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RESEARCH ARTICLE

Trade-offs in rooting strategy dimensions along an edaphic gradient in a grassland ecosystem

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Abstract

1. Roots are essential to the diversity and functioning of plant communities, but trade-offs in rooting strategies are still poorly understood.
2. We evaluated existing frameworks of rooting strategy trade-offs and tested their underlying assumptions, guided by the hypothesis that community-level rooting strategies are best described by a combination of variation in organ-level traits, plant-level root:shoot allocation and symbiosis-level mycorrhizal dependency. We tested this hypothesis using data on plant community structure, above- and below-ground biomass, eight root traits including mycorrhizal colonisation and soil properties from an edaphic gradient driven by elevation and water availability in sandhills prairie, Nebraska, USA.
3. We found multidimensional trade-offs in rooting strategies represented by a two-way productivity-durability trade-off axis (captured by root length density and root dry matter content) and a three-way resource acquisition trade-off between specific root length, root:shoot mass ratio and mycorrhizal dependence. Variation in rooting strategies was driven to similar extents by interspecific differences and intraspecific responses to soil properties.
4. Organ-level traits alone were insufficient to capture community-level trade-offs in rooting strategies across the edaphic gradient. Instead, trait variation encompassing organ, plant and symbiosis levels revealed that consideration of whole-plant phenotypic integration is essential to defining multidimensional trade-offs shaping the functional variation of root systems.

KEYWORDS
edaphic gradient, functional traits, root economic space, rooting strategies

1 | INTRODUCTION

At the whole-plant level, plant species are thought to be arrayed along ecological strategy spectra based on the consequences of trade-offs in function for demography (Kitajima & Myers, 2008; Rüger et al., 2018; Russo et al., 2021). Above- and below-ground traits should therefore be phenotypically integrated (Marks & Lechowicz, 2006; Pigliucci, 2003; Westoby et al., 2002) in a way that enables a given whole-plant ecological strategy to be achieved (McCarthy & Enquist, 2007; Poorter et al., 2014; Wahl & Ryser, 2000). For leaves, organ-level trait variation is well-described by the leaf economic spectrum (LES), which aligns leaf functional traits along a fast-slow axis (Reich, 2014; Shipley et al., 2006; Wright et al., 2004). Early root economic frameworks posited that root trait variation should follow a parallel fast-slow spectrum, but this has not received incontrovertible empirical support (Kochsiek et al., 2013; Ostertag, 2001; Weemstra et al., 2016, 2020). Plants optimise below-ground allocation to support above-ground photosynthetic carbon acquisition (Givnish, 1988; Wahl et al., 2001). Thus, organ-level root traits should be functionally coordinated with biomass allocation to roots to maximise whole-plant fitness (Ledder et al., 2020; Wahl & Ryser, 2000).

The complication is that for most plants, below-ground resource acquisition does not only depend on roots alone but also mycorrhizal fungi (Brundrett, 2017). Bergmann et al. (2020) improved upon earlier root economic frameworks by incorporating mycorrhizae and proposed that rooting strategies are defined by a two-axis root economic space: a do-it-yourself (DIY) versus outsourcing axis defined by specific root length (SRL) versus root diameter (RD), which was used as a proxy for mycorrhizal dependency, and an orthogonal fast-slow trade-off axis represented by root nitrogen to root tissue density (RTD). This framework was supported across species in multiple phylogenetic lineages (Bergmann et al., 2020). Using root trait data and plant species' climatic niche data from databases, one study found that while root traits were associated with species' occurrences along gradients, the proposed trade-offs were not observed (Laughlin et al., 2021). However, some of the root economic framework's assumptions have not been thoroughly tested, and whether it applies at the community level, at which resource availability and rooting strategies are in part determined (Farrior, 2014; Laughlin et al., 2021), remains unclear. First, whether RD is a good proxy for the degree of mycorrhizal dependency has not been substantiated. Root diameter can vary for reasons unrelated to mycorrhizal colonisation space. For instance, the fraction of aerenchyma confounds the postulated trade-offs between SRL and RD (Eissenstat et al., 2000; Laughlin et al., 2021). Second, because rooting strategies were defined based only on organ-level traits, above- versus below-ground allocation trade-offs are not accounted for (McCarthy & Enquist, 2007; Poorter et al., 2012). For instance, higher SRL is only one way to 'DIY': another is to increase root biomass (Körner & Renhardt, 1987; Weemstra et al., 2020). Third, the focus on interspecific variation across large phylogenetic scales does not account for how intraspecific trait variation and species turnover shape rooting strategies across environmental gradients. Understanding drivers of community-level trait shifts is essential for investigating ecosystem function (Schmitz et al., 2015). As plants are plastic in root traits (Bachle et al., 2018; Hanslin et al., 2019; Wahl et al., 2001), below-ground allocation (Poorter et al., 2012; Reich, 2002) and allocation to mycorrhizae (Gavito & Olsson, 2003; Kiers et al., 2011), these sources of variation may confound the detection and interpretation of trade-offs in rooting strategies based on organ-level patterns among species (Laughlin et al., 2017; Russo & Kitajima, 2016).

The goals of this study were to evaluate existing frameworks of rooting strategy trade-offs and to test their underlying assumptions. Our study was guided by the hypothesis that community-level rooting strategies are best described by trade-offs involving variation in organ-level traits, plant-level root:shoot allocation and symbiosis-level mycorrhizal dependency operating at the interspecific and intraspecific levels. To test this hypothesis, we analysed community-level rooting strategies in relation to plant community structure and soil properties along an edaphic gradient driven by elevation and water availability in a sandhills prairie that is considered one of the last remaining intact grassland systems on Earth (Scholtz & Twidwell, 2022). As the soil is up to 95% sand, water availability shapes the variation in vegetation with elevation (Barnes & Harrison, 1982), allowing us to examine the community-level trade-offs in rooting strategies while accounting for changes in plant species composition. Specifically, we addressed the following questions: (Q1) How do plant communities (structure and above-ground biomass) and rooting strategies vary with soil properties along the edaphic gradient? (Q2) What is the relative importance of interspecific versus intraspecific effects on variation in rooting strategies along the edaphic gradient? (Q3) What are the fundamental trade-offs in root economic space that define rooting strategies at the community level? To address these questions, we quantified community-level variation in rooting strategies based on eight variables and analysed their variation with respect to plant above-ground biomass, community structure and diversity and soil properties (Table 1) in three elevational habitats differing in water availability at two sandhills prairie sites.

2 | STUDY SITES AND METHODS

2.1 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Community	Across three habitats within communities	20–25 within each of three habitats at each of two sites

2.2 | Study sites and field sampling

This study was conducted at two sites in the sandhills prairie of the Great Plains in western Nebraska, USA: Arapaho Prairie (41.5° N, 101.8° W) (Barnes & Harrison, 1982) and University of Nebraska-Lincoln Gudmundsen Sandhills Laboratory (42.1° N, 101.4° W) (Adams et al., 1998), hereafter referred to as Arapaho and Gudmundsen. This grass-stabilised sand dune system comprises the largest active dune system in the western hemisphere (Whitcomb, 1989). This region is characterised as semiarid continental climate, with livestock replacing the natural grazers that were once a key part of the Great Plains (Samson et al., 2006). In this region from 2010 to 2020, the annual mean temperature was 8.9–11.1°C (22.1–26.9°C), and the mean annual precipitation was

TABLE 1 Description of variables quantified in this study.

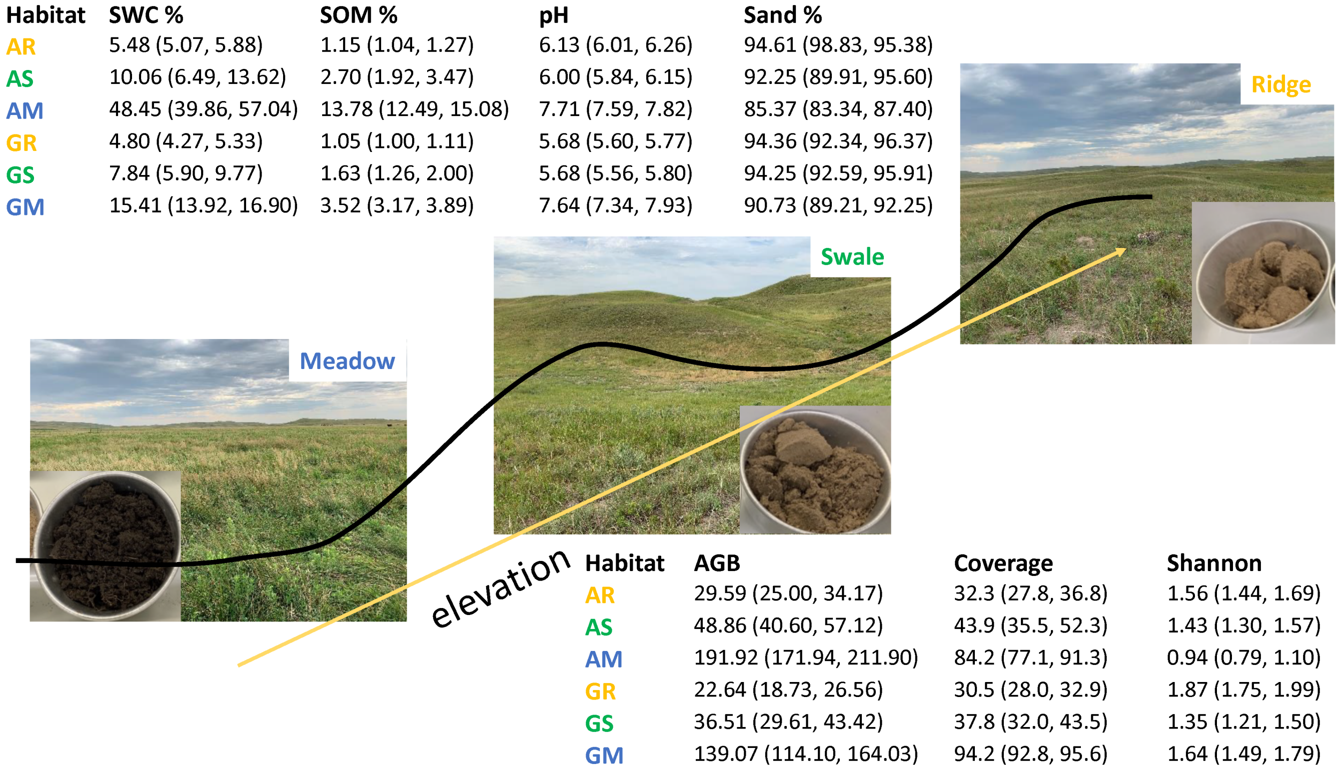
Abbreviation		Description	Units
Soil properties			
% sand		Percent sand in soil texture	percent
% clay		Percent clay in soil texture	percent
% silt		Percent silt in soil texture	percent
pH		pH	unitless
SWC		Gravimetric soil water content (g/g dry soil)	percent
SOM		Soil organic matter (g/g dry soil)	percent
Plant community structure			
AGB		Above-ground biomass	g
Coverage		Percent of the quadrat covered by plant canopies	percent
Species richness		Number of plant taxa	count
Species diversity		Shannon diversity	unitless
Rooting strategy			
Organ level	RD*	Average diameter	mm
	SRL*	Specific root length	cm/g
	RDMC*	Root dry matter content	g/g
	RTD*	Root tissue density	g/cm^3
Plant level	RLD	Root length density, soil core volume = 304.02 cm^3	cm/core
	RSR	Root:shoot mass ratio	g/g
Mycorrhizal dependence	AMF rate*	Percent of fields of view where AMF structure was present	percent
	AMF intensity*	Average of the percent of root space occupied by AMF structure	percent

Note: Each variable was estimated at the quadrat level and for surface soil (0–15 cm) for below-ground variables. Asterisk indicates variables that were quantified only on fine roots (<1 mm in diameter); all other root variables were quantified on all roots.

550.6 mm, with on average 60% precipitation occurring between May to August (National Weather Service, NOAA). The soil derives from aeolian sand (over 90% sand in many areas) overlaying Jurassic and Cretaceous sediments (Whitcomb, 1989).

We chose these sites because they are not heavily grazed, and the dune topography causes a clear gradient in water availability with elevation (Barnes & Harrison, 1982; Gosselin et al., 2006). Arapaho was ungrazed and not hayed for 32 years before 2016; since then it was grazed in mid spring at around 0.2 animals/ha and hayed in July each year, but all sampling was performed prior to haying. Gudmundsen is grazed at around 0.07–0.2 animals/ha (Raynor et al., 2021). Three distinct habitat types were defined in this study: ridge, swale and meadow (Figure 1). Specifically, the ridge is the top of a dune (~1140 m at Arapaho and ~1100 m at Gudmundsen), the swale is a lower-elevation depression between two ridges (~1130 m at Arapaho and ~1080 m at Gudmundsen), and the meadow is the lowest elevation area in large interdunal valleys, which are sub-irrigated by groundwater at some times of year (~1110 m at Arapaho and ~1060 m at Gudmundsen) (Barnes & Harrison, 1982; Gosselin et al., 2006). On average, the ridge and swale respectively have been found to have a depth of 30 and 40 cm in the AC horizon, beyond which is pure sand (Wang et al., 2008). The meadow soil shares similar profile but reaches the water table at approximately 90 cm, depending on rainfall (Mousel et al., 2007). We refer to the gradient from meadow to ridge as an edaphic gradient because although the lithology remains the same (aeolian sand), long-term variation in water drainage and plant cover have led to topographic differences in soil properties, which we quantified as described below.

The field sampling was conducted with permission from the landowners of Arapaho and the university field station manager of Gudmundsen. In June and July 2020, in each study site, ridge and swale were sampled on two sand dunes, and one meadow was sampled due to limited availability of suitable meadows near the ridges and swales. We sampled in 50 cm × 50 cm quadrats placed approximately 1.5 m apart from each other along 20-m transects running perpendicular to the prevailing slope. We sampled 10–15 quadrats/transect, for a total 105 quadrats across all habitat × site combinations. The latitude and longitude of each quadrat were recorded using a handheld GPS instrument (Earthmate PN60, DeLorme Inc., Yarmouth, ME, USA) and used to calculate the geographic distances



Habitat	SWC %	SOM %	pH	Sand %
AR	5.48 (5.07, 5.88)	1.15 (1.04, 1.27)	6.13 (6.01, 6.26)	94.61 (98.83, 95.38)
AS	10.06 (6.49, 13.62)	2.70 (1.92, 3.47)	6.00 (5.84, 6.15)	92.25 (89.91, 95.60)
AM	48.45 (39.86, 57.04)	13.78 (12.49, 15.08)	7.71 (7.59, 7.82)	85.37 (83.34, 87.40)
GR	4.80 (4.27, 5.33)	1.05 (1.00, 1.11)	5.68 (5.60, 5.77)	94.36 (92.34, 96.37)
GS	7.84 (5.90, 9.77)	1.63 (1.26, 2.00)	5.68 (5.56, 5.80)	94.25 (92.59, 95.91)
GM	15.41 (13.92, 16.90)	3.52 (3.17, 3.89)	7.64 (7.34, 7.93)	90.73 (89.21, 92.25)

Habitat	AGB	Coverage	Shannon
AR	29.59 (25.00, 34.17)	32.3 (27.8, 36.8)	1.56 (1.44, 1.69)
AS	48.86 (40.60, 57.12)	43.9 (35.5, 52.3)	1.43 (1.30, 1.57)
AM	191.92 (171.94, 211.90)	84.2 (77.1, 91.3)	0.94 (0.79, 1.10)
GR	22.64 (18.73, 26.56)	30.5 (28.0, 32.9)	1.87 (1.75, 1.99)
GS	36.51 (29.61, 43.42)	37.8 (32.0, 43.5)	1.35 (1.21, 1.50)
GM	139.07 (114.10, 164.03)	94.2 (92.8, 95.6)	1.64 (1.49, 1.79)

FIGURE 1 Description of habitats in the sandhills study sites in Nebraska, USA. The black curve shows an approximation of the profile of the elevation gradient at the Arapaho (A) and Gudmundsen (G) sandhills prairie study sites. Images are from the habitats in Gudmundsen prairie, and related soil images were from soil cores taken within each habitat (R, ridge, S, swale, M, meadow). The table shows average and 95% confidence intervals (in parenthesis) of soil properties (top left) and plant community variables (bottom right) in each habitat at each site. AGB, above-ground biomass; SOM, soil organic matter content; SWC, soil water content. Also see Table S2 and Figures S2 and S3. For SWC, $n = 5$–8. For other variables, $n = 20$–25 in ridge and swale and $n = 10$ in meadow.

between quadrats using the R package '*geodist*' (Padgham, 2021; R Core Team, 2023). Transects were sampled in a haphazard temporal sequence across sites and habitats within the shortest possible timeframe to capture the cover of both cool and warm-season grasses. However, one of the dominant cool-season grass species in one Gudmundsen swale transect, *Poa pratensis*, went into dormancy before we finished sampling all the quadrats within the same transect. We calculated the average ratio of *Poa pratensis* to litter coverage in early sampled quadrats along the same transect. This ratio was used to estimate *Poa pratensis* coverage in quadrats where it was dormant, based on the litter coverage.

2.3 | Plant community structure

We quantified three variables describing plant community structure: above-ground biomass (AGB), species richness and species diversity (Table 1). Within each quadrat, plant community composition was estimated based on the percentage canopy coverage of living plants, bare ground and litter in increments of 1%. Due to the difficulty in identifying sedges to the species level without reproductive organs, *Carex* species were grouped and treated as a single species (*Carex* spp.). Cover of living plants was estimated for each species, then all above-ground live vegetation was clipped, separated into four functional groups [grasses, grass-like species (sedges and rushes), forbs and legumes] and placed into separate plastic bags on ice in a cooler. In the lab, we measured the fresh mass and then dry mass after oven-drying at 65°C for at least 48 h. Data from forbs and legumes were aggregated because both were rare. For each quadrat, the biomass ratio of each growth form was calculated as the dry mass of the growth form divided by the total AGB. In each quadrat, species richness was estimated as the number of species, and species diversity was estimated using the Shannon-Wiener Index:

$$H = -\Sigma p_i \times \ln(p_i),$$

where p_i was the proportion of total plant cover of species i.

2.4 | Soil properties

We quantified five soil properties: soil water content (SWC), texture, moisture, organic matter content (SOM) and pH (Table 1). After clipping, two cylindrical soil cores (0–15 cm in depth, 5.08 cm in diameter) were taken haphazardly within each quadrat for quantification of soil properties and rooting strategies. Soil was placed into air-tight Whirl-pak bags and stored in a cooler on ice until returning to the lab for processing and analysis of soil properties. Soil pH was measured immediately in a soil: water ratio of 1:2 (m/v) using Orion 3-Star pH meter (Thermo Fisher Scientific, Waltham, USA) (Robertson et al., 1999a). The remaining soil was air-dried and passed through a 2-mm sieve before further analysis. For SOM, around 5 g of air-dried soil was pre-heated overnight at 105°C, weighed to obtain total dry mass and then ashed in a muffle furnace at 530°C for 3 h before final cooling and weighing. Percent organic matter was determined by mass difference before and after ashing divided by the mass at 105°C (Schulte & Hopkins, 1996). The ashing temperature has been tested on our samples to be efficient in ashing organic matter. Soil texture was measured using glass hydrometers after dispersion in 5 g/L sodium hexametaphosphate solution in a temperature-controlled room (Robertson et al., 1999b).

For SWC, after quickly removing discernable roots, additional soil samples were taken from 5 to 8 quadrats (0–15 cm) per transect into air-tight 50 mL centrifuge tubes. All soil samples for SWC were taken on the same day within 2 h in the morning at each site. Soil was weighed immediately and was weighed again after drying at 105°C for at least 48 h. SWC was calculated as the mass loss divided by dry soil mass expressed on a percentage basis.

2.5 | Rooting strategies

Rooting strategies were defined by hierarchical mechanisms governing root system functions: organ-level root traits, plant-level allocation and symbiosis-level mycorrhizal dependency (Table 1). In our study sites, previous work has shown that more than 75% of the root mass to depth of 1 m are concentrated in surface soil (0–15 cm depth) and that roots are sparse between 15 and 100 cm (Moore & Rhoades, 1966; Mousel et al., 2007). Fine roots (defined here as roots <1 mm) are generally considered to be the active roots that are primarily responsible for nutrient acquisition (Freschet et al., 2021; Weemstra et al., 2020), and the fibrous root systems of grasses, the dominant growth form in our study sites, are mainly comprised of roots <1 mm in diameter (Liu et al., 2010; Reinhardt & Miller, 1990). Thus, all organ-level traits (described below) were quantified on fine roots, which comprised most of the root biomass of our samples (Figure S1), within 15 cm of the soil surface.

All living roots were carefully separated from the soil, rinsed and scanned (Epson Perfection V700, Seiko Epson Co., Suwa, Nagano, Japan) for image analysis using WinRhizo Reg 2013e (Regent Instruments Inc., Canada). Rhizomes were excluded because they are underground stems, not roots. After scanning, roots were gently patted dry in layered paper towels, weighed for fresh mass and dried at 65°C for at least 48 h to obtain dry mass. We quantified the following organ-level root traits for fine roots at the community level: average diameter (RD), SRL, root dry matter content (RDMC) and RTD (Table 1). RD was estimated as a weighted average based on relative root length of each diameter category <1 mm. SRL was estimated as fine root length per soil core divided by dry mass. RDMC was estimated as fine root dry mass divided by fresh mass, and RTD was estimated as fine root dry mass divided by fine root volume. The plant-level allocation root variables, root:shoot mass ratio (RSR) and root length density (RLD; Table 1) were estimated at the community level. RSR was estimated following Hooper (1998) by converting the dry root mass of one soil core to the quadrat scale based on the area ratio of quadrat: soil core (2500:20.27), then dividing that product by AGB. This approach assumes that the one core used to sample root biomass was representative samples of the entire quadrat. RLD was estimated based on total root length in a soil core (Table 1) (Han et al., 2020; Wilson & Tilman, 1991; Yin et al., 2021).

Mycorrhizal dependency was estimated as the colonisation rate and intensity of arbuscular mycorrhizal fungi (AMF) in living fine roots, as they represent the active roots in this grassland system (described above). Living fine roots from the second soil core were cleaned, preserved in FAA (37% formaldehyde:alcohol:acetic acid:water, 2:10:1:7) and stored at 4°C. AMF colonisation was estimated following a modified line-intersect method (McGonigle et al., 1990). Briefly, fine roots were rinsed with de-ionised water, cleared in 10% KOH (m/v) at 65°C for 90 min and then stained in 0.5% Trypan blue in lactoglycerol (lactic acid:glycerol:water = 1:1:1) at 65°C for 10 min. The stained fine roots were mounted and observed under 200× magnification. In each field of view, AMF% was estimated as the percentage root area colonised by arbuscules, vesicles and hyphae that formed coils connected with AMF structures, taking care to distinguish AMF from other fungal endophytes (e.g. Chytridiomycota). About 10 fields of view were sampled on each slide, and three slides were sampled from each quadrat, totalling ~30 fields/quadrat:

$$\text{AMF rate} = \frac{\text{number of fields where AMF structure present}}{30} \text{ and}$$

$$\text{AMF intensity} = \frac{\Sigma(\text{AMF\% in each field})}{30}.$$

2.6 | Statistical analysis

All analyses were performed in R statistical software version 4.3.1 (R Core Team, 2023). Figures were generated using the package '*ggplot2*' (Wickham, 2016).

To address Q1, we performed one-way analyses of variance (ANOVA) across habitat × site combinations for soil properties, AGB, above-ground plant coverage, AGB ratio of different growth forms, species richness and Shannon diversity. Using the '*vegan*' package, we performed the following analyses (Oksanen et al., 2022). Principal coordinates analysis (PCoA) using Bray–Curtis dissimilarity was used to analyse variation in plant community composition, followed by permutational multivariate analysis of variance (PERMANOVA) with habitat × site combinations as the grouping variables. To visualise the effects of soil properties on plant community structure, we performed canonical correspondence analysis (CCA) using soil properties (Table 1) as constraining variables. To visualise the effects of soil properties on community-level rooting strategies, we performed redundancy analysis (RDA) using soil properties (Table 1) as constraining variables. The choice to use CCA or RDA depends on the length of the first axis from detrended correspondence analysis. If the first axis >4 SD, CCA was used, otherwise RDA was used (Šmilauer & Lepš, 2014).

To address Q2, we first performed Pearson's correlation analyses between rooting strategy variables (Table 1) and plant Shannon diversity. We then performed multiple regression on distance matrices (MRM) (Lichstein, 2007) based on 9999 permutations using the '*ecodist*' package (Goslee & Urban, 2007). Gower's distances (Gower, 1971) between quadrats in the rooting strategy variables were the response variables, and Cao's distance in plant community structure (Cao et al., 1997), Gower's distances in soil properties and geographic distance (package '*geodist*'; Padgham, 2021) were predictors. To estimate the relative contribution of interspecific and intraspecific effects on rooting strategy variation, we used partial R^2. We assumed that the partial R^2 for plant community structure should capture the unique contribution of interspecific effects owing to species turnover along the gradient and trait differences between species, whereas the partial R^2 for soil properties should capture the unique contribution of intraspecific effects owing to the impact of soil properties on root systems.

To address Q3, one-way ANOVA was performed across habitat × site combinations for all rooting strategy variables (Table 1). Pairwise Pearson correlations were performed for all rooting strategy variables and visualised in a correlation network using the '*igraph*' package (Csardi & Nepusz, 2006). To visualise trade-off axes in rooting strategies, we performed principal component analysis (PCA) on all rooting strategy variables using the '*vegan*' package (Oksanen et al., 2022). The biological significance of the PCA was evaluated using the package '*PCAtest*' (Camargo, 2022). The significance of the PCA, PC axes and loadings was determined by comparing empirical values of test statistics generated from bootstrapped PCA ordinations that resample quadrats, but preserving the relationships among traits within a quadrat and the number of quadrats sampled, to a null distribution created by permuting the data among quadrats for each trait.

We excluded the % silt and SWC from all analyses other than ANOVAs (Q1). For % silt, because of its necessary relationship with % sand and % clay in texture analysis (% silt = 1 − % sand − % clay), it cannot be included in the CCA or RDA with % sand and % clay. SWC was not sampled in every quadrat due to the necessity to complete all SWC sampling on a single rain-free day. SWC strongly correlated with SOM ($r = 0.98$, $p < 0.001$; Table S2), which thus likely captured the variation in SWC.

3 | RESULTS

3.1 | Plant communities and rooting strategies vary with soil properties along the edaphic gradient

Soil properties covaried strongly with each other (Table S2) and also varied significantly among habitats, with the greatest differences between the meadow versus ridge and swale (Figure 1; Figure S2). At both sites, SWC decreased with increasing elevation from meadow to ridge (Figure 1), but the only habitats that were significantly different from each other were meadow and ridge (Figure 1; Figure S2a). There was a corresponding decrease in SOM and increase in % sand among habitats with increasing elevation (Figure 1; Figure S2b,d). Soil pH strongly depended on whether the habitat is affected by ground water, as the meadow from both sites had significantly higher pH than both the swale and ridge (Figure 1; Figure S2c).

For both sites, AGB and plant coverage decreased, and alpha diversity increased with elevation along the edaphic gradient (Figure 1; Figures S3 and S4). Meadows had the highest AGB and plant coverage, but alpha diversity was lowest there compared to the swale and ridge (Figure 1; Figures S3 and S4), although differences in alpha diversity between habitat pairs were not always consistent between sites.

Plant community structure differed significantly across habitats and was similar within habitats between sites (Figure 2a). However, the composition of the meadows at Arapaho and Gudmundsen differed significantly (Figure 2a), possibly due to higher SWC and haying in the Arapaho meadow (Figure 1; Figure S2a). The swale habitat at Gudmundsen separated into two clusters (Figure 2a), which were principally differentiated by the two sand dunes sampled.

Among the 63 plant taxa found (Table S1), most showed strong habitat preferences (Figure 2b). We found that 16.7% of the variation in plant community structure was explained by the first two CCA axes describing soil properties. The first axis differentiated the Arapaho meadow and the ridges and swales based on variation in SOM and % sand. The second axis differentiated the Gudmundsen meadow from other habitats and sites mainly based on variation in pH (Figure 2b; Figure S2c).

Community-level rooting strategy variables showed strong variation across different habitats (Figure S5). The variation of community-level rooting strategies was strongly driven by soil properties, mainly pH and SOM (Figure 2c). A total of 33.5% of the variation in multivariate rooting strategies was explained by the first two RDA axes describing soil properties. Similar to the result from the CCA on plant communities, the first axis differentiated the meadows and the ridges and swales based on SOM and pH, whereas the second axis differentiated ridges and swales (Figure 2c).

3.2 | Rooting strategies vary owing to inter- and intraspecific variation but show little association with plant alpha diversity

Rooting strategy variables did not show consistent variation with Shannon diversity of the plant community (Figure S6). Among all rooting strategy variables, only RTD was consistently positively correlated with Shannon diversity across the two sites (Figure S6f), whereas the other variables were independent from plant diversity (Figure S6b,g,h). However, rooting strategies were more similar among quadrats that were more similar in plant community structure and soil properties (Table S3; $p = 0.001$). Based on analyses of

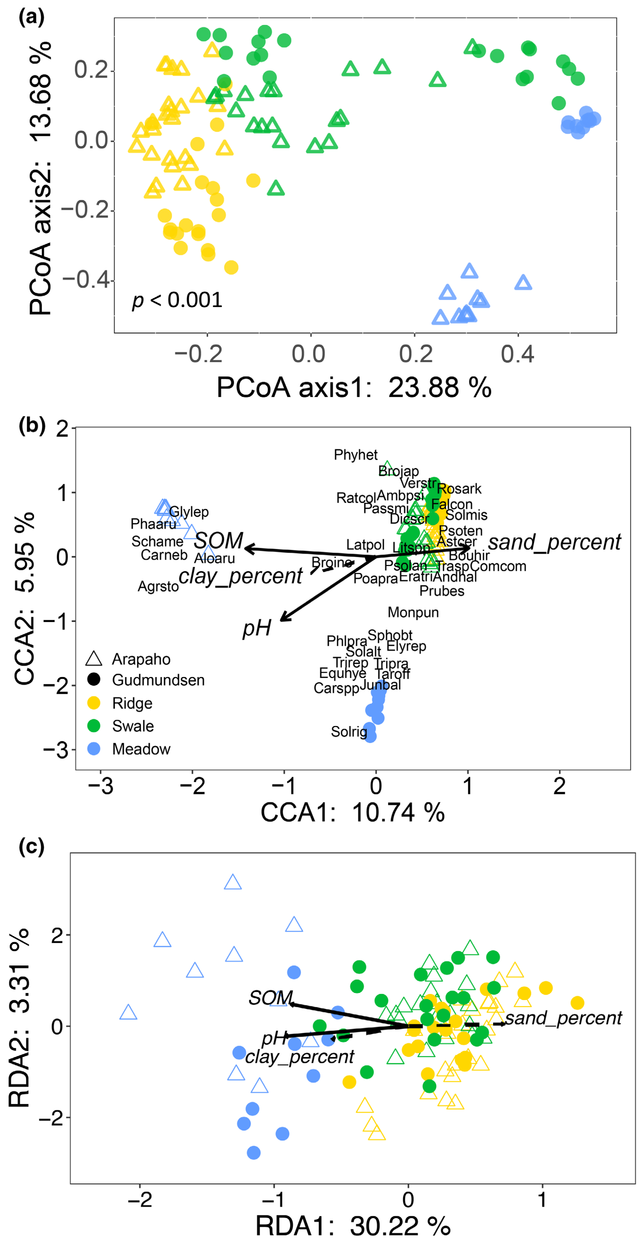


FIGURE 2 Distinct plant communities and rooting strategies across habitats driven by soil variation along an edaphic gradient in sandhills prairie, Nebraska, USA. (a) Principal coordinate analysis (PCoA) of plant communities across different habitat types based on Bray–Curtis dissimilarity. (b) Canonical correspondence analysis (CCA) on plant communities using soil properties as constraints (CCA1 and CCA2 are the first two axes of the CCA). Acronyms of common plant species from each habitat (Table S1) are also mapped in the figure. (c) Redundancy analysis (RDA) on rooting strategy variables using soil properties as constraints (RDA1 and RDA2 are the first two dimensions of the RDA). Soil properties (see Table 1 for abbreviations) with significant marginal effects on the variation of plant communities or rooting strategies are shown as solid arrows ($p < 0.05$). Shapes represent different sites, and colours represent different habitats as shown in the in-figure legend. The percent of variance explained is indicated for each axis.

dissimilarities, a total of 38% of the variation in rooting strategies was co-explained by plant community structure (30%), soil properties (30%) and geographic distance (1%).

We assumed that the variance in rooting strategies across the gradient that is uniquely explained by plant community dissimilarity captures the effects of species turnover and interspecific variation. Conditioning on plant community dissimilarity, the variance uniquely explained by dissimilarity in soil properties captures the effects of intraspecific variation. Based on these assumptions, interspecific and intraspecific effects on rooting strategies across the gradient were similar in magnitude because plant community structure and soil properties had similarly high unique explanatory power (partial $R^2 = 0.082$ and 0.078, respectively; Table S3).

3.3 | Multidimensional trade-offs shape community-level rooting strategies along the edaphic gradient

Overall, we found significant covariation among rooting strategy variables across habitats (Figure 3; Figures S7–S11). The first three PCs accounted for 78% of the overall variation, and the first two PCs explained a statistically significant amount of variation based on bootstrap resampling ($p < 0.01$, Figure S7), which also showed that all traits had significant loadings on the first PC ($p < 0.05$, Figure S7d).

There was a clear trade-off between RLD versus RDMC and RTD in both multivariate (Figure 3a–c) and bivariate relationships (Figures 3d and 4a,b). Even after removing data from meadow and only quantifying these relationships within the meadow, RLD and RTD were still significantly negatively correlated for both sites ($r = -0.57$ and $p < 0.001$ for ridge and swale, $r = -0.55$ and $p = 0.01$ for meadows only), even though the slopes of these relationships differed. Since RLD is partly driven by plant size and thus can reflect plant growth, this result confirmed the fast-slow trade-off axis reported in previous studies (Bergmann et al., 2020; Carmona et al., 2021). However, neither AMF dependency nor RD supported the previously proposed DIY versus outsourcing axis (Bergmann et al., 2020) based on their relationships with SRL, since we found SRL and AMF colonisation rate and intensity to be generally orthogonal to RD (Figures 3d and 4g,h; Figures S8a and S11c). Instead, stronger relationships were found between SRL, RSR and AMF colonisation rate and intensity (Figure 3), but, unlike RLD versus RDMC and RTD, these variables were not aligned along a single trade-off axis. Instead, SRL, RSR and AMF colonisation rate and intensity were arranged in a three-way trade-off aligned with the first three PCs of the PCA of rooting strategy variables (Figure 3a–c). SRL and AMF colonisation rate and intensity were positively correlated (Figure 4d,f), and both were negatively correlated with RSR (Figures 3d and 4c,e), but these bivariate relationships had low coefficients of determination, consistent with their multivariate influence on each other.

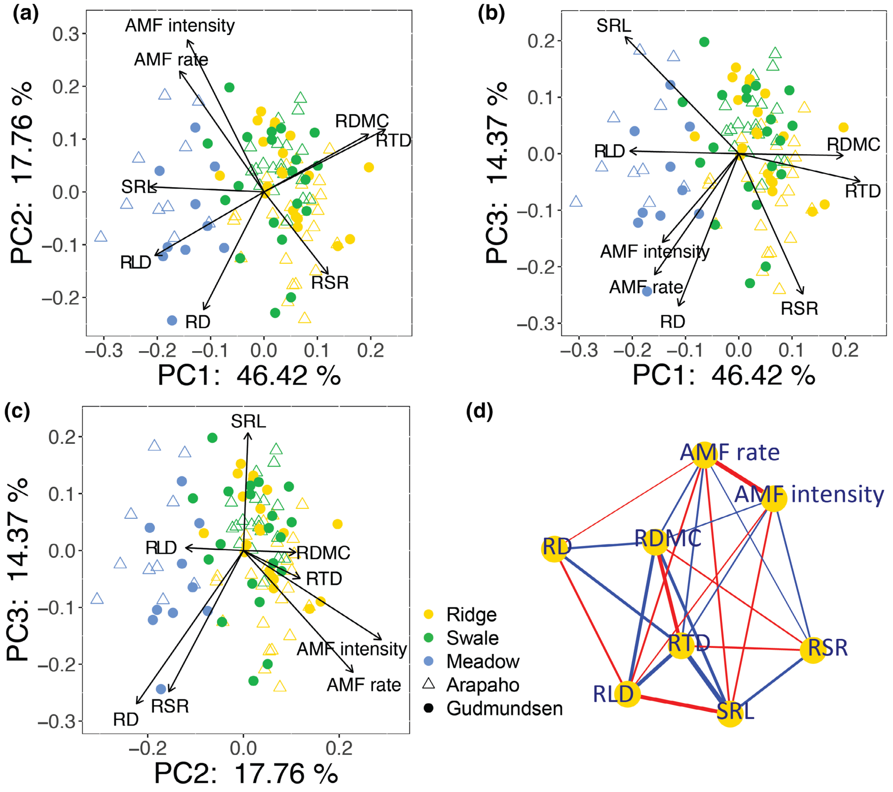


FIGURE 3 Multidimensional rooting strategies along an edaphic gradient in sandhills prairie, Nebraska, USA. (a–c) Principal component analysis on root traits across different habitats. Shapes represent different sites, and colours represent different habitats. (d) Correlation networks of univariate rooting strategies. Only significant correlations ($p < 0.05$, red: positive, blue: negative) are shown as edges. Widths of edges correspond to Pearson's *r* values. Abbreviations for traits are in Table 1. See Figure 4 for bivariate trait relationships.

4 | DISCUSSION

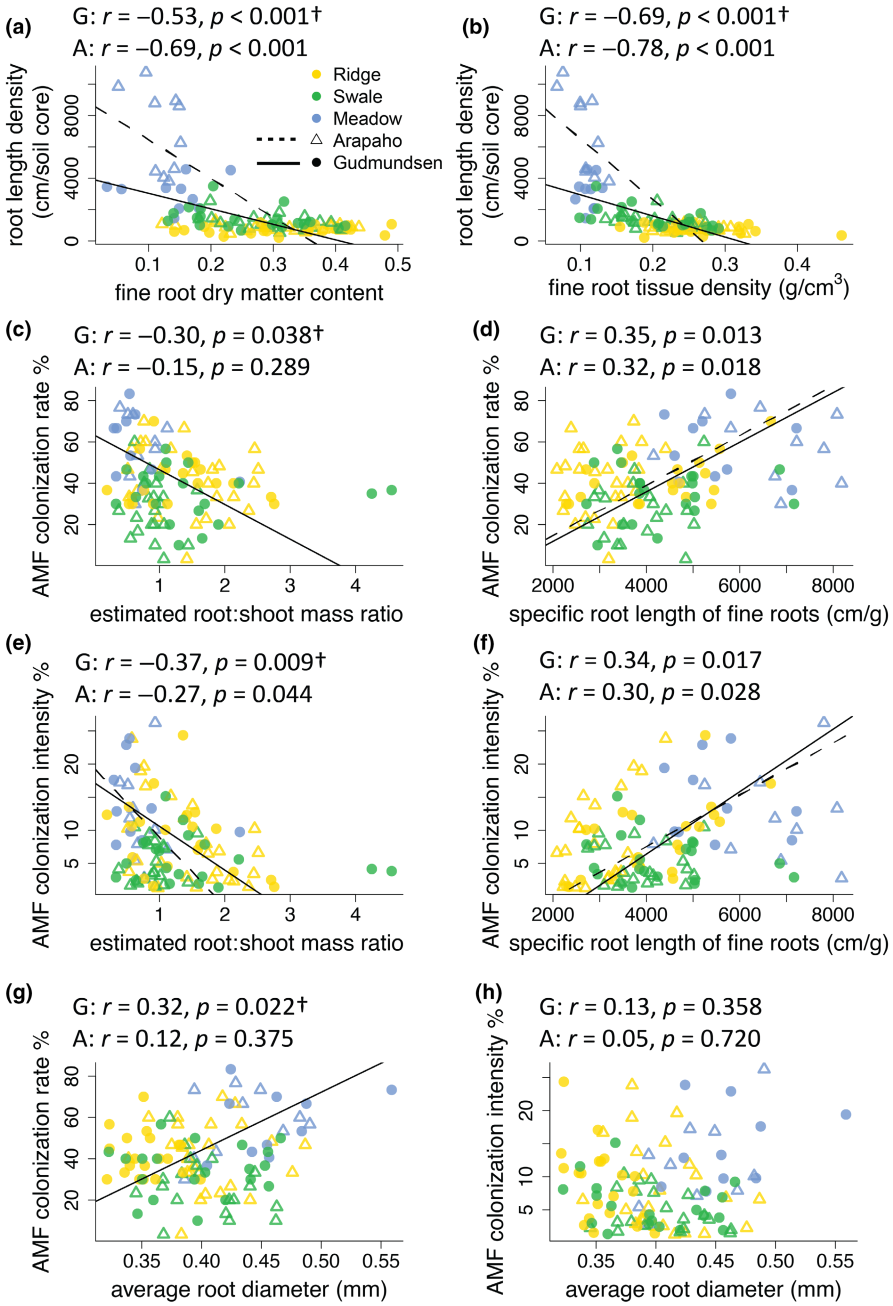
Our study revealed that at the community level, rooting strategies can be defined by multiple trade-off axes: a root productivity-durability trade-off axis represented by RLD versus RDMC and RTD that can be interpreted as a fast-slow axis, and a three-way resource acquisition trade-off represented by organ-level SRL, whole-plant-level RSR and symbiosis-level mycorrhizal dependency (Figure 5). The fast-slow trade-off axis has also been reported in previous studies using organ-level traits only (Bergmann et al., 2020; Carmona et al., 2021). However, novel findings of our work show that trade-offs in mechanisms of below-ground resource acquisition are more complex than depicted in previous root economics frameworks and that RD may not be a good proxy for mycorrhizal dependency. Namely, we found evidence in this prairie community for a three-dimensional strategy space defining below-ground resource acquisition that, importantly, spans multiple levels of integration of the plant and its mycorrhizal symbionts. The significant variation explained uniquely by soil properties, as opposed to interspecific effects owing to species turnover, suggests that intraspecific variation is likely to substantially contribute to community-level variation in rooting strategies, and points to the need for greater understanding of phenotypic plasticity at multiple biological levels of organisation in root systems. We propose that the multidimensional rooting strategy space incorporating organ, whole-plant and symbiosis-levels of variation suggested by our study can serve as a more comprehensive framework for understanding below-ground economies that should be tested in other ecosystems to assess its general applicability.

4.1 | Response of plant communities to the edaphic gradient

Habitats in our study are close to each other and do not differ in climatic regimes. However, the coarse-textured soils and dune-related elevation gradient make water availability and its long-term effects on soil properties the major environmental factors affecting vegetation of this region (Barnes & Harrison, 1982; Wang et al., 2008). Previous studies suggested SOM was a long-term indicator of water availability (Kerr & Ochsner, 2020). Consistent with that, we found that the correlation between SWC and SOM was extremely high. The correlation of pH and SWC, however, is likely due to the soil alkalinity caused by deposition of salts from ground water during repeated cycles of drying and wetting in the moister, sub-irrigated meadows (Ginsberg, 1985).

Along the edaphic gradient, AGB decreased with declines in SWC and SOM. However, the expected positive relations between AGB and diversity (Liang et al., 2016; Tilman et al., 1996) were not consistently supported. Instead, it has been suggested that the relative abundance of dominant species were more responsible for the productivity of the system than the richness of rare species (Avolio et al., 2019; Smith & Knapp, 2003). For instance, greater below-ground resource availability intensifies above-ground competition for light and space and causes negative effects on diversity (Fargione & Tilman, 2006; Hautier et al., 2009; Holmgren et al., 1997; Russo et al., 2005). The edaphic gradient defined by the soil properties we measured successfully separated distinct plant communities by habitats, although it did not capture most of the variation in plant community structure. Other factors

FIGURE 4 Bivariate relationships of rooting strategy traits along an edaphic gradient in sandhills prairie, Nebraska, USA. The Pearson's correlation coefficient and corresponding p values are shown in each panel from the two sites (G: Gudmundsen, A: Arapaho). Standardised major axis regression lines are plotted for statistically significant relationships. †, slopes on the two sites are different ($p < 0.05$). Shapes represent different sites, and colours represent different habitats.



beyond the focus of our study, such as microclimate heterogeneity (Fridley et al., 2011; Opedal et al., 2015), soil microbiota (Dastogeer et al., 2020; Hartnett & Wilson, 2002; van der Heijden et al., 1998), seed dispersal and within-habitat competition could contribute to spatial variation in plant communities, yet may not align with the edaphic gradient. We did not measure soil nutrient variation, but previous studies in this area (Hartman, 2015; Moore & Rhoades, 1966) found water to be the most limiting below-ground resource. Although soil nitrogen was also a limiting resource, it was highly correlated with SOM (Hartman, 2015; Lueking & Schepers, 1985; Moore & Rhoades, 1966). Thus, the soil properties we measured are likely to capture the principal factors generating the edaphic gradient in our system.

4.2 | Drivers of rooting strategies

At the community level, we found that multiple rooting strategy variables strongly differed along the edaphic gradient mainly driven by variation in soil texture, pH and SOM. Although soil properties explained a relatively low proportion of the variation in plant community composition, we found that soil properties were strongly associated with variation in rooting strategies at the community level, explaining more than a third of the variation. This difference in explained variation suggests that the edaphic gradient has stronger effects on community-level strategies than on community composition. Our findings focused on roots within 15 cm of the soil surface because they have been found to contribute the majority root

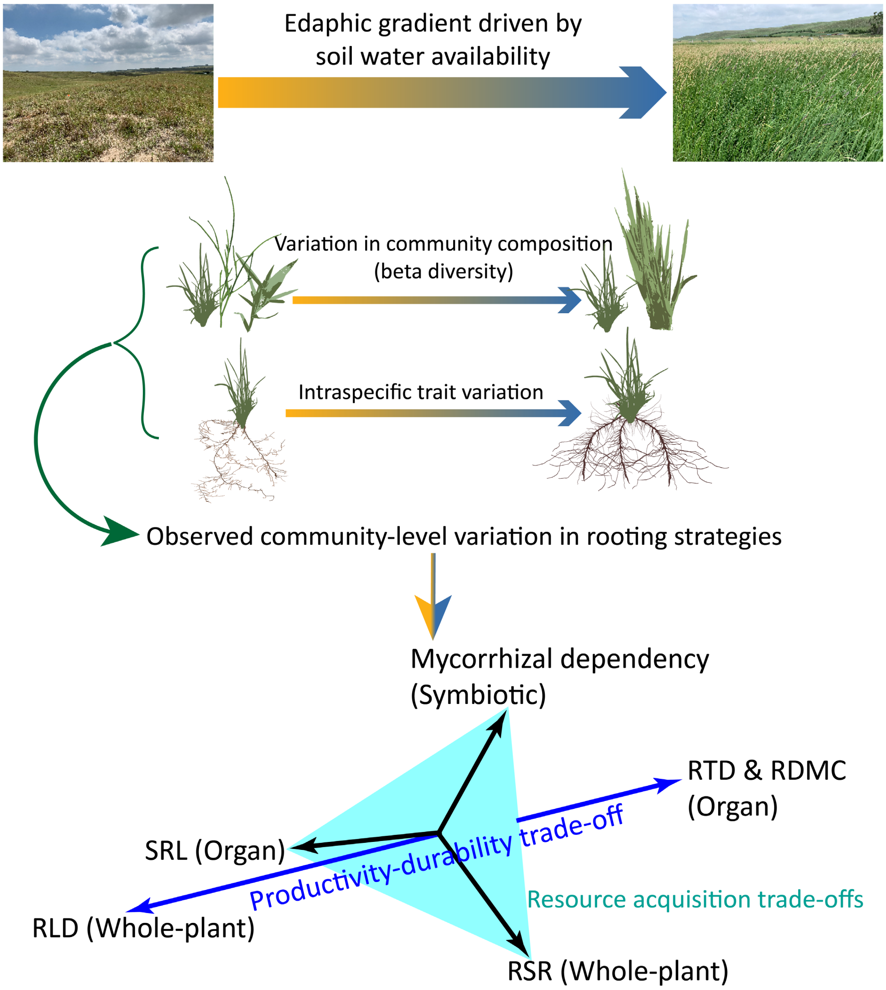


FIGURE 5 Conceptual framework of community-level trade-offs underlying rooting strategies along an edaphic gradient in a prairie ecosystem. Variation of community-level rooting strategies results from turnover in species composition (beta diversity) and intraspecific trait variation along the gradient. Rooting strategies are shaped by multidimensional trade-offs: a single trade-off axis representing investment in root productivity versus durability (dark blue line) and a three-way trade-off representing different ways that plants can acquire below-ground resources (light blue triangle; note that the shape of the triangle can vary). The productivity-durability trade-off captures a root strategy spectrum associated with investment in root growth (root length density, RLD) versus investment in durable, long-lived roots (root tissue density, RTD, and root dry matter content, RDMC). The three-way trade-off is comprised of organ-level and whole-plant level allocation traits enabling do-it-yourself (DIY) resource acquisition by increasing specific root length (SRL) and root:shoot mass ratio (RSR) and symbiosis-level traits mediated by outsourcing resource acquisition to mycorrhizae (mycorrhizal dependency).

mass in this grassland system (Nippert & Holdo, 2015; Weaver & Darland, 1949), yet we acknowledge that deeper roots may also play important roles during particularly dry periods.

Community-level functional variation in response to the environment can be divided into two sources enabling phenotype-environment matching. Environmental filtering can favour species with different mean trait values, resulting in a change of community-level trait variation due to species turnover (Kraft et al., 2015; Westoby & Wright, 2006). Intraspecific trait variation, including genotypic variation and phenotypic plasticity, can also cause a change of community-level trait values (Russo & Kitajima, 2016; Zheng et al., 2022). The effects of species turnover and interspecific trait variation can outweigh the effects of intraspecific trait variation (Ryser & Eek, 2000), but intraspecific effects on community-level trait variation are often not negligible, especially under environmental stress (Luo et al., 2023; Niu et al., 2020; Zheng et al., 2022).

In rooting systems, it is often impractical to estimate inter versus intraspecific variation because of the difficulty of linking individual roots to species in natural systems. While approaches such as the genetic barcoding of roots show promise (Bardgett et al., 2014; Luo et al., 2021), this method may often not be feasible, particularly in grasslands. Our approach was to indirectly estimate the relative contribution of interspecific versus intraspecific effects based on their partial R^2, or the unique explanatory power of species turnover versus variation in soil properties. A limitation of this approach is that it only estimates the portion of intraspecific variation responding to measured soil properties. However, other factors also influence intraspecific variation, such as local adaptation and unmeasured abiotic and biotic environmental factors (Russo & Kitajima, 2016; Sultan, 1995; Whitman & Agrawal, 2009), which are not accounted for here. Keeping in mind these caveats, we found that the portion of root strategy variation attributable to intraspecific effects was similar to the proportion attributable to interspecific variation in our grassland system. This result emphasises the importance of within-species sources of phenotypic variation, which are not accounted for when only species-average trait values are used in large-scale studies of plant strategies.

4.3 | Multiple trade-off dimensions in rooting strategies

Multivariate analyses of root variables revealed clear multidimensional trade-offs defining variation in community-level rooting strategies along the edaphic gradient. We found a strong negative correlation of RLD with RDMC and RTD, supporting a root productivity-durability trade-off axis, as proposed in existing root economic frameworks (Bergmann et al., 2020; Carmona et al., 2021; Craine et al., 2001; Weemstra et al., 2016; Yan et al., 2022). Although these relationships sometimes exhibited variation in slopes among habitats and sites, their consistent, significant, negative correlation regardless of habitat and site provided strong support for this trade-off axis. RLD is a proxy for rooting surface area (Eissenstat, 1991), but since RLD is scaled by soil volume rather than plant biomass, it reflects the above- and below-ground plant productivity supported by the environment. Ideally, root lifespan would be estimated from root turnover (Ostertag, 2001), but RDMC and RTD have been used as surrogates for longevity, which is often longer in resource-poor soil (Craine et al., 2002, 2005; Eissenstat et al., 2000; Kochsiek et al., 2013; Weemstra et al., 2020). Our results showing higher RLD in wetter soil, but higher RTD and RDMC in drier soil, is consistent with previous findings (Hanslin et al., 2019; Searles et al., 2009) and suggest that these traits may be reasonable proxies of root productivity and root longevity, respectively.

We did not, however, find a one-axis DIY versus outsourcing trade-off represented by SRL and RD, as proposed in previous root economic frameworks (Bergmann et al., 2020; Carmona et al., 2021). RD is considered a mycotrophic trait because higher RD is thought to provide more cross-sectional space for mycorrhizal fungi (Eissenstat et al., 2015; Weemstra et al., 2016) and therefore to be a stand-in for the degree of mycorrhizal dependence. However, in our grassland system, RD was not or was only weakly correlated with our more direct measures of mycorrhizal dependency (AMF colonisation rate and intensity) and was not correlated with SRL. Thus, our findings suggest not only that RD is likely to be an inadequate proxy for mycorrhizal dependency, but also that a single axis of DIY versus outsourcing may not fully capture the different mechanisms of below-ground resource acquisition.

Instead of the one-dimensional DIY versus outsourcing axis, we found a three-way trade-off encompassing organ-level, plant-level and symbiosis-level rooting strategy variables, as represented by covariation between SRL, RSR and AMF colonisation rate and intensity, which did not align on a single axis. The three-way trade-off was also supported by the weak bivariate correlations between each pair of the three variables (because any pair of the three variables cannot align on a single axis due to influence of the third variable), which in contrast to the stronger bivariate correlation of RLD with RTD and RDMC that were involved in the one-dimensional root productivity-durability trade-off. SRL and RSR are two distinct mechanisms for increasing root surface area (Poorter et al., 2012; Weemstra et al., 2020), and increased fine root length can also functionally substitute for reduced mycorrhizal dependence (Körner & Renhardt, 1987). Our findings indicate that at the community level, plants may use varying combinations of these mechanisms for below-ground resource acquisition, depending on the whole-plant strategy and environment. The more productive communities in wetter habitats had either higher SRL or AMF dependency and more acquisitive roots (higher RLD and lower RDMC), whereas the less productive communities in drier habitats had higher RSR and more conservative roots (higher RTD and RDMC). Following previous studies (e.g. Han et al., 2020; Hooper, 1998; Wilson & Tilman, 1991; Yin et al., 2021), we estimated RSR by converting the root mass from one core to the quadrat level, at which AGB was measured. Measuring above- and below-ground biomass at the same scales may provide more accurate estimates of RSR. Together, these results showed that there can be multiple ways to 'DIY' in below-ground resource acquisition, but these may not always compromise mycorrhizal dependency.

Much remains unknown concerning mycorrhizal-related traits (Chagnon et al., 2013; Chaudhary et al., 2022), which can vary across environments and evolutionary lineages of both fungi and plants (Koch et al., 2017; Mensah et al., 2015; Shi et al., 2023; Wipf et al., 2019). Our measurements of AMF colonisation provided insights on the abundance of AMF interacting with roots (Barceló et al., 2020; Bell et al., 2021). However, measurements of mycorrhizal colonisation are uncommonly made in studies of plant rooting strategy trade-offs, which can neglect key aspects affecting plant performance and influencing trade-offs (Schaffer-Morrison & Zak, 2023). Even so, AMF colonisation provides an incomplete picture of AMF dependency, which at the community level may be more related to root length colonised than RD and which may depend on other mycorrhizal traits, such as the allocation ratio of mycorrhizal fungal structures inside versus outside the roots (Barceló et al., 2020). Our study provides novel insights as to how mycorrhizae shape trade-offs in rooting strategies along environmental gradients.

Based on our findings, we propose a new trade-off framework of rooting strategies at the community level (Figure 5). Because our framework is defined at the community level, it cannot directly explain natural selection on rooting strategies at the species level. However, we posit that it is still informative for understanding the evolution of rooting strategies because below-ground resources and plant strategies to obtain them depend on community-level responses (Farrior, 2014; Suding et al., 2008). Moreover, functional traits, including rooting strategy variables, are shaped by environmental variation and have a high degree of intraspecific variation and plasticity (Lambers & Poorter, 1992; Wahl et al., 2001), which cannot be fully captured by largescale species-level studies that decouple trait values from their environments.

5 | CONCLUSIONS

Our study advances our understanding of the functional ecology of rooting strategies in several ways. We posit that focusing solely on organ-level traits is insufficient for capturing trade-offs in rooting strategies and how they vary along environmental gradients. Instead, we suggest that rooting strategies are defined by multidimensional trade-offs encompassing organ, whole-plant allocation and mycorrhizal symbiosis-levels that reflect the strong influence of phenotypic integration of root system functioning into whole-plant ecological strategies. Although mycorrhizal symbiosis is widely recognised to influence plant function, direct measures of mycorrhizal dependency are often not quantified along with other rooting strategy traits at the organ and whole-plant level, as we have done here. Integrating our findings, we present a novel, multi-dimensional trade-off framework for understanding rooting strategies that links rooting strategy variation across multiple levels of biological organisation. Future studies should test the generality of our multidimensional root strategy framework in other soil types, plant communities and ecosystems.

AUTHOR CONTRIBUTIONS

YY and SER conceived and designed the study. YY conducted data collection and analysis. YY and SER wrote the manuscript.

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CONFLICT OF INTEREST STATEMENT

Sabrina E. Russo is an Associate Editor of Functional Ecology but took no part in the peer review and decision-making processes for this paper. The authors declare no conflicts of interests with other organisations.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from UNL data archive: https://doi.org/10.32873/unl.dr.20230705 (Yang & Russo, 2023).

STATEMENT ON INCLUSION

This project was carried out by a diverse set of researchers. Undergraduate and high school field assistants on this project included women and underrepresented groups. We appreciate the contributions and support of all parties involved, which are acknowledged above. The literature cited includes works published by scientists from the local region, as well as scientists from diverse backgrounds and career stages.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: List of species found in this study in sandhills prairie in Nebraska, USA, their taxonomy, and corresponding abbreviations.

Table S2: Correlation of soil properties in sandhills prairie in Nebraska, USA.

Table S3: Results from multiple regression of distance matrices relating rooting strategy variables to soil properties, plant community composition, and geographic distances across three habitats at two sandhill prairie sites, Nebraska, USA.

Figure S1: Fine root biomass percent in three habitats along an edaphic gradient in two sandhills prairie sites, Nebraska, USA.

Figure S2: Variation in soil properties among three habitats along an edaphic gradient in two sandhills prairie sites, Nebraska, USA.

Figure S3: Variation in plant above-ground biomass and diversity along an edaphic gradient in sandhills prairie, Nebraska, USA.

Figure S4: Variation in above-ground traits across three habitats along an edaphic gradient at two sandhills prairie sites, Nebraska, USA.

Figure S5: Univariate differences of rooting strategy variables across three habitats along an edaphic gradient in two sandhills prairie sites, Nebraska, USA.

Figure S6: Pearson's correlation between rooting strategy variables and plant Shannon diversity across habitats in two sandhills prairie sites, Nebraska, USA.

Figure S7: Validation of principal components analyses of rooting strategy variables across habitats in two sandhills prairie sites, Nebraska, USA.

Figure S8: Pearson's correlation between organ-level root traits across habitats in two sandhills prairie sites, Nebraska, USA.

Figure S9: Pearson's correlation between plant-level allocation and organ-level root traits across habitats in two sandhills prairie sites, Nebraska, USA.

Figure S10: Correlations between mycorrhizal colonization rate and other rooting strategy variables across habitats in two sandhills prairie sites, Nebraska, USA.

Figure S11: Pearson's correlation between mycorrhizal colonization intensity and other rooting strategy variables across habitats in two sandhills prairie sites, Nebraska, USA.

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