Prosopis glandulosa persistence is facilitated by differential protection of buds during low- and high-energy fires

Heath D. Starns [a, *], Carissa L. Wonkka [b], Matthew B. Dickinson [c], Alexandra G. Lodge [d], Morgan L. Treadwell [e], Kathleen L. Kavanagh [f], Douglas R. Tolleson [a], Dirac Twidwell [g], William E. Rogers [d]

[a] Rangeland, Wildlife and Fisheries Management Department, Texas A&M AgriLife Research, Sonora, TX, 76950, USA
[b] USDA ARS, Northern Plains Agricultural Research Lab, Sidney, MT, 59270, USA
[c] US Forest Service, Northern Research Station, Delaware, OH, 43015, USA
[d] Department of Ecology and Conservation Biology, Texas A&M University, College Station, TX, USA
[e] Rangeland, Wildlife and Fisheries Management Department, Texas A&M AgriLife Extension Service, San Angelo, TX, USA
[f] College of Forestry, Oregon State University, Corvallis, OR, 97331, USA
[g] Department of Agronomy and Horticulture, University of Nebraska, Lincoln, NE, USA

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ABSTRACT

Rangelands worldwide have experienced significant shifts from grass-dominated to woody-plant dominated states over the past century. In North America, these shifts are largely driven by overgrazing and landscape-scale fire suppression. Such shifts reduce productivity for livestock, can have broad-scale impacts to biodiversity, and are often difficult to reverse. Restoring grass dominance often involves restoring fire as an ecological process. However, many resprouting woody plants persist following disturbance, including fire, by resprouting from protected buds, rendering fire ineffective for reducing resprouting woody plant density. Recent research has shown that extreme fire (high-energy fires during periods of water stress) may reduce resprouting capacity. This previous research did not examine whether high-energy fires alone would be sufficient to cause mortality. We created an experimental framework for assessing the "buds-protection-resources" hypothesis of resprouting persistence under different fire energies. In July–August 2018 we exposed 48 individuals of a dominant resprouting woody plant in the region, honey mesquite (*Prosopis glandulosa*), to two levels of fire energy (high and low) and root crown exposure (exposed vs unexposed) and evaluated resprouting capacity. We censused basal and epicormic resprouts for two years following treatment. Water stress was moderate for several months leading up to fires but low in subsequent years. Epicormic and basal buds were somewhat protected from low- and high-energy fire. However, epicormic buds were protected in very few mesquites subjected to high-energy fires. High-energy fires decreased survival, caused loss of apical dominance, and left residual dead stems, which may increase chances of mortality from future fires. Basal resprout numbers were reduced by high-energy fires, which may have additional implications for long-term mesquite survival. While the buds, protection, and resources components of resprouter persistence all played a role in resprouting, high-energy fire decreased mesquite survival and reduced resprouting. This suggests that high-energy fires affect persistence mechanisms to different extents than low-energy fires. In addition, high-energy fires during normal rainfall can have negative impacts on resprouting capacity; water stress is not a necessary precursor to honey mesquite mortality from high-energy fire.

1. Introduction

Over the past century, rangelands worldwide have experienced changes in vegetation cover and structure, and large portions of once grass-dominated landscapes are now woody-plant dominated (Archer et al. 2017; Fuhlendorf et al. 2017). In many cases, such state shifts are driven by overgrazing and decades of fire suppression (Bragg and Hulbert, 1976; Archer, 1989; Brown and Archer, 1989; Briggs et al., 2002;

Archer et al. 2017) with climatic changes and increasing CO_2 levels modulating the shift in many grasslands (Kulmatiski and Beard, 2013; Wilcox et al. 2018). These state shifts can have broad-scale impacts to biodiversity in addition to reducing productivity for livestock (Anadon et al. 2014; Andersen and Steidl, 2019). Due to the negative effects of encroachment on herbaceous biomass, state shifts from grasslands to shrublands or woodlands are not often easily reversed (Fuhlendorf et al., 1996; Twidwell et al. 2013a; Ratajczak et al. 2016). Grassland to woodland conversions are frequently subject to such hysteresis because woody-plant-dominated states are more stable than graminoid-dominated states; therefore restoring drivers that maintain grassland dominance is often insufficient to restore grass dominance (Fuhlendorf et al., 1996; Twidwell et al. 2013a; Ratajczak et al. 2016). Largely, this hysteresis results from highly fire-adaptive persistence mechanisms exhibited by woody species. As a result, once a state shift occurs, restoration to a grassland state is not often possible via traditional management practices such as prescribed fire (Ansley and Castellano, 2006; Ratajczak et al. 2016).

Persistence in ecosystems characterized by frequent fire, such as grasslands and savannas, requires survival and regrowth or repair of consumed or injured tissues. For many encroaching woody species, persistence is achieved through resprouting (Bond and Midgley, 2001). However, successful persistence through resprouting is determined by the development of a bud bank, protection of meristematic tissue during fire, and a capacity to provide resources to buds until they become self-sufficient (Anderegg et al. 2012; Pratt et al. 2014; Sevanto et al. 2014). The Buds Protection Resources (BPR) framework of Clarke et al. (2013) highlights the integration of these three components of resprouter persistence via plant traits selected for by the common disturbance regime and resource environment of an ecosystem. Variation in and trade-offs among these three components – abundance and location of buds, protection of buds, and storage, mobilization, and delivery of nonstructural carbohydrates to support resprouting – drives species-specific thresholds of persistence following fire under differing environmental conditions.

Mesquite species (*Prosopis* spp.) are globally well-known for their invasive tendencies (Shackleton et al. 2014), as well as their ability to resprout following aboveground disturbance including fire, mechanical, and some chemical treatments. Indeed, mesquite is reported to increase in number of basal stems, canopy area, and leaf area in response to any aboveground disturbance (Ansley et al. 2010; Ansley et al. 2010b). Historical livestock management and fire suppression practices have allowed honey mesquite (*P. glandulosa*) to increase in dominance and abundance in the southern Great Plains (e.g., Texas, Oklahoma, Kansas) since the beginning of Euro-American settlement (Bray, 1904; Archer, 1989). Due to the expense of mechanical and chemical treatment, prescribed fire is often the most cost-effective option for treating large areas of honey mesquite (van Liew et al. 2012), despite incomplete mortality. Although prescribed fire continues to gain social acceptance as a viable and safe practice (Twidwell et al. 2013b), norms often restrict fires to conditions which minimize fire intensity (Wonkka et al. 2015; Twidwell et al. 2016, 2019). However, low-intensity fires rarely cause mesquite/woody plant mortality (Wright and Bailey, 1980; Ansley et al. 1998), especially when they are performed as a single treatment rather than as part of a comprehensive management plan (Ansley et al. 1998; Taylor et al. 2012; Starns et al. 2020). Although mesquite is notoriously difficult to kill with fire (Ansley et al. 2006, 2010a; Bovey, 2016), mortality has been achieved in isolated studies when executed in conditions beyond those typical of most prescribed fires (Wright et al., 1976; Twidwell et al. 2016). For instance, Twidwell et al. (2016) found 35–55% fewer resprouting woody plants (including mesquite) after conducting prescribed fires when fuel moisture was extremely low because of severe drought. Drought increased fire intensity by lowering fine fuel moisture, but also increased water stress of resprouting woody plants. Hydraulic-related stress increases woody plant vulnerability to cavitation (Tyree and Sperry, 1989), and water stress following fire

could reduce the ability of buds to develop into resprouts because of limited plant-available water (Pratt et al. 2014). By conducting the extreme fire during drought, fire intensity effects on resprouting woody plant mortality were not distinguishable from effects related to plant water stress. In addition, extreme fire effects on resprouting have not been systematically studied in a manner consistent with BPR resprouting theory. Given the importance of intact meristematic tissue, non-structural carbohydrate remobilization, and hydraulic function to resprouting potential and survival (Anderegg et al. 2012; Pratt et al. 2014; Sevanto et al. 2014), we experimentally assessed the contribution of these components of BPR theory for mesquite persistence to fire. It is well-established that mesquite has many dormant buds (Fisher et al., 1946) typically located just below the inner bark along the entire length of the stem (Meyer, 1971) that are released following disturbance to distal points (fulfilling the Buds component of BPR theory). We examined the potential for bud protection (Protection component) during a fire by testing the following hypotheses:

H1: (Protection) Buds (epicormic) along stems of trees are protected (by bark) from fire.

H2: (Protection) Buds on the base of trees are protected from fire by soil around the basal stem.

If H1 is an important component of mesquite persistence, we expect mesquites to survive fire by resprouting from epicormic meristematic tissues (we measured all aerial resprouts and refer to them collectively as epicormic throughout for simplicity). If H2 is an important component of mesquite persistence, we expect them to survive fire by resprouting basally from the root collar (hereafter referred to as basal resprouting); additionally, we expect mesquites with soil removed from the base of the stem to exhibit lower resprouting vigor following fire due to increased heat exposure. We use honey mesquite (*P. glandulosa*) as a representative species for improving knowledge on management of the globally invasive *Prosopis* genus, as well as understanding persistence dynamics of resprouting woody plants in general. The concept of BPR resprouting theory, and our experimental research, is to differentiate among the relative contributions of H1 and H2, with the understanding that these hypotheses are not acting independently but instead are integrated. As such, we anticipate that H1 and H2 are integrated components of mesquite persistence to fire. We therefore compare persistence following low-energy fires and high-energy fires. We conducted this experimental research during a period of low-moderate water stress, which allowed us to assess effects of fire energy independently of plant water stress.

2. Methods

2.1. Study site

Our study was conducted at the Texas A&M AgriLife Sonora Research Station (SRS) in the Edwards Plateau ecoregion of Texas, approximately 56 km south of Sonora, Texas USA. The site is characterized by rolling topography and highly variable inter- and intra-annual precipitation. Soils are of the Tarrant silty clay series, of the clayey-skeletal, montmorillonitic, thermic family of Lithic Haplustalls, at an elevation of 730 m. The generally bimodal annual precipitation ranges from 156 to 1054 mm (median = 557 mm), with most rainfall resulting from spring and autumn thunderstorms. Herbaceous vegetation is comprised mainly of discontinuous mid- and shortgrass species. The growing season in the region lasts from April until early November. The portion of SRS used for this study was treated with an extreme (high ambient temperature, very low relative humidity) prescribed fire in August of 2000. It was subsequently used for grazing by sheep and goats, but livestock were excluded for one growing season (2017) prior to our experimental fires in 2018 and for the duration of monitoring. Year-to-date (2018) precipitation (104 mm) was slightly lower than the long-term mean during July–August but precipitation in the months immediately following fire was high (494 mm), such that 2018 rainfall was

slightly above average (598 mm). The two subsequent years had rainfall amounts near the long-term mean (522 mm in 2019 and 609 in 2020).

2.2. Experimental design and treatments

We created 10 m × 10 m plots centered around 72 individual mesquite trees and randomly assigned each a factorial treatment combination of fire energy (no fire, low intensity, and high intensity) and basal exposure (yes or no) as described below, resulting in 12 replications of each fire energy*basal exposure combination. Focal trees were selected to be similar in size and growth form. Hay was spread evenly across each plot prior to ignition to create a continuous fuel bed and cut juniper fuel was added to plots assigned high-energy treatments (Fig. 1). Fuel was added to each plot the same day it was burned. For
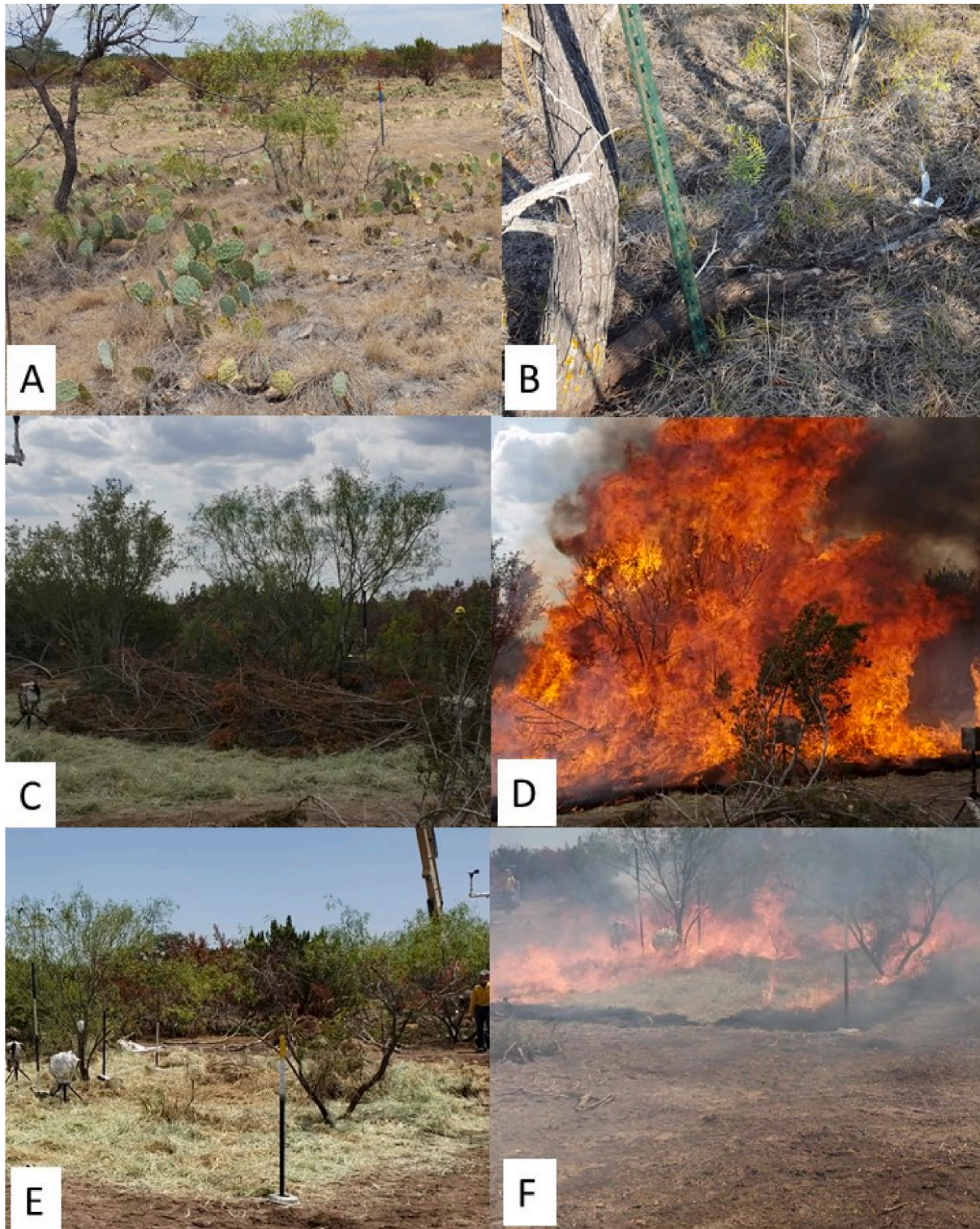

Fig. 1. (A) Pre-treatment photo of ambient fuels and landscape in study area. (B) Up-close image of a focal tree with ambient fuels. (C) Fuel additions for high-energy fire. (D) High-energy fire in progress. (E) Fuel additions for low-energy fire. (F) Low-energy fire in progress. Photo credit: H. Starns.

further detail on fuel additions, see Hiers et al. (2021). Fires were ignited individually in a "ring fire" pattern using two drip torches beginning at the downwind corner and meeting at the upwind corner. Burns were executed between July 30-August 4, 2018. Soil around the bases of all focal mesquite trees were carefully excavated between July 24 and July 27 to locate the shallowest root >1 cm diameter. Roots were reburied on all focal trees except for those assigned basal exposure treatment, because mesquite basal buds are typically located above the shallowest root.. Temperature, relative humidity, and pre-fire wind speed at 3.05 m height above ground (averaged over 10 min prior to ignition) was collected with HOBO micro-station instruments located at the plot corners. Year to date precipitation was 103.6 mm (data from on-site RAWS station, Mesowest.utah.edu, RAWS ID = EDWT2). Immediately prior to ignition, volumetric soil moisture was recorded at three random points within each plot using an EXTECH MO750 soil moisture probe (FLIR Commercial Systems, Nashua NH, USA) inserted to a depth of 20 cm.

2.3. Measurements

Mesquites were monitored for resprouting activity for two growing seasons following application of fire. For each focal mesquite, we assessed the post-fire status (live/dead) and censused the number of live basal and epicormic resprouts (Fig. 2). If there was no resprouting activity (basal or epicormic), the mesquite was recorded as having a status of "dead"; if there were any resprouts, the status was "alive". Fire energy was calculated from consumed fuel loading (kg/m^2) and a constant heat of combustion (18600 kJ/kg). Fuel mass and moisture content were measured prior to fires; woody fuels that were not consumed were re-weighed after fires to calculate consumed dry-loading. A negligible amount of hay remained after some fires and was not re-weighed. Because fire energy clustered into two distinct and vastly different groups separated by more than an order of magnitude as a function of woody fuel addition (high-energy plots averaged 104,759 ± 14,799 kJ/m^2; low energy plots averaged 10,174 ± 1150 kJ/m^2), we treated fire energy as a categorical variable for purposes of analysis.

2.4. Statistical analysis

We modeled resprouting of focal mesquite trees in April 2019 and July 2020. Our response variables were a binary response indicating resprouting status (resprouting or not) based on visible live tissue for each of the two sampling periods, total number (per focal tree) of live resprouts, a binary response indicating epicormic resprouting status (resprouting epicormically or not), number of epicormic resprouts, a binary response indicating basal resprouting status (resprouting basally or not) and number of basal resprouts. Only those focal mesquites that were resprouting were included in analyses of number of resprouts. We used negative binomial regression to analyze number of resprouts (total, basal, and epicormic) by treatment because these were overdispersed count data, as determined by dispersion tests of Poisson-modeled residuals. We used Firth's logistic regression to analyze the binary resprouting data because logistic regression revealed quasi-complete separation for several variables (Firth, 1993). Predictor variables for all models were fire energy (High versus Low), whether the root crown (stem base) was exposed (Yes or No), the interaction between these two treatments, average soil moisture of the plot at the time of burning, wind speed in kilometers per hour, and relative humidity at the time of ignition. We did not include ambient temperature in models, as this would have introduced multicollinearity due to the inherent correlation between relative humidity and temperature; relative humidity was the more variable of the two. We included the number of basal resprouts as a predictor variable in the model for number of epicormic resprouts because we hypothesized that basal resprouting might inhibit epicormic resprouting and vice-versa. Non-significant interactions were removed from models. To account for heteroscedasticity, we calculated robust standard error estimates following the White method (White, 1980;

White and Domowitz, 1984). We omitted control plots from the analysis because there was neither mortality nor resprouting in control trees during the study period, so we focused on comparing low- and high-energy fire treatments to assess differences in mortality and resprouting number for conventional (low-energy) and extreme (high-energy) prescribed burning. Due to the destructive nature of exposure to high-energy fire, we were unable to permanently identify each stem on each focal tree for post-fire monitoring. As such, we were unable to include stem diameter in our models.

All analyses were performed in the R statistical computing environment (R Core Team, 2021) with the glm function to fit the logistic regression models and glm.nb from the MASS package (Venables and Ripley, 2013) to fit negative binomial models. Dispersion tests were conducted using the dispersion test function from the AER package (Kleiber and Zeileis, 2008). Robust estimation of standard errors was conducted using the sandwich package (Zeileis 2004, 2006).

3. Results

3.1. Environmental conditions

Soil moisture averaged 13.3% on the day of burning and ranged from 4.2 to 20.9%. Relative humidity at the time of ignition averaged 27.2% and ranged between 20.3 and 35.2%. Wind speed at the time of ignition averaged 8.2 km/h and ranged between 4.15 and 15.7 km/h. Ambient temperature at time of ignition ranged from 32.2 °C to 39.4 °C. Depth to shallowest root >1.0 cm in diameter ranged from 0.5 cm to 21 cm, with a mean of 4.96 cm.

3.2. Total resprouts

All but 5 of the 48 burned focal mesquites were top-killed by fire. The 5 that were not top-killed were all in low-energy plots and had <10% of their pre-fire crown remaining. All but 7 focal mesquites had resprouted within 2 years post-fire; the 7 that did not resprout were all in high-energy plots. At the end of the study period, 7 of the 48 focal mesquites were dead, all in high-energy plots; 4 of the 7 had bases exposed (Table 1).

Fire energy was the only significant predictor in both years. Holding all other variables constant, being in a low fire energy plot increased the odds of a focal mesquite having at least 1 live resprout by a factor of 49 (confidence interval ~7–1085) and 13 (confidence interval ~1.4–1747) in 2019 and 2020 respectively (Table S1).

One year post fire, in 2019, there was a significant interaction between fire energy and basal exposure in the model for total resprouts (Table S2). High energy plots had fewer resprouts than low energy plots regardless of base exposure; however, low fire energy plots with bases exposed had fewer resprouts than low fire energy plots with intact bases while high fire energy plots had similar numbers of resprouts in plots with bases exposed and those with bases intact (Fig. 3). In 2020, the interaction between fire energy and basal exposure was no longer significant, so it was removed from the model; however, a significant interaction manifested between fire energy and wind speed, which was not evident in 2019 (Table S2). High fire energy plots had fewer resprouts than low fire energy plots at lower windspeeds, but that difference did not hold under higher wind speeds as the number of resprouts in low energy plots decreased with increasing windspeed (Fig. 3). Basal exposure was no longer a significant predictor of total resprouts in 2020 (Table S2, Fig. 3).

3.3. Epicormic resprouting

About 40% of the burned mesquites resprouted epicormically, but only one was in a high-energy treatment plot. Fire energy was a significant predictor in both years. Holding all other variables constant, being in a low fire energy plot increased the odds of a focal mesquite having at
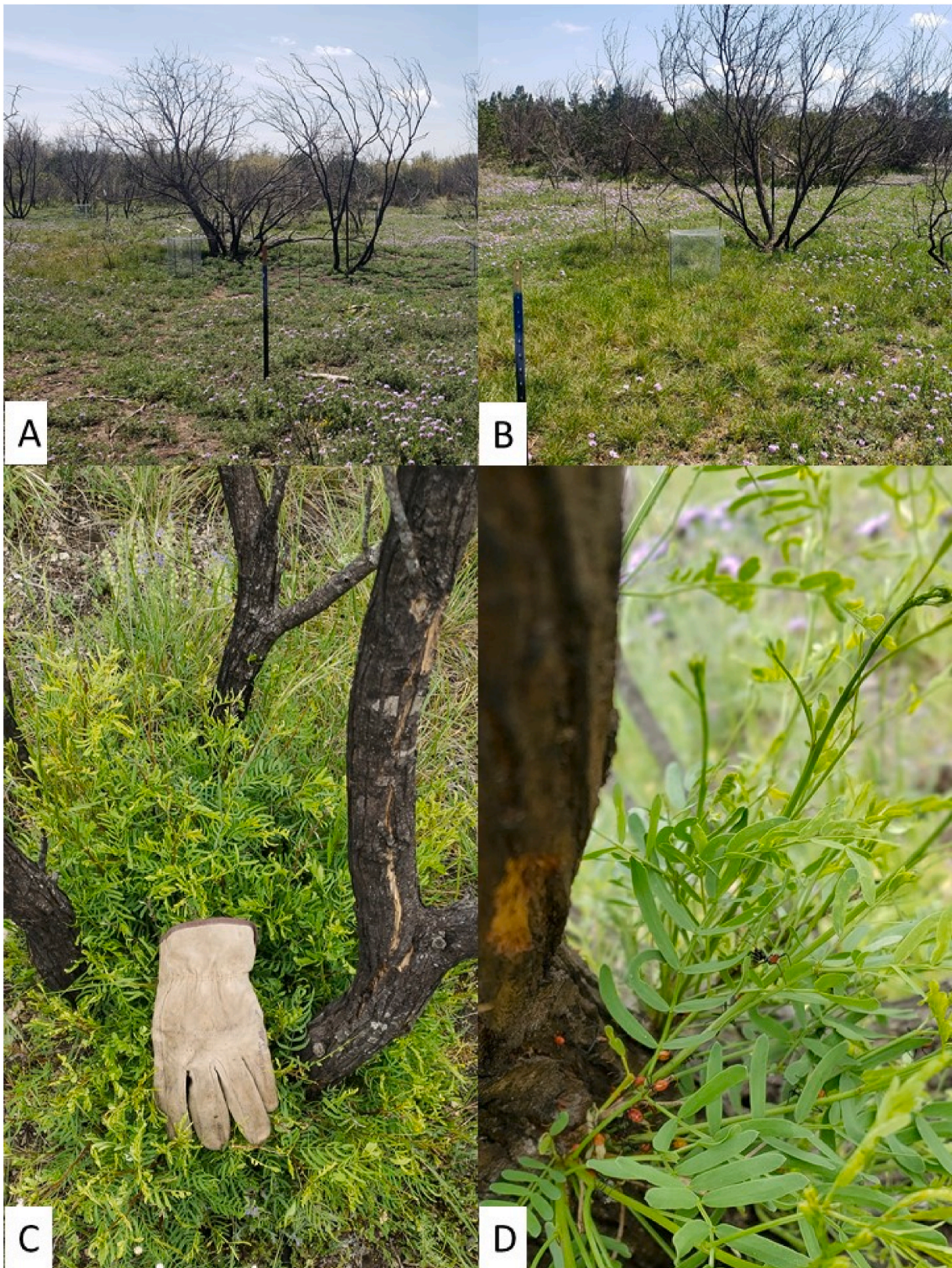
Fig. 2. (A) High-energy focal tree seven months post-fire. (B) Low-energy focal tree seven months post-fire. (C) Basal resprouts from high-energy focal tree. (D) Close-up photo of epicormic resprouts from low-energy focal tree, approximately 100 cm above ground-level. Photo credit: H. Starns.

Table 1

Contingency table for resprouting status and count of mesquites with epicormic and basal resprouts by fire energy.

	Epicormic Only	Basal Only	Both Basal and Epicormic	No Resprouts
2019				
Low Energy	7	4	12	1
High Energy	0	5	1	18
2020				
Low Energy	7	6	11	0
High energy	0	16	1	7

least one live epicormic resprout by a factor of 47 (confidence interval ~8–760) and 45 (confidence interval ~ 7–767) in 2019 and 2020 respectively (Table S3). Wind speed was also a significant predictor of whether a focal mesquite had an epicormic resprout, with a one kph increase in wind speed reducing the odds of a focal mesquite having at least one live epicormic resprout by a factor of 39 (confidence interval ~ 0.03–0.66) in 2019 and 48 (confidence interval ~0.15–0.73) in 2020 (Table S3).

Because only a single high-energy focal mesquite resprouted epicormically, fire treatment was not included in the assessment of number of epicormic resprouts. Basal exposure was not a significant predictor of

epicormic resprouts in 2019 or 2020 (Table S4, Fig. 4). Wind speed was a significant predictor of mean number of epicormic resprouts in both years. For each kph increase in wind speed, the mean number of epicormic resprouts decreased by 30% (confidence interval~ 3–50%) in 2019 and 37% (confidence interval ~6–65%) in 2020 (Table S4). The number of basal resprouts was not a significant driver of number of epicormic resprouts in either year (Table S4), although there was a marginally significant tendency for fewer epicormic resprouts in trees with more basal resprouts (Fig. 5).

3.4. Basal resprouting

Equal numbers of mesquites exposed to low- and high-energy fires resprouted basally, but those exposed to high-energy fire were nearly exclusively limited to basal resprouting while epicormic resprouting was common in low-energy treatments. Fire energy was a significant predictor of basal resprouting in 2019 but not 2020. Holding all other variables constant, being in a low fire energy plot increased the odds of a focal mesquite having at least one live basal resprout by a factor of 6.7 (confidence interval ~2–31) in 2019 but did not change the odds of having at least one live basal resprout in 2020 (Table S5).

In 2019, high energy plots had fewer resprouts than low energy plots, but by 2020 high and low energy plots had similar numbers of basal resprouts (Table S6, Fig. 6). Basal exposure was also a significant predictor of basal resprouts in 2019, but was not in 2020. Plots with bases exposed had 1–83% fewer basal resprouts than intact plots regardless of fire treatment in 2019, but by 2020, exposed and intact plots had similar
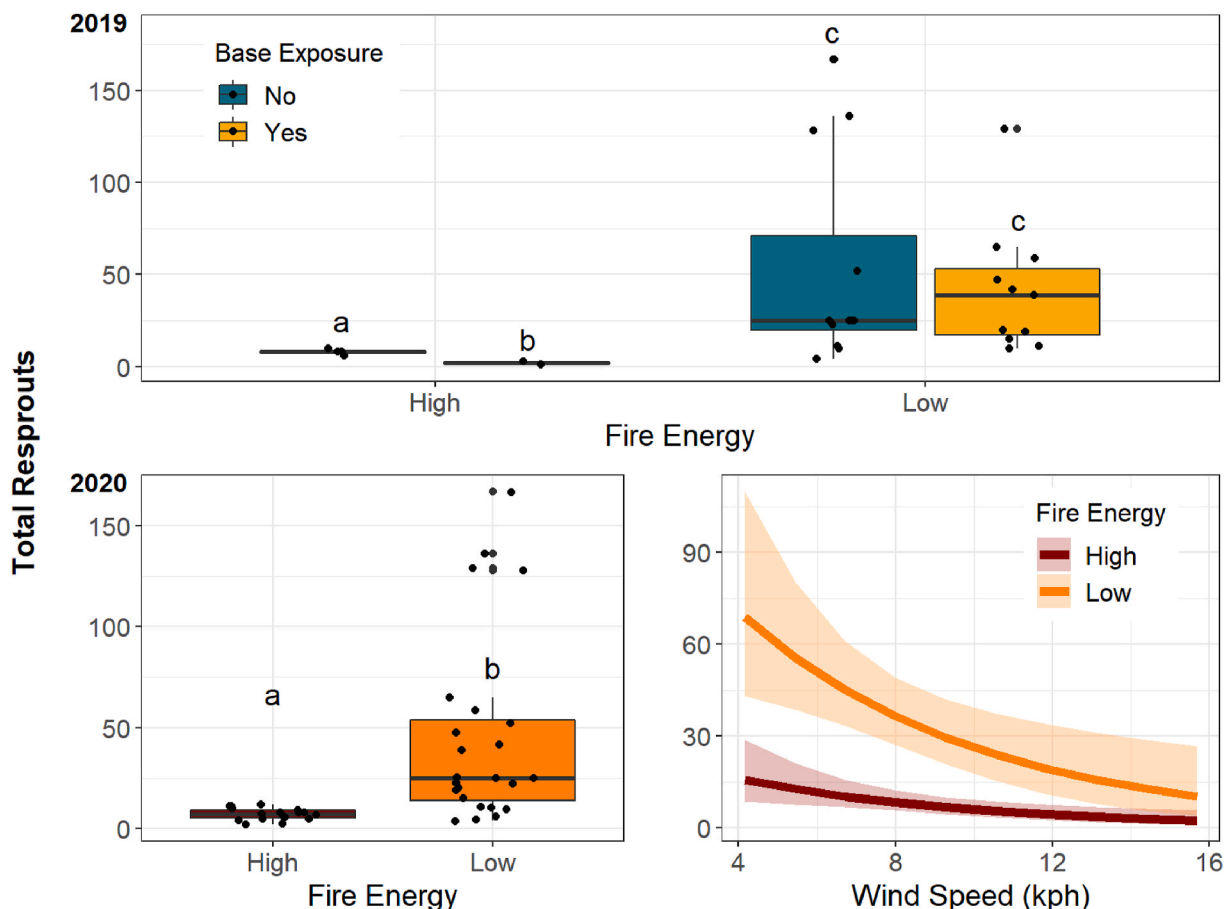

Fig. 3. Total number of resprouts in 2019 (top) broken down by fire energy and basal exposure and in 2020 (bottom) shown for different levels of fire treatment (left; different basal exposure treatments are combined in this figure because there was not a significant effect of basal exposure in 2020), and predicted values for number of total resprouts by wind speed (right). Significant differences are denoted with different letters. There was a significant interaction between fire energy and basal exposure in 2019, but not in 2020; in 2020 there was a significant fire energy by wind speed interaction, with increasing wind speed leading to fewer resprouts for low-energy plots but not high-energy plots.
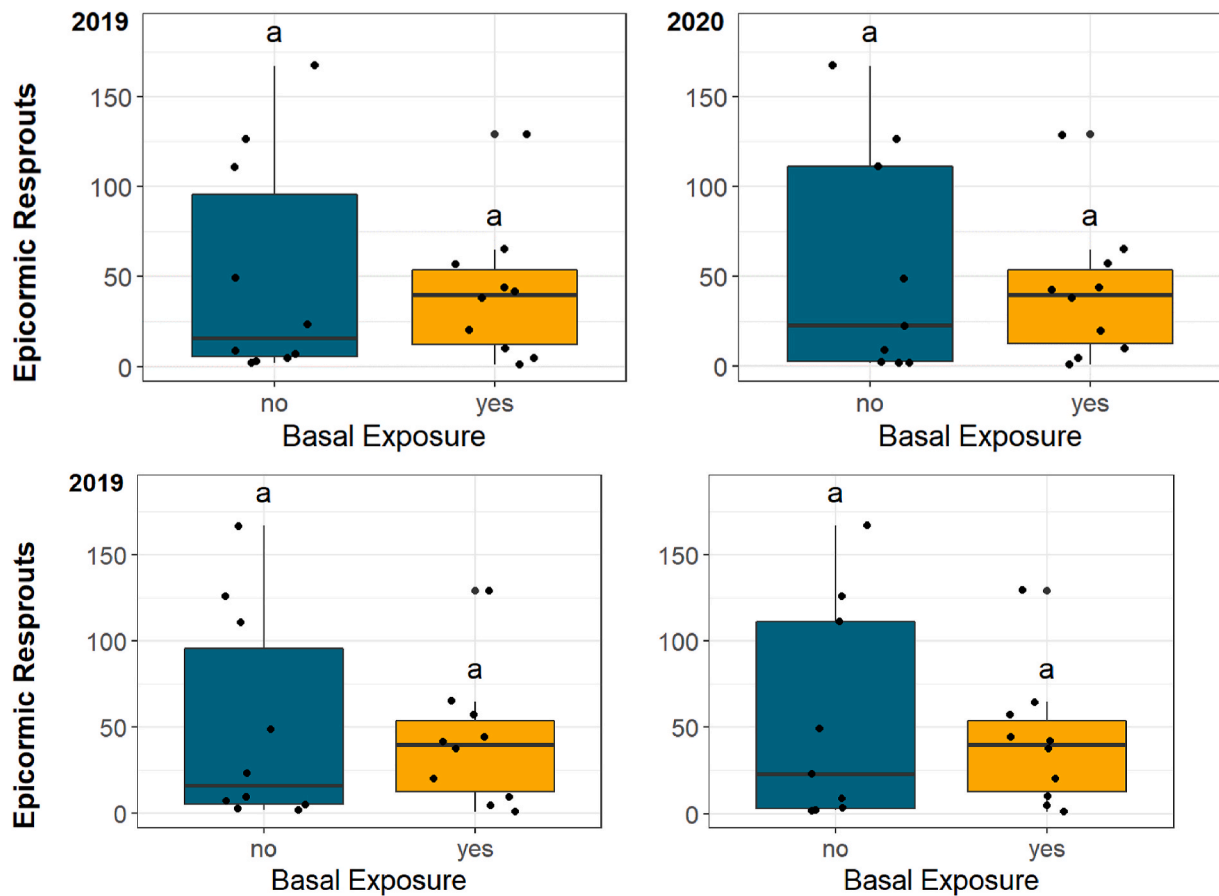
Fig. 4. Number of epicormic resprouts in 2019 (left) and in 2020 (right) by basal exposure. Data from low- and high-energy treatments were pooled. Significant differences are denoted with different letters within a panel.
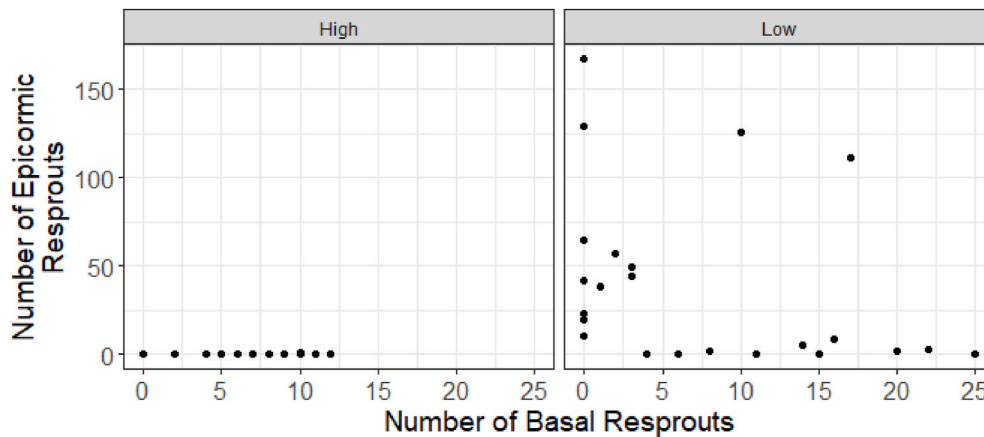

Fig. 5. Scatter plot of number of epicormic resprouts by the number of basal resprouts for high-energy plots (left) and low-energy plots (right) in 2020.

numbers of basal resprouts (Table S6, Fig. 6). In addition, relative humidity was a significant predictor of mean basal resprouts in 2019, but not 2020. For each percent increase in relative humidity, the mean number of basal resprouts increased by ~10% (Confidence interval: 2–18%) in 2019 (Table S6).

4. Discussion

As we expected based on BPR theory, mesquites have multiple adaptations to fire. Epicormic resprouting is a common response to low-energy fires (H1). In the event of high-energy fires that kill critical

tissues aboveground, basal resprouting (H2) is necessary for persistence. Counter to our expectations, however, high-energy fires did not overcome mesquite persistence. Although we did see a reduction in the number of resprouts and decreased likelihood of survival with high-energy fires, both persistence mechanisms did occur in high-energy plots. Over 70% of the focal mesquites burned in high-energy fires had produced resprouts by the end of the study and both persistence mechanisms were evident in high-energy plots. High-energy fires did cause a reduction in epicormic resprouting, with a focal mesquite producing epicormic resprouts in only one of twenty-four high-energy plots. It also lowered number of resprouts, with fewer basal and total resprouts
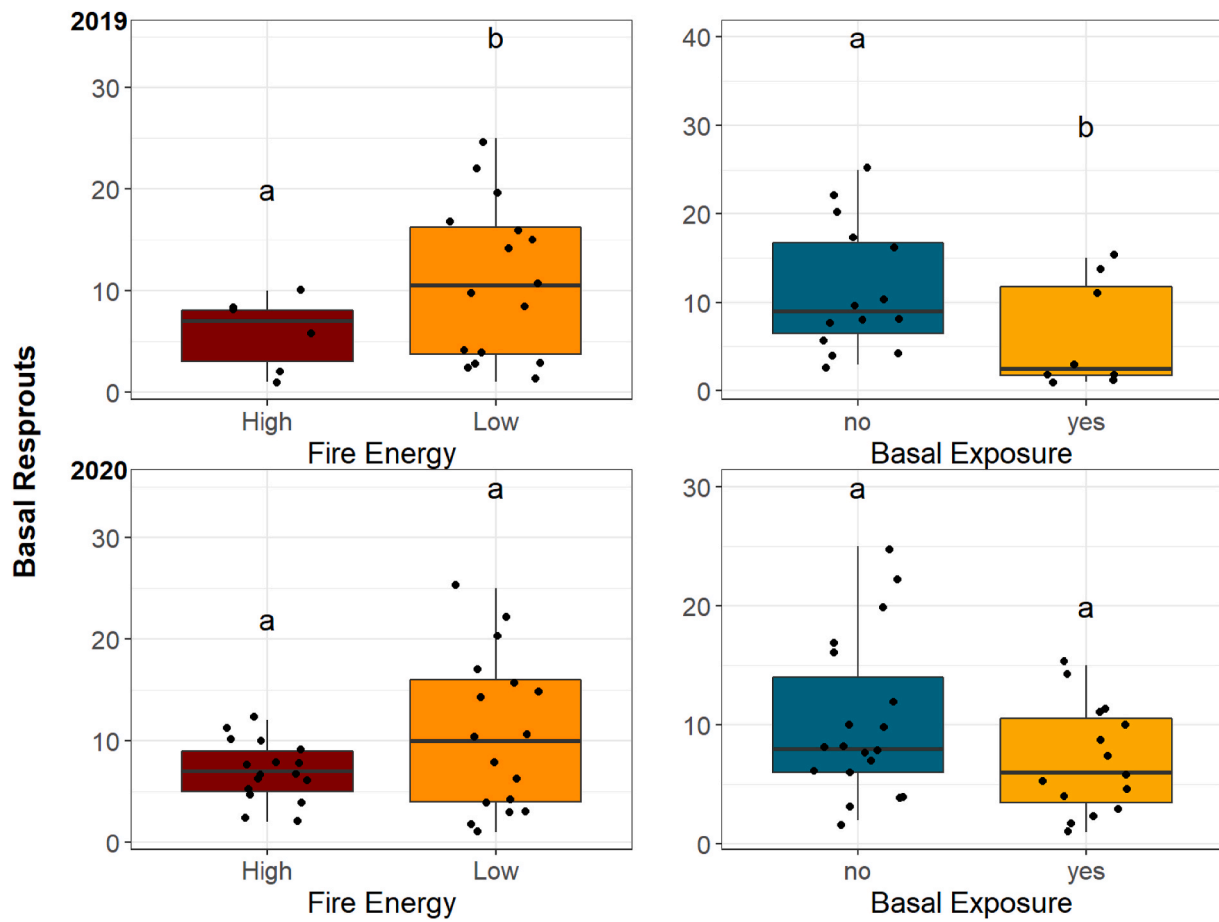
Fig. 6. Number of basal resprouts in 2019 (top) and in 2020 (bottom) by fire energy (left) and basal exposure (right). Fire energy and basal exposure are displayed separately since there was not a significant interaction between them in either year. Significant differences are denoted with different letters within a panel.

overall in high-energy plots relative to low-energy plots at least in the first growing season following fire, which can have lasting impacts on resprouting plant survival over the long term. In addition, high-energy fires decreased likelihood of survival. Twenty-nine percent of focal mesquites in high-energy treatments failed to resprout, while 100% of focal mesquites subjected to low-energy fire resprouted. While we refer to these mesquites as dead, the last status measurements were made 2 years following fire, which is not long enough to truly assess mortality as they might still resprout in subsequent growing seasons. Mesquite have been shown to produce resprouts after being dormant for as many as 3 years following high energy fire (Twidwell et al., 2016). However, any additional resprouting after two years with no resprouts could represent low resprouting vigor and could have implications for long-term mesquite survival, growth, and reproduction (Moreira et al., 2012).

Our results are novel in that we demonstrate that fire can kill mesquite in the absence of drought. Ours is the first study (to our knowledge) to disentangle the interaction between drought and extreme fire, whereas Twidwell et al. (2016) could not separate the effects of high-intensity fire from those of a multi-year intense drought. It is important to note that drought alone can lead to mortality of woody plants, although mortality of mesquite is limited (Johnson et al. 2018). Our study was conducted under more typical precipitation conditions. Year-to-date precipitation was slightly lower than average, but precipitation in the months immediately following our fires was high (2018 total precipitation was 598 mm), and the two subsequent years had near-average rainfall (522 mm in 2019 and 609 in 2020). By conducting our study without drought, we were able to confirm that some mortality of mesquites can be attained with high-energy prescribed fire regardless of drought conditions. This suggests that increased vulnerability to

xylem cavitation as a result of water stress is not a necessary precondition for mesquite mortality from high-energy fire and that protection of buds and cambium might be more important than protection of xylem for mesquite persistence in the face of high-energy fire.

Our findings, consistent with BPR theory (Clarke et al. 2013) showed H1 and H2 are integrated components of mesquite persistence in the face of fire. Mesquites survived fire by resprouting from epicormic buds (H1) and basally from belowground buds (H2); those without soil removed from the base of the stem exhibited more basal resprouting following fire (H2). We discuss the findings relative to each of these hypotheses in more detail below.

H1. Buds in the stems of trees are protected from fire

Mesquite is known to have meristematic buds along the stem and branches (Meyer, 1971). These buds are suppressed primarily by auxins produced by dominant buds when the mesquite has apical dominance and are released from dormancy following injury to branches and leaves and an attendant reduction in auxin production (Kormanik and Brown, 1969; Wilson, 1994). The extent to which apical and epicormic buds are protected from fire is not well understood. Our study showed that although epicormic buds in branches and stems of mesquite trees have some protection from fire by their location in the inner bark where they are protected by outer bark (Meyer, 1971), this protection is largely insufficient to protect against high-energy fire. Thirty-nine percent of burned focal mesquites resprouted epicormically. This aligns with current mesquite literature; mesquite is reported to resprout from stems and branches when damage occurs to any part of the leaves, branches, or stems (Meyer, 1971) and previous studies indicate that low-energy prescribed fires are unable to cause thermal damage to epicormic buds

(Wright et al., 1976; Ansley and Jacoby, 1998; Ansley et al. 1998). High-energy fires in our study caused more damage to epicormic buds and/or the tissues which support them. Only a single mesquite in the high-energy plots produced epicormic resprouts, suggesting that this persistence mechanism could be less effective with increases in fire intensity. Epicormic resprouting tends to be more prevalent in ecosystems that typically have low-intensity surface fires, while basal resprouting is more dominant in areas prone to more intense crown fires (Clarke et al. 2013). While high-energy fires did decrease the likelihood of epicormic resprouting, they did not completely preclude epicormic resprouting as a mechanism of mesquite persistence, so the fire energy threshold for overcoming apical bud protection likely differs among individuals. The reason this one mesquite resprouted epicormically is unclear – it was not related to size. The single epicormic resprouter in our high-energy treatments was similar in size to other focal trees; we controlled for differences in mortality related to size by selecting focal plants similar in size and growth form. We were therefore, not able to assess if size alters the dynamics of shrub response to fire energy. Another important unknown related to this is whether the vascular cambium was damaged for the mesquite that resprouted epicormically. If so, the long-term survival of these resprouts is not likely as the cambium is required for stem growth. Protection of stem meristematic tissues can only be considered a persistence mechanism if protection of water and nutrient transport channels is also supported (Michaletz and Johnson, 2007). We were unable to assess differences in number of epicormic resprouts resulting from fire energy because only one high-energy focal mesquite resprouted epicormically. However, that mesquite only produced a single epicormic resprout, while number of resprouts in low-energy plots varied substantially but was as high as 167 resprouts, suggesting that high fire energy could reduce the number of epicormic resprouts in mesquites that do persist via epicormic bud protection.

Higher numbers of basal resprouts were not strongly associated with lower numbers of epicormic resprouts, but the scatter plot revealed a relationship between the two types of resprouts for the low-energy treatment. This relationship suggests that in plots where epicormic tissues experienced greater thermal damage, basal buds were released from dormancy to a greater degree (Meier et al., 2012). However, damage to stems and branches in low-energy treatments was insufficient to shift resprouting predominantly from epicormic to basal, as was the case for high-energy fires.

Weather parameters were also significant predictors of epicormic resprouting for low-energy treatments, in which there were many more epicormic resprouts per stem. We included weather variables in the model because of their potential to alter the heat exposure of the focal mesquite, altering subsequent resprouting dynamics. Due to our small plot sizes, we considered a possibility that increased wind speeds could have moved the heat plume horizontally rather than vertically (mainly in low-energy treatments), thereby reducing heat exposure and increasing resprouting. Such was not the case, however, as resprouting decreased at higher wind speeds and lower RH levels. This result suggests that high wind and low RH led to higher heat release rates and greater stem heating and is consistent with previously established effects of weather on fire effects (Britton and Wright, 1971; Rothermel, 1972; Wright and Bailey, 1982).

H2. Buds in the base of trees are protected from fire

Basal buds were also protected from fire. Sixty percent of burned mesquites were top-killed (had no epicormic resprouts by the end of the study) but still resprouted from the base. This mechanism of persistence was only partially overcome by high fire energy; 70% of mesquites burned in high-energy fires resprouted basally. This seems to be the dominant mode of persistence in the face of high-energy fire. However, because they were capable of causing mortality in some focal mesquite (~29%), high-energy fires may remain a viable option for reducing resprouting of mesquite even in the absence of drought when incorporated into comprehensive management plans that use repeated fires at historically relevant intervals (Starns et al. 2020). In addition to moderate direct reduction in mesquite density, high-energy fires reduce apical dominance. Therefore, land managers can increase the susceptibility of resprouts to subsequent fires (basal resprouts are more exposed to surface fire than epicormic). In addition, most high-energy fires left standing dead stems, which could be ignited by future fires, potentially causing mortality via heat transfer to basal buds through combustion and smoldering of the dead stem (Britton and Wright, 1971; Wright et al., 1976; McPherson et al., 1990; Twidwell et al. 2016). Feedbacks resulting from increases in grass biomass with mesquite top-kill could also contribute to subsequent mortality of resprouting mesquite. Increased herbaceous biomass provides additional fine-fuel for conducting follow-up fires while resprouts are still within the fire trap (Bond and Midgley, 2001), keeping mesquite from developing a sufficient density of photosynthesizing resprouts to maintain growth and survival (Schutz et al., 2009).

Although basal resprouting was common in high-energy plots, basal resprout number tended to be lower in high fire energy plots than in low fire energy plots and in plots with bases exposed. In 2019, high fire energy plots had fewer resprouts than low fire energy plots and plots with bases exposed had fewer basal resprouts than unexposed base plots. Increased heat release rates resulting from lower relative humidity probably increased basal resprouting due to release from pre-fire apical suppression. Basal resprout number has been shown to decrease with increasing fire intensity in other mesquite resprouting studies (Ansley et al. 1998; Drewa, 2003), which suggest that increasing fire intensities potentially result in more direct damage or mortality to basal buds (Matlack et al., 1993; Drewa, 2003). In our study, after 2 years following prescribed fires, trees exposed to high-energy fires had resprouted enough that there was no longer a statistically significant difference in number of resprouts relative to low energy plots or base exposure plots relative to plots without basal exposure and the relationship with relative humidity was no longer evident. This suggests that even the low number of resprouts in the high-energy plots and base-exposed plots were sufficient to allow survival and persistence of the burned mesquite. However, the slower rate of resprouting in high-energy plots (fewer resprouting immediately after the fire), base exposed plots, and plots burned during lower relative humidity could have long-term impacts on resprouting vigor. Resprouting success depends on not only initiating resprouting which requires dormant buds to survive the fire and have sufficient resources and transport channels to mobilize them (Vesk and Westoby, 2004), but also on resprouting vigor and survival (Moreira et al., 2012). Studies of various resprouting plants have shown vigor to be highly related to resprout survival; higher photosynthetic efficiency associated with rapid production of photosynthesizing leaves leads to a higher probability of long-term survival (Arianoutsou and Margaris, 1981; Lloret and López-Soria, 1993; Schutz et al., 2009). While we assessed resprouting number and not growth rates or total biomass, resprout number is often included in calculations of resprouting vigor (see e.g. (Moreira et al., 2012; Casals and Rios, 2018), where resprouting number is multiplied by length as a proxy for vigor), indicating that there is a relationship between resprouting number and vigor. Studies of other resprouting woody plants show a negative relationship between fire intensity and resprouting vigor (see e.g. (Kayll and Gimingham, 1965; Malanson and Oleary, 1985; Malanson and Trabaud, 1988; Lloret and López-Soria, 1993)). Therefore, despite similar numbers of basal resprouts among all focal mesquites by 2020, the slower resprouting expressed by trees in high-energy plots could reduce the probability of resprouting mesquite survival over the long term.

4.1. Management implications

Our study supports the potential for high-energy fires to reduce the density of mesquite in semi-arid systems. In this complex landscape, which is primarily used for livestock and wildlife forage, managers can re-create high-energy fires by using mechanical means to place junipers

at the bases of mesquites. This method of increasing fire intensity is currently being employed in other parts of the Great Plains USA to counteract woody plant encroachment (Bielski et al. 2021). Furthermore, careful livestock management can facilitate accumulation of herbaceous biomass sufficient to conduct high-energy fires (Twidwell et al., 2016). Both practices of fuel accumulation are being actively used within the southern Great Plains to facilitate high-energy summer burning intended to reduce *Juniperus* spp. abundance (Twidwell et al., 2013a, 2013b). Our findings show that high-energy fires could also reduce densities of resprouting shrubs despite well-developed persistence mechanisms in the face of fire.

5. Conclusion

Honey mesquite persistence in our study was driven by the integration of all three persistence mechanisms of BPR theory, but the importance of those mechanisms differed in response to two different levels of fire energy. Protection of epicormic meristems was more important during low-energy fire, while protection of basal meristematic tissues in the base was integral for persistence during high-energy fire. Despite the resprouting ability of mesquite, our data suggest that prescribed high-energy fires may be a viable option for overcoming mesquite persistence and reversing the trajectory of encroachment. We offer empirical evidence to support the ongoing efforts of land managers in our study region to reverse mesquite encroachment by implementing extreme prescribed fires (Twidwell et al. 2013b). Our results offer insight into potential management regimes for global rangelands facing encroachment by *Prosopis* and other resprouting woody plants. Future research is warranted to determine whether a fire energy threshold exists at a level between our high- and low-energy treatments. In addition, further investigation into the effects of repeated fires and interactions between fire energy and other disturbances (e.g., herbivory) may provide insight into whether the resprouting capability of mesquite can be overcome.

Author contributions

WER, MBD, KLK, CLW, DT, DRT, MLT, HDS and AGL conceived the ideas and designed methodology; HDS, DRT, AGL, and MBD collected the data; CLW analyzed the data; HDS and CLW led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2021.114141.

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