

Herbaceous vegetation responses to experimental fire in savannas and forests depend on biome and climate

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Editor: Sally Archibald

Abstract

Fire–vegetation feedbacks potentially maintain global savanna and forest distributions. Accordingly, vegetation in savanna and forest ecosystems should have differential responses to fire, but fire response data for herbaceous vegetation have yet to be synthesized across biomes. Here, we examined herbaceous vegetation responses to experimental fire at 30 sites spanning four continents. Across a variety of metrics, herbaceous vegetation increased in abundance where fire was applied, with larger responses to fire in wetter and in cooler and/or less seasonal systems. Compared to forests, savannas were associated with a 4.8 (± 0.4) times

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larger difference in herbaceous vegetation abundance for burned versus unburned plots. In particular, grass cover decreased with fire exclusion in savannas, largely via decreases in C_4 grass cover, whereas changes in fire frequency had a relatively weak effect on grass cover in forests. These differential responses underscore the importance of fire for maintaining the vegetation structure of savannas and forests.

KEY WORDS

fire, herbaceous vegetation, C_3 and C_4 grasses, fire–vegetation feedbacks, prescribed burns, experimental fire, fire frequency, alternative stable states, savanna–forest bistability, biome distributions

INTRODUCTION

Fire may be a key determinant of global savanna and forest distributions (Lehmann et al. 2011; Staver et al., 2011b), but the importance of fire for stabilizing savannas is debated (see, e.g., Good et al., 2016; Veenendaal et al., 2018) and its effects on herbaceous vegetation across biomes are unelucidated. Frequent fires may allow savannas to persist where climate and soils might otherwise allow forests to dominate (Bond et al., 2005; Sankaran et al., 2005); these fire regimes may sharpen transitions between savannas and forests (Lloyd et al., 2008; Veenendaal et al., 2018). Vegetation influences fire in turn, and fire–vegetation feedbacks thus potentially maintain savannas and forests as alternative stable states (Beckage et al., 2011; Staver et al., 2011a). In savannas, a continuous layer of highly flammable herbaceous vegetation promotes frequent fires (Cardoso et al., 2022), which inhibit the maturation of tree seedlings and saplings via topkill (Hoffmann et al., 2009). Meanwhile, tree cover in forests inhibits herbaceous vegetation accumulation, thereby limiting fire spread and maintaining the closed canopy (see, e.g., Nowacki & Abrams, 2008). However, others propose that differences in fire regime are not necessary to explain savanna–forest distributions and that climate and soils primarily determine the vegetation structure of these two biomes (Good et al., 2016; Veenendaal et al., 2018). Evaluating vegetation dynamics in response to fire across a range of environmental conditions is therefore essential for both understanding vegetation distributions and developing sustainable ecosystem management plans.

Snapshot analyses have demonstrated that savannas and forests can occur in similar climate envelopes across both tropical and temperate regions, and they have suggested that these biomes are alternative stable states (Aleman et al., 2020; Dantas et al., 2016; Staver et al., 2011a). Regions where both woody and herbaceous vegetation are present and where climate could theoretically support either savanna or forest vegetation structure are considered part of the ‘savanna–forest complex’. Studies of woody vegetation dynamics provide support for bistability in the savanna–forest complex. For example, a recent data synthesis by Pellegrini et al. (2021) demonstrated that fire exclusion in savannas leads to an increase in woody basal area and, sometimes, transitions

to forest-like tree cover and composition. Applying fire in forests, however, does not always lead to a substantial loss of woody basal area (Pellegrini et al., 2021; Veenendaal et al., 2018), since mature trees are more resistant to surface fire effects (Grady & Hoffmann, 2012; Hood et al., 2018) and fire intensity is lower. These asymmetric responses suggest that fire effects on woody vegetation, at least on a decadal timescale, may depend on a system's initial condition as either a savanna or forest. Research that extends beyond woody vegetation dynamics is therefore warranted for a more complete understanding of the role fire plays in shaping vegetation structure in these systems.

Synthesis work in the savanna–forest complex has largely neglected effects of fire on the abundance of herbaceous vegetation, despite its mechanistic role in fire–vegetation feedbacks. Herbaceous vegetation is the primary fuel for fires in many savannas, and greater herbaceous vegetation abundance generally increases fire frequency, fire intensity and burned area (see, e.g., Govender et al., 2006; Kahiu & Hanan, 2018). In forests, shading from a closed canopy may not only increase fuel moisture by creating a wetter microclimate (Hoffmann et al., 2012), but also reduce herbaceous vegetation fuel load via competition for light (Lloyd et al., 2008; Reich et al., 2001). In some forests and woodlands, fires may instead be fuelled by leaf litter and woody debris (Keane, 2015), yet surface fires in forests under normal climatic conditions typically neither kill nor topkill the adult trees that dominate the forest canopy (Brando et al., 2014). Herbaceous vegetation abundance is thus a key component of fire–vegetation feedbacks across savanna–forest boundaries, meriting direct evaluation of its response to fire.

Different components of the herbaceous vegetation layer contribute differentially to propagating fire and thus to fire–vegetation feedbacks. While forbs contribute little to fire intensity or spread (Wragg et al., 2018), grasses, a major component of the herbaceous vegetation layer in savannas, are highly flammable (Simpson et al., 2016; Zanzarini et al., 2022), and grass biomass is positively correlated with fire intensity (Cardoso et al., 2022). Some grasses—especially C_4 grasses—have traits associated with flammability, including low fuel bulk density (Simpson et al., 2016), which results in fires that spread faster and are more intense (Hoffmann et al., 2012).

Because herbaceous vegetation in general and grasses in particular play a central role in mediating fire–vegetation feedbacks, we predict that asymmetric fire effects between savannas and forests should be observed in herbaceous vegetation responses to fire, inversely related to woody vegetation responses (Pellegrini et al., 2021). Excluding fire in savannas should result in a decrease in herbaceous vegetation due to shading from woody vegetation that has been released from fire-induced topkill (Hoffmann et al., 2009; Reich et al., 2001). On the other hand, introducing more frequent fires into forests should induce weaker responses than in savannas because relatively sparse herbaceous vegetation in the forest understorey may fuel only mild fires incapable of killing mature forest trees (Brando et al., 2014). Work at individual sites provides patchy support for these hypotheses: frequent burning maintains herbaceous vegetation abundance in savannas (see savanna references in Table S1). However, frequent fire application in forests also increases herbaceous vegetation abundance (see forest references in Table S2). Insights across studies are further obscured by differences in climatic factors that modulate herbaceous vegetation responses to fire (see, e.g. Govender et al., 2006). This question requires a synthesis comparing the magnitude of fire responses across different sites.

Here, we examine herbaceous vegetation responses to experimental fires at 30 sites across four continents encompassing broad biogeographical and climatic scales within the savanna–forest complex. Specifically, we ask whether fire effects on herbaceous vegetation depend on the initial condition of the ecosystem, predicting larger effects of fire exclusion in savannas than of frequent fire applications in forests. By compiling measurements of herbaceous vegetation abundance and grass cover in plots burned at different frequencies, we evaluate (1) whether herbaceous vegetation in general and grass in particular are more responsive to fire in savannas than in forests; (2) whether responses to fire differ between C_3 and C_4 grasses; and (3) how climatic variables including mean annual precipitation (MAP), precipitation seasonality and mean annual temperature (MAT) moderate or amplify responses to changing fire regimes.

MATERIALS AND METHODS

Study area selection

We synthesized data from prescribed fire experiments in the savanna–forest complex across four continents. We incorporated plot-level percent cover data that were collected in the same sites as woody-layer data reported in Pellegrini et al. (2021). These sites spanned a range of savanna and forest types in the temperate, subtropical and tropical zones. Sites differed in dominant species types and land use histories prior to the establishment

of the experiment. Sampling designs differed across sites given the differences in management and spatial scale; the methods are described in detail in the corresponding papers cited in Table S1.

We supplemented this data synthesis effort with results from references for sites listed in table S1 of Veenendaal et al. (2018) as well as results from additional experiments via a literature search. Using Google Scholar, we searched for relevant articles with the following keywords: fire exclusion experiment, experimental burn plot, prescribed fire experiment, ‘fire experiment’ savanna and ‘fire experiment’ forest. We scanned the first 50 results for each keyword in November 2020; articles ranged in publication date from 1970 to 2016. We examined each article and included those (1) in ecosystems with both herbaceous and woody vegetation, (2) that did not experience stand-replacing crown fires, (3) that included at least one burned plot and at least one unburned plot, (4) that did not entirely exclude herbivores and (5) that manipulated fire for three or more years. We chose 3 years as the minimum experiment duration to include a variety of sites in which herbaceous vegetation may begin to change in response to fire manipulation, with the recognition that a complete state transition is unlikely to occur on the shorter end of this timescale.

Data collection

Of the 71 fire manipulation experiments identified (Tables S1, S2), 30 sites met our criteria and reported relevant herbaceous vegetation data (Table S1). For these 30 sites, we classified the biome a priori based on the surrounding landscape as either savanna or forest (see Table S8). While the sites included in this study span a large range of regions and vegetation types, these terms refer broadly to open-canopy, mixed tree-grass systems for savannas and systems with dense woody vegetation or closed canopies for forests. We used three separate methods for classification: (1) site descriptions including overstorey cover and vegetation types from references associated with each site as listed in Table S1; (2) published photographs, satellite imagery and/or first-hand knowledge of the site; and (3) RESOLVE biomes based on site location (Dinerstein et al., 2017). All three methods agreed for 25 sites. For the other 5 sites (indicated with an asterisk in Table S8), we prioritized the first two criteria to classify biome, since RESOLVE does not capture finer scale variation. As an added precaution, we re-ran the analysis while excluding these five sites and found that the results were not substantially dissimilar from the full dataset (see Tables S9 and S10). We did not change any site classifications during or after data analysis.

From the dataset of herbaceous vegetation collected concurrently with the data from Pellegrini et al. (2021), we had percent cover data for all recorded species at the

individual plot level for 239 plots in 7 savanna sites and 5 forest sites. For these studies, we summed percent cover for all Poaceae species to calculate grass cover for each plot. We then classified each grass species according to whether it uses the C_3 or C_4 photosynthetic pathway according to a database compiled by Osborne et al. (2014). For each plot, we calculated the total C_3 and C_4 grass cover. For the remaining sites, we used published graphics or data tables to capture percent grass cover for every reported fire frequency at each site. For articles that did not publish grass percent cover data, we extracted grass biomass, herbaceous biomass, herbaceous percent basal cover, grass stem density or herbaceous stem density data for every reported fire frequency at each site (Table SI). For all sites, we also extracted the coordinates as well as the duration of the experiment at the time of data collection.

To determine whether climate modified herbaceous vegetation responses to changing fire regimes, we examined data on three characteristic climate variables based on ecologically relevant a priori hypotheses. First, we included MAP because of its well-documented positive correlations with tree cover and nutrient availability (Lehmann et al., 2011; Staver et al., 2011b). Second,

we included precipitation seasonality because wet season precipitation is thought to increase fuel accumulation, whereas the dry season likely promotes fuel curing (Kahiu & Hanan, 2018). Both MAP and precipitation seasonality are also thought to constrain the distribution of savannas and forests (Hirota et al., 2011; Staver et al., 2011b). Third, we included MAT because cold temperatures can reinforce savanna–forest bistability (Hoffmann et al., 2019; Joshi et al., 2020). All climate data were obtained from WorldClim, which integrates 30 years of weather station data from approximately 60,000 points, as well as topographic maps and satellite data to provide values for each location (Fick & Hijmans, 2017). We used the WorldClim database in the raster package (Hijmans, 2020) in R to obtain MAP, the coefficient of variation (CV) of monthly precipitation as a measure of seasonality, and MAT based on the coordinates of each site.

Of the 30 sites that met our selection criteria, 20 were savannas and 10 were forests (Table SI; Figure 1). Climate variable ranges were similar across the two biomes: MAP ranged from 407 to 1696 mm in savannas and 722 to 1683 mm in forests; precipitation seasonality ranged from a CV of 13 to 115 in savannas and 13 to 80

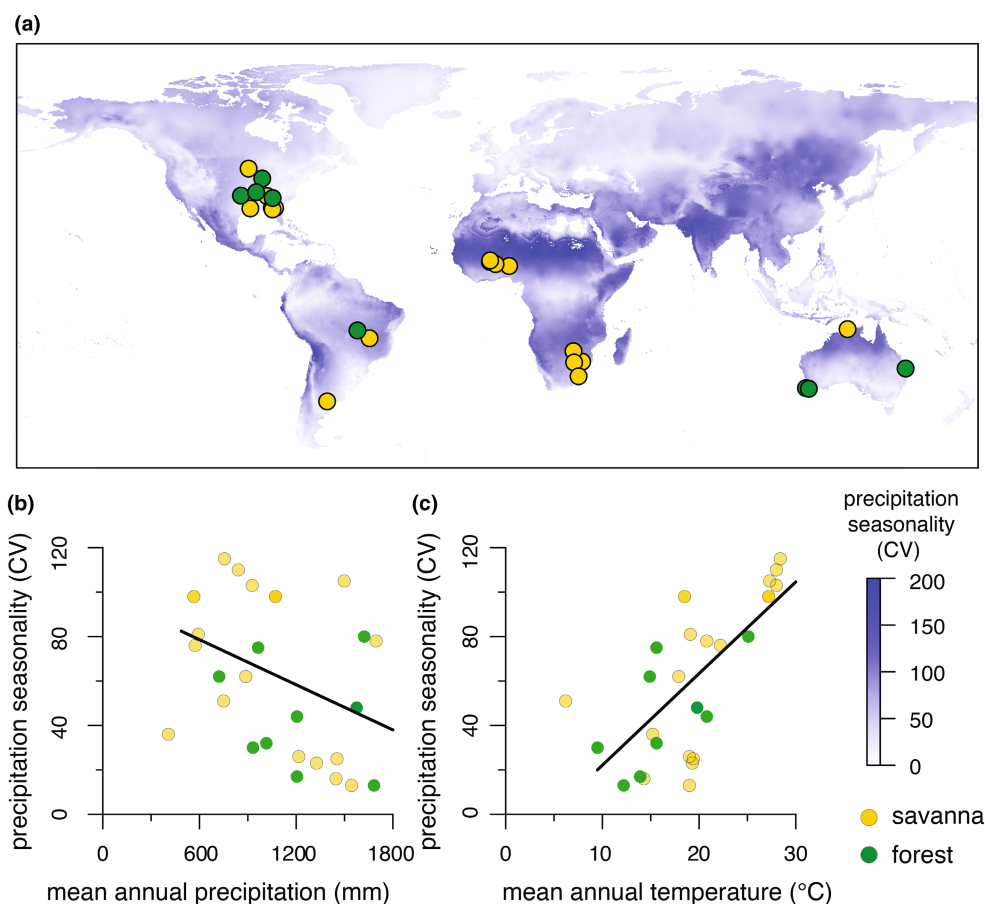


FIGURE 1 Global distribution of savanna and forest sites and relationships between climate variables included in this study. Sites are overlaid on a map of precipitation seasonality (a), with scatter plots for mean annual precipitation vs. precipitation seasonality ($r = -0.38$, $p < 0.05$) (b) and mean annual temperature vs. precipitation seasonality ($r = 0.71$, $p < 0.01$) (c).

in forests; and MAT ranged from 6.2 to 28.4°C in savannas and 9.5 to 25.1°C in forests (Table S1). Experiment duration ranged from 3 to 60 years for savannas and 6 to 64 years for forests (Table S1).

Statistical analysis

We used the available grass cover and herbaceous vegetation metrics (see *Data collection*) at each site to calculate response ratios, which were defined as the average metric at a given fire frequency divided by the average metric for the unburned plots at each site. Here we report log response ratios because they are widely used to estimate effect sizes when multiple different metrics need to be compared across studies and are simple to interpret; values greater than zero represent greater herbaceous vegetation abundance for plots with fire as compared to plots without fire. We tested all pairwise correlations between predictor variables and excluded one variable for pairs with $r > 0.6$ (see Table S10). Precipitation seasonality and MAT were the only correlated pair with $r > 0.6$ in this dataset (see Table S10), so we only used seasonality in the main model but also included a model with MAT (see Table S11) and interpret both variables. Using the log response ratios, we built a linear model with biome (savanna vs. forest), MAP (mm), precipitation seasonality (CV of monthly rainfall; unitless), experiment duration (years) and fire frequency (fires per year). Since we were interested in evaluating the role each of these variables had on responses to fire, we also included the interaction between each predictor and fire frequency. To account for differences between sites, we also fit a linear mixed-effects model with site as a random effect. The results were similar to the main model and are thus omitted from the main text (but see Table S7).

To specifically evaluate determinants of grass cover, we fit a linear mixed-effects model using the available plot-level data. For each plot, we square-root-transformed grass cover, which better satisfied the model assumptions and also most closely approximated a normal distribution as compared to untransformed or log-transformed data (but see Table S7 for untransformed data results). We then fit the model with the same variables as the model for the log response ratios. We also included the site of each plot as a random effect to account for site-level differences not captured by the other variables. When evaluating the data after separating C_3 and C_4 grass cover, we included the photosynthetic pathway and its interaction with fire as additional predictors in the full model. We also built linear mixed-effects models for C_3 and C_4 grasses on their own, with the same predictor variables as the original grass model.

Although we chose to fit linear models for interpretability, we also fit a logit-linked beta regression, as recommended by Damgaard and Irvine (2019) for proportional data, using the same predictor variables as the

linear model that included photosynthetic pathway. To fit the range (0,1), we adjusted the proportions by changing 0 to 0.001 and 1 to 0.999 before fitting the model. The results of the beta regression were similar to those of linear regressions and thus are omitted from the main text (but see Table S7).

For all models, we scaled the continuous predictor variables to have a mean of 0 and a standard deviation of 1. We then created model subsets for every combination of fixed terms in the full model and ranked each according to the Akaike information criterion (AIC). We selected the simplest model within two of the lowest AIC value as the best statistical model. Analyses were done in R, version 4.0.1, using the packages lme4 (Bates et al., 2015), glmmTMB (Brooks et al., 2017), MuMIn (Barton, 2020), visreg (Breheny & Burchett, 2017) and raster (Hijmans, 2020).

RESULTS

Herbaceous vegetation abundance, across 20 savanna and 10 forest sites (see Figure 1 and Table S1), was generally higher in fire treatments than in treatments without fire. There were widespread positive log response ratios to fire across sites (Figure S2) and metrics (e.g. biomass, cover). However, log response ratios varied. Biome had the strongest effect on the response of herbaceous vegetation to fire (see Table S3 for best model results and Table S6 for model selection), with an estimated $481 \pm 37.7\%$ larger herbaceous vegetation response to fire in savannas than in forests (Figure 2a). Climate also mattered: for every additional 100 mm in MAP, the estimated response of herbaceous abundance to fire was $20 \pm 3.9\%$ larger (Figure 2b), indicating that herbaceous vegetation in wetter sites was more responsive to fire. For every 10-unit decrease in precipitation CV, the estimated response of herbaceous abundance to fire was $16 \pm 5.2\%$ larger (Figure 2c).

Grass cover, from 239 plot-level measurements across 7 of the 20 savanna sites and 5 of the 10 forest sites, showed similar responses to fire as those described above (see Table S4 for best model results and Table S6 for model selection). Here, we were able to directly model grass cover instead of relying on response ratios, since measurement and sample units were comparable across sites. We found that the interaction between biome and fire frequency was significant: fires had relatively weak effects in forests (Figure 3a), but much more strongly increased grass cover in savannas (Figure 3b). In forests, an increase in fire frequency of 0.2 fires per year (e.g. from no fire to one fire every 5 years) increased the square root of grass percent cover by an estimated 0.974 ± 0.170 (Table S4). When back-transformed, this relationship was non-linear: for example, increasing fire frequency by 0.2 fires per year increased grass cover that started at 25 to 36% and at 50 to 65%. Grass cover in

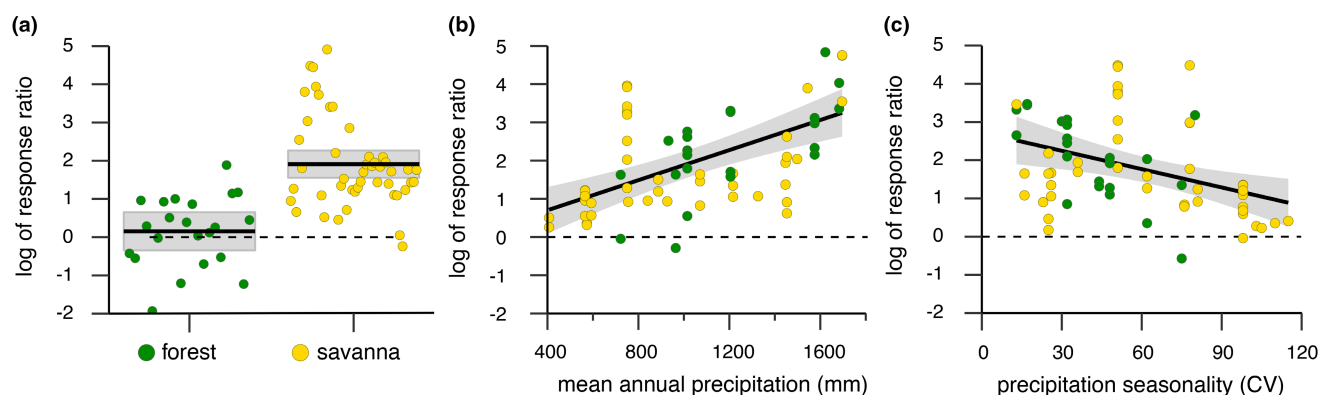


FIGURE 2 Herbaceous vegetation responses to fire (as log response ratios of fire to no-fire treatment values) depending on biome (a), mean annual precipitation (b) and precipitation seasonality (c). Plots show partial dependences from the best fitted model (see Table S3). Also shown are regression lines (black lines) and 95% confidence intervals (grey shading). Dashed lines indicate where herbaceous vegetation with fire is equal to herbaceous vegetation in the absence of fire.

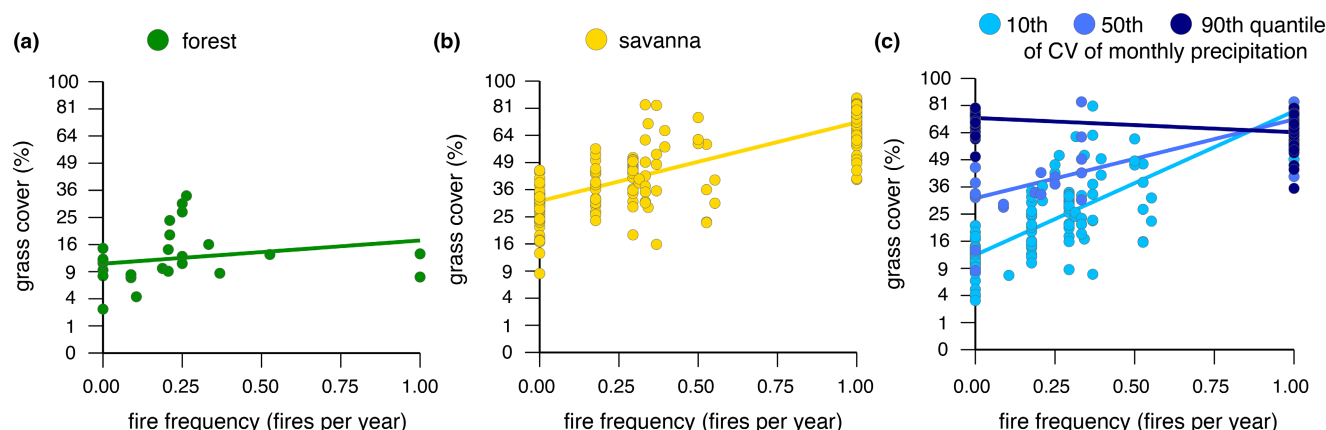


FIGURE 3 Grass cover responses to fire frequency in forest (a), in savanna (b) and depending on rainfall seasonality (c). Plots show partial dependences of grass cover from the best fitted model (see Table S4). Also shown are regression lines. Note that numbers on the y- (grass cover) axis have been back-transformed from the square root of grass cover and ranges were limited to 100%.

savannas (Figure 3a) was more responsive to fire than that in forests (Figure 3b). In savannas, increasing fire frequency by 0.2 fires per year increased the square root of grass percent cover by an estimated 1.4 ± 0.4 (Table S4), thereby, for example, increasing back-transformed grass cover that started at 25 to 41%, at 50 to 71% or at 75 to 100%. Note, however, that at high levels of initial grass cover or over large changes in fire frequency, this model can predict grass cover of above 100%, a limitation of this type of model.

Climate also influenced grass cover responses to fire. Grass cover was generally greater at more seasonal sites (measured as the CV of monthly precipitation; Table S4), but the effect of fire on grass cover decreased with seasonality (Figure 3c) and/or MAT (Table S11). This result is consistent with herbaceous vegetation response ratios, showing weaker responses to fire at more seasonal sites (Figure 2c). However, MAP was included in the best model for log response ratios but not for grass cover

(Table S6), perhaps because seasonality and MAP covary (see Figure 1 and Table S10).

Fire–climate interactions were also important when we considered C_4 grasses separately from C_3 grasses. A model that distinguished between C_3 and C_4 grass cover yielded a comparable model to the total grass cover model, but also included photosynthetic pathway and its interaction with fire as predictors of cover (see Table S5 for best model results and Table S6 for model selection). Overall, C_4 grass cover was much more responsive to fire than C_3 grass cover (Figure 4). When C_3 and C_4 grass cover were modelled separately (with C_3 grasses found in 119 plots across 9 sites, and C_4 grasses in 162 plots across 8 sites), the C_4 model was most similar to the total grass cover model (see Table S5 for best model results and Table S6 for model selection); fire was broadly associated with greater C_4 grass cover, with stronger responses in savannas and in less seasonal systems, while C_3 grass cover increased

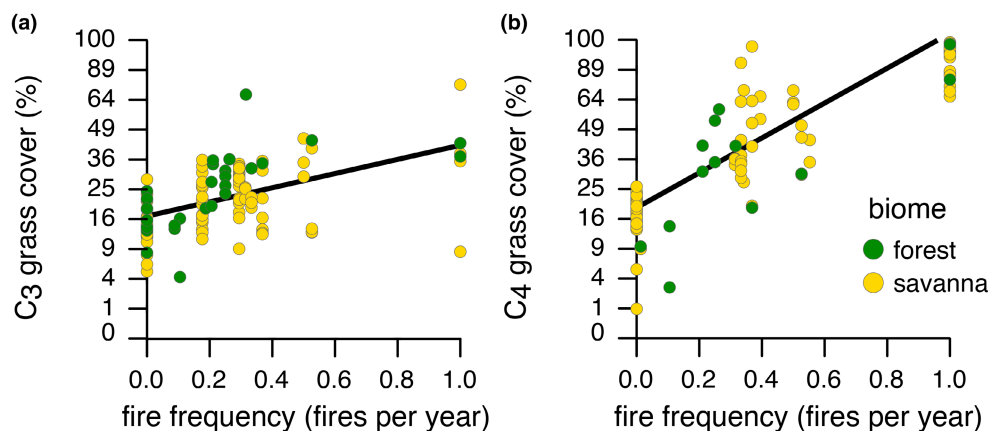


FIGURE 4 C_3 (a) and C_4 (b) grass cover responses to fire frequency. Plots show partial dependences from the best fitted model (see Table S5). Also shown are regression lines. Note that numbers on the y- (grass cover) axis have been back transformed from the square root of grass cover and ranges were limited to 100%.

weakly with fire frequency, irrespective of biome or seasonality.

DISCUSSION

Across 30 experimental sites spanning North and South America, Africa and Australia, we found widespread increases in both herbaceous vegetation abundance and grass cover in response to fire. Fire effects were greater in savannas than in forests, and grass cover responses were mostly driven by C_4 grasses. Climate also mediated responses: fire effects were larger in wetter, in less seasonal, and/or in cooler sites.

Our overall finding that herbaceous vegetation abundance increased with fire is consistent with interpretations of past work across both savannas and forests (see references in Table S1). Here, we further demonstrated that herbaceous vegetation responses to fire were larger in savannas, so much so that fire exclusion in savannas resulted in decreases to forest-like levels of grass cover, whereas burning in forests had more subtle effects on grass cover. Herbaceous vegetation responses to fire thus inversely reflect the responses of woody vegetation, which increases with fire exclusion in savannas (Pellegrini et al., 2021) but does not change or changes minimally with fire introduction in forests (Pellegrini et al., 2021; Veenendaal et al., 2018). Because herbaceous vegetation responses to fire, like woody vegetation responses, depended on the initial condition of the system as either a savanna or forest, our results accord with our expectations based on the savanna–forest bistability hypothesis.

Herbaceous vegetation responses to fire largely resulted from changes in C_4 grass abundance. Like overall grass cover, C_4 grass response to fire was greater in savannas and less seasonal systems. In contrast, C_3 grasses may have responded weakly to fire and increased with fire over longer experiment durations but did not

depend on biome or climate. This finding is consistent with past work showing that, while C_3 grasses may be more prevalent in the forest understorey (Ratnam et al., 2011), C_4 grasses are particularly well adapted to open, fire-prone systems because of their high resource use efficiency and their flexibility in biomass allocation (Simpson et al., 2016). These physiological traits contribute to both rapid resprouting and higher probabilities of survival after fire. Indeed, the Miocene expansion of savannas has been linked to climate elements that promoted frequent burning and, thus, to landscape opening; simultaneously, increased light levels may have increased productivity of C_4 grasses, which, in turn, may have resulted in greater fuel loads to support continued fires (Keeley et al. 2005; Karp et al., 2018). Our results here do not disentangle whether C_4 grasses simply dominate in open systems or whether they are particularly fire adapted and fire promoting, but they are consistent with literature documenting a strong association between C_4 grasses and open, fire-prone ecosystems (see, e.g., Peterson et al., 2007; Solofondranohatra et al., 2018).

Fire effects also depended on climate. Within the intermediate rainfall climate envelope represented here, herbaceous vegetation responses to fire were stronger in wetter sites, and responses of both herbaceous vegetation and grass cover were stronger in less seasonal sites. Two mechanisms may be at play. First, greater MAP is associated with greater herbaceous fuel load accumulation (Govender et al., 2006) and thus greater fire intensity (Govender et al., 2006) and burned area in savannas (Archibald et al., 2009). Second, strong rainfall seasonality may inhibit the development of a closed forest canopy (Staver et al., 2011b), limiting ecosystem responses to fire exclusion. Either way, this result supports the suggestion that long dry seasons are not necessary for fire to spread and maintain savannas. Here, because precipitation seasonality and MAT were positively correlated, herbaceous vegetation responses to fire may also have been stronger at cooler sites. Cooler locations may experience

more frequent frost events, which reinforce fire effects on vegetation by preventing maturation of tree seedlings and saplings at some sites (Hoffmann et al., 2019; Joshi et al., 2020). However, we did not explicitly examine probability of frost, nor did we assess whether temperate sites may be more responsive to changes in fire frequency. More work at sites that represent a wide range of environmental conditions is necessary to understand climatic mechanisms, but it is clear that climate does mediate the effects of fire on herbaceous vegetation.

While our findings support our hypotheses based on the bistability framework, there are several other explanations and data limitations that warrant further investigation. First, we did not directly evaluate mechanisms, including those related to other fuel types or microclimate (Hoffmann et al., 2012) or phylogenetic constraints (Cavender-Bares & Reich, 2012), that may contribute to differential responses of vegetation in savannas and forests; many of these processes are not mutually exclusive with savanna–forest bistability, and some may in fact be part of fire–vegetation feedback loops. Importantly, we were not able to directly evaluate hysteresis, since that would require re-applying fire in the same systems that transitioned from savanna to forest when fire was suppressed. Nor were we able to compare closely co-located savanna and forest dynamics at the same site (as in Peterson et al., 2007), which is another potential avenue for future investigation since soil and other environmental factors may modify vegetation response to fire.

Second, it is worth noting that we compare across broad geographical areas, including from some continents where there is a mismatch in the number of savanna and forest sites with relevant data. For example, there are no forest sites in this study from Africa and only one from South America. While the tropical forest site and temperate savanna sites are consistent with the results from temperate forests and tropical savannas, the limited amount of data complicates disentangling temperate versus tropical and subtropical effects. Additionally, it is important to acknowledge the limits of understanding state transitions while including some shorter experiments; continuing to monitor and evaluate long term dynamics in fire manipulation experiments will be paramount to better resolving the effects of disturbance on vegetation.

Furthermore, we considered only fire applied under typical environmental conditions, showing that regular managed fires have relatively small effects on herbaceous vegetation abundance in forests. Extreme fires may have very different ecosystem impacts. Fires that result from drought and other extreme weather can penetrate into forests that resist fires under normal circumstances (Beckett et al., 2022; Brando et al., 2020), resulting in massive fire-induced tree mortality (Barlow et al. 2008) as higher air temperature and lower relative humidity dry out fuels (Brando et al., 2014). In the case that a single intense fire is followed by the establishment of a regular

fire regime, a transition to savanna is possible (Beckett et al., 2022; Silvério et al., 2013). Importantly, regular fires seem to decrease the severity of fire extremes across forest ecosystems, even in the Amazon (Brando et al., 2014). As extreme fire weather and droughts become increasingly common under climate change, the breakdown of typical fire–vegetation feedbacks may break down, destabilizing forest ecosystems otherwise resilient to low-intensity fires (De Faria et al., 2021).

Overall, this study contributes further evidence that may be relevant in understanding savanna–forest bistability (Hirota et al., 2011; Staver et al., 2011a) and vegetation dynamics. Herbaceous vegetation fuels frequent fires in open-canopy grassy systems (Cardoso et al., 2022), thereby maintaining open savanna canopies, whereas closed forest canopies inhibit herbaceous vegetation growth (Lloyd et al., 2008), resulting in less frequent and/or less intense fires in forests. Thus, both woody and herbaceous vegetation contribute to the fire–vegetation feedbacks that appear critical for maintaining savannas and forests as alternative stable states.

This work also offers insights into the possible impact of fire management on vegetation in a changing climate. While this study focused neither on finer scale community composition related to different fire regimes (see, e.g., Cavender-Bares & Reich, 2012) nor on possible effects of fire on species invasions (see, e.g., Silvério et al., 2013), it does support the idea that fire is important for maintaining vegetation structure in the savanna–forest complex. Applying appropriately managed fire in forests does not necessarily result in transitions to savannas; however, in savannas, fire does maintain the open canopy and high grass cover. Proactively managing fires in savannas is therefore necessary (Bond & Parr, 2010) because woody encroachment via fire exclusion (Nowacki & Abrams, 2008; Stevens et al., 2017) cannot always be reversed by simply re-applying the previous fire regime (Buisson et al., 2019). Designing fire management programmes based on vegetation responses to changes in fire frequency, instead of implementing broadscale fire suppression, will thus be key to minimizing wildfire risk and maintaining resilient ecosystems.

AUTHOR CONTRIBUTIONS

ZJG and ACS developed the study's concept and design. AFAP, RJA, MLB, PMB, DGB, NB, ACF, SWH, WAH, KPK, PBR, PS, DS, KS, JMV, DDW and AW contributed data. ZJG, AFAP and TKR compiled the data. ZJG analysed the data, with feedback from AFAP and ACS. ZJG prepared the first draft of the manuscript, with input from ACS and early feedback from AFAP. All authors provided feedback and contributed to manuscript revisions.

ACKNOWLEDGEMENTS

We would like to thank the Staver Lab and three anonymous reviewers for their helpful comments on the

manuscript. Funding for this work was provided by a grant from the National Science Foundation (PI: ACS; NSF-MSB #1802453) and by the Grace Hopper College Richter Summer Fellowship. Participation of ACF was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; grant #311362/2019-2) and of SEH and PBR by grants from the National Science Foundation, including the Cedar Creek Long Term Ecological Research Program and the ASCEND Biology Integration Institute (NSF-DEB #1831944 and NSF-DBI #2021898).

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study and the associated code are openly available. DOI: <https://doi.org/10.5061/dryad.m37pvm71>.

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How to cite this article: Gold, Z.J., Pellegrini, A.F.A., Refsland, T.K., Andrioli, R.J., Bowles, M.L., Brockway, D.G. et al. (2023) Herbaceous vegetation responses to experimental fire in savannas and forests depend on biome and climate. *Ecology Letters*, 26, 1237–1246. Available from: <https://doi.org/10.1111/ele.14236>