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BOTANICAL BRIEFING

# Does fire-induced bud mortality reduce phenotypic variability?

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• **Background and Aims** For plants that resprout after fire, burning creates a strong before–after contrast in which lost biomass must be rebuilt under altered environmental conditions. In species that regenerate through protected below-ground buds (basal resprouters), postfire resprouting may lead to increases in subindividual variability through the activation of dormant buds. In contrast, in species where regeneration depends on the survival of stem buds (aerial resprouters), fire might impose a filter favouring well protected buds that might lead to a reduction in variability. We tested whether frequent low-severity fires act as a phenotypic filter in aerial resprouters, reducing variability in bud protection and associated leaf traits.
• **Methods** We studied the shrub *Palicourea rigida* (Rubiaceae) in the Brazilian Cerrado, and sampled three populations with contrasting fire histories. We quantified bud mortality, bud protection (using terminal stem diameter and height above ground) and leaf phenotype (leaf area, dry mass, moisture content and specific leaf area), and assessed fire-driven changes in phenotypic variability at subindividual and population scales.
• **Key Results** In high fire frequency populations, bud mortality strongly depended on terminal stem diameter, while in the fire-excluded population it depended solely on bud height. These patterns were associated with reduced variability in stem diameter and leaf traits under frequent fires at both population and subindividual scales. Leaf phenotypes also differed between fire histories, with frequently burned populations showing more conservative leaf traits.
• **Conclusions** Frequent low-severity fires can reduce subindividual phenotypic variability in aerial resprouters by selectively removing poorly protected buds. This contrasts with the increased subindividual variability reported for basal resprouters and highlights that fire effects on plant variability depend on resprouting strategy, and ultimately on fire regime. Incorporating subindividual variability into fire ecology provides new insights into how disturbance shapes plant form, function and resilience.

**Key words:** Aerial resprouting, bud mortality, leaf phenotype, postfire resprouting, *Palicourea rigida*, stem diameter, subindividual variability.

## INTRODUCTION

Plants living in fire-prone ecosystems must either survive fire or recruit postfire from a persistent seed bank (Keeley and Pausas, 2022). Some species survive fire by locating their buds far above fire and by insulating their basal meristems with bark (e.g. trees in surface fires, the 'lanky' strategy in savannas; Keeley, 2012; Dantas and Pausas, 2013). However, many plants grow within flame height (e.g. herbs, shrubs, 'corky' trees; Clarke *et al.*, 2013; Dantas and Pausas, 2013) and must therefore protect their primary meristems from direct heat exposure. Under these conditions, some species regenerate lost above-ground biomass from well-protected buds located below ground (basal resprouting; Clarke *et al.*, 2013; Pausas *et al.*, 2018), whereas others have evolved strategies that promote stem and bud survival even when exposed to flames (e.g. thick bark, low flammability or epicormic resprouting; Hoffmann *et al.*, 2009; Lawes *et al.*, 2011; Pausas, 2017; Pausas *et al.*, 2017; Pausas and Keeley, 2017). After a fire, these species resume vegetative growth from well-protected above-ground buds, either dormant or active before the fire (epicormic and apical resprouting, respectively; Clarke *et al.*, 2013; Pausas and Keeley, 2017). Consequently, effective bud insulation through bark, cataphylls or trichomes is a key trait in these species (Charles-Dominique *et al.*, 2015; Pausas, 2017; Chiminazzo *et al.*, 2021).

Here we focus on this latter group: woody plants with low flammability that resprout postfire from above-ground protected buds. Such species are common in ecosystems with frequent low-to-medium-severity fires, such as tropical mesic savannas (Charles-Dominique *et al.*, 2015; Pausas and Keeley, 2017, Fig. 2; Scalon *et al.*, 2020; Pilon *et al.*, 2021), and are therefore repeatedly exposed to fire through their lifespan (i.e. they have polypyric life cycles; Pausas and Keeley, 2014). Specifically, we ask how this polypyric life cycle alters plant phenotype through the differential mortality of aerial buds.

Fire damage is not homogeneous within individual plants. In surface fire ecosystems, such as savannas, heat exposure follows a vertical gradient (Franklin *et al.*, 1997), and accordingly the protection of meristematic tissues also varies with height, with basal portions being more protected (Jackson *et al.*, 1999; Schwilk *et al.*, 2013; Graves *et al.*, 2014). As a result, differential bud mortality across plant structure and development can induce architectural changes, for example shifting individuals from single- to multi-stemmed forms (Saiz-Blanco *et al.*, 2025; Chiminazzo *et al.*, 2026). Here, we explore the potential phenotypic consequences of this process, building on similar fire-driven changes in plant form reported in a Mediterranean basal resprouter, where they are associated with broad shifts in phenotype (Saiz-Blanco *et al.*, 2025).

Buds constitute the primary source of postfire regeneration. Their development is controlled by a complex interplay between endogenous and exogenous mechanisms (Andrés *et al.*, 2021; Zeng *et al.*, 2024), and their phenotype, as well as their environmental context (Savvides *et al.*, 2017), strongly influences organ-level characteristics such as size (Sinnott, 1921; Grafius, 1978; Cottrell and Dale, 1984) and the number of constituent parts (Stevens *et al.*, 1972). Consequently, within individual variation in bud and meristematic traits is a major driver of subindividual variability in plant organs (Herrera, 2009). Thus, subindividual patterns of bud mortality or development could have cascading effects on plant form and function (Chiminazzo *et al.*, 2023*b*; 2026).

In plants with aerial resprouting subjected to frequent low-severity grass fires, both the activation of accessory dormant buds (i.e. epicormic sprouting; Pausas and Keeley, 2017) and the selective mortality of poorly protected buds (Charles-Dominique *et al.*, 2015; Scalon *et al.*, 2020; Chiminazzo *et al.*, 2021) could have contrasting effects on subindividual variability. While the activation of dormant buds is expected to increase within-individual trait variability (Saiz-Blanco *et al.*, 2025), bud mortality is likely to reduce it. Thus, the direction of fire effects on subindividual variability may depend on the dominant resprouting mode as well as on the relative effect of each of these processes on trait variability.

We study the effects of bud mortality on subindividual variability in *Palicourea rigida* (Rubiaceae), a non-flammable aerial resprouter commonly found in Cerrado ecosystems. We use terminal stem diameter (TSD; Fig. 1) and bud height above ground (BH) as key traits. First, we examine the relationship between TSD, BH and bud mortality across three populations with contrasting fire histories: two with high fire frequency (6–20 burns since 1985) and one from a fire-excluded area that has not burned for at least 23 years. We then assess whether TSD and BH are correlated with leaf phenotype.

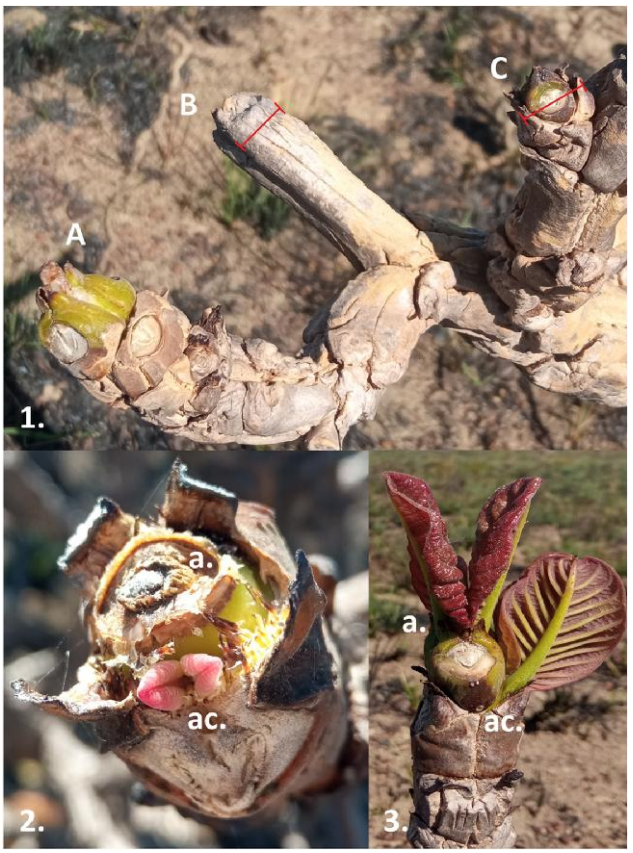


FIG. 1. Buds and resprouting in *Palicourea rigida* 2 weeks after fire. Panel 1 shows three apical buds; buds A and C are alive, while B is dead. Lines indicate terminal stem diameter (TSD). Panels 2 and 3 show leaf formation postfire. Note that postfire resprouting happens from the terminal section of branches, from apical (a.) and/or accessory (ac.) buds. Photos by J. Saiz-Blanco.

## MATERIALS AND METHODS

*Palicourea rigida* (Rubiaceae) is an evergreen shrub or small tree reaching up to 3 m, commonly found across the entire Cerrado, the Brazilian savanna (Ratter *et al.*, 2003; Flora e Funga do Brasil, 2020). This species is highly adapted to fire, exhibiting thick corky bark, sparse and highly sclerophyllous leaves, and the ability to sprout and flower shortly after fire (Vieira *et al.*, 1996; Trevizan *et al.*, 2025). Although postfire resprouting can take place from below-ground structures or from the internodes, it usually happens from thick and well protected buds (apical and/or accessory) located in the terminal portion of the stem (Fig. 1). In this work we use TSD as a key trait. TSD varies within individuals and is related to meristem protection and mortality (Lawes *et al.*, 2013; Rosell, 2016; Hoffmann *et al.*, 2020) as well as to bud size and leaf phenotype (Corner, 1949; Bond and Midgley, 1988).

In June 2025, we sampled three populations of *P. rigida*, two located inside the protected area of Parque Nacional da Chapada dos Veadeiros, Goiás, Brazil (14°10′S 47°30′W; Supplementary Data Fig. S1A, B) and one within a fire-

excluded area just outside the park (14°10.58′S 47°38.62′W; Supplementary Data Fig. S1C). This latter area has not burned for at least 23 years, while the other two populations burn frequently (6–20 fires since 1985). Of the frequently burned populations, one burned 1 year prior to sampling (May 2024) and the other ∼2 weeks before sampling (mid-May 2025). Consequently, plants of this latter population had not yet developed leaves at the time of sampling (Fig. 1) and thus are not considered for leaf phenotype analyses (see below).

We selected 10–16 individuals per population ($n = 43$). For each individual, we recorded BH and TSD (Fig. 1), two proxies of bud protection from heat, as well as bud mortality for approximately 10 buds per plant ($n = 285$). Buds bearing leaves were considered alive; leafless buds were sectioned to assess internal tissue colour and classified as alive when green tissues were present. We also measured plant height and stem diameter (30 cm above the ground).

In the two populations with living foliage at the time of sampling (fire-excluded vs frequently burned sampled 1-year postfire), we selected a subset of individuals ($n = 23$) to examine the relationship between bud traits and leaf phenotype. For each individual, we selected approximately five living buds and collected one or two fully developed leaves per bud ($n = 112$ leaves). For each leaf, we measured leaf area, fresh mass, dry mass (after 48 h at 60 °C), moisture content ((fresh mass − dry mass)/fresh mass), and specific leaf area (SLA; $cm^2\ g^{-1}$ dry mass). Leaf area was measured using an Epson Perfection V800 photo scanner and ImageJ software (Schneider *et al.*, 2012). Leaves were weighed to the nearest 0.01 g using a BEL precision scale.

### *Statistical analyses*

We analysed the relationships between TSD, bud mortality and leaf phenotype using mixed-effects models. Bud mortality was analysed with a binomial mixed model, with bud state (alive/dead) as the response variable. Leaf phenotype was analysed using linear mixed models, with each trait (leaf area, dry mass, leaf moisture content and SLA) considered separately as the response variable. In all models, fixed effects included plant diameter and height, BH, TSD, population and fire history (frequently burned vs fire excluded) as well as all possible interactions between fire history, TSD and BH. Plant individual was included as a random effect in all models. Model selection was performed using the dredge function from the MuMIn package, based on the corrected Akaike information criterion (AICc) (Bartoń, 2026). We report the best-supported models, defined as those with the lowest AICc; when multiple models differed by less than four AICc units, we selected the model with the most ecological sense.

In order to test for changes in TSD variability we calculated the coefficient of variation (CV; ratio between standard deviation and mean) for branches with living buds at the population and individual level. For CV values per individual (measure of subindividual variability; $n = 43$) we also fitted a simple linear regression with fire history as the sole predictor.

TABLE 1. Results of the Anova test for the mixed model analysing the effects of terminal stem diameter (TSD), bud height above ground (BH) and plant height and diameter on bud mortality ($n = 285$). All predictors have 1 degree of freedom except for population (2).

| Predictor | $\chi^2$ | *P*-value |
|---|---|---|
| Fire history (FH) | 0.238 | 0.626 |
| Population | 0.232 | 0.891 |
| **TSD** | **22.788** | **<0.001** |
| **BH** | **3.904** | **0.048** |
| **Plant height** | **6.661** | **0.010** |
| Plant diameter | 2.101 | 0.147 |
| TSD × BH | 0.047 | 0.828 |
| **TSD × FH** | **16.182** | **<0.001** |
| **BH × FH** | **3.086** | **0.079** |
| TSD × BH × FH | 1.817 | 0.178 |

Statistically significant predictors are highlighted in bold typing.

Mixed models were fitted using the glmer or lmer function of the lme4 package (Bates *et al.*, 2025) and simple linear models with the lm function of the stats package (R Core Team, 2024). Goodness of fit was evaluated with the simulateResiduals function of the DHARMa package (Hartig *et al.*, 2024). The significance of fixed effects was evaluated using the Anova function of the car package (Fox *et al.*, 2024).

In order to integrate differences in leaf phenotype between populations under different fire histories (fire-excluded vs high fire frequency), we conducted multivariate analysis based on Gower dissimilarity matrices calculated from leaf-level trait values ($n = 112$). We used leaf area, SLA and moisture (leaf weight was excluded since there were strong correlations with leaf area; marginal $R^2 = 0.91$). Matrices were calculated with vegdist, and differences between groups (i.e. the two fire histories) in centroid position and in data dispersion were tested using the betadisper and adonis2 functions, all three from the vegan package (Oksanen *et al.*, 2025). To specifically assess changes in subindividual variability, we separated the dataset by fire history and, within each group, ran adonis2 analyses grouping observations by individual plant. To represent the differences between fire histories in leaf phenotype we performed non-metric multi-dimensional scaling (NMDS) analyses using the metaMDS function from the vegan package.

## RESULTS

Bud mortality was negatively associated with BH and TSD. However, we detected interactions between each of these traits and fire history (Table 1). In the case of BH, the reduction in mortality of higher-located buds was stronger under fire exclusion (Fig. 2, right; marginal interaction). Meanwhile the TSD effect on mortality varied more abruptly among plants under different fire histories (Fig. 2, left). In the populations with high fire frequency, TSD was

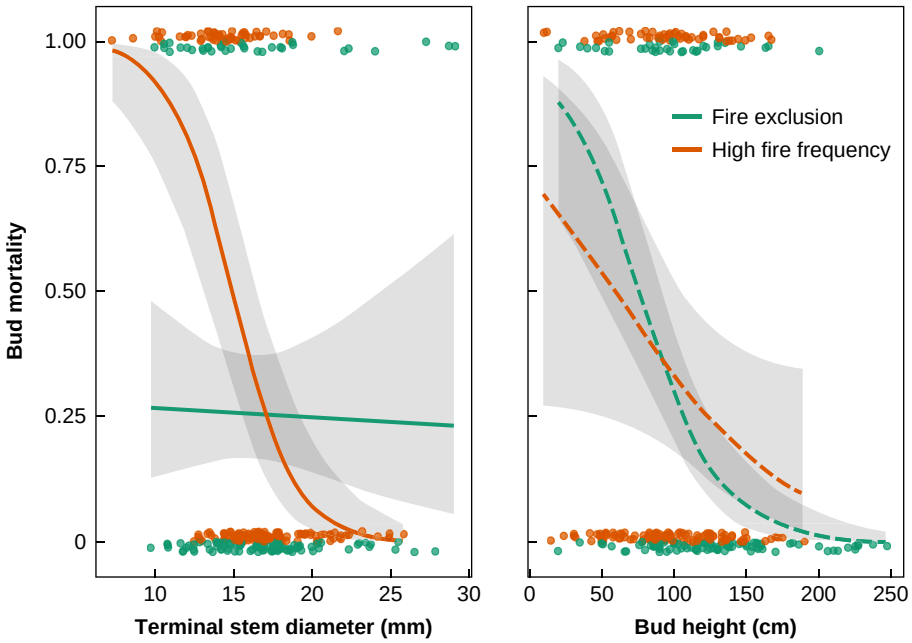


FIG. 2. Effect of TDS (left) and BH (right) on bud survival in plants growing under fire exclusion ($n = 121$, in green) and under frequent fires ($n = 164$, in orange). The latter include the two populations sampled (1 year old and recently burned) as they exhibit the same response (Supplementary Data Fig. S2). Lines represent model predictions (solid lines, significant interaction; dashed lines, marginal interaction), shaded areas indicate 95 % confidence intervals, and points represent observed data. For details of the model see Table 1.

TABLE 2. Results from the best model fit for each leaf trait studied. The $\chi^2$-values and *P*-values come from ANOVA analysis for each model. All leaf traits except moisture content were log-transformed. Note that, except for this last trait, TSD is always a significant predictor of trait value.

| Model | Predictor | Estimate | Standard error | $\chi^2$ | *P*-value | Marginal $R^2$ |
|---|---|---|---|---|---|---|
| Leaf area | TSD | 0.094 | 0.016 | 32.631 | <0.001 | 0.351 |
| | Population (high frequency) | −0.222 | 0.067 | 11.081 | 0.001 | |
| Leaf weight | TSD | 0.116 | 0.019 | 39.165 | <0.001 | 0.301 |
| | Population (high frequency) | −0.145 | 0.07 | 4.33 | 0.037 | |
| SLA | TSD | −0.019 | 0.005 | 15.598 | <0.001 | 0.491 |
| | BH | −0.024 | 0.005 | 18.438 | <0.001 | |
| | Population (high frequency) | −0.073 | 0.016 | 19.566 | <0.001 | |
| Moisture content | Population (high frequency) | −4.650 | 2.246 | 4.285 | 0.038 | 0.320 |
| | BH | −1.283 | 0.727 | 3.117 | 0.077 | |
| | Plant height | 3.498 | 1.122 | 9.718 | 0.002 | |

negatively related to mortality. In contrast, in the fire-excluded population bud mortality was independent of TSD and depended only on BH. We also detected a positive effect of plant height on mortality (estimate = 0.743; s.e. = 0.266; Table 1), probably because plant height is a proxy for total plant size, and bigger plants have more buds.

Variability of TSD on branches with living buds also differed among fire histories. At the population level, the fire exclusion area showed higher levels of variance (CV = 22.01) than the frequently burned areas (CV = 16.43). The same was true at the subindividual level, with a positive effect of fire exclusion on within-individual variance (Estimate = 3.66; S.E. = 2.51; $F = 4.01$; $P = 0.027$; Supplementary Data Fig. S3).

Terminal stem diameter was also significantly correlated to leaf phenotype (Table 2). Wider stems produced larger and heavier leaves with lower SLA values. Besides, there were also significant differences between fire histories. Leaves from plants under high fire frequency were smaller and had lower SLA and leaf moisture content than those from the fire-excluded area (Table 2, Fig. 3).

Multivariate analysis showed that leaves from the plants of high fire frequency and fire-excluded areas occupied distinct phenotypic spaces (adonis2: $R^2 = 0.23$, $F = 26.34$, $P = 0.001$; Fig. 3). Trait dispersion was significantly lower in the area with high fire frequency (betadisper: $F = 6.25$, $P = 0.014$), indicating reduced phenotypic variability at the population scale. Finally, variance partition (adonis2 analyses) performed at each area showed lower levels of subindividual variance in the high-frequency area (27.5 %) compared with the fire-excluded area (46.3 %).

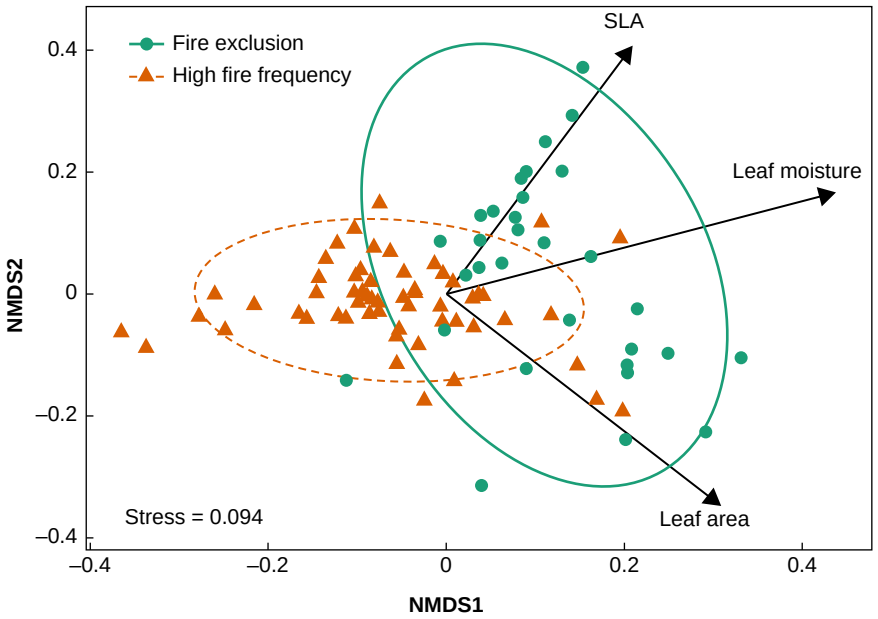


FIG. 3. Ordination (NMDS) of leaf phenotype. Symbols represent individual leaves from plants under high fire frequency (orange triangles) and from plants under fire exclusion (green circles). Ellipses depict 95 % confidence intervals for each area (solid line: fire exclusion; dashed line: frequently burned). The two areas occupy distinct phenotypic spaces, primarily driven by differences in leaf moisture. Leaves from the area with high fire frequency show reduced dispersion, indicating lower phenotypic variability.

## DISCUSSION

The relationship between bud mortality and fire protection traits (i.e. TSD and BH) differed among populations of *P. rigida* with contrasting fire histories. In frequently burned plants, bud mortality was strongly dependent on TSD and BH, whereas in the fire-excluded ones it depended solely on BH (Fig. 2).

The effect of BH on bud mortality is likely driven by a combination of factors, including ontogeny, light availability and protection from disturbances. Buds located higher in the canopy are younger, receive more light and are less exposed to fire heat, which together may enhance their probability of survival (Archibald and Bond, 2003). Besides, TSD is correlated with insulation capacity and resistance to fire (Lawes *et al.*, 2013; Rosell, 2016; Hoffmann *et al.*, 2020). We interpret the differences in the effect of TSD on bud mortality among fire histories as changes in the importance of heat insulation.

Taken together, these results suggest that bud mortality patterns emerge from the interplay of processes that vary across fire regimes. In the fire-excluded area, bud mortality appears to be primarily shaped by ontogenetic and light-related factors, as reflected by the dominant role of BH (Fig. 2). In contrast, in frequently burned areas fire acts as a strong filter, increasing the importance of TSD and reducing the relative effect of BH (Fig. 2). These results are consistent with the well-established relationship between fire frequency and bud protection at community (Charles-Dominique *et al.*, 2015; Scalon *et al.*, 2020) and intraspecific scales (e.g. bark production of generalists in areas with contrasting fire histories; Chiminazzo *et al.*, 2023*a*).

However, additional processes, such as fire-driven changes in plant architecture, are also likely to contribute to these mortality patterns (Chiminazzo *et al.*, 2023*b*). In this study, the *P. rigida* individuals located in frequently burned areas were shorter and started their canopy closer to the ground (Supplementary Data Fig. S4). Similar intraspecific architectural effects of fire have been described in other Cerrado species (Chiminazzo *et al.*, 2026; but see Archibald and Bond, 2003).

Despite the higher mortality of buds located on thin branch tips (low TSD) in the high fire frequency area, we did not detect an increase in the mean size of surviving stems ($\chi^2 = 1.64$; $P = 0.20$). Instead, we observed a reduction in TSD variability at both subindividual and population scales, consistent with a filtering effect of fire on less protected branches. Other fire-related processes, such as the changes in plant architecture mentioned above, may also influence TSD variability, since this trait is also correlated to bud ontogeny. In addition, because we did not distinguish among bud types (orthotropic, secondary and reproductive in *P. rigida*), we cannot fully disentangle these mechanisms. Nevertheless, given that TSD is correlated to bud size (Corner, 1949; Bond and Midgley, 1988) and consequently to leaf phenotype (Table 2; Sinnott, 1921; Grafius, 1978; Cottrell and Dale, 1984), the reduced variability in TSD in frequently burned areas is likely linked to the observed reduced variability in leaf traits through cascading effects (Fig. 3).

Despite this reduction in variability, the leaves produced under high fire frequency are not a subset of those found in the fire-excluded population (Fig. 3). Instead, plants in frequently burned sites explore a distinct phenotypic space, producing drier and more conservative leaves (i.e. smaller and with lower SLA; Wright *et al.*, 2004; Table 2, Fig. 3). Again, this shift is likely driven by a combination of factors, particularly fire resistance and light availability. Plants in low fire frequency environments, which are typically more shaded, tend to produce more acquisitive leaves (larger,

with higher SLA), whereas those in frequently burned, high-light environments exhibit more conservative strategies (smaller leaves with lower SLA). Similar patterns have been widely reported in community-based studies (de Souza *et al.*, 2016; Pellegrini *et al.*, 2023; Dai *et al.*, 2025), including those in Cerrado ecosystems (Hoffmann *et al.*, 2005; Dantas *et al.*, 2013; Moura *et al.*, 2023).

The reduction in subindividual variability after fire reported here contrasts with the increase in subindividual variability previously described for the Mediterranean basal resprouter *Anthyllis cytisoides* (Fabaceae; Saiz-Blanco *et al.*, 2025). We propose that these opposing patterns arise from differences in resprouting mechanisms, and ultimately from different historical fire regimes. Postfire resprouting may increase subindividual variability in species with basal resprouting under high-intensity fires as it triggers architectural changes through the recruitment of new shoots (e.g. a shift from single- to multi-stemmed individuals; Saiz-Blanco *et al.*, 2025). In contrast, in aerial resprouters that rely on bud survival (typically in low-intensity fire regimes), fire imposes a filter on bud traits (e.g. protection, size; Charles-Dominique *et al.*, 2015; Chiminazzo *et al.*, 2021), limiting the bud phenotype. Although fire-related changes from single-stem to multi-stem have also been described in savanna species with the ability to resprout both from underground and aerial buds (Chiminazzo *et al.*, 2026), once these species switch from basal resprouting to aerial resprouting (i.e. once they escape the fire trap; Hoffmann *et al.*, 2012) we expect to find patterns similar to those we describe here.

Our results also contribute to the growing evidence supporting the importance of incorporating the subindividual scale when assessing fire effects on plant survival and architecture. More specifically, we propose that postfire resprouting mode might broaden the range of mechanisms by which fire can alter the phenotypic mosaic of plants (*sensu* Harder *et al.*, 2019).

## SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following. Figure S1: the three populations sampled during this work. Figure S2: relationship between TSD and bud mortality probability for each of the three populations studied. Figure S3: effects of fire history on subindividual variability of TSD. Figure S4: architectural differences between *Palicourea rigida* individuals in areas with different fire histories.

## FUNDING

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## CONFLICT OF INTEREST

None declared.

## AUTHOR CONTRIBUTIONS

Conceptualization: J.S.B., J.G.P. (lead) and N.P. (support). Investigation, data curation and formal analysis: J.S.B. Writing (first draft): J.S.B. Writing (review and editing): J.S.B., J.G.P. and N.P. Funding acquisition and supervision: J.G.P.

## IA ASSISTANCE

ChatGPT (GPT-5.5) was used for minor text editing.

## DATA AVAILABILITY

All data used in this work area available in the FigShare repository (https://doi.org/10.6084/m9.figshare.31160737).

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