RESEARCH ARTICLE

Forbs, grasses, and grassland fire behaviour

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Abstract

1. In grasslands and savannas, fire regime—frequently a major determinant of woody encroachment, herbaceous species composition and diversity, and nutrient cycling—is influenced by the quantity and characteristics of plant fuel. Laboratory studies reveal variation in flammability among herbaceous species, but field experiments are needed to assess whether herbaceous species composition meaningfully affects ecosystem-scale fire behaviour.

2. In our North American tallgrass prairie study system, grasses' thinner leaves and longer leaf retention appeared to create a finer, more aerated, more connected fuel bed than forbs. We tested the hypothesis that grasses promote fire spread area, fire intensity, and associated facets of fire behaviour more strongly than an equivalent mass of forbs.

3. We characterized spring fires over multiple years in 315 annually ignited plots spanning profound gradients of plant biomass, cover, and grass:forb ratio that resulted from species richness and composition treatments, in a 20-year grassland biodiversity experiment.

4. Grasses increased fire spread and associated facets of fire behaviour, compared with an equivalent biomass or cover of forbs. Grass dominance increased fire spread area—or equivalently increased fire frequency at any given point. For fire to spread through 50% of the 9 m × 9 m plot area required approximately twice as high an abundance of forbs as of grasses. Grass dominance also resulted in fires that advanced faster, were more intense (higher rates of heat release per unit fireline length), caused more damage to plants, and released heat to greater heights. Fire temperature at 50 cm above-ground was about twice as high in plots with only grasses as in plots with the same biomass of forbs.

5. *Synthesis.* Even within herbaceous ecosystems that may appear homogenously flammable compared with less flammable woody ecosystems, fuel quality—specifically, the proportional abundance of grasses—combines with fuel quantity and ignitions to determine effective fire regime at a given point. In spring burns, grass-dominated plots burn more completely and generate higher temperatures, and thus better suppress woody plants and volatilize more nutrients, than forb-dominated plots (holding all else equal).

KEYWORDS
ecosystem function and services, fire intensity, fire spread, flammability, forb, fuel load, functional composition, grass

1 | INTRODUCTION

In grasslands and savannas, the frequency, spread and intensity of fire can be a major determinant of the abundances of woody and herbaceous species (Bond, Woodward, & Midgley, 2005; Cavender-Bares & Reich, 2012). It seems plausible that the species composition of plant communities may in turn influence the characteristics of fires (Mutch, 1970), and thus might create feedbacks that could lead to alternate woody-dominated and herbaceous-dominated states (Bond et al., 2005; Staver, Archibald, & Levin, 2011). Plant composition can affect fuel quantity and other characteristics. Higher fuel quantities promote fire spread and intensity (Byram, 1959; Cheney, Gould, & Catchpole, 1993; Pausas, Keeley, & Schwilk, 2017). Independent of fuel quantity, the fraction of biomass that is dry, fine, loosely packed, well aerated and connected is positively associated with fire spread area, fire intensity (the rate of heat release per unit fireline length), maximum temperature, rate of spread, flame length and flaming zone depth (Byram, 1959; Pausas et al., 2017; Schwilk, 2015). Accordingly, finer herbaceous fuels (grasses and forbs) carry fire more readily per unit fuel quantity than coarser woody fuels (trees and shrubs). Within these broad categories, there is evidence, mainly from laboratory studies, for variation in flammability among woody species (De Magalhães & Schwilk, 2012; Mutch, 1970; Zhao, Cornwell, van Pomeren, van Logtestijn, & Cornelissen, 2016) and among herbaceous species (Simpson et al., 2016). Field experiments, though, are needed to assess whether herbaceous species composition meaningfully affects ecosystem-scale fire behaviour, independent of fuel quantity (Fernandes & Cruz, 2012; Prior et al., 2017; Schwilk, 2015).

The effects of grassland and savanna plant community composition on fire spread and intensity have been difficult to study experimentally in field conditions because local variability in the species compositions of plant communities is rarely at a scale suitable for replicated experimental burn units. Here, we report on the Cedar Creek biodiversity experiment, created in 1994 with more than 300 independently burned 9 m × 9 m plots planted with 1, 2, 4, 8, 16 or 32 perennial grassland species, with about 30 replicates of each diversity level having randomly chosen species compositions and an equal number of additional plots having randomly chosen functional group compositions (Tilman, Dodd, et al., 1997). Annual above-ground productivity turned out to be an increasing function of species richness (Tilman, Knops, et al., 1997). Thus, in total, the experimental treatments created plots with a wide range in biomass (and fuel) types and amounts that enabled us to examine how plant species composition and plant productivity impact fire behaviour under annual ignitions. In this North American tallgrass prairie, grasses appeared to create a finer, better aerated, more connected fuel bed than forbs because the grasses have narrower and longer leaves and retain leaves longer; we tested the hypothesis that grasses promote fire spread area, fire intensity, and associated facets of fire behaviour more strongly than an equivalent mass of forbs.

We proceeded in three steps. In many landscapes, fire extent is most limited by the quantity and characteristics of plant fuel, but the frequency and timing of ignitions and weather can also influence fire regime (Archibald, Roy, Van Wilgen, & Scholes, 2009). Thus, we first characterized the influence of fuel vs. ignition and weather on fire behaviour, using the fact that fuel loads in each experimental plot were relatively consistent across years whereas ignition pattern and weather varied.

Our second step was to characterize the influence of fuel quantity—measured as herbaceous biomass or cover—on fire behaviour. The quantity of herbaceous biomass available to fuel grassland and savanna surface fires depends on herbaceous productivity and rates of loss to herbivory and decomposition. Herbaceous productivity and loss rates, in turn, depend on external factors including climate, soil parent material, and topography; but also on species richness and composition. Biodiversity experiments in perennial herbaceous systems, including the one we report here, have shown that biomass increases strongly with increasing planted species richness (Tilman, Naeem, et al., 1997). Biomass is our principal measure of plant abundance and fuel quantity, but we also used cover as an equivalent measure during the early years of this experiment, when cover rarely reached 100%.

Our third and focal step was to test whether herbaceous species composition influenced fire behaviour independent of productivity. We focus on grasses vs. forbs (i.e. non-grass herbaceous plants, all broad-leaved dicotyledons in this experiment) because most grass species have narrower (finer) leaves which should dry and ignite more readily, and longer leaves that may increase fuel connectivity and ignitability (Pausas et al., 2017), compared with leaves and stems of many forb species. Moreover, grasses tend to retain their leaves over winter and form a well-aerated fuel bed for spring fires, compared with forbs, which—at least in our study system—tend to drop more of their leaves in winter, resulting in a litter layer on the soil surface with little aeration that may reduce fire spread and intensity (Schwilk, 2015). However, fire spread and intensity tend to be correlated with flame length, flaming zone depth, and maximum temperature, other facets of fire behaviour can vary more or less independently depending on the system, including total heat release (Pausas et al., 2017; Schwilk, 2015), fire residence time (Prior et al., 2017), and reaction intensity (the rate of heat release per unit area). These other facets have been proposed to influence soil heating and mortality of underground plant structures (Gagnon et al., 2015), but we do not have expectations for how these differ between grass and forb fuels: residence time and reaction intensity depend on how fast the fire moves and on how deep the flaming zone is (Byram, 1959), and grass effects on spread rate and flaming zone depth could offset each other to an unpredictable extent.

Forbs are abundant in many grasslands and savannas (Peterson, Reich, & Wrage, 2007), and co-dominate or dominate in some calcareous grasslands (Willems & van Nieuwstadt, 1996), old fields (Tilman, 1987), tallgrass prairie (Fuhlendorf & Engle, 2004), and montane meadows (Harte & Shaw, 1995). The possibility that forbs and grasses may differentially impact fire behaviour has received little attention but could be of importance. Positive feedback cycles can occur when grasses displace forest by increasing fire frequency and intensity, which in turn promotes fire-tolerant grasses

over fire-intolerant trees (Brooks et al., 2004; D'Antonio & Vitousek, 1992). This feedback may maintain grassland or savanna as alternate stable states in areas climatically suitable for forest (Bond et al., 2005; Staver et al., 2011). Forbs are rarely mentioned in this context, but if grasses create more intense fires they may suppress tree establishment more strongly than forbs, with implications for biome distributions. In addition, different effects of grasses vs. forbs on fire may influence grassland species composition (Ellair & Platt, 2013; Gagnon, Harms, Platt, Passmore, & Myers, 2012; Thaxton & Platt, 2006). Finally, if grasses result in greater fire spread and higher fire temperatures, this could lead to greater volatilization of nitrogen, and potentially of phosphorus and sulphur which volatilize only in hotter fires; this could in turn reduce ecosystem pools of these nutrients.

We tested the hypothesis that grasses promote fire spread, intensity and correlated fire measures more strongly than forbs for a given abundance. We assessed the influence of herbaceous fuel quantity and quality by measuring fire behaviour in a 20-year grassland biodiversity experiment, where species richness and composition treatments created highly replicated gradients in plant abundance and the ratio of grasses to forbs. We measured three complementary suites of fire behaviour variables in replicate plots. (1) Fire spread area (the area burned following one ignition) and fire spread distance. The larger the fire spread area, the more frequently any given point within a parcel burns (i.e. the higher the "point fire frequency," as we call it), holding ignition frequency constant. (2) Fire intensity, fire temperature at two heights, rate of spread, flame length, flaming zone depth, fire residence time and reaction intensity. (3) Fire severity, which we assessed using fire damage to plants. We ask how these facets of fire behaviour are influenced by (1) fuel (i.e. the properties of a plot, principally fuel quantity and characteristics) vs. other factors such as weather or ignition pattern, (2) the quantity of herbaceous fuel, i.e. total herbaceous biomass or cover, and (3) the relative abundance of grasses vs. forbs. Finally, we tested whether plots with higher fire spread or intensity accumulated soil N at lower rates.

2 | MATERIALS AND METHODS

2.1 | Experimental design

We addressed our questions in the Big Biodiversity experiment (experiment number E120) at Cedar Creek Ecosystem Science Reserve, Minnesota, USA (Tilman, Dodd, et al., 1997). This experiment was established in 1994 using dominant and common perennial species of tallgrass prairie oak savanna, which dominated this region before European settlement.

A grid was established of 342 plots, each 9 × 9 m, separated by mown aisles at least 4 m wide. Of these plots, 154 core plots were randomly placed across this full grid and were assigned random draws of 1, 2, 4, 8, or 16 species from a pool of 18 species (Tilman et al., 2001) and maintained by weeding through 2014. The species pool had four species each of C4 grasses, C3 grasses, legumes,

and non-legume forbs, as well as two woody species (*Quercus* spp.; Tilman et al., 2001). Additional plots were planted with 1, 2, 4, 8, 16 or 32 species from an expanded species pool containing an additional four species of each of the four herbaceous groups (Tilman, Knops, et al., 1997); for the years in which they were also sampled (until 2000), we analysed these plots combined with the core plots for a total of up to 315 plots. We refer to non-grasses as forbs because woody plants were removed in 2010 before collecting most of the data reported here and were very rare during the earlier fire measurements (1996–1999, when their mean cover was 0.04% and their maximum cover was 2%).

The experiment was established in an old field where organic matter had been depleted by cultivation. Moreover, the year before the experiment was established, the top 6–8 cm of soil was removed by bulldozer to reduce the seedbank and the soil was ploughed (Fornara & Tilman, 2008).

2.2 | Fire conditions

Fire scar records indicate that fire was approximately annual before European settlement (Tilman et al., 2000). Most fires in the past 200 years in a nearby oak savanna occurred when trees were dormant, outside of the late summer lightning peak, suggesting that ignitions by people were important even before European settlement (Wolf, 2004).

The experiment was burned every spring, as soon as possible after snow-melt and while vegetation was still dormant; burn dates ranged from 25 March to 28 April in the years that fire behaviour was measured, 1997–2000 and 2010–2014.

Until 2006, the experiment was burned as one block by first establishing blacklines along the downwind edges and then igniting headfires in the upwind row of plots and allowing fire to jump from plot to plot. Burning the whole experiment took about 2 hr. From 2007 onwards, each plot was ignited independently along its entire upwind edge using a driptorch: rows of plots were ignited sequentially, starting with the down-wind row and working up-wind, which took about 4 hr. The spatial positions of plots did not significantly influence the results. There was no evident spatial pattern in the fire behaviour measures when mapped nor plotted against their *x* and *y* co-ordinates. Nor was there significant spatial autocorrelation in the residuals from our multiple regressions of fire behaviour response measures against grass and forb biomass (Mantel tests for correlation between differences in residuals and distances in space between plots: $p > .15$, mostly much larger). Moreover, the species richness and composition treatments were randomly allocated to plots, so any correlation among plots in fire behaviour would not lead to spurious associations with treatments.

Mean air temperatures, recorded hourly and averaged over the duration of each burn, ranged from 8.5 to 18.4°C in 1997–1999, and 0.4–24.3°C in 2010–2014. Mean relative humidity ranged from 21% to 32% in 2010–2014; mean wind speeds ranged from 2.7 to 4.3 m/s in 1997–1999, and 1.5–3.9 m/s in 2010–2014. We mostly present averages for these two sets of years, but we also present year-specific

data for 2000, 2011 and 2013; in these burns, respective mean air temperatures were 14.7, 18.0 and 24.3°C, and mean wind speeds were 1.9, 2.9 and 2.8 m/s. Mean relative humidity in 2011 was 32%, and in 2013 was about 34%. Weather was measured about 1 km from the experiment (Cedar Creek dataset E080), except for humidity in 2013 (measured 8 km away).

2.3 | Fire behaviour

We characterized fire behaviour in two broad ways: (1) the areal and linear extent of fire spread; and (2) the characteristics of the fire's behaviour within the area that it burned.

First, we visually estimated fire spread area as the percent of each plot that burned following one ignition in 2010, 2011, 2013 and 2014. Each year, plots that had not burned completely following one ignition were re-ignited; this modestly increased the proportion burned in some plots, though many remained incompletely burned. Fire spread area was estimated following any re-ignitions each year 1997–1999 and 2010–2014. (i.e. in 2010, 2011, 2013 and 2014 fire spread area was estimated both following one ignition and again after any re-ignitions.) We supplemented areal fire spread with a measure of linear fire spread. Each year 2010–2014, we inferred from post-burn photographs whether fire had spread a distance of at least 7 m following one ignition, from each plot's upwind ignited edge to a line 7 m downwind. Video of fire spread through subsets of plots (23 plots in 2010, 13 in 2011, and 69 in 2013) confirmed photographic inferences.

Second, we measured fire temperature as our main metric of fire behaviour within burned areas. Fire temperature was estimated using metal tags—pyrometers—with Omega Laq paints (Omega Engineering, Stamford, CT, USA) of varying melting points, placed in each plot before burning (Wally, Menges, & Weekley, 2006). In 2011, 13 paints with melting points spanning 79–788°C were spotted on copper plant tags (National Band and Metal, Newport, KY, USA), covered by a second tag, and placed at ground level and on stakes 50 cm above-ground at three corners of a 5 × 5 m square centred in each of the 154 core plots. After the burn, we estimated the proportion of a circle with 20 cm radius around each pyrometer that carried fire. We used identical tags in a subset of 100 plots in 2010 and 90 plots in 2014. We verified the paints' rated melting points by placing sample tags in a calibrated muffle furnace for 1 min at increasing temperatures and scored whether paints had melted using a dissecting microscope and reference images. Tags were assigned the melting temperature of the highest melted paint; when no paints were melted, they were assigned 20°C to approximate ambient temperature. We calculated the median fire temperature at each height for each plot in each year.

We also measured flame height and angle, flaming zone depth (the distance from the flame front to the back of the flame zone), and the time required for the flame front to advance 5 m, all in the central 5 × 5 m of each plot (which was marked with stakes of known height that served as dimensional references in digital video recordings). From these measurements, we calculated flame length and

forward rate of spread. To calculate fireline intensity (rate of energy release per unit length of fire front, Byram, 1959), we multiplied the forward rate of spread by the fuel load (approximated as biomass per unit area late the previous summer) and the approximate heat of combustion 20 MJ/kg (Williams, Gill, & Moore, 1998). We assumed the heat of combustion to be constant across species compositions because it is very similar across herbaceous species (Byram, 1959; Kidnie, 2009). We calculated reaction intensity per unit area by dividing fireline intensity by the flaming zone depth.

2.4 | Fire severity

As a biotic index of fire severity, we measured fire damage to similarly sized individuals of two plant species in a subset of plots that spanned the species richness gradient. First, we planted and marked 12 seeds of *Quercus macrocarpa*, the dominant tree in bur oak savanna at this site, at systematic locations in each of 32 plots after the spring 2010 burn and assessed how the spring 2011 burn damaged the 372 resulting seedlings. Second, we marked 99 systematically selected flowering plants of the forb *Liatris aspera* in 37 plots in fall 2013 and assessed how the spring 2014 burn damaged them.

2.5 | Plant abundance and fuel load

Climate is continental, and most growth is during summer from May until August. Cold winters, largely below freezing, inhibit decomposition and herbivory, so we measured plant cover and biomass in late summer the previous year to represent the fuel for spring fires. Each late July from 1996 to 1999, percent cover of each species was estimated using four 1 m^2 quadrats in each plot. These estimates indicate absolute (not relative) abundance of plants: plants, bare ground and litter together summed to 100%. Simultaneously, dry plant biomass, excluding litter from previous years, was measured by clipping strips (Tilman, Reich, & Knops, 2006); this biomass was not sorted to species, and included *Quercus* spp. tree seedlings in addition to herbs, but woody cover was negligible as described above. Woody plants were removed from the experiment in 2010. Each late July from 2010 to 2014, dry herbaceous biomass was measured using clip strips and sorted to species and previous years' litter. Litter from previous years was excluded from analyses; it was minimal and including it did not change results (not shown).

To assess how well summer (late July) biomass represented fuel loads the following spring, we clipped biomass (not separating previous-season biomass from older litter) immediately before burning in spring (March) 2015 in strips adjacent to those clipped the previous summer in 30 plots ranging from grass-dominated to forb-dominated. Spring herbaceous biomass, that is, actual fuel load, was closely related to herbaceous biomass the previous summer (correlation coefficient $r = .87$, $p < .001$). Moreover, a multiple regression of spring biomass vs. biomass the previous summer and its interaction with the proportion grass the previous summer, with the intercept set at zero, showed that forb-dominated plots did not lose significantly more biomass than grass-dominated plots (interaction

$p = .131$). This regression estimated that in exclusively forb plots spring biomass (i.e. fuel load) was 67% of previous summer biomass whereas in exclusively grass plots spring biomass was 79% of previous summer biomass (Figure S1).

2.6 | Soil nitrogen

Soil N samples were collected in summer 1994 and 2015. In each plot in each year, nine cores to 20 cm depth were aggregated by plot, sieved to remove roots, and analysed for total N using methods detailed by Fornara and Tilman (2008).

2.7 | Analyses

We assessed the effects of grasses vs. forbs on measures of fire behaviour and severity using multiple regressions with both plant types as independent variables. To perform two-tailed tests for whether the two plant types differed in their effects on fire, we used 10, 000 bootstrap samples (each drawn randomly with replacement from the data rows) to estimate the sampling distribution of the difference between their coefficients. Fire spread area, a percentage, was logit-transformed when used as a dependent variable to linearize its relationship with independent variables (Warton & Hui, 2010). The logit transformation, $\log(p/1-p)$ where p is a proportion, is not defined for $p = 0$ (0%) or $p = 1$ (100%), so before transforming we added 0.1% to values below 50% and subtracted 0.1% from values above 50%.

Because plots without fuel have zero fire spread and intensity, we fit these regressions through the origin by omitting intercepts. For logit-transformed dependent variables, and for logistic regressions, omitting an intercept fits the regression through 0 on the logit scale, or 0.5 on the probability scale, when the independent variables are 0; to instead fit the regression through approximately 0 on the probability scale, we used the logit of 0.1% as an offset (Gelman & Hill, 2007). (The logit transformation is undefined for 0; our conclusions were not sensitive to using 0.1% vs. other arbitrarily small values.) For the fire temperature dependent variables, we fit lines through the ambient temperature when the independent variables were 0 by subtracting the ambient temperature from the dependent variables before fitting regressions and adding the ambient temperature to fitted values for plotting.

We estimated variance components and mixed-effects regression models using reduced maximum likelihood with the R package lme4 (Bates, Maechler, Bolker, & Walker, 2014). We performed bootstrapping using the R package boot (Canty & Ripley, 2015) and calculated other statistics using standard R functions.

3 | RESULTS

3.1 | Fire behaviour controlled principally by fuel

Most of the variance in fire spread area and fire temperature was accounted for by the abundances of the (perennial) plants which changed slowly across years, or other similarly stable plot characteristics, according to variance components analyses using random effects regressions (with plot and year as non-nested random effects and an intercept as a fixed effect). A random effect representing persistent plot effects (i.e. variation among plots that is consistent across all years in an analysis) accounted for most of the variance in fire spread area in 1997–1999 (79% of variance) and in fire spread area following a single ignition in 2010–2014 (59% of variance), as well as in fire temperature in 2010–2014 (62% of variance at ground level, 61% at 50 cm above-ground). Only 2%–6% of the variance in these measures was attributed to a random effect representing variation among years (averaging across plots) due to either weather before and during burns or mean fuel properties. The remaining 19%–35% of variance in fire spread area and temperature arose from a combination of measurement error and variation in plot effects between years, which could be due to minute-to-minute variation in burn weather, or year-specific variation among plots in ignition pattern or fuel properties.

3.2 | Fuel quantity, driven by plant species richness, affects fire behaviour

Herbaceous biomass increased linearly with increasing log planted species richness treatments (Figure 1c, $F_{1,152} = 156.6$, $p < .001$), as previously reported for this experiment (Reich et al., 2012; Tilman, Knops, et al., 1997, 2001). Accordingly, fire spread area and fire temperature increased similarly and significantly ($p < .001$) with herbaceous biomass, cover, and planted species richness (in regressions with biomass, cover, or species richness as the sole independent variable, an estimated intercept, and responses transformed as described in captions to Figures 1 and 2). Of these three independent variables, we focus on biomass as our main independent variable because it is closer to the mechanism driving fire spread than is species richness, and because we have more data on biomass than on cover. Fire also responded similarly to effective species richness, e^H, where H is Shannon diversity estimated from species' relative biomass (not shown).

Fire spread through a larger percentage of the area of plots that had more plant biomass late the preceding summer, after igniting each plot once along its upwind edge (Figure 2a). Plots with more than about 300 g/m^2 of summer biomass consistently burned completely whereas, in plots with less biomass, fire spread area varied from near zero to near complete, both averaged across multiple years (2010–2014, Figure 2a) and in one representative year (2011, Figure S2a). Increased fire spread area is equivalent to increased effective fire frequency at each point, or fire return interval: a given point within a plot would be expected to burn every 1/(proportion burned) years. Thus, given annual ignitions, a fire spread area of 20% is equivalent to a point fire frequency of every 5 years; a fire spread area of 100% is equivalent to an annual point fire frequency.

Fire spread area showed a similar saturating increase with plant cover (Figure 2d) as with biomass (Figure 2c), averaging over the years (1997–1999) that both abundance measures were estimated, consistent with an approximately linear relation between cover and biomass observed during this period (Pearson's correlation
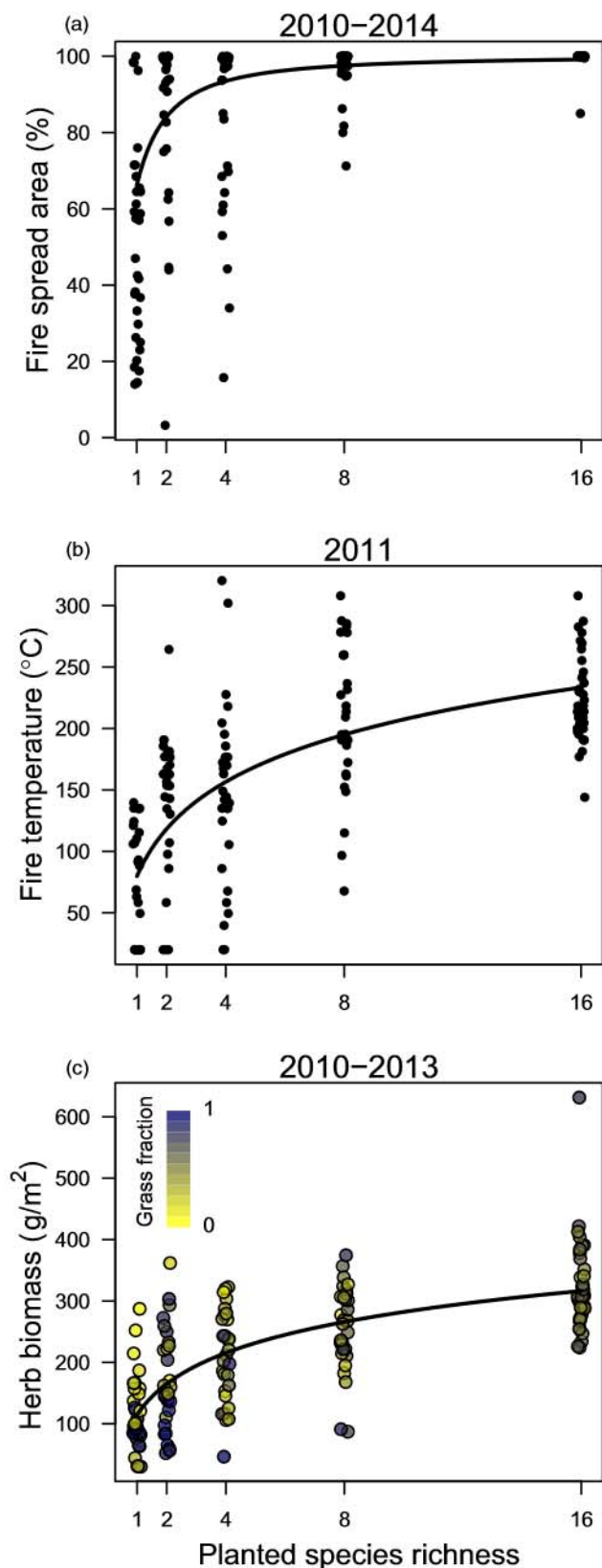
(a) 2010–2014
Fire spread area (%)

(b) 2011
Fire temperature (°C)

(c) 2010–2013
Herb biomass (g/m^2)
Grass fraction

Planted species richness

FIGURE 1 Among 154 grassland plots seeded to establish a species richness gradient in 1994 and maintained by weeding non-planted species and annual burning, plots with higher planted species richness had fire spread through a larger percentage of the plot area following one ignition (a), higher fire temperature at ground level (b), and higher herbaceous plant biomass (c). Fire spread area (a) was averaged for each plot over 2010, 2011, 2013 and 2014; late summer biomass (c) was averaged over available preceding years (2010, 2012, 2013). Fire temperatures are medians of three measurements per plot. Curves are linear fits against log planted species richness; fire spread area was logit-transformed to fit the curve. Planted species richness treatment is jittered for clarity [Colour figure can be viewed at wileyonlinelibrary.com]

with fire spread probability increasing at a threshold plant abundance (inflection point) of about 200 g/m^2 (Figure 2c) or 40% cover (Figure 2d, black curve), though this relationship is noisy without distinguishing grasses from forbs (done below). In 1997–1999, fire spread area was estimated after re-igniting incompletely burned plots; fire spread area may have been modestly over-estimated at low cover compared with 2010–2014 when we report fire spread area after igniting each plot once. However, this effect was likely small: re-ignition increased fire spread by only 5.4% of the plot area, on average, in 2010, 2011, 2013 and 2014 when spread was estimated both before and after any re-ignitions.

Fire spread through a larger fraction of plots' areas as planted species richness increased from 1 to 16 (Figure 1a), as it did for biomass and cover. Averaged over 4 years, fire spread following one ignition in monocultures ranged from less than one-fifth of plot area to complete, but in 16-species plots was consistently near-complete. Mean fire spread approached completeness even in an average four-species plot but became more consistently complete with further increases in species richness.

However, fire spread area saturated at 100%, fire temperature increased approximately linearly with increasing total plant biomass (Figure 3a, Figure S3a) and cover (Figure S3b) late the preceding summer, and with log planted species richness (Figure 1b). Plot-level median fire temperatures were about 300°C at ground level in plots with 400 g/m^2 of biomass the previous year, near the upper limit of above-ground productivity in this experiment, in 2011 (Figure 3a). Similarly, in 2000 median temperatures of about 300°C were measured 10 cm above the ground in plots with 400 g/m^2 of biomass (Figure S3a) or a mean plant cover of about 80% (Figure S3b). Every 16-species plot had a higher median fire temperature than any monoculture (Figure 1b).

Next, we examine how composition of plant fuel influenced fire behaviour independent of total plant abundance.

3.3 | Grass and forb relative abundance affects fire spread

Fire spread area following one ignition increased more strongly with grass biomass than with forb biomass in the 154 core plots, in multiple regressions forced through the origin (bootstrap test of

coefficient $r = .79$). In 1997–1999, only 3–5 years after the experiment was established from seed in 1994, numerous plots still had low biomass (<50 g/m^2). Most of these low-biomass plots had low fire spread and formed a lower tail of a sigmoid curve consistent

FIGURE 2 In grassland biodiversity experiment plots, fitted values from multiple regressions with grass and non-grass abundance as independent variables show that fire spread area (a, d) and probability of carrying fire at least 7 m (b) was predicted to increase significantly more strongly with abundance in plots containing only grasses (blue/dark grey curves) than in plots containing only forbs (yellow/light grey curves). (b) The fraction of years that fire carried at least 7 m, for each plot. Y axis values in (b) are jittered for clarity. Here, p-values are bootstrap tests of the equality of grass and non-grass biomass effects. Black curves are fitted values from linear regressions against total biomass or cover, regardless of grass/forb composition. Regressions were forced through the origin and were either linear regressions with logit-transformed fire spread area as response (a, c, d) or a logistic regression with the number of years that fire was carried (of 5 trial years) as response (b). Fire spread area was averaged across years for each of 154 plots in 2010–2014, when there were single ignitions (a, b), and 315 plots in 1997–1999, when there may have been more than one ignition (c, d). All burns were in spring; late summer biomass or cover measures the preceding years were averaged [Colour figure can be viewed at wileyonlinelibrary.com]

equality of the coefficients of the grass biomass and forb biomass independent variables: $p = .011$ for 2010–2014 means, Figure 2a; $p = .036$ in 2011, Figure S2a). The figures plot predicted values from these multiple regressions for plots containing only grasses (blue/dark gray lines) or only forbs (yellow/light grey lines): a given level of fire spread was attained at a lower total biomass if that biomass was entirely grasses than if it was entirely forbs. For example, fire was predicted to spread through 50% of a plot's area for approximately 120 g/m² of exclusively grass biomass vs. 210 g/m² of exclusively forb biomass (Figure 2a). These estimates of the differences between grass and forb effects are conservative: the grass-dominated points in Figure 2a, and more flexible curves (not shown), indicate that fire spread rose even more steeply with grass cover, reaching 50% at approximately 50 g/m² of grass biomass. Plots with a mix of grasses and forbs were predicted to be intermediate.

The difference in the effects of grass vs. forb abundance on fire spread area appeared even stronger from 1997 to 1999, when species' relative abundances were assessed using their percent cover instead of their biomass and more plots (315) were sampled: a multiple regression predicted fire spread of 50% in plots with 30% grass-only cover, or 80% forb-only cover (Figure 2d). Re-igniting incompletely burned plots before measuring fire spread area in 1997–1999 is unlikely to have contributed to the higher measured flammability of grasses: in 2010–2014, both absolute and proportional increases in fire spread area due to re-ignition were weakly and non-significantly *lower* in grass-dominated plots (Spearman's correlation coefficient between proportion grass and absolute or relative increase in fire spread area $\rho = -0.06$, $p = .23$, absolute increase; $\rho = -0.04$, $p = .44$, relative increase).

Another measure of a plot's propensity to carry fire is whether it carried fire a certain distance following one ignition. Much like fire spread area, with which it was tightly correlated ($\rho = 0.85$, 2010–2014 means), the probability of carrying fire at least 7 m increased
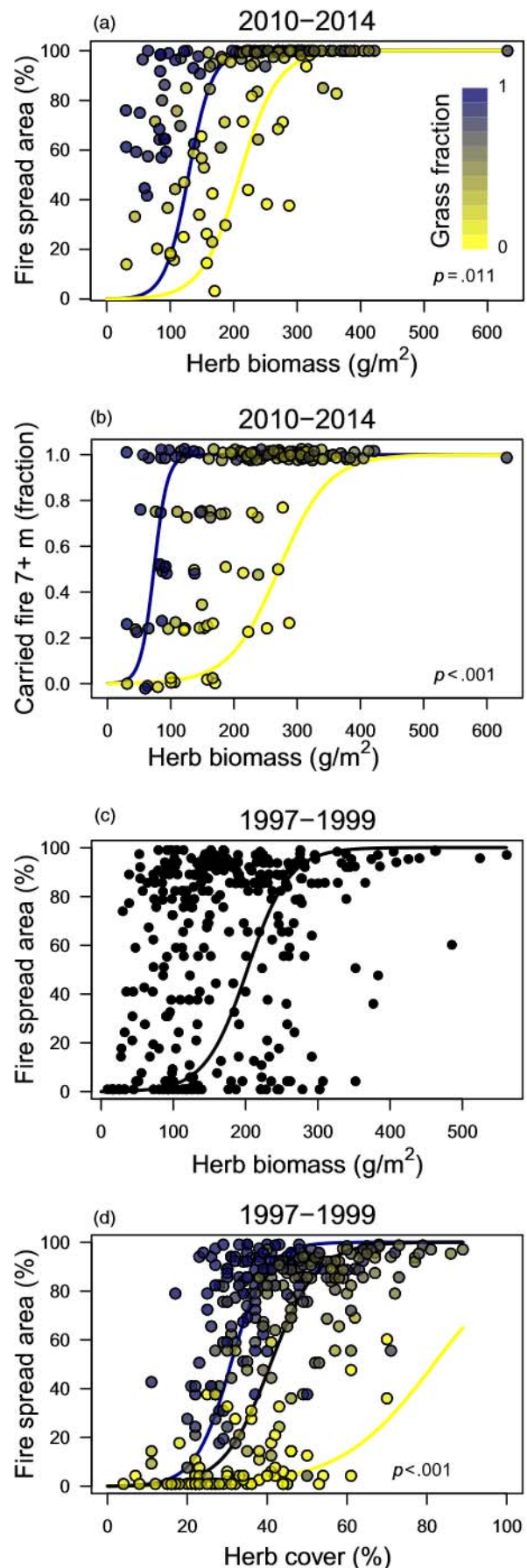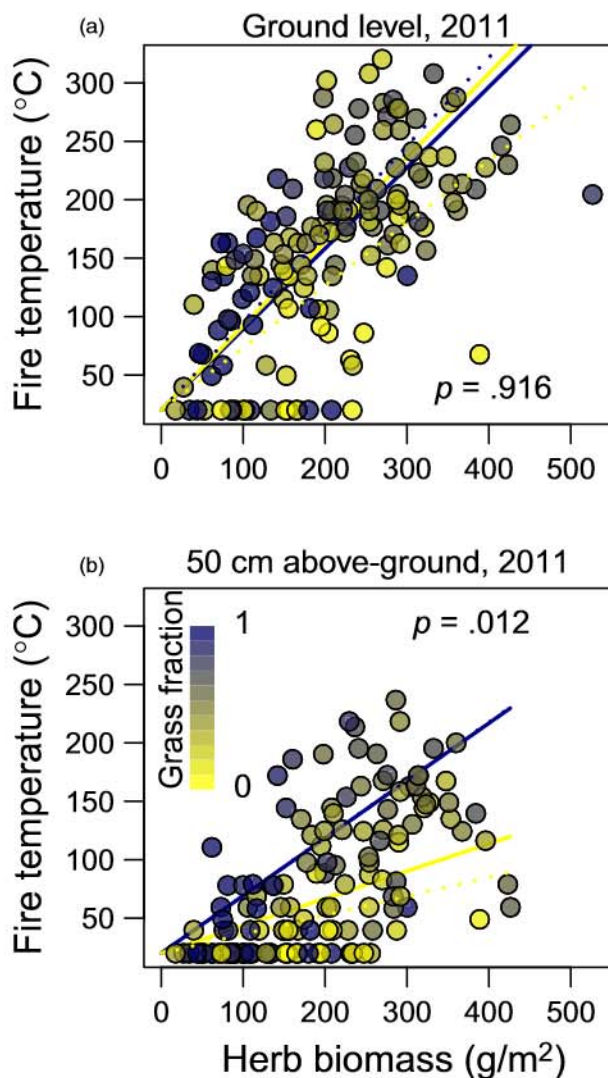
FIGURE 3 In grassland biodiversity experiment plots, median fire temperature of three pyrometers in each of 154 plots at ground level (a) did not increase more strongly with grass biomass than with forb biomass, whereas temperature of similar pyrometers in a subset of 135 plots at 50 cm above-ground (b) did. Lines are fitted values for plots with only grass biomass (blue/dark grey) or only forb biomass (yellow/light grey), from multiple regressions forced through the origin with grass and forb biomass as independent variables. Here, p-values are bootstrap tests of the equality of grass and forb biomass effects. The relationship between measured temperatures and unadjusted grass and forb biomass (shown by the points and dotted lines, statistics not shown) conflates fire temperature with whether fire spread around pyrometers. To isolate the effects of *burned* biomass on fire temperature, independent of fire spread, we fit regressions to grass and forb biomass independent variables that had been multiplied by the mean proportion of area burned in a 20 cm radius around the pyrometers in a plot (solid lines and p-values) [Colour figure can be viewed at wileyonlinelibrary.com]

more rapidly with grass biomass than with forb biomass, both averaged over 2010–2014 ($p < .001$, Figure 2b) and in 2011 ($p = .001$, Figure S2b). The multiple regression fitted to 2010–2014 means

indicates that a 50% probability of carrying fire required about 70 g/m^2 of exclusively grass biomass, or about 270 g/m^2 of exclusively forb biomass (Figure 2b).

3.4 | Grass and forb relative abundance affects fire intensity

Multiple regression showed that fire temperature at ground level increased similarly with previous-season grass biomass and forb biomass in 2011 ($p = .916$ for test of equality of grass and forb coefficients, Figure 3a), after adjusting biomass for the proportion of the area within 20 cm of pyrometers that burned. (Measured fire temperature would have depended on whether the fuel around a pyrometer burned, as well as how hot it burned; multiplying plot biomass by the mean proportion burned around pyrometers in that plot accounted for whether the fuel burned, to reveal effects on fire temperature independent of effects on fire spread.) In contrast, at 50 cm above-ground fire temperature depended strongly on species composition even after adjusting biomass for the proportion burned around the pyrometers ($p = .012$, Figure 3b). For a biomass of 300 g/m^2, the fitted temperature was twice as high (about 160°C) in plots with only grasses compared with plots with only forbs.

Aspects of fire behaviour related to spread rate also increased more strongly with grass than forb biomass and were correlated with fire temperature. In 2013, multiple regressions indicated that flame length (Figure 4a) and forward rate of spread (Figure 4b) both increased more strongly with grass biomass than with forb biomass ($p = .005$ and $p = .002$, respectively). At a biomass of 300 g/m^2, plots with only grass were estimated to have flames 2.8 m long advancing at 0.8 m/s, about three times greater than plots with only forbs. Both flame length and rate of spread were more strongly correlated with fire temperature 50 cm above-ground (Pearson's $r = .86$ and .64, respectively) than with fire temperature at ground level ($r = .70$ and $r = .55$, respectively), across 15 plots with suitable measurements in 2010 or 2011. The difference in flame length between grass- and forb-dominated plots arose from differences in flame height, not angle (not shown). Fireline intensity, the rate of heat release per unit time per unit length of fire front, increased more strongly with grass biomass than with forb biomass (Figure 4c, $p < .001$). Using a multiple regression, plots with 300 g/m^2 of grass-only biomass had fitted values of approximately 4,500 kW/m, more than double that of forb-only plots with similar biomass. Fireline intensity was correlated similarly with fire temperature at ground level ($r = .75$) or 50 cm above-ground ($r = .76$).

In contrast, reaction intensity, the rate of heat release per unit time per unit area, tended to increase slightly more strongly with forb than with grass biomass, though this difference was not significant ($p = .157$, not shown). This was because the flaming zone extended farther behind the fire front in grass-dominated than forb-dominated plots (Figure 4d, $p < .001$): for a biomass of 300 g/m^2, the fitted flame zone depth was about 3.5 m for plots with only grass and about 0.8 m for plots with only forbs. Thus, the greater intensity per length of fireline in grass-dominated plots was spread over a

FIGURE 4 In 63 grassland biodiversity experiment plots, flame length (a), rate of forward spread (b), fireline intensity (rate of energy release per length of fire front (c), and flaming zone depth (d) all increased more strongly with grass biomass than with forb biomass. Lines are fitted values for plots with only grass biomass (blue/dark grey) or only forb biomass (yellow/light grey), from multiple regressions forced through the origin with grass and forb biomass as independent variables. p-values are bootstrap tests of the equality of grass and forb biomass effects [Colour figure can be viewed at wileyonlinelibrary.com]

larger area, compared with forb-dominated plots of similar biomass. Also in contrast to the other measures, reaction intensity was more tightly correlated with ground level temperature ($r = .65$) than with temperature 50 cm above-ground ($r = .40$).

Fire spread area and fire intensity measures were not redundant: all six measures of fire intensity in Figures 3 and 4 were low to moderate in incompletely burned plots (fire spread area <95%) but were highly variable in completely burned plots (Figure S4).

## 3.5 | Grass and forb relative abundance affects fire severity

Two plant species, each with pre-marked individuals of consistent size, showed a stronger increase in fire damage with increasing grass biomass than with increasing forb biomass in multiple regressions (both $p < .001$, Figure 5). Seedling Q. macrocarpa trees in 2011 and adult L. aspera forbs in 2014 were fitted as reaching half of their maximum damage scores in plots with about 200 g/m² of grass biomass, vs. about 300–350 g/m² of forb biomass. Pre-fire plant size varied relatively little within species (height M ± SD: Quercus = 6.55 ± 0.22 cm, Liatris = 78.2 ± 15.2 cm), and did not significantly influence damage score when added as a predictor to multiple regressions (not shown). Fire damage scores were correlated with ground level fire temperature (Spearman's rank correlation rho = 0.79–0.89) and fire spread area (rho = 0.67–0.82); these fire behaviour measures predicted fire damage just as well as plot herbaceous biomass did (not shown).

3.6 | Fire, plants, and soil nitrogen accumulation

Total soil N from 0 to 20 cm depth increased over 21 years more strongly in plots with higher mean fire spread ($p < .001$, $R^2 = .10$) or higher mean fire temperature ($p < .001$, $R^2 = .29$), in separate simple linear regressions with percent soil N in 2015 minus percent soil N in 1994 as the response variable and the fire behaviour variables averaged over all available years (spanning 1997–2014).

4 | DISCUSSION

Species richness and composition treatments established profound gradients in plant biomass and cover, and in functional composition,
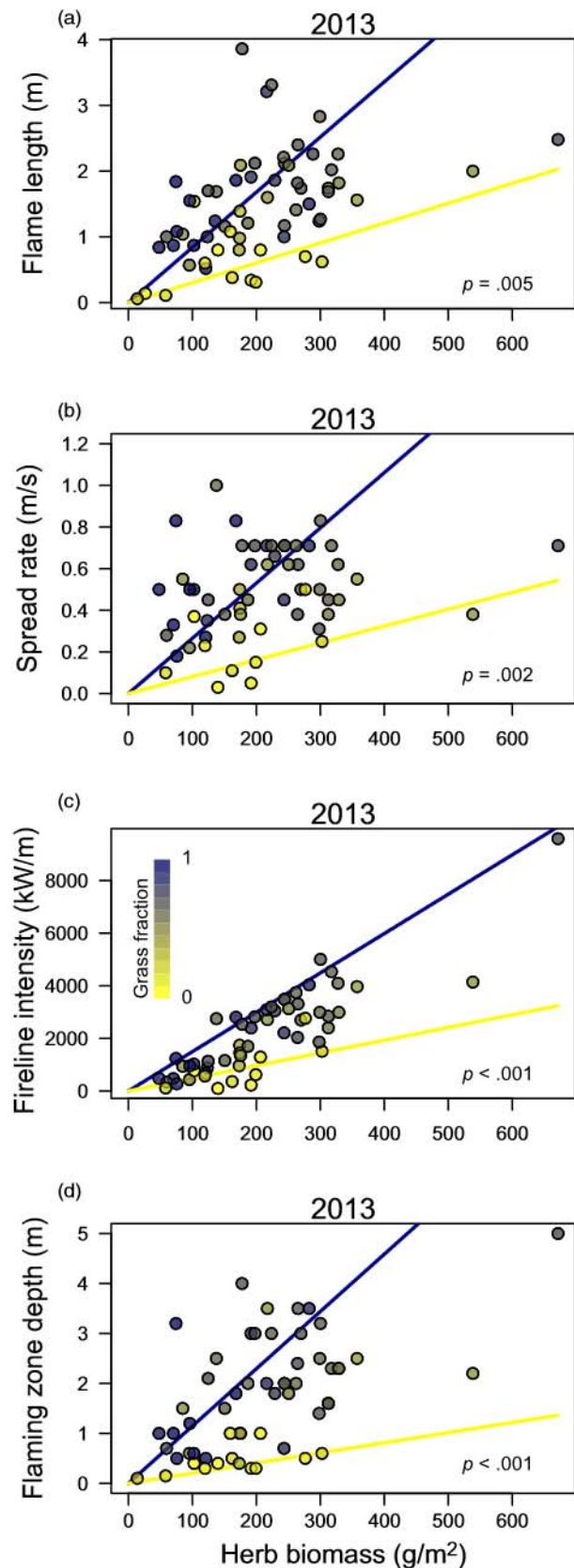
that were independent enough to reveal that grasses increased fire spread and associated facets of fire behaviour, compared with an equivalent abundance of forbs: grass dominance increased fire
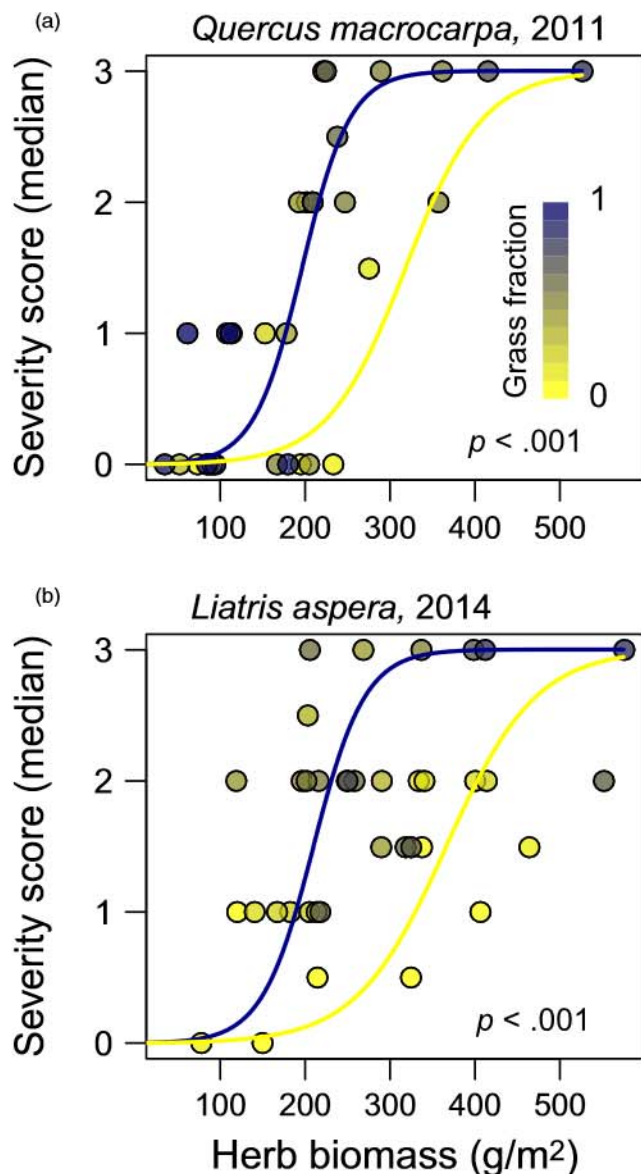
FIGURE 5 Severity of fire effects on plants increased more strongly with grass biomass than with forb biomass, measured the preceding late summer. Severity of fire damage to similarly-sized marked individuals was scored: 0 unburned, 1 scorched (darkened), 2 severely damaged (black or stem fallen), 3 consumed; points are medians of 12 1-year-old *Quercus* seedlings in each of 32 plots (a) or of two to five reproductive *Liatris* plants in each of 37 plots (b). Curves are fitted values for plots with only grass biomass (blue/dark grey) or only forb biomass (yellow/light grey), from mixed effects multiple regressions forced through the origin with grass and forb biomass as independent variables, logit-transformed severity score of each plant as response, and plot as a random intercept. *p*-values are bootstrap tests of the equality of grass and forb biomass effects [Colour figure can be viewed at wileyonlinelibrary.com]

spread area—or equivalently increased point fire frequency, or decreased point fire return interval—and resulted in fires that advanced faster, were more intense (higher rates of heat release per unit fireline length), caused more damage to plants, and released

heat to greater heights. These results are consistent with grasses forming finer, more aerated, better connected fuel beds than forbs in this system. This highly replicated vegetation-scale field experiment complements plant-scale lab flammability studies (Fernandes & Cruz, 2012; Schwilk, 2015; Simpson et al., 2016) in providing evidence that herbaceous plants vary meaningfully in their influence, per unit abundance, on ecosystem fire behaviour. This experiment also complements a continent-scale study linking fuel sampling with remotely sensed fire measurements (Prior et al., 2017) that found that grasses increased fire spread compared with more densely packed litter from other plants.

4.1 | Fuel controls fire behaviour

We infer from associations between plant abundance and fire behaviour that plant abundance influenced fire behaviour, because fuel quantity and characteristics are known from first principles to influence fire behaviour (Byram, 1959) and no other persistent plot characteristics (e.g. spatial variables) could explain why plots differed profoundly in fire behaviour in ways that were consistent across years. There may have been little variation in fire spread area and fire temperature between years (2%–6% of total variation) because most burns were conducted under low-humidity and mildly windy conditions conducive to fire, after fuels had dried. We infer that temporally consistent plant abundances were stronger controls of fire spread than inconsistent plot ignition patterns or weather at the moment of burning, because a) year × plot interactions combined with measurement error contributed only modestly (19%–35%) to variation in fire spread area after a single ignition, and b) re-igniting incompletely burned plots increased the percent area burned by only 5.4% on average.

4.2 | Herbaceous plant abundance promotes fire spread

Our results are broadly consistent with measurements of fireline intensity in relation to total fuel load from African, South American, and Australian savannas (Govender, Trollope, & Van Wilgen, 2006; Trollope, Trollope, Potgieter, & Zambatis, 1996; Williams et al., 1998); with measured flame heights in South African savannas (Trollope et al., 1996); and, for our grass-dominated plots, with rates of forward spread in grass-dominated African savannas (Trollope et al., 1996) and Australian grasslands (Cheney et al., 1993). Nonetheless, there are some factors to consider when interpreting our fire behaviour measures. Biomass and cover late the previous summer overrepresented fuel loads for spring fires because some growth and decomposition occurred between late summer abundance sampling and spring burning; in a sample of 30 plots, spring fuel biomass averaged 73% of previous-summer peak biomass. Our estimates of rates of heat release are upper bounds because they assume that fuel was entirely consumed (Stronach & McNaughton, 1989). However, any overestimation is likely modest because fuel consumption typically appeared fairly complete (P. D. Wragg pers. obs.), consistent with

fuel consumption >99% in early spring fires in tallgrass prairie elsewhere (Bragg, 1982); further, another method of estimating grassland fireline intensity using an established relationship with flame length (Alexander & Cruz, 2012) yielded median values 19% *larger* than those presented. Fires might have been more intense had they occurred in autumn before fuel was compressed by winter snowpack and before most forbs dropped their leaves, because these factors likely reduced aeration and convective and conductive heat transfer similarly to how cutting grass before burning it reduced fire spread rate by 18% (Cheney et al., 1993). Conversely, severe winter cold cured (killed) herbaceous fuels, enabling them to dry more rapidly (favouring fire) in spring than they would have in autumn. Fire intensity may have been higher in more extensive burns (Byram, 1959), and fire spread would be faster uphill and slower downhill than in this flat experiment.

The planted species richness treatments influenced fire spread area and temperature indirectly through their effects on biomass. Planted species richness increased biomass, on average, as reported previously from this experiment (Reich et al., 2012; Tilman, Knops, et al., 1997, 2006) and explained by mechanisms including complementary resource use and positive feedbacks with soil fertility (Reich et al., 2012) as well as more diverse mixtures being more likely to include the most productive species, which were C4 grasses (Tilman, Knops, et al., 1997). Biomass, in turn, influenced fire. Planted species richness may also have weakly increased fire spread area and temperature over and above its effects on biomass, for example, through increased probability of including highly flammable species, but the variation in fire behaviour uniquely explained by species richness (and not total biomass) was small (not shown). The wide variation in fire spread within low-diversity plots implies that even low-diversity mixtures can achieve maximum fire spread if they include highly productive or flammable species.

4.3 | Why do grass and forb relative abundances affect fire behaviour?

There are three groups of explanations for differences between grass and forb effects on fire. First, differences in heat released per unit of fuel burned, and the completeness with which fuel burned, are unlikely to explain why grasses increased fire intensity more strongly than did forbs per unit biomass. We assumed a constant heat yield per unit biomass because the heat of combustion of various grass and forb species had a coefficient of variation in only 5.3% in a Canadian tallgrass prairie (Kidnie, 2009), and 1.2% in a South American grassland (Britton, Dodd, & Weichert, 1976). We also assumed complete combustion; if (coarser) forbs were less completely consumed by fire than (finer) grasses then intensity would be overestimated for forbs more than for grasses, making our inference that grasses more strongly increase fireline intensity conservative.

Second, biomass (or cover) the previous summer may have overestimated spring fuel loads more for forbs than for grasses; this likely contributed modestly to the more positive effect of grass than forb abundance on fire behaviour. Plant abundance was measured

in late July, when cover and biomass were near their maxima, and these abundances are unlikely to be biased because grasses and forbs did not differ consistently in their phenology (Whittington, Tilman, Wragg, & Powers, 2015). However, forbs may have had higher decomposition or herbivory. Multi-site analyses have found that forbs decompose faster that graminoids (Cornwell et al., 2008; Reich, Wright, & Lusk, 2007), and C4 grasses—particularly in tribe Andropogoneae, which includes three of our four species—tend to have relatively low decomposition and herbivory rates due to high tissue C:N and lignin:N ratios (Bond, Midgley, & Woodward, 2003; Cornwell et al., 2008; Hobbie, 1992; Taylor, Parkinson, & Parsons, 1989). Conversely, there was strong overlap between prairie grasses and forbs in decomposition-related traits at this site (Craine et al., 2002). Seedlings of some of the grass species from this experiment tending to be less palatable to crickets than some of the forbs (Burt-Smith, Grime, & Tilman, 2003), implying that insect herbivory during autumn could have targeted forbs over grasses; herbivores larger than mice were excluded. However, the net effect was that biomass was reduced from one summer to the following spring only 12% more in forb-dominated than in grass-dominated plots, which can be only a small part of why grasses increased fire spread and intensity about twice as strongly as forbs per unit abundance.

The third, apparently most influential, set of factors that can explain why fires in grass-dominated plots tended to spread more rapidly and intensely than fires in forb-dominated plots with similar plant abundance involves differences in leaf retention, as well as leaf and stem morphology. These factors apparently contributed to grasses forming a more aerated, fine, connected fuel bed (P. D. Wragg & T. Mielke pers. obs.), though we cannot separate traits' roles because grasses differ from forbs in many ways. Grasses tended to retain their senesced leaves over winter and form a well aerated fuel bed in the spring, whereas the forb leaves in this experiment tended to drop during winter into a compact, poorly aerated litter layer (Figure 6). After leaf fall, the forb stems formed fuel that was coarser (thicker in diameter, and for several species somewhat woody) than grass stems. The forb species (all dicotyledons) had shorter and broader leaves than the grass species, perhaps also contributing to coarseness, though leaf thickness, surface area:volume ratio, specific leaf area, and leaf dry matter content—associated with flammability elsewhere (Lavorel & Garnier, 2002; Murray, Hardstaff, & Phillips, 2013)—did not differ consistently between grasses and forbs in this experiment (unpubl. data; Cadotte, Cavender-Bares, Tilman, & Oakley, 2009). Grass-dominated fuels may also be better connected than forb-dominated ones, at least above the less flammable compact litter layer, which would also promote fire spread area and intensity (Brooks et al., 2004; Pausas et al., 2017). The leafless upright forb stems were disconnected, whereas the grasses formed a connected fuel bed. Spatial arrangement of stems can also influence fuel connectivity, but grasses and forbs did not appear to differ consistently in this (P. D. Wragg pers. obs.). The more upward distribution of heat in grass- than forb-dominated plots, indicated by higher temperature at 50 cm above-ground (but not at ground level) and longer flame lengths for a given total biomass, may have arisen

FIGURE 6 Fire spread more completely, and was more intense, in grass- than forb-dominated plots of similar biomass. Photos of fire spread (a–k) were taken of the same set of three plots at different times: immediately before burns in April 2011 (wide views, a–c) and April 2015 (close views, d, f), and immediately after burns in April 2011 (wide views, g–i and close views, j, k). Averaging across annual spring burns in years with data (1997–1999 and 2010–2014), fire spread through 98% of the grass-dominated plot (mean late summer biomass across these years 114 g/m^2, of which 89% grass–principally the C$_4$ bunchgrass *Schizachyrium scoparium*: left column, a, d, g, j), compared with 45% fire spread in a plot dominated by the legume forb *Lespedeza capitata* (mean biomass 132 g/m^2, of which 92% forb: middle column, b, e, h, k) and just 14% fire spread in a plot dominated by the Asteraceae forb *Liatris aspera* (mean biomass 143 g/m^2, 97% forb: right column, c, f, i). Compared with grasses that formed well aerated and connected fuel beds of fine leaves and stems (d), forbs formed fuel beds of poorly aerated fallen leaves and disconnected coarse stems (e) or coarse and weakly connected leaves and stems (f) that burned incompletely (k). Other plots illustrated that when fire did spread, flames were longer and the flaming zone was deeper in plots dominated by grasses (M: mean biomass 188 g/m^2, 66% grass, principally *Panicum virgatum*) than in plots dominated by forbs (N: mean biomass 180 g/m^2, 91% forb, principally the legume *Dalea purpurea*; and P: mean biomass 143 g/m^2 of which 97% forb, principally *L. aspera*, same plot as c, f, i). A higher-biomass plot illustrates a more intense fire (L: mean biomass 366 g/m^2, 56% grass and 44% forb). Photos (l–o) were taken in April 2010 [Colour figure can be viewed at wileyonlinelibrary.com]

through the same processes that lead to faster spread, because these facets of fire tend to be correlated (Byram, 1959; Schwilk, 2015); there was no consistent difference in live height between grass and forb species in this experiment (Cadotte et al., 2009), though greater leaf drop by forbs may have resulted in a lower fuel height distribution for forbs at the time of burning. Our results are directly relevant to prescribed burns conducted during the spring. Grasses and forbs likely differ less in their effects on lightning fires during late summer, before forbs have dropped their leaves into a compact litter bed, and likely differ to an intermediate degree (more than in late summer, less than in spring) in their effects on prescribed fall burns, when forbs have dropped some leaves.

However, fire spread and severity and several facets of fire intensity (intensity, flame length, flame zone depth, temperature at 50 cm above-ground) were correlated and greater in grass- than forb-dominated plots, other measures—fire temperature at ground level, residence time, and rate of heat release per unit area—were independent of the spread-associated variables and not associated with grass vs. forb abundance, because increased fireline intensity in grass-dominated plots was offset by a deeper flaming zone and more upward heat distribution. Both the correlation of the fire spread-associated variables and the independence of the other variables are consistent with other studies (Pausas et al., 2017; Schwilk, 2015). Below-ground damage and mortality of resprouters such as those in this study, as well as heat scarification of legume seeds, may be more closely associated with measures such as fire residence time, which may better predict soil heating, than with spread-associated measures (Bradstock & Auld, 1995; Gagnon et al., 2015). In that case, mortality and scarification may be independent of grass:forb ratio, as fire residence time is. Too few marked *Liatris* and *Quercus* individuals (2%) failed to resprout following our burns to analyse correlates of mortality.

4.4 | A lower fire spread percolation threshold for grass-dominated plots

The sigmoidal increase in proportional fire spread area with increasing plant cover (Figure 2d) is consistent with fire spread as a percolation process, and grasses resulted in fire spread at a much lower apparent percolation threshold than forbs. Percolation processes exhibit thresholds in occupancy—in this case, the fraction of the landscape that has flammable fuel that ignites readily under the conditions of the burn—at which the probability of fire spreading from one patch to at least one other patch rapidly increases from zero to one (Cox & Durrett, 1988). The apparent threshold in our data was about 40% total plant cover irrespective of composition, or 30% for exclusively grass plots (Figure 2d), suggesting that the threshold is lower for grasses than for forbs. Indeed, the fitted line for forb-only plots suggested a much higher threshold of about 80% cover. The lower cover threshold for percolation in grass-dominated than forb-dominated plots may be due to a higher probability of fire spreading between grasses than forbs because grasses are finer fuels (see above).

Our results are consistent with invasive grasses radically increasing fire spread area in arid shrublands in the Mediterranean (Grigulis et al., 2005) and the North American Great Basin (Balch, Bradley, D'Antonio, & Gómez-Dans, 2013). Invasive grasses are understood to have made the landscape more connected in terms of fire spread. Our results suggest this could be due to either an increase in total fuel above a percolation threshold or a lower percolation threshold with more flammable fuel.

Steep declines in burn area as tree cover increases above 40% (Archibald et al., 2009), presumed to correspond to flammable grass cover falling below 60%, have been interpreted as consistent with a theoretical percolation threshold of 59% (Abades, Gaxiola, & Marquet, 2014; Cox & Durrett, 1988; Schertzer, Staver, & Levin, 2014). The apparent threshold in our grass-dominated plots (~30%, Figure 2d) may have been lower than the theoretical 59% for at least three reasons. First, fire burning with wind is biased percolation, which may have a lower threshold for spread (Ohtsuki & Keyes, 1986). Second, the theoretical threshold is for well mixed landscapes; clumping of flammable patches allows fire to spread at lower cover (O'Neill, Gardner, Turner, & Romme, 1992). Third, our estimates of percent cover may have been at a finer scale than the scale of fire spread. Models in which fire can jump over unoccupied patches predict lower percolation thresholds and are equivalent to coarser resolution models (O'Neill, Milne, Turner, & Gardner, 1988). Cover was estimated with a grain size as fine as 1 cm^2. Except in the sparsest plots, much of the estimated bare ground was composed of numerous small bare patches interspersed between plant matter, likely jumped readily by fire (P. D. Wragg pers. obs.). Therefore, our measures of plant cover would correspond to higher cover values at a coarser resolution that accounts for the ability of fire to jump over small gaps, resulting in a threshold estimate closer to the theoretical value.

We focus on how grasses vs. forbs influence fire behaviour holding abundance constant, but C4 grasses can also promote fire by increasing total plant abundance and fuel load. In this experiment, the presence of C4 grasses in a plot strongly increased herbaceous productivity, apparently because their lower tissue N allowed them to produce more biomass per unit area than C3 plants (Tilman, Knops, et al., 1997); similarly, C4 plants can have higher water use efficiency (Ehleringer & Monson, 1993). C4 grasses' low N and high lignin contents can also increase fuel loads by inhibiting decomposition and herbivory (Ehleringer & Monson, 1993; Masubelele, Bond, & Stock, 2007). Thus, in addition to having lower fire percolation thresholds due to grasses' high flammability per unit abundance, grasslands dominated by C4 grasses may also be more likely to exceed their percolation threshold—and thus to burn—because C4 grasses can increase fuel load.

4.5 | Forbs, tree-grass interactions, and biome shifts

The hypothesis that feedbacks between vegetation and fire can lead to grassland, savanna or forest as alternate stable states hinges on grasses promoting and being promoted by fire, and trees suppressing

and being suppressed by fire (Abades et al., 2014; Bond et al., 2005; Grimm, 1983; Schertzer et al., 2014; Staver & Levin, 2012; Staver et al., 2011). Forbs are missing from these treatments, implying that they are assumed to be (1) negligible in either abundance or per-abundance impact, or (2) equivalent to grasses. Forbs may indeed be negligible in abundance in many tropical savannas and other ecosystems. However, our results suggest that forbs have substantial per-abundance impacts on fire behaviour and that these differ from the effects of grasses. Where forbs are abundant, considering them separately from grasses could improve understanding of fire behaviour, tree demography, and fire-mediated biome shifts in two ways. First, for a given herbaceous biomass, grass-dominated fuels produced more extensive fires that were more intense and released heat higher above-ground and were thus more likely to top-kill trees by damaging their aerial buds or other tissues (Trollope, Trollope, & Hartnett, 2002). Increased fire spread with increased biomass and cover, especially of grasses, profoundly inhibited the establishment of oak trees (*Q. macrocarpa* and *Quercus ellipsoidalis*) in this experiment (Wragg, 2015): fire held trees in a "fire trap" (Bond & van Wilgen, 1996) by repeatedly top-killing them before they could grow large enough for their stems to survive fire. Second, our results suggest the percolation threshold for fire spread, may be steeper and occur at lower herbaceous cover for grass- than forb-dominated systems (Figure 2d). To the extent that percolation processes contribute to the suddenness of biome shifts (Schertzer et al., 2014), this implies that shifts between grassland or savanna and forest may be more sudden and occur at lower herb abundances in grass- than forb-dominated systems.

A stronger positive influence of grasses than of forbs on fire spread and tree suppression could help explain why acid, sandy soils that favour grasses over forbs tend to be grassland or savanna whereas more basic, clay-rich soils that favour forbs over grasses tend to be forested, in some regions. Soil texture only weakly predicts tree cover globally (Lehmann et al., 2014; Sankaran et al., 2005), perhaps because its effects can reverse depending on context. For example, high clay content may be associated with high tree cover (forest) in South America (Ruggiero, Batalha, Pivello, & Meirelles, 2002), yet high clay content may be associated with low tree cover in some Australian and African savannas where clay suppresses trees through water-logging or high grass productivity and fire intensity (Bond, 2008; Williams, Duff, Bowman, & Cook, 1996). High clay content may favour trees through high water holding capacity and nutrient availability that increase tree growth rate and thus the likelihood that trees avoid top-kill by fire (Murphy & Bowman, 2012). Our findings raise another possibility. In European grasslands and perhaps other regions, soils with high clay content are often also rich in cations and relatively basic, and cation-rich and basic soils promote forb dominance in at least some regions (Tilman, 1982; Tilman et al., 1994; Willems & van Nieuwstadt, 1996). Thus, if basic soils rich in clay promote forbs over grasses, and if this reduces fire intensity, this could help explain why such soils are more likely to be forested than sandier, more acid soils. Similarly, N deposition favours grasses over forbs in European and other grasslands (Stevens et al., 2009;

Xia, Niu, & Wan, 2009; Xia & Wan, 2008), which could increase flammability and thus favour grassy biomes over forest.

4.6 | Fire-mediated interactions between plant functional groups

Grasses and forbs may influence neighbouring vegetation through their profoundly different per-abundance effects on fire behaviour, in addition to other mechanisms such as resource consumption. How might differences in fire behaviour between grasses and forbs affect different plant functional groups in perennial-dominated grasslands and savannas? Woody plants tend to be inhibited by grass-driven increases in fire, because fire that destroys above-ground tissue requires small woody plants to regrow from the base (if not killed) instead of compounding previous-season growth. Thus, in addition to inhibiting tree establishment (discussed above), grass-driven fire may inhibit woody subshrubs (such as *Amorpha canescens* in this experiment) that are commonly considered forbs because they never grow taller than the grass layer yet can grow from woody previous-season stems. Within true herbs, however, there are not such clear-cut differences in response to fire. Species' responses to fire are understood mostly at the level of qualitative traits, such as seeding vs. re-sprouting after fire, which classify all the herb species in this experiment as "perennial resprouting herbs" (Lavorel & Garnier, 2002). Accordingly, grasses and forbs do not appear to differ consistently in their response to fire. For example, in some tallgrass prairies and mesic grasslands, forb and grass abundance responded similarly to fire frequency (Engle & Bidwell, 2001; Kirkman et al., 2014). If grasses and forbs differ in their effects on fire but not in their response to fire, that would accord with synthetic findings that traits that determine plants' impacts on fire are largely different than, and not necessarily correlated with, traits that determine their response to fire (Lavorel & Garnier, 2002).

However, high fire frequency did promote grasses over forbs in at least one tallgrass prairie, Konza Prairie (Collins, 1987; Gibson & Hulbert, 1987). In particular, C4 grasses may respond more positively to high fire frequency than mostly C3 forbs and C3 grasses (Forrestel, Donoghue, & Smith, 2014; Li, Zuo, & Knops, 2013), for several reasons. First, C4 grass growth tends to be more concentrated in the middle of the summer growing season than growth of C3 forbs and C3 grasses, so C4 grasses are less likely to be green and vulnerable during spring and autumn fires. Second, many C4 grasses are intolerant of litter that builds up when fire is infrequent (Knapp & Seastedt, 1986). Third, C4 grasses' lower tissue N concentrations may give them a competitive advantage (Tilman, 1990) where high fire frequency depletes N. If grasses promote fire (relative to forbs), C4 grasses respond positively to fire (relative to C3 forbs, especially subshrubs), and C3 grasses are uncommon (as is the case in many subtropical and tropical grasslands), then positive feedbacks between C4 grass abundance and fire could establish C4 grass-dominated and forb-dominated patches as alternative stable states.

4.7 | Implications of grass vs. forb effects on fire for nutrient losses

Nitrogen (N), phosphorus (P), and sulphur (S) were more likely to be volatilized by fire and lost in plots dominated by grasses than in plots dominated by forbs with equivalent biomass. Nitrogen was likely volatilized at a higher rate in grass-dominated plots due to both higher fire spread and higher canopy fire temperatures. First, higher fire spread in grass-dominated plots would certainly have caused higher N volatilization because fire temperatures near the ground were high enough to volatilize N (above 70°C; Knops, Bradley, & Wedin, 2002) in all but the barest plots (>65 g/m^2, Figure 3a and Figure S3a; >15% cover, Figure S3b). Second, within areas that burned, grasses likely promoted nutrient volatilization more strongly than did forbs through higher canopy fire temperatures: temperatures high enough to volatilize N at 50 cm above-ground required only 100 g/m^2 of grass biomass but more than 200 g/m^2 of forb biomass. Temperatures were also more likely high enough to volatilize P (at 281°C) and S (at 444°C) in grass-dominated plots (Haynes, Bruno, & Lide, 2014; Kauffman, Cummings, & Ward, 1994). Plot median temperatures ranged up to approximately 300°C at ground level (in 2011), 400°C at 10 cm above-ground (in 2000), and 250°C at 50 cm above-ground (in 2011); our highest pyrometer measurement was 610°C. These measures are comparable with results from similar pyrometers in Kansas tallgrass prairie (Gibson, Hartnett, & Merrill, 1990). However, higher temperatures may have occurred—making volatilization of P and S more likely—because pyrometer estimates of maximum fire temperature are conservative compared with maximum (Iverson et al., 2004; Kennard, Outcalt, Jones, & O'Brien, 2005) or peak 1-min mean (Wally et al., 2006) temperatures from continuously logged thermocouples, and actual flame temperatures can be even higher than thermocouple measures (Martin, Cushwa, & Miller, 1969).

Why did total soil N *increase* with increasing fire spread (corresponding to higher point fire frequency) and increasing fire temperature in this experiment, in contrast with multi-decade fire manipulations in which high fire frequency typically reduced total N in surface soil (Pellegrini et al., 2017)? In this experiment, plant abundance and species composition strongly determined both effective fire frequency (this paper) and soil N accumulation (Fornara & Tilman, 2008). Soil N accumulates in proportion to organic matter inputs from root biomass in early-successional, infertile old fields like this one (Knops & Tilman, 2000; Li, Knops, Zuo, & Laungani, 2014), and soil N increased especially strongly with the abundance of C4 grasses in this experiment (Fornara & Tilman, 2008). Relatively little N was volatilized by fire from shoot and litter biomass, compared with the much larger amount of N in unburned root biomass: roots constituted approximately 84% of total plant biomass in this experiment in 2006 (Fornara & Tilman, 2008). Thus, plant abundance and species composition confounded the effect of fire spread on soil N. This confounding may be stronger here than in experiments that directly manipulate fire frequency. It may also be stronger in early-successional, infertile old fields like this experiment (in which mean soil N increased from 0.045% in 1994 to 0.059% in 2015) than later in succession. Early in succession, when plant—and especially C4 grass—abundance powerfully promotes soil N accumulation (via root biomass) as well as fire frequency (via above-ground biomass), fire-driven N losses may not detectably affect total soil N. Accordingly, in another infertile old field at Cedar Creek undergoing natural succession and rapidly accumulating soil N, manipulating fire frequency over 27 years did not alter total soil N (Li et al., 2014). In contrast, studies that found that frequent fire reduced soil N—at Cedar Creek (Knops, Ritchie, & Tilman, 2000; Norris & Reich, 2009; Reich, Peterson, Wedin, & Wrage, 2001) and often elsewhere (Pellegrini et al., 2017)—were in unploughed grasslands and savannas with soil N levels closer to steady state. In unploughed prairies, if anthropogenic N deposition increases the ratio of grasses to forbs (Stevens et al., 2009; Xia & Wan, 2008; Xia et al., 2009) and thus increases fire spread and nutrient volatilization, this may reduce soil N availability (and increase surface light) and mitigate species loss due to eutrophication (McLauchlan, Craine, Nippert, & Ocheltree, 2014).

5 | CONCLUSIONS

Fire spread area, point fire frequency, fire intensity and associated facets of fire behaviour increased more strongly with grass than with forb abundance, holding total fuel quantity constant, in this long-term, replicated field experiment with annual spring ignitions and randomized species richness and composition (and hence fuel quantity and quality) treatments. This highlights that, even among herbaceous species, fuel quality is a major determinant of effective fire regime. Moreover, these results imply that forbs and grasses may play distinct roles in fire-mediated interactions between plants, including interactions between herbaceous and woody vegetation that influence biome boundaries, and have distinct effects on nutrient loss through volatilization.

Widespread decreases in grassland and savanna fire intensity, resulting from changing ignition regimes, fire suppression, and land management (Archibald, Lehmann, Gómez-Dans, & Bradstock, 2013), may increase the importance of the distinctly higher flammability of grasses and the impacts of this higher flammability on ecosystem dynamics.

AUTHORS' CONTRIBUTIONS

P.D.W., T.M. and D.T. conceived the ideas and designed methodology; P.D.W. and T.M. collected the data; P.D.W. and D.T. analysed the data; P.D.W. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

The data are available through both the Cedar Creek Ecosystem Science Reserve data catalog (http://cedarcreek.umn.edu/research/data) and the LTER Network Data Portal (http://portal.lter net.edu/). Weather: https://doi.org/10.6073/pasta/ac1b5f99b4cb 838860adf30545da9413 (Seeley, 2018); plot coordinates: https://doi.org/10.6073/pasta/940934edb437799bba2ca0a996cf072c (Tilman, 2018c); fire behaviour: https://doi.org/10.6073/pas ta/ce4fa7fbbe6f5979e84ca1e15f9c8353 (Wragg, 2018a); fire temperatures: https://doi.org/10.6073/pasta/c7866d02970685eee6e3 d1dbf774a529 (Wragg, 2018d); fire severity: https://doi.org/10. 6073/pasta/09fdbccac15ab171f6ea58cfc4a49c81 (Wragg, 2018c); plant cover: https://doi.org/10.6073/pasta/ae57e6e9d87dd5fd2044 22eeec37b442 (Tilman, 2018b); plant biomass: https://doi.org/10. 6073/pasta/341cc088f591a5dc7dfb27e517ecfc5d (Tilman, 2018a); spring fuel load: https://doi.org/10.6073/pasta/037b3d380a1c641 d589462aca0aba86e (Wragg, 2018b); soil nitrogen: https://doi.org/ 10.6073/pasta/c2bc09303d540666cdcd2cd3a98121fe (Tilman, 2018d).

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