

Spreaders, igniters, and burning shrubs: plant flammability explains novel fire dynamics in grass-invaded deserts

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Abstract. Novel fire regimes are an important cause and consequence of global environmental change that involve interactions among biotic, climatic, and human components of ecosystems. Plant flammability is key to these interactions, yet few studies directly measure flammability or consider how multiple species with different flammabilities interact to produce novel fire regimes. Deserts of the southwestern United States are an ideal system for exploring how novel fire regimes can emerge when fire-promoting species invade ecosystems comprised of species that did not evolve with fire. In these deserts, exotic annual grasses provide fuel continuity across landscapes that did not historically burn. These fires often ignite a keystone desert shrub, the fire-intolerant creosote bush, *Larrea tridentata* (DC.) Coville. Ignition of *Larrea* is likely catalyzed by fuels produced by native plants that grow beneath the shrubs. We hypothesize that invasive and native species exhibit distinct flammability characteristics that in combination determine spatial patterns of fire spread and intensity. We measured flammability metrics of *Larrea*, two invasive grasses, *Schismus arabicus* and *Bromus madritensis*, and two native plants, the sub-shrub *Ambrosia dumosa* and the annual herb *Amsinckia menziesii*. Results of laboratory experiments show that the grasses carry fire quickly (1.32 cm/s), but burn for short duration (0.5 min) at low temperatures. In contrast, native plants spread fire slowly (0.12 cm/s), but burn up to eight times longer (4 min) and produced hotter fires. Additional experiments on the ignition requirements of *Larrea* suggest that native plants burn with sufficient temperature and duration to ignite dead *Larrea* branches (time to ignition, 2 min; temperature at ignition 692°C). Once burning, these dead branches ignite living branches in the upper portions of the shrub. Our study provides support for a conceptual model in which exotic grasses are “spreaders” of fire and native plants growing beneath shrubs are “igniters” of dead *Larrea* branches. Once burning, flames produced by dead branches engulf the entire shrub, resulting in locally intense fires without historical precedent in this system. We suggest that fire models and conservation-focused management could be improved by incorporating the distinct flammability characteristics and spatial distributions of spreaders, igniters, and keystone shrubs.

Key words: biological invasions; fire behavior; fire modeling; fuel treatments; Mojave desert, USA; native annuals; non-fire adapted systems; prescribed fire; Sonoran desert, USA; species interactions.

INTRODUCTION

A major challenge in ecology is to better understand how species, communities, and ecosystems respond to altered disturbance regimes in a changing world (Bender et al. 1984, Vitousek et al. 1997, Moretti and Legg 2009, Supp and Ernest 2014). Some of the most striking examples of altered disturbance regimes involve changes in the frequency, intensity, and seasonality of fires that are driven by climate change (e.g., temperature and precipitation patterns; Grissino-Mayer and Swetnam 2000,

Littell et al. 2009), biotic change (e.g., introduction of invasive species; Vila et al. 2001, Pauchard et al. 2008, Gaertner et al. 2014), and land-use change (Lavorel et al. 2007, Cochrane and Barber 2009, Aldrich et al. 2014). Improved understanding of altered fire regimes is especially important in systems that rarely burned historically (e.g., tropical forests; Nepstad et al. 1999, Brando et al. 2012) or that are highly dependent on frequent fires (e.g., savanna-grasslands; Veldman et al. 2015). As such, both increases and decreases in fire frequency/intensity can either threaten or maintain biodiversity and ecosystem services, depending on whether the ecosystems in question evolved with or without frequent fires.

Plant functional characteristics related to fire tolerance and flammability are key factors that can help explain

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the responses of species and communities to natural and novel fire regimes (Bowman et al. 2014, Pausas 2015). Among these characteristics, plant flammability (i.e., the ability of a fuel to ignite and sustain fire; Anderson 1970, Varner et al. 2015) is crucial to our understanding of vegetation–fire feedbacks (Beckage et al. 2009), which ultimately determine community composition, ecosystem distributions, and fire regimes (i.e., frequency, timing, and intensity of fire). A clear understanding of the evolutionary origins of flammability remains elusive (e.g., Bowman et al. 2014), and there is still much that we do not know about the role of flammability in plant–fire dynamics (Troumbis and Trabaud 1989, Keeley et al. 2011). Nonetheless, it is clear that plant flammability is important to species interactions (Bond and Midgley 1995) and ecosystem functioning (e.g., fire regimes; Kane et al. 2008). Consequently, a better understanding of the role of flammability in systems that are experiencing altered fire regimes is essential for developing conceptual and predictive models of fire and vegetation dynamics that are able to inform management decisions.

Invasions by flammable grasses are among the most globally important causes of altered fire regimes (D’Antonio and Vitousek 1992, Rossiter et al. 2003, Ehrenfeld 2010) and their study offers insight into fire-mediated interactions between fire-promoting and fire-sensitive species. For example, the invasive exotic annual grasses *Schismus arabicus* Nees and *Bromus madritensis* L. (hereafter *Schismus* and *Bromus*) in the Sonoran and Mojave deserts of southwestern North America spread fire across landscapes that rarely burned historically (Haines et al. 2002, Brooks et al. 2004, Balch et al. 2013). Seeds of these annual grasses persist during droughts and then exploit infrequent rains to establish in open areas between shrubs, dramatically increasing fuel continuity (Brooks and Matchett 2006, Abella et al. 2011). In contrast, native herbaceous plants are patchily distributed in these deserts, often restricted to “fertility islands” created by perennial shrubs (Facelli and Temby 2002, Schafer et al. 2012). By serving as spreaders of fire, exotic annual grasses have transformed these deserts through fire-induced mortality of keystone shrubs and reduction of the high soil nutrient availability, typically associated with fertility islands (Fuentes-Ramirez et al. 2015a,b).

As a consequence of the extremely low historical frequency of natural fires, native species of the Sonora and Mojave deserts are poorly adapted to fire. Native herbaceous plant communities are less diverse in burned compared to unburned deserts (Brooks 2002, Engel and Abella 2011), and desert shrubs, such as the creosote bush, *Larrea tridentata* (DC.) Cov. (Zygophyllaceae; hereafter *Larrea*), are very fire sensitive. *Larrea* is a slow-growing, deep-rooted, and long-lived (up to 11,700 yr; Vasek 1980) shrub that is uniquely adapted to survive intense droughts, but not fire (post-fire resprouting rate of 3–30%; Abella 2009). Contributing to its vulnerability, *Larrea* has several characteristics that are maladaptive to fire. Dead branches retained at the base of the shrub

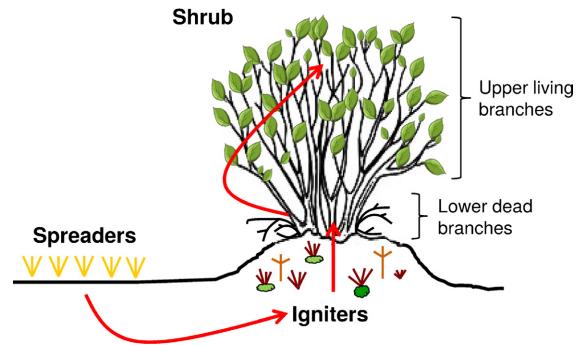


FIG. 1. Conceptual model of a novel fire dynamic involving spreaders, igniters, and burning shrubs. Exotic annual grasses (spreaders) provide fuel continuity across inter-shrub areas, to native herbaceous fuels beneath the shrubs (igniters), which ignite dead branches at the base of the shrub, and in turn ignite the entire shrub (including the living upper branches). In our study system, spreaders are the exotic invasive grasses *Bromus* and *Schismus*, igniters are the native annual herb *Amsinckia* and the small perennial shrub *Ambrosia*, and the burning shrubs are the fire-sensitive *Larrea*.

increase local fuel loads and may increase the likelihood of ignition of the entire individual (Fig. 1). Also contributing to local fuels loads, the relatively moist, shaded microhabitat beneath shrubs (Titus et al. 2002, Butterfield and Briggs 2009) promotes establishment and growth of native plants (Schafer et al. 2012) that may ignite the larger-diameter dead *Larrea* branches. These native fuels beneath *Larrea* are of little consequence in deserts without exotic annuals capable of spreading fire. However, where invasive grasses are abundant, these shrub islands are prone to burn (Brooks 2002). In this study, we seek to understand the flammability of native and invasive desert plants that produce a novel fire dynamic, wherein low-intensity surface fires spread and ignite *Larrea* shrubs, creating locally intense fires that can kill this keystone species.

Toward that end, we measured flammability metrics of five species that represent components of a proposed model of fire dynamics in grass invaded deserts (Fig. 1). In this model, exotic invasive grasses (i.e., *Bromus* and *Schismus*) are “spreaders” of fire between shrub fertility islands; native plants that grow beneath shrubs (i.e., *Amsinckia menziesii* (Lehm.) Nelson & J.F. Macbr and *Ambrosia dumosa* (A. Gray) Payne; hereafter *Amsinckia* and *Ambrosia*) are “igniters” of dead shrub branches; and once ignited, dead branches produce sufficient heat to burn living shrub branches. This process represents a novel fire dynamic, in which a long-lived shrub with low flammability that evolved in a fire-free environment, ignites, burns, and typically dies. We expect this novel fire dynamic to be due to synergies produced by distinct flammability characteristics of spreaders, igniters, and shrubs. We hypothesize that the very fine fuels (i.e., high surface area to volume ratios) produced by spreaders will burn quickly, produce fast flame spread rates, and produce relatively cool fires. In contrast, we predict

“igniters” to spread fire slowly, but to burn hot and long enough to ignite the thick, woody *Larrea* branches.

To test our model and these hypotheses (Fig. 1), we used lab-based experiments to quantify species-specific flammability characteristics (Kane et al. 2008, but see Fernandes and Cruz 2012). These experiments evaluated the relative flammability of exotic annual grasses (i.e., spreaders) that invade inter-shrub areas, native plants that grow beneath shrub canopies (i.e., igniters) and *Larrea* (i.e., burning shrubs, including both dead and live-collected branches). Our study was designed to determine: (1) How do invasive grasses, small-statured native plants, and keystone shrubs in southwestern American deserts differ in flammability? (2) Are native species better able to ignite *Larrea* shrubs compared to invasive grasses? (3) What flame temperatures and duration are required to ignite *Larrea* branches of varying size and moisture content? Answering these questions will demonstrate how species-specific flammability characteristics result in novel fire dynamics involving synergies between exotic invasive and native plant species.

MATERIALS AND METHODS

Study system

We studied the flammability of plant species that occur in alluvial fans (“bajadas”) of the Sonoran and Mojave deserts of the southwestern United States. The Sonoran study area is in the Barry M. Goldwater Range, Arizona, USA (US Air Force; mean annual temperature [MAT] of 23.4°C and mean annual precipitation [MAP] of 135 mm; Western Regional Climate Center, Gila Bend weather station). This area experiences two rainy seasons during June–August and January–March. The Mojave study area is in the Fort Irwin National Training Center, California, USA (US Army; MAT of 18.8°C, MAP of 131 mm; Western Regional Climate Center, Barstow weather station), where the majority of precipitation occurs in January–March. Native plant communities of the Sonoran and Mojave desert lowlands are characterized by scattered perennial shrubs, cacti, and annual forbs and grasses, separated by areas of bare and sparsely vegetated soil (Abella 2010). These communities are typically dominated by the perennial shrub *Larrea* with native annual plants, including *Amsinckia*, *Phacelia* spp., and *Pectocarya* spp., growing beneath *Larrea* canopies. In the Mojave Desert, the small, co-dominant perennial shrub *Ambrosia* (burro bush) also commonly grows near or beneath *Larrea* (Vasek and Barbour 1977, Fonteyn and Mahall 1981). Where invasive grasses occur, they colonize inter-shrubs areas during periods of high moisture availability (e.g., following monsoonal rains), and create a continuous layer of fine fuel capable of spreading fire across the landscape (Brooks et al. 2004).

Flammability of spreaders and igniters

We assessed the flammability of two potential fire spreaders, the exotic annual grasses *Bromus* and *Schismus*, as well as two potential shrub igniters, the native annual *Amsinckia* and native perennial *Ambrosia*. In January and February of 2014 we randomly collected fuels produced by these species from two plots of 1 ha each in both deserts. In each plot, we clipped standing fuels at ground level and collected identifiable litter from the ground. For *Ambrosia*, we collected fuels from different parts of the shrub, to include the range of branch sizes from 0.8 to 5.5 mm in diameter. Field-collected samples were carefully handled and stored to maintain fuel structure. To supplement our field-collected fuels, we collected seeds of the exotic annual grasses, which we grew in a greenhouse at Iowa State University (Ames, Iowa, USA) and harvested once senesced. The greenhouse grown fuels accounted for 50% and 30% of *Schismus* and *Bromus* material used in our experiments, respectively.

To assess the role of exotic and native plant fuels in spreading fire to and igniting *Larrea* shrubs, we used a burning device modified from Ganteaume et al. (2011, Fig. 2a). This device consisted of a round metal tray

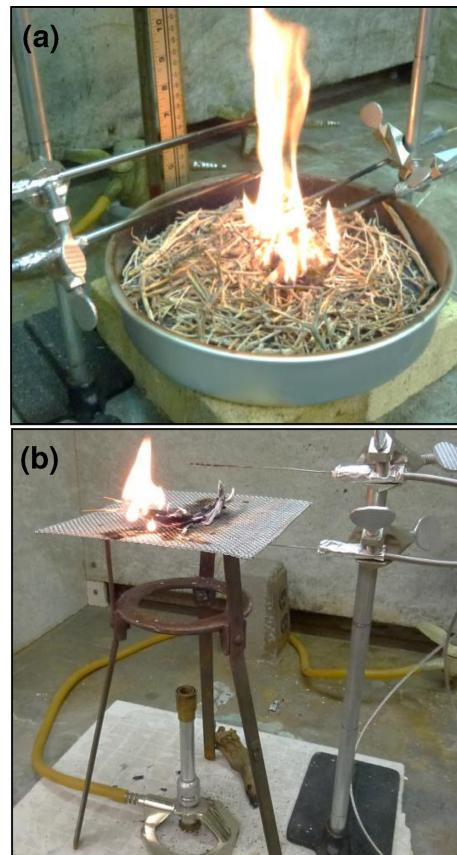


FIG. 2. Devices used to assess flammability of (a) spreaders and igniters (modified from Ganteaume et al. 2011), and (b) *Larrea* branches.

(25 cm in diameter with a 3 cm high edge) mounted over a concrete block. At the bottom of the tray we placed a lining of cement fiber (HardieBacker, 1.25 cm thickness) to avoid overheating. We monitored temperatures at 1-s intervals with a Reed SD-947 data logger connected to four type K mineral insulated thermocouples (DTC brand, -40 to 1000°C operating temperature, 0.1° accuracy, 1 mm sensor) mounted at 1, 2, 5, and 10 cm above the tray; these heights are representative of the distance from the soil surface to the lowest *Larrea* branches. Given that thermocouples provide imperfect measures of fire temperatures (Bova and Dickinson 2008), the flame temperatures we report should be viewed as a relative metric, as opposed to an absolute measure, of fire intensity for each fuel type. Similarly, it is important to note that laboratory studies are typically unable to mimic conditions of fires in the field (Fernandes and Cruz 2012). Nonetheless, lab-based experiments do have value in providing an understanding of the flammability characteristics of different fuels (Varner et al. 2015) and represent a reasonable first step for determining how differences in flammability among species underlie fire behavior observed in the field.

Between 30 June and 28 July 2014, we conducted $n = 30$ flammability trials per species, with experimental fuel loads that ranged from 4 to 24 g for *Bromus* and *Schismus*, 24 to 86 g for *Ambrosia*, and 11 to 58 g *Amsinckia*. These ranges reflect: (1) the minimum quantity of fuel able to ignite and hold fire, as determined in pilot experiments, (2) the maximum quantity of litter that fit within the metal tray, (3) typical range of biomass produced in a wet year within 20×20 cm plots in our study areas, and (4) fuel loads small enough to be safely burned in the laboratory. Before each burn trial, we oven-dried the fuel to be tested at 70°C for 72 h, immediately weighed the fuel to determine dry mass, and then waited another 24 h before burning so that the fuels would reabsorb moisture from the laboratory air (45% humidity). Prior to ignition, fuels were evenly distributed across the metal tray. Although this approach does not exactly replicate the physical structure of the fuels in the field, our primary aim was to determine the relative flammabilities of different plant fuels, not necessarily fuel structure. After placing the fuels on the tray, we ignited them using a long-necked butane lighter positioned beneath the center of the tray (modified from Ganteaume et al. 2011). Mean room temperature and relative humidity during the experiments were 22.4°C and 45%, respectively, measured with a Kestrel 3000 weather meter. The order of the trials was randomized by species and initial fuel mass.

We measured several flammability metrics for each species. To assess flame spread rate (FLSP; cm/s) we used a stopwatch to mark the time required for flames to spread from the center to the edge of the tray. We also timed how long each sample sustained fire (SUST; e.g., flame duration; min). To measure maximum flame height (FLHT; cm), we reviewed a video recording of each trial

to assess flame height in relation to a metal ruler positioned behind the burning device. Fuel consumability (CONS; percentage of initial dry mass) was determined by weighing each sample before and after burning. We determined the maximum flame temperature above the litter sample at the four heights of the thermocouples (i.e., TEMP₁, TEMP₂, TEMP₅, and TEMP₁₀).

Flammability of *Larrea*

To determine the ignition requirements and burning characteristics of *Larrea*, we evaluated the flammability of two types of shrub fuels: “dead” and “live-collected” *Larrea* branches, including a wide range of diameters and moisture content. We expected the dead branches that accumulate at the base of *Larrea* to be much more flammable than living branches in the upper portion of the shrub. These potential differences in flammability could be due to differences in fuel moisture content, as well as structural differences due to weathering of dead branches in hot, dry desert conditions. For example, dead branches tend to be brittle and cracked with peeling bark, whereas live branches are covered in smooth bark, with presumably lower surface area and higher moisture content.

During January and February 2014 in the Sonoran and Mojave sites, we collected 90 live and 40 dead *Larrea* branches from both the upper and lower portion of 20 shrubs. After collection, we cut each branch to a standard length of 14 cm, resulting in branches that ranged in dry mass from 1.7 to 26.3 g and in diameter from 3.8 to 21.4 mm (measured at the base of the branch). After transport to the lab at Iowa State University, we stored the samples in paper bags at room temperature ($\sim 23^{\circ}\text{C}$ and 26% relative humidity; RH) for 1 month before the experiments. Given the time that passed between harvesting of the live-collected branches and the experiments, our comparisons of dead and live-collected branches are meant to evaluate qualitative differences in flammability of different *Larrea* fuel types, since the live-collected branches we tested are drier than live branches in the field. Thus, the ignition requirements determined for live-collected *Larrea* branches in the laboratory are likely underestimates of the intensity of fires required to ignite live branches, with higher moisture content, in the field. For this reason, we also tested the flammability of rehydrated live-collected *Larrea* fuels (see description of moisture manipulations).

To test *Larrea* flammability, we placed dead or live-collected branches (40 replicates of each) on a burning device that consisted of a metal mesh platform (supported by a tripod), on which we laid the *Larrea* branch samples (Fig. 2b). We positioned a propane Bunsen burner under the platform with the tip of the flame 5 cm below the sample. We used two type K thermocouples (as described previously) to record the temperature when *Larrea* ignited and the temperature of the flame that was produced from its combustion. To record the temperature at ignition, we placed the first thermocouple

immediately beneath and in contact with the branch (exposed to the burner, but 5 cm above the tip of the flame). We recorded the *Larrea* flame temperature with a second thermocouple positioned 5 cm above the burning branch. The two thermocouples were connected to data loggers that recorded temperature at 1-s intervals. We started a digital timer at the beginning of each trial (i.e., when the burner was lit) and recorded when the *Larrea* branch ignited and the time when combustion ended (the burner was turned off once the branch ignited). The flame duration was the time period during which there was a visible flame produced by the fuel. During these trials, the mean room temperature and relative humidity were 21.3°C and 9.1% RH, respectively. Each day between 28 January and 10 February 2014, we conducted five to 10 trials, randomized by branch diameter and fuel type (i.e., dead vs. live-collected). Once again, due to the limitations of thermocouples (Bova and Dickinson 2008), the temperature at ignition and flame temperature we report should be viewed as relative metrics of *Larrea* ignitability and burning intensity. Of particular note, the temperature at ignition was read by the thermocouple in contact with the branch at the time of ignition, and is thus an overestimate of the temperature of the fuel itself at ignition (i.e., we did not measure ignition temperature). Nonetheless, the temperature at ignition measured by the thermocouple provides a metric of relative fire intensity required to ignite *Larrea* fuels.

To determine the influence of moisture on *Larrea* flammability, we manipulated fuel water content, and employed the same burning device described previously for the dead and live-collected branches. To manipulate branch moisture content, we first oven-dried live-collected *Larrea* branches at 70°C for 120 h, recorded the dry masses, and then placed the branches in water for 72 h. After removal from the water, we recorded the wet mass of each branch every 30 min to determine the percent moisture content by mass. For these flammability trials, we used samples that spanned a moisture gradient from 1.5% to 45% moisture by mass. The upper end of this range (30–45%) represents fuel moisture content measured in live stems of desert shrubs in other parts of the world, e.g., Israel (Sternberg and Shoshany 2001) and China, (Xu et al. 2007). We conducted $n = 50$ burning trials randomly stratified across five moisture classes: 1–5%, 5–10%, 10–20%, 20–30%, and 30–45% moisture by dry mass. Once we established the moisture content for a sample, we sealed the branch in a plastic bag for use in a burn trial on the same day. From 15 to 23 April 2014, we conducted 10 trials per day from one of the five randomly selected moisture classes. Mean laboratory temperature and relative humidity during the experiment were 21.8°C and 24.7% RH, respectively (Kestrel 3000 weather meter).

Statistical analyses

We used multiple regression analyses to determine how different species (i.e., the spreaders *Bromus* and *Schismus*

and the igniters *Ambrosia* and *Amsinckia*) and fuel loads (i.e., grams of initial dry biomass) influenced flame spread (i.e., FLSP), flame height (i.e., FLHT), consumability (i.e., CONS), flame duration (i.e., SUST), and maximum flame temperature (TEMP). We tested separate models for each response variable, with initial mass (i.e., grams of dry biomass) as a continuous predictor variable and species as a categorical variable. We also conducted ANOVA's to test the main effect of species on the mean flammability responses, followed by Tukey's tests to determine differences among species.

To evaluate *Larrea* flammability we used multiple regression to model temperature at branch ignition, flame temperature, time to ignition, and flame duration as a function of diameter and branch type (i.e., dead vs. live-collected branches). We did not include branch mass in the model because diameter was strongly correlated with mass, a reasonable proxy for size of branch (Spearman correlation = 0.96 and $P < 0.001$). We then used ANOVAs to determine the main effect of branch type on the mean temperature at ignition, flame temperature, time to ignition, and flame duration. To assess the effect of water content on flammability of *Larrea*, we conducted regression analyses with separate models for temperature at ignition, flame temperature, time to ignition, and flame duration, using percentage of water by dry mass as a continuous explanatory variable. All statistical analyses were performed with R 3.1.3 (R Development Core Team 2013).

RESULTS

Flammability of spreaders and igniters

Flame spread rate (FLSP) for spreaders, *Bromus* and *Schismus* (1.32 and 1.22 cm/s, respectively), ranged from three to 10 times faster than for the igniters, *Ambrosia* and *Amsinckia* (0.12 and 0.38 cm/s, respectively; Table 1). FLSP was negatively correlated with initial fuel load for *Bromus* ($P = 0.021$, $r^2 = 0.18$), whereas fuel load had no effect on FLSP of *Schismus*, *Ambrosia*, and *Amsinckia* (Fig. 3a, b). FLSP was slower for *Ambrosia* compared to the other three species ($P < 0.001$, Table 1), and was slower for *Amsinckia* compared to *Bromus* and *Schismus*, but did not differ between the spreaders (Table 1).

Flame height (FLHT; cm) was similar between spreaders and igniters (i.e., no effect of species; $P = 0.19$, multiple $r^2 = 0.6$, Table 1). FLHT was positively correlated with fuel load for all spreaders and igniters ($P < 0.001$, Fig. 3c, d). Mean consumability (CONS) for the igniters *Ambrosia* (83.3%) and *Amsinckia* (71.5%) exceeded that of the spreaders, *Bromus* (49.8%) and *Schismus* (34.8%). CONS was negatively correlated with fuel load for *Bromus* ($P < 0.001$, $r^2 = 0.37$, Fig. 3e), but positively correlated for *Ambrosia* ($P < 0.01$, $r^2 = 0.25$, Fig. 3f). Differences in CONS among the species were all statistically significant ($P < 0.001$ for all comparisons, Table 1).

TABLE 1. Summary of flammability results for spreaders (*Bromus* and *Schismus*) and igniters (*Ambrosia* and *Amsinckia*), including: flame spread rate (FLSP), flame duration (SUST), maximum flame height (FLHT), consumption (CONS), and maximum flame temperature (TEMP) recorded at four heights above the burn platform (1, 2, 5, 10 cm) for each plant species.

Species	FLSP (cm/s)	SUST (min.)	FLHT (cm)	CONS (%)	TEMP (°C)			
					1 cm	2 cm	5 cm	10 cm
<i>Ambrosia</i>	0.12 ^a (0.01)	4.17 ^a (0.15)	30.8 ^a (2.1)	83.3 ^a (2.1)	837.7 ^a (13.5)	779.6 ^a (23.5)	724.6 ^a (31.1)	572.4 ^a (35.8)
<i>Amsinckia</i>	0.38 ^b (0.02)	1.91 ^b (0.09)	26.9 ^a (2.6)	71.5 ^b (2.1)	655.1 ^b (23.7)	566.8 ^b (32.7)	453.5 ^b (37.5)	331.4 ^b (35.6)
<i>Bromus</i>	1.32 ^c (0.05)	0.55 ^c (0.03)	28.2 ^a (1.9)	49.8 ^c (1.7)	579.4 ^b (29.5)	605.3 ^b (34.2)	587.2 ^b (33.9)	437.4 ^b (36.3)
<i>Schismus</i>	1.22 ^c (0.05)	0.76 ^c (0.06)	24.1 ^a (2.1)	34.8 ^d (2.2)	588.9 ^b (28.6)	572.4 ^b (30.1)	536.6 ^b (42.4)	363.7 ^b (38.1)

Notes: Means are shown with standard error (SE) in parentheses. Statistical differences at $P < 0.05$ are shown with different superscripted lowercase letters.

Igniters produced longer fires (SUST) than spreaders ($P < 0.001$, Table 1). The spreader *Bromus* had the lowest SUST (flame duration), with a mean of 0.55 min, followed by *Schismus* and *Amsinckia* (0.8 and 1.9 min, respectively; Table 1). The igniter *Ambrosia* had the longest mean flame duration (4.17 min). For all spreaders and igniters SUST and initial fuel mass were positively correlated (all P values < 0.05 , Fig. 3g,h).

The maximum flame temperatures at 1, 2, 5, and 10 cm above the fuels (i.e., TEMP₁, TEMP₂, TEMP₅, and TEMP₁₀, respectively) was produced by the igniter *Ambrosia*, with significantly hotter temperatures across all heights compared to the other species ($P < 0.01$, Table 1). The spreaders, *Bromus* and *Schismus*, and igniter, *Amsinckia*, produced similar maximum temperatures across the different heights ($P > 0.05$ for all comparisons, Table 1).

Flammability of *Larrea* branches

Live-collected branches required higher temperatures to ignite compared to dead branches (Δ temperature = 153.3°C, Table 2, $F_{1,77} = 54.67$, $P < 0.001$). For both dead and live-collected branches, diameter had no effect on temperature at ignition or flame temperature. (Fig. 4a,b). Dead *Larrea* branches produced hotter flames compared to live-collected branches (mean flame temperature 799.6 and 668.8°C, respectively, Table 2).

The time required to ignite *Larrea* increased with branch diameter for both dead and live-collected branches ($P < 0.01$, Fig. 4c). Branch type had no effect on time to ignition (Table 2). Flame duration was positively correlated with the diameter of both *Larrea* branch types ($P < 0.001$, Fig. 4d). Dead *Larrea* branches burned

2.6 times longer than live-collected branches ($P < 0.001$, Table 2).

Regardless of their size, wetter *Larrea* branches required hotter temperatures to ignite ($P < 0.001$, Fig. 5a), but water content had no effect on flame temperature (Fig. 5b). Higher water content delayed time to ignition ($P < 0.001$, Fig. 5c), and also reduced flame duration ($P = 0.046$, Fig. 5d). In sum, wetter branches required hotter and longer fires to ignite, and once burning, they produced cooler fires and shorter flame durations compared to drier branches.

DISCUSSION

Through experimental assessments of plant flammability, this study details how novel fire dynamics can emerge as a result of the burning characteristics of three distinct, but interacting, functional groups: spreaders, igniters, and keystone shrubs. Consistent with our conceptual model (Fig. 1) and flammability hypotheses, the exotic grasses *Bromus* and *Schismus* spread fire quickly, burn for a very short duration, and produce relatively cool fires, with only 35–50% mass consumption. By comparison, the native igniters *Ambrosia* and *Amsinckia* spread fire slowly, burn up to eight times longer, and produce hotter fires that consume more of their mass (mean CONS 83%; Table 1). The temperature and duration of flames produced by these native species (specifically *Ambrosia*) are sufficient to ignite dead *Larrea* branches, which accumulate at the base of the shrub (Fig. 6). Once burning, these dead branches ignite living branches (with higher moisture content) in the upper portions of the shrub (Fig. 6), producing locally intense fires.

TABLE 2. Summary of flammability characteristics (mean \pm SE) for dead and live-collected *Larrea* branches.

Fuel type	Temp. at ignition (°C)	Flame temp. (°C)	Ignition time (min)	Flame duration (min)
Dead branches	595.7 ^a \pm 10.4	799.6 ^a \pm 19.5	1.9 ^a \pm 0.1	2.9 ^a \pm 0.3
Live-collected branches	692.8 ^b \pm 7.2	668.8 ^b \pm 25.9	2.1 ^a \pm 0.3	1.1 ^b \pm 0.1

Note: Statistical differences at $P < 0.05$ are shown with different superscripted lowercase letters.

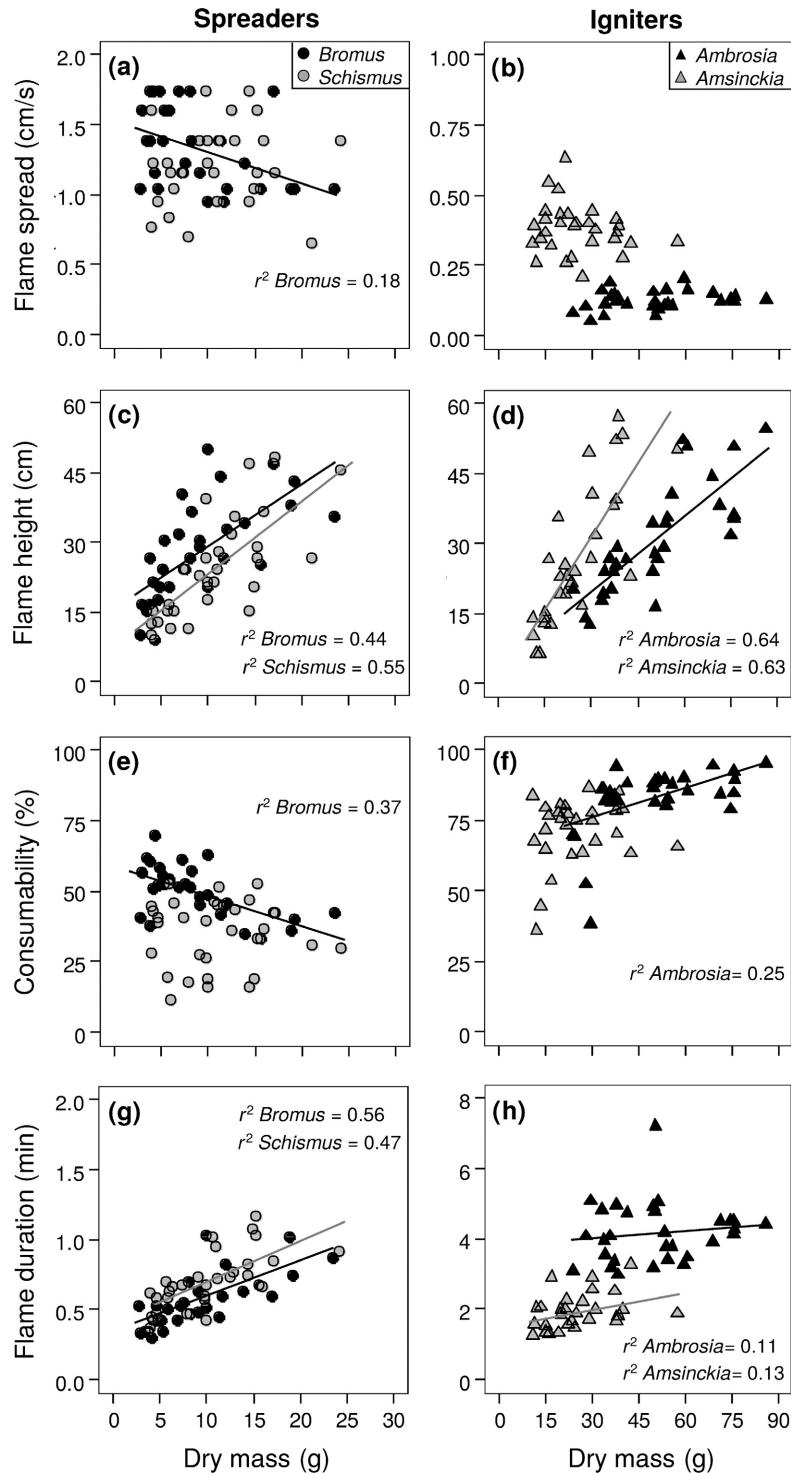


FIG. 3. Relationship between fuel loads (i.e. total dry mass) and (a, b) flame spread, (c, d) flame height, (e, f) consumability, and (g, h) flame duration for spreaders (*Bromus* and *Schismus*, left panels) and igniters (*Ambrosia* and *Amsinckia*, right panels). Best-fit lines and r^2 are displayed for relationships significant at $P < 0.05$. Note the different x- and y-axis scales for spreaders and igniters

Most studies of grass invasions typically focus on a single species, and infer rather than directly measure flammability. In contrast, our results demonstrate that

synergies among multiple species with different burning characteristics can provide mechanistic insight into novel fire dynamics in grass-invaded ecosystems. Indeed, there

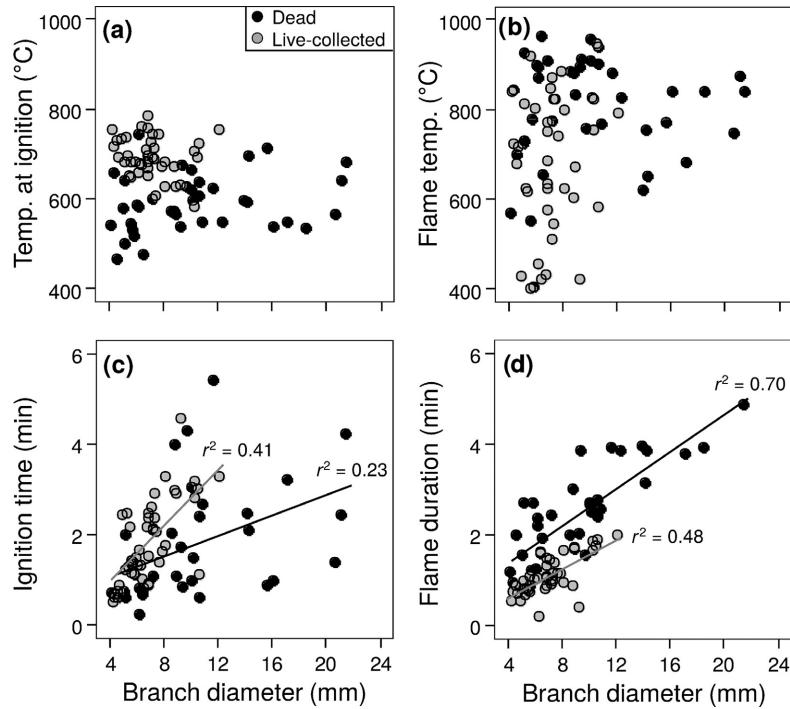


FIG. 4. Flammability metrics of *Larrea* fuels in relation to branch diameter and branch type (i.e., dead and live-collected) for (a) temperature at ignition, (b) flame temperature, (c) ignition time, and (d) flame duration. Best-fit lines and r^2 are displayed for relationships significant at $P < 0.05$.

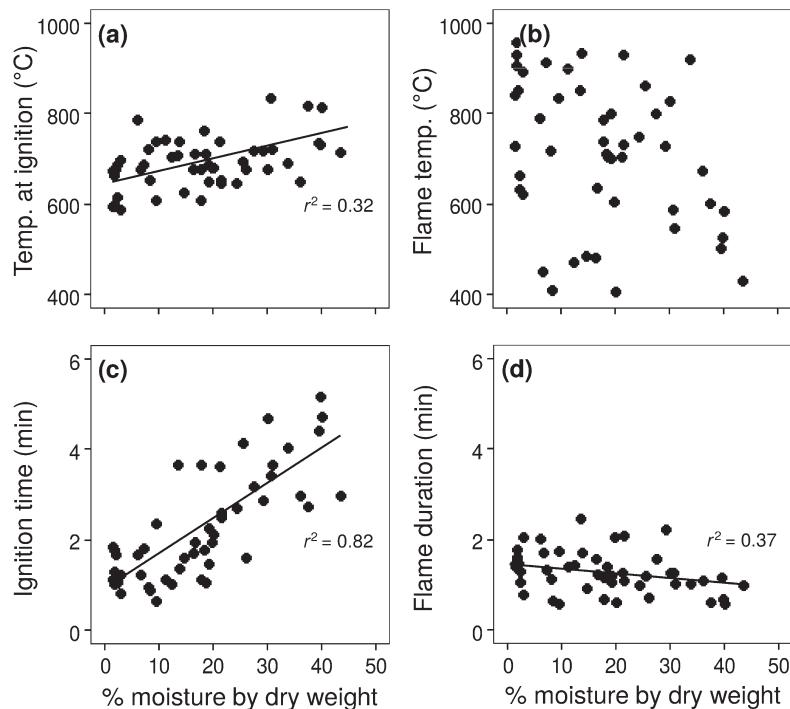


FIG. 5. Effects of fuel moisture content of (rehydrated) live-collected *Larrea* branches on (a) temperature at ignition, (b) flame temperature, (c) ignition time, and (d) flame duration. Best-fit lines and r^2 are displayed for relationships significant at $P < 0.05$.

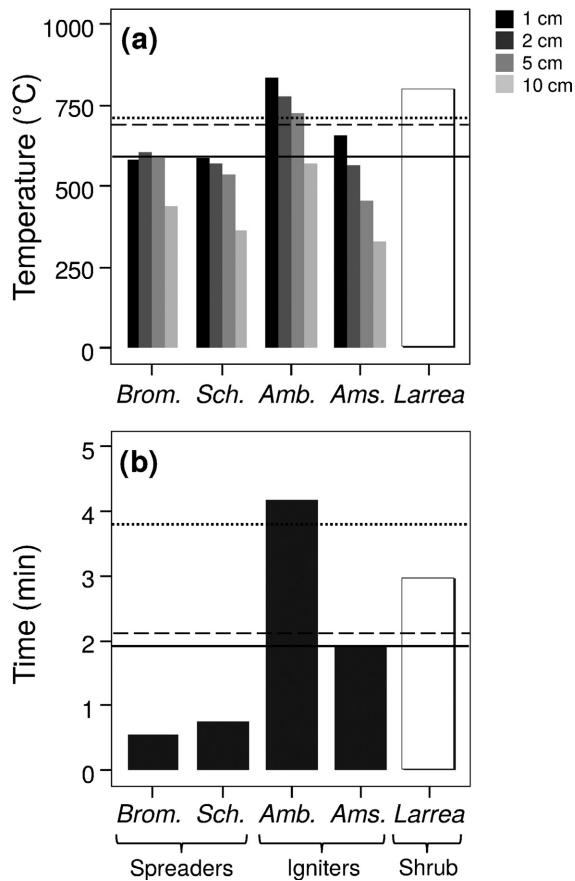


FIG. 6. The potential of spreaders (*Bromus* and *Schismus*), igniters (*Ambrosia* and *Amsinckia*), and dead *Larrea* branches to ignite dead and live-collected *Larrea* branches. (a) Maximum flame temperature at 1, 2, 5, and 10 cm above spreaders and igniters and 5 cm above dead *Larrea* branches (measured with different protocols, see *Methods*). (b) Flame duration for spreaders, igniters, and dead *Larrea* branches. Horizontal lines represent (a) mean temperature at ignition and (b) mean ignition time for three *Larrea* fuel types: dead branches (solid lines), live-collected branches (dashed lines), and live-collected branches rehydrated to 30–45% moisture by dry mass (dotted lines).

is growing recognition that species interactions are critical to novel fire regimes (Varner et al. 2015). For example, Metz et al. (2013) documented high mortality rates in the normally fire-tolerant coast redwood (*Sequoia sempervirens*) as a result of extremely intense fires that were fueled by native mid-story trees infected with and/or killed by an exotic fungal pathogen. Given that fire regimes represent complex climate–vegetation–human–fire interactions (Iglesias et al. 2015), we should expect these sorts of synergistic species interactions to be both common and of critical importance for modeling and management of fire–vegetation dynamics in many novel and natural ecosystems.

Among the complexities of fire regimes in our desert study system, climate change is contributing to more frequent, high-intensity rainfall events (United States Environment Protection Agency (EPA) 2015), which

promotes establishment, growth, and fuel production by invasive and native plant species (Brooks and Matchett 2006). Whereas low precipitation can greatly constrain fuel production and ecosystem flammability (the situation in most deserts), small increases in desert precipitation and productivity, driven by climate change, can greatly increase ecosystem flammability (Moritz et al. 2012). We should expect that rates of fire-induced mortality of *Larrea* shrubs in the Sonoran and Mojave deserts will increase as changing precipitation patterns contribute to a greater abundance of spreaders and increased fuel loads produced by igniters during wetter than average years, especially those years with extreme rainfall events. The effects of increased precipitation should not be confused with the potential of increased fuel moisture content to reduce plant flammability (Alessio et al. 2008, De Lillis et al. 2009); given the long dry periods and extreme seasonality of deserts, any increases in periodic rainfall are unlikely to reduce flammability of *Larrea* through effects on fuel moisture. Rather, our results suggest that to understand the effects of climate change on ecosystem flammability and *Larrea* mortality, future studies should consider how precipitation influences invasion by exotic spreaders (and thus landscape-scale fuel continuity) as well as fuel production (e.g., augmented growth) by native igniters.

Although we focused on grass-invaded deserts, our conceptual model (Fig. 1) reflects the broader importance of the spatial arrangement of fuels for understanding fire dynamics in a variety of systems. For example, in Australia the fire-sensitive conifer *Callitris intratropica* forms patches of low-flammability vegetation within a matrix of highly flammable grass-dominated savanna (Trauernicht et al. 2012). These fire-sensitive patches are prone to burn if prescribed fires are implemented in the late dry season (i.e., when fuels are very dry, Russell-Smith et al. 2010) or when domestic livestock are excluded from the system (i.e., removal of grazers permits fuels to accumulate, Trauernicht et al. 2013). Similarly, in African savannas, native perennial grasses spread fires across landscapes in which scattered trees form fertility islands, which like *Larrea* promote locally high herbaceous plant productivity (Belsky et al. 1989). Spatial patterns of tree cover and fire spread in these African savannas are both a product and cause of landscape-scale heterogeneity in fuels and megafaunal herbivory (Holdo et al. 2009). In savannas of the southeastern United States, the spatial distributions of plant communities of species with distinct flammabilities result in local-scale heterogeneity in fire intensity (Wenk et al. 2011). In these same systems, restoration of fire to long-unburned savannas often results in duff fires that can be lethal to normally fire-tolerant pines (Varner et al. 2015). Apparently, the highly flammable litter produced by these pines is advantageous when fires are frequent (Fonda 2001), but becomes a liability when fuels accumulate around the base of the plant, similar to the

dead branches that accumulate beneath *Larrea*. In sum, like the grass-invaded deserts in our study, an understanding of fire dynamics in these systems from Australia, Africa, and North America requires consideration of the landscape-scale distribution of plant species, the spatial arrangement of the fuels those species produce, the relative flammability of those species, and how those fuels are influenced by human factors (e.g., management of fire and herbivores).

CONCLUSIONS

In deserts of southwestern North America, ancient *Larrea* shrubs, which evolved to survive aridity but not fire, are being consumed by fires spread by exotic annual grasses. Our results suggest that these invasive grasses, although well known for their ability to carry fire across landscapes (Brooks et al. 2004), are unable to burn with sufficient intensity to ignite shrubs. Instead, these grasses spread fires to native herbaceous and perennial plants growing beneath scattered shrubs, which in turn produce fires that are hot enough and of sufficient duration to ignite *Larrea*. Indeed, Brooks (2002) measured such temperature peaks directly under shrubs during fires. Although difficult to ignite, once these shrubs begin to burn, they can produce intense fires that do not occur in non-invaded deserts. Thus, the synergy between exotic invasive grasses, native annuals, perennial shrubs, and their distinct flammability characteristics help to explain novel fire dynamics in a system that did not historically burn. Given the global importance of grass invasions and altered fire regimes, our proposed model of spreaders, igniters, and keystone shrubs should be useful for conceptualizing the contributions of both native and invasive species in determining ecosystem flammability and fire behavior.

We suggest that predictive fire models and fuel management could be improved through better incorporation of the distinct spatial distributions and flammability characteristics of fire spreaders, igniters, and woody plants. For example, where fire-spreading invasive grasses cannot be easily controlled, managers should consider the feasibility of reducing the quantity of fuels that accumulate beneath fire-sensitive woody plants. This strategy could be applied to produce firebreaks designed to limit the spread of wildfire during years of particularly high fire risk. Such fuel reduction treatments have proven useful in other systems to protect species of conservation interest (e.g., Williams et al. 2006). Specific methods for removing fuels around *Larrea* need to be developed and tested, but will likely involve manual removal (e.g., clipping and raking) of native plant fuels (i.e., igniters) and dead *Larrea* branches. Study of such treatments should try to determine whether the benefits of fuel removal to protect shrubs from grass fires outweigh the potential costs of altering the microenvironment around keystone species that provide critical habitat to a host of desert plants and animals.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1371/supinfo>

DATA ACCESSIBILITY

All data associated with this paper for (1) plant litter trials, (2) *Larrea* branches trials, and (3) moisture content trials are available in Appendix S1: file 1, 2 and 3, respectively.