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RESEARCH ARTICLE

Variation in plant belowground resource allocation across heterogeneous landscapes: implications for post-fire resprouting

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PREMISE: Resource availability affects biomass allocation in ways that could influence plant responses to disturbance such as fire. This is important because fire also varies across landscapes in ways that are correlated to resource availability. We hypothesized that plants growing in landscape microsites with a shortage of nutrients and water allocate more biomass and resources to belowground structures (and thus promote traits that enhance post-fire resprouting ability) than plants in more mesic sites.

METHODS: We selected sites in three contrasting topographies (3 gullies, 3 midslopes, and 3 ridges) that supported different vegetation types and fire regimes, in Jalisco, Mexico. At each site, we measured soil nutrient and water content and light availability. Then we sampled biomass and root starch allocation in three post-fire resprouting shrubs that grow across a wide range of microenvironmental conditions.

RESULTS: The ridges showed the highest values of solar radiation and the lowest of soil N and water content. Overall, we found a significant tendency for higher root-to-shoot (R/S) ratios, greater fine root biomass, and higher root starch content, in individuals growing in ridges or midslopes compared to the values of the plants living in gullies.

CONCLUSIONS: Plants located in open canopy sites, characterized by a shortage of nutrients and water, tend to allocate more biomass belowground than plants in wet and fertile sites. Thus, plants in wet and fertile forests should be more vulnerable to increased disturbance such as wildfires.

KEY WORDS Ageratina choricephala; disturbance ecology; Euphorbia schlechtendalii; fine roots; optimal partitioning theory; resource availability; root allocation; root-to-shoot ratio; soil nitrogen; Solanum nigricans; starch.

Availability and distribution of water and nutrients in the soil are spatially variable and affect plant biomass allocation (Haynes and Gower, 1995; Müller et al., 2000; Knox and Clarke, 2005) and root morphology and architecture (Paz, 2003; Linkohr et al., 2002). Low content of soil organic matter and nutrients, particularly nitrogen, can limit growth (Ericsson, 1995). In such conditions, an increase in the root-to-shoot (R/S) ratio can improve nutrient uptake (Ericsson, 1995; Hermans et al., 2006). In contrast, high nutrient availability can inhibit elongation of the lateral roots (López-Bucio et al., 2003; Hermans et al., 2006) and the production of fine (<2 mm diameter) roots (Gower and Vitousek, 1989; Bae et al., 2015). This resource allocation tradeoff is summarized in the optimal partition theory (Bloom et al., 1985). This theory proposes that, when aboveground resources (e.g., light and CO_2) are limited, plants allocate a greater amount of biomass to their aerial parts, while under low availability of soil resources (e.g., water and nutrients), plants allocate biomass mainly to the roots to improve soil resource acquisition. Environmental variability across the landscape is likely to explain some of the intraspecific variability in plants, including variability in belowground traits and response to various disturbance agents. The relationship between resource allocation and environmental variability is particularly important in resprouting species, since these depend on belowground resource allocation for a successful response and survival after disturbance (Moreira et al., 2012).

Resprouting ability is a phylogenetically widespread and ancient trait (Pausas and Keeley, 2009; Keeley et al., 2012), which allows the persistence of plant populations under frequent aboveground disturbance (Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Clarke et al., 2013; Pausas et al., 2016). It is therefore considered a key functional trait in many ecosystems worldwide (Clarke et al., 2013; Pausas and Keeley, 2014; Pausas et al., 2016, 2018; Ottaviani et al., 2017). In fire-prone environments, the capacity and strength of post-fire resprouting depends mainly on carbohydrates stored belowground and on dormant buds and meristems that are protected from the heat of fire by soil, bark, or other specialized structures (Knox and Clarke, 2005; Moreira et al. 2012; Clarke et al., 2013; Paula et al., 2016; Pausas et al., 2018), although other mechanisms may also be important (e.g., Just et al. 2017).

Starch is considered the most important carbohydrate reserve among woody plants and has often been used as the main indicator of plant carbohydrate content (Kozlowski, 1992; Pallardy, 2010). In stressful environments with limited resources, plants often increase the proportion of photosynthates allocated to storage, such as nonstructural carbohydrates (starch accumulation; Wyka, 2000). This starch storage pattern can be advantageous for post-fire resprouting species, particularly those growing in soils with low fertility and water availability (Knox and Clarke, 2005). Carbon reserves in post-fire resprouting plants also imply greater biomass allocation to storage tissue, which is reflected in a higher R/S ratio, as well as a potentially stronger resprouting response (Bell, 2001; Bond and Midgley, 2001; Knox and Clarke, 2005). Despite the fact that resprouting is commonly considered a binary character (Pausas et al., 2004), the simple classification of resprouters vs. non-resprouters is of limited value outside of regions with a Mediterranean-type climate (Pausas et al., 2016). A much wider variability in resprouting is often observed (and understudied) in highly heterogeneous landscapes such as tropical and subtropical ecosystems (Vesk and Westoby, 2004). In these communities, intraspecific variability in biomass allocation to roots and root starch content in post-fire resprouting species could be explained by differences in resource availability across the landscape. If this relationship is true, the resprouting ability of the plants will also vary, either as a plastic or genetically fixed response, across the landscape. Because fire regimes and changes in these regimes also vary across the landscape, understanding how resource allocation partners with resprouting is important for the management and conservation of fire-prone ecosystems.

Climate change models predict an increase in the frequency of dry years, an extension of the fire seasons, and a concomitant change in the frequency, severity, and extent of fires in several ecosystems (Flannigan et al., 2009). These changes include a potential increase in fire incidence in areas of the landscape that historically are never or only rarely subject to fires (e.g., fire-protected gullies). Thus, understanding the variability of resource allocation patterns may provide an insight into the variability of post-fire resprouting success and survival across the landscape in a global changing world.

We hypothesized that plants growing in parts of the landscape with limited soil resources (nutrient and water availability) will allocate more resources to belowground structures and thus be better prepared for resprouting than those in sites with abundant soil resources. We therefore predicted a higher R/S ratio and more starch allocation to the roots in drier and more unfertile landscape microsites. We tested this prediction in the Sierra de Manantlán Biosphere Reserve (SMBR) in Mexico, a geomorphologically diverse area with abundant gullies, midslopes, and ridges intermingled across the landscape. Each of these topographic features have different vegetation types and fire regime, making the SMBR an ideal location in which to study the implications of landscape heterogeneity for the potential response of plants to disturbance.

MATERIALS AND METHODS

Study area

The study was conducted at Las Joyas Scientific Station (LJSS), located in one of the core areas of the SMBR in the state of Jalisco, western Mexico (19°34′14″–19°37′30″N, 104°14′49″–104°18′16″W). The climate is temperate sub-humid with a mean annual temperature of 15.72 ± 1.52°C, relative humidity of about 80.16 ± 14.50%, and a mean precipitation of 1758.78 ± 203.42 mm (mean ± SD) (Zuloaga-Aguilar, 2019). The rugged orography of LJSS maintains a high microenvironmental heterogeneity with

TABLE 1. Linear mixed-effects models fitted by maximum likelihood to test the relationship between edaphic and microenvironmental characteristics in the three topographic positions considered (3 sites per position, *n* = 9) at Las Joyas Scientific Station, Jalisco, Mexico. Means and standard deviations are shown. Values in bold are significant at $\alpha < 0.05$.

Variable	Gullies	Midslopes	Ridges	$F_{2,6}$	*P*
Soil nutrients					
Organic matter (%)	26.92 ± 6.55	14.02 ± 1.70	20.51 ± 4.24	4.65	0.06
Inorganic N (ppm)	64.33 ± 26.88a	15.67 ± 0.47c	24.00 ± 5.71b	5.37	**0.04**
K (ppm)	356.00 ± 24.34	485.33 ± 146.51	314.33 ± 39.88	2.01	0.21
Na (ppm)	237.33 ± 20.49	294.33 ± 85.20	263.33 ± 30.02	0.56	0.59
Ca (ppm)	5130.33 ± 2269.62	3238.00 ± 1823.55	1306.67 ± 150.24	2.58	0.15
Mg (ppm)	498.33 ± 68.05	467.33 ± 171.27	262.00 ± 10.03	2.90	0.13
Zn (ppm)	1.70 ± 0.70	1.40 ± 0.74	1.17 ± 0.49	0.32	0.73
Fe (ppm)	8.43 ± 1.10	10.17 ± 0.20	9.67 ± 0.04	3.79	0.08
Cu (ppm)	0.75 ± 0.11	0.81 ± 0.09	0.54 ± 0.11	3.50	0.09
Mn (ppm)	9.33 ± 5.30	11.87 ± 1.14	13.27 ± 3.22	0.59	0.58
Microenvironmental variables					
PAR ($\mu \cdot m^2 \cdot s^{-1}$)	36.15 ± 69.67b	362.55 ± 319.57a	437.62 ± 368.15a	32.23	**6.17^{-04}**
Soil water content ($m^3 \cdot m^3$)	0.18 ± 0.03a	0.15 ± 0.03b	0.07 ± 0.04c	14.10	**5.39^{-03}**

a variety of vegetation types, including montane cloud forest in the gullies, pine-broadleaf mixed forest on the midslopes, and pine forest on the ridges and upper slopes (Cuevas and Jardel, 2004). This environmental heterogeneity promotes a range of potential fire regimes in the area, with different frequency and intensity of fires (Jardel et al., 2006; Llamas-Casillas, 2013). Gullies rarely burn due to their high humidity and provide fire refuge for many species; however, when fire does occur, it is severe and most of the trees are killed (Asbjornsen et al., 2005). On the other hand, on the midslopes and ridges (oak and pine–oak forests sites), low severity surface fires (which do not affect the forest canopy) are frequent during the dry season (April–May), with a fire return interval of <35 years (Jardel et al., 2006). In SMBR, 64.3% of fires that took place between 1995 and 2003 were located in the oak and pine–oak forests. These communities cover 53.75% of the total surface of this protected natural area (Jardel et al., 2004).

Study sites and microenvironmental variables

We selected nine forests stands (sites) in three topographic positions: three gullies (i.e., small valleys), three midslopes, and three ridges. Distance between sites ranged between 1000 and 3800 m. To our knowledge, none of these sites had been affected by fire in the 10 years before sampling. At each site, we established three circular plots of 500 m^2 (ca. 25 m diameter) at least 50–100 m apart. In each 500 m^2 plot (n = 27), we performed the following tasks: (1) We estimated the amount of light reaching the understory, from 10 measurements of photosynthetically active radiation (PAR) measured at a height of about 1.6 m, using a linear quantum light sensor (model MQ-301, Apogee Instruments, Logan, UT, USA). (2) During the dry season (May), we measured soil water content at 5 cm soil depth in 10 random locations using an S-SMD-M005 sensor connected to a data logger (model H21-002, Onset Computer Corp., Bourne, MA, USA). These measurements were then averaged for each site. And (3), we collected a sample of the mineral soil (i.e., after removing the litter) of approximately 330 g from the uppermost 30 cm soil layer at the center of the plot. The soil samples for each of the three plots of a site were mixed into a composite sample of approximately 1 kg for each site (n = 9). Nutrient content (inorganic N, K, Na, Ca, Mg, Zn, Fe, Cu, Mn, and organic matter) were determined for each composite soil sample at the University of Guadalajara (Laboratory of Organic Fertilizers, University Center of Biological and Agricultural Sciences, Zapopan, Jalisco, Mexico).

Species selection and sampling

We selected the following three common post-fire resprouter shrub species (Cuevas and Jardel, 2004; Zuloaga-Aguilar et al., 2016): *Ageratina choricephala* (B.L.Rob.) R.M.King and H.Rob. (Asteraceae), *Solanum nigricans* M.Martens and Galeotti (Solanaceae), and *Euphorbia schlechtendalii* Boiss. (Euphorbiaceae).

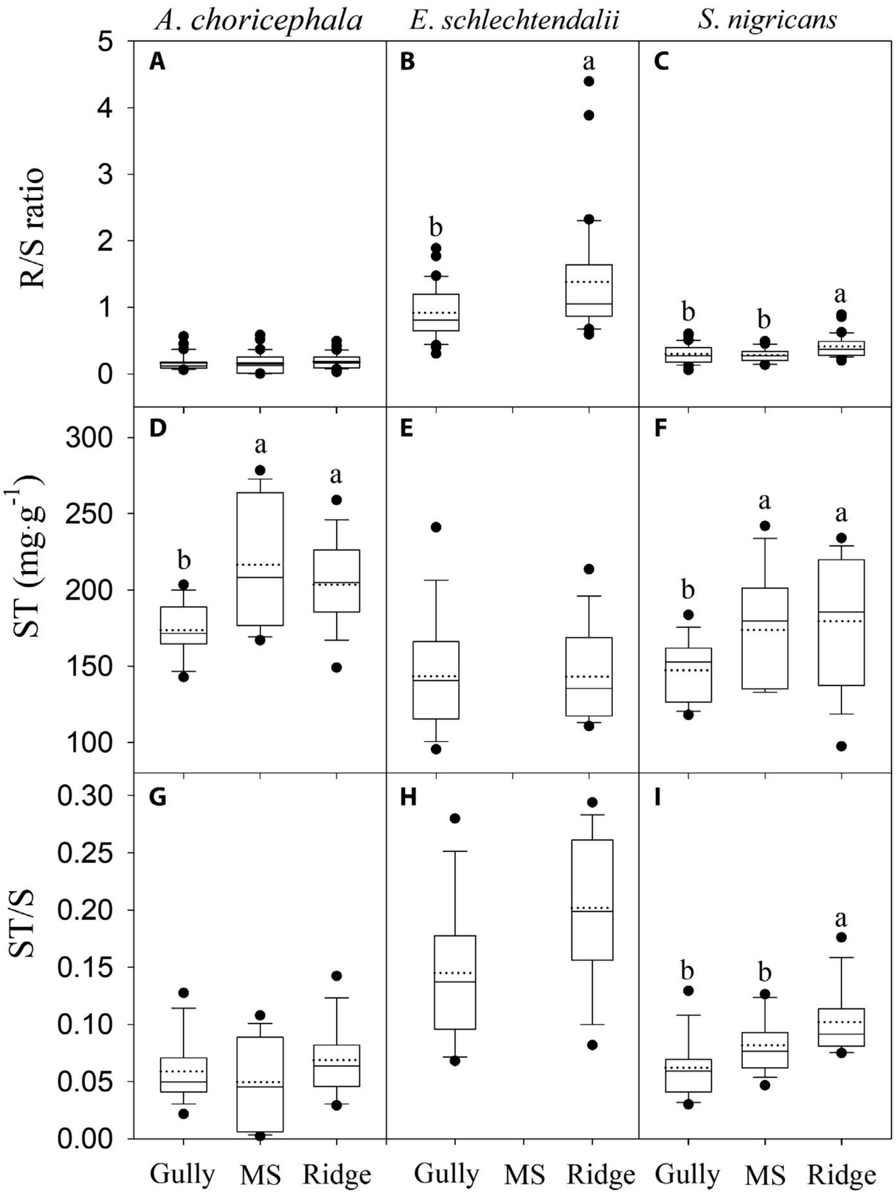

FIGURE 1. Variation in root-to-shoot ratio (R/S), root starch concentration (ST), and root starch/shoot biomass ratio (ST/S) of *Ageratina choricephala* (A, D, G), *Euphorbia schlechtendalii* (B, E, H), and *Solanum nigricans* (C, F, I) individuals growing in gullies, midslopes (MS), and ridges at Las Joyas Scientific Station, Jalisco, Mexico. Boxplots show the median (horizontal solid line), mean (horizontal dotted line), quartiles (boxes), 1.5-times the interquartile range (whiskers), and extreme values (dots). The letters over boxes indicate significant differences at $\alpha < 0.05$.

In each site, the aboveground part (stem, branches, and leaves) and the roots of 10 adult individuals of similar stem diameter (averages: *A. choricephala*, 0.58 ± 0.07 cm; *E. schlechtendalii*, 1.52 ± 0.08 cm; *S. nigricans*, 1.15 ± 0.14 cm) were collected by carefully digging to a soil depth of 50 cm at a 50-cm radius around the stem. Each root was then carefully immersed in water to remove the soil and extracted with a sieve (0.355 mm opening), taking care not to lose fine roots. Individuals of the first two species were collected in the gullies, midslopes, and ridges (9 sites), while *E. schlechtendalii* was only collected in gullies and ridges (6 sites), since this species was absent on the midslopes.

The collected plant material was placed in a drying oven (model Ed 140-UL, Binder, Tuttlingen, Germany) at 80°C for 8 days (Moreira et al., 2012). The dried roots of each individual were then separated into fine (<2 mm diameter) and coarse (>2 mm diameter) roots, which were weighed separately (see Appendix S1). The dry mass of plant material (above- and belowground) was determined with an analytical balance (XT 120A, Precisa Gravimetrics AG, Dietikon, Switzerland). To evaluate root starch content, samples of lateral roots 5 cm in length were collected at the point of branching from the main root from five individuals per species at each site. The collected samples were stored immediately in a portable freezer (So-Low U85-13, Environmental Equipment Co, Cincinnati, OH, USA) at 0°C for transport and subsequent drying using the method described above. Once dried, roots were crushed through a sieve (mesh size <1 mm). Starch was extracted with hydrochloric acid and sodium hydroxide and its concentration determined with the phenol-sulfuric reaction at an absorbance of 487 nm (DuBois et al., 1956). Root starch concentration was expressed as starch content per unit dry mass of root ($mg \cdot g^{-1}$; Appendix S2).

Resource allocation variables

To characterize the resource allocation of each plant, we considered the following four resprouting-related traits (response variables): root-to-shoot ratio (R/S), fine root-to-shoot ratio (FR/S), root starch concentration (ST), and root starch in relation to the shoot biomass (ST/S). The R/S was estimated as (Root dry mass – Root starch content)/Shoot dry mass. The FR/S was estimated in the same way, but considering the dry mass of fine roots only. The ST/S was estimated as the root starch content of each plant divided by its shoot dry mass.

Statistical analyses

(1) We first assessed the environmental differences between topographic positions (gullies, midslopes, and ridges) using linear mixed-effects models fitted by maximum likelihood. Site (9 replicates) was considered the random factor and each microenvironmental variable a fixed factor (see Table 1). (2) To assess the differences in resource allocation (response variables) among topographic positions, we again used linear mixed-effects models. This analysis was performed for all species together (with individuals within site and species as the random factor; overall test) and separately for each of the three species considered (including individuals within site as the random factor). Pairwise differences between the topographic positions were tested by contrasts (a priori "contrasts" function; Crawley, 2009). Finally, based on the result of the previous mixed model (1), we chose the significant microenvironmental variables among the topographic positions (PAR, soil N content, and soil water content: independent variables; see Table 1). (3) The relationship among each independent variable and each of the four response variables was assessed using one-way linear-mixed models. This analysis was also performed for all species together with individuals within site and species as the random factor (overall test) and separately for each of the three species (i.e., with individuals within site as the random factor). To standardize the data, we transformed all quantitative variables [log10 (data + 1)] before analysis. The assumptions of linearity, variance homoscedasticity, as well as the normal distribution of the model and residuals

TABLE 2. Linear mixed-effects models to test the relationship between the environmental variables (PAR, soil N, soil water contents) and the root/shoot (R/S), fine root/shoot (FR/S), root starch/shoot ratios (ST/S), and root starch concentration (ST) for *Ageratina choricephala*, *Euphorbia schlechtendalii*, and *Solanum nigricans* at Las Joyas Scientific Station, Jalisco, Mexico. The correlation of fixed effects for each linear-mixed model is reported (*r*). Values in bold are significant at $\alpha < 0.05$. The significant relationships are displayed in Figs. 2 and 3.

	PAR			Soil N concentration			Soil water content		
Species, Variable	F_{df}	P	r	F_{df}	P	r	F_{df}	P	r
A. choricephala									
R/S	$0.28_{1,80}$	0.59	-	$0.95_{1,7}$	0.36	-	$3.17_{1,80}$	0.07	-
FR/S	$0.23_{1,80}$	0.63	-	$1.36_{1,7}$	0.28	-	$0.02_{1,80}$	0.88	-
ST	$7.44_{1,35}$	**0.01**	0.42	$17.70_{1,7}$	**0.004**	–0.54	$0.25_{1,35}$	0.61	-
ST/S	$0.02_{1,35}$	0.87	-	$0.71_{1,7}$	0.42	-	$3.58_{1,35}$	0.06	-
E. schlechtendalii									
R/S	$12.88_{1,53}$	**7^{-04}**	0.95	$9.16_{1,4}$	**0.04**	–0.98	$4.70_{1,53}$	**0.03**	–0.87
FR/S	$0.03_{1,53}$	0.84	-	$6.94_{1,4}$	0.06	-	$1.04_{1,53}$	0.31	-
ST	$0.04_{1,23}$	0.84	-	$0.002_{1,4}$	0.97	-	$0.29_{1,23}$	0.59	-
ST/S	$8.55_{1,23}$	**0.008**	0.48	$8.16_{1,4}$	**0.04**	–0.47	$3.26_{1,23}$	0.08	-
S. nigricans									
R/S	$1.58_{1,80}$	0.21	-	$0.02_{1,7}$	0.87	-	$7.35_{1,80}$	**0.008**	–0.91
FR/S	$3.06_{1,80}$	0.08	-	$8.27_{1,7}$	**0.02**	–0.98	$2.36_{1,80}$	0.13	-
ST	$6.22_{1,35}$	**0.01**	0.97	$9.90_{1,7}$	**0.02**	–0.98	$4.12_{1,35}$	**0.04**	–0.91
ST/S	$9.87_{1,35}$	**0.003**	0.97	$4.27_{1,7}$	0.07	-	$9.97_{1,35}$	**0.003**	–0.91

were verified. Statistical analyses were performed using the programming language R ver. 3.5.1 (R Core Team, 2018); the models were fitted using the lme function in the nlme library (Pinheiro et al., 2018).

RESULTS

Microenvironmental variation

Soil water and inorganic N content and PAR differed significantly among topographic positions (Table 1). Soil water content values were up to 250% higher in gullies than in ridges, while soil inorganic N content was 3 and 4 times higher in the gullies than on the midslopes and ridges, respectively. No significant differences were found among topographic positions in terms of average organic matter content and for most of the soil nutrients analyzed. The gullies received much lower PAR values at the understory level (about one tenth) compared to the ridges and midslopes (Table 1).

Allocation patterns

The root to shoot ratios of *S. nigricans* ($F_{2,6}$ = 7.04, P = 0.02) and *E. schlechtendalii* ($F_{1,4}$ = 7.75, P = 0.04) were 1.4 and 1.2 times greater in individuals living on ridges compared to those on midslopes and in gullies, respectively (Fig. 1B, C). Individuals of *A. choricephala* ($F_{2,6}$ = 8.66, P = 0.02) and *S. nigricans* ($F_{2,6}$ = 5.49, P = 0.04) growing in gullies had the lowest ST values (173.66 ± 9.26 and 155.77 ± 9.34 mg·g^{-1}, respectively) compared to those on ridges (203.48 ± 6.95 and 198.62 ± 5.68 mg·g^{-1}, respectively) and midslopes (216.60 ± 10.71 and 185.54 ± 9.18 mg·g^{-1}, respectively) (Fig. 1D, F). We found significant differences among topographic positions in the ST/S ratio in *S. nigricans* ($F_{2,6}$ = 10.85, P = 0.01) but not in *A. choricephala* ($F_{2,6}$ = 0.44, P = 0.65) and *E. schlechtendalii* ($F_{1,4}$ = 6.08, P = 0.06). The values recorded for individuals of *S. nigricans* growing on the ridges were 1.3 and 1.8 times higher than in those of the midslopes and gullies (0.1 ± 0.007, 0.07 ± 0.003, and 0.05 ± 0.002 mg, respectively: Fig. 1I). The differences in the R/S ratio, ST, and ST/S ratio among topographic positions were confirmed when all three species were included in the same analysis (overall test: R/S, $F_{2,19}$ = 4.21, P = 0.03; ST, $F_{2,19}$ = 6.76, P = 0.006; ST/S, $F_{2,19}$ = 5.66, P = 0.01, respectively). Overall, there were no significant differences among topographic positions in allocation to FR/S ($F_{2,19}$ = 1.11, P = 0.34).

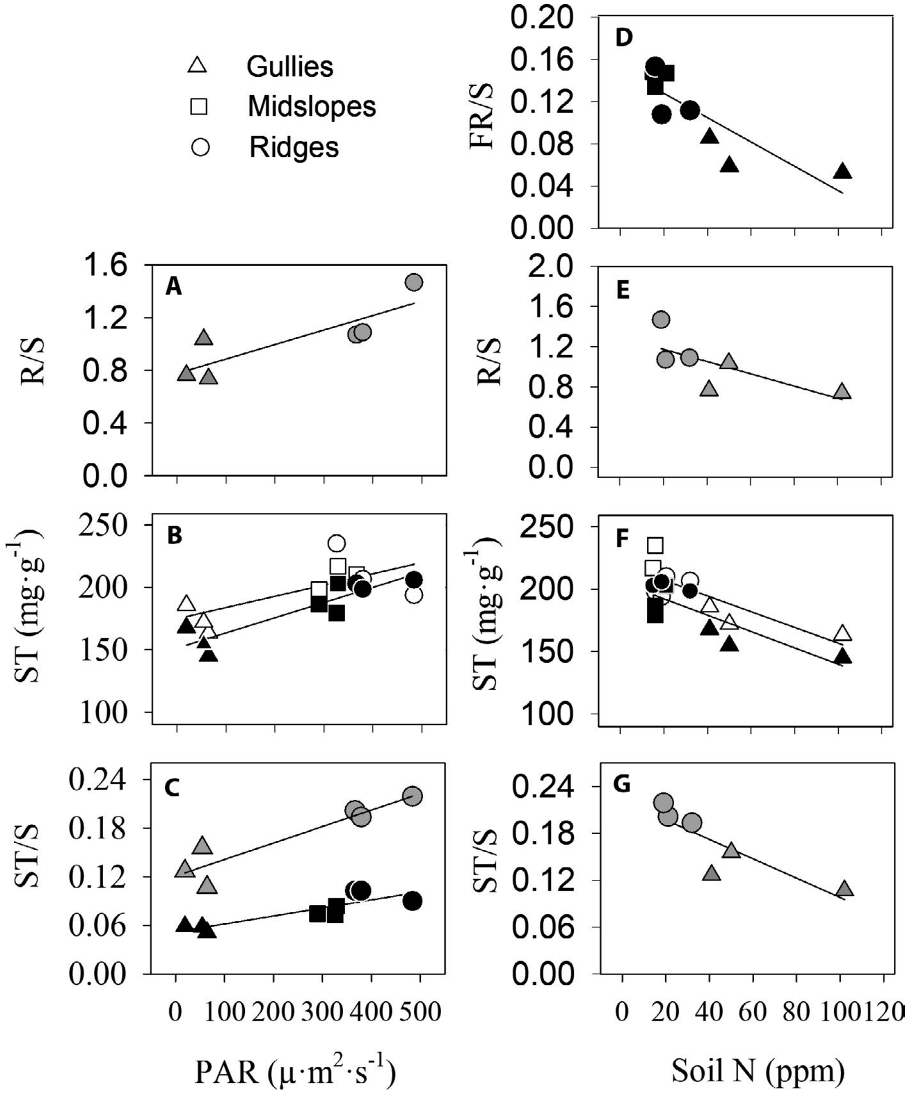

FIGURE 2. Relationships between environmental variables PAR and soil N and allocation variables root-to-shoot biomass ratio (R/S), fine roots-to-shoot biomass ratio (FR/S), root starch concentration (ST), and root starch/shoot biomass ratio (ST/S) for *Ageratina choricephala* (white symbols), *Euphorbia schlechtendalii* (gray symbols), and *Solanum nigricans* (black symbols). The data include sites in gullies (triangles) and on midslopes (squares) and ridges (circles) at Las Joyas Scientific Station in Jalisco, Mexico. All relationships are significant at $\alpha < 0.05$.

Relationship between microenvironmental variables and root allocation

Overall, we found a significant positive relationship between PAR and R/S ratio ($F_{1,215}$ = 7.51, P = 0.007, r = 0.31), ST ($F_{1,95}$ = 6.86, P = 0.01, r = 0.75), and ST/S ($F_{1,95}$ = 6.73, P = 0.01, r = 0.54). Negative relationships were found between soil inorganic N concentration and ST ($F_{1,20}$ = 13.9, P = 0.001, r = −0.87) and between soil water content and ST/S ($F_{1,95}$ = 11.18, P = 0.002, r = −0.34). The R/S ratio, ST, and ST/S increased more than 70% in individuals growing in sites with low soil N and water contents but with high PAR, compared with those growing in low PAR and high soil resources. No significant relationships were found among the remaining variables (P > 0.15).

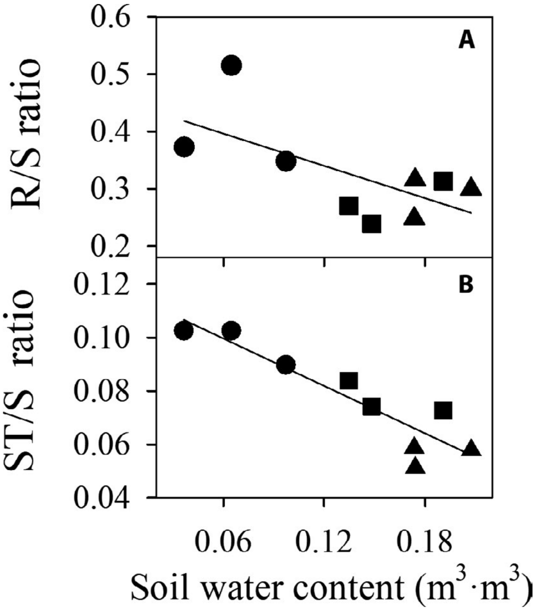

FIGURE 3. Relationships between soil water contents (*x*-axis) and (A) root-to-shoot ratio (R/S), and (B) root starch/shoot biomass ratio (ST/S) for *Solanum nigricans* in gullies (triangles), midslopes (squares), and ridges (circles) at Las Joyas Scientific Station in Jalisco, Mexico. All relationships are significant at $\alpha < 0.05$.

Despite the overall positive relationship with PAR and negative with soil resources, the significance for each biomass allocation variable varied among species (Table 2, Fig. 2). In relation to PAR, *S. nigricans* had a significant positive relationship for ST and for ST/S, while *E. schlechtendalii* had a significant relationship for R/S and for ST/S, as did *A. choricephala* for ST (Fig. 2A–C). For soil N, the relation was negative and significant in *S. nigricans* for FR/S and ST, *E. schlechtendalii* for ST/S, and *A. choricephala* for ST (Fig. 2D–G). A similar negative relationship was observed between soil water content and R/S (Fig. 3A), ST, and ST/S (Fig. 3B) for *S. nigricans* and between R/S for *E. schlechtendalii* (Table 2).

DISCUSSION

Our results suggest that intraspecific variability in root biomass allocation and starch concentration in resprouting species is influenced by variation in resource availability across the landscape. Specifically, these allocation variables suggest that, for a given species, plants growing in open, dry, and nutrient-poor sites (with high solar radiation and low soil N and water availability) tend to allocate more to belowground biomass than those in closed nutrient-rich forests; therefore, our hypothesis was confirmed. This pattern was especially clear in *S. nigricans*. Our result suggests that plants in open sites may be better prepared for resprouting after disturbance than those growing in shady, moist, nutrient-rich sites. These microenvironmental characteristics (open vegetation with dry and poor soils) are not randomly distributed but are specific to certain areas of the landscape, mainly on the upper midslopes and ridges, where fires are more likely (Jardel et al., 2006).

The observed intraspecific variability in biomass allocation patterns can be explained by optimal partitioning theory (Bloom et al, 1985), which in our case is related to soil N and water content and PAR. The results are consistent across species, but the specific biomass allocation variables that had a significant response to resources varied among species (Fig. 2). The R/S ratio was higher in *E. schlechtendalii* and *S. nigricans* grown in nutrient-poor and dry soils (with low soil N and water content and with high light incidence), conditions typical of fire-prone ridges and midslopes. The pattern was similar for the root starch concentration in *A. choricephala* and *S. nigricans* and in the ratio of root starch to shoot biomass in *S. nigricans*. Our results show that PAR is an important resource determining biomass allocation patterns; specifically, for *S. nigricans* and *E. schlechtendalii*, at least two of the resprouting-related traits recorded had a positive relationship with increased PAR availability. Another limiting resource for plants is the availability of nitrogen; N deficiency limits aboveground growth and development, leading to greater allocation of biomass to roots (Ericsson, 1995; López-Bucio et al., 2003; Paz, 2003). Moreover, N deficiency causes rerouting of the primary metabolism and accumulation of sugars in the leaves, which increases the transport of sugars to the root and therefore increases the R/S ratio and modifies the root morphology (Hermans et al., 2006). Growth and lateral branching of the roots and fine root production stimulated by soil nutrient and water deficiency improve the foraging capacity of the root system (Hermans et al., 2006; Paula and Pausas, 2011; Yavitt et al., 2011). We found more fine roots and root starch in *S. nigricans* in areas with greater light availability and lower availability of nitrogen. Thus, for this species, greater production of fine roots in nutrient-poor environments could improve acquisition of water and essential minerals (Yavitt et al., 2011), such as N, which is key to the photosynthetic process. Given that light is not a limiting resource under these conditions, the production and storage of root starch could be favored, which in turn would enhance resprouting (Bond and Midgley, 2001, 2003; Clarke et al., 2013; Pausas et al., 2016). However, more extensive research is necessary to fully describe the role of fine roots in starch storage. The significant differences found among topographic positions in the root starch concentration of *A. choricephala* and *S. nigricans* and in the ratio of root starch to shoot biomass of *S. nigricans* suggest that individuals in sites with lower soil N and water content, but higher light availability (midslopes and ridges) are able to store reserves through the process of accumulation (Chapin et al., 1990; Wyka, 2000); i.e., because growth is limited by the nutrient-poor, dry soil, photosynthetic carbon is diverted to the roots. This pattern is important because the ridges and some midslopes in our study area harbor pine and pine–broadleaf mixed forests—plant communities with a record of recurrent fires (Jardel, 1991; Jardel et al., 2006; Llamas-Casillas, 2013). Indeed, the initial ability to resprout (even intraspecifically) is related to the pre-disturbance condition of the plant; i.e., plants with greater reserves of starch have a higher probability of initiating resprouting (Moreira et al., 2012). Thus, greater belowground biomass allocation could be an advantage for individuals of these species growing in these sites, since it could enhance post-fire resprouting ability (Bell, 2001; Bond and Midgley, 2001; Knox and Clarke, 2005) and thus their long-term persistence. Thus, our results reveal a mechanism by which wet and fertile forest are likely more vulnerable to increased fire activity (low resource allocation to belowground in shady conditions). In fact, preliminary results of an experimental clipping (E. Magaña-Hernández et al., unpublished data) showed that individuals of *A. choricephala* and *S. nigricans* growing in dry and less-fertile sites resprout vigorously after recurrent clipping, in contrast to individuals living in resource-rich sites, where nearly all individuals died after the first clipping. The occurrence of fires in nonfire-prone communities (e.g., due to increased fire intensity under climate change) would thus be detrimental for some typical montane cloud forest species. Determining the extent that the observed pattern of resource allocation to belowground can be generalized to other ecosystems requires further work.

CONCLUSIONS

Intraspecific variability in patterns of belowground biomass allocation is influenced by resource availability across the landscape. Plants growing in well-illuminated, dry sites with poor soils (upper midslopes and ridges) had a higher R/S ratio, greater biomass allocation to fine roots, and/or higher root starch content, compared to those living in shady, N-rich, moist sites (gullies). These patterns are also related to the probability of fire because midslopes and ridges are more fire-prone than gullies; yet gullies do burn in very dry years. Given that the frequency of dry years is increasing as global warming escalates, our results suggest that plants in gullies are more vulnerable to increased fire activity. Determination of the extent to which intraspecific variability is a plastic response or whether they are genetically fixed by selection imposed by different conditions (microenvironment and fire regime) requires further research. Nevertheless, our results allow us to make a new prediction: individuals of the studied species living in gullies will have poorer resprouting ability (i.e., higher mortality) than those growing in more exposed sites (upper midslopes and ridges). Future studies should test the validity of this prediction.

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AUTHOR CONTRIBUTIONS

All coauthors participated in the design of the study. E.M. was responsible for data collection in field and laboratory analysis. The analyses and manuscript preparation were performed by E.M. and supervised closely by S.Z., J.G.P., and R.C.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Data on root and shoot biomass (g) and corresponding water contents ($m^3 \cdot m^3$), PAR ($\mu \cdot m^2 \cdot s^{-1}$) and N concentration (ppm) for each of the 10 plants of each species and site.

APPENDIX S2. Data on starch concentration and amount (mg/g) and corresponding root and shoot biomass (g), water content ($m^3 \cdot m^3$), PAR ($\mu \cdot m^2 \cdot s^{-1}$), and N concentration (ppm) for each of the five plants of each species and site.

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