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Burn hot or tolerate trees: flammability decreases with shade tolerance in grasses

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In ecosystems where trees and grasses coexist, some grass species are found only in open habitats and others persist under trees. The persistence of shade intolerant grasses in ecosystems such as open woodlands and savannas depends on recurrent fires to open the tree canopy. Therefore, grasses that depend on open sites might benefit from high flammability. We tested if shade intolerant grasses are more flammable than shade tolerant grasses and if flammability differences affected post-fire grass growth. We examined the relationship between shade tolerance and flammability by determining individual-level flammability and species shade tolerance of 17 grass species. We also measured grass traits to determine trait effects on flammability and the post-fire response. Grass species varied in flammability, mainly in the amount of heat produced during burning. Shade tolerant species produced less heat at 50 cm above the ground. Biomass and live fuel moisture had the greatest effects on heat release. However, the negative effect of live fuel moisture on heat release at the soil surface was weakened in plants with high specific leaf area. In addition, grass bulk density negatively influenced heat release at 50 cm height. Heat release at the soil surface negatively influenced post-fire growth. However, the influences of soil heating and species-specific traits on individual survival were more complex with 2- and 3-way interactions. Shade tolerance was negatively correlated with a major axis of flammability variation: shade tolerant grasses produced less heat where that heat could damage tree boles. Such heterogeneity in grass flammability may help maintain the tree–grass mixture in natural plant communities. If shade tolerant grasses near trees cause less fire damage to woody plants, especially tree saplings, this may weaken positive grass-fire feedbacks and thus aid the long-term coexistence of trees and grasses.

Keywords: ecological strategy, fire, flammability, grass, post-fire response, shade tolerance

Introduction

The persistence of shade intolerant grasses in ecosystems where woody plants can establish depends on recurrent disturbances to reduce light competition. In regions where closed-canopy ecosystems can establish, disturbances such as fires and herbivory limit

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tree density (Peterson and Reich 2001, Carla Staver et al. 2009, Van Auken 2009, Nano and Clarke 2010, Prior et al. 2010). Grass-fueled fires are fast-moving fires with short residence times and fire return intervals (Miranda et al. 1993, Jensen et al. 2001). Such fires can damage or kill tree saplings, yet spare many grasses that have meristems well protected from heat by leaf sheaths or soil. Fires remove aboveground biomass, open the canopy and provide a pulse of nutrients to favor post-fire recovery in grasses (Romanyà et al. 2001). In fueling frequent and fast-moving fires, grasses thus may act as niche constructing organisms creating favorable environments for their own growth and for their propagules (Schwilk and Kerr 2002, Schwilk 2003, Bowman et al. 2014). Grass species differ, however, both in their tolerance of shading by trees and in their resilience to fire (Weltzin and Coughenour 1990, Naumburg et al. 2001, Ripley et al. 2015, Moore et al. 2019). This suggests the hypothesis that shade tolerance and fire response are correlated with one another and part of an overall ecological strategy: shade intolerant grasses might be more fire resilient given the benefit (e.g. increased light) they gain from recurrent disturbances. However, this conjecture has never been investigated.

Ecosystems where tree cover varies abruptly in space create light environments that can support multiple grass shade tolerance strategies. For example, in savannas and open woodlands, light intensity under tree canopies can be 50% of that in open areas (Belsky 1994, Breshears et al. 1997, Ludwig et al. 2001, Valladares and Guzmán 2006). Grass species composition varies between these light environments with some species preferring under canopy habitats while others dominate in open areas (Whittaker et al. 1979, Weltzin and Coughenour 1990). These contrasting preferences in microhabitat associated with tree cover might result from variation in tolerance of shade (Cardoso et al. 2018, Charles-Dominique et al. 2018, Pilon et al. 2020) or from other microhabitat effects of tree cover (e.g. nurse plant effects, Belsky 1994, Ludwig et al. 2001).

Although shade tolerant grasses can occur under trees, the persistence of grasses preferring open habitats is dependent on recurrent fires or disturbance by animals to reduce canopy cover where climate and soil environment do not limit tree cover (Scholes and Archer 1997, Peterson et al. 2007, Charles-Dominique et al. 2018). Shade intolerant grasses might benefit from higher flammability if such traits foster recurrent fires and reduce competition for light (Cardoso et al. 2018, Charles-Dominique et al. 2018). Recently, species specific variation in flammability has been shown for grasses (Fill et al. 2016, Simpson et al. 2016, Cardoso et al. 2018, Gao and Schwilk 2018, Padullés Cubino et al. 2018). If grass species differ in their flammability as well as in their fire response, then fire, as a selective process, might act jointly on flammability and on shade tolerance traits. We aimed to determine if flammability and shade tolerance are inversely related in grasses (Fig. 1).

Flammability is multidimensional and variation along flammability axes can indicate different plant strategies in a fire-prone ecosystem (Pausas et al. 2017). Fire has long been an evolutionary agent and plants have evolved different flammability strategies to cope with specific fire regimes (Schwilk and Ackerly 2001, Pausas and Keeley 2009, He et al. 2012). Current empirical evidence suggests that there are two main axes of variation in flammability: heat release and rate of heat release (de Magalhães and Schwilk 2012, Engber and Varner 2012, Cornwell et al. 2015, Alam et al. 2020). However, with generally fast rates of spread and short combustion duration, grass fuels mainly vary in their total heat release (Gao and Schwilk 2018, Padullés Cubino et al. 2018). This specific combination of fire characteristics may depict a 'kill thy neighbor'

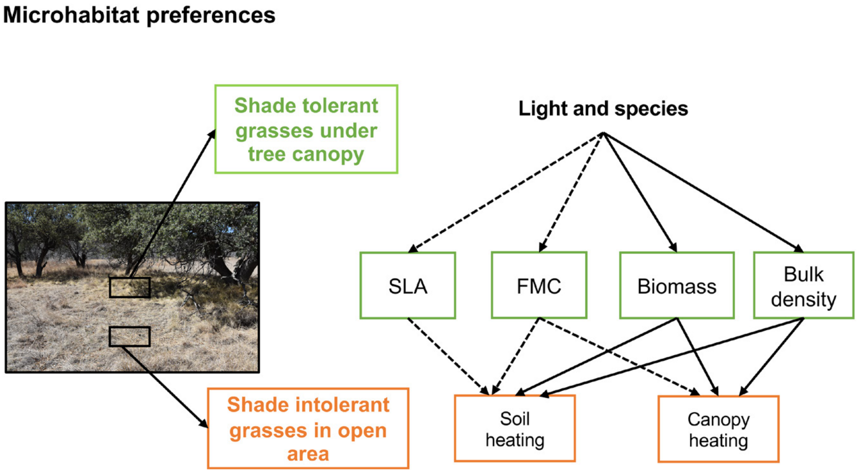

Figure 1. Conceptual diagram relating microhabitat preference, ecological strategy and flammability in grasses. Photo on the left side of the diagram was taken at the Nature Conservancy Davis Mountain Preserve, Texas, USA in an open oak woodland/savanna. Grass species underneath the canopy of *Quercus grisea* is *Piptochaetium fimbriatum*. In the open area, the predominant species include *Eragrostis* spp., *Bouteloua* spp. and *Aristida* spp. Solid lines and dashed lines on the right side of the diagram indicate hypothesized positive and negative effects respectively. Notice that we only hypothesized light effects on plant traits specifically. Changes in species composition in different light environments will also influence flammability via species-specific traits, which is difficult to predict.

strategy (Bond and Midgley 1995): a grass species with high heat release, especially if such heat can damage tree boles or canopies, can be detrimental to coexisting woody plants. If such heat release is away from the soil, it will have little effect on grass surface or belowground meristems (D'Antonio and Vitousek 1992, Gagnon et al. 2010, Bowman et al. 2014).

Plant ecological strategies involve combinations of traits. Associations between different strategies can arise from traits that have multiple effects: for example, shade tolerance traits might have direct effects on flammability. Shade response traits that might alter fire behavior include canopy architecture and leaf morphology. To efficiently capture light in shady environments, plants tend to develop fewer branches to reduce self-shading (Niinemets 2010). The resulting less densely packed biomass in turn can negatively influence heat release (Fill et al. 2016, Gao and Schwilk 2018). Moreover, leaves under low light are often thinner and broader with a high specific leaf area (Poorter et al. 2019, Solofondranohatra et al. 2021), which can positively influence the rate of spread (de Magalhães and Schwilk 2012, Engber and Varner 2012). In addition to the direct trait effects on flammability, reduced solar radiation in shady habitats creates wetter environments where fuel moisture is higher and that reduces flammability (Cardoso et al. 2018, Kreye et al. 2020). Furthermore, plant phenology such as the seasonal changes in dead to live biomass ratio during fire seasons can vary dramatically across species (Pearcy and Ehleringer 1984, Charles-Dominique et al. 2018, Pilon et al. 2020), which in turn affects fire behavior (Dimitrakopoulos and Bemmerzouk 2003, Pellizzaro et al. 2007a, Padullés Cubino et al. 2018, Emery et al. 2020).

Our novel contribution with this work was to test if shade tolerance strategy is correlated with flammability across 17 grass species. We also examined how fire behavior, species shade tolerance and pre-fire tiller number influence post-fire survival and resprouting vigor; and how biomass, fuel moisture content, canopy architecture and leaf morphology influence flammability. We expected that species growing well in open habitats but not under shade will be more flammable and more resilient to fire. In contrast, species that still maintain growth under shade will be less flammable and decline in abundance after fire because of competition by other species and the high energy demanded by resprouting. Post-fire survival and resprouting can also be influenced by fire behavior and other species-specific traits. Although surface and belowground meristems are often protected by leaf sheaths or soil, prolonged soil heating can kill buds (Choczynska and Johnson 2009, Gonzalez et al. 2015). Moreover, pre-fire tillers can positively influence post-fire survival (Moore et al. 2019). Although there is no flammability difference between C_4 and C_3 grasses (Simpson et al. 2016), C_4 grasses are more fire resilient than C_3 grasses due to a higher below ground carbon storage in high light environments (Ripley et al. 2010, Moore et al. 2019, Pausas and Paula 2020).

In light of these expectations, we predicted that: 1) shade intolerant grasses produce more heat than shade tolerant grasses; 2) increased soil heating reduces grass survival and aboveground biomass recovery; 3) grasses with lower shade tolerance, C_4 photosynthesis or more pre-fire tillers have higher survival and recovery in aboveground biomass after fire than grasses with greater shade tolerance, C_3 photosynthesis or fewer pre-fire tillers; and 4) in addition to positive biomass and negative fuel moisture effects on flammability, biomass density and specific leaf area increase flammability.

Material and methods

Our study included three stages. In the first stage, we grew 17 grasses species under two light environments (50% and 0% shade) in the greenhouse to characterize shade tolerance by species. During this stage, we also measured leaf and canopy traits to determine traits effects on flammability and post-fire responses. In the second stage, we burned plants to assess flammability. In the third stage, we returned burned plants to the greenhouse all under high light conditions (to mimic a high light post-fire light environment) to evaluate post fire survival and aboveground biomass recovery. Therefore, our shade tolerance trait is measured at a species level, but morphological traits, flammability and post fire response are measured at the individual level. Some traits required destructive harvests which necessitated some pairing of individuals as explained below.

Study species

We selected 17 grass species from 16 genera and 9 tribes for our study (Table 1). Species were chosen according to three criteria: 1) all were perennial grasses that are common in grassy ecosystems including semi-arid grasslands, juniper-mixed grasslands, pinyon–juniper open woodlands and mesic woodlands in the southwestern United States (Supporting information); 2) we aimed for equal representation of potential shade

Table 1. Grass species included in this study. Scientific names follow United States Department of Agriculture Plants Database (<https://plants.usda.gov/java/>). Information for species tribe and photosynthetic pathway was obtained from Waller and Lewis (1979) and Soreng et al. (2015).

Scientific name	Tribe	Photosynthetic pathway
Agrostis scabra	Poeae	C_3
Andropogon ternarius	Andropogoneae	C_4
Aristida purpurea	Aristideae	C_4
Bothriochloa saccharoides	Andropogoneae	C_4
Bouteloua gracilis	Cynodonteae	C_4
Chasmanthium latifolium	Chasmanthieae	C_3
Digitaria californica	Paniceae	C_4
Elymus virginicus	Triticeae	C_3
Eragrostis curvula	Eragrostideae	C_4
Festuca rubra	Poeae	C_3
Nassella viridula	Stipeae	C_3
Nassella tenuissima	Stipeae	C_3
Panicum hallii	Paniceae	C_4
Pappophorum vaginatum	Cynodonteae	C_4
Piptatheropsis micrantha	Stipeae	C_3
Poa compressa	Poeae	C_3
Setaria scheelei	Paniceae	C_4

tolerant and intolerant species according to the qualitative species shade tolerance information from the USDA plant database (these data are largely based on anecdotal observations, <https://plants.usda.gov/topics.html>); 3) we aimed to maximize the number of genera and tribes represented to maximize variation in plant traits and increase generalizability. Most of the study species can occur in ecosystems with at least some trees, but microhabitat preferences related to tree canopy is unknown. The fact that most species can occur in ecosystems where woody plants also occur indicates the existence of multiple light environments and thus the potential for variation in shade tolerance and microhabitat preference. Seeds of these species were obtained by either purchasing from a seed company or requesting from the National Plant Germplasm System, United State Department of Agriculture (<www.ars-grin.gov/npgs/>, Supporting information).

Greenhouse methods and light treatments (stage 1)

A greenhouse experiment was necessary to assess quantitative species shade tolerance. Seeds were germinated during April 2018. All species germinated within 2 weeks with at least 50 available seedlings. We selected 10–12 seedlings per species that reached the height of 5 cm to measure initial aboveground biomass for each species before applying different light treatments. We then selected 20 seedlings of similar heights per species for conducting the shading experiment to assess species shade tolerance and flammability.

To allow for spatial variation in temperature and relative humidity, we applied a split-block design to 5 blocks in the greenhouse and evenly split each block into 0% and 50% shade treatment. We chose 50% shade because it is a common shade level underneath trees in ecosystems with open canopies (Belsky 1994, Ludwig et al. 2001, Valladares and Guzmán 2006). We constructed frames with PVC pipe, and covered each frame with polypropylene shade cloth at a height of 1.2 m above the workbench surface. Frames without shade cloth were also built for the 0% shade treatment. A 20 cm wide gap between the shade cloth and workbench surface was left for venting. We randomly assigned each seedling to one of the light treatments in each block with 5 replicates per light treatment per species in total. Seedlings were transplanted into 4.3-l pots with greenhouse potting soil. Given the destructive biomass measurement (see shade tolerance assessment below) and limited greenhouse space, we planted paired seedlings in each pot: one for biomass measurement, and the other one for the flammability experiment. Plants were randomly placed and relocated within each treatment every month. Plants were watered regularly and fertilized once each week (15–5–15 cal-mag at 150 ppm N). The light treatments were established during late April in 2018.

Leaf trait measurements

In July 2018, we randomly selected and marked one plant from each pot for aboveground biomass measurements, and sampled three fully expanded leaves from the other plant that was assigned for flammability experiment. We scanned each leaf using a flatbed scanner at a fixed resolution (300 dpi) along with a printed ruler as scale reference. We then calculated leaf area using Image J (Rasband 2018). To estimate leaf area for species with needle-like leaves, we took leaf sections with known lengths, assumed each was a cylinder, and measured two perpendicular diameters. All leaf samples then were oven-dried to measure dry mass for specific leaf area (SLA) calculations.

Shade tolerance assessment, canopy traits, peak biomass and pre-burn biomass

To assess species tolerance to 50% shade, we measured total aboveground biomass four months after the shading treatment began in late August 2018. This was our estimate of peak growing season biomass. The individual in each pot designated for destructive harvest was cut at the soil surface and all above ground tissue dried. The mean relative aboveground biomass gained by plants grown under 50% shade (aboveground biomass of plant under 50% shade divided by aboveground biomass of plants under 0% shade from the same block) was calculated for each species and used as an index of species shade tolerance (Fynn et al. 2011). Greenhouse temperature control was terminated in early November of 2018 to mimic winter conditions and allow dormancy to occur before the flammability trials the following spring.

To measure live fuel moisture and live to dead biomass ratio, a sample of approximately 10% of the total aboveground fresh biomass was randomly taken from each one-year-old plant that includes both dead and live tissue prior to each burning trial in spring of 2019. As plant phenology determines live to dead biomass ratio, thus fuel moisture content (Pellizzaro et al. 2007a), we also measured live to dead biomass ratio to determine phenology effects on live fuel moisture in addition to the influence by light environments (Wittich 2011). These samples were separated into live and dead portions for fresh and oven-dried biomass measurement. To measure total aboveground fresh biomass, we measured initial plant weight (including the weight of the pot, soil and plant) prior to ignition and final plant weight (including weight of pot, soil and belowground biomass) after burning but first removing any aboveground fuel or ash that was left. The difference between the two measurements was our estimate of total aboveground fresh biomass. Total aboveground biomass was then estimated as the product of live fuel moisture and total aboveground fresh biomass. These are probably slight overestimates because our calculations assume that combustion did not change water content of the soil and belowground biomass when it could have some drying effect.

We measured plant height and width prior to flammability trials to estimate plant canopy volume (Supporting information). We then calculated bulk density by dividing total aboveground biomass by plant canopy volume (Gao and Schwilk 2018). We counted the number of tillers for each plant the day prior to flammability trials for use in models predicting post fire survival and resprouting vigor.

Flammability trials and measurements (stage 2)

From late March through early May 2019, we conducted indoor flammability experiments at the Lubbock Fire Department. To mimic natural burning conditions, we ceased watering and drought stressed experimental plants for three weeks before each was burned. Mean soil volumetric moisture content was 11.6 ± 6.8%. Burning was conducted in an incomplete block design: we randomly chose a greenhouse block and eight or nine species from the block on each burning day and always took plants from both light treatments for the chosen species for flammability trials. Flammability data were always collected for all plants from the same block within two consecutive burning days. Flammability trials of plants from two different blocks were separated by a minimum of three days to avoid potential temporal autocorrelation that might be due to short-term weather effect. To maintain an upright canopy (necessary for some species such as *D. californica* and *B. saccharoides* that tended to lean when grown in individual pots), we added a wire cylinder (30 cm in height and 12.6 cm in diameter) to all plants after the first trial (Supporting information).

To estimate heat released (J) at the soil surface and at 50 cm height, we placed a matte black aluminum disc (3.65 mm in thickness, 9.0 cm in diameter, 53 g in mass) at each location (Supporting information). We chose the two heat release measurements based on a priori reasoning: heat release determines meristem survival in grasses and fire damages in trees (Choczynska and Johnson 2009, Bowman et al. 2018). We measured the maximum temperature of the aluminum disc before ignition, near the end of flaming combustion when flame was stopping to touch each disc (with multiple measurements for each but only recorded the maximum temperature), and when no ember was in vision with an infrared thermometer gun (TG56, FLIR Systems). Temperature measurements of aluminum discs at the soil surface and at 50 cm height were converted to heat absorbed by the aluminum disc at each location as the product of specific heat content of aluminum and the difference between disc temperature measured before ignition and near the end of flaming combustion. We ignited the plant base by igniting a cotton ball to which 10 ml pure ethanol was added and then placing the burning cotton ball by the plant base for a maximum of 45 s. We removed the cotton ball 5 s after ignition occurred. Ignition was counted as a failure if the plant did not ignite after exposure to the ignition source for 45 s. We recorded relative humidity and air temperature for the room every 5 min during combustion using a HOBO temperature and humidity sensor.

In addition to heat release measurements of interest for this study, we also measured other flammability variables (Supporting information), which provide information about other fire behavior metrics that might be of interest to other researchers.

Post fire recovery assessment (stage 3)

We returned all plants to the greenhouse after the burning trials, where they were arranged in a fully random design. All plants were subjected to full light and were watered regularly with fertilizer being applied once each month. Plant positions were re-randomized every two weeks. We assessed plant survival two months after the burn by counting the number of tillers that emerged: plants with any post-fire tillers were counted as surviving. We then harvested aboveground biomass three months after the fire from late June to early August 2019 to assess resprouting vigor. To control for plant size effects, we calculated resprouting vigor as the percentage biomass recovered.

Data analysis

We did not foresee the canopy leaning problem for two species until the first day of burning. Therefore, we dropped observations (16 observations from eight species with one replicate per treatment per species) from the first trial for heat release at 50 cm height because the presence or absence of the wire cylinder influenced mid-canopy heat release (Supporting information). We included all leaf and canopy trait measurements in further analysis.

To determine if shade intolerant grasses are more flammable than shade tolerant grasses, we built two linear mixed effects models with shade tolerance and light treatment as fixed effects to predict heat release at the soil surface and at 50 cm height. Given that C_3 photosynthesis requires less light energy to fix CO_2 and thus a physiological advantage in tolerating shade compared to C_4 photosynthesis (Pearcy and Ehleringer 1984, Ehleringer and Monson 1993, Osborne and Freckleton 2009), it is possible that variation in flammability arises from morphological and phenological differences between C_3 and C_4 species rather than from variation in shade tolerance directly (but see Ripley et al. 2015 for flammability of C_3 and C_4 grasses). Thus, we included photosynthesis type as a covariate to account for potential unmeasured differences between C_4 and C_3 grasses. The relationship between shade tolerance and photosynthesis pathway was tested to examine if there is close correlation between the two variables (Supporting information). Some species (e.g. *B. gracilis*, *N. tenuissima*, *N. viridula*, *C. latifolium* and *A. purpurea*) under 0% shade did not reach the same size as mature plants we observed in the field (Sorensen et al. 2012, Peláez et al. 2013, Gao and Schwilk 2018). Variation in aboveground biomass can contribute to flammability variation that may not be observed in mature perennial grasses. Therefore, we also included biomass as a model covariate. The final linear mixed effects models thus included species shade tolerance, light treatment, photosynthesis type and total aboveground biomass as fixed effects with all possible 2- and 3-way interaction terms. We allowed intercepts to vary by species to account for other potential species-specific variation and applied this random effect term to all the following mixed effects models.

A logistic model was built to determine how fire behavior and plant traits influenced post-fire survival. Species shade tolerance, pre-fire tiller number and heat release at the soil surface were included in the model as fixed effects. To account for potential effect of photosynthetic pathway on post-fire responses, we also included photosynthesis type in the model as a covariate. We included all possible 2- and 3-way interactions among predictor variables. However, given the small sample size, we were not able to include species as random effect in this logistic model. We then built a linear mixed effect model with all the same predictors including species as random effect but only for observations that did resprout to examine how surviving plants varied in percentage biomass recovered.

To determine plant trait effects on heat release at the soil surface and at 50 cm height, we built linear mixed effect models including biomass, live fuel moisture, biomass density and specific leaf area as fixed effects. To account for air temperature variation during burning trials, we included temperature in each model as a fixed effect without any associated interaction terms. We included all possible 2- and 3-way interactions among plant traits. Light treatment was not included in the heat release models because we aimed to determine the mechanism by which environment might influence flammability and we therefore assumed that we included all important plant traits in our model that can vary under light treatments to influence flammability.

To distinguish the effects of leaf traits and species phenology on live fuel moisture from other light treatment effects, we built a linear mixed effect model including specific leaf area, live to dead biomass ratio, and light treatments as fixed effects with all possible interaction terms.

All mixed effects models were built with the lme4 package in R (Bates et al. 2015, <www.r-project.org>). Independent variables were standardized as z-scores to make fixed effects comparable. We log-transformed dependent variables to avoid violating the assumption of the normal-distribution of residuals during linear regression. We examined the significance of fixed effects using the *Anova()* function from the car package (Fox et al. 2013). Type 3 sums of squares were calculated for testing hypothesis including interaction effects (Shaw and Mitchell-Olds 1993, Hector et al. 2010). Approximate degrees of freedom and p-values were calculated using the Kenward–Roger approximation to avoid unacceptable type 1 error (Luke 2017). Data and code can be found at <https://github.com/XiulinGao/shade-flammability>.

Results

Inverse relationship between grass shade tolerance and heat release

As expected, aboveground biomass positively influenced heat release at the soil surface ($p = 0.012$) and at 50 cm height ($p < 0.001$, Fig. 2). In addition, plants grown under 50% shade produced less heat at both locations than did plants grown under 0% shade (soil surface: $p < 0.001$; 50 cm: $p = 0.004$, Table 2). In addition to these plastic effects of

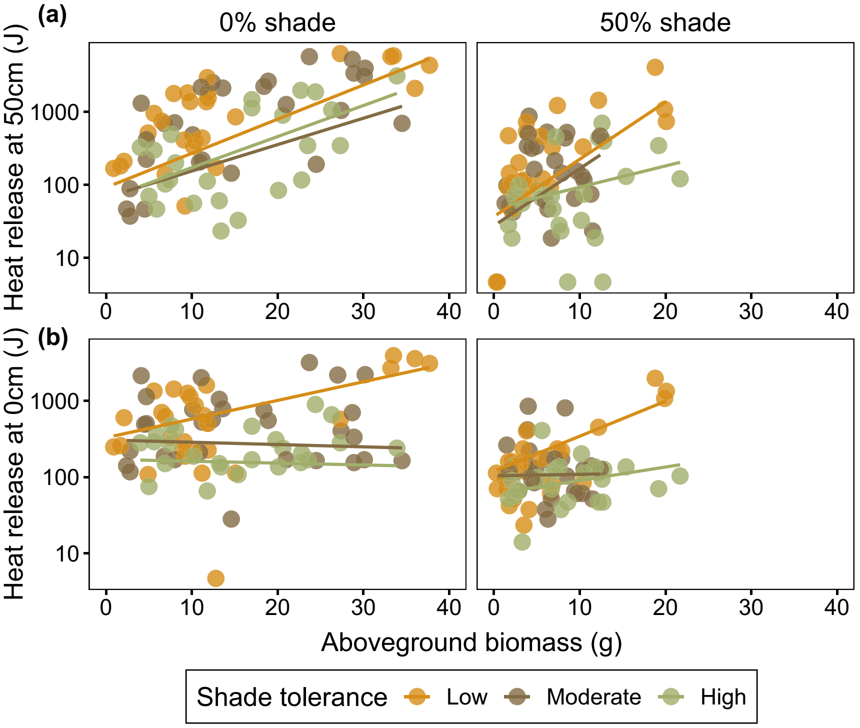

Figure 2. Relationship between total aboveground biomass, light environment, shade tolerance and heat release at 50 cm height (a) and the soil surface (b). Lines indicate the fitted linear mixed effects models. Points are individual observations. Cutoff values used for grouping species by shade tolerance for visualization were −0.7 and 0.3 (in standardized values), which were chosen to ensure a similar number of species in each shade tolerance group. Notice that shade tolerance was a continuous numeric variable in the model, grouping of shade tolerance was just for visualization in figure.

light environment, there was a strong effect of species shade tolerance: shade tolerance had a negative effect on heat produced at 50 cm height across light treatments (p = 0.001). In addition, the positive biomass effect on heat release at 50 cm height was weaker in species with higher shade tolerance (interaction coefficient = −0.155, p = 0.008). There was no effect of shade tolerance on heat release at the soil surface. We did not find any relationship between photosynthesis type (C_3 versus C_4) and flammability measurements.

Relationship between soil heating, plant traits and fire response

We did not detect any main effect of heat release at the soil surface, nor did we detect an effect of tiller number, photosynthesis type or shade tolerance on individual survival (Table 3, all p > 0.05). However, in general, plants with more pre-fire tillers were less affected by increased soil heating in terms of survival than were plants with fewer tillers (2-way interaction coefficient: 2.43, p < 0.001, Fig. 3). This positive interaction effect between soil heating and pre-fire tillers on individual survival was enhanced in species with greater shade tolerance (3-way interaction coefficient: 2.97, p = 0.011). Moreover, C_3 species were more negatively affected by soil heating in terms of post-fire survival (2-way interaction coefficient: −1.70, p = 0.028). There was also a positive 3-way interaction effect among species shade tolerance, pre-fire tillers and C_3 photosynthesis on individual survival: C_3 species with more pre-fire tillers had higher survival rate if they were also shade tolerant species (3-way interaction coefficient: 1.81, p < 0.001). We only found a negative effect of heat release at the soil surface on percentage biomass recovered (p = 0.005, Fig. 4).

Plant trait effects on heat release

Plants with more biomass produced more heat at 50 cm height (p < 0.001, Fig. 5a, Table 4) and at the soil surface (p = 0.047, Fig. 5b, Table 5). In contrast, fuel moisture content had negative effects on heat release at both locations (p < 0.001). In addition, fuel moisture content interacted with specific leaf area to influence heat release at the soil surface. For plants with higher SLA, the dampening effect of fuel moisture content on heat release at the soil surface was lessened (interaction coefficient: 0.20, p = 0.005, Fig. 5b) compared to that in plants with lower SLA. Furthermore, bulk density negatively influenced heat release at 50 cm height only (p = 0.022, Fig. 5a).

We further explored how specific leaf area, live to dead biomass ratio and light environment influenced live fuel moisture. Plants grown under 50% shade had higher moisture content at the time of fire than did plants grown under full sunlight (p < 0.001, Fig. 6, Table 6). As live to dead biomass ratio increased so did live fuel moisture (p < 0.001). However, the positive effect of live to dead biomass ratio on live fuel moisture was strengthened in plants from the high light treatment (p < 0.001). We did not detect any effect of specific leaf area on live fuel moisture content.

Table 2. Mixed effect model coefficients and ANOVA table for predictors of flammability. Results of linear mixed model fit with *lmer()* in the R package lme4 (Bates et al. 2015). Approximate effective degrees of freedom, F-statistics and p-values were calculated by Kenward–Roger approximation (Kenward and Roger 1997) using the car package in R (Fox et al. 2013). All numeric predictors were standardized to be mean-centered with unit standard deviation. ST: shade tolerance, M: biomass, Li: 0% shade, C_3: C_3 photosynthesis. Significant effects are highlighted in bold.

	Biomass (g)	Shade tolerance	Light (0% shade)	C_3	ST:M	M:Li	ST:Li	M:C_3	ST:C_3	Li:C_3	M:ST:Li	M:ST:C_3	M:Li:C_3	ST:Li:C_3
Log-transformed heat release at 0 cm														
Estimate	0.153	−0.080	0.190	0.023	−0.080	−0.042	0.027	0.005	−0.058	0.007	−0.025	0.032	0.047	−0.069
p	**0.012**	0.236	**< 0.001**	0.735	0.185	0.432	0.430	0.923	0.368	0.861	0.608	0.478	0.381	0.048
Log-transformed heat release at 50 cm														
Estimate	0.346	−0.207	0.118	0.006	−0.155	0.016	0.003	0.102	−0.101	−0.034	0.056	−0.087	0.030	0.001
p	**< 0.001**	**0.001**	**0.004**	0.908	**0.008**	0.742	0.919	0.087	0.066	0.385	0.240	0.057	0.556	0.956

Table 3. Coefficients and ANOVA table for logistic model predicting post-fire survival rate, and for linear mixed effect model predicting percentage post-fire biomass recovered. Results of logistic model and linear mixed effect model fit with *glm()* and *lmer()* in R respectively (Bates et al. 2015, <www.r-project.org>). All predictors were standardized to be mean-centered with unit standard deviation. C_3: C_3 photosynthesis, Sh: soil heating, Pt: pre-fire tiller, ST: shade tolerance. Significant effects are highlighted in bold.

	Soil heating (J)	Pre-fire tiller	Shade tolerance	C_3	Sh:Pt	Sh:ST	Pt:ST	Sh:C_3	Pt:C_3	ST:C3	Sh:Pt:ST	Sh:Pt:C_3	Sh:ST:C_3	Pt:ST:C_3
Post-fire survival														
Estimate	−1.206	−0.053	−0.496	−0.393	2.437	−1.419	0.001	−1.702	0.628	0.185	2.972	−0.554	−1.548	1.814
p	0.127	0.912	0.310	0.312	**< 0.001**	0.197	0.997	**0.028**	0.147	0.723	**0.011**	0.321	0.167	**< 0.001**
Post-fire biomass recovery (%)														
Estimate	−0.709	−0.178	−0.194	−0.005	0.328	−0.123	0.067	−0.422	0.050	0.083	0.130	0.117	−0.028	0.089
p	**0.005**	0.225	0.320	0.976	0.068	0.658	0.617	0.082	0.723	0.665	0.517	0.262	0.917	0.368

Discussion

We hypothesized that grass flammability strategy and tolerance of tree canopies are related and that this strategy axis includes on one end shade tolerant, less flammable grasses that can coexist with trees, and on the other end shade intolerant, flammable grasses that burn frequently and keep the canopy open. Our results were consistent with this hypothesis: we found that more shade tolerant grasses produced less heat at 50 cm height than did shade intolerant grasses across both light treatments and the measured biomass range. Even under 50% shade, individuals of shade intolerant grasses that managed to maintain relatively higher biomass (biomass > 5 g) were more flammable than shade tolerant grasses of similar biomass (Fig. 2a). In addition, biomass played a less important role in influencing flammability in species with greater shade tolerance, especially under 50% shade (Fig. 2a). This might be due to a higher fuel moisture content in high shade tolerant, C_3 species, which tended to have higher live: dead biomass ratio under low light (Supporting information). This shows that shade tolerance and flammability are correlated in grasses because of differences in species-specific traits (e.g. plant phenology) other than biomass, and that differences in fire behavior are not due solely to plastic response to the light environment. Consistent with Ripley et al. (2015), we did not find C_4 grasses were more flammable than C_3 grasses, the correlation between shade tolerance and flammability is thus not due to the variation in photosynthesis type.

Fire-induced plant mortality is largely determined by heat exposure above lethal temperature in live plant tissues (Keyser et al. 2006, Catry et al. 2010, Bowman et al. 2018), therefore variation in heat release might result in differential fire effects and plant responses. Total heat release can increase plant mortality (Vilà et al. 2001, but see Bond and Van Wilgen 1996 for diverse post-fire plant responses). However, heat release at different locations can have different biological effects. Prolonged soil heating will decrease the survival of surface and belowground structures in both trees and grasses, and cause distortion and dysfunction of xylem in trees (Ryan and Frandsen 1991, Odion and Davis 2000, Dickinson 2002, Balfour and Midgley 2006). Increased heat release aboveground at higher locations can be detrimental to trees, especially when fire resistant traits such as thick bark are absent, as it damages cambium tissue or causes top-kill in tree saplings (Keyser et al. 2006, Catry et al. 2010, Smith et al. 2017). In contrast, if fire occurs during grass dormancy, no important grass tissues are exposed to such heat. Therefore, canopy heating is generally less lethal to grasses.

Species specific flammability can potentially create heterogeneity at small spatial scales that would help maintain tree and grass persistence. If grasses are homogeneously flammable, then positive grass-fire feedbacks can, in theory, lead to grass dominance (Rahlao et al. 2009, Bowman et al. 2014). However, if the grasses nearest trees that are still vulnerable to fires tend to produce less heat, then this positive feedback effect would be lessened, which should increase community stability. The lower heat release at 50 cm height in tree-associated

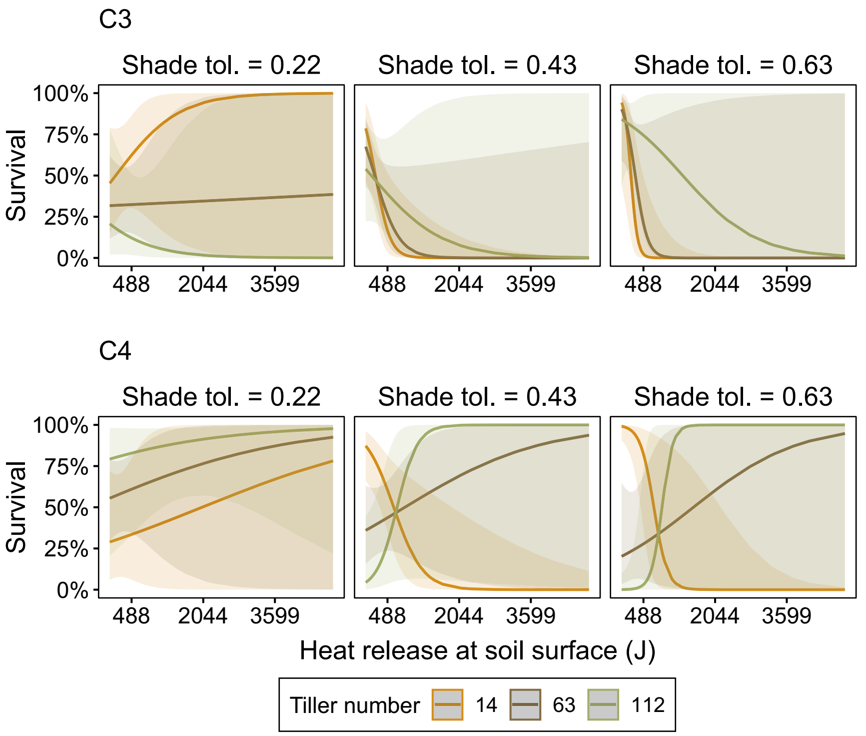

Figure 3. Predicted individual survival rate based on the logistic model. Prediction is based on all values of heat release at the soil surface, mean and mean ± standard deviation of species shade tolerance and pre-fire tiller number, and C_3 and C_4 photosynthesis type. This figure illustrates the 2-way and 3-way interaction effects among predictors on survival rate. Shaded areas represent 95% confidence intervals of model predictions.

grasses could lessen such positive feedback by resulting in less damage to tree saplings, and help maintain the tree–grass mixture occurring in plant communities such as juniper-mixed grasslands and oak savannas of the southwestern US.

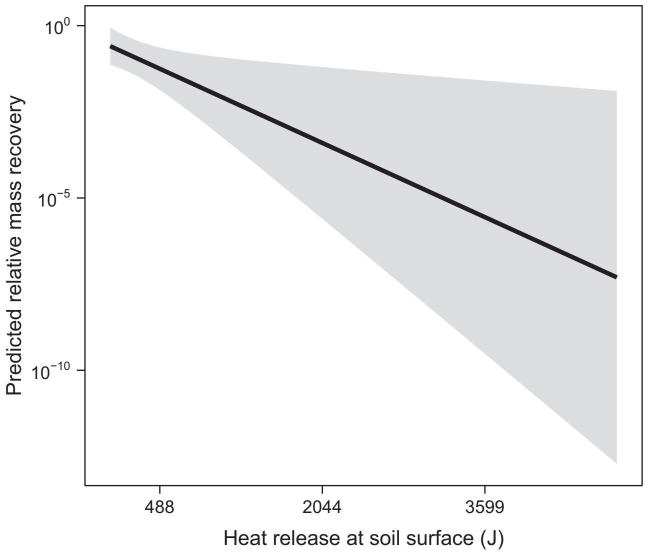

Figure 4. Predicted post-fire biomass relative to pre-fire biomass based on the linear mixed effect model Prediction is based on heat release at soil surface to show marginal effect of soil heating on post-fire percentage biomass recovery. Shaded area represents 95% confidence intervals of model prediction.

Grasses producing less heat at the soil surface recovered better after the fire; however, post-fire survival was influenced by fire behavior and plant traits in a complex way. Heat release at the soil surface directly influences surface meristem survival in resprouting, perennial grasses. Prolonged soil heating also increases heat transferred into the soil and increases the likelihood of belowground meristems being exposed to lethal temperature (Swezy and Agee 1991, Stephens and Finney 2002, Choczynska and Johnson 2009, Gonzalez et al. 2015). In contrast to previous work, we did not find higher survival rate with reduced soil heating (Gonzalez et al. 2015), or in plants with more pre-fire tillers (Moore et al. 2019). However, having more pre-fire tillers mitigated the damage of increased soil heating, and that interaction effect was enhanced in C_3 species with greater shade tolerance. It is likely that increased pre-fire tiller number provided a larger bud bank, increasing the chance of survival during a fire (Hendrickson and Briske 1997, Benson et al. 2004, Moreira et al. 2012). In addition, increased number of tillers in a defined area (e.g. the pot) might provide better heat isolation via reduced exposure surface, which might play a more important role in C_3, shade tolerant species that tended to burn with less heat release. Although we did not find that C_4 grasses were more fire resilient (in contrast to Ripley et al. 2015), increased heat release at the soil surface had less negative effects on C_4 individual survival, which might be due to C_4 species having higher belowground carbon reserves (Ripley et al. 2010).

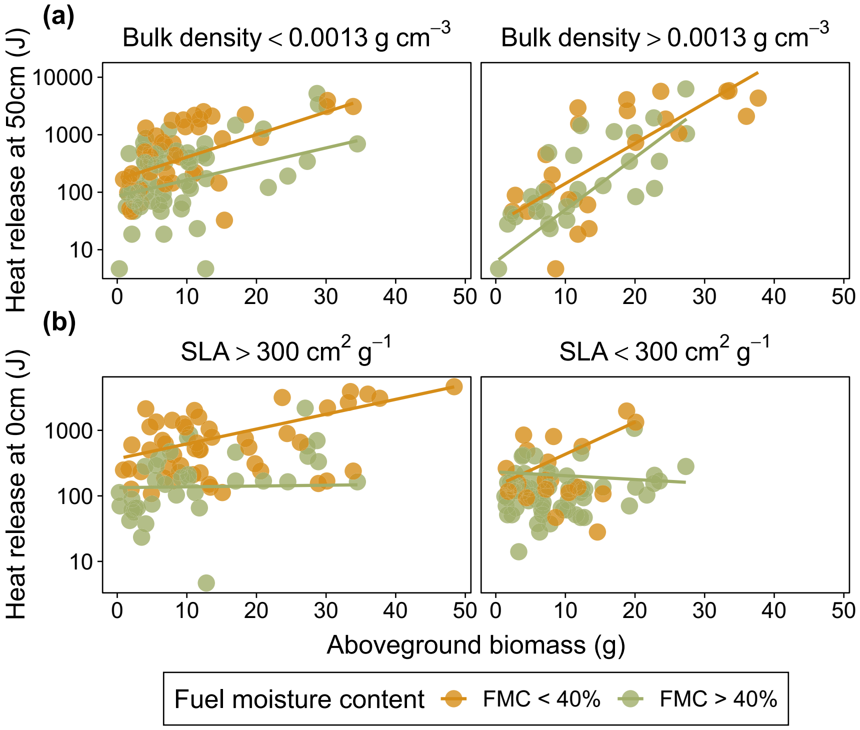

Figure 5. Relationship between plant traits and heat release at 50 cm height (a) and soil surface (b). Lines indicate fitted linear mixed effects model. Points are individual observations. Lines and points are color coded by fuel moisture content. Median value was chosen to divide the data for visualization purpose, all quantitative variables were included as continuous data in models.

Shade intolerant grasses were not more fire resilient than shade tolerant grasses. Previous work suggests that resprouting in grasses is related to both fire and grazing histories in natural habitats (Ripley et al. 2015, Archibald et al. 2019). As a common disturbance response trait, resprouting might only act as a precondition (e.g. adaptation to grazing and exaptation to fire) for the expansion of flammable, shade intolerant grasses in open habitats in the presence of fire, which can benefit from niche construction (Bond and Midgley 1995).

Table 4. Mixed effect model coefficient and ANOVA table for predictors of heat release at 50 cm height. Results of linear mixed model fit with *lmer()* in the R package lme4 (Bates et al. 2015). Approximate effective degrees of freedom, F-statistics and p-values were calculated by Kenward–Roger approximation (Kenward and Roger 1997) using the car package in R (Fox et al. 2013). All predictors were standardized to be mean-centered with unit standard deviation. M: biomass, FMC: fuel moisture content, BD: bulk density, SLA: specific leaf area. Significant effects are highlighted in bold.

	Estimate	Estimate df	p
Biomass (g)	0.700	85.618	**< 0.001**
FMC (%)	−0.285	136.255	**< 0.001**
Bulk density (g cm^{-3})	−0.237	58.394	**0.022**
SLA (cm^2 g^{-1})	−0.187	101.943	0.056
Temperature (°C)	0.048	127.323	0.444
M: FMC	−0.082	134.724	0.393
M: BD	0.102	134.313	0.214
M: SLA	−0.142	122.074	0.194
FMC: BD	0.035	133.938	0.596
FMC: SLA	0.085	135.255	0.200
BD: SLA	−0.102	136.934	0.337
M: FMC: BD	−0.035	134.122	0.627
M: FMC: SLA	−0.024	133.248	0.789
M: BD: SLA	0.150	136.594	0.145
FMC: BD: SLA	−0.064	136.343	0.551

Table 5. Mixed effect model coefficients and ANOVA table for predictors of heat release at the soil surface. Results of linear mixed model fit with *lmer()* in the R package lme4 (Bates et al. 2015). Approximate effective degrees of freedom, F-statistics and p-values were calculated by Kenward–Roger approximation (Kenward and Roger 1997) using the car package in R (Fox et al. 2013). All predictors were standardized to be mean-centered with unit standard deviation. M: biomass, FMC: fuel moisture content, BD: bulk density, SLA: specific leaf area. Significant effects are highlighted in bold.

	Estimate	Estimate df	p
Biomass (g)	0.219	108.479	**0.047**
FMC (%)	−0.381	150.993	**< 0.001**
Bulk density (g cm^{-3})	0.148	87.649	0.199
SLA (cm^2 g^{-1})	−0.197	107.826	0.054
Temperature (°C)	0.008	140.501	0.907
M: FMC	−0.028	145.630	0.795
M: BD	0.129	150.788	0.236
M: SLA	−0.166	138.079	0.117
FMC: BD	−0.003	148.939	0.968
FMC: SLA	0.206	149.789	**0.005**
BD: SLA	0.0601	145.430	0.642
M: FMC: BD	−0.110	145.878	0.270
M: FMC: SLA	−0.002	146.156	0.986
M: BD: SLA	−0.304	150.468	0.417
FMC: BD: SLA	−0.030	145.514	0.808

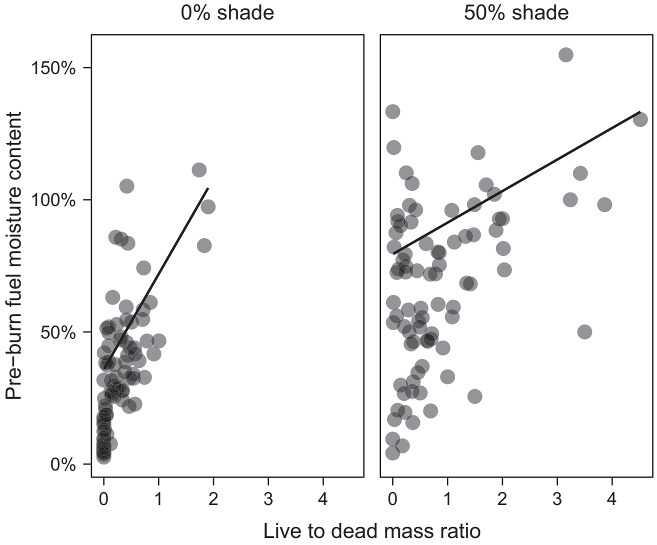

Figure 6. Relationship between live to dead biomass ratio, light environments and live fuel moisture. Lines indicate fitted linear mixed effects model. Points are individual observations. We changed transparency of each point for better visualization of overlapping observations, and different colors are due to the overlap of points.

Table 6. Mixed effect model coefficient and ANOVA table for predictors of live fuel moisture. Results of linear mixed model fit with *lmer()* in the R package lme4 (Bates et al. 2015). Approximate effective degrees of freedom, F-statistics and p-values were calculated by Kenward–Roger approximation (Kenward and Roger 1997) using the car package in R (Fox et al. 2013). All numeric predictors were standardized to be mean-centered with unit standard deviation. Significant effects are highlighted in bold.

	Estimate	Estimate df	p
SLA ($cm^2\ g^{-1}$)	0.069	147.254	0.056
Light (0% shade)	−0.120	159.930	**< 0.001**
Live/dead	0.334	159.513	**< 0.001**
SLA: light	0.006	151.728	0.845
SLA: live/dead	−0.035	159.842	0.440
Light: live/dead	0.154	153.661	**< 0.001**
SLA: live/dead: light	−0.037	152.113	0.378

In addition to biomass and fuel moisture effects on flammability, higher specific leaf area weakened the negative effect of live fuel moisture on heat release at the soil surface, and bulk density negatively influenced heat release at 50 cm height. High specific leaf area increases exposure to heat and leads to greater evaporation. This can accelerate the pre-heating process and thus mitigate the negative effect of fuel moisture on flammability. However, this interaction effect was not observed for heat release at 50 cm height. This may be due to the lower bulk density in canopy biomass compared to the more packed biomass at the plant base, which counteracts heat transfer during combustion and offsets the leaf trait effect (Schwilk 2015). In contrast to previous work on dry fuels (Gao and Schwilk 2018), we found that bulk density negatively influenced heat release at 50 cm height but not soil heating. It is possible that the effect of bulk density on soil heating was negligible in live fuel where high fuel moisture content suppresses combustion. The negative effect of bulk density on heat release at 50 cm mainly occurred in small plants (biomass < 20 g, Fig. 5a). In previous work, we found that as bulk density increases, there is less biomass allocated 10 cm above the ground (Gao and Schwilk 2018). It is likely that small plants would have much less fuel at 50 cm height, which negatively influenced heat produced.

As a key flammability trait, live fuel moisture is determined by environmental factors, leaf morphology and plant phenology. Precipitation and drought events directly influence live fuel moisture. However, fuel moisture content at the time of fire is determined by the interaction between the environment and plant traits (Pellizzaro et al. 2007b, Nelson and Hiers 2008, Jin and Chen 2012). Plant phenology controls the live to dead biomass ratio of a plant and thus influences fuel moisture (Wittich 2011, de Angelis et al. 2012). Phenology varies between cool- and warm-season grasses: cool season grasses start growth in early spring and have summer dormancy, and the contrasting patterns occur in warm season grasses (Peterson et al. 2002). Most high shade tolerant grasses were cool season grasses having higher live to dead biomass ratio in early spring when burning was conducted. Therefore, reduced flammability observed in grasses in the high shade tolerance group was probably in part a result of different phenology: at the time of burning, some cool season grasses had higher live to dead biomass ratio, and thus higher live fuel moisture.

We found a negative correlation between grass shade tolerance and flammability. In addition to the influence of biomass, variation in flammability largely resulted from different light environments and from plant phenology influencing live fuel moisture. Our study is the first work examining how grasses varying in shade tolerance behave as fuels at individual plant level. The study provides a novel perspective to understand fire-maintained stability of tree–grass mixtures in open woodlands and savannas by suggesting the possibility of alternative grass flammability strategies. The outcome will also benefit fire management and fire risk prediction of grassy ecosystems where species composition varies across space.

Speculations

Although our study did not address evolutionary questions and does not demonstrate any evidence of adaptation, it is possible that shade tolerance and flammability are two different plant strategies that are evolutionarily correlated in grasses. Ancestors of open-habitat grasses are from mesic, shady environments (Osborne and Freckleton 2009, Edwards and Smith 2010). The initial shift to open habitats in grasses is linked to the evolution of disturbance resistant traits (Bouchenak-Khelladi et al. 2010, Strömberg 2011, Linder et al. 2018). Fire in combination with drought then promoted the global expansion of open grassland and savanna habitats at the expense of trees, during which evolution of flammability traits could occur through vegetation-fire feedbacks (Keeley and Rundel 2005, Anderson 2006, Keeley et al. 2011). Future experiments incorporating grass phylogeny and a wider range of open and closed habitat species with more replicates per species could further examine the hypotheses we developed here. Moreover, a consistent pattern of correlated trait evolution from shade tolerant to shade intolerant species would provide evidence for the adaptive benefit of the shade intolerant, flammable strategy. Furthermore, to investigate the biological significance of any variation in grass flammability, field-scale burning experiments measuring fire behavior and tree fire response are required.

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Author contributions

Xiulin Gao: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Dylan W. Schwilk**: Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Writing – review and editing (equal).

Data availability statement

Data are available from Zenodo <doi:10.5281/zenodo.5791108> and the Dryad Digital Repository: <https://doi.org/10.7941/D17W62> (Gao and Schwilk 2022).

Supporting information

The supporting information associated with this article is available from the online version.

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