

# How important is fire-induced disturbance in the maintenance of a threatened perennial forb, *Solanum papaverifolium*?

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## ABSTRACT

**Context.** Many grassland forb populations have greatly diminished because their habitat coincides with prime agricultural land and remnants lack appropriate disturbance regimes. **Aim.** The aim of the current study is to examine the survivorship, vegetative recruitment, biomass and sexual reproduction of *S. papaverifolium* in response to burning in one of a few natural surviving populations in Queensland. **Methods.** We monitored the survivorship, vegetative recruitment, and reproduction of a rare native forb, *Solanum papaverifolium*, within a randomised replicated experiment by using 14 circular plots measuring 12.56 m<sup>2</sup> (2 m radius). **Key results.** Plant survival rate after 5 months was greater in the burnt plots (56%) than the unburnt plots (44%). Vegetative recruitment from suckers in the burnt plots was almost twice that in the unburnt plots. The probability of flowering was also enhanced by burning. Fruit set in new recruits was higher in the burnt plots (20%) than in the unburnt plots (5%). Whereas fruiting did not occur in unburnt plots for surviving plants that flowered, only 1% fruited in the burnt plots. Seedling production was not observed. **Conclusion.** Previous studies have demonstrated that the subtropical grassland flora in the study region is unaffected by burning, whereas the present study suggests that some grassland species respond positively to burning. **Implications.** Although fire increased flowering in this species, suggesting that fire may be a useful tool to stimulate sexual reproduction, ongoing research is required to understand the precise factors that promote flowering after burning and the barriers to seedling reproduction.

**Keywords:** competition and inter-tussock species, disturbance, fire, plant survival, *Solanum papaverifolium*, subtropical grassland, vegetative recruitment and reproduction.

## Introduction

Grasslands in arable landscapes are imperilled by conversion to crop production (Helkowski and Norman 1997; Hoekstra *et al.* 2005; Valkó *et al.* 2012; Williams *et al.* 2015; Cronk 2016; Bernardo *et al.* 2020). Subtropical grasslands in Australia have largely been cultivated and remaining remnant grassland patches are threatened by invasive plant species (Fensham 1997, 1998; Lewis *et al.* 2008; Fensham *et al.* 2016). Unsurprisingly, many grassland species persist only in small populations in isolated remnant grassland (Morgan 1999b; Kéry *et al.* 2000; Matthies *et al.* 2004). In addition, a large proportion of rare and threatened grassland plants are inter-tussock species (Pavlovic 1994; Lunt 1995; Morgan 1997; Price *et al.* 2019), which are less competitive than dominant tussock grasses (Munk *et al.* 2002; Valkó *et al.* 2012). For their persistence, these species depend on disturbances to reduce competition from dominant grasses (Lunt 1995; Munk *et al.* 2002; Valkó *et al.* 2012).

Diversity is commonly maintained at moderate levels of disturbance (Vujnovic *et al.* 2002; Roxburgh *et al.* 2004). However, grassland communities comprise species whose response to disturbances may be idiosyncratic (McIntyre *et al.* 1999). Fire is an example of a natural disturbance that is commonly used to maintain grassland diversity, particularly the inter-tussock flora (Pavlik *et al.* 1993; Menges and Gordon 1996; Lesica 1999; Menges and Quintana-Ascencio 2004). Although other methods such as grazing

and mowing can increase canopy gaps (Williams et al. 2007; Araújo et al. 2013), fire eliminates dead plant material and aboveground biomass and modifies resource availability (MacDougall and Turkington 2007). Furthermore, heat and smoke generated by fire also break seed dormancy of fire-dependent species (Whelan 1995; Clarke and French 2005; White et al. 2020) and fire can enhance light availability and nutrients for seedlings (Burke and Grime 1996; Morgan 1998).

Lunt and Morgan (2002) reported increased germination of some herbaceous perennial species following prescribed burning in grassland plant communities in Australia. Also, fire enhances seedling recruitment of the endangered perennial forb *Silene spaldingii* in a Montana prairie reserve, USA (Lesica 1999). Conversely, fire has a modest negative impact on seedling recruitment of a threatened perennial herb *Trioncinia retroflexa* in a subtropical grassland in Australia (Fensham et al. 2002).

Recruitment of new individuals arises either from genets (seeds) or ramets (vegetative resprouts from stolons, rhizomes or roots) and in most species where both modes of reproduction exist, reproduction from ramets is dominant (Pausas 2001; Pausas et al. 2004; Clarke et al. 2013; Zhao et al. 2013). Vegetative resprouters are commonly associated with frequent burning, whereas regeneration from seed (reseeders) occurs under less frequent fire (Hoffmann 1999). In fire-prone ecosystems, resprouters allocate resources to protective structures and the remobilisation of reserves of non-structural carbohydrate in the roots and unburnt stems aid in enhancing their resilience and survival after fire (Clarke et al. 2013; Simpson et al. 2021). Re-seeders germinate from the soil seed bank or newly dispersed seeds (Whelan 1995; Pausas et al. 2004).

*Solanum papaverifolium* is an endangered perennial forb found in subtropical grassland (Fensham 1997). This rhizomatous forb of short stature (<50 cm high) is capable of both vegetative and sexual reproduction (Bean 2004). Although there are no ecological studies of *S. papaverifolium*, previous studies have shown that fire promotes production of *S. centrale* (Walsh and Douglas 2011) and flowering, fruit set and germination of *S. prinophyllum* (Kubiak 2009). However, these congeners are not grassland species and the response of *S. papaverifolium* to fire is uncertain, especially as experimental burning, applied twice over 3 years in the same grassland system, did not affect species richness and composition significantly (Fensham et al. 2017). Nevertheless, it is possible that the rarity and/or decline of some grassland species, such as *S. papaverifolium* has been exacerbated by the lack of appropriate disturbance (Silcock and Fensham 2018; Silcock et al. 2021). The aim of the current study was to examine the survivorship, vegetative recruitment, biomass and sexual reproduction of *S. papaverifolium* in response to burning in one of a few natural surviving populations in Queensland.

## Materials and methods

### Study area

The study took place in grassland on the alluvial floodplain of the Darling Downs, 16 km north-west of Dalby, Queensland (lat. -27.1345, long. 151.1256). The climate is subtropical, with mean maximum and minimum temperatures of 27°C and 12°C respectively. The mean annual rainfall was 584 mm for the period of 1992–2021. The grasslands have been extensively converted to croplands and remnants are confined to roadsides, railway lines and travelling stock routes. Subtropical grassland in this region are now classified as threatened ecosystems (Fensham 1997). The soil at the study site is a heavy clay classified as a vertosol. Generally, fire was an important management tool in natural grassland in Queensland until the 1960s, after which the use of fire drastically declined with the expansion of cropping on pastoral land (Pressland 1982). The area does not appear to have been mechanically disturbed in recent times.

### Description, distribution and habitat of *S. papaverifolium*

*Solanum papaverifolium* (Solanaceae) is a weak-stemmed, rhizomatous perennial forb that grows to a height of 0.6 m (Fig. 1). The leaves are broadly ovate, deeply lobed and spiny. Adult plants typically commence flowering in October, producing three to five solitary flowers and fruiting occurs in April–May. The aboveground portion of the plant dies each year but the rhizome is persistent. *S. papaverifolium* grows on clay-rich soil in grassland and open eucalypt woodland in Queensland and New South Wales in Australia (Bean 2004) and the loss of populations over the past two decades in the Darling Downs (R. J. Fensham 2018,



Fig. 1. *Solanum papaverifolium* plant, 25 cm tall. (Photo: Joachim Froese).

unpubl. data) indicates that the species is threatened with extinction. The natural habitat of *S. papaverifolium* has declined with agriculture and roadsides are being degraded by exotic invasive species and road construction and there are no records from conservation reserves (Bean 2004). *S. papaverifolium* is considered one of the most threatened plants in grassland and it is listed as 'Critically Endangered' under the *Queensland Nature Conservation Act, 1992*.

## Experimental design

In late March 2020, 14 circular plots measuring 12.56 m<sup>2</sup> (2 m radius) were established within a population of *Solanum papaverifolium* that occupied an area of about 1200 m<sup>2</sup>. A permanent marked peg was placed in the centre of each plot and the location was recorded using a GPS. Plot locations were selected to represent a relatively moderate and uniform density of *S. papaverifolium* plants. The location of each *S. papaverifolium* plant from the centre peg was ascertained by measuring the distance and bearing from the centre peg with the aid of a measuring tape and a compass respectively. The height of each stem was also measured at this time. Seven of the circular plots were randomly selected and a 1 m wide strip was mowed around each plot as a fire break. On 6 October 2020, these seven plots were burnt and the other seven plots were left unburnt. The dry fuel weight was not measured but similar grassland sites have between 1.5 and 4.3 t ha<sup>-1</sup> (Fensham *et al.* 2017). The wind speed at the time of the burn was 19 km h<sup>-1</sup> and the fires were lit down-wind of the plots such that the fire crept slowly against the wind. The precipitation for the 12-month periods prior to March 2020 was below average (340.1 mm) and prior to March 2021, it was about average (575.3 mm). All stems in burned plots were removed by fire, and all aboveground stems in the unburnt plot died back to below the ground surface.

All plots were monitored in mid-March 2021. Minor excavation and the appearance of the stems indicated that all plants were ramets regenerating from rhizomes. As such, stems re-emerging from the same ramet location as original stems were categorised as surviving and where no stems re-emerged they were considered to have died. Stems emerging from different locations from those originally mapped were treated as recruits. We also examined the fruits to assess whether viable seeds were formed after fruit development.

During monitoring we measured the height of each stem, as well as which stems were flowering or not and the number of flowers per individual plant. We returned in May 2021 to see whether the plants that had flowered during our March 2021 visit had produced any fruits.

## Data analysis

All statistical analyses were performed with R version 4.0.2 (R Development Core Team 2020). Analyses were undertaken

at both the stem and plot scales. At the stem scale, height of individual stems (including surviving stems and recruits) was log-transformed and modelled as a function of burning treatment in a linear mixed-effects model by using the lmer() function in the lme4 package (Bates *et al.* 2015) with plot ID included as a random effect. Survival, flowering and fruiting (of those plants that flowered) were coded as binary response variables. Each of these variables was modelled as a function of burning treatment in generalised linear mixed effects models (GLMMs) with a binomial error distribution and logit-link function using the glmer() function, again with plot ID being included as a random effect. For the plants that flowered, the number of flowers was modelled as a function of burning treatment using a GLMM with Poisson error distribution and log-link function. The flowering and fruiting response variables were analysed separately for surviving and recruiting plants. In the models of flowering probability and flower number, plant height (log-transformed) and its interaction with burning treatment were included to account for size effects. Non-significant variables (as shown by model estimates and *P*-values) were sequentially removed to improve model parsimony, starting with interactions and then main terms. The interaction was included to test for differences in flowering–height relationships between the burnt and unburnt treatments. In the fruiting model, only stems that flowered were included and we did not account for height effects. Even though these analyses were undertaken at the stem scale, most are graphically represented as plot-scale proportions in the results figures.

At the plot scale, we calculated the change in the total number of stems (no. stems before / no. stems after × 100) and counted the number of new recruits (excluding surviving stems). To estimate the change in plot-scale biomass before versus after the treatments were applied, we first summed the height of all stems in each plot before and after the treatments. We then calculated log response ratios for each plot as:

Summed height response ratio

$$= \log(\text{summed height after}) - \log(\text{summed height before})$$

Positive values of this response ratio indicate an increase in summed plant height, zero indicates no change and negative values indicate a decline in summed plant height. These plot-scale response variables were modelled as a function of burning by using a linear model.

## Results

### Effects of fire on survival, recruitment rates and biomass

Prior to treatment, the number of individual stems for the unburnt and burnt plots was 115 and 130 respectively.

On average, burnt plots had more stems in 2021 than in 2020 (average increase of 62%), whereas unburnt plots had fewer stems in 2021 than in 2020 (average decrease of 38%), and this difference was significant ( $P = 0.027$ , Fig. 2a).

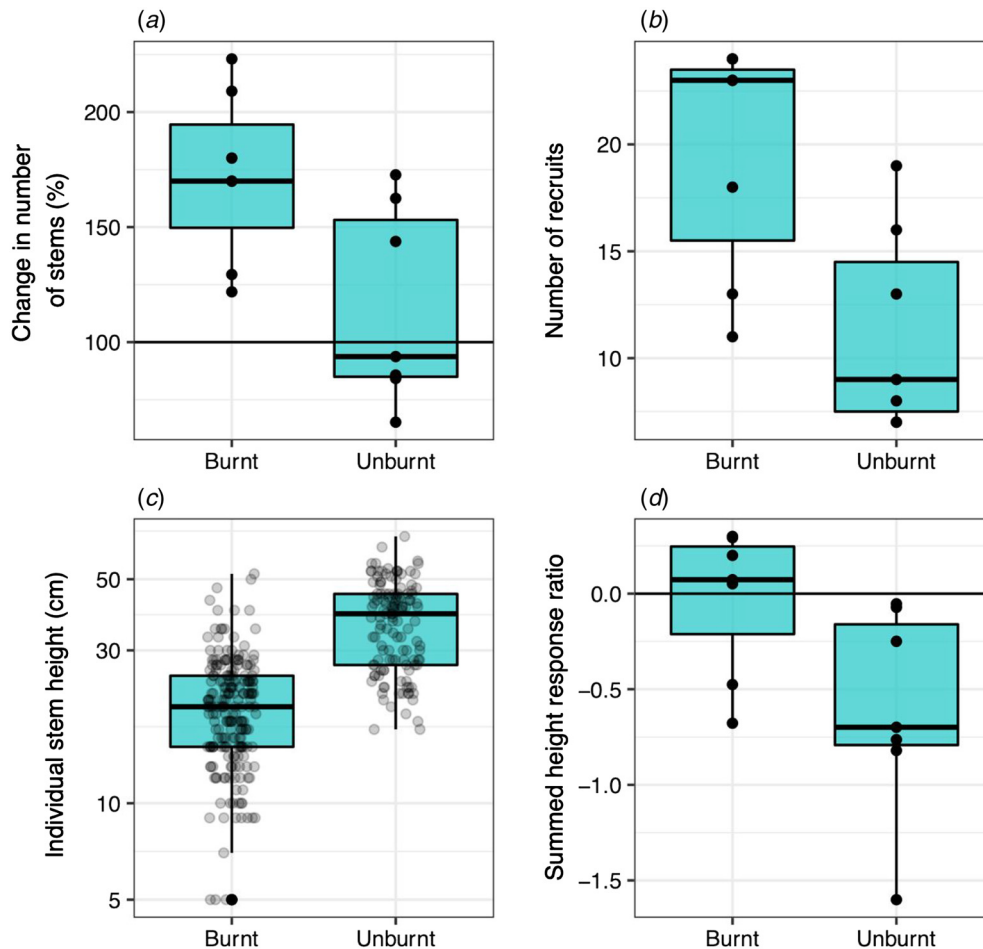
We recorded 215 new *S. papaverifolium* recruits for existing ramets, of which 136 were in the burned plots and 79 in the unburnt plots and the mean number of recruits per plot was significantly greater in burnt than unburnt plots ( $P = 0.012$ , Fig. 2b).

The probability of survival was higher (0.56) in the burnt plots than the unburnt plots (0.44,  $Z = -1.975$ ,  $P = 0.048$ ). Individual stems in burnt plots were 19 cm tall, on average, compared with 36 cm tall in unburnt plots, and this difference was significant ( $t = 11.00$ ,  $P = <0.001$ ; Fig. 2c). On average, the summed height response ratio in the unburnt plots decreased from the original value after treatment (depicted as zero) and in the burnt plots it slightly increased from zero after treatment and this difference was

significant (Fig. 2d;  $P = 0.042$ ). These results indicate clear differences in biomass allocation between the burning treatments. Burning resulted in the emergence of many shorter stems the heights of which summed to pre-burning levels, whereas the summed heights in unburnt plots declined despite stems in these plots being taller on average.

### Effect of treatment on flower and fruit production in surviving and recruiting plants

In the model of flowering probability for recruits, the interaction between treatment and height was not significant and was removed. In the resulting model, the effect of height was positive and significant (Table 1, Fig. 3a) and the effect of treatment (unburnt compared with burnt) was negative and strongly significant (Table 1). For a 30 cm tall recruit, the probability of flowering in a burnt plot was 0.82 (95% confidence intervals = 0.70–0.90) compared with



**Fig. 2.** The effect of burning on the %change in (a) number of stems, (b) number of vegetative recruits, (c) height of individual stems and (d) summed height response ratio (proxy for biomass) of *S. papaverifolium* plants. In all panels, mid-lines are medians, boxes show the 25th and 75th percentiles and vertical lines indicate the range. Raw data are overlaid as black points. The solid horizontal lines at 100 and 0 in a and d respectively are the reference points, which correspond to the values before treatment.



0.23 (0.17–0.42) in an unburnt plot (Fig. 3a). For survivors, the interaction between treatment and height was significant (Table 1) and indicated that flowering probability in burnt plots was unrelated to height (probabilities were ~0.6 regardless of height), whereas flowering increased strongly with height in the unburnt plots (Fig. 3b). For a 30 cm tall survivor, the probability of flowering was 0.62 (0.40–0.80) in a burnt plot compared with 0.05 (0.006–0.28) in an unburnt plot (Fig. 3a). The number of flowers per plant was not significantly related to plant, burning treatment or their interaction (Supplementary Table S1).

For the new recruits that flowered, burning significantly increased the probability of fruiting ( $P = 0.012$ , Fig. 4).

**Table 1.** Summary of fixed effects from the binomial mixed-effects models of flowering probability for recruits and surviving stems.

Item	Estimate (logits)	Z-value	P-value
<b>Recruits</b>			
Intercept (Burnt)	−4.048	−2.944	0.003
Treatment (Unburnt)	−2.494	−4.907	<0.001
log(Height) (Burnt)	1.641	3.531	<0.001
<b>Surviving stems</b>			
Intercept (Burnt)	1.118	0.438	0.661
Treatment (Unburnt)	−22.207	−2.464	0.014
log(Height) (Burnt)	−0.187	−0.220	0.826
log(Height):Treatment (Unburnt)	5.492	2.296	0.022

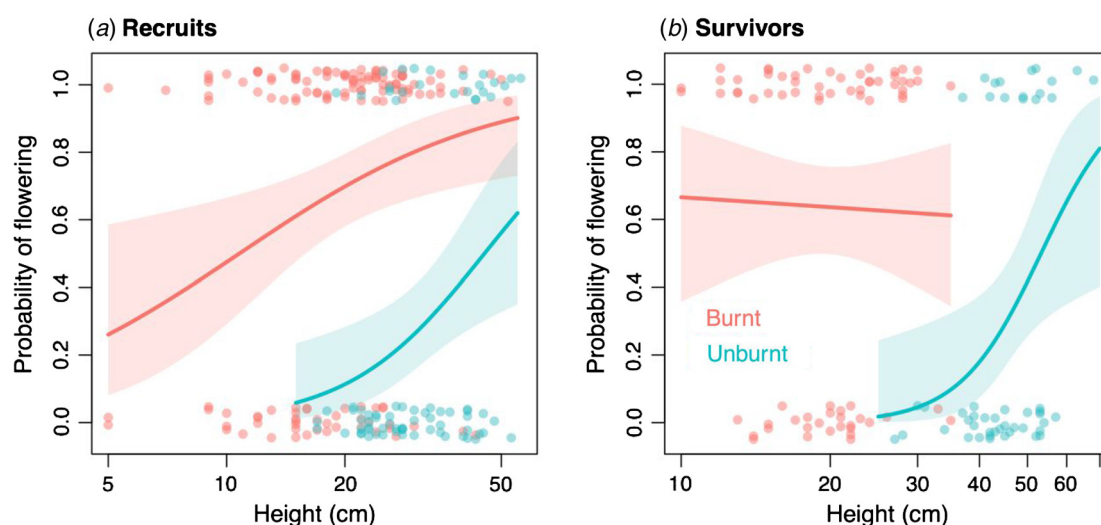
In the model for recruits, the interaction between log(Height) and Treatment was not significant ( $P = 0.271$ ) and was subsequently removed. Refer to Fig. 3 for plots of model fits.

For the surviving stems that flowered, only burnt stems produced fruit (Fig. 4). In addition, our examination of the fruit showed that seeds were absent in fruits of *S. papaverifolium* plants.

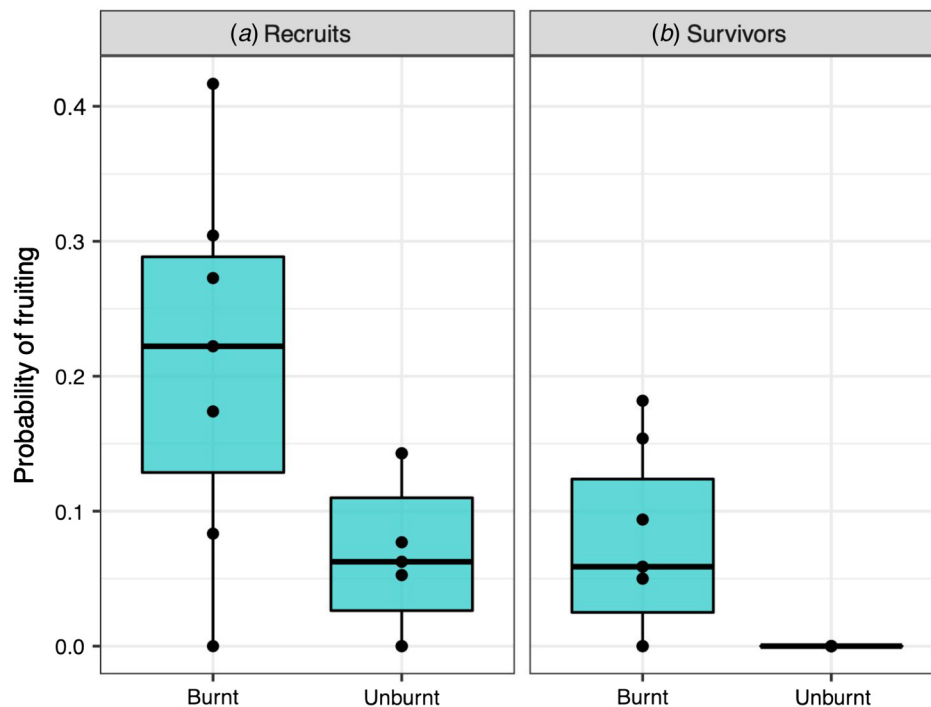
## Discussion

The single application of fire promoted the asexual recruitment of *S. papaverifolium* in subtropical grassland. Overall, the number of stems increased in burnt and remained constant in the unburnt plots (Fig. 2a). The number of recruits was significantly greater in burnt than unburnt plots (Fig. 2b). Some studies have shown that climatic conditions influence demographic responses to disturbance (Fensham *et al.* 2002; Moore *et al.* 2019; Griffith and Rutherford 2020). In the present study, rainfall in the preceding year was below average and about average during the experiment. During wetter conditions, perennial grasses are known to have a competitive advantage over smaller-statured forb species for resources such as water, light and nutrients (Bond and Parr 2010; Collier *et al.* 2013). The competitive effects of increased grass growth with average rainfall is a potential explanation for the decline in the number of ramets in unburnt plots at the start of the experiment compared with the previous year.

The greatly increased number of stems in burnt plots was partly offset by their smaller size than in unburnt plots. This suggests that belowground resources provide a partial limitation to aboveground biomass. However, the net result of burning overall was a greater height-response ratio (proxy for biomass) in the burnt plots (Fig. 2d), suggesting



**Fig. 3.** Probability of flower production for (a) new recruits and (b) surviving *S. papaverifolium* plants versus stem height (cm), for both burnt and unburnt treatments. Points are raw binary data that have been jittered to show overlapping data. Fitted lines are from binomial mixed-effects models and envelopes are associated 95% confidence intervals.



**Fig. 4.** Box and whisker plots showing the effect of burning on the probability fruiting for (a) new recruits and (b) surviving plants. The mid-lines indicate the median, boxes show the 25th and 75th percentiles and vertical lines indicate the range. Raw proportions for each plot are overlaid as black points.

that fire does promote aboveground growth. Other studies have suggested that rhizomatous resprouters require fire or grazing to stimulate regrowth by axillary buds (Fidelis *et al.* 2010, 2014; Clarke *et al.* 2013; Zhao *et al.* 2013; Vidaller *et al.* 2019). Consistent with our findings, on semi-arid steppe in China, fire increased the density of recruits emerging from suckers, rhizomes, tillers and stolons (Zhao *et al.* 2013).

Stems of *S. papaverifolium* die back to below the ground during the subtropical dry season, even in the absence of fire. Thus, it was not the loss of aboveground parts in the burnt plots that triggered the positive response in the burnt plots. The positive response was either to smoke of the fire, or to nutrients from ash (Saulnier and Reekie 1995) or was a response to the temporary release from grass competition (Milton and Dean 2000). Future research could separate the influence of fire and competition experimentally by using burning and clipping surrounding perennial grasses (to remove biomass without fire).

The probability of flowering increased with plant height except for burnt survivors (Fig. 3b). Fire had a positive effect on flowering regardless of plant height, although this effect was complicated by an interaction between height and burning for survivors (Fig. 3b). Sixty-two per cent of plants flowered in the burnt plots compared with 30% in the unburnt plots, despite the burnt plants being shorter. This result is consistent with the documented positive

effects of fire on flowering in grassland species (Table S2, Cummings *et al.* 2007; Pavlovic *et al.* 2011; Fidelis and Blanco 2014; Valkó *et al.* 2018; Griffith and Rutherford 2020). For instance, there were flushes of flower production after fire for the perennial herb *Blandfordia grandiflora*, particularly in the second post-fire year in Australian heathland (Griffith and Rutherford 2020). Although the reason for the increase in flower flush in *S. papaverifolium* after fire remains unknown, other studies have identified increased light availability and large stores of carbohydrate reserves as the triggers for increased flowering among fire-adapted plants (Abrahamson 1984; Saulnier and Reekie 1995; Bellingham and Sparrow 2000; Huffman and Werner 2000; Wyka and Galen 2000; Fidelis and Blanco 2014; Simpson *et al.* 2021).

Despite the positive effects of fire on *S. papaverifolium* flowering, it promoted fruiting only in 20% of the flowering stems among the new recruits in the burnt plots. In contrast, only 5% of the flowering stems in the unburnt plots were able to form fruits (in new recruits only). Limited fruit production and the rarity of recruitment from seeds appears to be offset by prolific vegetative reproduction in *S. papaverifolium*, a persistence strategy not uncommon for perennial species in grasslands (Morgan 1999a; Zhao *et al.* 2013). Increased probability of flowering after fire suggests that the resprouting recovery of aboveground biomass did not have a

significant drain on root reserves, although this was not investigated in this study. We do not know whether repeated burning would sustain the positive response associated with flowering in these species. Future research would investigate whether pollination is limited after a fire.

## Conclusions

Burning increased the number of ramets, total biomass and reproductive effort in *S. papaverifolium*. However, the importance of fire to the persistence of this threatened plant species remains uncertain. The proliferation of rhizomatous stems is contained within the pre-existing population of the species, and with the small-scale burns of this experimental trial, *S. papaverifolium* did not spread beyond where it originally occurred. Recruitment from seed and the constraints on the dispersal and distribution of this species need further investigation, especially because this study showed that even though fire promotes vegetative reproduction and flowering of this threatened herb, it may not be essential for population persistence. Ongoing research is required to understand the precise factors that promote flowering after burning and the barriers to seedling reproduction.

## Supplementary material

Supplementary material is available [online](#).

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**Data availability.** Data are available at <https://cloudstor.aarnet.edu.au/plus/s/ed3LvDb4NuzRab>.

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