improve our understanding of how fuels affect fire behavior in wiregrass-dominated stands, which can potentially extend to other grass-dominated ecosystems. Furthermore, the extreme sensitivity of wiregrass to soil disturbance limits its presence to native communities (Hedman et al., 2000; Kirkman et al., 2004b), making the link between wiregrass and natural fire behavior an important conservation issue.

To develop AGB allometric relationships for wiregrass, we destructively sampled wiregrass from 20 stands across the core of its distribution. Our objective was to develop allometric equations based on easily measured attributes in the field. We also tested to see whether TSB, species (*A. stricta* or *A. beyrichiana*), and site type (clayhill, flatwood, or sandhill) influenced allometric relationships of this Coastal Plain foundation species at a regional scale.

MATERIALS AND METHODS

Wiregrass tussocks were collected from six locations from Florida to North Carolina during the growing season in 2017 (Fig. 1). Climate in this region is humid subtropical, with a hot, humid summer growing season and a mild winter dormant season (Bailey, 1980). Precipitation occurs year-round, but is greater in the summer months. Stands were located in sandhills (soils in the Entisol order), flatwoods (soils in the Spodosol order), or clayhills (soils in the Ultisol order). Sandhill locations included Sandhills Game Lands (SHGL) in Richmond County, North Carolina; Aiken Gopher Tortoise Heritage Preserve (AGT) in Aiken County, South Carolina; and Ordway-Swisher Biological Station (OSBS) in Putnam County, Florida. Flatwood locations included Bladen Lakes State Forest (BLSF) in Bladen County, North Carolina and Webb Wildlife Center and Game Management Area (Webb) in Hampton County, South Carolina. Clayhill stands were located at Pebble Hill Plantation (PHP) in Grady County, Georgia. At each location, two to five stands were selected across a range of TSB, from 1 to 50 years (Table 1). All stands had a dominant overstory primarily of longleaf pine, with some slash pine (*Pinus elliottii* Engelm.), shortleaf pine (*P. echinata* Mill.), and scattered oaks (*Quercus* spp.). Wiregrass was abundant in all stands with the exception of the long-unburned stand (50 years) at OSBS, which had a noticeably lower grass density and greater pine and oak overstory. The presence of wiregrass indicated that these stands did not have a history of agriculture (Hedman et al., 2000; Kirkman et al., 2004b).

At each stand, approximately 20 wiregrass tussocks were selected by a random toss of a small object and cutting the nearest tussock at ground level with clippers. Tussocks were sampled so that the full range of available sizes was collected at each stand. A total of 396 wiregrass tussocks were sampled. For each tussock, two basal diameter measurements were taken, one at the widest diameter and the second perpendicular to the first. Wiregrass tussocks occasionally have a "doughnut" habit in which the central portion of the tussock dies and no longer grows new leaves (Clewell, 1989; Fig. 2). In these instances, the central "hole" was also measured in the same manner as stated above.

In the laboratory, tussocks were separated into live leaves, dead leaves, and flowering culms (if present) and oven-dried at 60°C for 48 h to obtain AGB measurements. Intermixed non-wiregrass material such as pine needles were discarded from the sample before drying. The lengths of 10 random live leaves were measured (including sheath) in each tussock and averaged together (L_{avg}).

Basal area (BA) of each tussock was calculated using the formula for an ellipse: $BA = \pi r_1 r_2$, where r_1 and r_2 are the long and perpendicular radii of the tussock base, respectively. Tussocks displaying the "doughnut" habit also had the area of the "hole" calculated in the same manner and subtracted from the BA measurement. Exploratory analysis suggested that there was high stand-to-stand variability in the relationship between tussock basal area and total AGB (Fig. 3), so tussock volume (vol) was used to incorporate any differences in leaf lengths between stands. Volume was estimated as done by Johnson et al. (1988) using the basal elliptic cylinder substituting leaf length for plant height: $vol = BAL_{avg}$.

For volume measurements, tussocks displaying the "doughnut" habit had the volume of the hole subtracted from the initial volume measurement (i.e., a hollow cylinder). Previous studies have estimated wiregrass volume using a half ellipsoid (Fill et al., 2016), which more accurately reflects the habit of the plant and is useful in bulk density estimation. We chose to use a cylinder (or hollow cylinder) because there was the possibility that measurements for a half ellipsoid may change in different weather conditions. For instance, clump height and clump radius are affected by the degree of arching

TABLE 1. Summary table of wiregrass (*Aristida beyrichiana*/*A. stricta*) measurements.

Location	Stand	Lat	Lon	Time Since Burn (years)	BA_{avg} (cm^2)	BA_{max} (cm^2)	BA_{min} (cm^2)	L_{avg} (cm)	L_{max} (cm)	L_{min} (cm)
AGT	1	33.505	−81.413	2	165.9	579.2	12.8	44.0	80	37
AGT	2	33.5067	−81.41	1	116.1	395.8	14.1	46.6	66	36
AGT	3	33.4917	−81.424	3	141.2	471.2	23.8	45.4	77	38.5
BLSF	1	34.7088	−78.477	3	105.5	328.3	1.6	49.9	80	37.5
BLSF	2	34.718	−78.492	4	115.8	373.1	6.9	49.2	66	46
BLSF	3	34.731	−78.528	7	90.9	404.1	0.7	49.2	85	41
BLSF	4	34.7119	−78.566	8	126.0	461.8	5.5	56.8	115	51
BLSF	5	34.7273	−78.576	10	137.7	530.5	4.7	45.4	83	34
OSBS	1	29.6857	−81.989	1	153.0	1249.6	8.2	39.0	67	34.5
OSBS	2	29.6946	−81.963	2	110.2	420.2	0.1	41.5	65	29
OSBS	3	29.7023	−81.944	1	98.9	340.5	2.4	41.6	70	34
OSBS	4	29.6958	−81.963	50	29.3	110.7	4.5	50.8	84	43
PHP	1	30.7704	−84.096	1	125.0	392.7	8.2	53.9	89	38
PHP	2	30.7704	−84.096	3	133.8	440.6	0.9	55.1	99	54
PHP	3	30.7704	−84.096	2	185.2	510.8	10.9	53.8	88	45
PHP	4	30.7704	−84.096	5	188.6	1043.4	7.3	53.3	109	49
SHGL	1	34.966	−79.542	1	88.6	208.5	6.9	43.1	74	27.5
SHGL	2	34.9642	−79.541	2	79.1	205.8	2.9	46.6	77	23
Webb	1	32.6198	−81.284	1	112.0	293.7	2.4	65.8	98	68
Webb	2	32.5942	−81.3	3	137.0	480.7	2.4	65.4	102	65

AGT = Aiken Gopher Tortoise Preserve; BLSF = Bladen Lakes State Forest; OSBS = Ordway-Swisher Biological Station; PHP = Pebble Hill Plantation; SHGL = Sandhills Game Lands; Webb = Webb Wildlife Preserve; and BA = basal area; L = leaf length.

FIGURE 2. The common "doughnut" habit of wiregrass.

of wiregrass leaves, whereas leaf length and basal area measurements do not change. Regression analysis was used to create models at the individual stand level and collectively at a range-wide level. For stand-level regressions, simple least squares regressions were fit using the formula Ln (AGB) = $a + b$ Ln (vol).

For the range-wide regression, we tested 32 mixed effect models for the allometric relationship between live, dead, and total AGB and different variables such as vol, BA, and TSB (see Appendix S1 for list of all models; Table 2 lists all fixed effect variables used in the tested models). For each model, stand was included as a random effect. Volume and BA were included as predictors in separate models as these predictors have been used in previous allometric studies on other bunchgrass species (Johnson et al., 1988; Oliveras et al., 2014). It is unknown whether the allometry of *A. beyrichiana* differs from *A. stricta*, so species was coded as either *e* or 1 and included in the study. Site type (sandhill/flatwood/clayhill) was coded with two binary variables (flatwood and clayhill) as either *e* or 1 (Table 2). Because we sampled along a latitudinal gradient, latitude was included as a predictor as well.

Traditional allometric studies fit a power-law relationship by taking the natural log transformation of both sides of the equation and fitting a linear model. Some authors argue that fitting a nonlinear function to the data on the original arithmetic scale is more appropriate (Packard, 2013). The major difference between the two methods lies in how the error term is treated within the model. In traditional allometry, the error term is additive on the logarithmic scale, which then is multiplicative when back-transformed to the arithmetic scale. Nonlinear fitting assumes the error is additive on the arithmetic scale (Xiao et al., 2011; Mascaro et al., 2013; Packard, 2013). We tested both log-transformed linear regression and nonlinear regression methods following the guidelines provided by Xiao et al. (2011), which suggested that log transformation was more appropriate for our models. Only the log-transformed results are presented here. Models were fit using the lmer function in the R package lme4 (Bates et al., 2015).

Model selection

We compared the fit of the 32 models with maximum likelihood estimation using the model.sel function in the R package MuMIN (Barton, 2018). We included the marginal and conditional estimates of the coefficients of determination (R^2_m and R^2_c, respectively), residual standard error (RSE), corrected Akaike information criterion (AIC_c), and Akaike weights (w) in our comparisons. The marginal and conditional coefficients of determination are interpreted in a similar manner as the traditional R^2, with the amount of variance explained by the fixed effects (R^2_m) and both fixed and random effects combined (R^2_c) (Nakagawa and Schielzeth, 2013; Johnson, 2014). Akaike weights provide an additional metric for model selection, providing a probability that a given model is the best model to describe the data out of the given candidate models (Wagenmakers and Farrell, 2004). The model with the lowest AICc and highest Akaike weight was selected for the model verification process.

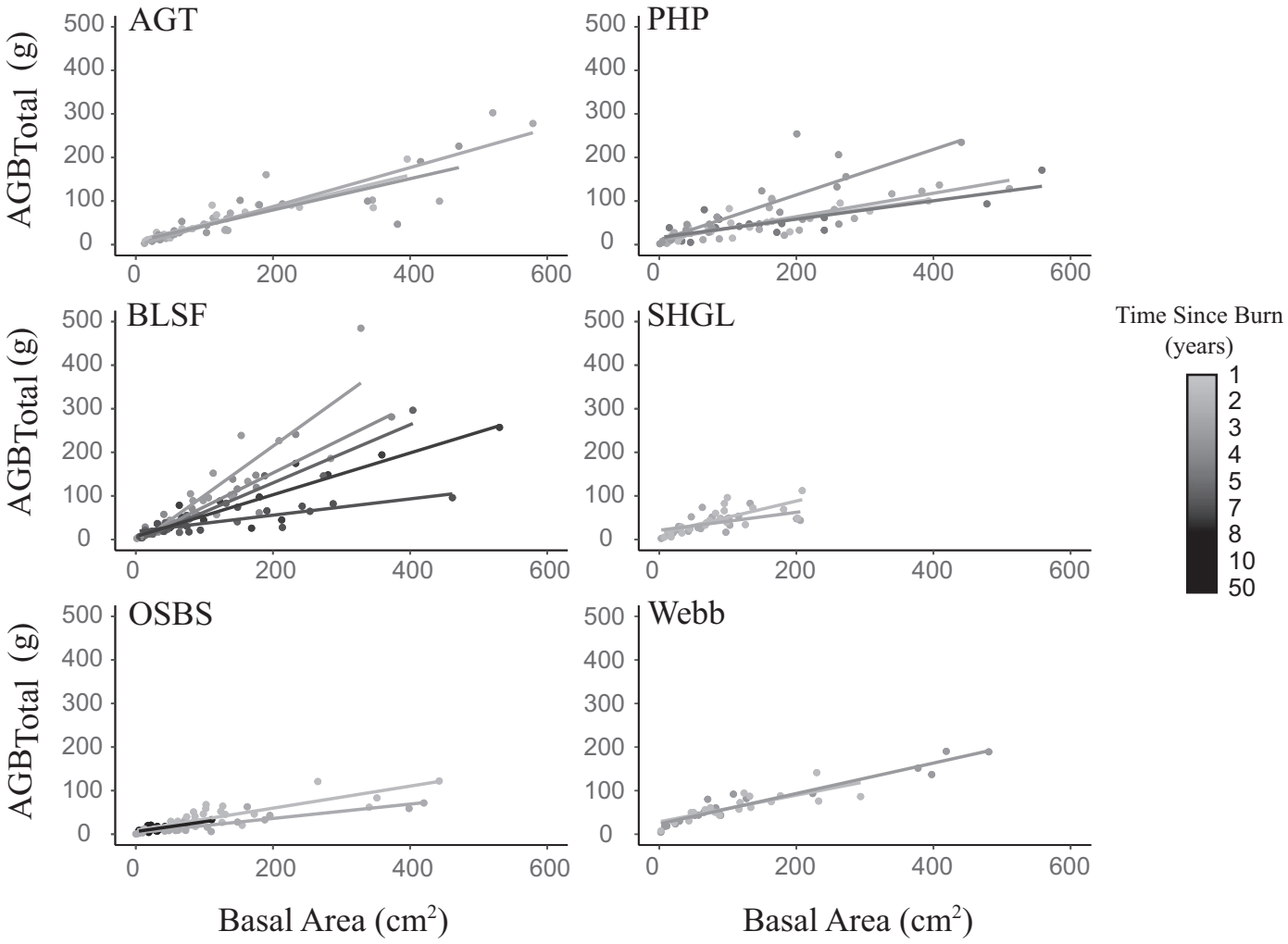

FIGURE 3. Exploratory data showing the relationship between total aboveground biomass (AGB) and basal area of wiregrass tussocks. AGT = Aiken Gopher Tortoise Heritage Preserve; BLSF = Bladen Lakes State Forest; OSBS = Ordway-Swisher Biological Station; PHP = Pebble Hill Plantation; SHGL = Sandhill Game Lands; Webb = Webb Wildlife and Game Management Area. Trendlines are simple linear models on untransformed data.

TABLE 2. Fixed effects tested in the development of allometric equations for aboveground biomass of wiregrass (*Aritida beyrichiana/A. stricta*).

Variable	Type	Units/Values	Abbreviation
Basal area	Continuous	cm^2	BA
Basal elliptic volume	Continuous	cm^3	vol
Latitude	Continuous	°N	Lat
Site type	Categorical	Clayhill { clayhill = *e*, flatwood = 1	clayhill/flatwood
		Flatwood { clayhill = 1, flatwood = *e*	
		Sandhill { clayhill = 1, flatwood = 1	
Species	Categorical	*A. beyrichiana* = *e* *A. stricta* = 1	SPP
Time since burn	Continuous	years	TSB

e = Euler's number ≈ 2.7183.

Model verification

To verify the accuracy of our models, we randomly divided the data set into training (70% of the data) and testing (30% of the data) subsets. The best model identified in our model selection was fit to the training data set. The coefficients were back-transformed as needed and the back-transformed equation was used to predict the test data. The final model included a correction factor (CF) to account for the bias introduced when back-transforming the model equation as suggested by (Baskerville, 1972):

$$\mathrm{CF} = e^{\left(\frac{\mathrm{MSE}}{2}\right)},$$

where MSE is the mean square error of the regression. Model accuracy was determined by summing the actual AGB for all individuals in the test data and comparing it to the summed predicted AGB. Prediction error for individual tussocks was calculated by subtracting the actual AGB from the predicted AGB. All analyses

TABLE 3. Regression results fit to the equation Ln (AGB_{total}) = a + b Ln (vol) for each sampled stand.

Location	Stand	a	b	r^2	P
AGT	1	−4.0429	0.9247	0.94	<0.01
AGT	2	−2.8813	0.7962	0.94	<0.01
AGT	3	−2.8067	0.7789	0.86	<0.01
BLSF	1	−2.8414	0.8630	0.97	<0.01
BLSF	2	−2.5188	0.8004	0.83	<0.01
BLSF	3	−2.8233	0.8079	0.87	<0.01
BLSF	4	−1.2007	0.5623	0.75	<0.01
BLSF	5	−2.7810	0.8020	0.89	<0.01
OSBS	1	−1.6092	0.6302	0.93	<0.01
OSBS	2	−1.9887	0.5909	0.84	<0.01
OSBS	3	−3.3295	0.8119	0.90	<0.01
OSBS	4	−1.3130	0.5269	0.46	<0.01
PHP	1	−1.4263	0.5889	0.76	<0.01
PHP	2	−2.4161	0.7596	0.91	<0.01
PHP	3	−2.7331	0.7341	0.75	<0.01
PHP	4	−1.0606	0.5495	0.59	<0.01
SHGL	1	−2.5427	0.7714	0.89	<0.01
SHGL	2	−1.6759	0.6454	0.80	<0.01
Webb	1	−0.6309	0.5410	0.89	<0.01
Webb	2	−1.4121	0.6387	0.96	<0.01

AGT = Aiken Gopher Toroise Preserve; BLSF = Bladen Lakes State Forest; OSBS = Ordway-Swisher Biological Station; PHP = Pebble Hill Plantation; SHGL = Sandhills Game Lands; and Webb = Webb Wildlife Preserve.

were conducted in R statistical package (version 3.3.3, https://www.R-project.org/).

RESULTS

All stand-level regression equations for wiregrass were significant at $\alpha < 0.01$. The R^2 values ranged from 0.46 to 0.97, with the majority of stands having R^2 values over 0.75 (Table 3). Slopes and intercepts from the different stands varied from 0.53 to 0.92 for slope and −4.04 to −0.63 for intercept ranges (Table 3).

Of the 32 model forms tested for the range-wide regression, the best model (using all of the data) for AGB_{Live} included tussock volume, latitude, site type, and TSB as predictors (Table 4, see Appendix S2 for R^2_m, R^2_c RSE, AIC_c, and w values of all models):

$$\text{Ln}(AGB_{Live}) = -13.84 + 0.631\ \text{Ln (vol)} + 3.245\ \text{Ln (Lat)} + 0.380\ \text{Ln (flatwood)}\ 0.281\ \text{Ln (clayhill)} + -0.148\ \text{Ln (TSB)}.$$

Fixed effects accounted for approximately 79% of the variance, and the random effect of site accounted for an additional 4% (Table 4). The correction factor for back transformation was 1.097. Site type was not significant in the best AGB_{Dead} model:

$$\text{Ln}(AGB_{Dead}) = -11.960 + 0.754\ \text{Ln (vol)} + 2.447\ \text{Ln (Lat)} + 0.159\ \text{Ln (TSB)}.$$

Fixed effects in our best dead AGB model accounted for 74% of the variance with the random effect of site accounting for approximately 7% (Table 4). The correction factor for back transformation was 1.13. Our best total AGB model, which included live, dead, and flower culms (if present) was:

$$\text{Ln}(AGB_{Total}) = -13.03 + 0.709\ \text{Ln (vol)} + 3.105\ \text{Ln (Lat)}.$$

Fixed effects for AGB_{Total} accounted for 83% of the variance, with the random effect accounting for approximately 3% (Table 4). The CF for AGB_{Total} was 1.08.

Our range-wide models fit to the randomly split training data was able to predict the summed AGB of the test data with an accuracy of 91.8% for AGB_{Live}, 83.9% for AGB_{Dead}, and 89.3% for AGB_{Total} when predicting the test data set (Table 4). The majority of the error across the six study locations were similar, with average errors ranging from −5.1 to 0.5 g across all locations for AGB_{Live}, −13.3 to 4.0 g for AGB_{Dead}, and −13.2 to 5.3 g for AGB_{Total} (Fig. 4). The range in errors across all locations was smallest in AGB_{Live} predictions, with the worst predictions being off by approximately −37.3 g and 30.9 g (Fig. 5). Dead and total AGB predictions error ranges were larger, with AGB_{Dead} having an error range of −133.5 and 42.4 g and AGB_{Total} having an error range of −147.0 and 71.8 g (Fig. 5).

The average LDR per stand declined as a power function with time since burn (Fig. 6). Although time since burn was significant ($P = 0.008$), the variability of LDR within sites—particularly in the 1-yr since burn sites—gave the model relatively low explanatory power ($r^2 = 0.29$). The final equation for LDR (including correction factor) was $LDR = 1.31 \times TSB^{-0.2691}$ where TSB is time since burn in years.

DISCUSSION

At the stand level, tussock basal elliptic cylinder volume was an accurate predictor of total wiregrass AGB as evident in the good fits in our stand level results. Advances in fire ecology in surface-fire regimes require more accurate quantification of heat transfer in direct relation to plant response (O'Brien et al., 2018). For grasses, reliance on traditional clip plots for AGB estimation at stand levels do not have the resolution to relate AGB to fire effects (Rowell et al., 2016), particularly at scales that dominate fire effects on biodiversity in this ecosystem (Dell et al., 2017). Relationships of tussock dimensions to AGB also offer a significant opportunity to advance the use of terrestrial LiDAR and remote sensing estimates for bunchgrass fuel load without disrupting critical fuelbed characteristics such as continuity (Rowell et al., 2016).

Our results are consistent with allometric equations for other grass species in the literature. For example, Johnson et al. (1988)

TABLE 4. Best model equations for live, dead, and total AGB of *Aristida* spp.

Model	R^2_m	R^2_c	E	AICc	W	Accuracy(%)
Ln (AGB_{Live}) = a + b Ln (vol) + c Ln (Lat) + d Ln (flatwood) + eLn (clayhill) + fLn (TSB)	0.79	0.83	0.4391	521.4	0.45	91.8
Ln (AGB_{Dead}) = a + b Ln (vol) + c Ln (TSB) + d Ln (Lat)	0.74	0.81	0.5132	647.8	0.27	83.9
Ln (AGB_{Total}) = a + b Ln (vol) + c Ln (Lat)	0.83	0.86	0.3962	436.0	0.28	89.3

AGB = aboveground biomass; flatwood/clayhill are dummy variables indicating whether the site is flatwood, clayhill, or sandhill; R^2_m/R^2_c = marginal/conditional coefficent of determination; RSE = residual standard error; AICc = corrected Akaike's information criterion; w = Akaike weight.

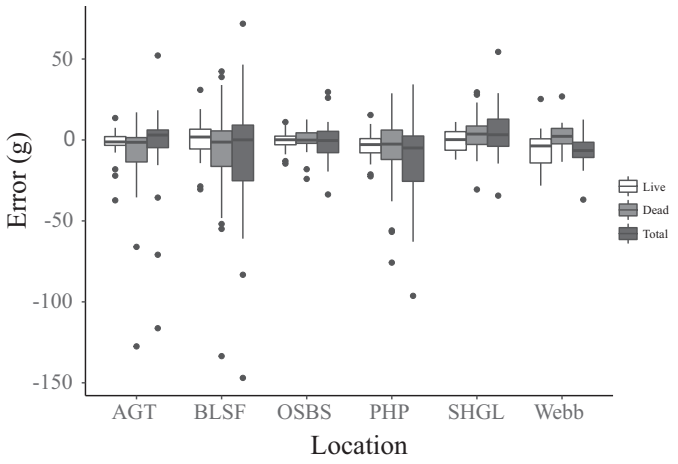

FIGURE 4. Prediction errors for the models predicting live, dead, and total AGB of wiregrass across the six study locations. AGT = Aiken Gopher Tortois Preserve; BLSF = Bladen Lakes State Forest; OSBS = Ordway-Swisher Biological Station; PHP = Pebble Hill Plantation; SHGL = Sandhill Game Lands; Webb = Webb Wildlife and Game Management Area.

found that the basal elliptic cylinder volume of crested wheatgrass [*Agropyron desertorum* (Fisch. Ex Link) Schult.] explained approximately 67 to 87% of the variation in AGB. Oliveras et al. (2014) developed allometric equations for four species of tussock grasses combined in high altitude grasslands of Peru. Although they did not use volume as a predictor specifically, the best model to predict total AGB included basal area, maximum height, and canopy area (Oliveras et al., 2014). Johnson et al. (1988) also considered canopy area in their elliptical cone volume predictor, which produced slightly better fits than their basal elliptical cylinder equations, but suggested that the error in the measurement of canopy diameters in bunchgrasses may be excessive.

Our results also revealed that there is considerable stand-to-stand variation in the relationship between wiregrass AGB and the measured variables investigated. The best general model for live, dead, and total AGB all included latitude as a significant predictor, which is likely a proxy variable for some unmeasured predictor(s). For example, precipitation monitored by nearby remote automated weather stations (RAWS) also varied along the same latitudinal gradient (Fig. 7), suggesting that precipitation, soil moisture retention, growing season length, or a combination may be responsible for the differences in allometric coefficients that we observed. Wiregrass grows on many types of sites from extremely wet, poorly drained soils, to extremely xeric well-drained soils (Parrott, 1967; Clewell, 1989), which also influences its growth. For example, Parrott (1967) observed that wiregrass tussocks in poorly drained wet soils tended to grow more via tillering than via rhizomes, with leaves elevated approximately 10 cm above the soil surface. Site type was included in our best live AGB model with flatwood and clayhill sites both having positive coefficients suggesting that the rate of AGB increase relative to volume is higher on these sites compared to sandhill sites. Site type was not included in our best dead and total AGB models, possibly due to higher decomposition rates of dead AGB in flatwood and clayhill sites. Additionally, site type was coded with two variables, and the AICc estimator penalizes models with more predictors (Hurvich and Tsai, 1989), which may have lowered the

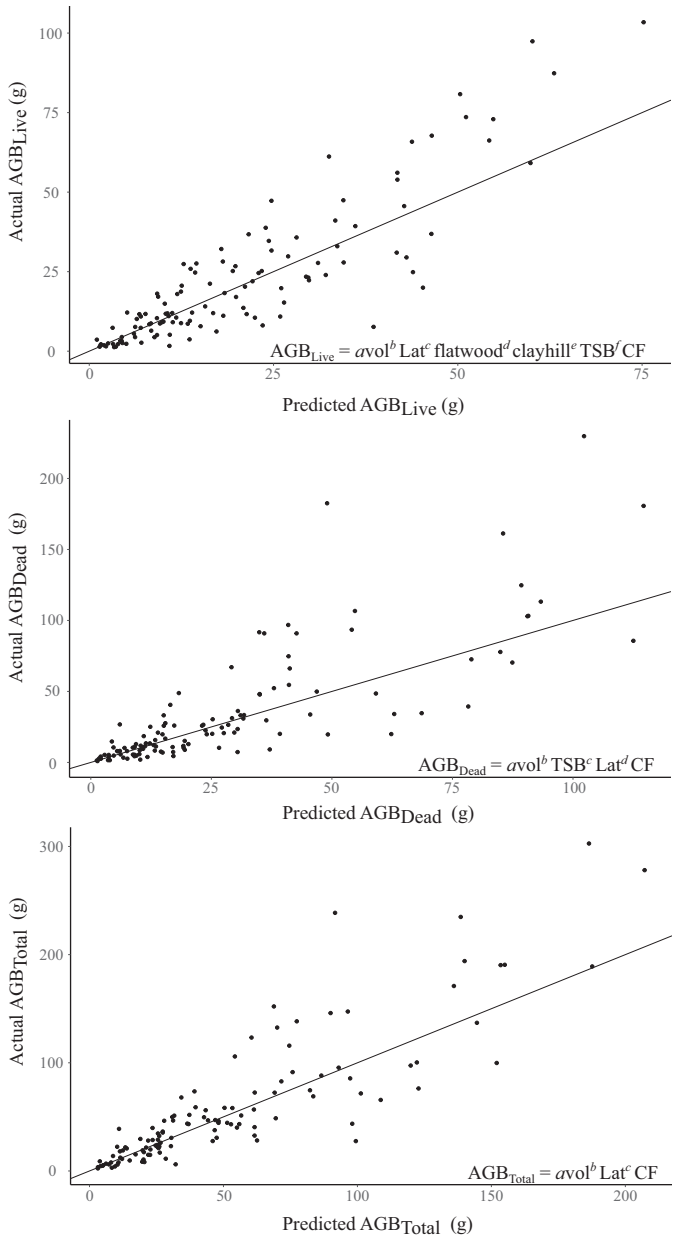

FIGURE 5. Results of the range-wide model for predicting wiregrass above ground biomass (AGB). Data were fit to 277 randomly selected tussocks using the best mixed model for live, dead, and total AGB. Stand was included as a random effect. Predictions were made using the back-transformed equation of the fixed effects on a separate data set of 119 tussocks. vol = Tussock volume; Lat = stand latitude; flatwood/clayhill = dummy variables indicating site type; TSB = time since burn (years); and CF = correction factor. Line indicates 1:1 actual to predicted.

model's rank. For instance, site type was included in the second best model for total AGB (Appendix S2). Genetic variation may also account for difference in allometric coefficients as well. For example, Kindell et al. (1996) found evidence for local adaptation in *A. stricta* sensu lato in flatwood and sandhill sites.

Time since burn was significant for both live and dead wiregrass AGB, but not for total AGB. For live AGB, the TSB coefficient was

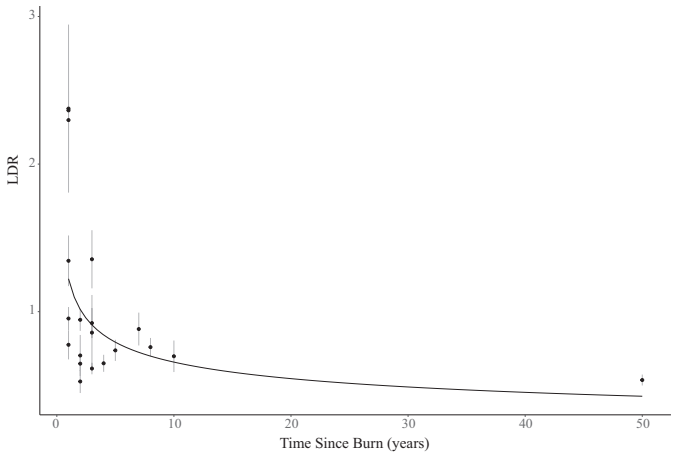

FIGURE 6. Ratio of live to dead leaves (LDR) averaged for each stand (±1 SE). Power function line was fit to the equation Ln (LDR) = Ln (TSB) where TSB is time since burn (years).

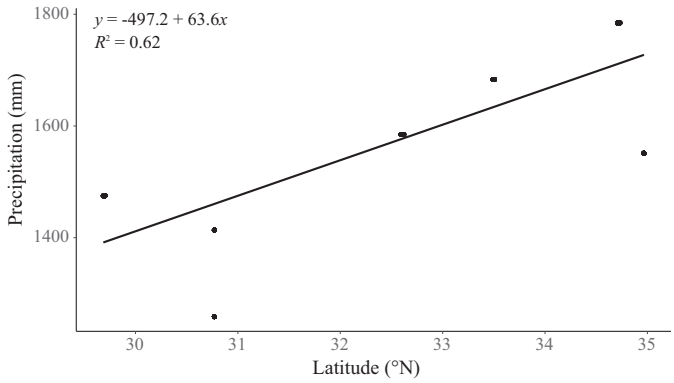

FIGURE 7. Total precipitation for the 12 months before collection of 396 wiregrass tussocks. Precipitation data were obtained from the nearest Remote Automated Weather Station (RAWS, https://raws.dri.edu/). Trendline was fit using least squares regression.

negative, indicating that wiregrass vigor decreases with TSB, a relationship that has been observed previously (K. Robertson, unpublished data). The effect of TSB on the growth of wiregrass is likely due to increased intraspecific competition over time as understory gap sizes decrease (Hovanes et al., 2018). For instance, Menges and Kimmich (1996) found that increased TSB led to increases in woody shrubs and decreases in open patches, which led to reduced survival, growth, and fecundity of *Eryngium cuneifolium* Small. in Florida scrub habitats. Another possibility is that aboveground productivity is sacrificed for belowground storage of carbohydrates reserved for resprouting following fire, as wiregrass shows considerable aboveground productivity following fires after extended periods of fire exclusion (K. Robertson, personal observation). For dead wiregrass AGB, the TSB coefficient was positive, indicating that dead AGB accumulates with TSB, similar to observations of Parrott (1967) and Clewell (1989). The reduction in live AGB and increase in dead AGB over time appear to have resulted in the nonsignificant response of total AGB to TSB.

Similar to our study, others have found that allometric coefficients change based on site characteristics. Site-specific allometric equations often perform poorly at predicting new data from a different site (e.g., Koerper and Richardson, 1980; Brix and Mitchell, 1983; Grier et al., 1984; Feller, 1992). Couso and Fernandez (2012) found that increasing drought levels of three different Patagonian grass species resulted in a decrease in tillering rate (number of tillers produced per day) and subsequent tiller density in potted plants. In wiregrass, Parrott (1967) commented that maximum leaf length and mass were dependent on environmental conditions. These environmental conditions may also dictate whether a wiregrass tussock devotes more resources to basal expansion (via expanding tillers or rhizomes) or to increased leaf or tiller density. These differences underscore the importance of using a broad range of sites to calculate a more comprehensive and less-biased allometry for range-wide models as done in this study, including inputs for latitude and specific community types.

The finding that the allometric coefficients differ from stand to stand also suggests that allometry could be sensitive over time and to changing environmental factors that influence coefficients. For example, Johnson et al. (1988) found substantial differences in the allometric coefficients in crested wheatgrass fit to individuals from three different growing seasons. This sensitivity to annual environmental fluctuations may be less apparent in the allometry of woody species because AGB is retained in the perennating structures that make up a majority of the plant volume (Johnson et al., 1988).

Although wiregrass does retain dead leaves for multiple years, our study suggests that the LDR reaches an asymptote within a few years, confirming Parrott's (1967) observations. In the first year following a fire, LDR is relatively high, with most of the marcescent, dead material burned in the fire. Parrott (1967) noted that roughly 85% of wiregrass leaves die back within the first year of growth as illustrated in the decline in LDR in plots that had more than 1 year since the last fire. Clewell (1989, p. 226) remarked that wiregrass tussocks after at least 2 years since fire "virtually 'begs' to be ignited." Fill et al. (2016) did not find a significant effect of LDR (range, 0–0.58) on the flammability of wiregrass at AGT.

Our study shows a wide range of LDR even within the first year following fire, likely due to the rather coarse scale of TSB being in calendar years from when the tussock was sampled, and possibly also due to the time of year when the tussock was burned. Wiregrass can begin regrowth aboveground within a day after a fire, so a fire early in the growing season enables time for new leaves to grow and die relative to fires late in the growing season or the dormant season. Thus, we would expect wiregrass in early growing season fires to have lower LDR the following year. The rapid accumulation of dead material with its marked reduction in moisture content (8.7% dead versus 71.4% live, T. Shearman unpublished data) likely contributes to the ability of wiregrass to burn even in humid conditions (Fill et al., 2016). Over time, this accumulation plateaus as decomposition removes dead biomass, which can be seen in wiregrass tussocks 50 years since fire having similar LDR to those sites that are only a few years since burn. Any effect of LDR on flammability would likely only be seen in the higher ranges of LDR.

Our best range-wide models were successful at predicting the summed wiregrass AGB of the test data. On the individual tussock, our models performed well also, with few exceptions. These exceptions with errors in excess of 100 g may have been due to the fact that larger tussocks tend to have increased internal leaf gaps due to dieback (Fig. 2) and therefore had higher prediction errors. Alternatively, measurement errors of the tussock basal area may result from some tussocks that are irregular in shape

and challenging the assumption of an ellipse to estimate the basal dimensions of larger tussocks. As the basal area of tussocks increases, they fragment vegetatively, forming new individuals. Clewell (1989) suggested that this fragmentation begins when the base of a tussock reaches approximately 15 cm in diameter. There might also be an age effect, but we are unable to determine the age without knowing when the seed germinated. While there remain chances for individual irregularities to induce error to stand-level estimations, sufficient sampling of individuals within a stand using these equations should yield accurate results as evident in the high accuracy of our models at predicting the summed AGB of the test data (Table 4).

We did not find evidence for differences between the two species of wiregrass, *A. stricta* and *A. beyrichiana*. Tested models with species as a predictor variable were not selected as the best model (Appendix S2). The two species ranges are separated by the "wiregrass gap", an area in northern South Carolina where wiregrass is absent (Peet et al., 1993; Weakley, 2015). Because the northern *A. stricta* and the southern *A. beyrichiana* fall on a latitudinal gradient, they are thus confounded in our analysis with latitude. The same latitudinal trend was observed in looking at just the subset of *A. beyrichiana* sites (data not shown), suggesting that any significance of species as a predictor of AGB is based solely on the fact that the two species fall on the same latitudinal gradient.

Our study provides a tool that can be used to further our understanding of how fuels influence fire behavior. The development of physics-based fire models requires accurate estimation of the fine scale heterogeneity of fuel structure and biomass loadings (Kremens et al., 2010). Our models can be used with data obtained from terrestrial laser scanners to develop three-dimensional distributions of fuels and biomass (Rowell et al., 2016). Understanding the environmental variables that influence the allometry of wiregrass would be useful to increase the precision of AGB estimates and the subsequent effects on fire behavior and effects on neighboring vegetation. Beyond wiregrass as a fuel source for fires, the equations developed here have great utility for other plant ecological studies including carbon and nutrient cycling, plant competitive or facultative interactions, herbivore forage production, and wildlife cover and habitat. Understanding the biology and morphology of wiregrass and other functionally important species will provide greater insight into how species interact in fire-prone ecosystems.

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AUTHOR CONTRIBUTIONS

T.M.S: Study concept and design, data acquisition, data analyses, manuscript drafting. J.M.V.: Study concept and design, data acquisition, manuscript drafting. K.R.: Data acquisition, manuscript drafting, J.K.H.: Data acquisition, manuscript drafting.

SUPPORTING INFORMATION

All models tested and full model selection statistics are available in Appendices S1 and S2. Raw data used in these analyses are available in Appendix S3.

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Model forms tested in allometry of wiregrass (*Aristida* spp.).

APPENDIX S2. Model comparisons. See Appendix S1 for model number form. Best models are indicated with L (live), D (dead), and T (total).

APPENDIX S3. Raw data used in the analyses described here.

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