Applied Soil Ecology 180 (2022) 104615

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Maize varieties and their root trait variation mediate the development of rhizosphere arthropod diversity

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ARTICLE INFO

Keywords:
Maize
Rhizosphere
Root trait
Soil arthropod
Thailand

ABSTRACT

While ecological roles of rhizosphere arthropods are well documented, little is known about the relationship between the development of plant roots and soil arthropod communities in agroecosystems. In this study, we investigated the effects of maize varieties and their root traits on the diversity and community composition of soil arthropods over time. Soil arthropods and root traits were evaluated before planting and at 30 and 60 days after planting in four maize varieties with different root growth angles and lateral root branching. Arthropod diversity declined from day 0 to 30 but recovered by day 60 with the development of maize roots. Two maize varieties (Nei 542018 and Nei 542022) exhibited lower brace and crown root angles, and arthropod taxon richness was greater in these two varieties than in others. The highest abundance of detritivores and predators was found in one of the maize varieties (Nei 542018) which, in addition to lower root angle, attained greater root diameter and lateral root branching and length. Redundancy analysis indicated that soil arthropod composition was correlated with crown root angle. Our findings highlight the importance of root traits, especially the angle of the roots, to enhance arthropod biodiversity in the rhizosphere ecosystem.

1. Introduction

Arthropods are the most diverse and omnipresent multicellular organisms, and have been recognized as crucial drivers in soil ecological processes (Coleman et al., 2018; Eisenbeis and Wichard, 1987). Arthropods are involved in organic matter decomposition and mineralization of nutrients by acting as litter transformers and soil engineers, leading to improved soil chemical and physical structure (Culliney, 2013). Several studies have reported the relationships between soil arthropod diversity and plant roots from natural (e.g., forests) and agricultural areas (Bonkowski et al., 2009; Potapov et al., 2017). Arthropods generally inhabit the topsoil layer (approximately 0–20 cm of soil depth), where plant roots and organic matter are concentrated (Voroney and Heck, 2015). Arthropods, however, can also be found in the deeper soil layers (30–116 cm from the soil surface), but their abundance diminishes with decreasing root biomass (Hishi et al., 2008; Potapov et al., 2017). Experiments in microcosms revealed that the arthropod abundance in unplanted soils was 2 to 2.5 times lower than in planted soils (Eerpina et al., 2017), which illustrates the influence of roots on arthropods. Moreover, several indirect relationships between plant roots and arthropods were also reported in a review by Bonkowski et al. (2009). For example, the symbiont fungi attracted by plant roots indirectly promoted the abundance of springtails. Up to 50 % of the carbon content in soil arthropods was detected as root-derived due to the consumption of fungi on the root (Albers et al., 2006). Moreover, root exudates play important roles in the interaction between soil organisms and plants (Bais et al., 2006) by attracting natural enemies of herbivorous arthropods, for example, to suppress damage to plant roots and production (Bonkowski et al., 2009; Matsumoto, 1970).

Roots transport essential nutrients and water to above-ground plant parts (York et al., 2013), and also provide a suitable habitat in their rhizosphere for microorganisms and invertebrates (Bais et al., 2006; Garrett et al., 2001). The coexistence of plant roots and arthropods in the rhizosphere is likely a mutualistic relationship where plant roots provide shelter and root-derived carbon resources (Bonkowski et al., 2009), while soil fauna decompose organic matter and provide large pools of

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https://doi.org/10.1016/j.apsoil.2022.104615
Received 6 January 2022; Received in revised form 19 July 2022; Accepted 21 July 2022

nutrients in return (Pramanik et al., 2001; Wäckers et al., 2005). Plant roots and arthropods, therefore, together play an important role in maintaining energy flows within soil communities (Bonkowski et al., 2009; Scherber et al., 2010).

Despite the well-known relationships between soil arthropod biodiversity and plant roots, our knowledge on the relationships between soil arthropods and plant root traits is limited, and until now, only a few studies are available from forested habitats (Hishi et al., 2008). More studies are required on soil arthropods in the rhizosphere of crops, including maize *Zea mays*, a major crop supporting worldwide food demands (Bennetzen and Hake, 2009; O'Keeffe, 2009). Root traits have been widely studied to improve maize production (Lynch, 2007). For example, many varieties of hybrid maize have been bred with the aim of improving root structure, morphology and exudate, which consequently increase maize growth (Canellas et al., 2019; Zhao et al., 2018). Most of the new varieties bear a larger root system for supporting larger shoots and deeper roots to increase water and nutrient uptake (Tracy et al., 2020). Some maize varieties with shallower roots are known to better take up nutrients from the topsoil layer (Hund et al., 2009; Tracy et al., 2020). However, little is known about the relationships between the characteristics of maize roots and soil arthropod diversity. Root traits such as root diameter that are associated with root exudates (Matsumoto, 2008; Williams et al., 2021) may also be correlated with the arthropod community in the rhizosphere, which mainly consumes root matter (Scheunemann et al., 2015).

In this study, we investigated the dynamics of soil arthropod communities in the rhizosphere among four Thai inbred maize varieties with different root traits. Soil arthropod abundance, richness, and functional guild composition were analyzed to address our two objectives: (1) to investigate the effects of maize varieties on soil arthropod assemblages over time; and (2) to identify maize root traits that are relevant to soil arthropod diversity. We hypothesized that (1) the maize varieties with shallow roots are associated with greater diversity of arthropods that are concentrated in the top soil, and this in turn attracts predators; and (2) root traits such as greater root diameter are associated with arthropod diversity and composition.

2. Materials and methods

2.1. Plant materials

Four inbred varieties of Thai maize *Zea mays* (Nei 422004, Nei 492007, Nei 542018, and Nei 542022) with different root traits were chosen based on our preliminary screening study at Nakhon Sawan Field Crop Research Center (NSFCRC), Thailand (unpublished data). We have selected the maize varieties based on brace and crown root growth angles and lateral branching: both Nei 422004 and Nei 492007 typically have roots with steep angles with low and high lateral root branching, respectively (Supplementary Fig. S1); meanwhile, Nei 542018 and Nei 542022 both typically have shallow roots with high and low lateral root branching, respectively.

2.2. Field experiment

The study site was in a fallow area at Naraphirom Subdistrict, Banglen District, Nakhonpathom Province, Thailand (13° 55′ 11.04″ N, 100° 15′ 56.01″ E). The elevation is around 1–2 m above sea level. The annual temperature range between 28 and 30 °C and the mean precipitation is 1006 mm/year. Soil texture mainly was clay and contained 2.52 % organic matter, with a pH of 5.6. Prior to the field experiment, the study site was planted with common bean (*Phaseolus vulgaris*) and left with all crop residues after harvesting. The field experiment was conducted in rainy season from late June to early September 2019. The soil was tilled by tractor with 30 cm plow depth and approximately 4.3 kg of fertilizer (16 % N, 16 % P, 16 % K) was applied one week before maize planting.

The experiment employed a randomized complete block design with five replications. The field was divided into five 15×1.8 m rectangular blocks, and each block was separated approximately 1 m from the others. Each block was further divided into five equal plots (3×1.8 m). One of the plots was randomly selected and left as an unplanted area to serve as a control. The other four plots were randomly assigned to each of the four maize varieties. Each plot was divided into four rows with eight maize plants per row. The distance between rows was 0.70–0.75 m and the width between plants in the same row was 0.20 m. During the growing season, the entire study site, including the empty plots within each block, received regular watering and manual weed removal at the same frequency.

2.3. Soil and root sampling

Soil samples were collected three times during the experiment: on the day before planting (Day0), at 30 days after planting the maize (Day30), and at 60 days after planting (Day60). The period of 60 days was selected because this is the flowering period of maize and it also is used in the Shovelomics method for root trait measurements (see Trachsel et al., 2011). Soil sampling in the control plots was carried out by excavating a volume of soil (diameter 20 cm, depth 20 cm) with a shovel from a randomly selected area within each plot. In the planted plots, a maize, which was of typical height for the plot, was sampled from the middle rows (i.e., rows along the plot borders were avoided) and, for Day60, we selected maize plants of typical height in the middle rows, but away from the areas where Day30 samples were collected. The shoot was cut off at 3 cm aboveground. The roots with the surrounding soil bulk were then collected together, using the same method and soil volume as described for the control plot.

2.4. Root morphology evaluation

On Day30 and Day60, a total of five maize plants were sampled per plot to measure root morphological traits. We selected the five representative maize plants (having average height for their plot) from the middle rows. The maize roots were cleaned by gently removing the attached soil before measuring their morphology. Measurement of root traits followed the Shovelomics Scoring Method (Trachsel et al., 2011). Root trait measurements included the diameter of brace root, angle of brace root, lateral root branching of brace root, lateral root length of brace root, whorl number of crown root layer, number of crown roots, diameter of crown root, angle of crown root, lateral root branching of crown root, and lateral root length of crown root.

The countable traits, root whorl and number, were directly counted. For root angle measurement, each root was placed along the vertical center line of the semicircle on the shovelomic scoreboard (Supplementary Fig. S2). The angles of left and right arms of the root were measured (in degrees) and their average value was then used for further analyses. Root diameter was evaluated by a vernier caliper. For lateral roots, the length was measured with a ruler scale on the board (Supplementary Fig. S2), whereas the branching was scored by placing the brace and crown root along the bold horizontal line and comparing to patterns of lateral roots on the board (Supplementary Fig. S2). Three roots were selected for evaluation of root diameter, lateral root length, and lateral root branching, and they were measured at 3–5 cm from the point they emerged from the main stem of the crown or brace root.

2.5. Soil arthropod extraction and identification

Excavated soil from each plot was homogenized. Approximately 1000 cm^3 of homogenized soil was subsampled and placed on a 2×2 mm mesh sieve base in a Berlese-Tullgren funnel with a 25 W incandescent light bulb. Arthropods were extracted for seven days and preserved in 70 % ethanol.

Extracted specimens were sorted and studied under a stereomicroscope (ZEISS Stemi 305). Some small-sized arthropods were mounted on microscopic slides with Hoyer's medium. Arthropod identification was done at the family level following taxonomic literature (CSIRO Division of Entomology, 1991a, 1991b; Krantz and Walter, 2009). Functional guilds were assigned to each arthropod taxon based on literature and previous reports (CSIRO Division of Entomology, 1991b, 1991a; Gonçalves et al., 2020; Krantz and Walter, 2009). These guilds were herbivore, fungivore, detritivore, predator, and omnivore. Our soil arthropod data consisted of the number of individuals from each family per plot per sampling time. Animal use in this study was approved by the Faculty of Science, Mahidol University Animal Care and Use Committee SCMU-ACUC (MUSC 62-032-496).

2.6. *Data analyses*

The arthropod assemblages and root traits were analyzed using univariate and multivariate analyses implemented in R (version 4.0.2) (R Core Team, 2021). The control (unplanted soil) and four maize varieties (Nei 422004, Nei 492007, Nei 542018, and Nei 542022) are hereafter referred to as the experimental treatments. Preliminary data analysis showed that the root traits and arthropod taxon abundance did not vary among the blocks, but individual plots showed high variability. Therefore, we assigned plot as a random explanatory variable in the following univariate analyses.

Differences in individual root trait parameters among the four maize varieties were tested by generalized linear mixed models (GLMMs) in *lme4* (Bates et al., 2014). Days after planting (Day30 and Day60), maize variety, and their interaction were included as fixed factors. Root trait variables were either counts (i.e., lateral root branching of brace root, whorl number of crown root layer, number of crown root, and lateral root branching of crown root) or continuous numbers (remaining root traits), and we specified either Gaussian or Poisson family according to the distribution of the data in each response variable. When a GLMM was unable to converge for some root trait variables, the random explanatory variable was dropped and generalized linear models (GLM) were applied instead. When the effect of maize variety was significant, we conducted post-hoc comparisons in root traits among maize varieties using Tukey's pairwise comparison tests available in the *emmeans* package (Lenth et al., 2021).

We used non-metric multidimensional scaling (NMDS) in the *vegan* package (Oksanen et al., 2020) to visualize variation in arthropod assemblage composition among the days after planting (Day0, Day30, and Day60) and the experimental treatments (the control plus the four maize varieties). The abundance of arthropods was log-transformed to reduce the influence of highly abundant families. The ordinations of NMDS were based on Bray-Curtis dissimilarity with 20 random initializations using the *vegan* package. We tested effects of the days after planting, experimental treatments, and their interactions on overall arthropod assemblage composition using PERMANOVA sequential tests with 9999 permutations (*adonis2* function). We also tested the dispersion of arthropod assemblages (beta diversity) within Day0, Day30, and Day60 using the *betadisper* function.

Generalized linear mixed models using template model builder (glmmTMB) were performed using the *glmmTMB* package (Brooks et al., 2017) to evaluate the effects of the experimental treatments on total abundance, taxon richness, the abundance of individual taxa, and abundance of functional guilds. Sampling day, experimental treatment and their interactions were treated as fixed factors, while plot was a random factor. We employed glmmTMB to incorporate temporal autocorrelation of the arthropod data (which was sampled three times). Variance-covariance matrices were structured by specifying *ar1*, which builds covariance structures of unit-spaced intervals used for repeated sampling (Kristensen and Maeve, 2020). For the abundance of individual taxa, we included only arthropod families that occurred in >25 plots ($n = 75$) and with >30 individuals altogether, resulting in 23 taxa in total for the analysis. As we expected to see no differences in arthropod diversity in Day0 (before planting) and changes in the subsequent samples (Day30 and Day60), effects of the experimental treatments on arthropod abundance and richness were only considered significant when the interaction between the days after planting and the experimental treatments was significant. Differences between the experimental treatments were specified by post-hoc Tukey's pairwise tests in the *emmeans* package (Lenth et al., 2021).

Finally, distance-based redundancy analysis (RDA) was implemented using the capscale function in the *vegan* package to visualize and to test the correlation between maize root morphological traits and arthropod communities on Day30 and Day60, separately. To remove the influence of rare species that only constitute noise in the community-level response, we included only the 23 common arthropod families that were also used for univariate analyses described above. We used the Bray-Curtis dissimilarity index to quantify arthropod assemblage composition. The root trait values were all centered and then scaled. The significance of correlations between individual root traits and community composition were tested with 9999 permutations of the arthropod samples.

3. Results

3.1. *Phenotypic variation of maize root traits*

Results of generalized linear mixed model analysis are summarized in Supplementary Table S1 and phenotypic variation of root traits in Supplementary Table S2. All root traits showed significant variation among the four maize varieties. The angles of both brace and crown roots were significantly steeper in Nei 422004 and Nei 492007 than in Nei 542018 and Nei 542022 for both Day30 and Day60 (Fig. 1A, B). In contrast, the crown root lateral root length was significantly greater in Nei 542018 and Nei 542022 than in Nei 422004 and Nei 492007 (Fig. 1I). The number of crown roots was highest in Nei 422004, followed by Nei 492007, Nei 542018, and Nei 542022 (Fig. 1E). Both brace root diameter (Fig. 1B) and crown root diameter (Fig. 1G) were greatest in Nei 542018. Similarly, brace root branching was highest in Nei 542018, followed by Nei 542022, Nei 492007, and Nei 492004 (Fig. 1C). Significant interaction effects were found for brace root lateral length and crown root lateral root branching. The brace root lateral length of Nei 542018 was the highest on Day60 only (Fig. 1D), whereas crown root lateral root branching of Nei 542018 was the highest on both Day30 and Day60 (Fig. 1H).

3.2. *Assemblage compositions of arthropods in the rhizosphere*

We collected a total of 6436 individual arthropods (3321 from Day0; 815 from Day30; and 2300 from Day60), and classified them into 62 families. Oribatid mites showed the highest abundance (32.96 %), followed by springtails (20.90 %), and mesostigmatid mites (16.19 %). A list of family names with abundance from each sampling time is shown in Supplementary Table S3.

Assemblage composition of arthropods, as shown in NMDS ordination (Fig. 2), was different among the three sampling days, and PERMANOVA confirmed significant differences among the days after planting ($p < 0.001$) and the experimental treatments ($p = 0.004$). Assemblage composition on Day0 was similar among the experimental treatments, with the lowest beta dispersion of 0.194. During the maize growing period, arthropod composition was highly variable on Day30 (beta dispersion = 0.491), but became more similar on Day60 (0.385). These differences in beta dispersion among the sampling days were statistically significant at $p < 0.001$. The PERMANOVA suggested that the effect of the experimental treatments was significant at p = 0.004; however, the interaction between the days after planting and the experimental treatment was not significant ($p = 0.182$), suggesting that arthropod assemblages did not respond to the experimental treatments on Day30 and Day60 after planting maize (i.e., the interaction should have occurred if the effect of maize variety was significant as we

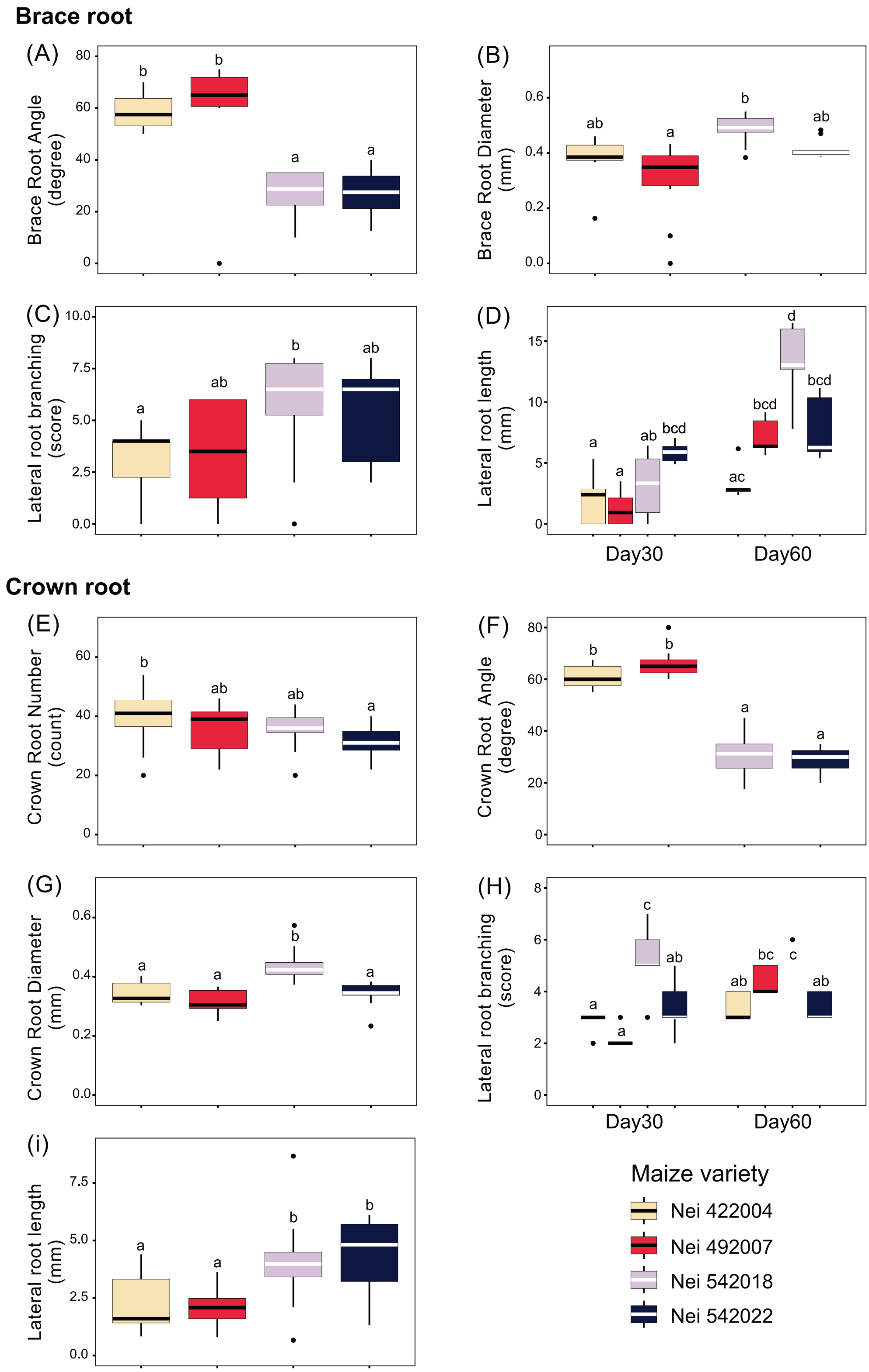

Fig. 1. Box plot of (A-D) brace root and (E-I) crown root traits across four maize varieties. When the interaction effect between days after planting and maize variety was significant (D and H), the box plot was split into Day30 and Day60. Different letters above bars indicate significant differences among maize varieties.

included Day0 in the analysis).

3.3. *Abundance and taxon richness of arthropods among treatments*

Both total abundance and taxon richness dropped on Day30, but recovered on Day60 (Fig. 3 and Supplementary Table S4). The generalized linear mixed models indicated significant effects of the days after planting and the experimental treatments on both total abundance and taxon richness of soil arthropods; however, a significant interaction effect was only found for total taxon richness (Supplementary Table S5; *p*

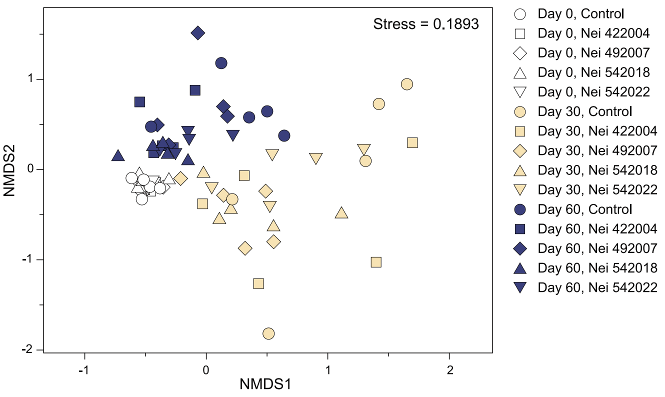

Fig. 2. NMDS ordination plot of assemblages of soil arthropods in control (unplanted) soil and rhizospheres of four maize varieties (Nei 422004, Nei 492007, Nei 542018, and Nei 542022) on three sampling days (Day0, Day30, and Day60).

= 0.009). Taxon richness was similar among the experimental treatments on Day0, but highly variable on Day30 and Day60 (Fig. 3B). On Day60, the highest taxon richness was found in Nei 542018 and Nei 542022 (Fig. 3B).

Most of the 23 common arthropod families showed significant differences in abundance among the sampling days (Supplementary Table S6). In contrast, effect of the experimental treatment was significant for only four families. Only one family (Scheloribatidae) showed a significant interaction effect between the days after sampling and the experimental treatments (Supplementary Table S6). The abundance of Scheloribatidae did not differ among the experimental treatments on Day0, but the highest abundance was found in Nei 542018 on Day30 and Day60 (see Supplementary Table S7). Two families of mesostigmatid mites, Ascidae and Rhodacaridae, showed the highest abundance in the rhizosphere of Nei 542018, and generally lower abundance in the control soil. The abundance of springtail family Sminthuridae was the highest on Day0. The abundances of individual arthropod taxa across the days after planting and the experimental treatments are summarized in Supplementary Table S7.

3.4. *Abundance of soil arthropod feeding guilds among treatments*

In total, five ecological feeding guilds of soil arthropods were identified in this study. Detritivores were the most dominant group, accounting for 53.0 % of all individuals, followed by fungivores (25.3 %), predators (17.0 %), omnivores (3.8 %), and herbivores (0.5 %).

The abundance of all feeding guilds significantly differed among the days after planting (Supplementary Table S8). Generally, the abundance of all feeding guilds dropped from Day0 to Day30 and then recovered on Day60 except for herbivores, whose abundance was higher on Day30 and Day60 than on Day0. Effects of the experimental treatments and the interaction were both significant for detritivores and predators. Abundance of detritivores and predators did not differ among the experimental treatments on Day0, but the abundance of these feeding guilds significantly varied among the experimental treatments on Day30 and Day60 (Fig. 4). On Day30, the abundance of detritivores was the lowest in the unplanted control plot, while in the maize plots, there was no significant difference among the varieties (Fig. 4A). On Day60, the lowest detritivore abundance was again found in the control plot, which was significantly lower than Nei 422004, Nei 542018, and Nei 542022 but there was also no significant difference among maize varieties (Fig. 4A). For predators, on Day30, their abundance in the unplanted control plot was the lowest, and significantly lower than Nei 492007, Nei 542018, and Nei 542022 (Fig. 4B). On Day60, predators showed the highest abundance in Nei 542018 (Fig. 4B). The unplanted plot and maize varieties with steeper root angle (Nei 422004 and Nei 492007) had lower predator abundance than those with shallower root angle (Nei 54108 and Nei 542022).

3.5. *Correlation between maize root morphological traits and soil arthropods*

Redundancy analysis (RDA) based on the ten root trait parameters explained 56.24 % of variability in the arthropod assemblage composition on Day30 (Fig. 5A, axis 1 = 33.71 %, and axis 2 = 22.53 %) and 55.31 % on Day60 (Fig. 5B, axis 1 = 32.12 %, and axis 2 = 23.19 %). The permutation test indicated that the crown root number and crown root lateral branching were both significant traits that influenced the composition of arthropod assemblages on Day30 (p = 0.002 and p = 0.023, respectively), whereas crown root angle was significant on Day60 (p = 0.028).

4. Discussion

4.1. *Collapse and recovery of arthropod diversity after maize planting*

Arthropod diversity substantially decreased from Day0 to Day30, suggesting the persistent impacts of tillage and maize planting. Tillage is known to cause a substantial disturbance in soil and detrimentally affect arthropod diversity (Doles et al., 2001; Rodríguez et al., 2006). Tillage could have altered arthropod diversity by disrupting soil aggregation, reducing litter input, increasing surface soil temp, and altering soil moisture regime due to the absence of plant cover (Curry, 2004). However, the tillage effect on the diversity of soil organisms seems to be a gradual progress, and generally subsides through time (Crittenden et al., 2014; Robertson et al., 1994). Crittenden et al. (2014) found that

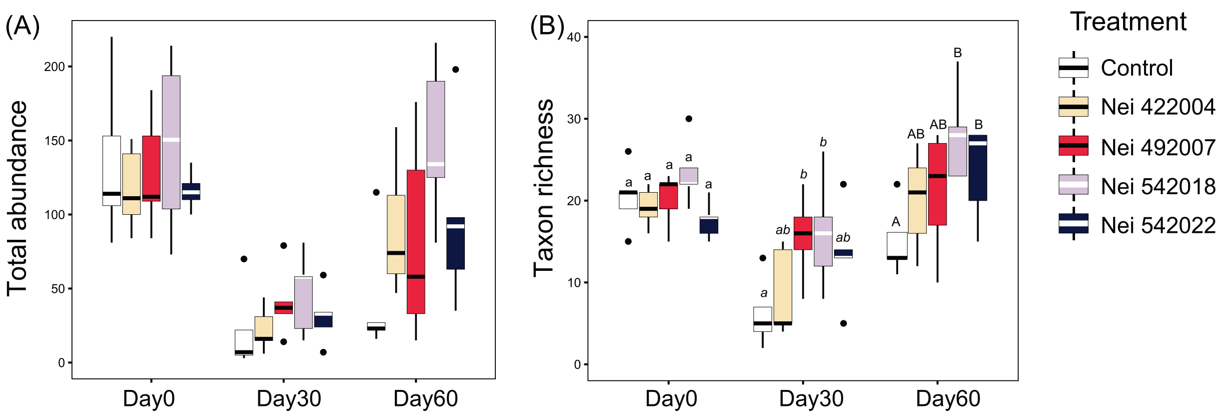

Fig. 3. Box plot of (A) total abundance and (B) taxon richness of arthropods. Different letters above bars indicate significant differences among treatments.

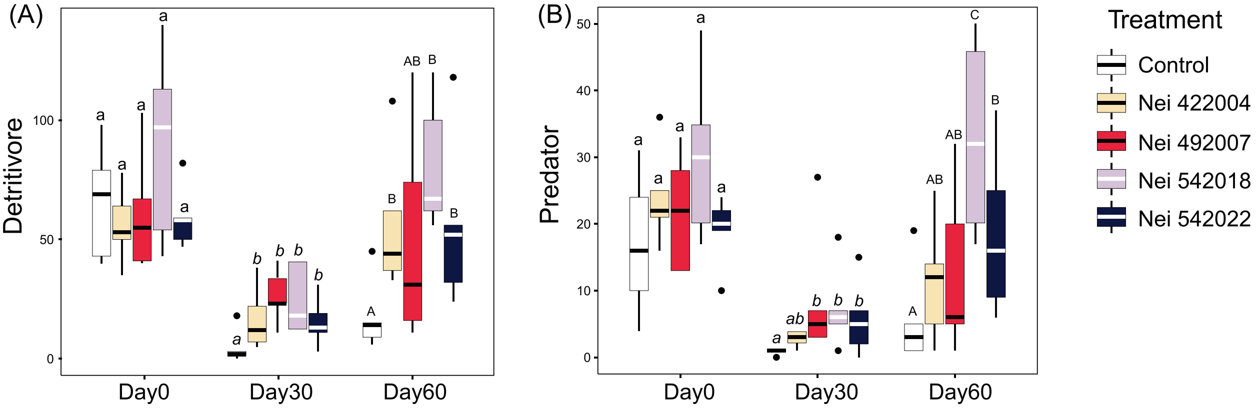

Fig. 4. Box plots showing abundance among treatments of (A) detritivores and (B) predators. Different letters above bars indicate significant differences among treatments.

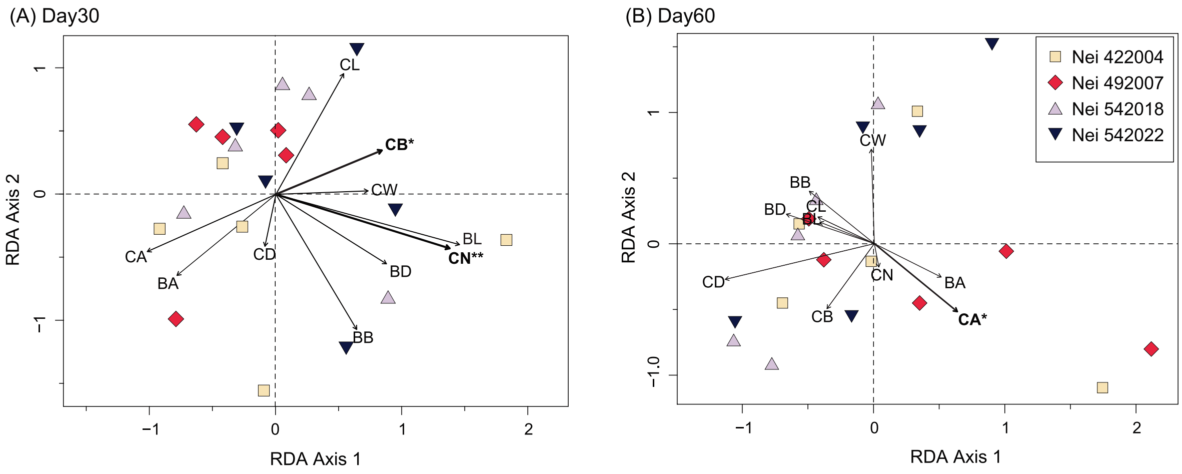

Fig. 5. Redundancy analysis (RDA) representing the correlation between maize root morphological traits and soil arthropod communities on (A) Day30 and (B) Day60. Quantitative root variables are indicated by arrows. BA: brace root angle, BD: brace root diameter, BB: lateral root branching of brace root, BL: lateral root length of brace root, CW: crown root whorl, CN: crown root number, CA: crown root angle, CD: crown root diameter, CB: lateral root branching of crown root, CL: lateral root length of crown root.

abundance of earthworm started to significantly decrease 15 to 35 days after soil plowing and the abundance began to recover around 53 days after plowing. Likewise, arthropod assemblage composition in our study was similar among plots on Day0 (sampled 5 days after the tillage), was highly variable on Day30, and recovered on Day60 (Fig. 2 and Supplementary Table S3). However, as expected, the recovery of arthropod diversity was highly variable among the maize varieties with different root trait characteristics.

4.2. Variation of maize root traits induces changes in arthropod diversity

The change in arthropod diversity between the unplanted and planted plots could be explained by niche availability in soil (Chase and Leibold, 2004). In the field used for our trial, regular weeding was carried out throughout the planting period. Hence, besides the main source of energy derived from accumulated plant residue from previous crops (Moore et al., 2004), the maize roots were the only prominent source of organic matter available to soil arthropods (Andresen et al., 2011). Similar results have been reported in studies of other rhizosphere fauna. Lower richness of microbes and higher abundance of nematodes were found in the maize rhizosphere compared to unplanted soil (Matus-Acuña et al., 2021; Szoboszlay et al., 2015). Both studies further mentioned that having plant roots in soil is more attractive for soil fauna, including the arthropods that rely on carbon sources released from roots (Curry and Ganley, 1977; Endlweber et al., 2009; Sabais et al., 2011; Scheunemann et al., 2015). Indeed, low diversity of arthropods was apparent in the control plot, where food resources were lacking after maize planting.

The phenotypic variation of root traits among maize varieties, as shown in Fig. 1, appeared to drive the arthropod community and diversity during the growing period. Among the rhizospheres of the four maize varieties, the different abilities of these microhabitats to support arthropod diversity may be related to root traits. In studies by Sweeney et al. (2021) and McCormack and Iversen (2019), root diameter was identified as a trait that was positively related to abundance of arbuscular mycorrhizal fungi in the rhizosphere. Increased niche availability, reflected by plant root biomass and possibly fungal abundance, was suggested to positively influence rhizosphere arthropod diversity (Hishi et al., 2008; Potapov et al., 2017). In our study, taxon richness of arthropods was greater in Nei 542018 and Nei 542022 (Fig. 3B), that both have shallow root angles. Shallowness of their roots means that their rhizosphere provides abundant root-derived resources along the horizontal axis, particularly in the topsoil, which is the most favorable location for soil arthropods (Potapov et al., 2017; Simoni et al., 2013).

Although the total abundance of arthropods did not differ significantly among the maize varieties after planting, greater abundance of Scheloribatidae and detritivores were found in Nei 542018. Scheloribatidae mites generally feed on plant litter and debris (Hubert et al., 2000), and our study suggests that the dense roots of Nei 542018 provided a suitable habitat for this mite family and other detritivores.

In addition, Nei 542018 also possessed higher root diameter, lateral root branching, and lateral root length than the other maize varieties, and this maize variety supported the highest diversity of arthropods. This suggests that increased rhizosphere habitats provided by Nei 542018 increased the diversity of soil arthropods, whereas notably lower arthropod diversity found in Nei 422004 and Nei 492007 may be related to their lower amounts of rhizosphere habitats, as possibly indicated by low lateral root branching and lateral root length. Moreover, the large root diameter of Nei 542018 could indirectly lure soil arthropods, as maize with greater root diameter generally has more area of root surface surrounding a root segment, potentially providing more plant exudates for soil arthropods (Williams et al., 2021). Root exudates of maize are known to be rich in amino acids, sugars, and enzymes (Williams et al., 2021). These compounds are important carbon sources, inducing a greater abundance of microbes and consequently more arthropods in the rhizosphere (Sweeney et al., 2021; Williams et al., 2021).

Moreover, higher rates of root exudates released from larger root seems to have a cascading effect on predatory arthropods as well, as the highest abundance of this feeding guild was found in Nei 542018 (Fig. 4B). It has been demonstrated that plants sometimes release volatile compounds to attract predators for suppressing herbivores that can harm their roots (Bonkowski et al., 2009; Matsumoto, 2008; Zhang et al., 2019). Thus, a maize root with large diameter may engage more abundant predators to the rhizosphere (Matsumoto, 2008; Williams et al., 2021), as was evidenced in Nei 542018 in our study (Fig. 4B).

4.3. Correlation between root traits and soil arthropod community

The results of redundancy analysis suggest that some variation in arthropod composition on Day30 can be explained by crown root number and lateral root branching of maize roots (Fig. 5A). The relationship between high arthropod diversity and greater root number and branching may be related to greater accessibility to root resources serving as food and habitat for the rhizosphere fauna, as we mentioned above.

The impacts of tillage, however, appeared to persist 30 days after planting, as arthropod abundance and taxon richness were substantially lower than at Day0, and assemblage composition was highly variable. Subsequently, arthropod assemblage composition substantially changed from Day30 to Day60, and different root traits explained the variation in arthropod composition. In contrast to the sample at Day30, the maize roots on Day60 appeared fully developed and were considered able to absorb resources to support the reproductive stage (O'Keeffe, 2009). On Day60, the crown root angle was associated with the arthropod assemblage composition. Shallow crown root angles were associated with Nei 542018 and Nei 542022, and indeed the arthropod assemblages from these two varieties were placed in the opposite direction from the crown root angle vector (Fig. 5B). Although both Nei 542018 and Nei 542022 improved abundance and richness of arthropods, the assemblage composition, as shown in Fig. 5 (constrained ordination), seemed highly variable and difficult to distinguish among the four maize varieties. This may suggest that although Nei 542018 and Nei 542022 both provide rhizosphere habitats for greater diversity of soil arthropods, the assembly process of soil arthropods is likely non-deterministic, even for arthropod assemblages collected from the same maize variety.

Nevertheless, plants with shallow roots or roots with larger diameter seem to promote greater arthropod density around the rhizosphere, as shown in this study, and could in turn provide more nutrients into the soil. Several studies reported the positive correlation between arthropod abundance and nutrient content in soil (e.g., Pramanik et al., 2001), suggesting that these soil organisms play a key role in increasing nutrients in soil. Therefore, mechanistic understanding of some specific root traits on arthropod communities could further be investigated and used as a criteria for maize variety selection in order to promote soil health and maize productivity.

5. Conclusions

Our findings indicate that root traits of maize influence arthropod abundance and diversity in the rhizosphere, and the effect was most pronounced for root angle. The maize with shallow roots supported higher abundance and taxon richness of arthropods, possibly due to greater availability of root-derived resources within the topsoil. Additionally, root traits which are directly related to carbon supply (e.g., root exudates) should further be considered in studies of the relationship between roots and the associated soil community.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This research was supported by Mahidol University. AN was supported by High-End Foreign Experts Program of the High-Level Talent Recruitment Plan of Yunnan Province, National Natural Science Foundation of China General Program (31770472) and Strategic Priority Research Program of Chinese Academy of Sciences (XDB31000000). We acknowledge members of ASME Laboratory and Root Laboratory, Department of Biology, Faculty of Science, Mahidol University, for their help with field and laboratory work. We extend our sincere thanks to Dr. Buntika A. Butcher for all her useful suggestions, Dr. Warut Siriwut and Dr. Natdanai Likhitrakarn for arthropod identification, and Mr. David J. Anderson for his help with linguistic editing of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2022.104615.

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