Letters

Grasses and fire: the importance of hiding buds

A response to Moore *et al*. (2019) 'Effects of drought and fire on resprouting capacity of 52 temperate Australian perennial native grasses'

Most research on plant response to fire has been performed on woody plants, and this is especially evident for research on postfire resprouting (Pausas *et al*., 2016). This bias is probably due to the considerable amount of research performed in Mediterranean-type shrublands (Keeley *et al*., 2012), and to the fact that grasslands have traditionally been linked to grazing systems (Coughenour, 1985; McNaughton, 1985). Fortunately, this is changing rapidly, and after the recognition that many grasslands worldwide are also maintained by fire (Bond, 2008), studies on the fire responses of native grasses are flourishing (Ripley *et al*., 2010, 2015; Simpson *et al*., 2016; Wragg *et al*., 2018; Russell *et al*., 2019).

A recent example of a resprouting study in grasses is the experiment performed on 52 Australian native grasses that combined fire and drought treatments (Moore *et al*., 2019). The results of this study are: (1) C_4 grasses survive better fire than C_3; (2) survival increased with leaf dry matter content (LDMC); and (3) drought increased postfire resprouting in both C_3 and C_4 species. The importance of the photosynthetic pathway in postfire survival can be explained by the fact that C_4 plants are able to fix more carbon under warm and sunny environments than C_3 grasses, and so providing more carbon resources for survival and growth after fires (Ripley *et al*., 2010). The results are also consistent with the idea that fire enhanced the spread of C_4 grasslands in the Late Miocene and Pliocene in regions previously dominated by C_3 forest and woodlands (Keeley & Rundel, 2005; Edwards *et al*., 2010; Bouchenak-Khelladi *et al*., 2014; Karp *et al*., 2018). One of the unanswered questions of this study is that if the capacity to efficiently fix carbon is the clue for fire response in grasses, we would expect the photosynthetic pathway to be a good predictor not only for postfire survival but especially for the strength of resprouting (e.g. Ripley *et al*., 2010). But apparently this was not the case (Moore *et al*., 2019). This suggests that carbon reserves are not the only limiting factor for resprouting. The first requirement for initial resprouting is the survival of the bud bank, which depends on the degree of bud protection (Pausas *et al*., 2018). Once the initial resprouting occurs, the carbon reserves and the new photo-assimilates should determine the resprouting vigour (Moreira *et al*., 2012). The number of surviving buds may also affect the strength of resprouting after fire, since the amount of sprouted buds likely affects the resprouted biomass (Moreira *et al*., 2012).

Here we propose that to fully understand the variability in postfire resprouting in grasses we need to consider the location and the degree of protection of the bud bank (Pausas *et al*., 2018). Specifically, we predict that bud location explains resprouting in grasses better than photosynthetic pathway and LDMC. To test this prediction, we use the data from Moore *et al*. (2019) and added to their models a variable related to the position of the resprouting buds with three categories (see Supporting Information Methods S1): stolons (aboveground), crown (root–shoot transition), and rhizome (belowground).

The position of the buds is shown to be a significant factor, and the resulting model is descriptive of the resprouting process (Figs 1, S1): survival depends not only on having a C_4 photosynthesis pathway, but also (and more importantly, i.e. with larger effect size) on the location of the buds. Furthermore, this is especially important for the strength of the postfire resprouting of surviving plants, either measured as the number of tillers postfire (as in Moore *et al*., 2019) or as the proportion of tillers in relation to the prefire conditions (Fig. 1). The mean proportion of tillers across treatments for each species and for all 52 species suggests that overall postfire resprouting response is lower for grasses with stolons, intermediate with those that resprout from the crown, and highest for the species with rhizomes (Fig. 2), as expected under the hypothesis of bud protection as a driver for the fire response. The results support the idea that the location of the bud bank is an important factor in determining fire response in grasses, and perhaps it is more important than the photosynthetic pathway or the LDMC. Even if the high efficiency of C_4 leaves allow greater allocation to storage (Ripley *et al*., 2010), the mechanism for bud survival (and thus plant survival and resprouting) is likely to be determined by the position (and soil protection) of the buds. In fact, previous studies already suggested that other traits indirectly related to C_4 photosynthesis could explain responses of C_4 grasses to disturbance (Edwards *et al*., 2010; Ripley *et al*., 2015); we propose that those traits are related to the location and protection of resprouting buds. Supporting this idea is a tendency for rhizomes to occur more frequently in species with C_4 photosynthesis than in those with C_3, as observed in three independent data sets from different continents (Notes S1). Further research is needed given that the experiment by Moore *et al*. (2019) was not designed to test this factor (bud location); however, our results suggest that we need to look at the position of the buds to better understand the underlying mechanisms of response to disturbances in plants (Ottaviani *et al*., 2017; Pausas *et al*., 2018).

The traditional view is that C_4 photosynthesis is more efficient in open, dry, and warm habitats (Ehleringer & Monson, 1993), and thus these habitats may have favoured C_4 grasses. However, these habitats are also likely to be fire-prone (particularly in the tropics), and thus their survival may depend on the bud protection mechanisms. Moreover, C_4 grasses

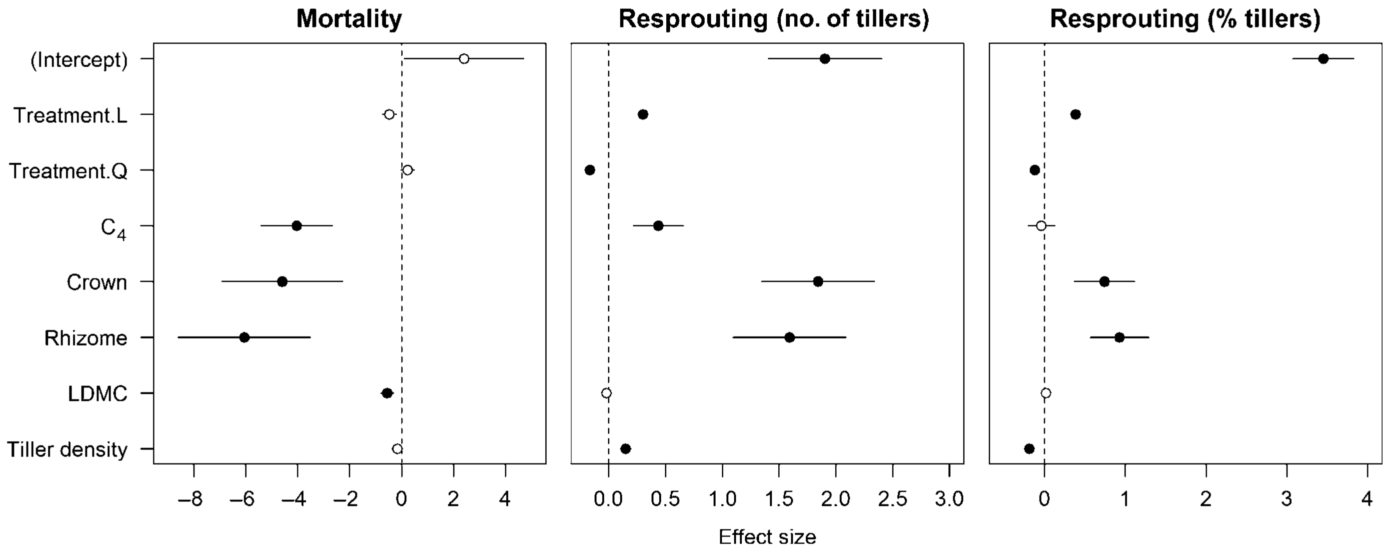

Fig. 1 Effect size (in logit units) of the different variables for the models of postfire mortality and resprouting (for the postfire survivors) of 52 Australian grasses (data from Moore *et al*., 2019). The variables included are: drought treatment (as ordered factor; L, linear; Q, quadratic response), photosynthesis pathway (C_3/C_4), bud location (stolons, crown, rhizome), leaf dry matter content (LDMC), and tiller density. Resprouting is modelled as number of postfire tillers (following Moore *et al*., 2019; middle panel) and as the proportion of postfire tillers in relation to prefire tillers (rightmost panel). The intercept represents the predicted logit probability of death or resprouting for C_3 grass in the 4-d drought treatment, and for species with stolons. Closed symbols are significant coefficients ($P < 0.05$), open symbols otherwise; variability refers to standard errors. For a comparison with the original models by Moore *et al*. (2019) see Supporting Information Fig. S1.

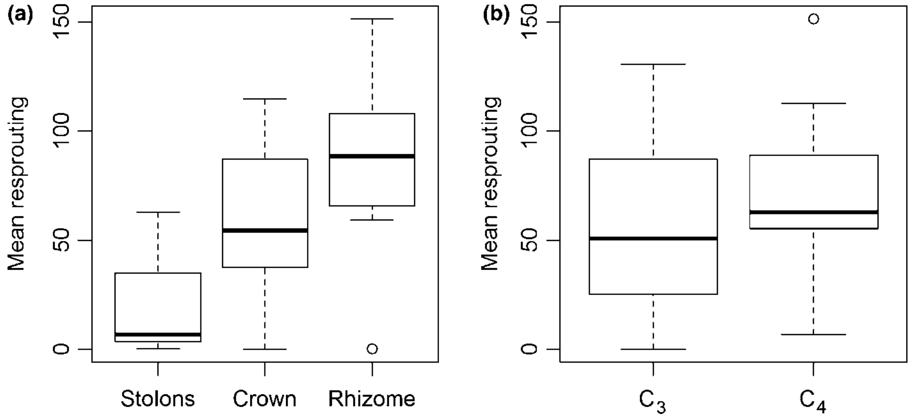

Fig. 2 Mean proportion of postfire tillers in relation to prefire tillers in Australian grasses across treatments aggregated by the species that have (a) different bud locations (stolons, crown, rhizomes), and (b) by the different photosynthetic pathway (C_3, C_4). The pattern is consistent when analysing each drought treatment separately. Variability is among species and includes all 52 species from Moore *et al*. (2019). Boxplots indicate the median (horizontal line), the first and third quartiles (box), the range that excludes outliers (i.e. 1.5 interquartile range; whiskers), and the outliers (points).

originated in the Eocene–Oligocene transition but they diversified and massively expanded during the Late Miocene (3–8 million years ago (Ma); Edwards *et al.*, 2010; Bouchenak-Khelladi *et al.*, 2014) thanks to enhanced rainfall seasonality that increased fire frequency, that in turn opened habitats (Keeley & Rundel, 2005; Karp *et al.*, 2018). Bud protection, together with C_4 photosynthesis, could have been beneficial during the C_4 grass expansion, and explain why these two traits are associated in fire-prone ecosystems (Notes S1). Studies on the correlated evolution of these two functional traits would shed light on this process.

A hidden belowground bud bank could also play a role for resprouting after grazing by vertebrates. However, grass tolerance to grazing is more likely related to the continuous elongation of leaves from their bases, than to the regrowth from a belowground bud bank (Coughenour, 1985). In fact, there is evidence suggesting that grazing favours stoloniferous plants against rhizomatous ones (Brock *et al.*, 1997; Pakeman, 2004; De Bello *et al.*, 2005). Thus, grasses may have followed different evolutionary pathways in relation to their bud banks depending on the main disturbance driver they were subject to through their history. Studies comparing the bud bank in grasslands driven by grazing (temperate climates, mainly C_3) and those driven mostly by fire (warm climates, mainly C_4) would be worthwhile, especially if they also include other traits like herbivory defences (palatability) and flammability traits.

Bud banks have different ecological functions in plants: growing, colonizing the space, and recovering from different disturbance-types (Ottaviani *et al.*, 2017). Because not all bud banks are equally efficient in each of these processes, different evolutionary pressures have shaped the variability of bud banks in plants (Pausas *et al.*, 2018). We encourage researchers to look at the position of the buds to better understand the underlying mechanisms of response to disturbances in plants.

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Author contributions

JGP designed the research, performed the statistical analysis, and wrote the first version of the manuscript. SP contributed to the idea, compiled and analysed the southern Africa data set (Notes S1), and contributed to the final version of the manuscript. JGP and SP compiled the Argentinian data (Notes S1).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Mean effect size of the different variables for the models of postfire mortality and resprouting.

Methods S1 Statistical methods.

Notes S1 The relation between the presence of rhizomes and the photosynthetic pathway.

Key words: bud bank, C_4, fire ecology, grasses, resprouting.

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The following Supporting Information is available for this article:

Methods S1 Statistical methods

Figure S1 Mean effect size of the different variables for the models of postfire mortality and resprouting

Notes S1 The relation between the presence of rhizomes and the photosynthetic pathway

Methods S1 Statistical methods

We use the raw data from Moore et al (2019) available at https://github.com/jscamac/postfire_grass_responses. We first (1) replicate their analyses and display the equivalent to their Fig. 1a and 2a. That is, we build a statistical model for the survival and resprouting of grasses after an experimental fire and drought. The variables considered were drought treatment (3 categories: 4, 8, and 11-days drought treatment), photosynthetic pathway of the species (C_3 / C_4), leave dry matter contents (LDMC) and tiller density. Quantitative variables (LDMC, tiller density) were centered and standardised previous to the analysis, and species identity was used as random factor. We modelled postfire mortality as a binomial model and resprouting (number of postfire tillers conditioned to the survival) as a negative binomial model with an overdispersion value of 3.44 (from Moore et al. 2019). The main difference from the Moore et al (2019) is that we used a maximum likelihood approach while they used a Bayesian approach; specifically we use a generalized linear mixed model as implemented in the library glmer in R. The other difference is that we considered Treatment as an ordered factor. Despite these differences, our results are the same as those reported by Moore et al. (2019) (see Fig. S1a,b).

Then (2) we add to the model (both to mortality and resprouting) a new variable also obtained from Moore et al. (2019): the location of the resprouting buds. We categorised this variable as: stolons (aboveground buds), crown (buds at the root-shoot transition), and rhizomes (buds belowground). Note also that *Paspalum distichum* can has both stolons and rhizomes; Moore et al. (2019) assumed rhizomes in Table 1 and stolons in the raw data; we used their raw data. Resprouting was analysed in two ways, as the number of tillers postfire (following Moore et al. 2019), and as the proportion of tillers postfire in relation to the number of tillers prefire.

Finally (3) we plotted the fire response (for all species) in relation to the position to the buds and in relation to the photosynthetic pathway, by averaging the resprouting (proportion of tillers postfire) across the three drought responses for each species. This provides an indicator of the overall response to fire.

Fig. S1 Mean effect size of the different variables for the models of postfire mortality and resprouting

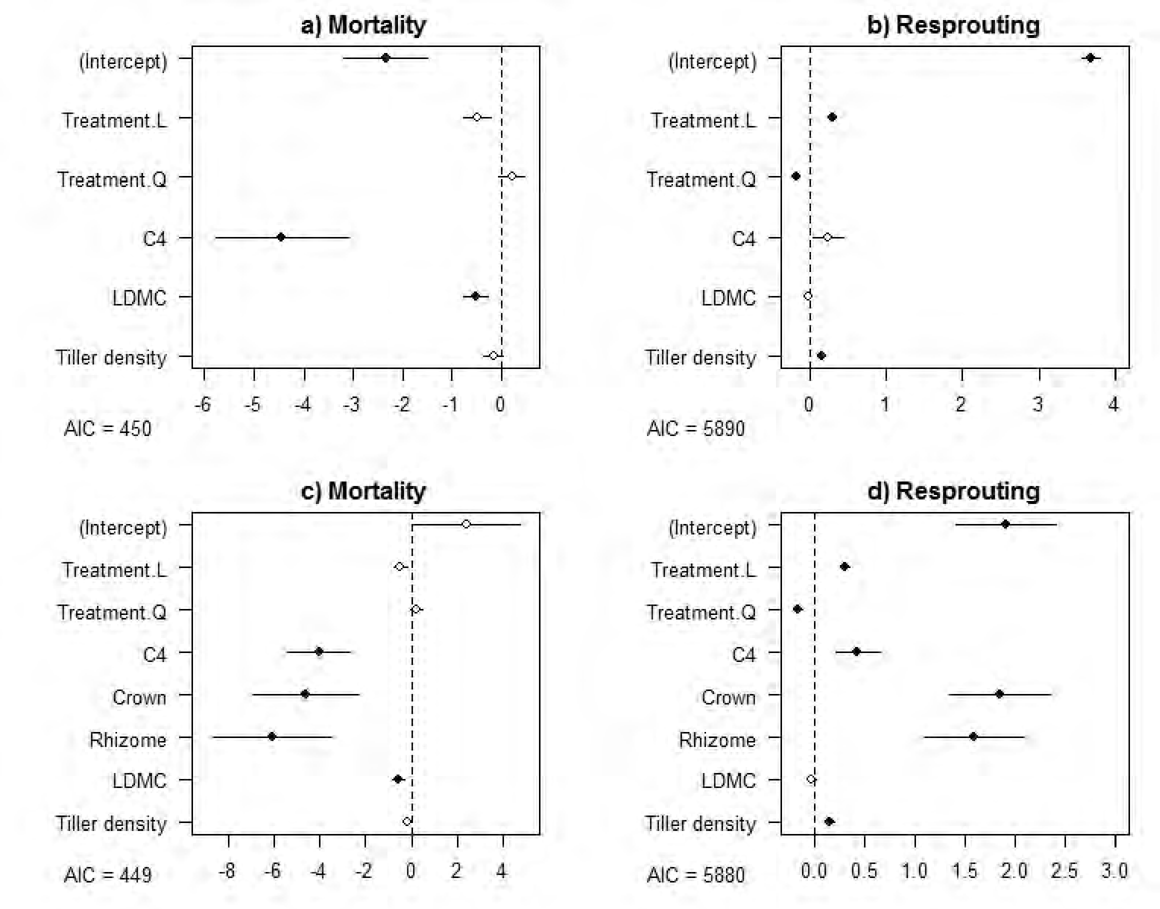

Fig. S1. Mean effect size (*x* axes, in logit units) of the different variables for the models of postfire mortality and resprouting (for the fire surviving) of 52 Australian grasses. Models in the top (**a, b**) are replicated from Moore et al (2019) but using an approach based on Generalised Mixed Linear Models instead of the Bayesian approach used by the original authors (see Notes S1); however the results are the same. Another difference is that we use Treatment (4, 8, or 11 days of drought) as ordered factor. These models include drought treatment, leaf dry matter contents (LDMC), tiller density, and photosynthesis pathway (C$_3$/C$_4$). Models in the bottom (**c, d**) are the same models but adding the categorical variables related to the bud location (stolons, crown, rhizome). Closed symbols are significant coefficients (p<0.05), open symbols otherwise; variability refers to standard errors. The intercept represents the predicted logit probability of death/resprouting for C3 grass in the 4-days drought treatment, and (in c and d) with stolons. Plots c and d are shown in the main text as Fig. 1a and 1b.

Notes S1 The relation between the presence of rhizomes and the photosynthetic pathway

We compiled the presence of rhizomes (yes/no) and the photosynthetic pathway (C_3 /C_4) on perennial grasses for three independent fire-prone areas:

(1) Southern Australia: rhizomes and the photosynthetic pathway from Moore et al. (2019). It includes 52 species from southern Australia.

(2) Southern Africa: data from Fish et al. (2015) which is a guide of grasses for southern Africa (i.e., Namibia, Botswana, Swaziland, Lesotho and South Africa). When the information on the presence of rhizome was missing, we used Clayton et al. (2006). We excluded exotic species, annuals, rare species, and species inhabiting wet habitats (wetlands, river beds), coastal dunes, halophytic soils, and extreme deserts. The final number of taxa with reliable data was 278 (37% C_3 and 63% C_4).

(3) Central Argentina: data from Jewsbury et al. (2016). This data set include grasses from fire-prone areas in the region of Córdoba, Argentina. We excluded annuals and alien species. The photosynthetic pathway was obtained from Cabido et al. (1997), Cavagnaro (1988), Liu et al (2011), and Kattge et al. (2011). The final number of taxa with reliable data was 63 (29% C_3 and 71% C_4).

For the total of 393 species, we compared the presence of rhizomes taxa in relation to the photosynthetic pathway by means of Generalized Lineal Model assuming a binomial distribution error. Rhizomatous taxa were significantly more frequent in C_4 than C_3 grasses ($p< 0.001$; overall: 50% and 29% respectively); neither the data set nor the interaction of the data set and the photosynthetic pathway were significant (Fig. 1 below) suggesting consistent results across data set.

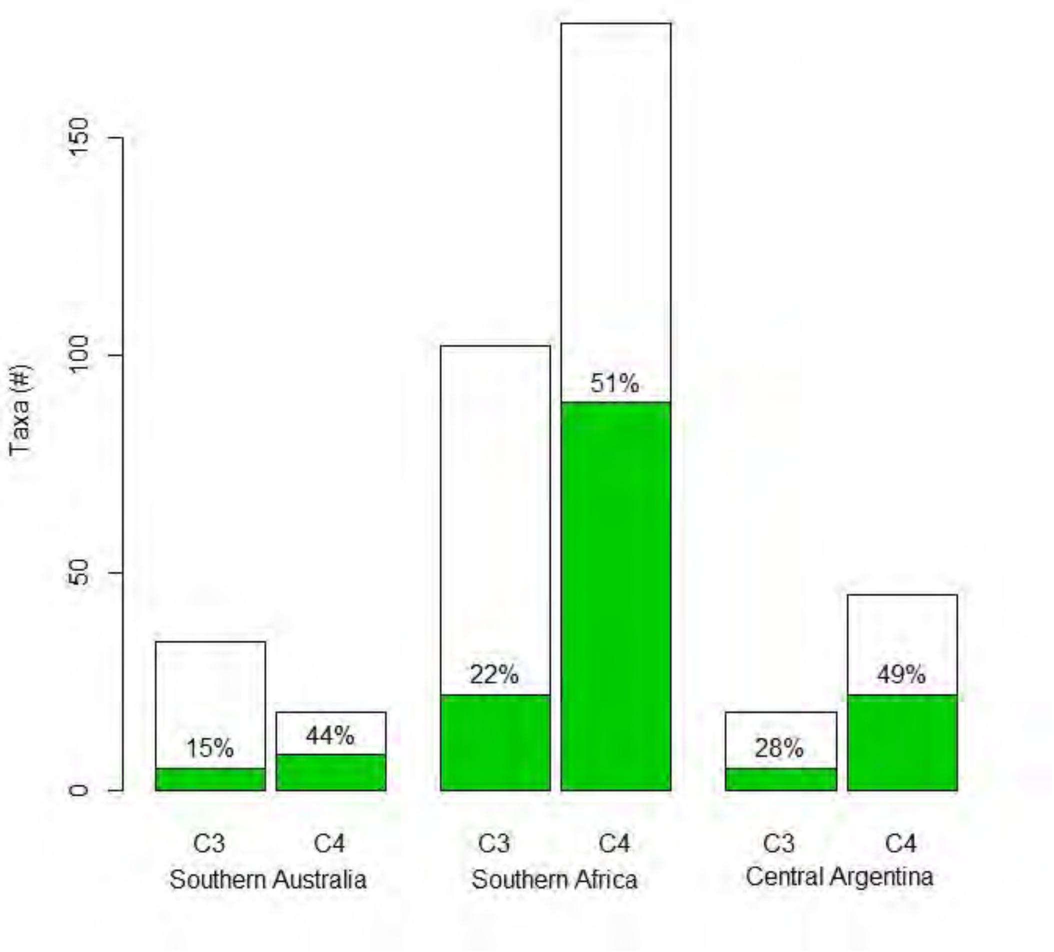

Fig. 1 in Notes S1. Number of rhizomatous (green) and non-rhizomatous (white) taxa for the three data sets considered (southern Australia, southern Africa, central Argentina). Overall, the proportion of rhizomatous taxa is significantly higher in C_4 than in C_3 grasses ($p< 0.001$); the data set and the interaction were not significant.

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