






RESEARCH ARTICLE

Variation in biomass allocation and root functional parameters in response to fire history in Brazilian savannas

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Abstract

1. Fire is a fundamental ecological factor in savannas because it affects vegetation dynamics and ecosystem functioning. However, the effects of fire on below-ground compartments, including biomass and root traits, and their regeneration remain poorly understood. In this study, we assess the variation of above- and below-ground plant components along fire-history gradients in Brazilian open savannas and investigate whether changes in vegetation and soil properties are associated with the responses of below-ground biomass and root traits.
2. The study was conducted in eight sampling areas of open savanna (*campo sujo*, i.e. vegetation having low woody cover) within the Cerrado (Brazilian savannas), located along a gradient of time since the last fire (1–34 years); the number of fires that occurred within the past 34 years (0–9 fires) varied by sampling area. In each sampling area, we measured above- and below-ground biomass, root depth distribution, root functional parameters and nutrient levels in the upper soil layers (0–10 cm).
3. Rapid recovery of above-ground live biomass after a fire was primarily due to re-sprouting of graminoids. This recovery was associated with an increase in absorptive root biomass in the upper soil layer in the most recently burnt sites, whereas root biomass was unaffected in deeper layers. Root parameters remained constant regardless of fire history but responded to variations in vegetation structure and soil properties. Specific root length (SRL) decreased with K, Mg²⁺, Al³⁺, N and C and increased with P concentration. In contrast, root tissue density (RTD) and absorptive root proportion were negatively correlated with soil P. RTD was strongly associated with the above-ground biomass of graminoids. Soil texture impacted the root system: the proportion of absorptive roots increased with fine sand content in the soil, inversely to transport root biomass. The relationship between fire and soil properties was insignificant.
4. *Synthesis.* In savannas, fire stimulates absorptive root biomass in response to the higher demand for below-ground resources. This response is correlated with shoot regrowth after a fire. Variations in morphological root parameters are not

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directly associated with fire history; instead, they reflect differences in soil chemistry, especially soil P and graminoid biomass changes.

KEYWORDS

absorptive root traits, below-ground biomass, *campo sujo*, Cerrado, morphological traits, root depth distribution, time since last fire

1 | INTRODUCTION

In many regions, fire is a significant determinant of plant community structure and ecosystem functioning, affecting nutrient cycling, carbon storage and plant regeneration (Higgins et al., 2007; McLauchlan et al., 2020; Pellegrini, Hobbie, et al., 2020). Fire regimes are modified in response to significant changes in land use and climate (Rogers et al., 2020). Open ecosystems, such as savannas, are shaped by recurrent surface fires (every 3–5 years in the Cerrado in Brazil, Miranda et al., 2009; Rissi et al., 2017). These fires maintain vegetation in an open state (Bond et al., 2004; Pausas & Bond, 2020), dominated by grasses and scattered shrubs and having few trees (Lehmann et al., 2014; Staver et al., 2011, 2017). Resprouting ability is a key functional trait in savannas to persist in such fire-prone environments (Clarke et al., 2013; Pausas & Keeley, 2014; Pilon, Cava, et al., 2021; Simpson et al., 2021; Zupo et al., 2021). Consequently, to cope with recurrent fires in savannas, the biomass is preferentially allocated below-ground (e.g. in coarse roots and other storage organs) especially in wetter environments (Pausas et al., 2018; Tomlinson et al., 2012; Wigley et al., 2019). However, fine roots play a critical role in nutrient acquisition by providing access to nutrient-rich substrates immediately after a fire. Although our current understanding of biomass allocation and root traits in savannas has primarily focused on tree species and coarse roots (Tomlinson et al., 2012; Wigley et al., 2019; Zhou et al., 2020), information about the response of fine root traits in plant communities dominated by grasses, such as open savannas (but see Oliveras et al., 2013; Simpson et al., 2021), is lacking. Therefore, we investigated whether root biomass and fine root traits associated with resource acquisition and conservation vary along a fire regime gradient.

Root responses to fire may be mediated by changes in vegetation structure at different times after a fire. Analysing temporal community responses by comparing sites with distinct fire histories is then relevant to examine how growing conditions change over time after a fire. Fires cause partial or total combustion of litter and dead plant biomass, allowing full light penetration that enhances the growth of species that recover rapidly, such as grasses (Edwards & Smith, 2010; Linder et al., 1999). On the other hand, a prolonged absence of fire causes the accumulation of dead biomass (Fidelis et al., 2013), changes in grass composition (Cardoso et al., 2018; Smith et al., 2013) or woody encroachment (Stevens et al., 2016) that may lead to changes in the below-ground biomass allocation and root traits (Case et al., 2020). Because grass species establish and develop more quickly than woody species, they become dominant

when fire frequency increases (Simpson et al., 2021), especially in more humid environments (Lehmann et al., 2011).

Fire also affects soil properties (McLauchlan et al., 2020; Santín & Doerr, 2016). After a fire, ash deposition increases soil pH, affecting nutrient availability (Carvalho et al., 2014; Silva & Batalha, 2008; Neary et al., 2005; Pivello et al., 2010; Santín & Doerr, 2016). However, there is no consensus on the effect of fire on soil nutrients (McLauchlan et al., 2020; Neary et al., 1999). Some studies report that high fire frequency decreases soil nitrogen (N) and carbon (C) content in shallow soil layers (Nardoto & Bustamante, 2003; Pellegrini et al., 2018). Other studies show no impact or increases of soil N and C (Coetsee et al., 2010; Silva & Batalha, 2008). Long periods without fire may lead to the accumulation of soil C and N (Pellegrini et al., 2014; Wardle et al., 2003) or decrease soil fertility (Carvalho et al., 2014). Fire does not seem to impact soil P and Ca; however, contrasting effects (increases or decreases) are reported for K in savannas (Silva & Batalha, 2008; Pellegrini et al., 2018; Pivello et al., 2010). When the time since last fire increases, soil pH tends to decrease, and Al increases (Silva & Batalha, 2008; Pivello et al., 2010). Such soil changes can constrain plant growth and roots may also respond to such modification in soil condition.

After a fire, savanna vegetation typically recovers rapidly (Pilon, Cava, et al., 2021; Zupo et al., 2021), taking an average of 2.5 years to fully recover the fuel load (Oliveira et al., 2021). Rapid regeneration is primarily determined by the ability of vegetation to resprout from fire-protected below-ground buds (Clarke et al., 2013; Ott et al., 2019; Pausas et al., 2018; Pilon, Cava, et al., 2021; Zupo et al., 2021). However, ensuring rapid regeneration and taking advantage of favourable post-fire environmental conditions to reach reproductive maturity also require that plants have root systems suitable to facilitate rapid resource acquisition (Forrestel et al., 2014; Kramer-Walter et al., 2016; Simpson et al., 2019, 2020).

The fine roots of graminoid species are often concentrated in the topsoil (De Castro & Kauffman, 1998; Linder et al., 2018; Oliveras et al., 2013) and might be directly affected by fire, whereas deeper roots remain unharmed (Neary et al., 1999). After a fire and on frequently burnt savannas, the biomass of fine roots typically increases near the soil surface (Hartnett et al., 2004; Oliveras et al., 2013; Simpson et al., 2019) as a strategy to increase nutrient acquisition and ensure rapid regrowth compared to unburnt sites. The morphology of fine roots may also favour post-fire regeneration by facilitating resource acquisition and plant regrowth. For example, fine roots with thin diameters, low tissue densities and high specific root length (SRL, i.e. ratio between

root length and biomass) have high capacities for the uptake of nutrients and water (Hodge, 2004; Reich et al., 1998; Zangaro et al., 2008) and are associated with high relative growth rates (Comas et al., 2002; Comas & Eissenstat, 2004; Kramer-Walter et al., 2016; Reich et al., 1998; Simpson et al., 2020). Although we know that resprouting grasses present leaf conservation strategies in fire-prone environments (i.e. lower leaf N; Simpson et al., 2021), below-ground strategies are poorly studied. Increasing fine root biomass or producing fine roots with high SRL and low diameter are expected to be two alternative strategies that facilitate soil exploration and ensure more rapid plant regrowth (Hertel et al., 2013; Li et al., 2019; Weemstra et al., 2020).

Changes in the root system should occur gradually in the post-fire period in open savannas, with shrubs eventually replacing grasses and causing associated changes in the below-ground compartment. Compared to shrubs and trees, grasses have a more fibrous root system: they are less deeply rooted and develop finer roots in the topsoil (February & Higgins, 2010; Reich et al., 2001). Such characteristics are frequently observed in sandy soils (Case et al., 2020). Grasses also have higher SRL and lower root diameter than woody species (Freschet et al., 2017). In addition, roots with thicker diameters and high tissue densities favour root persistence and resource conservation and storage. In some South African grasses, an absence of fire leads to a decrease in root branching and fewer fine roots and is correlated with an increase in arbuscular mycorrhizal fungi (AMF), an alternative strategy to increase nutrient uptake (Bergmann et al., 2020; Hartnett et al., 2004). In addition, changes in soil properties along a fire gradient affect root traits that depend on resource availability (Eissenstat et al., 2000; Freschet et al., 2017).

We investigated how above- and below-ground plant components responded to fire in the open savannas of the Cerrado (*campo sujo*) and whether they were associated with vegetation structure and soil properties to elucidate the below-ground effects of fire. We selected plots along a fire-history gradient ranging from 1 to 34 years since the last fire. Because we performed the study in natural systems, the number of past fire events (i.e. a proxy of fire frequency) varied between plots, ranging from 0 to 9 fires within the past 34 years. We examined the impact of fire history (i.e. time since last fire and number of fires) on above- and below-ground biomass, root depth distribution, functional parameters of absorptive roots

and soil properties. We examined the relationship of below-ground biomass and root parameters relative to vegetation structure and soil properties. The expected responses after a fire were rapid vegetation recovery and changes in vegetation structure. We hypothesised the following:

1. A decrease in below-ground biomass allocation due to a reduction in graminoid biomass and a gradual increase in shrub dominance, with increasing time since last fire and decreasing number of fires,
2. An increase in root depth and changes in root morphological parameters, such as higher root tissue density (RTD) as the time without fire increases and
3. Differences in root systems near the soil surface in response to the expected increase in soil nutrients after a fire, possibly due to a rise in absorptive root biomass in shallow soil layers or the production of roots with morphological traits that favour resource acquisition, such as high SRL and thin diameter.

2 | MATERIALS AND METHODS

The study was conducted in the southeastern edge of the Cerrado region in southeast Brazil (Figure S1). The climate in this region is humid subtropical, characterised by hot and humid summers (April–September) and dry winters (October–March; Escobar et al., 2018). The natural vegetation in the region is a mosaic of savanna patches with varying fire histories. The study was carried out in *campo sujo*: open savannas with a continuous species-rich herbaceous layer, composed primarily of grasses with scattered shrubs, dwarf palms and low tree cover (Figure S2). In that region, fires are of low-to-moderate intensity with intermediate frequency, and burnt areas are relatively small (Archibald et al., 2013).

We selected eight sampling areas (0.5–1.5 ha, Figure S1) of open savannas with varying times since the last fire (1–34 years; Table 1). The number of fires (a proxy of frequency) ranged from 0 to 9 fires between 1984 and 2018; in other words, frequencies ranging from no fires to a fire every 3–4 years (Conciani et al., 2021, Table 1). Fire intensity was considered low (<1,000 kW/m) when it occurred at the transition from the rainy to dry season in March (one study site) and

TABLE 1 Fire history of the eight sampling areas in open savannas of the Cerrado: time since last fire, number of fires (between 1984 and 2018) and date of last fire at the Ecological Station of Santa Barbara (ESSB) or Ecological Station of Itirapina (ESI; Figure S1)

Sampling area	Time since last fire (year)	Number of fires	Date of last fire	Site
1	1	4	August 2017	ESSB
2	7	4	July 2011	ESSB
3	7	2	July 2011	ESSB
4	9	3	August 2009	ESI
5	10	9	June 2008	ESSB
6	13	1	March 2005	ESI
7	17	2	August 2001	ESI
8	34	0	No fire	ESI

moderate (2,000–4,000 kW/m) when it occurred in the middle of the dry season (June–August; seven study sites; Table 1; Govender et al., 2006; Rissi et al., 2017). Because the sites were pristine open savannas subjected to natural fires, it was impossible to define a fire chronosequence at a single location.

The eight sampling areas were selected within two sites located 150 km apart (Figure S1). The first site (2,700 ha) is situated at the Ecological Station of Santa Barbara (22°46′–22°50′S, 49°16′–49°10′W, ESSB hereafter), with an average altitude of 640 m. The mean annual temperature is 21.1°C, and the mean annual precipitation is 1,440 mm (Hoffmann et al., 2019). The second site (2,300 ha) is located at the Ecological Station of Itirapina (22°11′–22°15′S, 47°51′–48°00′W, ESI hereafter), with an average altitude of 750 m. The mean annual temperature is 21.9°C, and the mean annual precipitation is 1,459 mm (Zanchetta et al., 2006). Both sites experienced irregular, low-intensity unplanned cattle grazing until 10 years before data were collected for this study.

2.1 | Above-ground biomass assessment

We randomly selected five circular plots (80 cm diameter, 0.5 m² area) in each sampling area. Sampling areas were open savannas dominated by grasses and shrubs, which dictated the method used for sampling. Samples were collected at the peak of vegetative growth (wet season, January–February 2018), and the total above-ground biomass (i.e. standing live and dead–still attached to the vegetation–biomass) was clipped. After separating dead and live biomass, the latter was sorted according to growth forms (i.e. graminoids, forbs, palms and shrubs), oven-dried at 80°C for 48 hr and weighed. Litter collected on the soil surface and dead biomass were also oven-dried at 80°C for 48 hr and then weighed.

2.2 | Root sampling

A soil core was taken in the middle of each plot immediately after above-ground biomass and litter were collected, every 10 cm up to 40-cm depth and then every 20 cm up to 100-cm depth with a 5-cm diameter auger. A total of 273 soil cores were collected and stored at –18°C before analysis (i.e. 39 plots × 7 depths; one plot was discarded due to the presence of a nearby termite nest). Harvested roots represented a mixture of roots from species occurring above and in the vicinity of the core. Soil cores were defrosted at the laboratory, and roots were sorted by type. Coarse roots (>2 mm diameter, including rhizomes) were manually separated from the soil and washed. Fine roots (≤2 mm diameter) attached to coarse roots were cut and pooled with the rest of the fine roots. The fine roots were then gently washed with water using 1.0-, 0.85- and 0.20-mm sieves (Pérez-Harguindeguy et al., 2013) and separated into absorptive and transport fine root samples following McCormack et al. (2015). Absorptive fine roots consisted of first-, second- and third-order

roots principally responsible for resource acquisition. In contrast, transport fine roots were higher-order roots characterised by secondary development and primarily responsible for the transport of water and nutrients.

Root morphological traits were measured using a representative sub-sample of fresh absorptive roots harvested at 0–10 cm depth. Absorptive roots were arranged on a transparent acrylic tray full of water to avoid root overlap and then scanned as greyscale images at a resolution of 1,200 dpi, using an EPSON Perfection V800 scanner (Bouma et al., 2000; Pérez-Harguindeguy et al., 2013). Each root sub-sample and the remaining absorptive, transport and coarse roots for each soil layer were oven-dried at 60°C for 72 hr and weighed to determine their dry mass. All digital images were analysed using WinRhizo software (version 2009, Regent Instruments Inc.) to determine average root diameter (mm), root length (cm) and root volume (cm³). Morphological and functional parameters of absorptive roots were calculated as follows: root tissue density (RTD, g/cm³) as the ratio between root dry mass and root volume, specific root length (SRL, m/g) as the ratio between root length and root dry mass and root length density (RLD, cm/cm³) as the root dry mass per unit of soil volume (g/m³) multiplied by the SRL. The proportion of absorptive roots was calculated as the ratio between the dry biomass of absorptive roots and total dry mass of fine roots (i.e. the sum of transport and absorptive root biomasses) for the entire soil profile (0–100 cm depth) and the 0–10 cm depth. The root:shoot ratio was calculated as the ratio between total dry root biomass (i.e. the sum of coarse, transport and absorptive roots) of the entire soil profile (0–100 cm depth) and the dry biomass of live shoots.

2.3 | Soil characterisation

We randomly collected three soil samples in each sampling area during the rainy season (January–February 2018) near the plots where above- and below-ground biomasses had been harvested. Each soil sample consisted of three pooled sub-samples taken at 10 cm depth, using a hand trowel. Samples were air-dried and sieved at 2 mm before analysis. Soil textures (i.e. silt, clay, or fine or coarse sand) of the fine fraction (<2 mm) were analysed at the soil laboratory of the Universidade de São Paulo, ESALQ. Other soil chemical analyses were performed at the soil laboratory of Viçosa Federal University, Viçosa, Minas Gerais (i.e. pH in water, N and organic carbon (C_{org}) in g/kg; P and K in mg/kg; Mg²⁺, Al³⁺ and Ca²⁺ in cmolc/kg). P, N and K were analysed with the Mehlich 1 extraction method; Ca²⁺, Mg²⁺ and Al³⁺ with 1 M KCl extraction; and C_{org} with the Walkley–Black method.

2.4 | Data analyses

Generalised additive mixed models (GAMMs) were performed to understand the relationships between the above-ground biomass

of each plant growth form (i.e. graminoids, forbs, palms and shrubs) and the time since last fire, the number of fires and site. The time since last fire and the number of fires were included as smooth terms in the GAMMS because we expected nonlinear responses, and sites were used as a parametric term. We included sampling areas as random factors in all models to compensate for spatial autocorrelation.

The effects of the time since last fire, number of fires and site on (i) above-ground biomass (litter, dead and live biomass); (ii) below-ground biomass, which includes the total root biomass (i.e. coarse and fine roots), absorptive and transport root biomass, and proportion of absorptive roots and the root:shoot ratio, and (iii) absorptive root variables in 0–10 cm of soil (absorptive root biomass, proportion of absorptive roots, RLD, SRL, RTD and average diameter) were tested first using generalised additive mixed models (GAMMs). Time since last fire and number of fires were included as smooth terms, site as a parametric term, and sampling area as a random factor. When the time since last fire or number of fires showed linear relationships with response variables, we performed linear mixed models using the time since last fire, the number of fires, and site as fixed factors and sampling areas as a random effect. We considered site as a fixed factor to control for the impact of site differences on our results (we only have two levels for that factor, and a higher number of random-effect levels is typically considered a random factor). Root:shoot ratio and total root biomass were log-transformed to fulfil normality and variance homogeneity requirements. We used log transformation of predictors (time since last fire) to analyse absorptive root biomass (0–10 cm) to account for the nonlinear relationship. Generalised linear mixed models were used to analyse the proportion of absorptive roots using beta family and logit link functions, considering the same fixed and random factors as previously explained.

The effects of soil depth, time since last fire, number of fires and site on absorptive root biomass were assessed using generalised linear mixed models, with Gamma family and link inverse. The initial model included depth, time since last fire, number of fires (between 1984 and 2018), sites, and their interactions as fixed factors, and sampling area as the random effect. Model simplification was then performed to identify the best model.

The effects of time since last fire, number of fires, and site on soil texture and chemical composition were assessed using linear mixed models with time since last fire, number of fires, and sites as fixed factors and sampling area as the random effect.

We computed correlations and their probabilities using the Pearson method between variables of below-ground biomass in the upper 100 cm soil and morphological parameters of shallow (0–10 cm) absorptive roots (RLD, SRL, RTD and average diameter) and (a) above-ground graminoid and shrub biomass and (b) soil texture and chemical composition. For soil texture and chemical composition, mean values based on the three soil samples collected from each sampling area were used in correlation.

Analyses were performed using the R version 4.0.3 (R Core Team, 2020), using the BETAREG (Cribari-Neto & Zeileis, 2010), the MGCV

(Wood, 2011), GLMMTMB (Brooks et al., 2017), PSYCH (Revelle, 2020) and the GGLOT2 (Wickham, 2016) packages.

3 | RESULTS

3.1 | Litter and above-ground biomass

The amount of litter, dead and live biomass did not exhibit consistent change with fire history; that is, time since last fire and number of fires (Figures 1a,b and 2a,b; Table 2; Table S1). However, litter and dead biomass were lower in the area sampled 1 year after fire relative to the other sampling areas (Figure 1a). In contrast, live biomass did not differ across the gradient of time since last fire (Figure 1b) and the number of fires (Figure 2b). On average, live biomass represented 21%–50% of the total above-ground biomass, consisting of 25%–78% graminoids and 12%–50% shrubs. Graminoid biomass decreased with time since last fire (Figure 1c) and increased with the number of fires (Figure 2c; Table 2; Table S2). On the contrary, although not significant, shrub biomass tended to increase with time since last fire (Figure 1d; Table 2; Table S2). Graminoid biomass differed between sites and was higher at the ESSB, whereas shrub biomass was higher at ESI (Table 2; Table S2).

3.2 | Below-ground biomass and absorptive root functional parameters

The total root biomass (i.e. coarse and fine roots) and the root:shoot ratio were unaffected by the time since last fire or the number of fires (Figures 1h and 2h; Table 2; Table S1). The absorptive root biomass in the upper 100 cm of soil decreased with time since last fire (Figure 1e; Table 2; Table S1). The proportion of absorptive roots increased with the number of fires, whereas the biomass of transport roots decreased (Figure 2f,g; Table 2; Table S1).

Overall, 39% of the absorptive roots were located in the upper 0–10 cm soil layer, and as expected, the absorptive root biomass decreased with soil depth (Figure 3; Table S3). Patterns of root depth distribution varied with time since last fire and site (Figure 3a; Table S3) but not according to the number of fires (Figure 3b). This result is primarily due to the higher absorptive root biomass within the upper soil layer (0–10 cm) in the most recently burnt areas (Figure 3a; Table 2; Table S4). The proportion of absorptive roots in the upper soil layer (0–10 cm) responded positively to an increase in the number of fires (Table 2; Table S4).

Considering the morphological parameters of absorptive roots in the upper soil (0–10 cm), SRL exhibited a consistent increase with time since last fire, whereas RLD, RTD and mean root diameter did not differ significantly (Figure 1i,j,k,l; Table 2; Table S4). RLD, SRL, RTD and mean root diameter were unaffected by the number of fires (Figure 2i,j,k,l; Table 2; Table S4). Absorptive root biomass, the

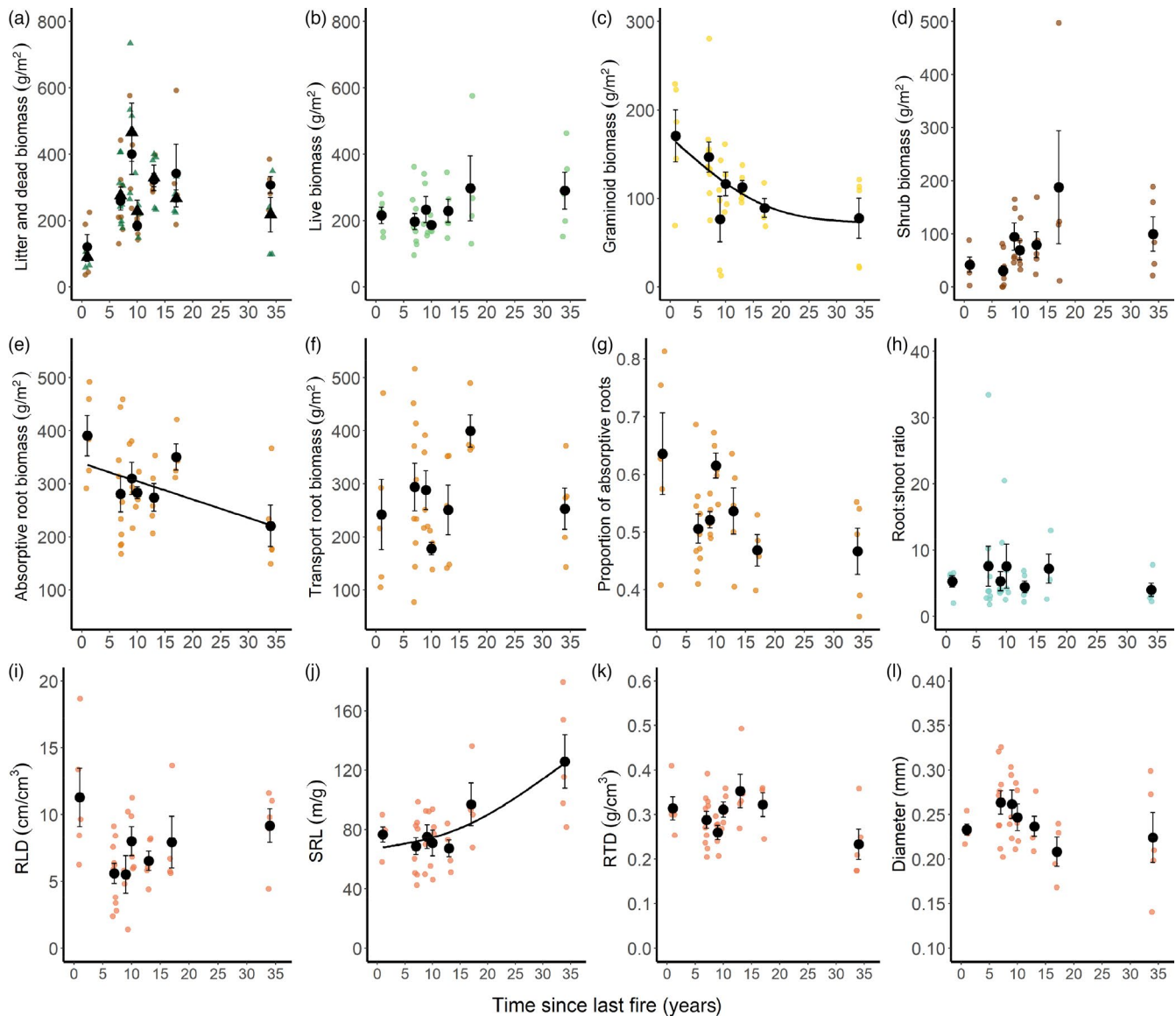


FIGURE 1 Above-ground (a–d) and below-ground (e–g) plant biomass in the upper 1 m of soil, root:shoot ratio (h), and morphological root parameters in the upper 0–10 cm soil (i–l) in relation to time since last fire in open savannas of the Cerrado. RLD, root length density; SRL, specific root length; RTD, root tissue density. In a, litter is represented as brown points and dead biomass as green triangles. Raw data are presented in colour, means and SE are in black, and linear and nonlinear relationships are drawn to illustrate significance (see Table 2; Tables S1 and S2 for more details)

proportion of absorptive roots, and morphological and functional parameters did not differ between sites (Table 2).

3.3 | Soil properties

Overall, soil samples were sandy (average sand content 920 g/kg), acidic (average pH 4.7) and nutrient deficient (Table S5). Clay content was slightly and positively associated with the time since last fire and the number of fires; P and Ca^{2+} contents increased with the time since last fire, whereas N and C increased slightly with the number of fires (Table S5). The two sites differed in soil chemical composition, with higher N, C_{org} , K, Mg^{2+} and Al^{3+} contents at ESSB.

3.4 | Relationship between below-ground parameters, vegetation structure and soil properties

The below-ground variables in the upper 100 cm of soil were not significantly correlated with vegetation structure; however, transport root biomass was positively correlated with shrub biomass (Table 3). Morphological parameters of absorptive roots in the upper 0–10 cm of soil were not significantly associated with shrub biomass. SRL showed a marginal negative correlation and RTD showed a positive correlation with graminoid biomass (Table 3).

The proportion of absorptive root in the upper 100 cm of soil depth was related to soil texture (i.e. positively with fine sand content

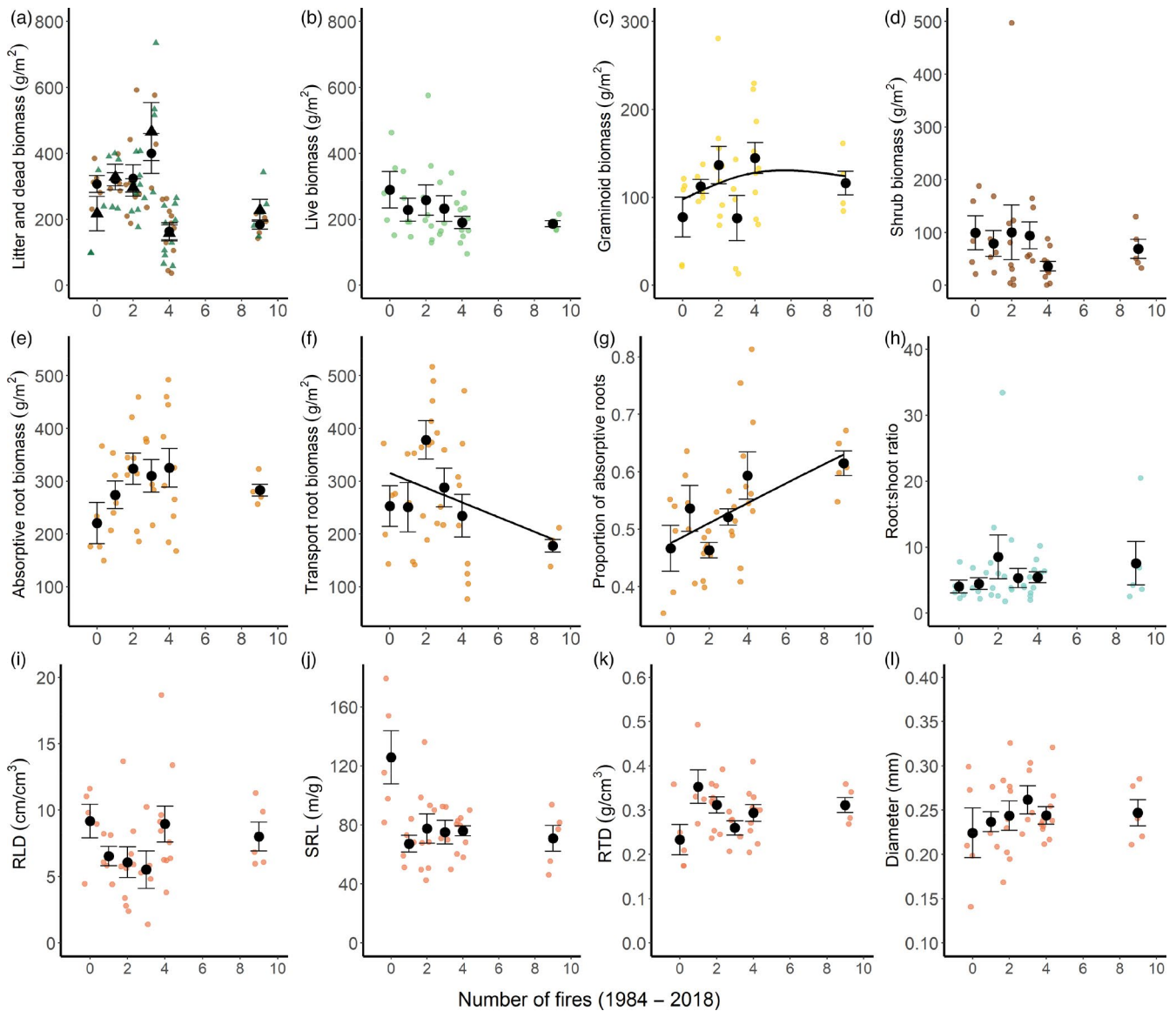


FIGURE 2 Above- (a–d) and below-ground (e–g) plant biomass in the upper 1 m of soil, root:shoot ratio (h), and morphological root parameters (in the upper 0–10 cm soil) (i–l) in relation to the number of fires (1984–2018) in open savannas of the Cerrado. RLD, root length density; SRL, specific root length; RTD, root tissue density. In a, litter is represented as brown points and dead biomass as green triangles. Raw data are presented in colour, means and SE are in black, and linear and nonlinear relationships are drawn to illustrate significance (see Table 2; Tables S1 and S2 for more details)

and negatively with coarse sand content; Table 3) in a manner opposite to that of transport root biomass (Table 3). The proportion of absorptive root in the upper 100 cm soil layer was positively correlated with soil N, C_{org} and Al^{3+} content but negatively correlated with soil P content. Again the opposite trend was observed with transport root biomass, which was positively correlated with soil P and pH (Table 3). SRL was the primary morphological trait associated with soil variables: it increased with P content and decreased with K, Mg^{2+} and Al^{3+} content (Table 3). RTD was negatively correlated with soil P, and the average diameter was positively associated with soil K content (Table 3). In contrast, RLD variations were not explained by differences in any soil variable.

4 | DISCUSSION

Fire history primarily affects absorptive root biomass but not fine root morphology in fire-prone grassy communities like open savannas. One year after a fire, the above-ground live biomass of plant communities had recovered to levels similar to sites with longer fire-free intervals, illustrating that above-ground recovery after a fire is rapid. This finding is consistent with other studies (Le Stradic et al., 2018; Oliveira et al., 2021) and primarily due to graminoids presenting higher biomass in the most recently burnt sites. Graminoid species in the open Cerrado have high annual productivity; they rapidly form a continuous ground layer after a fire and

Value	Intercept	Time since last fire	Number of fires	Site (ESSB)
Plant community composition				
Graminoids (g/m ²)	85.10***	1.00 (edf)(*)	1.58 (edf)(*)	63.64**
Shrubs (g/m ²)	117.97***	1.00 (edf)	1.00 (edf)	-81.75*
Forbs (g/m ²)	0.35	1.00 (edf)	1.00 (edf)	1.88*
Palms (g/m ²)	39.99*	1.00 (edf)	1.00 (edf)	-21.41
Above-ground biomass				
Litter biomass (g/m ²)	329.50***	1.49 (edf)	1.00 (edf)	-111.70
Dead biomass (g/m ²)	346.90***	1.31 (edf)	1.00 (edf)	-156.27
Live biomass (g/m ²)	238.42***	1.56	-4.61	-27.27
Below-ground biomass (upper 0–100 cm soil)				
Total root biomass (g/m ²)	7.00***	0.00	0.01	-0.15
Absorptive root biomass (g/m ²)	370.26***	-4.54*	-1.00	-28.25
Transport root biomass (g/m ²)	359.00***	-2.30	-16.21(*)	-15.65
Proportion of absorptive roots	0.08	-0.01	0.06(*)	-0.02
Root:shoot ratio	1.58***	-0.01	0.03	-0.04
Below-ground variables (upper 0–10 cm soil)				
Absorptive root biomass (0–10 cm; g/m ²)	134.67	-19.77 (log)*	3.31	-12.31
Proportion of absorptive roots	0.93	1.01	01.10*	0.96
RLD (cm/cm ³)	8.09***	1.00 (edf)	1.00 (edf)	1.21
SRL (m/g)	81.46***	1.54 (edf)**	1.68 (edf)	-1.34
RTD (g/cm ³)	0.31***	1.00 (edf)	1.63 (edf)	-0.03
Average diameter (mm)	0.24***	0.00	0.00	0.01

Abbreviations: RLD, root length density; RTD, root tissue density; SRL, specific root length.

Bold text indicates significance (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$) or marginal significance ((*), $p < 0.08$). (log) refers to log transformation.

are highly competitive for space and light (Pilon, Cava, et al., 2021; Pilon, Durigan, et al., 2021). Their caespitose architecture with buds and meristems protected between packed leaf sheaths and bunched tillers is particularly adapted to fire; it protects and ensures rapid recovery (Linder et al., 2018; Wigley et al., 2020). Because graminoids have no woody tissues, the energy cost of resprouting is devoted to producing photosynthetically active tissue, facilitating effective recovery after a fire (Linder et al., 2018; Simpson et al., 2021).

Graminoid biomass decreases gradually in the absence of fire and is often associated with increases in the establishment of woody species and shade (Pilon, Durigan, et al., 2021). In our study, woody species encroachment was not prominent because significant differences in woody vegetation between sites were not observed. Instead, there was only a tendency for shrub biomass to increase in the absence of fire. The time required for a site to experience woody species encroachment and achieve a closed canopy tends to be more extensive in sites with low fertility (Lehmann et al., 2011), which is the case for our study sites. In addition, high groundwater levels

seem to constrain woody species establishment in our study sites (cf. Leite et al., 2018). Our results suggest that coarser soil texture limits the proportion of absorptive roots and favours transport roots; therefore, soil texture also mediates shrub species establishment, consistent with previous studies (Case et al., 2020).

Dead biomass and litter accumulated rapidly after a fire. These components contribute to the fuel load, increasing the risk of wildfires in subsequent dry seasons and their intensity (Newberry et al., 2020). Dead biomass is derived mainly from dead leaves attached to grass tussocks (Fidelis et al., 2013). A substantial amount of accumulated litter is indicative of a low decomposition rate (Jacobson et al., 2011; Kozovits et al., 2007; Linder et al., 2018), likely due to poor-quality litter (Cornwell et al., 2008; Hättenschwiler et al., 2005). Resprouting grass species usually have leaf traits associated with conservative strategies, such as low leaf N content (Simpson et al., 2021) and a high resorption rate. These characteristics minimise nutrient loss (Abrahão et al., 2019; Kozovits et al., 2007; Nardoto et al., 2006; Paiva et al., 2015) but lead to poor-quality litter.

TABLE 2 Statistical models to analyse the plant community composition, above- and below-ground biomasses (upper 100 cm of soil), and below-ground variables (upper 0–10 cm of soil) relative to time since last fire, number of fires (1984–2018) and sites (ESSB corresponds to the alternative level). The model intercepts are also presented. Estimates of predictive variables are informed or effective degrees of freedom (edf) in the case of generalised additive mixed models. More details on the statistical analyses are available in the main text

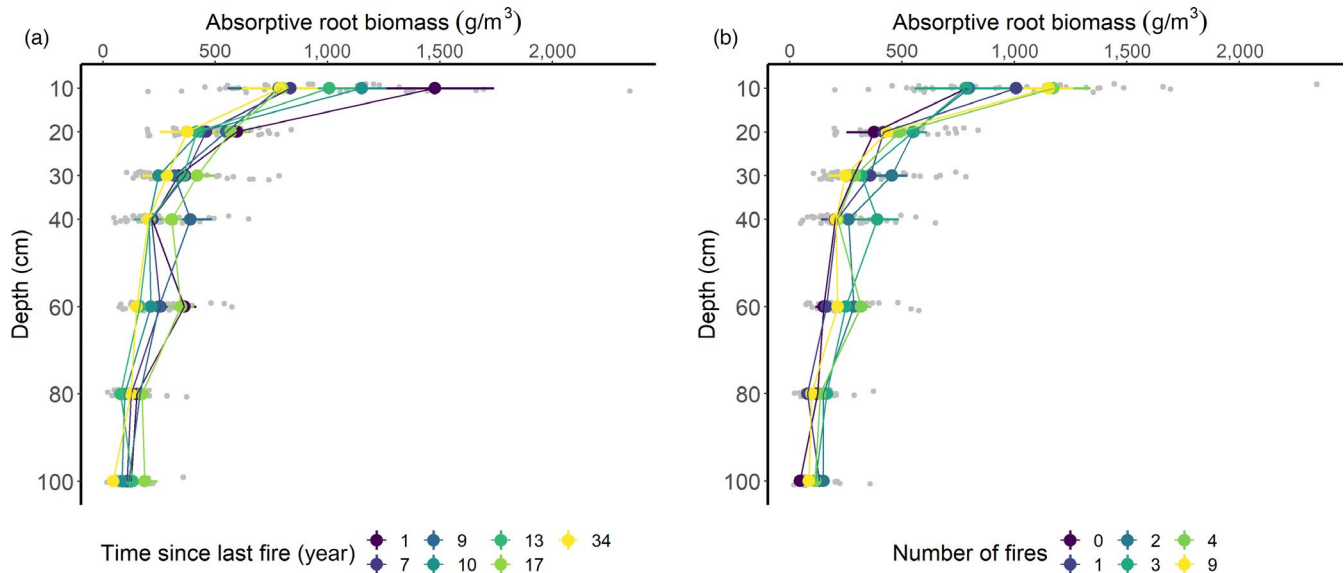


FIGURE 3 Below-ground distribution of absorptive root biomass in the upper 100 cm of soil in relation to time since last fire (a) and the number of fires (1984–2018) (b) in open savannas of the Cerrado. Raw data are presented in light grey, and means and SE for each depth are in colour (see Table S3 for statistical results)

In addition to the rapid recovery of above-ground live biomass, we observed an increase in absorptive root biomass in recently burnt sites. The positive effect of fire on absorptive root biomass was most frequently observed in the upper soil layer (0–10 cm), whereas the root biomass in deeper soil did not change. Temperature increases caused by fire occur only in the very top centimetres of soil (Miranda et al., 2002; Pivello et al., 2010), and shallow roots are more affected than deep roots (Neary et al., 1999). Shallow absorptive roots might be killed by fire but then recover rapidly to support shoot regrowth. Differences in root biomass in deep soil layers were not observed in our study, probably because such changes would occur only when fire frequency is high (Pellegrini, McLauchlan, et al., 2020) or when fire exclusion favours more woody vegetation (February & Higgins, 2010), which was not the case in our study sites. Transport roots were only slightly affected by fire history: first, because the biomass of woody species that have more transport roots than grasses did not differ significantly along the gradient; second, because transport roots are thicker and protected by dense tissues, they might be less vulnerable to an increase in soil temperature than absorptive fine roots.

After a fire, there is an increased demand for below-ground resources to promote shoot regrowth, and increasing the size of the absorptive root system allows that need to be met, as part of the regenerative strategy. Similarly, a higher proportion of absorptive roots in areas that experience frequent burning suggests that repeated fires promote higher production of absorptive roots than transport roots. Production of roots with high SRL could be an alternative strategy because SRL is typically associated with resource capture and a higher relative growth rate (Comas et al., 2002; Kramer-Walter et al., 2016; Simpson et al., 2020); however, this response was not observed in our study. Increasing the absorptive root biomass enhances the volume of soil explored and favours resource acquisition

after a fire (Hertel et al., 2013; Oliveras et al., 2013; Weemstra et al., 2017, 2020). Surprisingly, absorptive root biomass and SRL, two traits that reflect the extent of potential soil resource exploration and exploitation (Freschet et al., 2021) and are positively related to the plants' relative growth rate (Simpson et al., 2020), showed opposite patterns after a fire. An inconsistent response of SRL to environmental gradients is often reported (Freschet et al., 2015; Ryser, 2006; Weemstra et al., 2016, 2020). Our study demonstrated that SRL variation was primarily related to differences in soil nutrient content, as discussed below.

Soil P and Ca^{2+} concentrations increased with the time since last fire, whereas soil C_{org} and N slightly increased with the number of fires, contrary to our expectations and previous studies (Nardoto & Bustamante, 2003; Pellegrini et al., 2018; Pellegrini, McLauchlan, et al., 2020; Pivello et al., 2010; Reich et al., 2001). However, we need to acknowledge that many differences in soil properties may be associated with intrinsic differences between the study sites.

Differences in below-ground variables were also associated with differences in vegetation structure and soil properties. Transport root biomass was positively associated with shrub biomass, coarse soil texture, soil P and pH. In contrast, proportion of absorptive root was positively correlated with soil fertility (N and C_{org}) and fine soil texture but negatively correlated with soil P. Differences in species composition often correspond to nutrient availability (Ludwig et al., 2004; Oliveras & Malhi, 2016; Paganelli et al., 2020). For example, under fertile conditions, herbaceous biomass and competition for nutrients with tree seedlings may increase (van der Waal et al., 2009), whereas higher soil P and Ca^{2+} may favour woody species to the detriment of grass species in the Cerrado (Silva et al., 2013). An increase in transport root biomass was related to increases in soil P content and woody biomass, but further studies are needed to clarify the mechanism behind such changes and how

TABLE 3 Pearson correlations between vegetation or soil characteristics and below-ground plant biomass (upper 0–100 cm soil) or root morphological parameters (upper 0–10 cm soil) in open savannas of the Cerrado

	Below-ground biomass (0–100 cm)					Morphological parameters (0–10 cm)				
	Total root biomass	Root:shoot ratio	Absorptive root (g/m ²)	Transport root (g/m ²)	Absorptive root proportion	RLD (cm/cm ³)	SRL (m/g)	RTD (g/cm ³)	Average diameter (mm)	
Graminoid biomass (g/m ²)	-0.22	-0.09	0.17	-0.02	0.16	-0.16	-0.28(*)	0.43*	-0.02	
Shrub biomass (g/m ²)	0.15	-0.12	0.20	0.34*	-0.19	0.05	0.11	-0.18	-0.01	
Clay (g/kg)	0.12	0.12	-0.08	-0.21	0.17	0.16	0.10	-0.06	-0.02	
Silt (g/kg)	0.09	0.21	0.02	0.28	-0.24	-0.16	-0.17	0.24	0.05	
Coarse sand (g/kg)	0.12	0.06	0.04	0.50*	-0.54*	-0.23	0.23	-0.14	-0.05	
Fine sand (g/kg)	-0.15	-0.09	-0.02	-0.49*	0.53*	0.21	-0.25	0.14	0.06	
pH H ₂ O	-0.01	-0.09	0.26	0.34*	-0.20	0.16	0.30(*)	-0.12	-0.21	
N (g/kg)	0.09	0.18	-0.02	-0.26	0.30(*)	0.00	-0.30(*)	0.07	0.22	
Corg (g/kg)	0.09	0.19	0.02	-0.24	0.32*	0.03	-0.29(*)	0.08	0.19	
P (mg/dm ³)	0.09	0.06	-0.21	0.28+	-0.49*	-0.06	0.49*	-0.34*	-0.10	
K (mg/dm ³)	0.07	0.18	0.04	-0.20	0.29	-0.04	-0.34*	-0.02	0.29(*)	
Ca ²⁺ (cmolc/dm ³)	0.13	0.17	-0.08	0.07	-0.14	0.10	0.23	-0.12	-0.03	
Mg ²⁺ (cmolc/dm ³)	0.14	0.24	-0.01	-0.09	0.15	-0.13	-0.32*	0.07	0.24	
Al ³⁺ (cmolc/dm ³)	0.06	0.17	0.22	-0.18	0.42*	0.10	-0.40*	0.17	0.18	

Abbreviations: RLD, root length density; RTD, root tissue density; SRL, specific root length. Bold text indicates significance (* $p < 0.05$) or marginal significance (** $p < 0.08$).

soil fertility affects shrub and grass competition. Our results corroborated that soil texture impacts the root system in savanna ecosystems, with coarser soil texture favouring transport roots and a finer soil texture favouring absorptive roots (see also Case et al., 2020; Staver et al., 2017).

SRL barely varied with vegetation but was associated with differences in soil chemical composition. Although grasses may be expected to be more productive than other plants and have higher SRL (Freschet et al., 2017), SRL was marginally and negatively correlated with graminoid biomass in our study. However, soil chemical composition appears to be a major determinant of root morphological parameters in fire-prone grassy ecosystems, especially soil P content, but also K, Mg²⁺, N, C and Al³⁺. High SRL is often associated with nutrient-depleted soil and supports soil exploration and nutrient acquisition (Freschet & Roumet, 2017; Hill et al., 2006; Hodge, 2004; Kramer-Walter et al., 2016). Our results are consistent with previous reports that SRL increases with decreasing N, C_{org}, K and Al³⁺. We showed here that SRL is positively associated with increasing P availability. High SRL highlights the presence of species capable of elevated nutrient uptake and may denote a higher capacity to compete (Hodge, 2004; Mommer et al., 2011; Rajaniemi, 2007) or less need to uptake resources through mycorrhizal association when soil P increases (Bergmann et al., 2020). High RTD was positively correlated with graminoid biomass and negatively correlated with soil P content. High RTD reflects adaptation to infertile soil (Kramer-Walter et al., 2016) and is often associated with conservative strategies (Bergmann et al., 2020; Roumet et al., 2016), reduced rates of decomposition (Birouste et al., 2012; Prieto et al., 2016) and growth (Kramer-Walter et al., 2016). Conservative characteristics below-ground may ensure the persistence of savanna grass species (i.e. perennial resprouters in our case) in fire-prone ecosystems (see Simpson et al., 2021 for leaf traits).

Our finding that elevated absorptive root production is a regenerative strategy of plant species after savanna fires can affect competition between grasses and shrubs, especially for water (Case et al., 2020; February & Higgins, 2010). Indeed, the interception of water by dense rooting systems may limit other species (e.g. woody species) from accessing deeper water sources and may increase competition between grasses and woody species. Differences in vegetation structure and soil properties influence below-ground variables in grassy communities. Further studies are needed (e.g. in arid or semi-arid savannas and areas with more fertile soils) to disentangle the impacts of fire, vegetation structure, soil fertility and water availability on fine root biomass traits. In open savannas in wetter environments, root morphology remains relatively unaffected by fire history and responds primarily to differences in vegetation structure and soil properties. As fire changes vegetation and soil characteristics (Lehmann et al., 2014; Pellegrini et al., 2018), the associated effects on root traits have consequences to plant performance and ecosystem functioning, including nutrient cycling, carbon storage and plant regeneration (Freschet et al., 2021).

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CONFLICT OF INTEREST

Giselda Durigan is an Associate Editor of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper. The authors declare no further conflicts of interest.

AUTHORS' CONTRIBUTIONS

S.L.S. and A.F. conceived the ideas and designed the methodology with the help of G.D.; S.L.S. and L.C. collected the data; S.L.S. and C.R. analysed the data; S.L.S. wrote the first draft; S.L.S. and C.R. led the writing of the manuscript; all co-authors contributed to and approved the final version of this article.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13786>.

DATA AVAILABILITY STATEMENT

All the data that support the findings of this study are available on the Zenodo Repository (<https://doi.org/10.5281/zenodo.4322925>).

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