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RESEARCH ARTICLE

Effects of warming and parasitism on root traits and the root economics space

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Abstract

1. Plants infected by parasitic species might be further stressed by climate warming as both factors can influence the host plant's nutrient acquisition and growth. The root economics space, defined by root functional traits, reflects a plant's nutrient acquisition strategy. However, the combined effects of warming and parasitism on root functional traits and their positions within the root economics space have not been extensively studies.
2. We grew soybean plants in pot cultures outdoor in the absence or presence of parasitism by *Cuscuta gronovii* and with or without simulated climate warming using infrared heater lamps. We measured various root functional traits of soybean, including root morphological traits, symbiosis with arbuscular mycorrhizal fungi (AMF) and rhizobia and enzyme activity. Correlations among these traits were analysed, and principal component analysis was used to determine the position of the plants in the root economics space.
3. Parasitism significantly reduced AMF colonization rate, nodule biomass, root tissue density (RTD) and phosphatase activity in the rhizosheath, while increasing root nitrogen concentration (RN). Nodule biomass was positively correlated with AMF colonization, indicating an 'outsourcing' strategy for nutrient foraging. Parasitized soybeans occupied a trait space with higher RN and lower RTD, indicative of a 'fast' nutrient acquisition strategy. Warming did not significantly affect root functional traits or the plants' positions in the root economics space, regardless of parasitism presence.
4. This study is the first to demonstrate that rhizobial colonization, similar to AMF colonization, is part of the 'outsourcing' strategy and that parasitism shifts host plants from a 'slow' to a 'fast' nutrient uptake strategy. These findings provide new insights into plant below-ground strategies under warming and parasitism.

KEYWORDS
collaboration gradient, conservation gradient, elevated temperature, parasitization, plant–plant interactions

1 | INTRODUCTION

Global surface temperatures have risen by approximately 1.2°C since 1850 (NOAA, 2020) and are projected to increase by an additional 2.2°C by 2100 (Lyon et al., 2022). Climate warming can impact the fitness and distribution of plants by altering root morphology, symbiosis and nutrient acquisition strategies (Arndal et al., 2013; Dukes et al., 2005; Liu et al., 2013; Meza-Lopez & Siemann, 2017; Nijs et al., 1996; Olsrud et al., 2010; Qiu et al., 2021; Rillig et al., 2002; Wertin et al., 2017; Zhou et al., 2022). Alongside climate-induced abiotic stresses, plants face biotic stresses, such as herbivory, pathogen infection and parasitism by other plants (Albornoz et al., 2017; Bardgett et al., 2006; Sentis et al., 2020). Although the effects of climate change on herbivores and pathogens have been studied (Laughton et al., 2017; Lemoine et al., 2017), its impact on the interactions between host plants and parasites remains less understood.

Parasitic plants often cause serious damage to host plants by directly extracting nutrients from the host or indirectly reducing the host's nutrient acquisition capabilities (Yuan et al., 2021; Yuan, Gao, et al., 2023; Yuan & Li, 2022). To enhance nutrient uptake, plants have evolved various strategies involving different root functional traits (Carmona et al., 2021; Wang et al., 2023). First, to increase nutrient foraging efficiency and uptake, plants can grow longer and thinner roots, resulting in a higher specific root length (SRL) and specific root area (SRA), and a lower root diameter (RD). Symbiotic relationship with arbuscular mycorrhizal fungi (AMF) further enhances nutrient extraction from the soil (Yaffar et al., 2022). Second, to increase the nutrient uptake rate, plants can decrease root construction costs by having a lower root tissue density (RTD) and increase the metabolic rate by having a higher root nitrogen content (Bergmann et al., 2020; Ding et al., 2023; Wang et al., 2023). Enzymatic activities, such as acid phosphatase (APase) release, also play a role in nutrient availability by enhancing organic matter mineralization (Bi et al., 2023). Measuring the root functional traits of plants under different environmental conditions may help to predict how plant performance will respond to environmental change.

To better understand the relationships among root functional traits and to predict root responses to environmental changes, ecologists have recently used multiple root traits to define the 'root economics space' (Bi et al., 2023; Ding et al., 2023; Han et al., 2022; Kramer-Walter et al., 2016; Ren et al., 2023). This framework includes two primary dimensions: the collaboration gradient, ranging from a 'do-it-yourself' strategy with thin roots to an 'outsourcing' strategy with thick roots facilitating AMF symbiosis and the conservation gradient, ranging from a 'slow' resource acquisition strategy with high roots tissue density to a 'fast' resource acquisition strategy with high root nitrogen content (Figure S1) (Bergmann et al., 2020; Ding et al., 2020). The root economics space was initially based on RD, SRL, root nitrogen content and RTD (Bergmann et al., 2020). Several other root traits have aligned with the two main dimensions. For example, the percentage mycorrhizal colonization was found to be correlate with RD, reflecting the 'outsourcing' strategy. Furthermore, root phosphatase activity exhibited a positive relationship with SRL and a negative relationship with AMF colonization, indicating that root phosphatase activity contributes to the 'do-it-yourself' strategy along the collaboration gradient (Han et al., 2022). Additionally, nitrogen-fixing bacteria, like rhizobia in legumes, represent another form of nutrient acquisition outsourcing (Thilakarathna & Raizada, 2017), though their relationship with the root functional traits that define the root economics space remains poorly understood.

The position of plants in the root economics space has been used to predict their nutrient acquisition strategies (Carmona et al., 2021; Ren et al., 2023; Sun et al., 2021; Sweeney et al., 2021). For example, Wang et al. (2023) found that relative to tree species, liana species have higher SRL and nitrogen contents, positioning them on the fast resource acquisition side of the root economics space. It has also been shown that nutrient-rich grasslands are characterized by 'fast' plant communities, while moist grasslands are characterized by 'do-it-yourself' plant communities (Lachaise et al., 2022). Although many studies have assessed the position of different species and plant communities in the root economics space, few have examined how the position of individual species changes with environmental conditions.

Climate warming has been shown to affect individual root functional traits (Birgander et al., 2017; Qiu et al., 2021). For example, Qiu et al. (2021) found that warming increased AMF colonization and RTD while decreasing SRL in soybean (*Glycine max*). These results suggest that, in response to warming, soybean may shift in the root economics space towards the 'outsourcing' and 'slow' strategies. Recently, species distribution models predicted that climate warming could increase the potential niche overlap between soybean and one of its major pests, parasitic plants in the genus *Cuscuta*, by up to sixfold by 2070 (Cai et al., 2022; Shao, 1990). Parasitic plants can strongly suppress the growth of their host plants and decrease carbon allocation of host plants to below-ground structures (Yuan, Gao, et al., 2023; Yuan & Li, 2022; Yuan, Lin, et al., 2023). For example, one of our previous studies showed that *Cuscuta* parasitism decreased root growth and AMF colonization in *Bidens pilosa*, while increasing nitrogen and phosphorus concentrations (Yuan, Lin, et al., 2023). If this holds true for soybeans as well, parasitism may cause them to shift in the root economics space towards the 'do-it-yourself' and 'fast' strategies. Thus, the concurrent effects of warming and parasitism on root traits might neutralize each other.

To test whether the root functional traits of soybean and its position in the root economics space are affected by climate warming and parasitism by *Cuscuta gronovii*, we conducted a factorial pot experiment outdoors. On the host plants, we measured SRL, SRA, RD, root nitrogen concentration (RN), RTD, AMF colonization (MC), rhizobia nodule biomass (NB) and APase activity in the rhizosheath. We characterized changes in the relationships among these root traits and the positions of soybean plants along the axes of the root economics space in response to warming and parasitism. We hypothesized that (i) AMF and rhizobial colonization are positively correlated and align with the 'outsourcing' strategy within the root economics space; (ii) warming will shift soybean plants from a 'do-it-yourself' to an 'outsourcing' strategy by increasing colonization by both AMF and rhizobia, and from a 'fast' to a 'slow' nutrient acquisition strategy by producing roots with higher RTD and lower RN; (iii) parasitism will shift soybean plants from an 'outsourcing' strategy to a 'do-it-yourself' strategy by reducing colonization by both AMF and rhizobia, and from a 'slow' to a 'fast' nutrient acquisition strategy by producing roots with lower RTD and higher RN; and (iv) when plants are exposed to both warming and parasitism, their individual effects on root traits will neutralize each other.

2 | MATERIALS AND METHODS

2.1 | Plant materials

The host plant used in this study was soybean (*Glycine max* (Linn.) Merr.), cultivar 'Zhonghuang 37', with seeds sourced from the Chinese Academy of Agricultural Sciences. Stems of parasitic plant, *Cuscuta gronovii* Willd. ex Schult., were collected from a field population near Taizhou University.

2.2 | Experimental design and manipulations

The experiment was conducted in the outdoor research garden on the Jiaojiang Campus, Taizhou University, Zhejiang province, China (28°65′N, 121°39′E). The local climate is humid subtropical monsoon with an average annual precipitation ranging from 1100 to 2200mm. Soil used in the study was collected from the base of a mountain in the Jiaojiang District, Taizhou, China. This sandy soil had a pH of 6.14, organic carbon content of 3.35 $g\,kg^{-1}$, total nitrogen of 45.12 $mg\,kg^{-1}$ and available phosphorus of 12.62 $mg\,kg^{-1}$. The field soil was air-dried, mixed and sieved through a metal grid with a 1-cm mesh size before being filled into pots (diameter: 28cm, height: 19cm).

The experimental set-up included three blocks, each measuring 6.1m×2.1m (length×width) and containing two triangular plots (sides of 2.5m) spaced 1.1m apart. One plot in each block was warmed 24h a day using three infrared heater lamps (Model LPR2420/1500-L, Longpro Co., Ltd., Guangzhou, China), while the other plot served as a control. The infrared lamps were 2.5m above the ground in the warmed plots. Air temperature was monitored in all plots using a temperature sensor (Model DTE10T, Delta Co., Ltd., Taiwan, China) placed 0.5m above the ground. Following the IPCC (2022) scenarios predicting global temperature increase of 1.5–4.5°C, we simulated climate warming by elevating the air temperature by 3°C, similar to other studies (Meyer et al., 2021; Qiu et al., 2021). In each plot, eight pots (diameter×height, 25cm×20cm) filled with 3kg of field soil were randomly allocated to fixed positions, resulting in a total of 48 pots (3 blocks×2 plots×8 pots).

On 26 May 2022, soybean seeds were surface sterilized in a 0.5% NaClO solution for 10min and then washed three times with sterile water. Three seeds were planted into each of the 48 pots, resulting in three soybean plants per pot upon germination. One month later, 10cm long stem pieces of *C. gronovii* were wound around the stems of the soybean plants in four of the eight pots per plot to induce parasitism.

2.3 | Plant harvest and measurement of root trait parameters

On 21 August 2022, the soybean plants were harvested. Aboveground biomass was harvested by cutting the plants at the soil surface, then drying them at 65°C for 72h to determine the dry mass per plant (averaged across the three plants per pot).

Roots were washed free from substrate, and the roots of the three soybean plants in each pot were separated. Rhizobia nodules were separated from the host roots and dried at 65°C for 72h to determine their dry mass. Fresh roots of each plant were scanned using a flatbed scanner (Model perfection V850 Pro, Epson Co., Ltd., Japan) and analysed with WinRHIZO software (Regent Instruments, Inc. Quebec, Canada) to determine RD, root length (RL), root surface area (RA) and root volume (RV). Then roots were dried at 65°C for 72h to determine the root dry mass per plant. SRL was calculated by dividing the root length by the root dry mass. SRA was calculated by dividing the root area by the root dry mass. RTD was calculated by dividing the root dry mass by root volume (Xu et al., 2021). AMF colonization was determined on dried roots that had been cleared in 10% KOH and stained with acid fuchsin, evaluated using the modified gridline intersection method (Giovannetti & Mosse, 1980) with 200 intersections per root sample observed under a microscope at 20× magnification. Root parameter values were averaged across the three soybean plants per pot.

Before washing the roots, a joint sample of rhizosheath soil from the three soybean plants in each pot was collected. Phosphatase activity (APase) was measured on these samples using the soil phosphatase assay kit (Suzhou Michy Biomedical Technology Co., Ltd., Suzhou, China), following the manufacturer's protocol.

2.4 | Statistical analysis

All statistical analyses were performed using R 4.2.2 (R Core Team, 2022). Linear mixed-effects models were used to examine the effects of warming, parasitism and their interaction on the average values of soybean biomass and root traits per pot, implemented in the R package nlme (Pinheiro et al., 2023). Potential random terms included block only, plot only or plot nested within block. For each response variable, analyses were conducted with all three random models, selecting the one with the lowest Akaike information criterion. The block was used only as the random factor for RL and RN, while the plot was used for all other variables. Data were transformed to improve normality when necessary, using reciprocal transformation for RL and RN, and natural logarithm (loge) transformation for SRL and APase activity.

Pearson's correlation analysis was used to determine associations between root functional traits. Principal component analysis

(PCA) was performed to visualize these correlations, their definition of the root economics space and the positions of plants exposed to warming and parasitism treatments. Least significant difference tests were used to assess the significances of differences in mean scores of plants among different treatment combinations along the first and second principal component (PC) axes.

3 | RESULTS

3.1 | Biomass production

Warming did not significantly affect the biomass of the parasite *C. gronovii* (Figure S2). However, warming reduced the above-ground biomass of the soybean plants by −27%, although this effect was only marginally significant. Parasitism significantly reduced the above-ground biomass by −21% (Table 1; Figure 1A). Warming, parasitism or their interaction did not significantly affect the root biomass of the soybean plants (Table 1; Figure 1B).

3.2 | Root functional traits

None of the root functional traits measured on the soybean plants was significantly affected by warming (Table 1; Figure 2). RD, SRA and SRL were also not significantly affected by parasitism (Table 1; Figure 2A–C). However, parasitism significantly reduced RTD by −21% and APase activity by −35%, and significantly increased RN by +29% (Table 1; Figure 2D–F). The effect of parasitism on the functional root traits was not modified by warming (Table 1; Figure 2).

MC of the soybean roots was not significantly affected by warming (Table 1; Figure 2G), but was significantly reduced by parasitism by −28% (Table 1; Figure 2G). NB was reduced by warming by −30%, although the effect was only marginally significant and was significantly reduced by parasitism by −40% (Table 1; Figure 2H).

3.3 | Root trait dimensions

A PCA on the root traits measured showed that the first and second PC axes accounted for 34.92% and 33.48%, respectively, of the total variation (Table S1; Figure 3). These two orthogonal axes corresponded to the collaboration gradient and conservation gradient of the root economics space (Figure 3). SRL and SRA loaded negatively, while RD, MC and NB loaded positively on the first axis (the collaboration gradient) (Table S1; Figure 3). RN loaded negatively, and RTD and APase loaded positively on the second axis (the conservation gradient) (Table S1; Figure 3).

Warming and parasitism had no significant effects on the position of the soybean plants along the collaboration gradient of the root economics space (PC1; Figure 3). However, parasitism significantly shifted along the conservation gradient (PC2) from a 'slow' strategy with high RTD and APase but low RN values to a 'fast' strategy with low RTD and APase but high RN values (Figure 3).

3.4 | Associations of mutualists and APase with root morphological traits of the root economics space

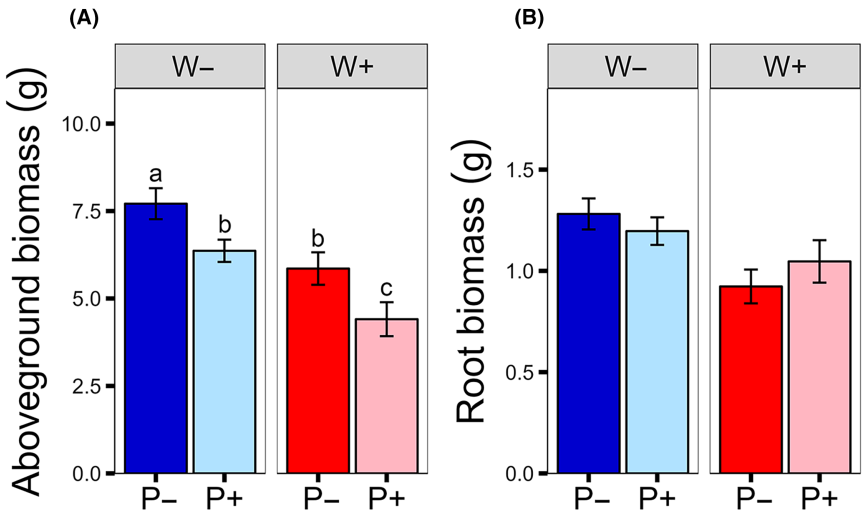
Across all treatments combined, the AMF colonization rate of soybean was significantly positively associated with nodule biomass

TABLE 1 Results of linear mixed models testing the effects of warming (W) and parasitism (P) on biomass and root functional traits of soybean.

	W		P		W × P				
Sources	df	F	df	F	df	F	SD block	SD plot	SD residual
Above-ground biomass	1, 4	**6.088**†	1, 40	**15.174*****	1, 40	0.020	–	1.022	1.219
Root biomass	1, 4	4.034	1, 40	0.064	1, 40	1.857	–	0.156	0.260
RD	1, 4	0.590	1, 40	2.514	1, 40	0.003	–	0.172	0.595
SRA	1, 4	0.892	1, 40	1.953	1, 40	0.099	–	52.716	137.631
SRL	1, 4	<0.001	1, 40	0.117	1, 40	0.045	–	0.095	0.512
RTD	1, 4	2.148	1, 40	**12.291****	1, 40	0.087	–	0.017	0.036
APase	1, 4	0.090	1, 40	**20.139*****	1, 40	0.018	–	0.189	0.298
RN	1, 41	0.504	1, 41	**121.634*****	1, 41	0.019	0.003	–	0.006
MC	1, 4	0.504	1, 40	**11.218****	1, 40	0.367	–	12.162	15.897
NB	1, 4	**5.144**†	1, 39	**31.750*****	1, 39	2.008	–	0.079	0.117

Note: *F* values are shown for the fixed terms, and standard deviations (SD) for the random terms. Significant *F* values ($p < 0.05$) are highlighted in bold.
Abbreviation: APase, acid phosphatase activity in the rhizosheath; df, degree of freedom; MC, AMF colonization rate; NB, nodule biomass; RD, root diameter; RN, root nitrogen concentration; RTD, root tissue density; SRA, specific root surface area; SRL, specific root length.
†$0.05 < p \le 0.10$.
**$0.001 < p \le 0.01$. ***$p \le 0.001$.

FIGURE 1 Effects of warming and parasitism on soybean biomass per plant. (A) above-ground biomass; (B) root biomass. Data are means ± SE. P−, Without parasitism; P+, With parasitism; W−, Soybean in unwarmed control plots; W+, Soybean in warmed plots. Different lowercase letters indicate a significant difference ($p < 0.05$) between treatment combinations.



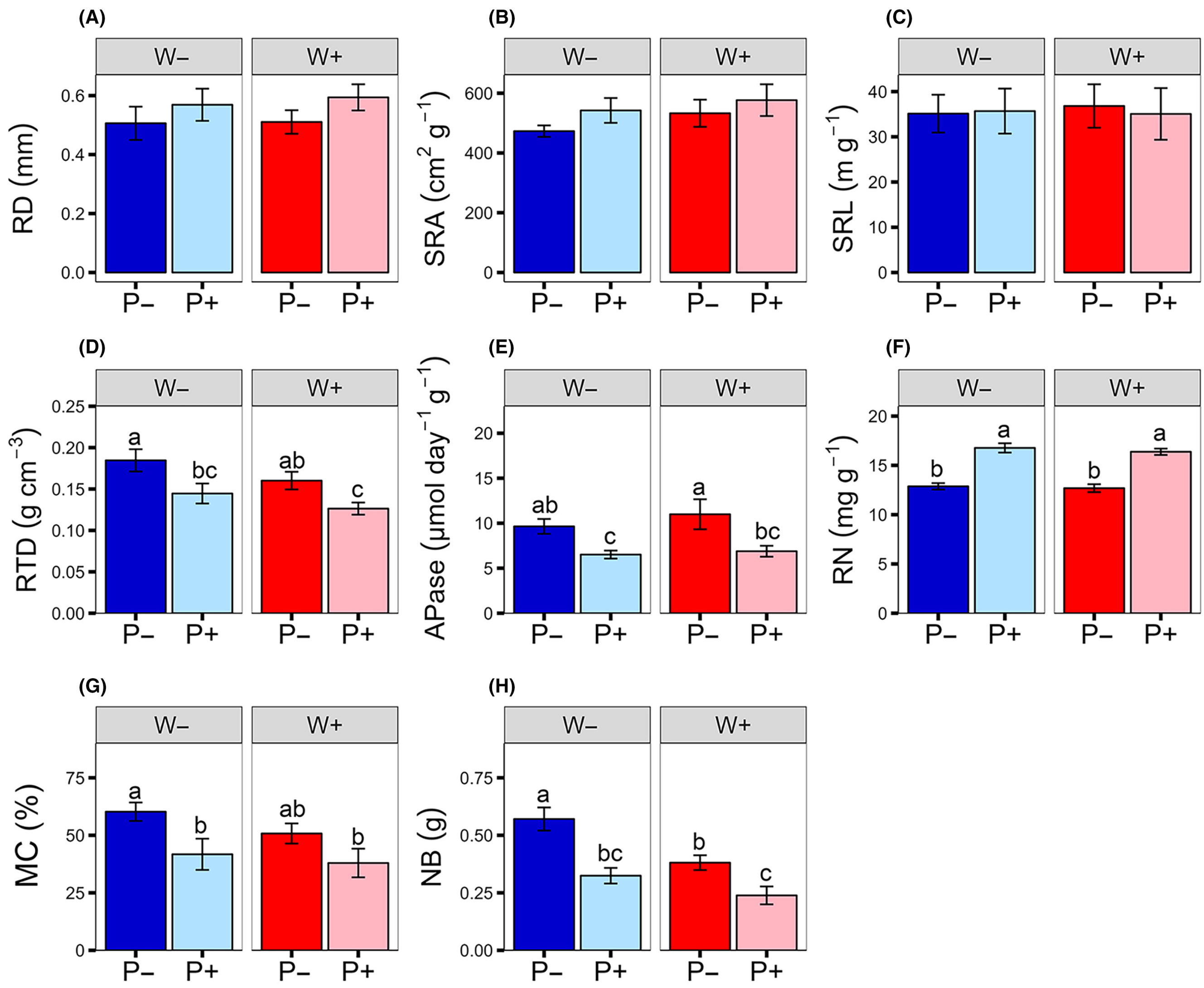


FIGURE 2 Effects of warming and parasitism on root functional traits of soybean. (A) root diameter (RD); (B) specific root area (SRA); (C) specific root length (SRL); (D) root tissue density (RTD); (E) acid phosphatase activity in the rhizosheath (APase); (F) root nitrogen concentration (RN); (G) AMF colonization rate (MC); (H) nodule biomass (NB). Data are means ± SE. P−, Without parasitism; P+, With parasitism; W−, Soybean in unwarmed control plots; W+, Soybean in warmed plots. Different lowercase letters indicate a significant difference ($p < 0.05$) between treatment combinations.

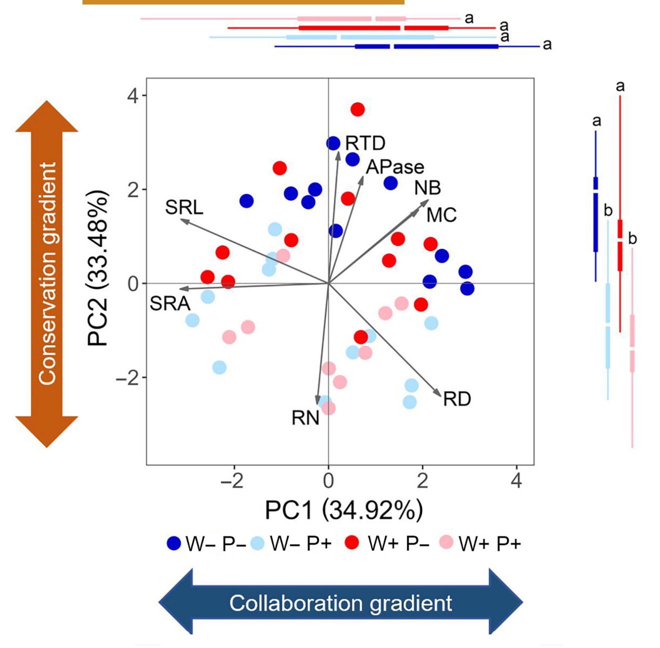


FIGURE 3 Principal component analysis (PCA) for root functional traits of soybean. Loading scores are shown in Table S1. Points indicate the position of the soybean plants along the first two axes. Box and whisker plots on the top and right of the panel show the median, upper and lower quartiles, and maximum and minimum of principal component axis 1, corresponding to the collaboration gradient, and axis 2, corresponding to the conservation gradient. Groups with different letters are significantly different ($p < 0.05$). APase, Acid phosphatase activity in the rhizosheath; MC, AMF colonization rate; NB, Nodule biomass; RD, Root diameter; RN, Root nitrogen concentration. W− P−, Soybean in unwarmed control plot without parasitism; RTD, Root tissue density; SRA, Specific root surface area; SRL, Specific root length; W− P+, Soybean in unwarmed control plot with parasitism; W+ P−, Soybean in warmed plot without parasitism; W+ P+, Soybean in warmed plot with parasitism.

(Figure 4a; Figure S3). SRA, but not SRL and RD, was significantly negatively associated with AMF colonization rate and nodule biomass (Figure S3). However, the correlations depended on the warming and parasitism treatments (Figure 4b–g). Significant correlations were, with one exception, only found for soybean plants without warming and without parasitization. In this treatment combination, MC and NB were significantly negatively correlated with SRL and SRA, and NB was significantly positively correlated with RD (Figure 4). The negative correlation between MC and SRA was also significant for parasitized plants without warming.

Across all treatments combined and when soybean plants grew in the warmed plots with parasitism, APase was significantly negatively associated with RN and significantly positively correlated with RTD (Figure 5; Figures S3 and S4).

4 | DISCUSSION

Root trait (co)variation within a single species, soybean (*Glycine max*), primarily aligned along a collaboration and a conservation gradient (Figure 3), consistent with findings across species (Bergmann et al., 2020) and among communities (Lachaise et al., 2022). The collaboration gradient is characterized by a negative correlation between RD and SRL, while the conservation gradient is marked by a negative correlation between RTD and RN (Ding et al., 2023). Root colonization by AMF and rhizobia was associated with the 'outsourcing' strategy along the collaboration gradient, and APase activity was aligned with the 'slow' strategy of the conservation gradient (Figure 3). Parasitism by *Cuscuta gronovii* and warming both negatively impacted soybean biomass, but only parasitism significantly altered root traits, shifting plants along the conservation gradient from a 'slow' to a 'fast' strategy (Table 1; Figure 3). Contrary to expectations, the effects of parasitism on root traits were not neutralized by warming.

Despite reports of competition between AMF and rhizobia (Larimer et al., 2014; Vázquez et al., 2001), the results demonstrated a positively correlation between AMF colonization and nodule biomass (Figure 4). This likely reflects that thicker roots facilitate both AMF and rhizobial colonization (low SRL and high RD), suggesting that AMF and rhizobia do not necessarily compete, as they provide complementary resources: phosphorus from AMF and nitrogen from rhizobia (Larimer et al., 2014; Liu et al., 2023). Additionally, both mutualists heavily loaded on the first PC axis (the collaboration gradient) and showed significant negative relationships with SRA, indicating a trade-off between maximizing root surface area for nutrients uptake and colonization by AMF and rhizobia. AMF is already widely recognized as an 'outsourcing' strategy (Bergmann et al., 2020), and it also seems evident that rhizobial colonization is a mechanism of outsourcing for plants. Furthermore, rhizobia can disperse along AMF hypha (Jansa & Hodge, 2021; Zhang et al., 2020) and promote AMF hyphal growth and extension (Xie et al., 2020). Therefore, rhizobial colonization could also contribute to the 'outsourcing' strategy by enhancing nutrient foraging by AMF.

Nodule biomass correlated positively with RTD and negatively with RN (Figure S3), suggesting alignment with the 'slow' strategy along the conservation gradient (Figure 3). The conservation gradient is characterized by a trade-off between slow and fast resource return on carbon investment (high RN indicates fast resource return, while high RTD indicates high carbon investment in root construction) (Figure S1) (Bergmann et al., 2020; Ding et al., 2020). The negative correlation between NB and RN and the positive correlation with RTD suggest a trade-off between carbon investment in rhizobial colonization and nutrient return. Thus, rhizobial colonization of soybean roots represents outsourcing nitrogen uptake and a high carbon investment for root construction.

Previous studies have shown varying effects of warming on plant roots and associated microbes, with positive (Norby & Jackson, 2000; Rillig et al., 2002), negative (Bai et al., 2010; Olsrud et al., 2010) or neutral (Arndal et al., 2013; Dukes et al., 2005) outcomes. In water-limited ecosystem, warming often induces drought stress, suppressing root growth and symbiosis formation (Bai et al., 2010; Olsrud et al., 2010). Conversely, warming can promote root growth in water-abundant conditions, allowing roots to explore a larger soil volume

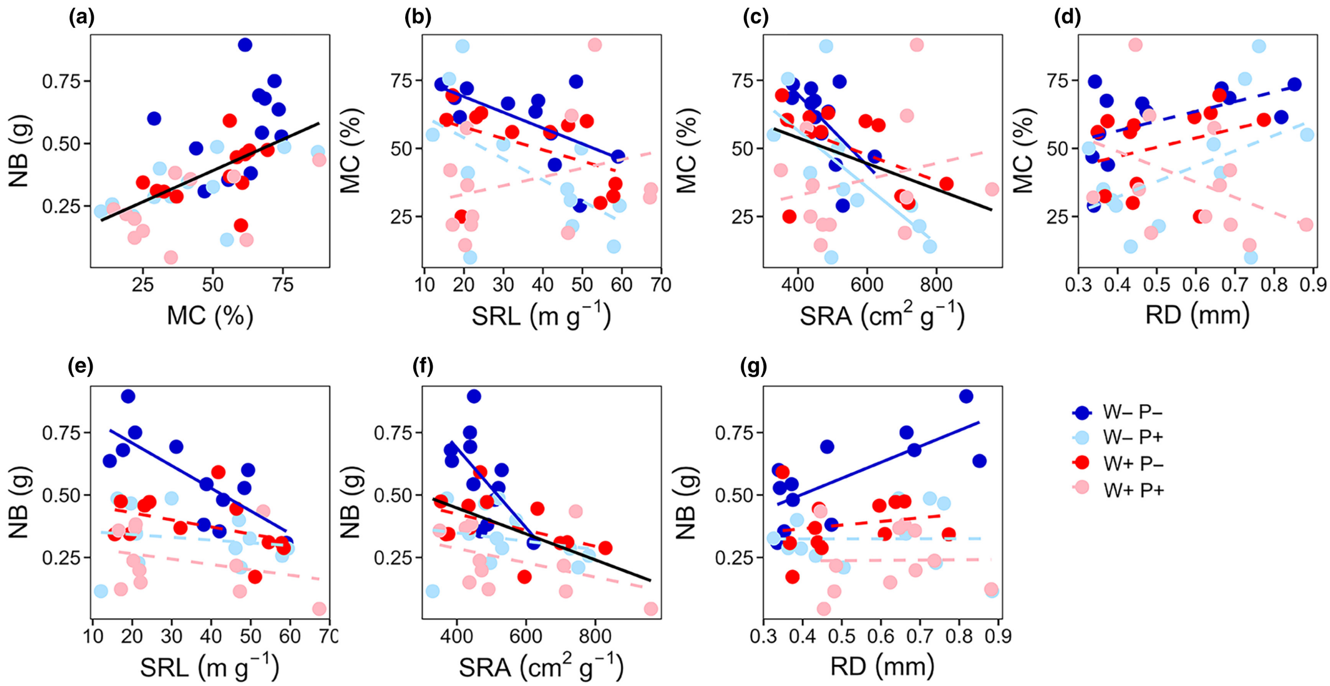


FIGURE 4 Correlations between AMF colonization rate (MC) and nodule biomass (NB) (a), MC and specific root length (SRL) (b), MC and specific root area (SRA) (c), MC and root diameter (RD) (d), correlations between NB and SRL (e), NB and SRA (f), NB and RD (g). W− P−, Soybean in unwarmed control plot without parasitism; W− P+, Soybean in unwarmed control plot with parasitism; W+ P−, Soybean in warmed plot without parasitism; W+ P+, Soybean in warmed plot with parasitism. Solid lines indicate significant correlations ($p < 0.05$), and dashed ones indicate non-significant correlations ($p > 0.05$). Solid black lines indicate significant correlations across the treatment combinations.

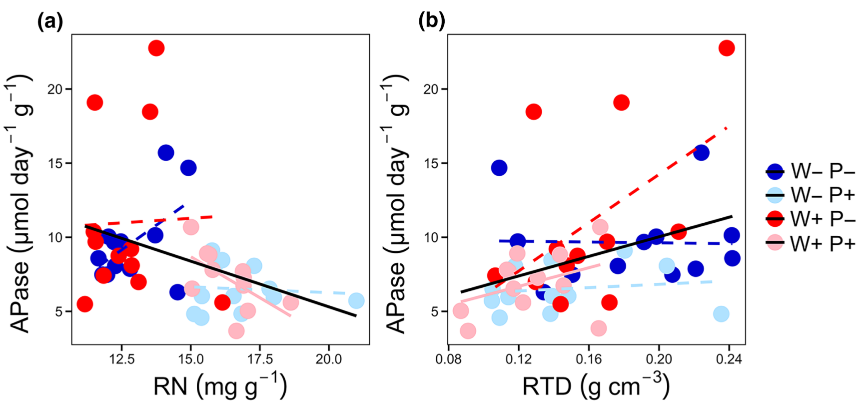


FIGURE 5 Correlations of acid phosphatase activity in the rhizosheath (APase) with root nitrogen concentration (RN) (a) and root tissue density (RTD) (b). W− P−, Soybean in unwarmed control plot without parasitism; W− P+, Soybean in unwarmed control plot with parasitism; W+ P−, Soybean in warmed plot without parasitism; W+ P+, Soybean in warmed plot with parasitism. Solid lines indicate significant correlations ($p < 0.05$), and dashed ones indicate non-significant correlations ($p > 0.05$). Solid black lines indicate significant correlations across the treatment combinations.

(Norby & Jackson, 2000; Rillig et al., 2002). In this study, warming had marginally significantly negative effects on above-ground and nodule biomass and significantly decreased root length (Table 1; Table S2; Figures 1 and 2; Figure S5). These results indicate that soybean plants in warmed plots are exposed to drought stress due to increased evapotranspiration, which leads to decreased growth, as indicated by lower soil water content in warmed plots (Figure S6). So, the light drought stress caused by the warming treatment may have reduced overall growth.

Previous studies have found that roots functional traits showed inconsistent responses to climate warming. Some studies showed that warming increased SRL (Chen et al., 2018; Kwatcho Kengdo et al., 2022), while other studies reported that warming decreased SRL (Kasurinen et al., 2016; Wan et al., 2004). This study found little warming effect on root morphological traits defining the root economics space. Although these results are inconsistent with the significant effects of warming on root traits reported by Qiu et al. (2021), they align with the absence of a warming effect on root biomass, SRL, RD and SRA found in a previous data synthesis study (Zhao et al., 2023). The overall inconsistent responses of root traits to climate warming may be attributed to different warming magnitudes, experiment durations or other experimental conditions (Wang et al., 2021). For example, the synthesis study by Zhao et al. (2023) found that warming duration significantly positively influenced the effects of warming on SRL, C:N ratio and root phosphorus concentration.

Parasitism decreased rhizobia and AMF colonization, but did not affect RD, SRL or the PC scores corresponding to the collaboration gradient. This indicates that parasitism did not affect root thickness but decreased mutualistic interactions. Some studies have shown a trade-off between SRL and AMF, with high SRL values typical for the 'do-it-yourself' strategy and AMF for the 'oursourcing' strategy (Ding et al., 2023; Qiu et al., 2021). Parasitism in this study likely decreased the host plant's carbon investment in mutualism with AMF and rhizobia without allowing compensation through increased SRL. So, the parasite may have affected the usual trade-off between SRL and AMF colonization. Indeed, we only found trade-offs between SRL and colonization with AMF and rhizobia when soybean grew in the control plots without parasitism. In response to parasitism, however, plants increased RN and decreased RTD, shifting along the conservation gradient towards a faster nutrient uptake strategy.

APase activity, an enzyme that can enhance nutrient availability (Bi et al., 2023), was positively correlated with RTD and negatively correlated with RN (Figure 3), aligning with the 'slow' strategy along the conservation gradient. This result is consistent with Bi et al. (2023), but contrasts with Han et al. (2022), who found that APase aligned with the 'do-it-yourself' strategy. APase in the rhizosheath can originate from roots, rhizobia and hyphosphere microbes (Jiang et al., 2021; Wen et al., 2019; Zhang et al., 2022), hydrolysing organic phosphorus (Wen et al., 2019). Possibly, APase was not strongly aligned with the collaboration gradient because it can be produced by the fine roots, characteristic for the 'do-it-yourself' strategy or by rhizobia and microbes associated with AMF, typical of the 'outsourcing' strategy. As parasitism significantly decreased APase activity, possibly due to the energy cost of APase synthesis (Allen et al., 2020), this might result in the association of APase activity with the 'slow' strategy of the conservation gradient in our study.

Although the experimental design allowed for testing the hypotheses, one limitation of this study was using pot cultures for growing soybean plants. This set-up could have affected root growth and morphological traits due to space restriction (Peterson et al., 1991; Tsakaldimi et al., 2009). Despite this potential limitation, the study demonstrated that parasitism resulted in a shift in the nutrient acquisition strategy of the host plants. Additionally, climate warming was simulated using infrared heaters. While these heaters are commonly used to simulate climate warming (Bai et al., 2013) and can precisely control energy input with minimal physical disturbance to the surroundings (Hou et al., 2013), they cannot simulate the advective effects of climate warming (Hou et al., 2013). Therefore, future studies should explore whether climate warming simulated with other methods such as open-top chambers, affects root morphology.

5 | CONCLUSIONS

This study on soybean demonstrated that rhizobial colonization of roots, like AMF colonization, is part of the 'outsourcing' strategy. Parasitism shifted host plants from a slow to fast nutrient uptake efficiency. Contrary to expectations, warming had little effect on the root nutrient acquisition strategy and did not neutralize the impact of parasitism on root traits. This study is the first time to reveal the position of rhizobial colonization in the root economics space and show how parasitism affects the root nutrient acquisition strategy of the host plant. The findings provide new insights into host plants' responses to parasitism and the impact of stem parasitic plants on soil nutrient cycling via cascading effects. Despite studying only one host plant and parasite in pot cultures, this research is a significant step forward in understanding rhizobial bacteria's and parasitic plants' roles in the nutrient acquisition strategies. Future studies should consider more host species, parasitic plant species and regions to test the generality of these findings.

AUTHOR CONTRIBUTIONS

Yongge Yuan and Junmin Li designed the study; Yongge Yuan performed the experiments, analysed the data and wrote the manuscript; Mark van Kleunen and Junmin Li improved the manuscript. All authors contributed to subsequent versions.

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CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from Figshare https://doi.org/10.6084/m9.figshare.26133550.

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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: Loading scores of the root functional traits in the PCA for soybean across all treatments.

Table S2: Results of mixed linear models on the effects of warming (W) and parasitism (P) on root traits of soybean.

Figure S1: A conceptual representation of the root economics space from Bergmann et al. (2020) and Ding et al. (2023), in which specific root length (SRL) and root diameter (RD) represent the collaboration grandient, and root tissue density (RTD) and root nitrogen (RN) concentration represent the conservation gradient.

Figure S2: Effect of warming on biomass of *Cuscuta gronovii*.

Figure S3: Pairwise Pearson's correlations among root traits of soybean plants across all treatments.

Figure S4: Pairwise Pearson's correlations among root traits of soybean plants in each of the four different treatment combinations: soybean plants in unwarmed control plot without parasitism (a); soybean plants in unwarmed control plot with parasitism (b); soybean plants in warmed plot without parasitism (c); soybean plants in warmed plot with parasitism (d).

Figure S5: Effects of warming and parasitism on root traits of soybean: root length (RL) (a); root area (RA) (b); root volume (RV) (c).

Figure S6: Effect of warming on soil moisture content.

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