



Shade alters the growth and architecture of tropical grasses by reducing root biomass

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Abstract

Tropical grassy biomes have variable tree cover and are often characterized by a flammable grassy ground layer where the dominating grass species have strategies to persist and proliferate with frequent fire. However, there is limited understanding of how grass growth and flammability traits respond to light availability. We experimentally grew 14 grass species characteristic of the Malagasy Central Highlands for one year with four treatments of light exclusion ranging from 0 – 60%. Eight plant functional traits and four leaf flammability traits were measured: plant height, bulk density, aboveground biomass, belowground biomass, ratio of root to shoot biomass, specific leaf area, leaf length, leaf width, leaf heat release capacity, temperature of maximum decomposition, total heat release and peak heat release rate. Belowground biomass, the ratio of root to shoot biomass, and bulk density were all negatively affected by decreasing light availability. Surprisingly, aboveground biomass showed no significant change with changing light availability, although there was a trend toward shorter plants in low light. At a leaf level, declining light availability increased specific leaf area, leaf length, and leaf width. In terms of leaf flammability, of the four traits measured, unexpectedly, only leaf total heat release was significantly positively related to declining light availability. These results suggest field alterations in grass flammability may be primarily related to plant architecture and microclimates. The shifts in allometry and substantial reduction in belowground biomass suggest that grasses would be rapidly lost from shaded environments with a diminished competitive capacity to resprout.

KEYWORDS

allometry, flammability, grassland, Madagascar, plant architecture, Poaceae, tree cover

1 | INTRODUCTION

Tropical grasslands and savannas are open ecosystems with variable tree cover and a continuous grassy ground layer (Bond, 2008; Ratnam et al., 2011). These ecosystems support frequent fire and tend to occur worldwide where feedbacks between disturbance, water availability,

soil characters, and vegetation traits promote variability in tree cover (Hoffmann, Jacons, et al., 2012). C_4 grasses dominate in these tropical open environments and where increasing tree cover reduces the abundance of C_4 grass biomass and C_4 grass diversity (Pilon et al., 2020; Scholes, 2003; Scholes & Archer, 1997). That is, in tropical grassy biomes, shade cast by trees acts as an environmental filter reducing light

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availability for C_4 grass species whose photosynthetic machinery is dependent on high light environments (Black, 1971; Hatch, 1992). A diversity of field studies observe abrupt thresholds in tree cover and tree leaf area index where grasses are excluded (Charles-Dominique et al., 2018; Hoffmann, Geiger, et al., 2012; Pilon et al., 2020; Pinheiro et al., 2016). Remarkably, there have been few tests of how changing light availability impacts grass growth, allometry, flammability, and biomass allocation, knowledge required to disentangle the mechanism for the abrupt exclusion of grasses with increasing tree cover.

Although shade can increase herbaceous biomass productivity under individual tree crowns (Belsky, 1994; Belsky et al., 1993), it can also lead to the exclusion of C_4 grass species (Parr et al., 2014). However, the tree cover thresholds at which C_4 grass exclusion occurs is both regionally variable and little investigated (Charles-Dominique et al., 2018; Pilon et al., 2020), while tree cover thresholds related to reduced fire spread has been shown to be around 40% (e.g., Staver et al., 2011). C_3 and C_4 grasses have been shown to have similar morphological responses to light availability but responses closely related to photosynthesis such as growth rate and biomass have been shown to be greater for C_4 grasses than C_3 grasses (Kephart et al., 1992; Sage & McKown, 2005). A common acclimation response to shading is the development of thinner larger leaves with no apparent differences between C_3 and C_4 grass species in response to shading (Louwerse & Zweerde, 1977; Ward & Woolhouse, 1986). Veenendaal et al. (1993) found that C_4 photosynthetic sub-types had different responses to shading where species of NADP-ME (using NADP-malic enzyme) and PCK (using PEP carboxykinase) sub-types were associated with more shaded habitats and had lower relative growth rate compared to NAD-ME (using NAD-malic enzyme) sub-types that were associated with open habitats.

Fire regimes in tropical grassy biomes can vary substantially in frequency, intensity, size, and season (Archibald et al., 2013), and this variation in fire regimes generally selects for functionally distinct traits in plants (Forrestel et al., 2014; Silva & Balatha, 2010). Changes in vegetation structure and composition can in turn alter vegetation flammability and fire regimes (Belcher et al., 2010; Brooks et al., 2004; Rossiter et al., 2003). Numerous grasses have life history strategies to persist in ecosystems with frequent fire via resprouting from protected buds and where numerous perennial C_4 grasses require removal of senesced biomass via fire to avoid the constraints of self-shading (Linder et al., 2018). Flammability traits, such as plant bulk density and leaf characteristics, influence fire behavior and vary greatly among woody species (e.g., Fonda, 2001; Pausas et al., 2012). However, flammability traits in grass species have been relatively little explored despite the recognition that flammability may both influence and be influenced by fire regime. Simpson et al. (2016) demonstrated that flammability of whole plants and leaves varied among grass species and can be predicted from plant functional traits where aboveground biomass and moisture content were key drivers of combustion and ignitability. It would be expected that grass flammability would shift with changing light availability, but the degree to which such changes are a product of changing microclimates, moisture contents, biomass, and fuel structure is unknown, and experimental data would provide new insights.

Madagascar's Central Highlands is a physiognomically heterogeneous landscape, characterised by a grassland-woodland mosaic interspersed with subhumid gallery forest (Moat & Smith, 2007) reflecting a light and tree cover gradient across vegetation types. In Madagascar, *Uapaca bojeri* (Phyllanthaceae) dominated savanna woodlands are characterized by variable tree cover ranging from 5 to 40% with the understorey dominated by C_4 grasses (Solofondranohatra et al., 2018). Here, intact gallery forests have tree cover greater than approximately 60%, with a ground layer partially composed of shade-tolerant C_3 grasses with abrupt boundaries between savanna and forest formations (Solofondranohatra et al., 2018). These open landscapes are subject to tree planting for reforestation and afforestation as part of carbon sequestration initiatives although fast-growing non-native species are largely prioritized (Malagasy Ministry of Environment and Sustainable Development). With such projects, rapid reductions in ground layer light availability across grass-dominated systems are expected with impacts on grass diversity and ecosystem function, information crucial to land management, unknown.

Here, we investigate how light availability alters grass biomass, allometry, functional traits, and leaf flammability of 14 grass species typical of Madagascar's Central Highlands. We aimed to test: (a) how does light availability affect grass species biomass, architecture, and allometry? and (b) how are leaf level flammability characters altered by light availability and, is there a relationship with specific leaf area? We predicted significant trait and leaf flammability relationships with declining light availability due to acclimation. Further we predicted that grass biomass, architecture, and allometry would both alter with light availability and covary due to the interdependent relationships among growth-related traits. Finally, specific leaf area and leaf size would increase with declining light availability to maximize light interception in shaded conditions with leaves expected to be less flammable.

2 | METHODS

2.1 | Plant material and growth conditions

The 14 grass species, representing six grass lineages were chosen as common and abundant species from open fire-maintained communities across the region (Solofondranohatra et al., 2018; Solofondranohatra, Vorontsova, Hempson, et al., 2020), comprised of four endemic and ten non-endemic species (Table S1). Fire-maintained grasslands are primarily composed of tall, caespitose species with narrow leaves and low bulk density (Solofondranohatra, Vorontsova, Hempson, et al., 2020). Grasses were established from young single tillers of existing plants and not grown from seed due to: 1) the lack of germination infrastructure such as germination cabinets and agar gel; 2) known poor germination rates of the study species and the difficulty in establishing from seed (Baskin et al., 1998); and 3) genetic consistency in plants among light treatments.

Plants were collected over the 2016/17 rainy season across the Central Highlands (i.e., the Ibity, Ambohitantely and Ankafobe

regions) with similar climates (mean annual rainfall 1000–1500 mm and a 5–7 month dry season, Rajeriarison & Faramalala, 1999) and soils (ferrallitic, on sandstone and basement gneiss, Moat & Smith, 2007). For each species, ten plants were collected along with roots and soil with plants kept in 15L pots with soils from the locality they were collected and transported to the experimental site. At the experimental site, plants were divided into individual juvenile grass tillers.

For 20 replicates of each of 14 species (total 280 pots), a single juvenile tiller was planted into a 15L pot with drainage holes and filled with the same amount of substrate (Figure S1) composed of 45% local soil, 45% sand and 10% compost. For two weeks, plants were watered regularly to facilitate establishment in sunlit conditions. For each species, replicates were then placed into three shade houses (light treatment) and grown for 12 months (March 2017 to February 2018). Each shade house was approximately 5 m × 15 m × 2 m tall. Commercially available shade cloth used in agriculture tested to exclude 20, 40, and 60% of light was used to build each shade house. Five further replicates were placed in the open, in full sunlight. Each treatment was categorized as: 0% shade/light exclusion, 20% shade/light exclusion, 40% shade/light exclusion and 60% shade/light exclusion. The four light levels were used as a proxy for light availability to mimic increasing tree cover.

Plants were watered weekly over the dry season from March to November 2017 but not watered during the rainy season. Fifty-one individuals, of which all individuals within 20% shade of *Panicum subhystris* of the 280 plants died during this period. Mortality was associated with species and treatment only for *Panicum subhystris*, the only C₃ grass in the experiment (ANOVA, $p < 0.001$). Hence, analyses were undertaken without *Panicum subhystris* from the 20% shade treatment.

2.2 | Grass functional traits related to light acquisition and flammability

After one year of growth, in March 2018, plants were destructively harvested to quantify morphology and architecture to capture functional traits as dimensions of life history strategies. We measured eight grass functional traits related to light acquisition, growth, and flammability: (a) plant height, defined as leaf table height; (b) bulk density defined as mass per unit volume; (c) aboveground biomass; (d) belowground biomass; (e) ratio of root to shoot biomass; (f) specific leaf area (SLA); (g) leaf length, and (h) leaf width. Full details on the function ascribed to each trait are presented in Table 1. Mean values of functional traits of plants from 0% shade are presented in Table S1.

2.3 | Trait collection

For each species, biomass allometry and allocation measurements required destructive harvesting. Roots were gently washed to

minimize loss of fine root biomass. Each plant was divided into belowground biomass (roots and the basal portion of the tillers from the point of root attachment to the beginning of photosynthetic tissue) and aboveground biomass (all aboveground material including senesced leaves to give an indication of total annual production). Plant material was stored in paper bags and oven dried at 70°C for 72 hours then weighed to determine dry mass with a two decimal place accuracy.

For leaf level measurements, SLA, leaf length and leaf width were measured on three young but fully expanded leaves (i.e., leaves with no evidence of senescence, Cornelissen et al., 2003). For SLA, leaves were placed in a sealed plastic bag with some moist paper to maintain turgor and in a constant environment until they were scanned. Leaves were scanned using an Epson flatbed scanner at 1200 dpi, and area measurements made using ImageJ software. All leaves were oven dried at 60°C for 72 hours and weighed to two decimal places.

2.4 | Leaf flammability

Leaf level flammability was measured on the same leaves harvested for specific leaf area. Unfortunately, it was not possible to source thermocouples to quantify plant level flammability metrics at our experiment. Hence, we report leaf level flammability metrics considered relevant to plant level flammability.

Four leaf flammability traits were measured for each sample on a g⁻¹ dry mass basis: (a) maximum temperature of decomposition, defined as the temperature at which the maximum rate of decomposition of virgin fuel is reached; (b) heat release capacity defined as the maximum capability of the material to release combustion heat per degree of temperature during pyrolysis, providing an indication of the resistance of leaves to thermal degradation (lower values indicate enhanced fire resistance); (c) total heat release which is the total energy released by the sample during combustion; and (d) peak heat release rate defined as the most intense flux of heat during the combustion of the material, indicating the maximum decomposition rate of the leaves which is related to the volatile gas flux of the material. Measurements properties, (b) to (d) describe flammability aspects of the leaf material while (a) provides a measure of how much heat must be applied to fuel before it reaches its peak burning flux. Hence, (a) is an indicator of the structural and biochemical integrity of leaf material. Therefore, variations in the maximum rate of decomposition may indicate variation in leaf biochemistry.

Leaf scale measures of flammability used a Federal Aviation Administration (USA, FAA) Microcalorimeter (Fire Testing Technology, East Grinstead, UK) that was developed to allow direct measurements of heat release rate with respect to material properties and chemical composition of materials (Simpson et al., 2016). The FAA microcalorimeter is a pyrolysis combustion flow calorimeter. It was used to reproduce the solid-state and gas phase processes of flaming combustion by heating approximately 10 mg of each sample of a grass leaf for each species in each treatment

TABLE 1 Description of eight measured plant and leaf functional traits alongside collection method and related function

Traits	Collection method	Related function
Leaf table height (H_{LT} , cm)	The height visually estimated to correspond to the ca 80th quantile of leaf biomass was measured on three individuals per species.	Plant height is a key functional trait with important role for light acquisition and vegetation flammability (Olff & Ritchie, 1998; Westoby, 1998). Some tall grasses are strong light competitors and very flammable (Simpson et al., 2016; Linder et al., 2018).
Bulk density (BD, g/cm ³)	Bulk density is the ratio between plant biomass and volume. It is calculated by dividing the total aboveground biomass by an estimate of the grass canopy volume. Volume was calculated using measures of the tuft basal diameter (D_B), leaf table height (H_{LT}) and leaf table diameter (D_{LT} , diameter at H_{LT}). It is calculated using the formula for a truncated cone: $V = \pi / 3 * H_{LT} * ((D_B / 2)^2 + (D_{LT} / 2)^2 + D_B * D_{LT})$.	Bulk density, the ratio between plant biomass and the volume it occupies, reflects its architecture. Low bulk density means the plant is assembled sparsely, allowing oxygen to circulate and making it more flammable compared with high bulk density plant (Hempson et al., 2019).
Aboveground biomass (g)	Aboveground biomass is determined by clipping, drying (at 70°C for 72 h) and weighing the parts of the individual for which the volume estimate was made.	Aboveground biomass is a key driver of plant flammability (Simpson et al., 2016). High aboveground biomass means high quantity of photosynthetic material, which facilitates light interception.
Belowground biomass (g)	Belowground biomass is determined by clipping roots and the basal portion of the tillers from the point of root attachment to the beginning of photosynthetic tissue, drying (at 70°C for 72 h) and weighing until constant weight.	Belowground biomass allow grass to resprout and regrow after defoliation by fire and grazing, with low root biomass affecting persistence in a repeatedly disturbed environment (Qian et al., 2017; Ripley et al., 2010, 2015).
Root to shoot biomass ratio	The ratio is determined by dividing the total belowground biomass with the total aboveground biomass.	The ratio of root to shoot biomass is related to plant persistence within the environment. A high ratio indicates that plant allocate more belowground biomass which allow them to persist after disturbances like fire. It is also linked to light availability with low ratio allowing plants to maximize light capture by investing more in the aboveground part (Allard et al., 1991; Cruz, 1997; Dias-Filho, 2000).
Specific leaf area (m ² /kg)	Specific leaf area was measured on three fully expanded leaves. It is calculated by dividing the area of the leaf with its dry weight. Area was calculated on scanned leaves using ImageJ software.	High-specific leaf area, that is, a greater surface area per gram leaf (thin leaf) has been shown to allow species to optimize light interception in shady conditions (Milla & Reich, 2007). This study also showed that large leaves are associated with low specific leaf area. Small leaves (high specific leaf area) arranged in an aerated canopy ignite easily and burn intensely, that is, more flammable (Schwilk, 2015).
Leaf size: Leaf length (cm) Leaf width (cm)	Leaf length and leaf width was measured on three fully expanded leaves with digital calliper.	Leaf size is related to light acquisition. Big leaves allow an optimization of light interception in shady conditions (Milla & Reich, 2007). Small-leaved woody species have been shown to be associated with more light in the understorey (Bragg & Westoby, 2002).

in a nitrogen stream whereupon the volatile gases that are driven off and oxidized at high temperature in excess oxygen. The micro-calorimeter then measures the rate of heat release based on the oxygen consumption history of the fuel. The samples were exposed to a heating program that ramped up to 750°C at a rate of 3°C per second.

2.5 | Analyses

All statistical analyses were performed in the R environment (R Core Team, 2013). Where necessary, data were log-transformed to improve normality and meet model assumptions.

To determine how species respond to changing light availability as a categorical variable, linear mixed-effects models were fitted with plant and flammability traits as response variables with species as a random effect. Models were fitted using the “lmer” version 1.1–21 R package (Bates et al., 2014). Coefficients of the random effects were plotted to assess the variance among each species (Figure S2).

The effect of species was assessed with analysis of variance (ANOVA) using the “stats” version 4.1.0 package. An ANOVA was also used to determine associations between plant and leaf flammability traits related to species endemism. All model formulations are presented in the Supporting Information Table S2. In addition, differences in means of functional traits among shade levels were assessed using one-way ANOVA.

To determine covariance among key plant traits, bivariate lines in allometry were fitted using standardized major axis (SMA) with the package “smatr” version 3.4–8 package (Warton et al., 2012) to establish relationships between belowground biomass and aboveground biomass and volume and aboveground biomass among shade treatments. SMA regression accounts for uncertainty where independence/dependence is unclear by minimizing errors in both directions and testing for variation in slope and intercept among experimental treatments. Relationships among leaf flammability traits (heat release capacity, temperature of maximum decomposition, total heat release and peak heat release rate), specific leaf area and leaf size were also established using linear regression. Pearson correlation coefficients were estimated to characterize all relationships between each pair of functional traits. Belowground biomass, aboveground biomass and volume were all log-transformed prior analysis to improve normality.

3 | RESULTS

3.1 | Variation of plant functional traits across shade treatments

Light availability was positively related with bulk density, belowground biomass and root to shoot ratio, such that values of these traits were reduced under increasing shading (ANOVA, $p = 0.02$; $p < 0.001$; $p < 0.001$, respectively). However, there was no relationship with plant height or aboveground biomass (ANOVA, $p = 0.32$; $p = 0.08$). Comparisons among treatments found little effect of light availability on leaf table height (Figure 1).

Bulk density of plants in the 20% and 40% treatments was similar to the 0% treatment. However, bulk density in the 60% treatment was significantly lower in comparison with other treatments (Figure 1, Table S1). Comparing bulk density between the 0% and 60% treatments demonstrated an average 30.3% ($\pm 5.90\%$) decrease in bulk density. On average, aboveground biomass in the 20%, 40%, and 60% treatments were similar relative to the 0% treatment. However, comparison of the 20% and 40% treatments with the 60% treatment found aboveground biomass decreased with decreasing light availability (Figure 1, Table S1). Large decreases in belowground biomass was found with declining light availability. While in the 0% and 20% treatments belowground biomass was similar, belowground biomass in the 40% and 60% treatments was significantly lower (Figure 1, Table S1). On average, and relative to the 0% treatment, belowground biomass of plants in the 40% and 60% treatments decreased by 39.7% ($\pm 7.17\%$) and 68.5% ($\pm 3.80\%$), respectively. The ratio of root to shoot biomass significantly decreased with declining light availability (Figure 1). Relative to the 0% treatment, root to shoot biomass ratio on average declined by 32.7% ($\pm 11.22\%$), 47.3% ($\pm 6.32\%$) and 64.7% ($\pm 5.19\%$) across the 20%, 40%, and 60% treatments, respectively. There was no significant difference in any of the measured plant traits between endemic ($n = 4$) and non-endemic ($n = 10$) species (ANOVA, all $p > 0.05$).

3.2 | Variation of leaf flammability and leaf traits across shade treatments

Among the four leaf flammability traits, declining light availability only had a significant effect on leaf total heat release (ANOVA, $p < 0.001$; Figure 2). Among flammability traits and relative to the 0% and 60% treatments, there was an average increase of 4.9% (SD $\pm 2.79\%$), 2.74% ($\pm 0.91\%$), 3.22% ($\pm 1.28\%$) and 5.68% ($\pm 3.03\%$) of heat release capacity, temperature of maximum decomposition, total heat release and peak heat release rate, respectively.

Specific leaf area, leaf length and leaf width were significantly affected by shade treatment (ANOVA, $p = 0.03$; $p < 0.001$; $p < 0.001$, respectively). Relative to the 0% treatment, SLA slightly decreased by 7.4% ($\pm 7.87\%$) in the 20% treatment although with high variability. However, in the 40% and 60% treatments SLA increased by 33.2% ($\pm 12.37\%$) and 76.5% ($\pm 21.89\%$), respectively. With leaf length and relative to the 0% treatment, in the 20% treatment, leaf length decreased by 2.41% ($\pm 1.51\%$) and then increased on average by 18.07% ($\pm 17.21\%$) and by 62.24% ($\pm 22.12\%$) in the 40% and 60% treatments, respectively. Relative to the 0% treatment, leaf width increased on average by 14% ($\pm 13.33\%$), 24% ($\pm 3.33\%$) and 16% ($\pm 42.6\%$) across the 20%, 40% and 60% treatments, respectively. Among the leaf flammability traits, no significant relationships were found with specific leaf area between endemic and non-endemic species (ANOVA, all $p > 0.05$). Although with respect to leaf shape, non-endemic species had significantly longer wider leaves compared with endemic species (ANOVA, $p < 0.001$).

3.3 | Variation among species in plant traits, leaf traits and leaf flammability

Random effects of species coefficients showed that all plant traits varied among species across all treatments (ANOVA, $p < 0.001$ for all traits) except for root to shoot biomass ratio (ANOVA, $p = 0.75$; Figure S2). The height of widespread species such as *Hyparrhenia rufa*, *Panicum maximum*, *Melinis repens* and *Sporobolus pyramidalis* had positive responses to shade with the two former species significantly so (ANOVA, $p = 0.005$ and 0.009 , respectively). Increasing shade had a significant positive effect on the aboveground biomass of both *Hyparrhenia rufa* and *Sporobolus pyramidalis* (ANOVA, $p = 0.007$ and 0.02 , respectively). Although no significant variation was found among the root to shoot ratios of the study species in response to shade, the four widespread species were the most affected with the lowest values of coefficients (Figure S2). Specific leaf area of *Panicum maximum* and *Melinis repens* responded positively to shade. Shade had a significant positive effect on the leaf length of all species except *Melinis repens*, *Aristida tenuissima* and *Panicum subhystris*. Leaf width of *Panicum maximum* and *Hyparrhenia rufa* significantly increased with shade (Figure S2). For some species such as *Loudetia simplex* and *Andropogon trichosyzygus*, none of the measured traits showed a significant response to shade.

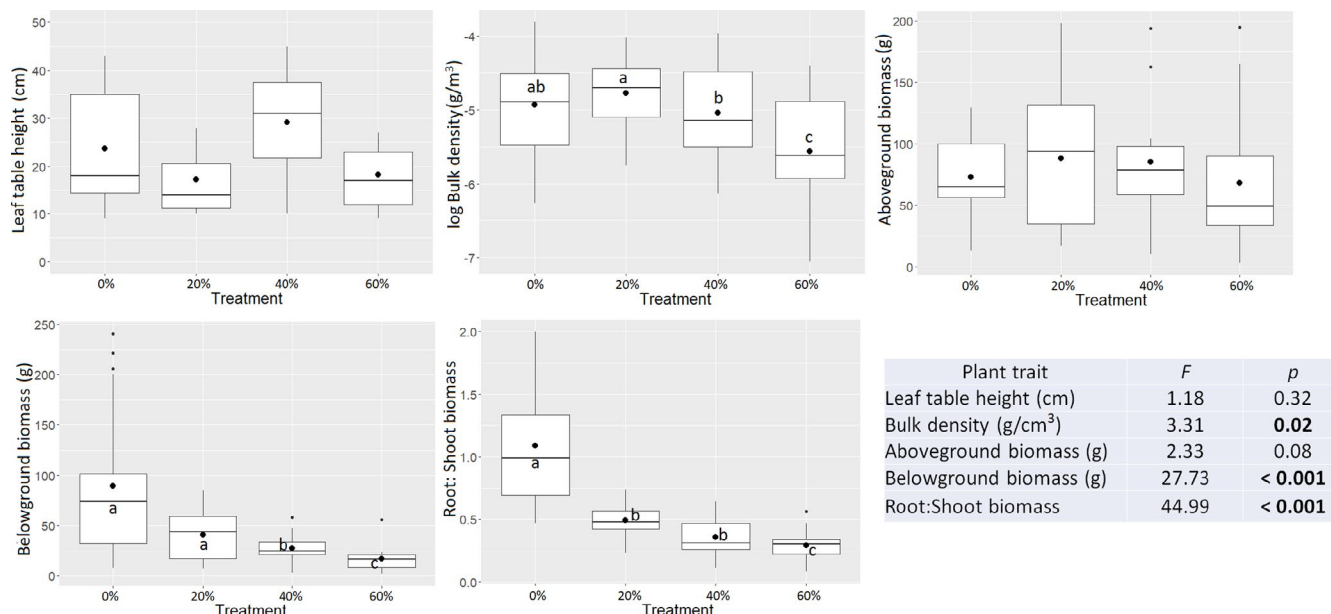


FIGURE 1 Plant traits of the 14 grass species compared between treatments. Letters indicate significance of difference of traits means between treatments with same letters indicating no significant difference and different letters indicating significant differences at $p = 0.05$. Black dots inside the boxplots indicate the means of each trait per treatment. The influence of treatment on plant traits is given on the table as indicated by F and p values obtained from ANOVA on the fitted linear mixed-effects models, using species as random effect. p values in bold are significant at $p = 0.05$

All measured leaf flammability traits varied significantly among all species across all treatments (ANOVA, $p < 0.001$). Increasing shade had a significant positive effect on *Sporobolus centrifugus* heat release capacity; negative effect on *Pennisetum pseudotritichoides*, *Sporobolus pyramidalis*, *Panicum maximum*, *Ctenium concinnum*, *Trachypogon spicatus* and *Schizachyrium sanguineum* temperature of maximum decomposition. Increasing shade positively affected *Panicum subhystris* (the only C_3 species in our dataset) total heat release capacity but negatively affected *Pennisetum pseudotritichoides*, *Hyparrhenia rufa* and *Panicum maximum*. *Sporobolus centrifugus* and *S. pyramidalis* peak heat release rate was positively affected by shade (Figure S2).

3.4 | Covariation of traits

Belowground biomass and plant volume both increased with increasing aboveground biomass (Figure 3). Pearson's correlation coefficients for 0%, 20%, 40%, and 60% treatments are equal to 0.75; 0.72; 0.57, and 0.70, respectively, between belowground and aboveground biomass and all these positive relationships are significant (ANOVA, $p < 0.001$ for all treatments). While the relationships are similar, on average plants in the 40% and 60% treatments were shorter than in the 0% and 20% treatments. Tests for common slopes and intercept differences showed heterogeneous slopes and differences in intercepts across treatments ($p = 0.04$ and < 0.001 , respectively).

Between plant volume and aboveground biomass, Pearson's correlation coefficients for 0%, 20%, 40%, and 60% treatments are equal to 0.30, 0.22, 0.26, and 0.33, respectively, and these positive relationships are all significant (ANOVA, $p < 0.001$ for all treatments except for 40% (ANOVA, $p = 0.004$)). Tests for common slopes and

intercept differences showed heterogeneous slopes and differences in intercepts across treatments ($p = 0.002$ for both coefficients). The relationships between leaf flammability traits and SLA across treatments showed a significant negative effect of SLA on the heat release capacity of leaves in 0% and 40% treatments (ANOVA, $p = 0.01$ and 0.03, respectively; Figure S3), where high SLA is associated to enhanced fire resistance. This negative effect was also apparent regarding peak heat release rate of plants in 0% and 40% treatments (ANOVA, $p = 0.009$ and 0.02, respectively; Figure S3). Leaf length was significantly negatively related with total heat release across all treatments (ANOVA, $p = 0.01$; 0.001; 0.03 and 0.01 from the 0% to 60% treatments, respectively; Figure S4). Long leaves were also associated with a low temperature of maximum decomposition in the 20% and 40% treatments (ANOVA, $p = 0.02$ and 0.03, respectively; Figure S4) where longer leaves thermally decompose faster. Relationships between leaf width and leaf flammability traits among treatments showed a significant negative effect of leaf width on the heat release capacity of leaves in 0% and 40% treatments (ANOVA, $p = 0.03$ for both); on the peak heat release rate of leaves in the 0% treatment (ANOVA, $p = 0.03$) and on the total heat release rate of leaves in 0% and 20% treatments (ANOVA, $p = 0.002$ and 0.03, respectively; Figure S4). Wide leaves are associated with low maximum fire intensities.

4 | DISCUSSION

Grass morphology, allometry and architecture are substantially altered by changing light availability (Figure 1), where declining light availability generates steep declines in both belowground biomass and the

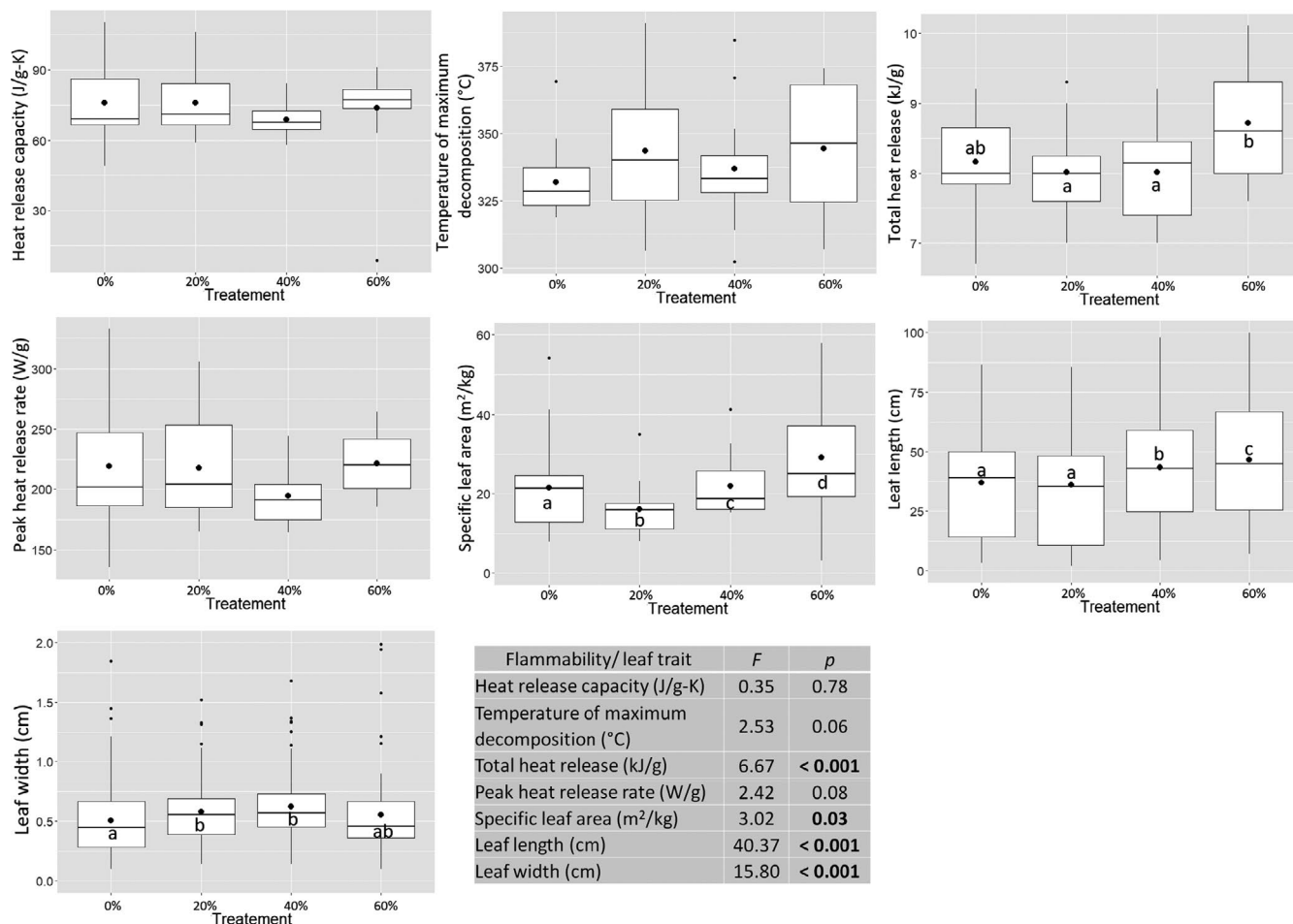


FIGURE 2 Leaf flammability traits and leaf traits of 14 grass species compared among treatments. Letters indicate significance of difference of traits means between treatment with same letters indicating no significant difference and different letters indicating significant differences at $p = 0.05$. Black dots inside the boxplots indicate the means of each trait per treatment. The influence of treatments on flammability traits and specific leaf area is given on the table as indicated by F and p values obtained from ANOVA on the fitted linear mixed-effects models, using species as random effect. p values in bold are significant at $p = 0.05$

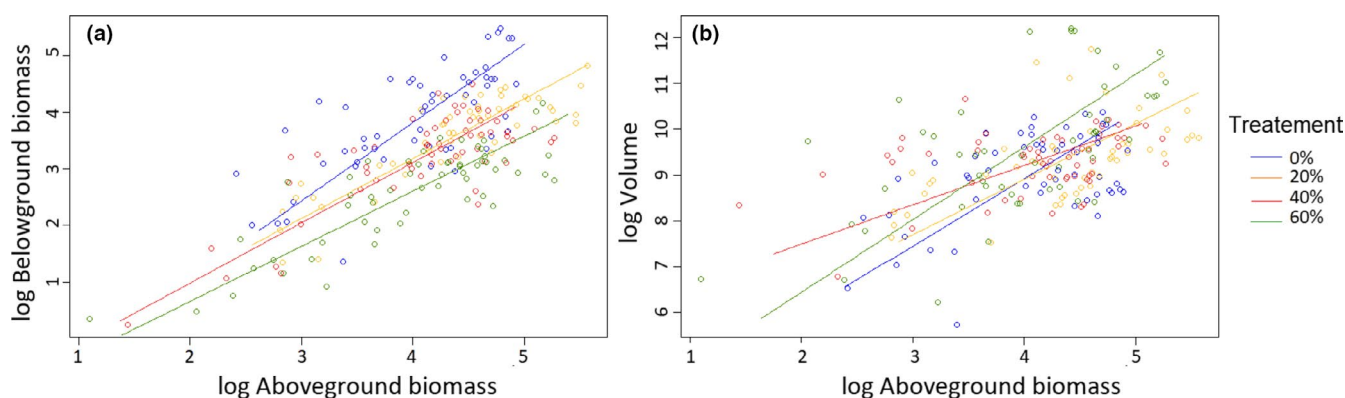


FIGURE 3 Relationships between (a) belowground biomass and aboveground biomass (values presented are log of biomass values in g), (b) plant volume (log of plant volume in g per cm³) and aboveground biomass across (log of biomass in g) 14 grass species for all treatments. Data points are shown as colored points with different colors per treatment. Lines indicate the standardized major axis (SMA) slope for each treatment. Tests for common slopes and intercepts differences: (a) Slopes heterogeneous, $p = 0.04$; differences in intercepts, $p < 0.001$, (b) slopes heterogeneous, $p = 0.002$; differences in intercepts, $p = 0.002$. p value and Pearson's correlation obtained from regressions are as follows: (a) $p < 0.001$ for all treatments; $r = 0.75$; 0.72 ; 0.57 and 0.70 , respectively, from 0% to 60% treatment, (b) $p < 0.001$ for all treatments except for 40% with $p = 0.004$; $r = 0.30$, 0.22 , 0.26 and 0.3 , respectively, from 0% to 60% treatment

ratio of root to shoot biomass (Figure 1). In contrast, and as expected, mean specific leaf area and leaf size increased substantially with declining light availability, suggesting an increase in photosynthetic leaf surface area of individual plants, supporting previous findings around acclimation to changing light environments (Dias-Filho, 2000; Evans & Hughes, 1961; Loach, 1970). Finally, contrary to expectations, changing light availability had a limited impact on leaf level flammability with respect to specific leaf area but there were large changes in plant bulk density that can alter the flammability of a fuel bed.

Plants adjust morphological and physiological characteristics in response to changing light environments (Allard et al., 1991; Dias-Filho, 2000; Evans & Hughes, 1961; Kephart et al., 1992; Loach, 1970; Pearcy, 1999). Hence, while it was no surprise shading significantly reduced belowground biomass, shaded plants allocated a significantly larger proportion of their total biomass to shoots than did plants grown in full sunlight to increase light harvesting capacity (Figures 1 and 3) as opposed to plants simply being smaller when grown at a lower light availability. As a first response to any decline in carbon assimilation, it has been shown that plants reduce the growth of root systems (Caldwell et al., 1981). While there was no significant change in aboveground plant size with reduced light, there was a trend to smaller plants at 40% and 60% shade compared with 0% and 20% shading (Figure 3). Kephart et al. (1992) reported adaptive responses of grasses to irradiance regime grown under 37%, 70% and 100% light availability with grasses shifting biomass allocation, favoring aboveground structures in detriment of roots to increase light harvesting capacity. By comparing the growth and biomass allocation of two species of *Brachiaria* in full sunlight and shaded to 30% light availability, Dias-Filho (2000) showed that plants had higher specific leaf area and allocated significantly less biomass to root and more to leaf tissue than high-light plants. While C_4 grass species can persist in low light levels utilizing carbon resources stored in underground structures (Pinheiro et al., 2016; Taylor et al., 2010; Zimmermann et al., 2010), it is only possible for a limited time before the plant must enter a carbon deficit (de Moraes et al., 2016; Pilon et al., 2020; Pinheiro et al., 2016). Crucially, reduced belowground allocation could result in reduced competitive ability and resprouting capacity relative to both fire and grazing that in turn would increase the likelihood of a species being filtered out of an ecosystem. Indeed, such substantial diminishment of belowground reserves observed here may explain the abrupt exclusion of grasses from the ground layer with increasing tree cover observed in field studies (Charles-Dominique et al., 2018; Hoffmann, Geiger, et al., 2012; Pilon et al., 2020; Pinheiro et al., 2016).

Grass flammability is altered by biomass quantity, bulk density, and leaf traits (Simpson et al., 2016). Grasses with very low bulk densities, that is, sparse architectures, associated with low aboveground biomass are poor fuel for fires as there is little material to combust and sustain fire (Simpson et al., 2016). Increasing bulk density increases fuel connectivity that enhances combustibility and fire spread rate, but this only applies up to a threshold beyond which poor ventilation will limit drying and combustion (Rothermel, 1972). Here, while in general decreasing light availability appeared

not to correlate with aboveground biomass or leaf level flammability, shade did decrease plant bulk density, particularly in 60% shade. We found that changes in bulk density were determined by increasing plant volume (Figure 3). Hence, while we found that specific leaf area was not associated with changes in leaf level flammability, it is likely to ultimately influence plant level flammability via reduced structural support. However, it is important to note that the relationship of plant flammability with bulk density is not linear and to date plant flammability experiments have offered limited insight into vegetation-fire dynamics interactions (Fernandes & Cruz, 2012).

In our experiment, leaf level flammability traits did not significantly shift with decreasing light availability to make an appreciable difference. While we did not measure leaf moisture contents, it is important to mention it as a key trait determining grass flammability (Simpson et al., 2016). Leaf water content is an important correlate of leaf flammability and plant species with high moisture content might be less flammable as they take longer to ignite (Gill & Moore, 1996; Schwilk & Caprio, 2011). The increase in leaf total heat release at the highest level of shade compared with the intermediate levels may be related chemical traits such as phosphorus content or terpenes that have been shown important to leaf flammability (Grootemaat et al., 2015; Ormenó et al., 2009; Scarff et al., 2012), although this is unknown in grasses and requires investigation. The strong positive response of leaf total heat release of *Panicum subhystris*, the only C_3 grass examined might be explained by biochemical differences between C_3 and C_4 plants (McNaughton et al., 1982; Wilsey et al., 1997) that may have been altered by shade, resulting in a higher energy released during combustion.

Acclimation capacity is likely key in determining grass competitive potential in different light environments and is likely important in explaining species distributions (Pierson et al., 1990). In our experiment, grass species varied significantly in response to shade and with widely distributed grasses being more flexible compared to the others. For example, *Hyparrhenia rufa*, *Panicum maximum*, *Melinis repens* and *Sporobolus pyramidalis*, all common species across the tropics had wide variation in morphology relative to light availability. Studies have shown that widely distributed grasses commonly have ecotypic variation to locally adapt to specific environment (e.g., Gray et al., 2014; Lowry et al., 2014; Theunissen, 1992). A common garden experiment growing grasses collected from varied fire frequencies found variation in leaf and plant functional traits unrelated to genetic differentiation, suggesting phenotypic plasticity as the mechanism behind these trait changes (Simpson et al., 2019). Further, plants grown at the lowest light had higher intraspecific variation in all functional traits except belowground biomass and root to shoot ratio. If in future experiments, grasses were to be collected from populations with differing levels of light availability, we may well observe different growth responses.

The substantial changes in belowground biomass and bulk density of grasses in our experiment suggests that in low light environments

grasses will be rapidly excluded from the environment because of a reduction in post-fire competitiveness. Previous studies have shown that increased tree cover in similar ecosystems results in a loss of biodiversity (Abreu et al., 2017). Future work examining grass resprouting resilience relative to light availability in concert with assessments of biodiversity will be crucial to understanding how tree cover change will impact ecosystem dynamics.

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AUTHOR CONTRIBUTIONS

CS, MV, and CL designed the research and methodology; CS collected data; RD and CB ran leaf flammability analyses, CS analyzed data; CS, MV, and CL wrote the paper. RD, CB, SC, and VJ contributed to the interpretation and the revision of the work.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.2jm63xsm6> (Solofondranohatra, Vorontsova, Dewhurst, et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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