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**Soil amelioration driven by diverse Herbaceous perennials
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activities, and organic carbon**

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Abstract

Subjected to long-term disturbances from urban site conditions and anthropogenic activities, green spaces frequently confront degradation issues such as soil compaction and nutrient limitation. Rational plant configuration represents an effective strategy for optimizing soil physicochemical properties; however, the ameliorative effects of different perennial flowers on urban green space soils in Northeast China remain largely unclarified. In this study, an *in situ* planting experiment was conducted on meadow black soil utilizing seven perennial flowers commonly used for landscaping in Changchun City. In the third year post-planting, soil samples were collected to evaluate the ameliorative impacts of these perennial flowers on soil aggregates, carbon fractions, and enzyme activities within the 0–20 cm bulk and rhizosphere soils, with unplanted bare land serving as a control.

The results indicated that the plant-induced ameliorative effects exhibited significant species specificity. P-PS (*Pseudolysimachion spicatum*) demonstrated the

optimal synergistic amelioration potential, significantly increasing the proportion and stability of water-stable macroaggregates while enhancing rhizosphere available nitrogen by 67.6% compared to the control. Additionally, P-PS, P-SJ (*Salvia japonica*), and P-HE (*Hosta ensata*) significantly elevated microbial biomass carbon (MBC). Although P-LL (*Lycopus lucidus*) and *Rudbeckia hirta* enhanced invertase activity, this process was accompanied by a short-term active consumption of soil organic carbon (SOC). Furthermore, the Mantel test revealed a highly significant correlation between variations in soil enzyme activities and the dynamics of SOC fractions ($P < 0.001$).

In conclusion, under conventional landscape management scenarios, P-PS can synergistically improve soil structure and augment nitrogen availability, exhibiting superior potential for soil amelioration and fertility enhancement. Therefore, it is highly recommended as a priority candidate plant to simultaneously sustain landscape aesthetics and soil health in Northeast China.

Keywords: Herbaceous perennials, Soil amelioration, Soil aggregates, Enzyme activities, Soil organic carbon

Introduction

Under the backdrop of rapid urbanization and long-term anthropogenic disturbances (such as trampling and topsoil stripping), the physicochemical properties of urban green space soils have undergone significant alterations. Consequently, green space soils in Northeast China frequently confront issues such as increased compaction, deteriorated permeability and aeration, and nutrient imbalances, which negatively impact their original physical structures and biochemical cycling processes [1-3].

Under conventional landscape maintenance conditions, the *in situ* ecological amelioration of soils using landscape plants, functioning as a Nature-based Solution (NbS), has emerged as an effective approach for optimizing urban soil structure and

enhancing soil fertility [4]. Among various landscape plants, perennial flowers—characterized by their well-developed root architectures, prolonged growth cycles, and exceptional environmental adaptability—can successfully establish and exert enduring ameliorative effects on soils through rhizosphere processes such as physical root penetration, exudate mediation, and residue turnover [5-7]. Compared with annual flowers, perennial flowers possess distinct advantages in enhancing soil carbon sequestration and improving aggregate structure [8-10]. However, most existing research on plant-induced soil amelioration has primarily focused on field crops or arboreal forestlands [11, 12], whereas studies on the systematic amelioration mechanisms and practical applications of perennial flowers remain relatively scarce. In particular, quantitative evaluations of the soil amelioration efficacy of typical perennial flowers under conventional landscape management scenarios are still lacking.

Soil aggregate composition and stability, in synergy with soil organic carbon (SOC) fractions, constitute core indicators for assessing soil structural quality and fertility enhancement [13]; their interactions directly determine the aeration, permeability, and nutrient retention capacity of the soil. Concurrently, soil enzyme activities, acting as sensitive indicators of microbial metabolic characteristics, drive organic carbon transformation and aggregate formation, thereby directly reflecting the evolutionary trends of soil microecology during the plant-driven amelioration process [14]. Although it is widely acknowledged that plants can enhance soil structure and elevate carbon pool levels [15], the differential impacts and underlying regulatory mechanisms of perennial flowers with diverse root architectures on the complex coupled system of "aggregates-SOC-enzyme activities" remain elusive, particularly in the context of high-latitude, cold urban green spaces in Northeast China. This research gap substantially constrains the precise configuration and application of perennial flowers in urban ecological landscapes.

This study aims to address the following two core scientific questions: (1) to evaluate the growth adaptability of different perennial flowers under conventional landscape maintenance and their comprehensive ameliorative effects on soil physical

structure (aggregate stability) and biochemical properties (carbon fractions and key enzyme activities); and (2) to elucidate the coupling relationships among soil enzyme activity variations, SOC fraction dynamics, and physical structural optimization during the plant-induced soil amelioration process. The findings of this study will provide profound insights into the ecological mechanisms by which perennial flowers ameliorate urban soils, offering a scientific basis for the precise configuration of landscape vegetation and the sustainable enhancement of comprehensive soil fertility in Northeast China.

1. Materials and methods

1.1. Description of the study area

The experimental site was located at the experimental field of the West Campus, Changchun University, in Changchun City, Jilin Province, China (125°18' E, 43°50' N). Situated in the hinterland of the Songnen Plain, this region is characterized by a mid-temperate continental monsoon climate. The region has a mean annual temperature of 5.2 °C, a mean annual precipitation of 570 mm, and an annual effective accumulated temperature of 2900 °C. According to the classification criteria of the Resource and Environment Science and Data Center, Chinese Academy of Sciences, the soil at the experimental site is classified as meadow black soil, with a predominantly clay loam texture. This site represents a typical urban green space soil habitat in Northeast China.

1.2. Experimental materials

In this study, seven representative perennial herbaceous flowers widely utilized in the urban landscaping of Changchun City were selected: P-LL (*Lycopus lucidus*), P-GP (*Gaillardia pulchella*), P-SJ (*Salvia japonica*), P-RH (*Rudbeckia hirta*), P-HF (*Hemerocallis fulva*), P-HE (*Hosta ensata*), and P-PS (*Pseudolysimachion spicatum*). None of these selected species are rare, endangered, or protected plants. We confirm that all experimental research and use of plant material in this study complied with all relevant institutional, national, and international guidelines and legislation.

1.3. Experimental design

This experiment was conducted from May 2023 to September 2025. To eliminate the interference of prior vegetation on soil physicochemical properties, all surface weeds were eradicated in May 2023, and the field was naturally air-dried for two weeks to prepare the planting bed. A total of eight treatments were established: monoculture plots for the seven tested herbaceous perennials and one unplanted bare land control (CK). Each treatment was arranged with three block replicates. The experimental plot area was set to 2 m × 2 m, and the planting density was uniformly controlled at 16 plants m⁻². In May 2023, vigorous seedlings of consistent age were transplanted into the experimental plots. Moderate irrigation was applied during the initial two weeks post-transplanting to ensure seedling establishment. Once the plants were established, conventional landscape maintenance was simulated; only periodic weeding was performed to guarantee the completely bare state of the CK plots and the monoculture status of each planted plot.

1.4. Measurement items and methods

Sampling was conducted in September 2025, at which point the canopy coverage of each treatment plot had stably reached over 85%. Within each plot, an "S"-shaped five-point sampling method was employed to randomly select five representative plants with uniform growth, which were entirely excavated. The loose soil on the roots was shaken off, and the soil firmly adhering to the roots (1–2 mm) was subsequently brushed off and collected as the rhizosphere soil sample. Bulk soil samples were collected from the 0–20 cm soil layer. The five samples within the same plot were pooled to form a single composite sample, resulting in three biological replicates per treatment (n = 3). After removing plant residues and gravel and mixing thoroughly, the rhizosphere soil samples were placed in sterile Ziploc bags and stored at 4 °C for the determination of chemical indicators such as enzyme activities. The bulk soil samples were naturally air-dried indoors and passed through sieves of various mesh sizes for the assessment of physical indicators, including soil aggregates.

The dry sieving method utilized a sieve series with mesh sizes of 5, 2, 1, 0.5, and

0.25 mm to fractionate the soil into six particle-size classes. The Le Bissonnais method was introduced to quantify the content of water-stable macroaggregates and to evaluate the soil's resistance to water disruption [16]. Soil organic carbon (SOC) and microbial biomass carbon (MBC) were determined using the Walkley-Black potassium dichromate oxidation method and the chloroform fumigation-extraction method, respectively [17]. The calculation of MBC was based on a standard extraction conversion factor ($K_{ec} = 0.45$). Soil enzyme activities were assayed as follows: catalase activity was measured via the potassium permanganate titration method [18]; phosphatase activity was determined using the disodium phenyl phosphate colorimetric method [19]; urease activity was analyzed by the sodium phenate-sodium hypochlorite colorimetric method [20]; cellulase and invertase activities were both quantified employing the 3,5-dinitrosalicylic acid (DNS) colorimetric method [21], utilizing a spectrophotometer to evaluate the mineralization efficiency of soil organic carbon.

1.5 Data processing and statistical analysis

The stability indicators of soil water-stable aggregates were expressed using the mean weight diameter (MWD) and geometric mean diameter (GMD):

$$MWD = \sum_{i=1}^n \frac{x_i w_i}{\sum_{i=1}^n w_i} \quad (1)$$

$$GMD = \exp \left[\frac{\sum_{i=1}^n w_i \ln x_i}{\sum_{i=1}^n w_i} \right] \quad (2)$$

$$P = \frac{\lambda_i w_i}{w} \times 100\% \quad (3)$$

where x_i is the mean diameter of aggregates in the i -th size class (mm); w_i is the percentage content of aggregates corresponding to x_i ; λ_i is the organic carbon content of aggregates in the i -th size class ($\text{g} \cdot \text{kg}^{-1}$); w is the total soil organic carbon content ($\text{g} \cdot \text{kg}^{-1}$); n is the number of aggregate size classes ($n = 4$); and P represents the contribution rate of organic carbon from aggregates in each size class.

All statistical analyses were performed using SPSS 25.0 software. Prior to the

significance analysis of differences, the Shapiro-Wilk test and Levene's test were employed to evaluate the normality of data distribution and the homogeneity of variances, respectively. The results indicated that all data met the aforementioned assumptions; subsequently, a one-way analysis of variance (ANOVA) combined with Duncan's multiple range test was conducted to assess the significant differences ($P < 0.05$) in soil aggregate distribution and stability, organic carbon content, and enzyme activities among the different herbaceous perennial planting treatments. Data visualization was generated using Origin 9.0 software, and the data presented in the figures and tables were expressed as "Mean $\pm$ standard deviation (SD)".

2. Results and analysis

2.1. Comprehensive effects of herbaceous perennials on soil physicochemical and biological properties

Although different herbaceous perennial treatments did not significantly alter soil bulk density and total porosity ($P > 0.05$), they significantly influenced pore size distribution and moisture characteristics (Table 1). Compared with the control (CK), P-HE significantly increased non-capillary porosity ($P < 0.05$), thereby improving the aeration conditions in deep soil layers. Furthermore, soil water retention capacity exhibited pronounced interspecific differences, with the P-HF treatment recording the highest soil moisture content (13.9%) and P-PS showing the lowest (5.1%). These findings indicate that the root systems of different herbaceous perennials can specifically ameliorate the soil micro-physical structure, which can provide a theoretical basis for balancing the "aeration-water retention" functions in practical plant configurations.

Table 1 soil physical properties

Treatment	BD ($\text{g}\cdot\text{cm}^{-3}$)	SMC (%)	PORT (%)	CP (%)	NCP (%)
CK	1.0 $\pm$ 0.1a	8.1 $\pm$ 1.7bcd	62.3 $\pm$ 3.8a	8.1 $\pm$ 1.9b	54.2 $\pm$ 4.2a
P-LL	1.1 $\pm$ 0.1a	10.7 $\pm$ 1.1abc	58.5 $\pm$ 3.8a	11.8 $\pm$ 1.6ab	46.7 $\pm$ 4.1a

P-GP	1.0±0.3a	10.4±4.4abc	62.3±11.3a	10.4±5.4ab	51.9±12.5a
P-SJ	1.0±0.1a	12.5±4.4ab	62.3±3.8a	12.5±4.6ab	49.8±5.9a
P-RH	1.2±0.1a	10.9±0.6abc	54.7±3.8a	13.1±1.3ab	41.6±4.0a
P-HF	1.2±0.1a	13.9±2.2a	54.7±3.8a	16.7±3.0a	38.0±4.8a
P-HE	1.1±0.1a	7.2±0.4cd	58.5±3.8a	7.9±0.8b	50.6±3.9a
P-PS	1.2±0.1a	5.1±1.2d	54.7±3.8a	6.1±1.5b	48.6±4.1a
p-value	>0.05	<0.05	>0.05	<0.05	>0.05

Note: BD, soil bulk density; SMC, soil moisture content; PORT, total porosity; CP, capillary porosity; NCP, non-capillary porosity; *P*-value, probability value.; 0-20 cm Bulk Soil ;Values are presented as means ± SE (*n* = 3). Different lowercase letters indicate significant differences among treatments at the *P* < 0.05 level (the same applies below).

P-RH and P-PS exhibited remarkable promotive effects on macroaggregate formation (Table 2). P-RH demonstrated the strongest cementation capacity for large macroaggregates (> 5 mm), showing an approximately 11-fold surge compared to the control (CK) and thereby achieving the highest mean weight diameter (MWD). Meanwhile, P-PS significantly elevated the proportion of > 2 mm aggregates; it exhibited outstanding MWD and geometric mean diameter (GMD) values, constructing a more balanced and erosion-resistant soil structure. Conversely, both MWD and GMD decreased under the P-SJ and P-LL treatments, where the soil displayed a distinct "fining" tendency. In summary, different herbaceous perennials can indeed significantly influence soil physical properties via their root systems, finely regulating soil structure primarily by driving macroaggregate formation and microaggregate transformation.

Table 2 The mass percentage of soil aggregates under the planting conditions of seven Herbaceous perennials.

Treatment	Size fraction (mm)					MWD	GMD	PAD	WSAS
	>5	5-2	2-1	1-0.5	0.5-0.25				
CK	0.5±0.1c	4.5±0.7d	24.3±1.1a	41.1±0.4c	31.8±2.2d	0.98±0.01c	0.59±0.01b	64.64	32.04
P-LL	0.3±0.3c	5.3±0.1cd	10.1±0.1d	26.8±0.5e	57.4±0.9a	0.77±0.02e	0.64±0.01e	50.88	45.24
P-GP	0.5±0.1c	1.6±0.1e	18.2±0.5c	34.4±1.0d	44.1±4.5b	0.78±0.01e	0.60±0.01d	67.27	30.14
P-SJ	0±0c	1.4±0.1e	0.1±0.2e	57.7±0.9a	37.8±1.8c	0.63±0.01f	0.78±0.02e	74.06	23.40
P-RH	6.2±0.3a	11.5±0.8a	2.4±0.1e	35.3±1.4d	43.1±0.6b	1.24±0.01a	0.71±0.01b	69.91	27.56

P-HF	0.3±0.1c	6.8±0.6b	21.5±2.7b	28.1±0.6e	44.6±1.1b	0.96±0.01d	0.77±0.01c	51.65	43.76
P-HE	0.4±0.4c	5.9±0.5c	17.4±2.1c	50.6±1.9b	26.4±0.9e	0.97±0.01c	0.78±0.01b	64.10	32.24
P-PS	3.5±0.5b	5.3±0.5cd	25.3±1.0a	41.6±1.1c	23.1±1.3e	1.17±0.01b	0.89±0.01a	61.42	35.22
p-value	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05

Note: MWD, mean weight diameter; GMD, geometric mean diameter; PAD, percentage of aggregate destruction; WSAS, water-stable aggregate stability; 0-20 cm Bulk Soil.

The seven herbaceous perennials significantly altered soil chemical properties and nutrient profiles (Table 3). Soil pH was maintained within a slightly alkaline range (7.3–7.5), whereas electrical conductivity (EC) exhibited strong interspecific differences: P-HE and P-LL significantly elevated EC, while P-HF significantly decreased it. Furthermore, the regulatory strategies for nitrogen cycling varied dramatically among species. P-LL significantly enriched total nitrogen (TN, 1.2 g kg⁻¹), and P-PS demonstrated a robust nitrogen mineralization capacity, boosting the alkali-hydrolyzable nitrogen (AN) content by 67.6%. Conversely, P-SJ and P-HF caused a dual deficit in both TN and AN. Additionally, most treatments depleted soil total phosphorus (TP). However, P-GP, P-PS, and P-RH all significantly increased the contents of total potassium (TK) or available potassium (AK), exhibiting excellent potassium activation and enrichment functions. In summary, different herbaceous perennials can indeed significantly influence and reshape the soil chemical environment through specific nutrient consumption and enrichment strategies.

Table 3 soil chemical properties and nutrient content

Treatment	EC ($\mu\text{S}/\text{cm}$)	pH	TN ($\text{g}\cdot\text{kg}^{-1}$)	TP ($\text{g}\cdot\text{kg}^{-1}$)	TK ($\text{g}\cdot\text{kg}^{-1}$)	AN ($\text{mg}\cdot\text{kg}^{-1}$)	AP ($\text{mg}\cdot\text{kg}^{-1}$)	AK ($\text{mg}\cdot\text{kg}^{-1}$)
CK	269.0±1.0d	7.5±0.1bc	0.8±0.0c	1.0±0.0a	6.0±0.1c	72.2±1.1d	84.8±0.8c	113.1±0.1h
P-LL	283.0±1.0b	7.3±0.0e	1.2±0.0a	0.9±0.0b	6.2±0.2b	85.9±1.4b	94.5±1.0a	194.4±0.1c
P-GP	256.3±0.6e	7.4±0.0cd	1.0±0.0b	0.8±0.0c	7.4±0.1a	76.2±1.5c	87.0±0.6b	197.0±0.2b
P-SJ	267.3±1.5d	7.4±0.0cd	0.7±0.0f	0.5±0.0f	5.9±0.1c	50.9±1.6f	47.7±0.5f	161.5±0.1e
P-RH	253.7±0.6f	7.4±0.0de	0.8±0.0c	0.6±0.0e	6.3±0.1b	55.1±0.7e	58.8±1.3e	203.8±0.3a
P-HF	230.0±1.0g	7.3±0.0e	0.6±0.0g	0.9±0.0b	5.9±0.1c	50.0±1.3f	73.8±1.4d	152.4±0.2f
P-HE	295.3±1.2a	7.5±0.0a	0.8±0.0d	0.8±0.0d	6.3±0.0b	73.6±1.2d	93.6±0.7a	129.8±0.1g
P-PS	271.7±1.5c	7.5±0.1ab	0.7±0.0e	0.8±0.0c	7.3±0.1a	121.0±1.3a	74.2±2.3d	175.2±0.4d
p-value	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05

Notes: EC, electrical conductivity; pH, Potential of hydrogen; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AP, available phosphorus; AK, available

potassium; Rhizosphere Soil.

2.2 Effects of seven herbaceous perennials on five soil enzyme activities

Regarding soil antioxidation and carbon metabolism, P-HF induced the strongest positive stimulation of catalase activity (Figure 1a). Furthermore, P-LL and P-RH significantly elevated sucrase activity (Figure 1c). P-HE substantially enhanced cellulase activity, whereas P-RH and P-HF exerted a profound inhibitory effect on it (Figure 1b). In the context of nitrogen (N) and phosphorus (P) cycling, contrary to the traditional positive priming effect, all tested herbaceous perennials induced a significant negative rhizosphere effect on phosphatase activity (Figure 1d). Urease activity exhibited a gradient differentiation; P-PS maintained the native N transformation potential, whereas P-RH and P-HF demonstrated severe inhibition (Figure 1e). Taken together, the different herbaceous perennials markedly reshaped the soil microecology via the specific regulation of enzymatic systems, exhibiting multidimensional functional trade-offs. Specifically, P-LL and P-HE were the most prominent in stimulating the activities of carbon cycle-related hydrolytic enzymes. Conversely, P-HF and P-RH tended to enhance singular metabolic functions and antagonize hydrolytic enzymes, reflecting a distinct ecological niche differentiation.

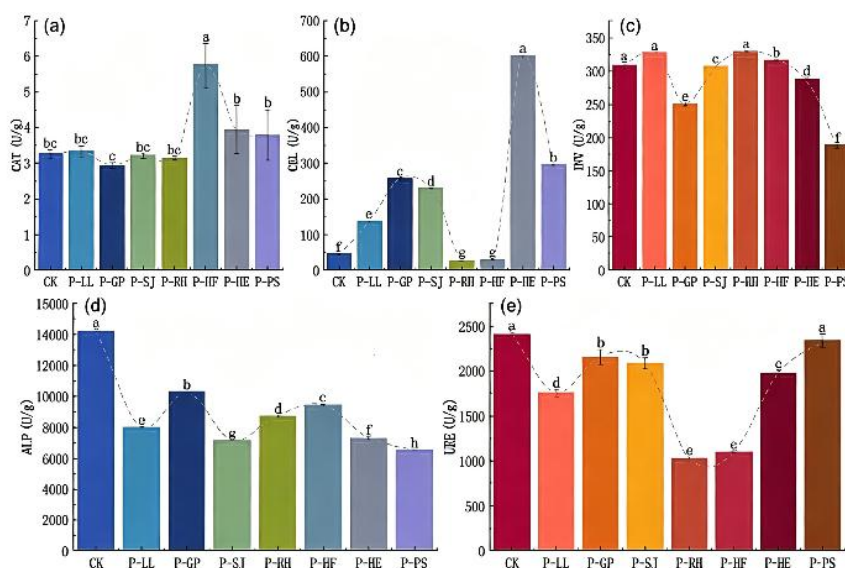


Figure.1 Effects of seven Herbaceous perennials on five soil enzyme activities

Note: (a) Catalase; (b) Cellulase; (c) Invertase; (d) Alkaline phosphatase; (e) Urease. Rhizosphere Soil. Different lowercase letters indicate significant differences among treatments ($P < 0.05$). The

same applies below.

2.3 Effects of Seven Herbaceous Perennials on Soil Organic Carbon and Microbial Biomass Carbon Contents

After two consecutive years of establishment and growth, the apparent soil organic carbon (SOC) and microbial biomass carbon (MBC) exhibited significant differences among the various herbaceous perennial treatments (Figures 2 and 3). Specifically, the detected SOC values under treatments such as *Rudbeckia hirta*, P-LL, and P-HF were significantly lower than those of the control group ($P < 0.05$). This significant short-term decline in SOC may be attributed to a strong rhizosphere priming effect induced by the plants. The well-developed root systems of herbaceous perennials release substantial amounts of labile carbon-rich exudates into the soil, which stimulate the activity of rhizosphere microorganisms. To meet the subsequently increased nutrient demands, these active microorganisms accelerate the mineralization and decomposition of the native stable organic matter, thereby leading to a short-term decrease in apparent SOC content. Concurrently, the MBC determination results further corroborate the sensitive response of the microbial community to different plant root inputs. As illustrated in Figure 3, treatments including P-SJ, P-PS, and P-HE significantly increased the MBC content. The extremely small standard deviations (SD) within these treatment groups demonstrate excellent data stability, accurately reflecting the specific impacts of different herbaceous perennials on the rhizosphere microenvironment. Collectively, the aforementioned variation characteristics of the carbon pool fractions manifest the highly dynamic carbon turnover processes within the plant ecosystem, providing robust data support for elucidating the regulatory mechanisms of the rhizosphere microecology of herbaceous perennials.

To explore the potential covariation characteristics among soil physicochemical properties, aggregates, enzyme activities, and carbon fractions, Pearson correlation analysis and Mantel tests (based on 999 permutations) were conducted (Figure 4). The results indicated that soil macroaggregates (> 5.0 mm and $2.0\text{--}1.0$ mm) and mean weight diameter (MWD) were significantly and positively correlated with multiple enzyme activities (CAT, CEL, ALP, and URE) ($P < 0.05$). The Mantel test

preliminarily suggested significant statistical couplings between the dynamic changes in SOC and MBC and the modules of physicochemical properties, aggregate distribution, and enzyme activities ($P < 0.05$). The aforementioned correlation network demonstrates that the introduction of herbaceous perennials may provide a favorable microenvironment for enzymatic reactions by improving the fundamental physical structure of the soil, which in turn is closely associated with the turnover of active carbon fractions. However, given the statistical limitations associated with a small sample size, these complex covariation relationships among multivariate factors and their potential causal driving mechanisms remain to be rigorously verified in future studies with larger sample sizes and longer observation periods.

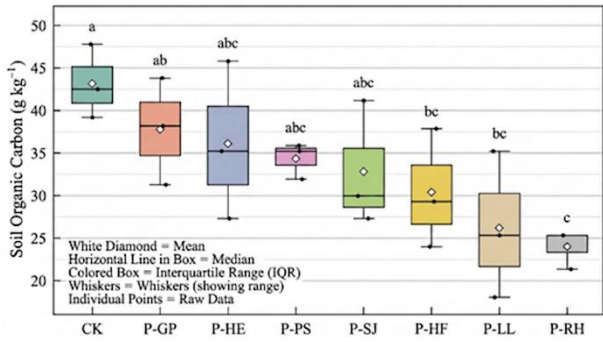


Figure.2 Effects of seven Herbaceous perennials on soil organic carbon content.
Note:Rhizosphere Soil.

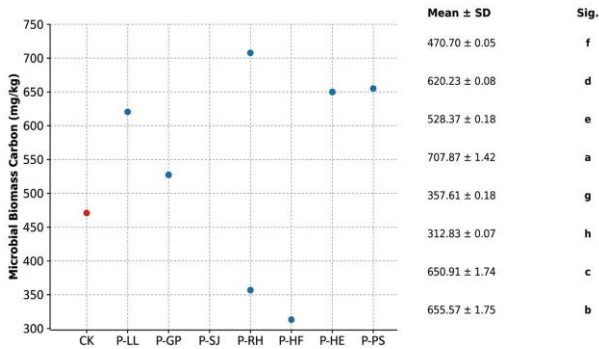


Figure.3 Effects of seven Herbaceous perennials on soil microbial biomass carbon content.
Note:Rhizosphere Soil.

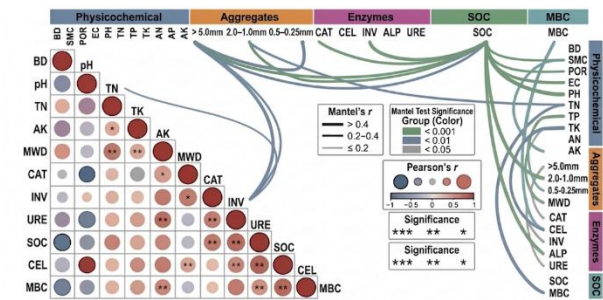


Figure.4 Mantel test and Pearson correlation analysis of soil factors and carbon components
Note: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; Note: Rhizosphere Soil.

3 Discussion

3.1 Effects of diverse herbaceous perennials on soil physical properties and aggregate structural stability

Through deep coupling between root systems and the soil, herbaceous perennials significantly reshape the rhizosphere physical microenvironment. The present study reveals that varying herbaceous perennials exert heterogeneous effects on soil bulk density and pore distribution due to their differentiated growth characteristics. Compared with the unplanted control (CK), species such as *Rudbeckia* and P-HF increased soil compaction and reduced total porosity. This was primarily attributed to the pressure generated by root growth, which rearranged soil particles, and the extensive root systems that clogged pre-existing pores [22]. Regarding moisture regulation mechanisms, despite the unfavorable structural condition characterized by a significant reduction in capillary porosity, P-HF exhibited an excellent capacity for soil moisture retention. This nonlinear correlation between structure and function compellingly validates the "aboveground microenvironment shielding hypothesis" [23]: its dense surface canopy effectively mitigates passive water loss from the topsoil via physical shielding, thereby compensating for the moisture regulation deficit caused by the deterioration of the physical structure. This mechanism resonates strongly with recent studies on plant-soil interactions. For instance, Gentsch et al. demonstrated that plant canopies with high crown closure not only promote the stable distribution of macroaggregates but also substantially enhance the matrix's water retention capacity through interception and microenvironment remodeling [24]. In contrast, the lower soil moisture content in the P-PS plots was closely related to its vigorous physiological water demand. This indicates that the shaping of the rhizosphere moisture environment by plants is a comprehensive consequence jointly driven by root reconstruction effects and aboveground resource trade-offs.

Rhizosphere nutrient dynamics reflect the differentiated resource acquisition

strategies of plants. P-LL significantly enriched total nitrogen, suggesting that its root exudates might have stimulated the activity of free-living diazotrophs in the rhizosphere [25]. Conversely, P-SJ and P-HF induced a substantial deficit in the nitrogen pool, revealing that these species adopt a "high-intensity nutrient mining" strategy to support rapid aboveground growth [26]. In the phosphorus cycle, the vast majority of plants exacerbated total phosphorus depletion, confirming the characteristic of phosphorus as a limiting factor in slightly alkaline soils. Notably, P-PS induced a substantial increase (+67.6%) in alkali-hydrolyzable nitrogen, indicating a strong priming effect on nitrogen mineralization within its rhizosphere microenvironment [27]. This discrepancy fundamentally reflects an ecological mechanism wherein plants selectively remodel microbial communities to meet their own stoichiometric demands by regulating rhizosphere carbon inputs. As emphasized by Liu in elucidating the "carbon-for-nitrogen" strategy, root exudates from specific plants can act as signaling molecules and carbon sources, profoundly altering microbe-mediated nitrogen transformation pathways and consequently determining the contribution rates of gross nitrogen mineralization and nitrogen fixation to the plant-available nitrogen pool [28]. Concurrently, *Gaillardia*, P-PS, and *Rudbeckia* were found to possess exceptional potassium activation capabilities, significantly elevating soil total potassium and available potassium contents (particularly prominent in *Rudbeckia*). The underlying micromechanism is likely closely associated with the secretion of low-molecular-weight organic acids by roots to promote mineral weathering, or the specific enrichment of potassium-solubilizing bacteria [29]. Simultaneously, the elevated electrical conductivity observed in P-HE and P-LL corroborates active rhizosphere ion exchange processes. This study fills a critical gap regarding the rhizosphere nutrient regulation mechanisms of urban ornamental plants, confirming that herbaceous perennials can actively remodel rhizosphere chemical cycling through "nitrogen fixation," "intensive mineralization," or "potassium activation." Such niche differentiation in nutrient utilization provides crucial microecological evidence for the future construction of low-input, self-sustaining mixed planting communities in urban landscaping.

3.2 Effects of diverse herbaceous perennials on soil nutrients and enzyme activities

Soil enzyme activities elucidate the metabolic adaptation mechanisms of the rhizosphere microecology. In this study, all investigated plants reduced phosphatase activity, which seemingly contradicts the traditional "resource scarcity-induced enzyme secretion" theory. However, considering the exceptionally high available phosphorus content in the background soil, we propose that this represents a typical "negative feedback inhibition" mechanism [30]. Given the sufficient available phosphorus pool, neither plants nor microorganisms are required to invest substantial metabolic energy into phosphatase synthesis; this "economic principle" is ubiquitous in eutrophic habitats [31]. Concurrently, the lower urease activity in planted soils compared to the unplanted bare land control (CK) was attributed to the fact that microorganisms in the CK, deprived of available nutrients, secreted massive amounts of urease to decompose organic nitrogen. Following plant establishment, however, root exudates functioned as natural urease inhibitors, deactivating free urease and resulting in significantly lower urease activity than that of the CK [32].

Regarding carbon and nitrogen metabolism, different species exhibited distinct functional trade-offs: the exceptionally high catalase activity in P-HF indicated its proactive construction of a highly oxidized rhizosphere to combat environmental stress. This may be the result of the plant actively secreting antioxidants to defend against pathogens or detoxify harmful rhizosphere metabolites [33]. Conversely, P-HE and P-LL generated a positive priming effect by elevating cellulase or invertase activities, thereby accelerating organic carbon turnover [34], which aligns with the significant enrichment of total nitrogen content in the rhizosphere soil of P-LL (Table 3).

3.3 Synergistic regulation effects of diverse herbaceous perennials on the compositional stability of soil aggregates and carbon fractions

Through the deep coupling of root systems and soil, herbaceous perennials significantly reshape the soil physical microenvironment. The formation and stability of soil macroaggregates ($> 2\text{ mm}$) serve as key indicators for evaluating the erosion

resistance of soil structure. In this study, plant root traits significantly influenced the evolutionary trajectory of soil aggregate structure. *Rudbeckia* and P-PS, characterized by high-density fibrous root systems, significantly promoted the accumulation of > 2 mm macroaggregates, likely through physical entanglement and exudate cementation [35, 36]. Conversely, owing to a higher degree of root lignification and fewer active fine roots in P-SJ and P-LL, macroaggregates were prone to disintegrate into microaggregates under external pressure in the absence of physical anchoring and biochemical cementing agents, leading to a "fining" trend dominated by microaggregates [37]. The significant increase in macroaggregates under the *Rudbeckia* and P-HF treatments implies that these species may possess stronger rhizodeposition capacities. This not only directly provides cementing materials but also indirectly promotes the biological aggregation of soil particles by stimulating rhizosphere microbial activity [38]. *Rudbeckia* and P-PS elevated the soil mean weight diameter (MWD) and geometric mean diameter (GMD), significantly enhancing soil porosity and erosion resistance; this fills a current gap in research on the soil ecological functions of ornamental plants. Based on a "morphology-function" oriented plant screening strategy, species with strong aggregate-promoting capabilities, such as P-PS, should be utilized as pioneer plants for urban soil amelioration [39, 40].

Herbaceous perennials profoundly alter the accumulation levels of core soil carbon fractions (MBC and SOC) through differentiated carbon input strategies. At the soil organic carbon (SOC) level, this study challenges the traditional paradigm that "vegetation cover inevitably enhances carbon sinks" [41]. Lacking root disturbance, the control group (CK) maintained a high level of SOC because its intact aggregate physical barrier effectively blocked the contact between substrates and microorganisms [42, 43]. The introduction of herbaceous perennials disrupted this equilibrium. *Gaillardia*, relying on a higher root biomass input, effectively compensated for the carbon loss caused by microbial respiration, thereby maintaining a dynamic balance in the carbon budget [44]. Conversely, following the introduction of *Rudbeckia* and P-LL, although the physical structure of the soil was improved, the

input of fresh root-derived carbon sources triggered a strong rhizosphere priming effect [45]. Analysis by Huo et al. (2017) demonstrated that the rhizosphere priming effect is ubiquitous across diverse ecosystems, where living plant roots frequently and significantly accelerate the decomposition of originally stable SOC [46]. According to the microbial co-metabolism theory, these fresh carbon sources provide "activation energy" for starved microorganisms, stimulating them to synthesize degradative enzymes and consequently consuming large amounts of old, stable SOC that was previously physically protected [47]. Regarding microbial biomass carbon (MBC), high-yielding root systems such as those of P-SJ release substantial quantities of active exudates, providing abundant substrates for underlying enzymatic reactions. This significantly stimulates microbial activity and promotes the accumulation of MBC and necromass carbon [48, 49]. Such active microbial metabolic processes are considered to potentially facilitate the accumulation of microbial necromass, which constitutes a core pathway for the formation of stable SOC pools [50]. In contrast, P-HF and *Rudbeckia* may induce microbial nitrogen limitation due to the allelopathic inhibition of secondary metabolites or the high carbon-to-nitrogen ratio of their litter, triggering a negative feedback loop of "structural impairment–microbial limitation" [51].

In summary, this study revealed a tightly coupled network between multidimensional environmental factors and soil carbon fractions via the Mantel test. Favorable basal physicochemical properties fundamentally determine the water and aeration permeability of the soil, creating an irreplaceable physical space for microbial colonization [52, 53]. Concurrently, the correlation network suggests that soil aggregates exert a dual regulatory function as a core "hub" within this micro-ecosystem: on one hand, macroaggregates can protect organic carbon from degradation through physical encapsulation; on the other hand, the aggregation process helps maintain stable enzymatic reaction efficiency by providing microhabitat refuge for extracellular enzymes. This optimization of the physical structure likely provides favorable conditions for the efficient transformation of substrates, which in turn is closely associated with the accumulation of core carbon pools (particularly the

active MBC) [54]. This coupling characteristic highly aligns with the cutting-edge theory that the carbon cycle is governed by the "dynamic equilibrium between physical protection and microbial accessibility" [55]. Therefore, in the future construction of mixed planting communities in urban landscaping, it is essential not only to evaluate the ameliorative potential of plants on soil physical structure but also to weigh the potential impacts of the rhizosphere priming effect—triggered by their fresh carbon inputs—on the stability of deep carbon pools, thereby maximizing the carbon sequestration benefits of urban green space ecosystems.

Conclusions

Under conventional urban greening scenarios, all tested herbaceous perennials exhibited robust adaptability, and their ameliorative effects on the soil microenvironment demonstrated significant species-specificity. Notably, P-PS possessed the optimal synergistic potential for “growth–amelioration”. It not only established the most stable and uniform soil aggregate network—recording the highest mean weight diameter (MWD) and geometric mean diameter (GMD) among all treatments—but also drove a substantial 67.6% increase in soil available nitrogen while maintaining exceptionally high urease activity and microbial biomass carbon. This dual functionality effectively resolved the traditional trade-off dilemma between physical structure optimization and nutrient depletion. In conclusion, P-PS perfectly aligns with the dual objectives of landscape enhancement and soil fertility improvement, rendering it an optimal candidate species for urban greening in Northeast China. For future landscaping practices, we recommend establishing multi-species mixed communities based on a morphological–functional complementarity strategy to ensure the long-term enhancement of comprehensive soil fertility in urban green spaces.

Author Contributions

Conceptualization, P.B. and Z.Q.; methodology, X.Z.; validation, Y.Z.; formal analysis, P.B.; investigation, P.B. and B.H.; resources, W.G.; data curation, Y.W.; writing—original draft preparation, P.B. and H.Z.; writing—review and editing, W.G.;

supervision, W.G.; project administration, W.G.; funding acquisition, W.G. All authors have read and agreed to the published version of the manuscript.

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Data Availability

The original contributions presented in the study are included in the article; further inquiries can be directed to the corresponding authors.

Competing Interests

The authors declare there are no competing interests.

References

1. Keesstra, S., et al. (2018). The significance of soils and soil science towards realization of the United Nations Sustainable Development Goals. *SOIL*, 4(1), 111–128. <https://doi.org/10.5194/soil-2-111-2016>
2. Tresch, S., et al. (2018). Urban soil quality assessment—A comparison of urban garden types in relation to different management practices. *Science of the Total Environment*, 644, 252–263. <https://doi.org/10.3389/fenvs.2018.00136>
3. Wang, X., & Liu, S. (2021). Impacts of human recreational disturbances on soil bacterial community composition and diversity in urban forest in Changchun, Northeast China. *Forests*, 12(10), 1341. <https://doi.org/10.3390/f16121798>
4. Celletti, S., Poreba, L., Wawer, R., Padoan, E., Comis, S., Bartosiewicz, B., & Schiavon, M. (2025). The potential of nature-based solutions for urban soils: Focus on green infrastructure and bioremediation. *Land Degradation & Development*, 32(14), 3822–3841. <https://doi.org/10.3389/fenvs.2025.1634662>
5. Ruihong Wang, Jialin Liu. (2026). Effect of herbaceous plant root traits on soil aggregate stability and erosion control in degraded soils. *Soil and Tillage Research*, 198, 104543. <https://doi.org/10.3390/app16052333>
6. Batista, A. M., Pessoa, T. N., Putti, F. F., Andreote, F. D., & Libardi, P. L. (2023). Root influences rhizosphere hydraulic properties through soil organic carbon and

microbialactivity. *Plants*.<https://doi.org/10.3390/plants13141981>

7.Ma.Y (2019). Plant root-microbe interactions in phytoremediation of degraded soils: Mechanisms and applications. *Science of The Total Environment*, 858, 159756. doi: 10.3389/fpls.2019.01519

8.Sokol, N. W., Slessarev, E., Marschmann, G. L., Nicolas, A., Blazewicz, S. J., Brodie, E. L., ... & Pett-Ridge, J. (2022). Evidence for the primacy of living root inputs, not root or shoot litter, in forming soil organic carbon. *New Phytologist*, 236(4), 1361–1375. <https://doi.org/10.1111/nph.15361>

9.Siddique, I. A., Grados, D., Schittenhelm, S., et al. (2023). Soil organic carbon stock change following perennialization: A meta-analysis. *Agronomy for Sustainable Development*, 43(4), 55. <https://doi.org/10.1007/s13593-023-00912-w>

10 Peixoto, L., Olesen, J. E., Elsgaard, L., Lønne Enggrob, K., C. Banfield, C., Dippold, M. A., Nicolaisen, M. H., Bak, F., Zang, H., Dresbøll, D. B., Thorup-Kristensen, K., & Rasmussen, J. (2022). Deep-rooted perennial crops differ in capacity to stabilize C inputs in deep soil layers. *Scientific Reports*, *12*, Article 5952. <https://doi.org/10.1038/s41598-022-09737-1>

11.Yang, Q., Peng, J., Ni, S., Zhang, C., Wang, J., & Cai, C. (2024). Soil erosion-induced decline in aggregate stability and soil organic carbon reduces aggregate-associated microbial diversity and multifunctionality of agricultural slope in the Mollisol region. *Land Degradation & Development*, 35(8), 2891–2905. <https://doi.org/10.3390/hydrology12100267>

12.Wang, Z., et al. (2021). Effects of different vegetation restoration on soil physical properties. *Scientific Reports*, 11, 14521. <https://doi.org/10.1038/s41598-021-93976-5>

13. Dorji, T., Field, D. J., & Odeh, I. O. A. (2020). Soil aggregate stability and aggregate-associated organic carbon under different land use or land cover types. *Soil Use and Management*, *36*(2), 308–319. <https://doi.org/10.1111/sum.12549>

14. Singh, N., Asha, Maurya, V. K., & Singh, D. (2024). Soil enzyme activities as bioindicators of soil health: Implications for sustainable agriculture. *Journal of Natural Resource Conservation and Management*, 5(2), 124–136. <https://doi.org/10.51396/anrcm.5.2.2024.124-136>

15. Dijkstra, F. A., Zhu, B., & Cheng, W. (2021). Root effects on soil organic carbon: A double-edged sword. *New Phytologist*, *230*(1), 60–65. <https://doi.org/10.1111/nph.17082>
16. Li, Y., Yu, P., & Shen, L. (2022). Changes in soil aggregate stability and aggregate-associated organic carbon during old-field succession in karst valley. *Environmental Monitoring and Assessment*, *194*(1), Article 15. <https://doi.org/10.1007/s10661-021-09662-2>
17. Li, J., Wu, X., Shen, J., & Wang, Y. (2023). Interactive effects of organic and inorganic fertilizers on soil organic carbon fractions and microbial community under long-term fertilization. *Journal of Soils and Sediments*, 23(5), 1945–1958. <https://doi.org/10.1371/journal.pone.0195144>
18. Song, R., Zhu, W. Z., Li, H., & Wang, H. (2024). Impact of wine-grape continuous cropping on soil enzyme activity and the composition and function of the soil microbial community in arid areas. *Frontiers in Microbiology*, 15, 1348259. <https://doi.org/10.3389/fmicb.2024.1348259>
19. Yu, J., Liu, Y., Wang, Z., Huang, X., Chai, D., Gu, Y., ... & Shen, Z. (2022). The cropping obstacle of garlic was associated with changes in soil physicochemical properties, enzymatic activities and bacterial and fungal communities. *Frontiers in Microbiology*, 13, 828196. <https://doi.org/10.3389/fmicb.2022.828196>
20. Li, Z., Li, C., Huang, C., et al. (2024). Effects of different ratios of nitrogen base fertilizer to topdressing on soil nitrogen form and enzyme activity in sugar beet under shallow drip irrigation. *PeerJ*, 12, e18219. <https://doi.org/10.7717/peerj.18219>
21. Kuang, H., Wu, B., Peng, F., Yu, Y., Ma, X., & Shangguan, Y. (2025). Sustainable remediation of heavy metal contaminated soil through phytostabilization with the in-situ immobilization by mercapto-based palygorskite. *Frontiers in Plant Science*, 16, 1659418. <https://doi.org/10.3389/fpls.2025.1659418>
22. Bodner, G., Leitner, D., & Kaul, H. P. (2014). Coarse and fine root plants affect pore size distributions differently. *Plant and Soil*, 380(1), 133–151. <https://doi.org/10.1007/s11104-014-2079-8>
23. Wang, D., Liu, C., Yang, Y., Liu, P., Hu, W., Song, H., Miao, C., Chen, J., Yang, Z.,

- & Miao, Y. (2023). Clipping decreases plant cover, litter mass, and water infiltration rate in soil across six plant community sites in a semiarid grassland. *Science of the Total Environment*, *861*, Article 160588. <https://doi.org/10.1016/j.scitotenv.2022.160588>
24. Gentsch, N., Riechers, F. L., Boy, J., Schweneker, D., Feuerstein, U., Heuermann, D., & Guggenberger, G. (2024). Cover crops improve soil structure and change organic carbon distribution in macroaggregate fractions. *SOIL*, 10(1), 139–150. <https://doi.org/10.5194/soil-10-139-2024>
25. Coskun, D., Britto, D. T., Shi, W., & Kronzucker, H. J. (2017). Nitrogen transformations in modern agriculture and the role of biological nitrification inhibition. *Nature Plants*, 3(6), 17074. <https://doi.org/10.1038/nplants.2017.74>
26. Dijkstra, F. A., Carrillo, Y., Pendall, E., & Morgan, J. A. (2013). Rhizosphere priming: A nutrient perspective. *Frontiers in Microbiology*, 4, 216. <https://doi.org/10.3389/fmicb.2013.00216>
27. Kuzyakov, Y., & Blagodatskaya, E. (2015). Microbial hotspots and hot moments in soil: Concept & review. *Soil Biology and Biochemistry*, 83, 184–199. <https://doi.org/10.1016/j.soilbio.2015.01.025>
28. Liu, Y., Evans, S. E., Friesen, M. L., & Tiemann, L. K. (2022). Root exudates shift how N mineralization and N fixation contribute to the plant-available N supply in low fertility soils. *Soil Biology and Biochemistry*, 165, 108541. <https://doi.org/10.1016/j.soilbio.2021.108541>
29. Zhao, Y., Liang, H., Zhang, J., Chen, Y., Dhital, Y. P., Zhao, T., & Wang, Z. (2024). Isolation and characterization of potassium-solubilizing rhizobacteria (KSR) promoting cotton growth in saline–sodic regions. *Microorganisms*, 12(7), 1474. <https://doi.org/10.3390/microorganisms12071474>
30. Nannipieri, P., Giagnoni, L., Landi, L., & Renella, G. (2011). Role of phosphatase enzymes in soil. In E. K. Bütemann, A. Oberson, & E. Frossard (Eds.), *Phosphorus in action: Biological processes in soil phosphorus cycling* (pp. 215–243). Springer. https://doi.org/10.1007/978-3-642-15271-9_9
31. Liu, M., Gan, H., Li, H., Xiao, S., & Song, X. (2022). Effects of nitrogen and phosphorus addition on soil extracellular enzyme activity and stoichiometry in Chinese

- fir (*Cunninghamia lanceolata*) forests. *Frontiers in Plant Science*, 13, 834184. <https://doi.org/10.3389/fpls.2022.834184>
32. Nascimento, C. A., Gupta, S., Yildirim, S., Andrikopoulos, B., Wille, U., & Roessner, U. (2023). Deciphering the interactions in the root–soil nexus caused by urease and nitrification inhibitors: A review. *Agronomy*, 13(6), 1603. <https://doi.org/10.3390/agronomy13061603>
33. Li, Y., Ma, J., Li, Y., Shen, X., & Xia, X. (2023). Microbial community and enzyme activity respond differently to seasonal and edaphic factors in forest and grassland ecosystems. *Applied Soil Ecology*, 191, Article 105167. <https://doi.org/10.1016/j.apsoil.2023.105167>
34. Yin, L., Dijkstra, F. A., Phillips, R. P., Zhu, B., Wang, P., & Cheng, W. (2021). Arbuscular mycorrhizal trees cause a higher carbon to nitrogen ratio of soil organic matter decomposition via rhizosphere priming than ectomycorrhizal trees. *Soil Biology and Biochemistry*, 157, Article 108246. <https://doi.org/10.1016/j.soilbio.2021.108246>
35. Zhao, Y., et al. (2024). Effects of riparian pioneer plants on soil aggregate stability: Roles of root traits and rhizosphere microorganisms. *Science of the Total Environment*, 940, Article 173584. <https://doi.org/10.1016/j.scitotenv.2024.173584>
36. Colombi, T., Braun, S., Keller, T., & Walter, A. (2017). Soil compaction and the architectural plasticity of root systems. *Journal of Experimental Botany*, 68(19), 6019–6034. <https://doi.org/10.1093/jxb/erx383>
37. Bardgett, R. D., Mommer, L., & De Vries, F. T. (2014). Going underground: Root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution*, 29(12), 692–699. <https://doi.org/10.1016/j.tree.2014.10.006>
38. Gould, I. J., Quinton, J. N., Weigelt, A., De Deyn, G. B., & Bardgett, R. D. (2016). Plant diversity and root traits benefit physical properties key to soil function in grasslands. *Ecology Letters*, 19(9), 1089–1100. <https://doi.org/10.1111/ele.12652>
39. Gould, I. J., Quinton, J. N., Weigelt, A., De Deyn, G. B., & Bardgett, R. D. (2016). Plant diversity and root traits benefit physical properties key to soil function in grasslands. *Ecology Letters*, 19(9), 1140–1149. <https://doi.org/10.1111/ele.12652>
40. Qiao, H., Wu, L., Li, C., Yuan, T., & Gao, J. (2024). Microbial perspective on

- restoration of degraded urban soil using ornamental plants. *Journal of Environmental Management*, 359, Article 120920. <https://doi.org/10.1016/j.jenvman.2024.120920>
41. Lal, R. (2016). Soil health and carbon management. *Food and Energy Security*, 5(4), 212–222. <https://doi.org/10.1002/fes3.96>
42. Totsche, K. U., et al. (2018). Microaggregates in soils. *Journal of Plant Nutrition and Soil Science*, 181(1), 104–136. <https://doi.org/10.1002/jpln.201600451>
43. Bölscher, T., Cardon, Z. G., Garcia Arredondo, M., Grand, S., Griffen, G., Hestrin, R., Imboden, J., Jamoteau, F., Lacroix, E. M., Pérez Castro, S., Persson, P., Riley, W. J., & Keiluweit, M. (2025). Vulnerability of mineral-organic associations in the rhizosphere. *Nature Communications*, 16, Article 5527. <https://doi.org/10.1038/s41467-025-61273-4>
44. Henneron, L., et al. (2020a). Rhizosphere control of soil nitrogen cycling: A key component of plant economic strategies. *New Phytologist*, 228(3), 881–896. <https://doi.org/10.1111/nph.16760>
45. Friggens, N. L., Hugelius, G., Kokelj, S. V., Murton, J. B., Phoenix, G. K., & Hartley, I. P. (2025). Positive rhizosphere priming accelerates carbon release from permafrost soils. *Nature Communications*, *16*, Article 3576. <https://doi.org/10.1038/s41467-025-58845-9>
46. Huo, C., Luo, Y., & Cheng, W. (2017). Rhizosphere priming effect: A meta-analysis. *Soil Biology and Biochemistry*, 111, 78–84. <https://doi.org/10.1016/j.soilbio.2017.04.003>
47. Zhang, Q., Feng, J., Li, J., Huang, C. Y., Shen, Y., Cheng, W., & Zhu, B. (2023). A distinct sensitivity to the priming effect between labile and stable soil organic carbon. *New Phytologist*, 237(1), 88–99. <https://doi.org/10.1111/nph.18458>
48. Lange, M., Eisenhauer, N., Sierra, C. A., Bessler, H., Engels, C., Griffiths, R. I., ... & Gleixner, G. (2015). Plant diversity increases soil microbial activity and soil carbon storage. *Nature Communications*, 6(1), 6707. <https://doi.org/10.1038/ncomms7707>
49. Sokol, N. W., & Bradford, M. A. (2019). Microbial formation of stable soil carbon is more efficient from belowground than aboveground input. *Nature Geoscience*, 12(1), 46–53. <https://doi.org/10.1038/s41561-018-0258-6>

50. Liang, C., Amelung, W., Lehmann, J., & Kästner, M. (2019). Quantitative assessment of microbial necromass contribution to soil organic matter. *Global Change Biology*, 25(11), 3578–3590. <https://doi.org/10.1111/gcb.14781>
51. Henneron, L., Cros, V., Picon-Cochard, C., Rahimian, V., Fontaine, S., & Chauvat, M. (2020b). Plant economic strategies of grassland species control soil carbon dynamics. *Journal of Ecology*, 108(2), 528–545. <https://doi.org/10.1111/1365-2745.13276>
52. Rabot, E., Wiesmeier, M., Schlüter, S., & Vogel, H. J. (2018). Soil structure as an indicator of soil functions: A review. *Geoderma*, 314, 122–137. <https://doi.org/10.1016/j.geoderma.2017.11.009>
53. Kravchenko, A. N., & Guber, A. K. (2017). Soil pores and their contributions to soil carbon processes. *Geoderma*, 287, 2–9. <https://doi.org/10.1016/j.geoderma.2016.06.027>
54. Jian, S., Li, J., Chen, J., Wang, G., Mayes, M. A., Dzantor, K. E., ... & Luo, Y. (2016). Soil extracellular enzyme activities, soil carbon and nitrogen storage under nitrogen addition: A meta-analysis. *Soil Biology and Biochemistry*, 101, 26–34. <https://doi.org/10.1016/j.soilbio.2016.07.003>
55. Cotrufo, M. F., Ranalli, M. G., Haddix, M. L., Six, J., & Lugato, E. (2019). Soil carbon storage informed by particulate and mineral-associated organic matter. *Nature Geoscience*, 12(12), 989–994. <https://doi.org/10.1038/s41561-019-0484-6>