

Effects of drought and fire on resprouting capacity of 52 temperate Australian perennial native grasses

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Summary

- It remains uncertain how perennial grasses with different photosynthetic pathways respond to fire, and how this response varies with stress at the time of burning. Resprouting after fire was examined in relation to experimentally manipulated pre-fire watering frequencies. We asked the following questions: are there response differences to fire between C₃ and C₄ grasses? And, how does post-fire resprouting vary with pre-fire drought stress?
- Fifty-two perennial Australian grasses (37 genera, 13 tribes) were studied. Three watering frequencies were applied to simulate increasing drought. Pre-fire tiller number, tiller density, specific leaf area and leaf dry matter content were measured as explanatory variables to assess response.
- Most species (90%) and individuals (79%) resprouted following experimental burning. C₄ grasses had higher probabilities of surviving fire relative to C₃ grasses. Responses were not related to phylogeny or tribe. High leaf dry matter content reduced the probability of dying, but also reduced the re-emergence of tillers.
- Post-fire tiller number increased with increasing drought, regardless of photosynthetic type, suggesting that drought plays a role in the ability of grasses to recover after fire. This has implications for understanding the persistence of species in landscapes where fire management is practiced.

Introduction

Fire has been a fundamental process in the evolution and dominance of grasses and grassland ecosystems across the globe (Bond & Keeley, 2005; Keeley & Rundel, 2005; Edwards *et al.*, 2010; Leys *et al.*, 2018; Linder *et al.*, 2018), shaping plant functional traits related to persistence, recovery after disturbance, and recruitment (Simpson *et al.*, 2016; Pausas *et al.*, 2017). Fire is an important ecological process in tropical C₄ grasses (Bond & Keeley, 2005; Edwards *et al.*, 2010), but our understanding of the relationship between C₃ grasses and fire is much less clear (Edwards *et al.*, 2010; Strömberg, 2011).

Drought is common in Australia, a product of El Niño–Southern Oscillation cycles that cause large interannual variation in precipitation (Vines *et al.*, 2004) and significantly affects net primary productivity in grasslands (Morgan *et al.*, 2016). It is also known to compromise post-fire regeneration of grasses (Carter *et al.*, 2012; Russell *et al.*, 2015) by reducing the metabolic functions and recovery rates of C₄ grasses (Knapp, 1985), a photosynthetic pathway that is generally assumed to be resilient to arid conditions (Ripley *et al.*, 2010; Taylor *et al.*, 2010). While the drought responses of Australian native grass species have been reported (e.g. Ghannoum *et al.*, 2002; Hodgkinson & Muller,

2005), interspecific links between water stress and fire have not been studied. In a world that is predicted to become drier and more flammable (Flannigan *et al.*, 2009; Krawchuk *et al.*, 2009; Cary *et al.*, 2012), it is critically important that we understand the effect of fire on grasses. Global climate change is expected to cause more frequent and severe droughts in many regions worldwide (IPCC, 2014), leading to potentially drier and more flammable vegetation. Fire regime changes are predicted to change the distributions of dominant grass types and create fire-fuel feedbacks that will likely impact future vegetation dynamics (Bradstock, 2010; Cary *et al.*, 2012). Indeed, such feedbacks may already be occurring (e.g. see Camac *et al.*, 2017).

Fire and drought response in grasses may need to be interpreted in the context of the phylogenetic and/or taxonomic relatedness of grasses (Bond & Midgley, 1995; Taylor *et al.*, 2011; Forrester *et al.*, 2014; McGlone *et al.*, 2014; Ripley *et al.*, 2015). Species from the Chloridoideae tribe, for example, are thought to have diversified into low productivity, xeric habitats which had low fire frequencies while species of the Andropogoneae dominate mesic habitats where fire has been historically more frequent (Strömberg, 2005; Visser *et al.*, 2012). This evolutionary history may affect how a grass species responds to contemporary fire (Elliott *et al.*, 2009; Bowman *et al.*, 2014). Identifying how grass

species respond to the combined effects of fire and drought, and whether their responses can be predicted by traits, phylogenetic relationships or higher taxonomic levels, will be critical for forecasting future change among ecosystems worldwide.

Here, we report the response of temperate Australian perennial grasses to experimental fire after different durations of water stress. We grew plants under three different water regimes, subjected them to fire, then monitored their post-fire survival and growth. We asked: (1) Does post-fire resprout capacity vary between C_3 and C_4 photosynthetic pathways? (2) Does post-fire resprouting vary with pre-fire drought stress? We also asked whether phylogenetic relationships or higher taxonomic levels (i.e. tribe) help explain the response of Australian perennial grasses to fire and drought?

Materials and Methods

To determine how fire and drought affect survival and resprouting capacity of temperate C_3 and C_4 grasses, a glasshouse experiment was conducted in January 2015 in Melbourne, Australia (37°42'S, 145°03'E).

Species selection and growing conditions

We selected 37 genera and 52 species, comprising 34 C_3 and 18 C_4 perennial species, spanning 13 grass tribes (Soreng *et al.*, 2017) that inhabit temperate grassland, woodland and forest habitats of southern Australia (Table 1). This region is characterised by predominately winter–spring rainfall and summer–autumn fire activity (Murphy *et al.*, 2013). It supports 64 genera of grasses, and *c.* 400 species, across a broad precipitation gradient (350–1000 mm) and a variety of fire regimes (Bradstock, 2010; Murphy *et al.*, 2013). Most genera (34) used in this experiment were represented by one species per genera. Three genera (*Austrostipa*, *Poa*, *Rytidosperma*) were represented by two, two and 14 species, respectively.

Plants were grown in 6 l pots using a standard native grass potting media for 6 months before treatments being applied. There were three drought treatments, with five blocks per treatment and one replicate of each species per block ($n = 5$ per treatment). Pots were arranged within a well-lit, temperature-controlled glasshouse (maximum daytime temperatures were 25°C, while minimum overnight temperatures ranged from 10–23°C). To reduce within-block shading of grasses, whole blocks were randomly shifted every 2 wk, with random re-arrangement within blocks.

Drought treatment

To test the effects of drought on fire response of grasses, we imposed three levels of drought for 35 d before burning. The drought treatments were based on watering frequency: (1) 'Control' (plants watered to field capacity every 4 d); (2) 'Moderate Drought' (plants watered to field capacity every 8 d); and (3) 'Severe Drought' (plants watered to field capacity every 11 d). On average, based on weight of moisture loss from field capacity

to the time of next watering, the treatments depleted soil moisture by $14.6 \pm 0.9\%$ (mean \pm 1 SE; Control), $19 \pm 1\%$ (Moderate Drought) and $40.7 \pm 1.1\%$ (Severe Drought).

Along with photosynthetic pathway and grass tribe, we also measured covariates that were expected to affect post-fire survival and growth: pre-fire density of tillers (cm^2) and leaf dry matter content (LDMC; dry leaf mass/water-saturated fresh leaf mass). Leaf dry matter content is considered a proxy for plant drought-stress response (Fernandez & Reynolds, 2000). Here, as drought stress increases and resource acquisition declines, LDMC should increase as a result of morphological reactions to reduce water loss (Fernandez & Reynolds, 2000; Rusch *et al.*, 2011). Pre-fire tiller density and LDMC were measured in the final week of drought treatment (35 d) before plants were burned. LDMC was measured for each species in each treatment block by collecting 10–20 leaves for each species for each drought treatment, across replicates. LDMC was calculated using the protocols of Cornelissen *et al.* (2003).

Fire treatment

All plants in the three drought treatments were burned *in situ* (within pots) using 4 mm concrete sheeting to prevent heat damage to plastic pots. Plants were burned at the end of a treatment drought cycle. Because of the differing drought treatments imposed, plants in each treatment were not fully cured at the time of burning; 11-d droughted plants typically had drier canopies than 4-d droughted plants (N. Moore, pers. obs.). As grasses retained different amounts of moisture and cured differently across treatments, they were unlikely to burn completely when ignited. Indeed, we observed that 11-d droughted plants typically had more flammable canopies than 4-d droughted plants. Hence, we tried to minimise heterogeneity of burns by using a hand-held gas torch to apply flames to each plant, with temperatures in the flaming zone ranging between 300–700°C. This ensured all plants had *c.* 100% leaf scorch and experienced a temperature range (measured near the ground) that is common in southern Australia tussock grassland fires (Morgan, 1999). Most plants took *c.* 10–15 s to combust. This approach eliminates inherent differences in flammability caused by factors such as biomass quantity, density and moisture content which effect ignitability, sustainability and combustibility (Simpson *et al.*, 2016).

After burning, plants were returned to the glasshouse and remained unwatered for 2 d. All treatment blocks were then returned to a 4-d watering cycle for a further 10 wk. Whole blocks were randomly shifted every 2 wk during this period, including random re-arrangement within blocks. After 10 wk, plant survival and the number of post-fire tillers per plant were recorded.

Data analysis

We used the number of post-fire tillers as a measure of resprouting strength. We modelled the strength of resprouting using a hierarchical zero-inflated negative binomial (ZINB) model. This

Table 1 Species attributes, and mean (\pm 1SE) post-fire tiller resprouting (as a % of pre-fire tiller number) for 52 grasses from Australia subjected to experimental drought before burning.

Tribe	Species	Photosynthetic pathway	Location of growing buds	Tiller resprouting (as a % of pre-fire tiller number)		
				4-d drought	8-d drought	11-d drought
Andropogoneae	<i>Bothriochloa macra</i>	C ₄	Crown	59 \pm 16	61 \pm 28	87 \pm 19
Andropogoneae	<i>Cymbopogon refractus</i>	C ₄	Crown	28 \pm 9	48 \pm 11	91 \pm 15
Andropogoneae	<i>Dichanthium sericeum</i>	C ₄	Crown	55 \pm 14	56 \pm 15	117 \pm 11
Andropogoneae	<i>Eulalia aurea</i>	C ₄	Crown	57 \pm 8	79 \pm 12	101 \pm 10
Andropogoneae	<i>Hemarthria uncinata</i>	C ₄	Rhizome	84 \pm 5	92 \pm 7	88 \pm 18
Andropogoneae	<i>Imperata cylindrica</i>	C ₄	Rhizome	108 \pm 20	105 \pm 21	124 \pm 5
Andropogoneae	<i>Themeda triandra</i>	C ₄	Crown	104 \pm 23	94 \pm 11	108 \pm 20
Cynodonteae	<i>Chloris truncata</i>	C ₄	Crown	20 \pm 7	41 \pm 9	76 \pm 12
Cynodonteae	<i>Distichlis distichophylla</i>	C ₄	Rhizome	79 \pm 17	126 \pm 20	94 \pm 12
Danthonieae	<i>Rytidosperma bipartitum</i>	C ₃	Crown	19 \pm 9	44 \pm 32	90 \pm 24
Danthonieae	<i>Rytidosperma caespitosum</i>	C ₃	Crown	26 \pm 10	6 \pm 5	30 \pm 13
Danthonieae	<i>Rytidosperma carphoides</i>	C ₃	Crown	60 \pm 17	135 \pm 25	141 \pm 15
Danthonieae	<i>Rytidosperma duttonianum</i>	C ₃	Crown	73 \pm 36	103 \pm 14	128 \pm 11
Danthonieae	<i>Rytidosperma erianthum</i>	C ₃	Crown	33 \pm 9	81 \pm 3	110 \pm 8
Danthonieae	<i>Rytidosperma fulvum</i>	C ₃	Crown	6 \pm 4	75 \pm 5	59 \pm 21
Danthonieae	<i>Rytidosperma geniculatum</i>	C ₃	Crown	43 \pm 24	73 \pm 25	77 \pm 52
Danthonieae	<i>Rytidosperma indutum</i>	C ₃	Crown	60 \pm 19	74 \pm 6	127 \pm 15
Danthonieae	<i>Rytidosperma laeve</i>	C ₃	Crown	12 \pm 3	36 \pm 13	67 \pm 16
Danthonieae	<i>Rytidosperma pallidum</i>	C ₃	Crown	4 \pm 2	9 \pm 7	3 \pm 3
Danthonieae	<i>Rytidosperma pilosum</i>	C ₃	Crown	85 \pm 24	124 \pm 19	110 \pm 17
Danthonieae	<i>Rytidosperma racemosum</i>	C ₃	Crown	1 \pm 1	42 \pm 20	57 \pm 14
Danthonieae	<i>Rytidosperma semiannulare</i>	C ₃	Crown	53 \pm 24	84 \pm 23	124 \pm 15
Danthonieae	<i>Rytidosperma setaceum</i>	C ₃	Crown	2 \pm 1	33 \pm 21	39 \pm 18
Ehrharteae	<i>Microlaena stipoides</i>	C ₃	Rhizome	48 \pm 4	75 \pm 9	176 \pm 47
Ehrharteae	<i>Tetrarrhena juncea</i>	C ₃	Rhizome	0	1 \pm 1	0
Eragrostideae	<i>Enneapogon nigricans</i>	C ₄	Crown	8 \pm 4	11 \pm 7	19 \pm 18
Eragrostideae	<i>Eragrostis brownii</i>	C ₄	Crown	29 \pm 5	52 \pm 7	82 \pm 9
Meliceae	<i>Glyceria australis</i>	C ₃	Rhizome	113 \pm 9	138 \pm 24	141 \pm 9
Molinieae	<i>Phragmites australis</i>	C ₃	Rhizome	97 \pm 9	93 \pm 15	120 \pm 14
Paniceae	<i>Digitaria brownii</i>	C ₄	Rhizome	52 \pm 6	70 \pm 8	66 \pm 3
Paniceae	<i>Neurachne alopecuroidea</i>	C ₃	Crown	34 \pm 4	58 \pm 12	52 \pm 17
Paniceae	<i>Oplismenus hirtellus</i>	C ₃	Stolon	0	0	0
Paniceae	<i>Panicum effusum</i>	C ₄	Crown	43 \pm 8	57 \pm 11	54 \pm 8
Paniceae	<i>Paspalidium jubiflorum</i>	C ₄	Rhizome	51 \pm 2	61 \pm 5	59 \pm 10
Paniceae	<i>Spinifex sericeus</i>	C ₄	Stolon	0	0	20 \pm 20
Paniceae	<i>Walwhalleya proluta</i>	C ₃	Crown	0	0	0
Paspaleae	<i>Paspalum distichum</i>	C ₄	Rhizome	51 \pm 8	80 \pm 13	58 \pm 10
Poeae	<i>Amphibromus nervosus</i>	C ₃	Crown	56 \pm 8	73 \pm 6	105 \pm 10
Poeae	<i>Deschampsia caespitosa</i>	C ₃	Crown	72 \pm 12	123 \pm 26	148 \pm 18
Poeae	<i>Deyeuxia quadriseta</i>	C ₃	Crown	31 \pm 11	51 \pm 15	71 \pm 19
Poeae	<i>Dichelachne sieberiana</i>	C ₃	Crown	0	0	0
Poeae	<i>Dryopoa dives</i>	C ₃	Crown	5 \pm 5	0	0
Poeae	<i>Echinopogon ovatus</i>	C ₃	Rhizome	114 \pm 22	183 \pm 26	157 \pm 44
Poeae	<i>Lachnagrostis avenacea</i>	C ₃	Crown	88 \pm 42	5 \pm 3	20 \pm 20
Poeae	<i>Pentapogon quadrifidus</i>	C ₃	Crown	70 \pm 9	83 \pm 10	76 \pm 21
Poeae	<i>Poa labillardieri</i>	C ₃	Crown	73 \pm 8	124 \pm 12	114 \pm 18
Poeae	<i>Poa sieberiana</i>	C ₃	Crown	18 \pm 11	24 \pm 13	34 \pm 21
Stipeae	<i>Austrostipa rudis</i> ssp <i>rudis</i>	C ₃	Crown	0	41 \pm 25	78 \pm 12
Stipeae	<i>Austrostipa scabra</i> spp <i>falcata</i>	C ₃	Crown	2 \pm 2	78 \pm 29	88 \pm 10
Triticeae	<i>Anthosachne scabra</i>	C ₃	Crown	66 \pm 11	99 \pm 20	85 \pm 11
Zoysieae	<i>Sporobolus virginicus</i>	C ₄	Rhizome	29 \pm 9	72 \pm 20	76 \pm 9
Zoysieae	<i>Zoysia macrantha</i>	C ₄	Rhizome	30 \pm 5	137 \pm 42	99 \pm 23

Location of growing buds is defined as the position where new shoots arise: stolon (above-ground), rhizome (below ground) or crown (position between the roots and shoot in tufted grasses). Classifications follow Soreng *et al.* (2017).

model form is commonly used for data that have far more observed zeros than expected in standard Poisson or Negative Binomial models (Zuur *et al.*, 2009). However, in accounting for

these inflated zeros, the model also simultaneously provides information on two biological processes: (1) the probability of survival; and (2) the strength of resprouting conditional on survival.

It does this by fitting the data as a function of two linear models: a binomial model which assesses the probability of death (i.e. did the individual resprout?), and a negative binomial model, which estimates the number of post-fire tillers conditional on the plant surviving (i.e. conditional on it resprouting). The over-dispersion parameter of our model was estimated to be $3.44 (\pm 0.22 \text{ SD})$.

Both probability of death and number of post-fire tillers were modelled as a function of manipulated (watering treatment: 0 = Control, 1 = Moderate, 2 = Severe) and unmanipulated covariates (photosynthetic pathway: $C_3 = 0$ or $C_4 = 1$; pre-fire tiller density cm^{-2} ; and LDMC mg g^{-1}). Both LDMC (mean $\pm 1\text{SD}$: 336.5 ± 56.8) and pre-fire tiller density (2.95 ± 2.7) were centred on zero (by subtracting the mean) and standardized by two standard deviations. Centering coefficients allows them to be interpreted more easily, with intercepts interpreted as average responses and slope terms as partial dependencies conditional on other continuous variables at their mean. Standardizing by two SDs allows the magnitude of effects to be compared between binary (C_3 vs C_4) and continuous variables at their mean (Gelman & Hill, 2007).

We also allowed the intercepts of both modelled processes to vary by tribe and species, so that the model accounted for the nested structure of the dataset (that is, individuals within species, species within tribes) and therefore accounted for nonindependence in observations. Another advantage of this was that it allowed us to partition both explained and unexplained variance at each level of the dataset (Gelman & Hill, 2007) and therefore assess at which level greatest variance occurred.

We fitted this model in R v.3.4.1 using the Bayesian package RSTAN 2.16.2 (Stan Development Team, 2015). Detailed information about the analysis is provided in the Supporting Information. Data and source code are available at: https://github.com/jscamac/postfire_grass_responses. In order to aid in the reproducibility of this work, our code was written using a remake framework (FitzJohn, 2015). This allows others to readily reproduce our analyses from data processing, running the models, and reproducing the figures by calling `REMAKE::MAKE()` in R. To safeguard against cross-platform issues and future software changes, we have embedded this framework within a Docker image (see github repository).

To examine whether phylogeny helps to explain the responses observed, we constructed a phylogenetic tree of all genera used in this study ($n = 37$), based on Thornhill *et al.* (2016), and map the fire responses (mortality, tiller resprouting) of each genera onto the phylogeny. We use the mean effect size ($\pm 95\%$ credible intervals) coefficients derived for mortality (dead, live) and post-fire tiller abundance (less than, equal to, more than pre-fire tiller number) and plot responses on the phylogenetic tree to examine patterns. For the three genera with $n > 1$ species (*Rytidosperma*, *Austrostipa*, *Poa*), we use the mean for the genera character state prediction.

Results

There were significant changes in LDMC (Kruskal–Wallis test: $H = 52.48$, $\text{df} = 2$, $P < 0.0001$) in response to watering treatment.

Mean LDMC across all species varied with time between watering, from 324 ± 3.7 (Control; mean $\pm 1 \text{ SE}$), to 313 ± 4.1 (Moderate Drought) to 351 ± 3.9 (Severe Drought).

Of the 780 plants burned, 616 (79%) survived fire. Six species were found to be fire sensitive, with $> 90\%$ mortality after fire across all drought treatments: *Dichelachne sieberiana* (Tribe Poaceae, C_3), *Dryopoa dives* (Poaceae, C_3), *Oplismenus hirtellus* (Paniceae, C_3), *Spinifex sericeus* (Paniceae, C_4), *Tetrarrhena juncea* (Ehrharteae, C_3) and *Walwhalleya prolata* (Paniceae, C_3). Ninety per cent of species recovered from fire by resprouting, to varying degrees (Table 1).

Watering treatment and species trait effects on post-fire mortality

We examined how watering treatment and species traits (LDMC, photosynthetic pathway) affected the probability that a grass would not resprout at 10-wk postfire (i.e. mortality) using the binomial sub-model of the ZINB model. We found that the probability of post-fire mortality decreased as the number of days between watering events increased from 4 to 11 d (Fig. 1a). Moreover, the sub-model also indicated that despite considerable uncertainty, species with a C_4 photosynthetic pathway (Fig. 1a,b) and high LDMC (Fig. 1a,c) had significantly (credible intervals do not cross zero) lower probabilities of mortality relative to low LDMC or C_3 species. An individual's pre-fire tiller density had no significant effect on probabilities of post-fire mortality (Fig. 1a,d).

Watering treatment and species trait effects on the strength of post-fire resprouting

The count sub-model of the ZINB model also allowed us to examine how watering treatment, LDMC and photosynthetic pathway affected the number of post-fire tiller resprouts (i.e. our measure of resprouting strength), conditional on the probability a grass resprouts. We found that, if a grass did resprout, the number of tillers at 10-wk post-fire was not significantly affected by the photosynthetic pathway. Rather, the number of post-fire tillers was found to increase with the length between watering events and the density of tillers pre-fire (Fig. 2a,b,d). We also found that species with higher LDMC tended to have fewer tillers at 10-wk post-fire (Fig. 2a,c).

Residual variation attributed to tribe and species classification In both linear sub-models (i.e. models estimating mortality and post-fire tiller abundance), we allowed the intercepts to vary as a function of two random variables, grass tribe and species. By doing this, we not only allowed for predictions to be made to tribes or species not included within our dataset but also were able to examine whether taxonomic differences at two-levels (tribe and species) accounted for variation that was otherwise not explained by treatment, individual (i.e. pre-fire tiller density) or species (i.e. photosynthetic pathway and LDMC) covariates. The expectation is that if the covariates do fully account for differences among tribes or species, then the estimated tribe or species

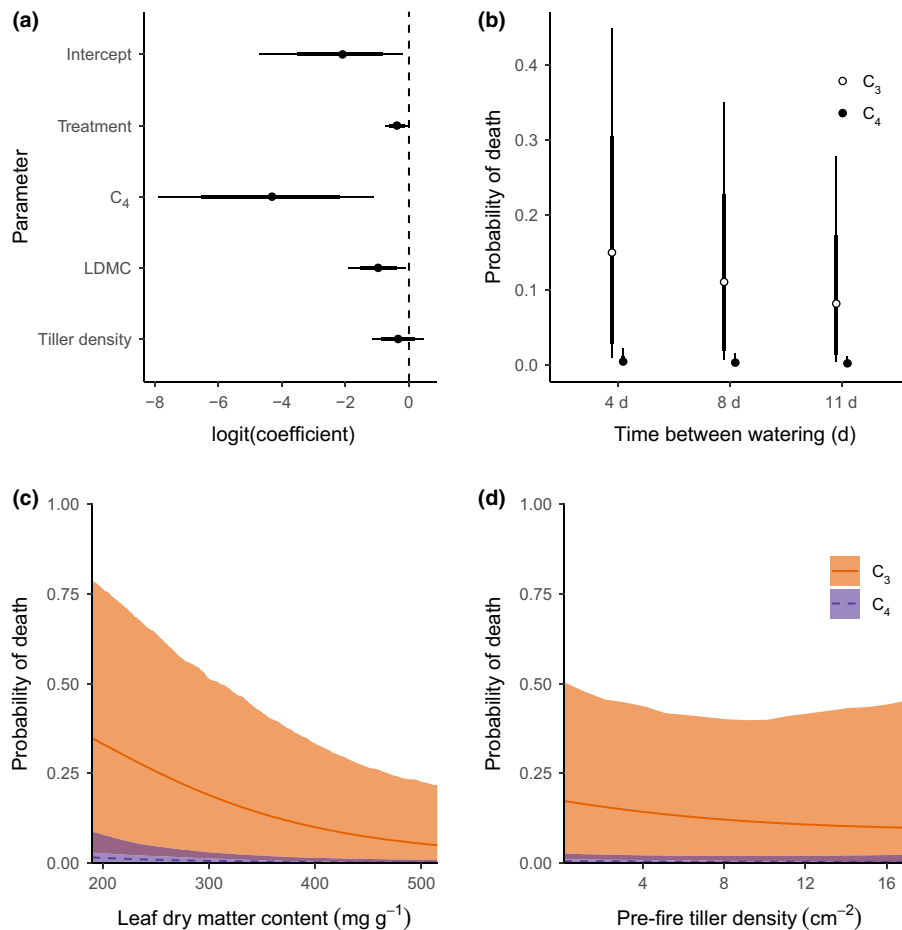


Fig. 1 Probability of death, as estimated from a zero-inflated negative binomial regression. (a) Coefficient plot showing logit mean effect sizes and 95% (thin line) and 80% (thick line) credible intervals. The intercept represents the predicted logit probability of death for a C₃ grass from an average grass tribe growing in the 4-d watering treatment with a leaf dry matter content (LDMC) of 337 mg g⁻¹ and a pre-fire tiller density of 2.95 cm⁻². Partial dependency plots for both C₃ and C₄ plants highlighting the estimated modelled relationship between the predicted probability of dying in the 4-d watering treatment and (b) watering treatment, (c) LDMC and (d) pre-fire tiller density. Note, because no significant interaction was detected among LDMC, density of pre-fire tillers and watering treatment, (c, d) only show the predicted response to the 4-d watering treatment. The 8-d and 11-d treatments have similar curves except that the intercept is lower.

effects should be small and groupings within each should have similar effect sizes. We found that in both mortality and resprouting sub-models, all 13 tribes used in this study responded similarly, with no single tribe deviating significantly from any other (Supporting Information Fig. S1).

By contrast, significant variation between species still existed after accounting for treatment, LDMC and photosynthetic pathway in both mortality and post-fire tiller abundance sub-models (Fig. 3a,b). In terms of mortality, *Spinifex sericeus* had an average estimated mortality rate of > 0.99 (note high logit effect; Fig. 3a) and *Pentapogon quadrifidus* had the lowest estimated probability of death post-fire of 0.02% (95% BCI range: 0–0.52). In terms of resprouting strength (Fig. 3b), *Microlaena stipoides* was the strongest resprouter with an expected mean of 3.23 tillers (95% BCI range: 1.9, 5.7), and *Oplismenus hirtellus* was the weakest with an expectation of 0.19 tillers (95% BCI range: 0.05, 0.55). As such, we found that there was considerably more residual variation among species relative to that found between tribes (Table 2).

Responses viewed from a phylogenetic perspective Phylogenetic patterns were not evident when assessing the response of grass genera to fire (mortality, Fig. S2a; post-fire tiller resprouting, Fig. S2b).

Discussion

In this large, comparative glasshouse study, we show that temperate Australian grasses vary in their response to fire, both within and between species. We found that interspecific fire responses were partially attributed to species traits such as photosynthetic pathway (as it effects mortality) and LDMC (which effects mortality and post-fire tiller abundance). Individual factors such as pre-fire tiller density and the drought stress experienced by the plant (as evidenced by increasing LDMC) at the time of burning contributed to the observed intraspecific variability. Hence, the effects of fire should not be assumed to be similar across temperate grass species, or under differing drought conditions. The response to fire in temperate Australian perennial grasses has, until now, largely been inferred because quantitative data have been lacking for genera other than grassland dominants such as *Themeda triandra* (Lunt & Morgan, 2002), *Austrostipa* species (Sinclair *et al.*, 2014) and *Poa* species (Prober *et al.*, 2007).

The 52 species in our study exhibited a spectrum of responses to fire, ranging from plants being killed outright to plant growth being stimulated. Six species in this study were highly sensitive to fire. These species are nonresprouters that recover from fire by seed stored in the soil; most are C₃ species, commonly found in shaded, wet forests (*Dryopoa dives*, *Tetrarrhena juncea*,

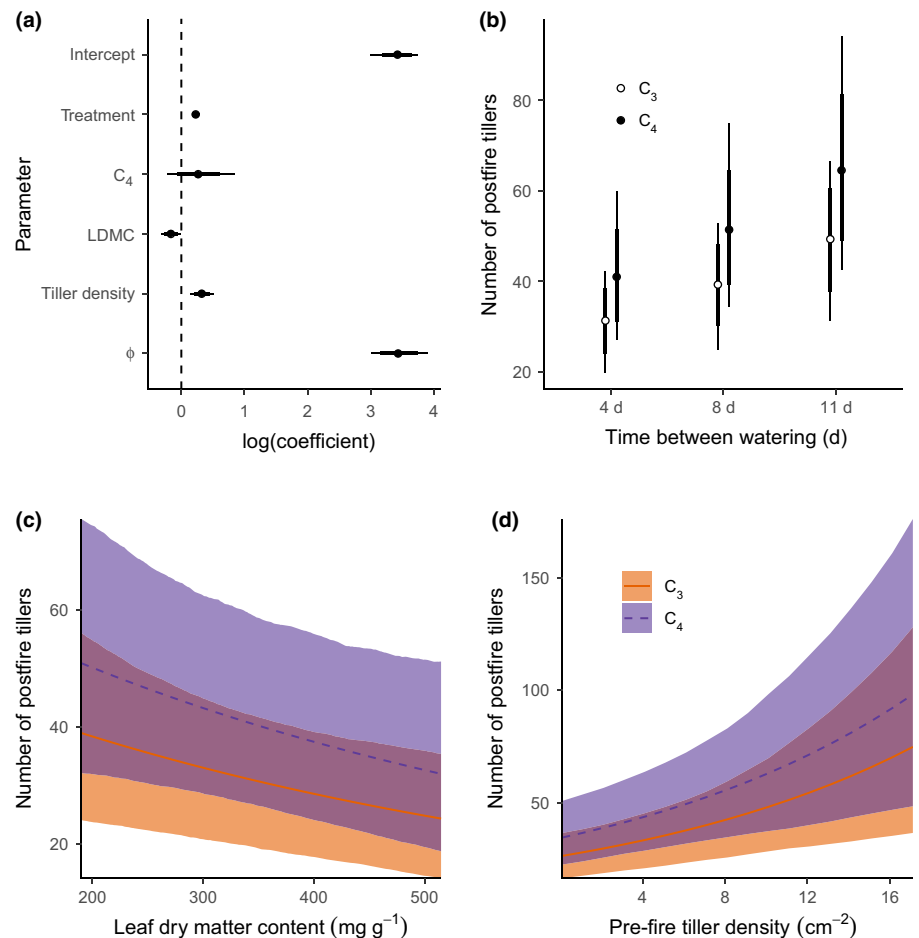


Fig. 2 Post-fire tiller abundance, as estimated from a zero-inflated negative binomial regression. (a) Coefficient plot showing log mean effect sizes and 95% (thin line) and 80% (thick line) credible intervals. The intercept represents the predicted log number of post-fire tillers for a C₃ grass from an average grass tribe growing in the 4-d watering treatment with a leaf dry matter content (LDMC) of 337 mg g⁻¹ and a pre-fire tiller density of 2.95 cm². Partial dependency plots for both C₃ and C₄ plants highlighting the estimated modelled relationship between the predicted number of post-fire tillers in the 4-d watering treatment and (b) watering treatment, (c) LDMC and (d) pre-fire tiller density. Note, because no significant interaction was detected among LDMC, density of pre-fire tillers and watering treatment, (c, d) only show the predicted response to the 4-d watering treatment. The 8-d and 11-d treatments have similar curves except that the intercept is higher.

Oplismenus hirtellus, *Dichelachne sieberiana*) while a fifth (*Walwhalleya proluta*) is common in grassy wetlands. The only fire-killed C₄ species (*Spinifex sericeus*) was found on coastal sand dunes. All of these habitats burn rarely due to site wetness (wet forest species), fuel discontinuity and low flammability (grassy wetlands), or lack of fuel (sand dunes). Nonresprouting grasses typically allocate resources to other functions, such as rapid growth and reproduction (Ripley *et al.*, 2010), and have been observed recovering *en masse* after intense forest fire from soil-stored seed (e.g. *Dryopoa dives*, Lindenmayer *et al.*, 2015). It is likely that the probability of disturbance and/or the type of disturbance may determine the relative resource allocation to buds versus seeds in perennial grasses (Dalglish & Hartnett, 2006; Klimešová & Klimes, 2007; Gagnon *et al.*, 2010) and this hypothesis is worthy of further investigation.

The interspecific differences in post-fire survival of temperate grasses were not because narrowly distributed species were more sensitive to fire (using area of occupancy as an estimate of the total area occupied by a taxon; $r^2 = 0.031$, $P = 0.213$, Fig. S3a). 'Good' resprouters (i.e. those that produced more tillers after fire than were present pre-fire), however, were those grasses that were more widespread in Australia ($r^2 = 0.12$, $P = 0.007$, Fig. S3b). Hence, species geographic range size provides some insight to explain the interspecific variation to fire we observed, but the

mechanism(s) that underpin this pattern need further exploration.

For many grasses, biomass quickly recovers after fire because most species are capable of quickly mobilizing stored resources from below ground required to support rapid post-disturbance regrowth (Ripley *et al.*, 2010; Wragg *et al.*, 2018). The ability to resprout quickly allows plants to capitalise on newly available resources, such as light or a nutrient flush (Vesk & Westoby, 2004), or to pre-empt resources from near neighbours (Davis *et al.*, 2000). Resprouting from meristems, however, is clearly a morphologically diverse trait in grasses, with plants recovering from bud banks located in a variety of organs such as root crowns, rhizomes and stolons. Tiller density (i.e. packing) had a positive effect on the capacity of grasses to regenerate after fire, reflecting an expectation that the density of axillary buds, and the capacity to maintain those bud reserves undamaged from fire, are higher in grass species that evolved with frequent fires (Russell *et al.*, 2015). Typically, such plants have traits that make them ignite easily and burn quickly (Pausas *et al.*, 2017). Having such traits, conferring fast flammability, increases fitness because it decreases fire residence time and the heat shock to the meristems and roots of the plant (Gagnon *et al.*, 2010), allowing buds to survive largely undamaged.

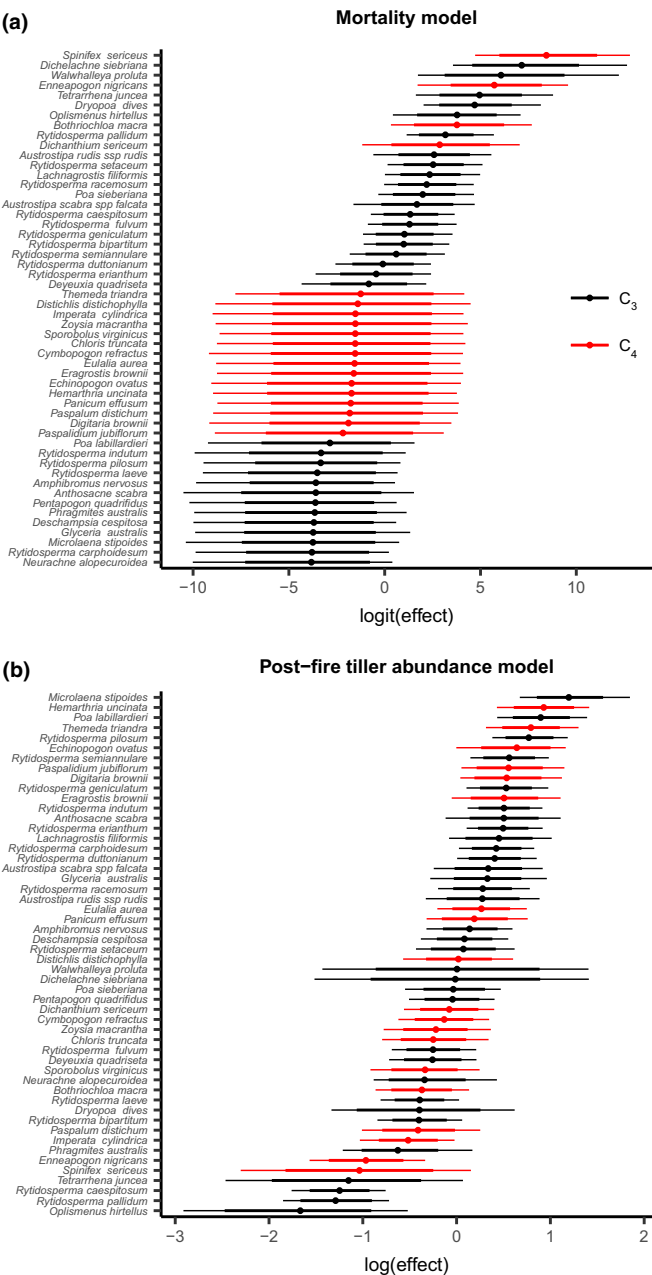


Fig. 3 Species random intercept terms estimated from a zero-inflated negative binomial regressions. (a) Probability of death model with logit mean effect sizes and 95% (thin line) and 80% (thick line) credible intervals for each species. (b) Count model of tiller count predictions post-fire with log mean effect sizes and 95% (thin line) and 80% (thick line) credible intervals for each species.

One potential explanation for why increasing drought benefited the survival and resprouting of grasses in this study may relate to the nature of experimental drought/fire treatment we employed. Longer intervals between watering may have led to leaf senescence (although we did not measure this) and hence, more-droughted plants may have lost proportionally less live biomass in the fire than well-watered grasses. Indeed, if droughted grasses have lower tissue N concentrations at the time of burning than nondroughted plants, one would expect such plants to have a

Table 2 Estimated posterior standard deviation and 95% quantile intervals for both binomial process model (i.e. mortality) and count process models (i.e. post-fire regrowth).

Process	Level	Mean	2.5%	97.5%
Mortality	Tribe	1.35	0.06	4.72
	Species	4.13	2.71	6.15
Post-fire regrowth	Tribe	0.20	0.01	0.66
	Species	0.71	0.53	0.95
	Phi	3.43	2.98	3.91

The over-dispersion parameter (phi) for the count process is also included.

higher capacity for leaf regrowth after fire (Wragg *et al.*, 2018). The general pattern of resilience to fire of the vast majority of species, and the individuals that comprised these species, however, suggests that burning across different fuel moisture contents presents a low risk to the persistence of many Australian grasses. This risk is likely to be lowest when grasses are most likely to be exposed to fire (i.e. late summer); at this time their foliage is cured and nutrient resources stored below ground in readiness for resprouting (Ripley *et al.*, 2010).

Our model predicted that grass species were less likely to die if they had higher LDMC. LDMC is positively associated with bud bank traits responsible for disturbance tolerance such as number and location of meristems (Rusch *et al.*, 2011), which may insulate buds more from extreme heat. Species that have consistently succumbed to experimental fire had lower LDMC values than resprouters (although this negative response was embedded amongst species with low LDMC that also survived fire and/or displayed high resprouting).

C₄ species survived fire better than C₃ species, as has previously been shown in other parts of the world (e.g. Bond *et al.*, 2003; Bond, 2008). C₄ grasses typically exhibit morphological adaptations to burning such as a well-protected bud bank (Keeley & Rundel, 2005; Edwards *et al.*, 2010). C₄ photosynthesis enables efficient use of water and nutrients, allowing a high proportion of biomass to be allocated to storage or roots (Ripley *et al.*, 2007), which can contribute to fast vegetative regeneration (Knapp, 1985). Determining if C₄ photosynthesis is adaptive for grasses in fire-prone environments, however, is complicated because the long evolutionary history of grasses may have resulted in selection for fire-related traits that are independent of photosynthetic type (Bond *et al.*, 2003; Edwards *et al.*, 2010).

The photosynthetic pathway effect on post-fire tiller abundance was uniform across watering treatments. Rather, the number of post-fire tillers was found to increase with the length between watering events and the density of tillers pre-fire. Water stress can reduce the photosynthetic advantage of C₄ over C₃ grasses (Ghannoum, 2009; Taylor *et al.*, 2011), with C₃ grass species having the capacity to increase their water-use efficiency during drought (Taylor *et al.*, 2011). This was evident in the resultant increase of post-fire tiller abundance in several C₃ species as days between watering increased (e.g. *Microlaena stipoides*, *Rytidosperma erianthum*), closing the gap in resprouting capacity between C₃ grasses and their C₄ counterparts under the

longest drought conditions. Hence, drought and the physiological status of grasses at the time of burning, as well as in the weeks after fire, may have an important role in the ability of perennial grasses to recover after burning (Knapp, 1985). Actively growing grasses (i.e. nonstressed plants) appear more vulnerable to fire than droughted grasses, perhaps because root carbohydrate stores are lower and meristems are actively growing at the time of burning. These findings contrast with observations of reduced tiller regeneration in burned, drought-affected prairie (Engle & Bultsma, 1984; Russell *et al.*, 2015). The season of burn affects fire intensity (Govender *et al.*, 2006) and has been shown to impact bud bank dynamics (Russell *et al.*, 2015), with implications for the abundance of species when fire occurs in the growing season vs dormant season (Forrestel *et al.*, 2014). This is particularly pertinent in south-east Australia where early season (i.e. growing season) fuel reduction burning for asset protection is being promoted ahead of late season (i.e. dormant season) fires.

We examined if fire responses could be understood from the perspective of higher taxonomic levels (i.e. tribe) or by viewing phylogenetic relationships. In our experiment, we found that all grass tribes responded similarly to fire, and a phylogenetic signal at the genus level was not obvious. This was somewhat unexpected; incorporating phylogeny and/or higher-level taxonomy to understand disturbance responses has proved useful elsewhere (e.g. Verdu & Pausas, 2007; Antonelli *et al.*, 2011; Ripley *et al.*, 2015). Forrestel *et al.* (2014) examined the responses of grasses in North American and South African savanna grasslands to fire regimes and found tribe effects in fire responses on both continents, driven primarily by species in the Andropogoneae. In our study, fire-response differences between distantly related tribes and species were not particularly apparent, perhaps highlighting a convergent response to filtering processes (e.g. frequently burned environments) across grasses in temperate Australia (Dwyer & Laughlin, 2017; Leys *et al.*, 2018). Fire is thought to have been a common landscape component in temperate Australian grasslands for at least 5 Myr (Morgan *et al.*, 2017), potentially shaping convergent fire responses across much of the grass flora. The response we observed may be a consequence of this long-exposure to fire, with only those grasses constrained to fire refuges (as suggested above), fundamentally differing in their resprouting capacity.

Conclusion

Our study is the first empirical documentation of the fire response of a large number of native grass genera from the temperate region of Australia. Until now, the effects of fire on these species have largely been inferred from studies of grassland dominants. This study also provides the first drought-related fire-response comparisons of Australian grasses. We asked: (1) whether post-fire resprout capacity varied between C_3 and C_4 photosynthetic pathways (it did, with C_4 grasses better at resprouting after fire than C_3 grasses); (2) whether responses could be explained by phylogenetic associations or the higher taxonomic level of tribe (it did not, perhaps the temperate grasses of

Australia have been exposed to a long history of fire); and (3) whether post-fire resprouting varied with pre-fire drought stress (it did, with more-droughted plants resprouting better than less-droughted plants). An obvious next step is to examine how the experimental fire responses we observed translate to the field and, in particular, to variations in season, frequency and intensity of fire? Given predictions that Australia will be warmer, drier and more flammable in the coming century (Cary *et al.*, 2012), plant functional trait responses to the changed season and intensity of fire are likely to maintain this disturbance agent as a strong community assembly filter on species distributions, as has been the general case in the evolution and subsequent spread of grasses (Linder *et al.*, 2018).

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Author contributions

JM and NM designed the study and performed the experiments. JC and JM analysed data. JM, JC and NM wrote the paper.

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Fig. S1 Tribe random intercept terms estimated from zero-inflated negative binomial regressions.

Fig. S2 Temperate Australian grass phylogeny (derived from Thornhill *et al.*, 2016) in relation to mortality and post-fire tiller resprouting of 35 perennial grass genera.

Fig. S3 The relationship between the area of occupancy (AOO, km²) of 52 Australian temperate perennial grass species in relation to the mean effect size for mortality and post-fire tiller resprouting capacity.

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