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Research article

Root foraging strategies and niche segregation of three mediterranean shrub species

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Shrubs are usually adapted to stressful environments in which soil resources are limited, and thus, roots are fundamental for their biological success. However, root measures are challenging to collect, especially in field conditions and at the individual level. For this study, we collected data on the three-dimensional distribution of fine root biomass of twenty-three individuals belonging to three shrub species in a mediterranean shrubland in central Spain: gum rockrose *Cistus ladanifer*, rosemary *Salvia rosmarinus*, and hairy-fruited broom *Cytisus striatus*. Our goal was to determine the soil-foraging strategies adopted by the plants. We hypothesized that plants would show stabilizing niche differences explaining the high plant biodiversity characteristic of mediterranean shrublands and that they would follow the game theory model's prediction of exploitative segregation of roots behaving territorially but also over-proliferating roots close to their stem and engaging in a root tragedy of the commons. We found that two-thirds to three-fourths of the biomass was belowground, and the system's productivity was roughly 500–600 g C m^{-2} $year^{-1}$. Only rosemary plants competed with neighbors following the exploitative segregation predictions. Broom plants had the shallowest and most widespread root systems but significantly reduced their root range toward competing neighbors. Gum rockrose presented deep, narrow root systems avoiding extensive overlap with neighbors but did not appear to respond to competitive pressure levels. Shrubs appeared to stratify their roots at different soil depths, supporting the niche segregation hypothesis.

Keywords: exploitative segregation of plant roots, root stratification, root territoriality, root, shoot ratio, stabilizing niche differences, tragedy of the commons

Introduction

Drylands represent almost half of the Earth's land cover (Lal 2004) and are expected to expand drastically due to desertification processes triggered by anthropogenic climate change (Huang et al. 2020). Shrublands are the third most widespread dryland

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vegetation after grasslands and barren deserts (Maestre et al. 2021), and they are expected to expand because shrub encroachment on grasslands is a characteristic process accompanying desertification (Eldridge et al. 2011). Xeric shrublands, besides covering a significant proportion of planetary land surface, play fundamental ecological roles such as representing hotspots for biodiversity (Olson and Dinerstein 1998, Myers et al. 2000), regulating ecohydrological cycles (Scott et al. 2006, Wang et al. 2012), and acting as a significant global carbon sink (Fusco et al. 2019). Nonetheless, shrubland ecosystems are threatened by climate change. They are susceptible to abrupt collapse as precipitation declines (Martinez-Garcia et al. 2023), giving rise to unproductive bare soil that is very difficult to restore (Karssenberg et al. 2017, Berdugo et al. 2020, Rietkerk et al. 2021).

Studying root competition and foraging strategies in drylands is fundamental to understanding the dynamics and functioning of these ecosystems (Freschet et al. 2021). Soil carbon is recognized as one of the leading global carbon sinks offsetting human emissions (Scharlemann et al. 2014), and plant roots represent the most critical input to belowground carbon sinks (Pausch and Kuzyakov 2018). It has been estimated that roughly half of the belowground net primary production globally corresponds to shrubland and savanna ecosystems (Gherardi and Sala 2020). This is unsurprising, given the sizeable root-to-shoot biomass and root-to-crown lateral spread often reported in shrubland biomes (Mokany et al. 2006, Lefever et al. 2009, Tumber-Dávila et al. 2022). Woody plants may have territorial crowns aboveground (Strigul et al. 2008), and still, the root systems of plants overlap largely, leading to intense competition for soil nutrients and water (Jones et al. 2011, Madsen et al. 2021). Additionally, belowground competition may be much more intense in drylands, where water is potentially the main limiting factor for plant growth, than in other biomes (Ottaviani et al. 2020). In this context, it is paramount to understand belowground processes in dryland vegetation systems such as shrublands.

Because roots cannot be observed and they forage for several resources simultaneously (Farrior et al. 2013), root competition is still a poorly understood, complex phenomenon (Schenk 2005, Lux and Rost 2012, Ward et al. 2013). One historical perspective on the study of root competition, the spatial approach, has focused on the lateral spread of roots in soil space. Generally, spatial studies report root territoriality, i.e., plants growing fewer roots toward their neighbors (Brisson and Reynolds 1994, Schenk et al. 1999). An alternative perspective, the economic approach, focuses on studying the biomass allocation of plants into their roots to maximize resource gain (Gersani et al. 1998, de la Riva et al. 2021). Following the latter perspective, game theory predicts that competing plants engage in a root tragedy of the commons, over-allocating biomass into their root systems as a response to competition (Gersani et al. 2001, Cabal 2022). While both perspectives seem to suggest opposing foraging strategies – the spatial approach indicates competition leads to shorter root range and the economic approach indicates plants overproduce roots when they compete, a recent theory, the exploitative segregation of plant roots, proves that both trends may complement each other and coexist: Cabal et al. (2020)'s game theory model accounts for both biomass allocation and explicit space. It predicts that plants may engage in a tragedy of the commons but also segregate their root systems when they compete. Namely, the model predicts that plants over-proliferate roots near their stems but under-proliferate roots far away as competitive pressure increases. However, no field evidence exists of such a phenomenon, where conditions may differ significantly from controlled settings (Poorter et al. 2016, Cabal et al. 2021).

Mediterranean-climate shrublands are generally considered hotspots for plant diversity (Cowling et al. 1996, Myers et al. 2000), and the shrubland from our study site, in particular, presents a remarkable diversity of canopy species, making it possible to find a dozen species within a few square meters (pers. obs.). Niche segregation theory states that such a high diversity of organisms with similar environmental requirements, which may seem paradoxical (Hardin 1960), is possible when interspecific competition is less intense than intraspecific competition at high population densities (hereafter, stabilizing niche differences) (MacArthur 1958, Levine and HilleRisLambers 2009). Species stratifying their root systems to forage at different soil depths (hereafter, root stratification) would lead to individuals competing more intensely with conspecifics when growing in such conditions (Cody 1991, D'Antonio and Mahall 1991, Palacio et al. 2017). Root stratification predicts a trade-off between shallow-rooted species being more water-efficient and engaging in preemptive competition strategies by rapidly using precipitation water right after precipitation events (Craine and Dybzinski 2013) and deep-rooted species being more resistant to droughts because they rely on less ephemeral hydrological sources (Ward et al. 2013). Phenotypic plasticity might be another essential factor for plant niche segregation (Callaway et al. 2003, Turcotte and Levine 2016, Herben et al. 2022) for species responding to non-self roots in soil can avoid completion with heterospecific neighbors.

In this study, we analyzed a dataset with detailed information about the aboveground and belowground biomass of individual plants of rosemary *Salvia rosmarinus* (Lamiaceae), gum rockrose *Cistus ladanifer* (Cistaceae), and hairy-fruited broom *Cytisus striatus* (Fabaceae), in a mediterranean shrubland in central Spain. We obtained individual-level root biomass distribution in spatially located soil samples by injecting different color dyes into different individuals within each experimental plot. With this method, we combined aboveground measures of the species with a detailed three-dimensional map of the root biomass distribution of several focal individuals. We use this information to investigate the three shrub species' root distribution, biomass allocation, and autecology. Our main goal is to test the three following general hypotheses: 1) the studied mediterranean shrubland is a significant carbon sink despite showing scarce biomass aboveground because most carbon is stored in roots. 2) Shrubs present plastic responses to competition in soil following the

exploitative segregation of plant roots. 3) The three studied species present root stratification leading to stabilizing niche differences.

Material and methods

Field site description

This study was carried out in a mediterranean shrubland in 'Las Tejoneras' (40°06′42.69″N, 5°16′32.46″W, 329 m a.s.l.), Candeleda (Avila, Spain). Las Tejoneras is a small, isolated granitic mountain that rises about 50 m above the surrounding plains beside the reservoir of El Rosarito. Pedologically, it is dominated by leptosols and superficial bedrock. The area presents a meso-mediterranean, sub-humid ombroclimate (Rivas-Matínez and Armaiz 1984) with characteristic arid summers, annual precipitation of 797.9 mm, and a mean temperature of 16.17°C during the last decade (from January 2010 to December 2019 both included, data from the AEMET meteorological station in Candeleda, 40°08′21″N, 5°18′41″W, 350 m a.s.l.). The vegetation associated with this region is a biodiverse mediterranean closed-canopy shrubland with over a dozen shrub species, dominated by gum rockrose *C. ladanifer*, mastic thyme *Thymus mastichina*, Spanish heather *Erica australis*, green heather *Erica scoparia*, rosemary *S. rosmarinus*, flax-leaved daphne *Daphne gnidium*, topped lavender *Lavandula stoechas* and hairy-fruited broom *C. striatus*. Shrubland canopy is generally between 1.5 and 2 m tall, but some individuals are up to 5 m tall. There are also scattered sclerophyllous holm oak trees throughout the area *Quercus ilex*, some stands of cluster pines *Pinus pinaster* at the base of the reservoir-oriented slope of the mountain, and some small stands of riparian forest species (*Salix* spp., *Populus* spp.) growing in small depressions and valleys.

Data collection

For this research, we selected three species among all the shrub species present in our study site to obtain enough replications of the measures from individuals of various sizes, from young saplings to the largest plants we could find, for each species in the area. Selected species for this study were gum rockrose *C. ladanifer*, rosemary *S. rosmarinus* and hairy-fruited broom *C. striatus*. Species were selected first because they were the most common in the area and second because they represent three different shrub families important in the Mediterranean Basin shrublands: Cistaceae, Lamiaceae and Fabaceae, respectively. Selected plants were seven rosemary, eleven rockroses, and five brooms of different sizes. We collected data reflecting each individual's aboveground size (height, dry weight of leaves and wood, crown surface area) and allometric predictors (stem diameter at the ground level, hardwood, and sapwood areas at the base of the stem).

We sampled twenty-three focal plants in six 2 × 2 meter plots selected in the shrubland. Up to five focal plants were selected in each plot, and their roots were first marked with five different dye colors (yellow, red, green, purple and blue) by injection from aboveground. Dyes (fresh cut flower colorant) were injected by cutting a branch of the individual plant, fitting a flexible, transparent PVC tube to the cut stem, introducing the dye inside the fitted tube, and exerting 1.5 bar pressure to the dye over 30 h (10 h per day, three days in a row, the dye was left in the tube overnight, but no pressure was applied). Dyes flowed through the xylematic vessels, staining the remaining leaves, stems, and roots of each individual internally. Soil samples were extracted using a rotary diamond drill core that cut through the abundant granitic rocks. We followed a regular sampling pattern within each plot. A total number of 81 soil cores were extracted and divided into vertical strata (usually three levels, 0–10, 10–30 and 30–70 cm depth, but this was variable, and the actual median depth of each sample was recorded), adding up to 216 soil samples three-dimensionally located in soil relative to the position of each focal plants in each plot. Cores had a significant size, roughly 11 cm in diameter and up to 80 cm in depth. Hence, we consider that they represented the root systems of surrounding plants well (Taylor et al. 2013). We measured the volume of stone and gravel within each sample, allowing us to determine the effective rooting volume of soil in each sample (subtracting the volume of stone and gravel from the total core volume). Roots from each sample could be linked to the different focal individuals from each plot based on the color observable inside the root fragment, as each focal individual's roots were stained in a different color (Fig. 1). A total of 2840 root fragments were identified, and their diameter and dry weight were recorded. Non-stained fresh roots were identified as roots from other competing shrubs in the plot surroundings. Root density (bulk or differentiating each focal individual) was calculated as the dry weight of roots divided by the effective rooting volume in each sample.

Preliminary treatment of the data yielded a dataset with each plant assigned to the root density per diameter class in each soil sample, the Euclidian distance between the plant and the centroid of the sample, and combining the features measured at each sample and the plant level (Supporting information). A thorough description of the data collection methods used in these plots and a preliminary data treatment leading to the data as presented in the Supporting information are published in Cabal et al. (2022) (for the present work, we only used the data obtained from shrubs identified using dye injection from the referred publication).

In a complementary dataset, we gathered information about the biomass allocation of two studied species, rosemary and rockrose plants, to reproduction and leaf and twig turnover. Twelve plants of each species representing a wide range of sizes were measured at our study site. Each of the plants was fenced to prevent disturbances by small predators, and a known surface area of litter collection trays was installed under the canopies. Plants were tracked for an entire year, from the first day of September 2018 until the last day of August 2019. We collected the tray content every two months and kept it dry in paper bags to minimize the potential biomass lost due

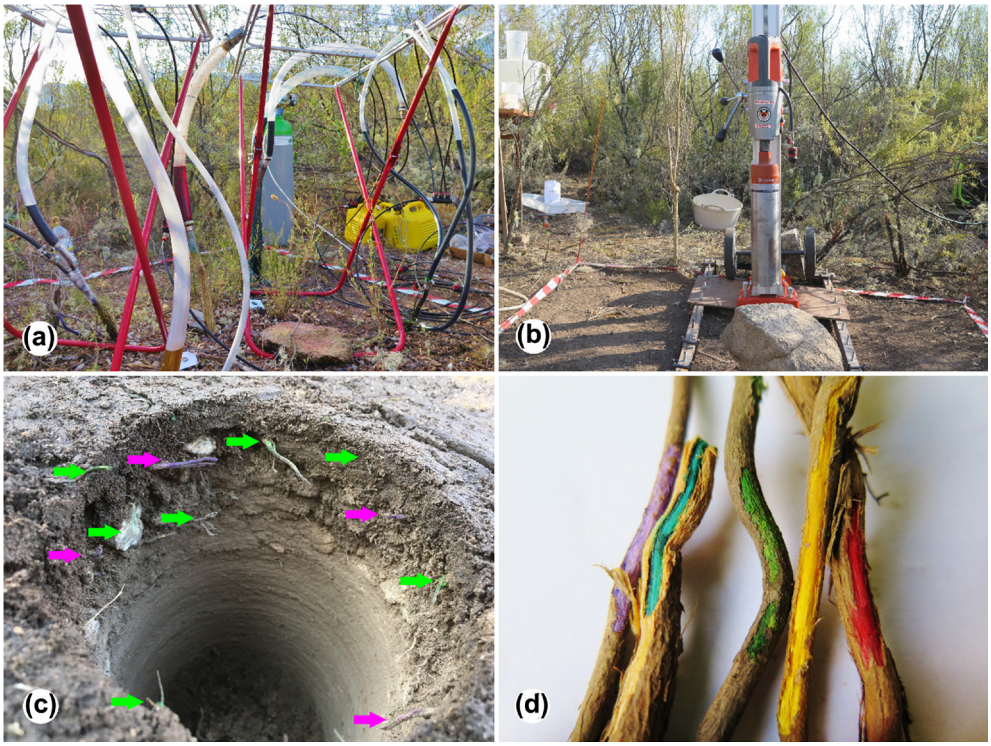


Figure 1. Photographs of the root sampling method. (a) Root injection setup with nitrogen tank for exerting pressure on PVC tubes with dyes fitted to the branches of the different individuals, with a different color for each. (b) Diamond core drill used to extract samples, able to cut through the granitic rocks in the soil. (c) Example of the hole left after extracting a 12 cm diameter sample, with superficial cut roots stained in green and purple, belonging to two different focal individuals, marked with arrows of the same colors. (d) Clean sampled roots of different individuals from different species, showing the color beneath the scratched root bark. Dye inside the root allowed the identification of root fragments at the individual level from the mixed samples.

to decomposition. All the material collected over the year was oven-dried, and litter was classified into photosynthetic material (leaves), non-photosynthetic materials (twigs and branch parts), and reproductive material (flower parts, fruit parts and seeds). Every litter fraction for each individual was weighted. For each plant, the crown area and the basal stem diameter in two directions were also measured at the start and the end of the observation period, and mean values were calculated.

Data analysis – spatially-explicit root distribution models

We fitted individual root density distribution (IRDD) models for fine roots for each species. IRDD models fundamentally predict for each soil coordinate the fine root density (root biomass per soil volume) of a plant as a function of the distance from the plant stem and the local presence of non-self roots, controlling for the plant size and the depth in the soil.

To predict the IRDD of fine roots (diameter < 2 mm), we assumed that the cost of building roots increases quadratically with the distance to the plant stem based on the exploitative segregation of plant roots (ESPR) model (Cabal et al. 2020), and hence that the root density decrease should be inversely proportional. We also assumed that the non-self root density distribution would have a multiplying effect as a variable measuring local belowground competition intensity. This effect was incorporated directly and through an interaction with the distance to the stem. This allowed us to fit the model to a case in which there is root over-allocation as a response to more intense competition close to the stem (positive direct effect) but a shift to local under-proliferation far away (negative interaction effect), as predicted by the ESPR. Because the soil resource concentration decays in the vertical soil profile, we incorporated a multiplier coefficient of soil depth. We assumed that the plant root density would vary with plant size following a power law, the functional relationship most commonly used for biological allometries (West et al. 1997). Finally, the intact model predicts that roots will tend to zero at an infinite distance, but the lower root density found on a soil sample was in the range of 0.05 mg cm^{-3}, therefore we assumed that the root density for an individual is null after it reaches the threshold of 0.05 in the model. To fit such a model for each species, using the plant's identity as a random effect, we used the *glmer* ('lme4' ver. 1.1-27) (Bates et al. 2015) function with Gamma distribution and the natural logarithmic link:

$$(\mathrm{RD}+0.05)\sim 1+\ln(E+\partial)\times \mathrm{NSR} + D+\ln(\mathrm{AW})+(1\,|\,\mathrm{plant})$$

where RD stands for root density (mg cm^{-3}) of fine roots (diameter < 2 mm), E is the Euclidian distance from the sample centroid to the plant insertion point (m), NSR stands for the non-self root density (mg cm^{-3}), D stands for the depth of the sample centroid (m), AW is the aboveground dry biomass (kg) of the plant, and plant represents the plant identity used as a random intercept factor. Because there are other costs to building roots than the transportation costs related to distance, the root density at the intercept (distance = 0) is not infinite (nor is the RD extremely large at a very small E). Therefore, we summed ∂ up the distance before transforming. In each case, the value ∂ was adjusted so that the power of the relation RD-distance was −2, following our mechanistic expectations from the ESPR model. We fitted three IRDD models, one for each plant species, to obtain IRDD predictions of plants of each species, i.e. predictions of RD across three-dimensional space. We thereby obtained an RD equations of the form:

$$\mathrm{RD} = \left(e^{\alpha+\beta\times\mathrm{NSR}+\delta D} \times \left(E+\partial\right)^{-2+\gamma\times\mathrm{NSR}} \times \mathrm{AW}^{\omega}\right) - 0.05$$

where α is the fitted intercept, and the coefficients to the explanatory variables are β for NSF, δ for the depth, ∂ being adjusted to obtain $\varepsilon \approx -2$, and γ for the interaction between the distance and NSR. However, when any of the coefficients were not significantly different from zero (including ε) at a confidence level of 95%, the corresponding explicative variables were removed in a step-by-step method, and a new model was fitted.

To predict the IRDD of coarse roots (IRDDc), we assumed that coarse roots transport the resources uptaken by fine roots from each soil patch to the insertion point of the plant stem. We fitted coarse RDc using the 'glmer' (lme4 ver. 1.1-27) (Bates et al. 2015) to the predicted fine roots RD for each observation, using a Gamma distribution and the identity link, and forcing the intercept to zero. In this model, we accounted for the plant identity for both predicting the RD and as a random intercept factor:

$$\mathrm{RD}_c \sim 1 + \mathrm{IRDD}$$

Data analysis – estimating productivity and carbon storage

We produced a plant-level database, including the plant-level information directly obtained from the field as described in previous sections and root information derived from the IRDD models. To produce plant-level root information, we used the fitted models to infer the full IRDD of each shrub in continuous space. We used the fitted model to make predictions of total root biomass for each diameter class across three-dimensional space. For each shrub's IRDD, we used as model intercept the plant-specific intercept, given that plant identity was used as a random intercept factor; the non-self root density was the mean value per plot, accounting for different competition levels in the different plots; model predictions were yielded for all depths at which root density was non-zero; Euclidian distance was calculated at each point of soil, based in the depth and an x-coordinate representing horizontal distance from the plant; to obtain actual root weights, we multiplied across space the predicted root density by mean rooting volume (1 – stone proportion) in each plot. Three-dimensional IRDD was obtained by rotation of the two-dimensional predictions, and total fine root biomass was obtained by integrating numerically the fine root density weighted by rooting volume across the three-dimensional space. Each shrub's total coarse root biomass was obtained similarly, fitting cIRDD models in the two-dimensional space based on fine root IRDD predictions, weighting by rooting volume, rotating the prediction to obtain three-dimensional predictions, and numerically integrating those predictions. Root ranges were also estimated based on the IRDD model. Using all plant-level data, we calculated the total belowground dry weight of plants, allometric and functional ratios, and other plant-level variables, as shown in the Supporting information.

Using the plant-level data, we ran plant- and ecosystem-level analyses. First, we tested for plant allometries, assuming they followed power laws by fitting a linear equation to log–log transformed data (Niklas 2004). For each case, we calculated Pearson's correlation between log-transformed variables and the t-distribution significance tests for Pearson's correlation (Hollander et al. 2003). We fitted allometries for gum rockrose and rosemary to establish ecosystem-level dynamics. We established allometric relations using basal diameter (stem diameter at the ground level) and plant biovolume as predictors and fitted leaf turnover, branch turnover, and reproduction allocation. Second, we established direct relations between age and the four standing biomass fractions, leaf, branch, coarse roots, and fine roots, all measures of dry biomass per unit surface area of the shrub crown. We estimated the aboveground and belowground net primary production (ANPP and BNPP, respectively) of plants of the two species for which we had collected reproduction and aboveground tissue turnover data based on the allometric curves. The labile plant fractions were measures of litter collected by year but were not linked to plant age because we did not have direct estimates of the age of the plants. Therefore, in the cases where significant allometry (alpha = 0.1) was identified, the age was linked to each plant observation through stem diameter. Belowground labile fractions, i.e. fine and coarse root turnover, were not directly measured in the field. To estimate BNPP, we assumed that fine root turnover was 0.5 $year^{-1}$ (Gill and Jackson 2000) and that structural tissue turnover belowground should be equal to aboveground to maintain a functional hydraulic architecture (Tyree and Ewers 1991), and calculated turnovers from standing biomass fractions.

The standing biomass plant fractions were biomass measures by crown area unit of the measured plant but were directly linked to the plant age. Therefore, the growth of such standing biomass per year could be obtained from the

Table 1. RD_i mixed model coefficients for rosemary plants. RD = root density (mg cm^{-3}), E = Euclidian distance from the sample centroid to the plant insertion point (m), NSR = non-self root density (mg cm^3), D = depth of the sample centroid (m), AW = aboveground dry biomass (kg) of the plant, ∂ = parameter summed to E to impede the intercept of E to grow to infinity and adjusted so that $\varepsilon = -2$, ε = power law for the decreasing costs of building roots with plant's proximity. Significance codes: 0 '***' 10^{-3} '**' 10^{-2} '*' 0.05 '·' 0.1 ' ' 1.

	Estimate	SE	t value	p-value
α (Intercept)	0.56731	0.30156	1.883	5.99 10^{-2}
ε (log (E + ∂))	−2	0.25661	−7.795	6.43 10^{-15}***
∂ (for ε = −2)	0.84970			
β (NSR)	0.13035	0.03711	3.513	4.43 10^{-4}***
δ (D)	−1.61621	0.31902	−5.066	4.06 10^{-7}***
ω (AW)	0.40772	0.13698	2.977	2.92 10^{-3}**
γ (log (E + ∂):NSR)	−0.16927	0.04355	−3.887	1.01 10^{-4}***

derivative of the cumulative biomass measured across the plant ages for each species. In cases where a significant allometry (alpha = 0.1) was identified, such a derivative was calculated and used as a growth predictor. When the biomass of a given fraction of standing plant tissues did not change significantly through plant age per crown area unit according to allometric calculations, we considered its value was constant across shrub ages and, therefore, its growth equal to zero.

To calculate carbon (C) storage, biomass measurements were converted to units of C using the IPCC default conversion ratio of 0.47 (McGroddy et al. 2004, Aalde et al. 2006). All the values of labile and standing C = 0.47 × biomass per surface area and year summed gave the plants' net primary production (NPP), which could be fractioned for each species as belowground (coarse roots and fine roots, BNPP) and aboveground (photosynthetic, aboveground non-photosynthetic, and reproductive materials, ANPP).

Data analysis – data and code

Datasets are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.brv15dvhz (Cabal et al. 2024) All our analyses and visualizations were performed using R ver. 4.0.4 (www.r-project.org) and R studio (ver. 1.4.1106).

Results

Plant competition in fitted IRDD models

In rosemary plants, the NSR coefficient β was positive, indicating local root over-proliferation near the plant stem. The interaction coefficient γ between the distance E and NSR was negative, indicating local root under-proliferation far from the plant stem as a response to interaction with other plants belowground. In broom plants, we only detected a significant positive signal of the NSR coefficient β, indicating that plants under-proliferated roots as a response to interaction with other plants belowground at any distance. In gum rockrose, no interaction term was found to be significant. All the other coefficients were significant for all three species; IRDD decreased with distance from the plant stem and soil depth and increased with aboveground plant size (Table 1–3, Fig. 2). All cIRDD models found a significant positive linear relationship between coarse roots and the predicted IRDD for fine roots (Table 4).

Root allocation and plant strategy

Root to shoot biomass ratio was found to be relatively constant across species, with values of 2.21 ± 0.41 (mean ± SE) in rosemary, 2.99 ± 1.18 in broom, and 3.03 ± 0.57 in rockrose, indicating that roughly between two thirds and three fourths of the dry phytomass was belowground. Root to crown lateral range was similar in rockrose and rosemary, with values of 6.11 ± 0.53 and 7.19 ± 0.70, respectively. Broom plants had much larger root-to-crown range ratios with a mean of 15.32 ± 3.28 (Fig. 3). In all cases, the potential surface overlap between root systems, proportional to the square of the range of the ratio (crown and root areas), was orders of magnitude larger in the case of roots than in the case of crowns.

Calculated ratios showed species-specific hydraulic strategies. We found the lowest ratio of fine root dry mass per cm^2 of sapwood area for rockrose with 177.55 ± 32.10 g and of dry biomass of leaves per cm^2 of sapwood area with 39.62 ± 7.72 g. This species also had the lowest fine root-to-leaf ratio, roughly equal to five. Rosemary plants showed 455.55 ± 98.04 g of dry biomass of fine roots per cm^2 of sapwood area and 46.25 ± 5.88 g of dry biomass of leaves per cm^2 of sapwood area. Finally, broom plants produced 747.36 ± 299.07 g of dry biomass of fine roots per cm^2 of sapwood area and 68.26 ± 16.20 g of dry biomass of photosynthetic material per cm^2 of sapwood area. Both species' fine root-to-photosynthetic

Table 2. RD_i mixed model coefficients for gum rockrose plants. RD = root density (mg cm^{-3}), E = Euclidian distance from the sample centroid to the plant insertion point (m), NSR = non-self root density (mg cm^{-3}), D = depth of the sample centroid (m), AW = aboveground dry biomass (kg) of the plant, ∂ = parameter summed to E to impede the intercept of E to grow to infinity and adjusted so that $\varepsilon = -2$, ε = power law for the decreasing costs of building roots with plant's proximity. Significance codes: 0 '***' 10^{-3} '**' 10^{-2} '*' 0.05 '·' 0.1 ' ' 1.

	Estimate	SE	t value	p-value
α (Intercept)	−1.04687	0.12148	−8.618	< 20^{-16}***
ε (log (E + ∂))	−2	0.13039	−15.351	< 20^{-16}***
∂ (for ε = −2)	0.33976			
δ (D)	−0.79106	0.23187	−3.412	6.46 10^{-4}***
ω (AW)	0.36035	0.07209	4.999	5.77 10^{-7}***

Table 3. RD_f mixed model coefficients for hairy-fruited broom plants. RD = root density (mg cm^{-3}), E = Euclidian distance from the sample centroid to the plant insertion point (m), NSR = non-self root density (mg/cm^3), D = depth of the sample centroid (m), AW = aboveground dry biomass (kg) of the plant, ∂ = parameter summed to E to impede the intercept of E to grow to infinity and adjusted so that $\varepsilon = -2$, ε = power law for the decreasing costs of building roots with plant's proximity. Significance codes: 0 '***' 10^{-3} '**' 10^{-2} '*' 0.05 '·' 0.1 ' ' 1.

α (Intercept)	2.62877	0.50484	5.207	$1.92\ 10^{-7}$***
ε (log (E + ∂))	−2	0.61492	−3.253	$1.14\ 10^{-3}$**
∂ (for ε = −2)	1.42276			
β (NSR)	−0.11462	0.02462	−4.656	$3.22\ 10^{-6}$***
δ (D)	−4.73642	0.78057	−6.068	$1.30\ 10^{-9}$***
ω (AW)	0.30383	0.09244	3.287	$1.01\ 10^{-3}$**

material dry weight ratios were nearly ten, twice as much as rockrose. This trend correlates with the mean vessel diameter of each species, with gum rockrose having the smallest vessel diameter, around 18.5 µm (Torres-Ruiz et al. 2017), followed by rosemary, with ~ 31 µm (Crivellaro and Schweingruber 2015) and broom with vessels as wide as ~ 100 µm (value estimated from our scanned stems).

Carbon storage and NPP in Mediterranean shrubland

The carbon stored by the studied species by canopy area unit was 2610.68 ± 246.54 g C m^{-2} (mean ± SE) for rockrose plants, which stored most of the carbon into coarse roots, and 1562.90 ± 325.44 g C m^{-2} in broom plants and 1554.04 ± 273.76 g C m^{-2} in rosemary plants, for which most was allocated to fine roots. Generally, we observed that gum rockrose stored more carbon in structural tissues than in functional tissues (leaves and fine roots). In contrast, the allocation into functional tissues was proportionally much larger in the other two species (Fig. 4). Unsurprisingly, given the shoot-to-root ratios, most carbon was found belowground, with specific values of 1896.46 ± 217.50 g C m^{-2} for rockrose plants, 1080.25 ± 258.77 g C m^{-2} in broom plants, and 1049.44 ± 235.21 g C m^{-2} in rosemary plants.

The total NPP for rockrose and rosemary ranged around 500–600 g C m^{-2} $year^{-1}$ values, respectively (Supporting information). Most NPP was allocated into labile tissues (turnover or reproduction), and structural aboveground wood was the only standing biomass fraction that seemed to increase per m^2 through shrub aging. When comparing BNPP and ANPP, rosemary allocated more belowground with a BNPP:ANPP ratio close to 5, and most of the carbon was invested into fine root turnover. For gum rockrose, the BNPP:ANPP ratio moves from 1.5 in younger individuals to 1 in older individuals. While gum rockrose had a smaller total NPP, the carbon allocated to wood growth (only standing biomass fraction growing) was constant across ages and larger (70 g C m^{-2} $year^{-1}$) than in rosemary, for which the initial value is similar, yet it decreases much faster as shrubs age.

Discussion

Shrublands in arid lands are usually considered systems with low carbon uptake and storage (Kicklighter et al. 1999, Serrano-Ortiz et al. 2009, Anderson-Teixeira et al. 2011, Yang et al. 2017). Hence, global vegetation models often neglect them (Laurent et al. 2004, Fusco et al. 2019). Considering that shrublands in our study site present a closed canopy, and that all studied species yielded similar productivity and carbon values, and assuming that the other less dominant species might not show very dissimilar ones, our results suggest that the mediterranean shrubland in Las Tejoneras stored roughly 2000 g C m^{-2}. Most of the carbon stored in plant tissues was found belowground, representing between two-thirds and three-quarters of the total carbon in the system. NPP calculations indicate that the total NPP in the study site ranged between approximately 500 and 600 g C m^{-2} $year^{-1}$. Subtropical dry forests in the mediterranean climate store about 5300 g C m^{-2}, of which about 2400 g C m^{-2} are stored belowground, and have an estimated total NPP of 1600 g C m^{-2} $year^{-1}$ of which 700 g C m^{-2} $year^{-1}$ corresponds to BNPP (Anderson-Teixeira et al. 2018, Cook-Patton et al. 2021). While mediterranean forests have higher C storage and NPP than our studied shrubland in the same biome, this is magnified by observations restricted to aboveground. Accounting for belowground carbon, mediterranean-climate shrublands may be an important carbon sink, accumulating more than one-third of the carbon stored in forests with similar climates.

The different soil resource-foraging strategies observed in the studied species indicate that stabilizing niche differences might explain the high species diversity in our study site. The three shrub species studied showed different root foraging strategies, including both root stratification and plastic responses to belowground competition (Fig. 5). In particular, rockrose presented the deepest root systems, followed by rosemary with intermediate rooting depths, and broom plants presented a shallow but laterally spread root system.

Gum rockrose plants had the largest rooting depth and the minimum lateral spread, consequently curtailing their root overlap with neighbors. We did not find any significant plastic response of root proliferation as a response to the levels of competition in rockrose plants. Our results indicate that rockrose plants having little lateral root spread avoid competition by developing root systems that minimize overlap with neighbors. Alternatively, they increase rooting depth and forage at soil depths other species do not reach. Rockrose plants might follow a drought resistance strategy according to root stratification theory predictions (Ward et al. 2013). Consistent with that expectation, they have the thinnest xylem vessels of the three species studied, hence being the most resistant to cavitation (Pockman and Sperry 2000), and

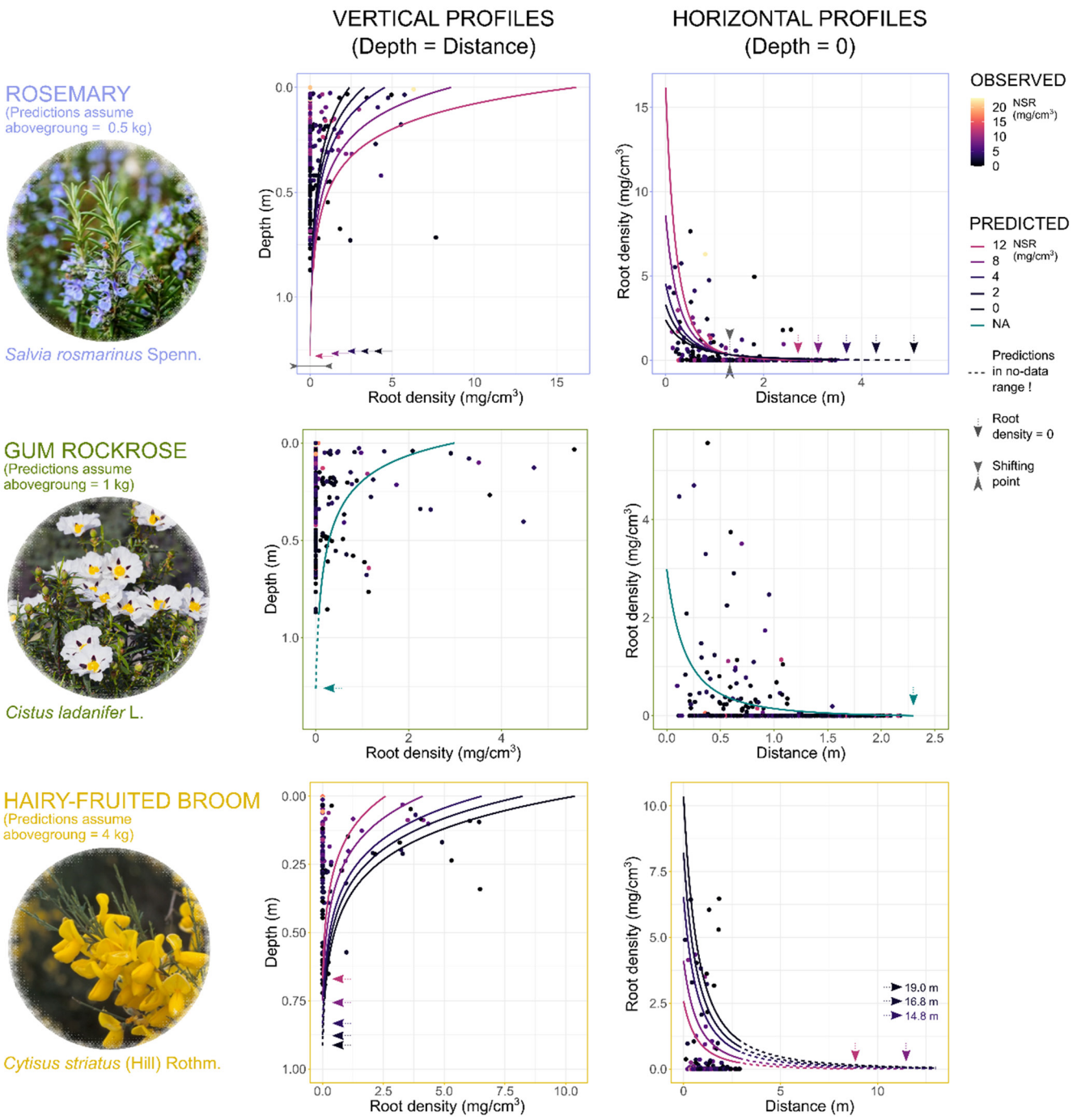


Figure 2. Observed and predicted IRDD for fine roots (diameter < 2 mm) of plants of the three different species and of given aboveground size. The first column shows the predictions for a vertical profile aligned with the plant insertion, i.e. when depth equals the distance from the insertion point. The second column shows the predictions for a horizontal profile at the ground level. Notice that all observed data for any depth and distance combination are plotted in both cases. In the case of rosemary, the shifting point represents the distance at which the local response to competition shifts from over- to under-proliferation.

they show the lowest ratios of leaf and fine root biomass to sapwood area, indicating they had the lowest water absorption rates and require relatively more sapwood to maintain transportation rates, following a conservative strategy. Rockrose plants invest about four times more biomass into coarse roots than fine roots and allocate most carbon to structural tissues and relatively little to leaves and fine roots, as opposed to the other two species.

Broom plants were, on the other extreme, the most shallowly rooted plants, yet they had the most extensive root range, potentially overlapping more with neighboring plants' roots. While the potential overlap is more extensive, we

Table 4. IRDDc mixed model results for each species (only one coefficient estimated). Significance codes: 0 '***' 10^{-3} '**' 10^{-2} '*' 0.05 '.' 0.1 ' ' 1.

	Estimate	SE	t value	p-value
μ Rosemary	0.17560	0.02514	6.985	$1.53\ 10^{-10}$***
μ Gum rockrose	4.004	0.363	11.03	< 20–16***
μ Hairy-fruited broom	0.2792	0.1084	2.575	$1.13\ 10^{-2}$*

also detected that the local response to increases in non-self roots was to decrease self root proliferation, therefore broom plants reduced significantly their root range extension toward patches of soil densely packed with competitor roots. Soil resource availability decreases in the vertical soil profile as nutrient-rich litter and precipitation water enter the soil by the surface, and only leftovers can progressively infiltrate to deeper layers (Schenk 2005). Plants following this strategy may benefit from developing shallow root systems to preemptively compete for these copious resources (D'Onofrio et al. 2015). Consequently, most plant roots are generally found foraging near the soil surface (Jackson et al. 1996). This opportunistic strategy requires adaptations to rapidly exploit the nutritive solution after precipitation pulses, which is in accordance with the allocation patterns and traits found in this species: wide xylem vessels allowing fast movement of sap, high allocation into absorbing fine roots rather than transporting coarse roots, and proportionally less sapwood area relative to foraging tissues.

Finally, rosemary plants showed intermediate average levels of rooting depth, segregating their roots from the other two species. Most interestingly, our results showed significant evidence for the exploitative segregation of plant roots (ESPR) in response to competition with neighbors (Cabal et al. 2020) for this species. This means that the rosemary's response to belowground competition is plastic and follows game theory exploitative predictions, engaging in a root tragedy of the commons. As a response to increased local competition, rosemary shrubs over-proliferated fine roots near their stem, over-allocating biomass. Still, they also under-proliferated roots far from their stem, reducing their root system lateral spread toward competing neighbors and segregating their root systems.

Speculations

We find it quite remarkable that the ESPR is proven for one out of three species in the first field study testing for it. Because the root tragedy of the commons is the result of the simplest exploitative foraging dynamics of roots (Cabal 2022), we expect it to be ubiquitous across plant species, and our results indicate that it may indeed be quite widespread. Even while our statistical analyses only found a significant trace in one species, all three could engage in ESPR, notwithstanding root

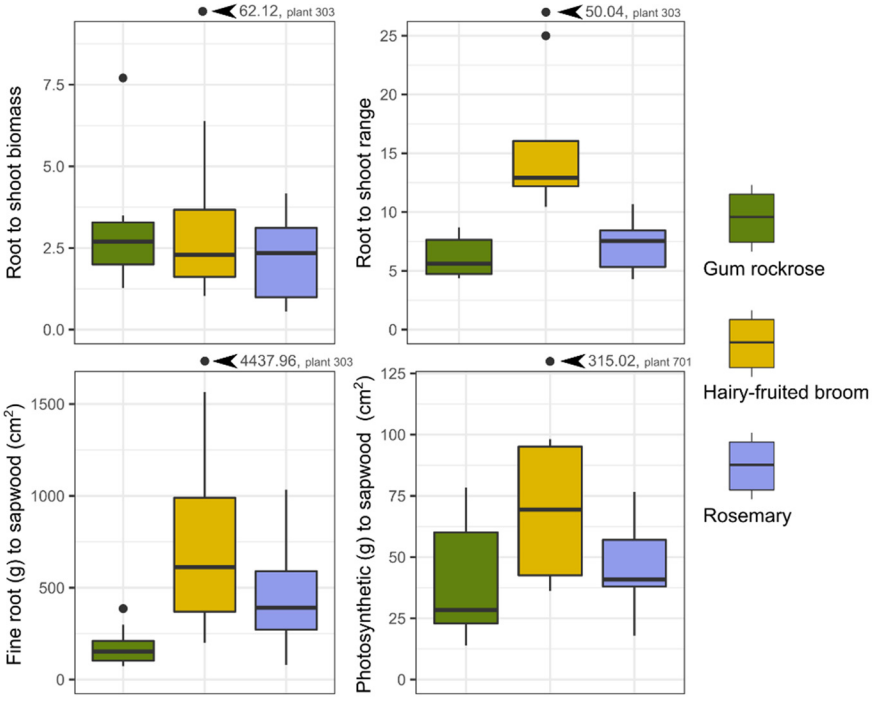


Figure 3. Boxplots showing each species' plant structural ratios (root-to-shoot biomass and root-range-to-crown range) and functional ratios (fine root biomass to sapwood area and photosynthetic material to sapwood area). Points on top of the plot area represent outliers corresponding to broom plants no. 303 or 701.

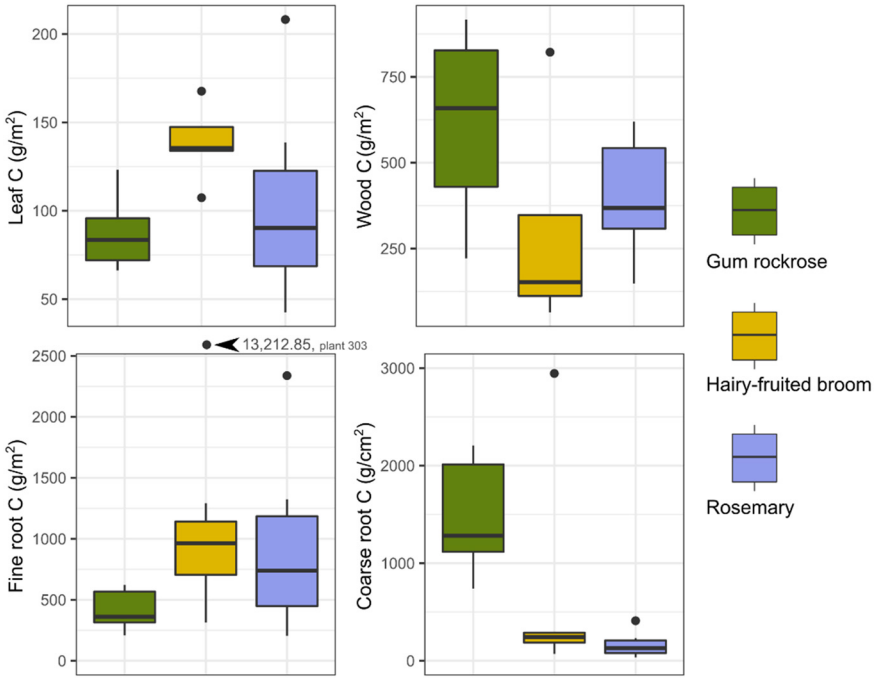


Figure 4. Boxplots showing plant carbon storage in the different fractions of biomass: leaves (photosynthetic material), wood (aboveground non-photosynthetic material), fine roots (diameter < 2 mm), and coarse roots (diameter > 2 mm). The point on top of the plot area represents an outlier corresponding to plant no. 303.

stratification. We may have been unable to prove the exploitative segregation for the other two species due to three statistical caveats: 1) ESPR is the model with the most parameters and requires maximal statistical power. 2) Broom plants had the lowest replication levels: five individuals, of which two behaved as outliers at some variables (Fig. 2–3). 3) Rockrose minimized the overlap with neighbors by producing deep, narrow root systems, and as a consequence, the variability in non-self root density in this species' root samples was low, potentially hindering the detection of effects of both non-self roots and its interaction with the distance to the plant in the fitted model.

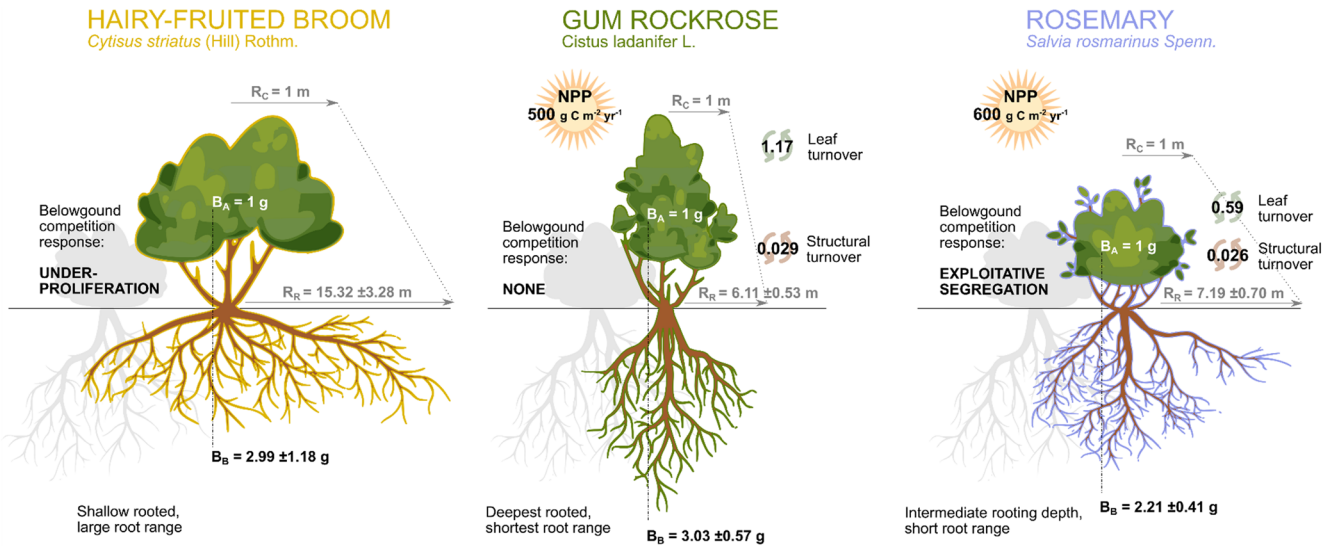


Figure 5. Schematic summary of the autoecology of the three shrub species studied. The figure shows the belowground competition strategy and general shoot-to-root allometries. R_R represents the root range-to-crown range ratio, i.e. the root range for a plant with one unit of crown radius R_C. B_A represents the shoot-to-root ratio, i.e., the root dry biomass per unit of shoot-dry biomass BA. The figure shows the estimated total net primary productivity (NPP) and the mean leaf and structural tissues (wood) turnover per year for the two species for which dynamic allocation was studied. Values correspond to mean ± SE.

Conclusions

Shrubs in this study stored 2000 g C m^{-2} and had an NPP of 550 g C m^{-2} $year^{-1}$, representing a third of the values reported for forests in similar climates. Developing technologies to study shrub roots, reporting belowground carbon storage in shrublands, and accounting for shrublands in vegetation and earth system models is fundamental for the large amount of carbon they can store and the vast amount of land they cover. Root foraging strategies of the studied shrubs indicate that stabilizing niche differences may play a fundamental role in species coexistence, explaining the high plant biodiversity in Mediterranean shrublands in Candeleda. We found evidence of root stratification, with gum rockrose presenting deep roots combined with other drought-resistance hydraulic traits, broom shrubs had shallow root systems spreading widely across the superficial soil layer, and rosemary presented intermediate values of root spread both laterally and in-depth. Rosemary and broom plants presented plastic responses to local competition: Both reduced their root range towards highly rooted soil patches (territoriality). Additionally, we found evidence of exploitative segregation of plant roots in one of the three species studied, the rosemary, which over-proliferated roots near its main stem (root tragedy of the commons) but also under-proliferated roots far as a response to increasing non-self root density. Further studies testing the exploitative segregation response to competition of diverse plant species in field conditions might show that this game-theory-based foraging strategy involving a root tragedy of the commons might be more widespread than previously thought.

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Author contributions

Ciro Cabal: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead). **Fernando Valladares**: Conceptualization (equal); Project administration (lead); Supervision (equal); Writing – review and editing (equal). **Stephen W. Pacala**: Conceptualization (equal); Funding acquisition (lead); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.brv15dvhz (Cabal et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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