

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

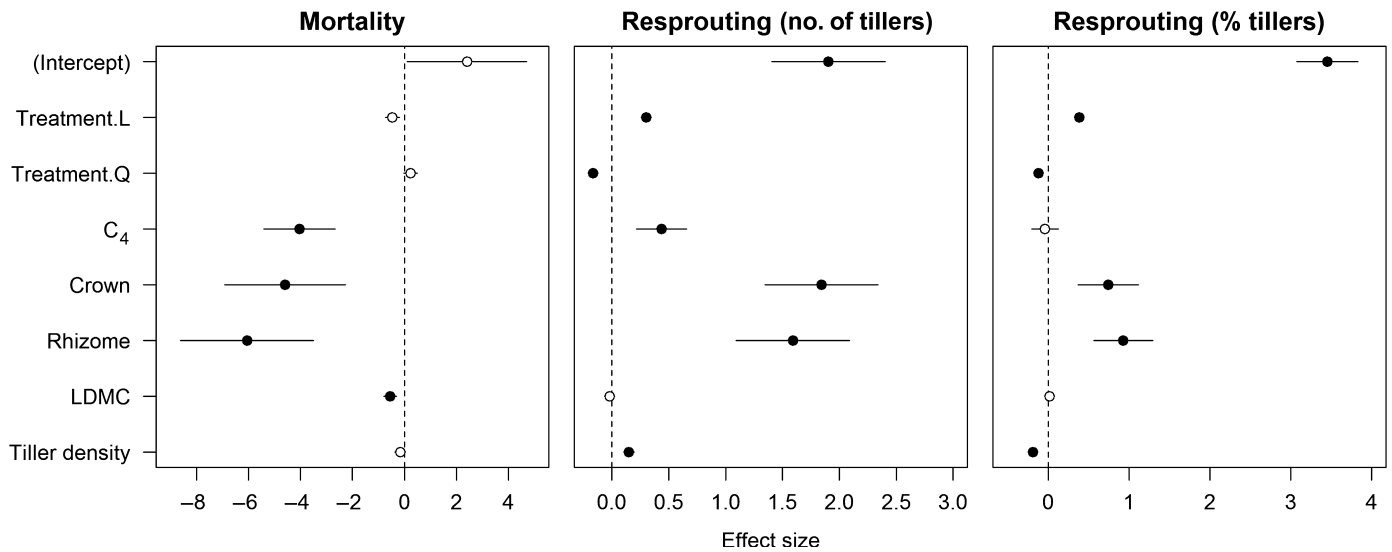


Fig. 1 Effect size (in logit units) of the different variables for the models of postfire mortality and resprouting (for the postfire survivors) of 52 Australian grasses (data from Moore *et al.*, 2019). The variables included are: drought treatment (as ordered factor; L, linear; Q, quadratic response), 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.

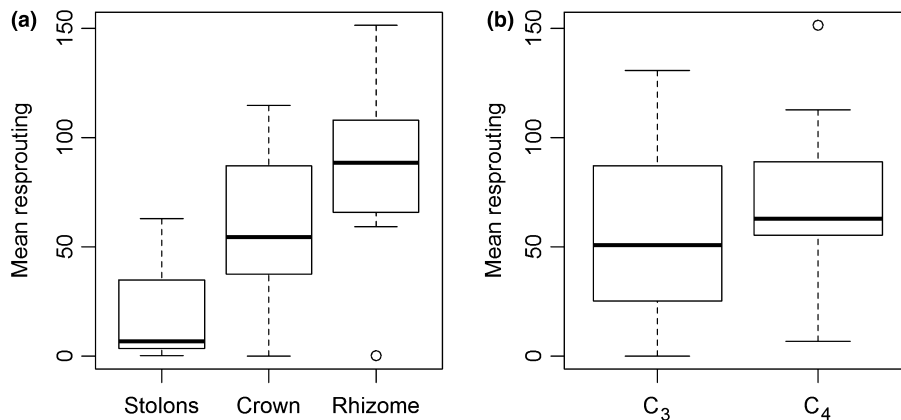


Fig. 2 Mean proportion of postfire tillers in relation to prefire tillers in Australian grasses across treatments aggregated by the species that have (a) different bud locations (stolons, crown, rhizomes), and (b) by the different photosynthetic pathway (C_3 , C_4). The pattern is consistent when analysing 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.

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