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Rootstock impacts on 'USDA-ARS-Pawnee' pecan growth, physiological traits, and soil microbial communities

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Introduction: Pecan (*Carya illinoinensis*), native to North America, is the most commercially significant species within the *Carya* genus, playing a vital role in nut production across the southern United States. Cultivated for its high-quality nuts, pecans are widely utilized in culinary applications, and their increasing global demand underscores the necessity for enhanced cultivation practices that ensure both economic sustainability and long-term viability. One critical factor influencing pecan production is rootstock selection, which affects growth, physiology, and overall orchard performance. This study investigates the impact of 12 different rootstocks on the growth and physiological characteristics of the 'USDA-ARS-Pawnee' scion to provide insights into optimal rootstock choices for pecan orchards.

Methods: The study was conducted over multiple years, assessing key traits including budbreak timing, tree morphology, leaf size, leaf retention, photosynthesis, leaf nutrient composition, and soil microbial community structure. Twelve distinct rootstocks were evaluated to determine their influence on scion development. Measurements of photosynthesis rate (PSR) and water use efficiency (WUE) were collected to establish correlations with leaf size. Leaf nutrient content and soil microbial diversity were analyzed to assess rootstock effects on tree health and orchard sustainability.

Results: Significant differences in budbreak timing were observed among the rootstocks, with northern rootstocks, particularly 'Peruque,' exhibiting the latest budbreak, while eastern rootstocks demonstrated the earliest budbreak. Growth performance varied across rootstock origins; southern (Mexican) rootstocks produced the tallest trees with the largest trunk diameters and canopy widths, highlighting their potential for enhancing orchard productivity. Leaf size differed among rootstocks, with northern and eastern rootstocks generally producing larger leaves, although statistical significance was not established. Larger leaves correlated positively with increased PSR and WUE, with 'Giles' (northern) and 'VC1-68' (western) exhibiting the highest values, while 'Elliott' (eastern) recorded the lowest. Leaf retention showed no significant differences, but northern and eastern rootstocks. Nutrient analysis revealed rootstock-dependent variations, with 'Riverside' containing the highest Zn levels and 'Peruque' the lowest, while

'Major' exhibited the highest B content, and 'Frutoso' the lowest. Soil microbial analysis identified distinct microbial compositions influenced by rootstock selection, with 'Peruque' fostering ectomycorrhizal fungi and '87MX5-1.7' supporting nitrogen-fixing bacteria, suggesting rootstock effects on soil microbial diversity and nutrient cycling.

Discussion: These findings highlight the importance of rootstock selection in optimizing pecan tree growth, physiological performance, and soil health. The superior growth of southern rootstocks suggests their potential for improving orchard productivity, while variations in PSR and WUE underscore the complex interactions between rootstocks and photosynthetic efficiency. Additionally, the microbial differences observed indicate that rootstock selection may influence soil nutrient dynamics, further emphasizing the role of rootstocks in sustainable pecan cultivation. Overall, this study provides valuable insights into rootstocks to enhance pecan orchard management.

KEYWORDS

Carya illinoinensis, provenance, seedstock, scion, horticultural traits, microbial diversity

Introduction

Pecan (*Carya illinoinensis*) is an economically and ecologically valuable nut tree in North America (Thompson and Grauke, 1991). The industry is a major contributor to the agricultural economy, with the United States being one of the largest global producers (USDA-NASS, 2024; INC, 2023). The growing demand for pecans, driven by their nutritional value which is rich in healthy fats, proteins, vitamins, and antioxidants, has increased the need for research to enhance production practices to ensure both economic viability and sustainability (Du et al., 2022; Yusufali et al., 2023).

Pecans thrive across diverse climates and soils in the United States, ranging from the warm, humid climates of the southeast to the arid areas of the southwest (Grauke et al., 2016; Thompson and Grauke, 1991). While their adaptability makes them a valuable crop, differences in cultivation environments poses challenges such as variable rainfall, low water quality, poorly drained soils, and early freeze. Regardless of growing region, one of the primary obstacles to successful pecan production is the long juvenile stage before fruit-bearing, combined with the high costs of establishing and maintaining pecan orchards, making efficient cultivation practices crucial to maximize yield and minimize costs (Fabrizio et al., 2018).

One of the most widely used techniques for improving pecan cultivation is grafting, a method that involves attaching a desired scion cultivar to a rootstock (Melnyk, 2017). By bypassing the lengthy juvenile phase, grafting facilitates faster and more predictable fruit production (Wells, 2024). However, its success relies heavily on selecting appropriate rootstocks (Grauke and O'Barr, 1996; Forner-Giner et al., 2020). Rootstocks influence more than just structural support; they play a central role in water and nutrient uptake, hormonal signaling, and root-to-shoot interactions (Rasool et al., 2020). Their effects on scion performance depend on genetic factors, as well as environmental conditions like soil composition, water availability, and temperature (Mir et al., 2023; Nawaz et al., 2016; Tworkoski and Miller, 2007; Wang et al., 2025b). These influences extend to critical growth aspects, including scion vigor, root development, nutrient uptake, and environmental stress tolerances such as drought, soil salinity, and diseases (Smith et al., 2014; Grauke and Thompson, 1995; Liu et al., 2019; Jamshidi Goharrizi et al., 2020; Rumbaugh et al., 2021; Barone et al., 1998).

Numerous studies have investigated the effects of different rootstocks on pecan tree performance. For instance, rootstock selection has been shown to influence a variety of traits such as scion tree size and growth rate (Grauke et al., 2003; Hasey et al., 2004; Nikpeyma, 2020; Tworkoski and Fazio, 2016). While some rootstocks promote more vigorous growth, others result in a more compact growth habit, which is advantageous for certain orchard management systems (Hayat et al., 2022; Mir et al., 2023; Morales Alfaro et al., 2023). Rootstocks also influence photosynthetic efficiency, leaf size, and overall canopy architecture, which directly affect a tree's capacity to capture sunlight and produce energy (Fallahi et al., 2001; Mickelbart and Arpaia, 2002). Additionally, they regulate nutrient uptake, which is critical for maintaining healthy tree growth and high-quality nut production (Reig et al., 2018; Ibacache et al., 2020; Brown et al., 1994). Studies have indicated that rootstocks enhanced the ability of pecan trees to acquire essential nutrients, such as nitrogen, phosphorus, and potassium, from the soil, thereby improving overall tree health and increasing nut yields (Walworth, 2020; Miyamoto et al., 1985).

Another emerging focus of rootstock research is their impact on soil microbial communities (Rasool et al., 2020; Ren et al., 2023; Palma et al., 2018). The rhizosphere, or the soil surrounding roots, hosts a diverse microbiome, including bacteria, fungi, and other microbes, which influence nutrient cycling, plant growth, and disease suppression. Studies suggest that rootstocks affect the composition and diversity of these microbial communities, which in turn impact overall tree health and growth (Ren et al., 2024, 2023; Palma et al., 2018). A healthy and balanced soil microbiome enhances nutrient availability, disease resistance, and improves soil structure, contributing to better tree performance (Bokszczanin et al., 2021). Therefore, understanding how different rootstocks shape soil microbial dynamics is crucial for developing sustainable and productive pecan orchard systems.

Pecan trees are highly heterozygous genetically, the openpollinated seeds are not completely true-to-type of their mother trees. However, growers and nurserymen primarily rely on seedling rootstocks due to the challenges in cloning and micropropagation. The open-pollinated seeds, resulting in genetic variability among rootstocks, which can lead to variability in tree vigor (Fabrizio et al., 2018; Sitton et al., 1939; Wang et al., 2025b), disease resistance (Sanderlin and Sanderlin, 2015), and adaptability to environmental conditions (Mir et al., 2023; Ren et al., 2024).

This study builds on existing knowledge of rootstock-scion interactions by evaluating the effects of 12 different rootstocks on the performance of the 'USDA-ARS-Pawnee' scion, a widely planted pecan cultivar in commercial orchards due to its high-quality nuts and early nut maturity. Conducted by the USDA ARS Pecan Breeding Program, the research began with seed germination in 2008 (Wang et al., 2025a), field trials in 2014, and evaluation of grafted scion trees from 2018 to 2023. The trial assessed a range of key parameters, including tree morphology, leaf size, photosynthesis and nutrition, and soil microbial community composition. By examining these factors, this study provides insights into how rootstocks influence pecan tree growth and health, with implications for improved orchard management practices.

Materials and methods

Three-year-old seedlings of 12 open-pollinated rootstocks (Wang et al., 2025a, b) were planted in an orchard in Somerville, TX (30° 31'21"N, 96°25'24"W) in 2012. The orchard consisted of four blocks, separated by a border row designed to provide pollination for the scion grafted on these rootstocks. Rows and trees were spaced 9.14 m by 9.14 m. Each block consisted of four rows and a total of 60 trees (Figure 1), arranged in a completely randomized design with five replications. In 2013 and 2014, a scion cultivar 'USDA-ARS-Pawnee' was grafted (if rootstock stem diameter was 35 mm or more) or budded (if rootstock diameter was blow 35 mm) onto the rootstocks (Wang et al., 2025b). The irrigation sprinklers were installed near each tree and used as needed. Fertilizers were applied based on the annual soil report. Zinc sprays were applied three times annually in the growing season. Insect control (casebearer) was performed once a year in the spring. The first block was monitored for the selected traits analyzed in this study.



FIGURE 1

College Station Rootstock Test (CSRT) block one field drone review map (center). Row 1 and 6 are border trees, and rows 2–5 are 'USDA-ARS-Pawnee' scion grafted onto 12 different rootstocks. Orange dots indicate the southern rootstock 87MX5-1.7, and blue dots represent the northern rootstock 'Peruque'. Root and rhizosphere soil samples were collected from these two rootstocks for microbial diversity analysis. One tree of each rootstock is shown on the right and left, respectively.

Budbreak

Budbreak was rated in the spring from 2020 to 2023 using an ordinal scale of 1 to 5, where 1 = dormancy, 2 = swelling, 3 = inner scale splitting, 4 = leaf burst, and 5 = leaflet expansion (Wang et al., 2025b). The date of budbreak scale 3 was transferred to Julian days to compare the length of budbreak time for statistical analysis.

Plant height, canopy width, and trunk diameter

The scion height and canopy width were measured in meters using a laser rangefinder (Vertex Laser Geo, Haglof, Sweden). The trunk diameter was measured 60 cm above ground using a digital caliper. All these three traits were collected in the dormant season in 2020-2023 (between December and January).

Leaf size

The end of July marks the peak of the growing season for pecans each year. On July 27, 2018, and July 27, 2022, ten pairs of the fourth leaflets from the middle compound leaves on a shoot, located in the outer middle section of the canopy, were collected. The leaflets were measured for length and width in millimeters using a digital caliper, and leaflet size (mm²) was calculated by multiplying length by width. Subsequently, the leaflets were dried in an oven at 70°C and ground for nutrient analysis.

Leaf nutrient

Total nitrogen (%) was determined by high-temperature combustion (McGeehan and Naylor, 1988). Plant minerals (B, Ca, Cu, Fe, K, Mg, Mn, Na, P, S, and Zn) (ppm) were analyzed by inductively coupled plasma (ICP) analysis after a nitric acid digest (Havlin and Soltanpour, 1980). Data in 2018 and 2022 were used for analysis.

Photosynthesis

Photosynthesis measurements were taken using LI-COR 6400XT portable photosynthesis system (LI-COR Biosciences, Inc.) from the fourth leaflet pair of a compound leaf located in the middle of a shoot at the outer edge of the middle canopy. Data was collected every 2.5 hours from 7:00 am to 7:30 pm on July 28, 2018.

Root and rhizosphere soil microbial community

The root and rhizosphere soil sampling of two rootstocks, 87MX5-1.7 and 'Peruque' (Figure 1) and analysis of microbial components followed the published methods (Ren et al., 2024). Briefly, roots with surrounding soil were collected from a depth of 5-20 cm, one meter away from the tree's main trunk base in May 2022. Total microbial DNA was extracted separately from roots and soil and then sequenced. The V4 region of bacterial 16S rDNA was amplified to explore the bacterial community, while the ITS2 region of fungi was amplified using universal primer pairs. The bioinformatics analysis was previously published in Ren et al. (2024). The test orchard is part of the USDA ARS Pecan Breeding Program in Somerville, TX (30° 31'21"N, 96°25'24"W). Based on U.S. climate data for Somerville, TX in 2022 (accessed on May 1, 2025, via US Climate Data), this region's annual climate features an average high temperature of 26.3°C (ranging from 16.1-35.6°C), an average low temperature of 12.9°C (ranging from 2.8-22.2°C), and an average annual precipitation of 8.18 cm (ranging from 4.80-11.35 cm). The soil is clay with a pH value of 6.5 (ranging from 5.9-6.9).

Data analysis

Statistical analysis was performed using $JMP^{\textcircled{R}}$ Pro 17.0.0 (SAS Institute Inc.). Rootstock effects were tested using a Generalized Linear Model and the overdispersion parameter was estimated by Maximum Likelihood. A one-way analysis of variance (ANOVA) was used to compare the mean values for each trait, with significance determined via the Tukey-Kramer HSD test. The effect of leaf size on photosynthesis rate and water use efficiency was assessed using a nominal logistic model, assuming rootstock independence.

Results

Budbreak

The 12 rootstocks significantly influenced the timing of budbreak in the 'USDA-ARS-Pawnee' scion (Table 1), with a 1–4-day difference observed over the four years from 2020 to 2023. The 'Peruque' rootstock exhibited a significantly (p = 0.05) later budbreak compared to the other 11 rootstocks, which did not differ significantly from one another (Table 2). Overall, northern rootstocks exhibited the latest budbreak, while eastern rootstocks showed the earliest. Southern and western rootstocks did not show significant differences in budbreak timing (Table 3).

Tree size

The scion growth performance varied significantly across the 12 rootstocks in terms of tree size metrics. Southern rootstocks generally outperformed northern ones, with southern (Mexican) rootstocks particularly effective in promoting significant increases in scion plant height, trunk diameter, and canopy width (Table 3). Specifically, the rootstock 87MX1-2.2 demonstrated the greatest vigor when compared to the other rootstocks (Table 2) and was significant (p = 0.05) in comparison to 'Elliott' (Eastern) and 'Peruque' (Northern). Rootstocks

		Budbreak (Julian days)		Height (m)		Canop	oy (m)	Diameter_Ro	otstock (cm)	Diameter_S	Scion (cm)	Retension (%) ^a		
Source	DF	L-R ChiSquare	Prob>ChiSq	L-R ChiSquare	Prob>ChiSq	L-R ChiSquare	Prob>ChiSq	L-R ChiSquare	Prob>ChiSq	L-R ChiSquare	Prob>ChiSq	L-R ChiSquare	Prob>ChiSq	
Rootstock	11	177.8744	<.0001**	183.7996	<.0001**	219.5023	<.0001**	258.5187	<.0001**	235.6469	<.0001**	12.957723	0.2961	
Rep	4	8.5960	0.0720	27.8607	<.0001**	40.5067	<.0001**	23.2833	<.0001**	36.8269	<.0001**	30.545721	<.0001**	
Year	3	1580.1247	<.0001**	645.4678	<.0001**	613.5126	<.0001**	781.1122	<.0001**	671.1102	<.0001**	168.16966	<.0001**	
Rootstock*Rep	44	76.7798	0.0016**	187.8832	<.0001**	193.6566	<.0001**	199.9311	<.0001**	220.1899	<.0001**	37.789952	0.7337	
Rootstock*Year	33	63.9690	0.0010*	6.6178	1.0000	16.8481	0.9911	13.8161	0.9987	5.6205	1.0000	37.511818	0.2699	
Rep*Year	12	21.3432	0.0456*	6.7618	0.8729	8.0130	0.7841	2.0956	0.9992	4.1829	0.9799	23.205138	0.0260*	
Rootstock*Rep*Year	132	140.9075	0.2819	31.4555	1.0000	45.1012	1.0000	24.3368	1.0000	18.9229	1.0000	138.53258	0.3312	

Generalized linear model fitted with an overdispersion parameter estimated by Maximum Likelihood in JMP Pro 17.0. Significance levels are indicated by *(p-value < 0.05) and **(p-value < 0.01). ^aData were collected in 2021 to 2024.

TABLE 2 Scion growth grafted on 12 different rootstocks from 2020 to 2023 in a replicated testing orchard.

Rootstock Provenance		Budbreak time (days)			Plant height (m)			Canopy width (m)				Trunk diameter (mm)				Leaf size (mm2)*				Leaf retention (%)**					
Rootstock	Provenance	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level
Moore	Eastern	87.15	3.77	1.69	ab	5.57	0.53	0.24	ab	2.75	0.54	0.24	ab	104.67	18.74	8.38	ab	27.23	4.36	1.95	abc	29.50	17.62	7.88	a
Elliott	Eastern	85.20	4.29	1.92	b	4.38	2.11	0.95	b	1.78	1.15	0.52	b	81.70	43.01	19.23	Ь	26.91	3.23	1.44	abc	29.00	16.36	7.31	a
Giles	Northern	88.80	2.84	1.27	ab	5.65	0.49	0.22	ab	2.90	0.14	0.06	ab	109.61	13.00	5.81	ab	24.62	4.59	2.05	abc	38.00	10.37	4.64	a
Major	Northern	90.00	1.98	0.88	ab	4.99	0.86	0.38	ab	1.91	0.44	0.20	ab	88.59	20.31	9.08	ab	24.60	4.82	2.16	abc	29.00	6.27	2.81	a
Posey	Northern	89.20	0.54	0.24	ab	4.79	0.80	0.36	ab	2.19	0.53	0.23	ab	84.65	18.89	8.45	ab	28.91	3.08	1.38	a	25.00	8.66	3.87	a
Peruque	Northern	92.35	1.15	0.52	a	4.21	1.00	0.45	b	1.60	0.64	0.29	b	78.01	24.37	10.90	b	26.39	6.34	2.84	abc	28.50	22.68	10.14	a
87MX1-2.2	Southern	87.50	2.46	1.10	ab	6.24	0.47	0.21	a	3.22	0.59	0.26	a	132.85	17.41	7.79	a	25.42	2.73	1.22	abc	34.50	11.65	5.21	a
Frutoso	Southern	89.80	0.80	0.36	ab	5.94	0.70	0.31	ab	2.51	0.60	0.27	ab	106.07	20.96	9.37	ab	22.70	1.75	0.78	bc	15.50	4.47	2.00	a
87MX5-1.7	Southern	86.60	1.43	0.64	b	5.80	0.75	0.34	ab	2.84	0.55	0.25	ab	110.77	20.78	9.29	ab	24.96	4.76	2.13	abc	27.50	15.41	6.89	a
VC1-68	Western	87.35	1.58	0.71	ab	6.11	0.38	0.17	ab	2.93	0.32	0.15	ab	120.85	4.93	2.21	ab	27.98	6.00	2.68	ab	28.50	12.07	5.40	a
San Felipe	Western	88.60	0.98	0.44	ab	5.27	0.20	0.09	ab	2.26	0.32	0.14	ab	95.55	6.38	2.85	ab	22.01	4.21	1.88	с	21.50	5.18	2.32	a
Riverside	Western	87.75	3.36	1.50	ab	4.57	1.94	0.87	ab	2.00	1.03	0.46	ab	84.22	32.33	14.46	ab	23.21	3.33	1.49	bc	22.40	15.59	6.97	a

*Leaf size was the average of 2018 and 2022 and **leaf retention was the average in 2021-2024. Comparisons between all pairs were conducted using Tukey-Kramer HSD, with levels not connected by the same letter considered significantly different at p = 0.05. The highest and lowest values for each trait were outlined in red and blue, respectively.

-				
*	Level	а	а	a
ition (%)*	Std Err Mean	5.07	2.99	3.45
saf reter	Std Dev	16.03	13.39	13.35
Ľ	Mean	29.25	30.13	25.83
	Level	а	а	a
e (mm²)*	Std Err Mean	1.14	1.07	0.86
Leaf size	Std Dev	3.62	4.80	3.32
	Mean	27.07	26.13	24.36
ي ل	Level	ab	p	a
neter (mr	Std Err Mean	10.60	4.85	5.67
unk diam	Std Dev	33.54	21.67	21.94
Тл	Mean	93.18	90.22	116.56
	Level	ab	p	a
vidth (m	Std Err Mean	0.31	0.15	0.16
anopy v	Std Dev	0.99	0.66	0.61
	Mean	2.27	2.15	2.86
	Level	ab	q	a
aight (m)	Std Err Mean	0.50	0.20	0.16
Plant he	Std Dev	1.58	0.91	0.63
	Mean	4.97	4.91	5.99
	Level	q	a	ab
ak (days)	Std Err Mean	1.25	0.49	0.54
Budbre	Std Dev	3.94	2.20	2.11
	Mean	86.18	90.09	87.97
	Provenance	Eastern	Northern	Southern

13.35 11.36 24.13 68.62 æ a 0.80 1.31 3.32 5.06 24.4024.30 B q 6.16 5.67 21.9423.84 96.911 100.21 æ ab 0.160.19 0.610.73 2.80 2.40 ab æ 0.16 0.32 0.63 1.25 66.C 5.32 ap ab 0.54 0.55 2.11 2.12 87.97 87.90 southern Western

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Leaf size

scion growth performance, we conducted a principal component analysis (PCA) based on four years of data (2020–2023). The analysis included budbreak, tree height, canopy width, and trunk diameter, accounting for rootstocks and replications. The PCA clarified the above results: northern rootstocks delayed budbreak (resulting in longer Julian days) and slowed tree growth, whereas southern

The average size of the leaflets was variable, with 'Posey' exhibiting the largest leaflets and 'San Felipe' the smallest (Table 2). On average, rootstocks from eastern and northern provenances produced larger leaflets compared to those from southern and western regions (Table 3). However, these differences were not statistically significant.

from eastern and western regions showed intermediate performance, with distinct differences when compared to both southern and

rootstocks (except for Frutoso) advanced budbreak (resulting in

shorter Julian days) and enhanced tree growth (Figure 2). The

effects of western and eastern rootstocks showed variability (Table 1).

To evaluate the contributions of rootstocks and their origins to

Leaf retention

Leaf size

northern seedstocks (Table 3).

Leaf retention, referring to the duration leaves remaining on the canopy before natural defoliation, was estimated as the percentage of leaves remaining on the canopy during the late growth season (with a maximum of >50% leaf defoliation). The scion leaf retention showed no significant difference across the 12 rootstocks but presented variation in years (Tables 1, 2) (p > 0.05) (. Although rootstock origin did not significantly affect leaf retention, northern and eastern provenances tended to retain more leaves than southern and western rootstocks in early November (Table 3). For instance, the northern rootstock 'Giles' had the highest leaf retention (38%), while the southern rootstock 'Frutoso' had the lowest leaf retention (15.5%). However, these differences were not statistically significant.

Leaf photosynthesis

Leaf photosynthesis rate (PSR) and water use efficiency (WUE) were assessed across the 12 rootstocks, revealing significant differences during most of the daylights with exception of no significance at 14:30 pm (Table 4). Two rootstocks, 'Giles' (northern region) and VC1-68 (western region)-showed the highest PSR and WUE (Figure 3). In contrast, 'Elliott', a rootstock commonly used in southeastern and southern pecan-growing regions, exhibited the lowest PSR and WUE at the time of the highest daily photosynthesis rate (5 p.m.), despite showing higher or at least moderate PSR during other periods of the day (Figure 3). The PSR and WUE had a higher positive correlation (r = 0.752). This study also indicated that scion leaf size has significant positive

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[ABLE 3 Scion growth on different rootstock provenances from 2020 to 2023 in a replicated testing orchard.



Principal Component Analysis (PCA) illustrating the contributions of 12 rootstocks from four provenances to 'USDA-ARS-Pawnee' scion growth performance, including budbreak time, height, canopy width, and trunk diameter.

TABLE 4	The effect tests of leaf size,	photosynthesis rate	(PSR) and water	use efficiency (WUI	E) of the 12 r	ootstocks on scion	'USDA-ARS-Pawnee' i	n
July 2018								

Time			7:00	9:30	12:00	14:30	17:00	19:30
Source	Nparm	DF	Prob>ChiSq	Prob>ChiSq	Prob>ChiSq	Prob>ChiSq	Prob>ChiSq	Prob>ChiSq
Leaf size	11	11	0.0031**	0.0882	0.0004**	0.0322*	0.0008**	0.6097
PSR	11	11	0.0976	0.0403*	0.0396*	0.5911	0.0004**	0.0473*
Leaf size*PSR	11	11	0.1256	0.0075**	0.2682	0.3103	0.0865	0.0956
WUE	11	11	0.0443*	0.0341*	0.2996	0.0002**	0.3057	0.0025**
Leaf size*WUE	11	11	0.0230*	0.0002**	0.1155	0.1152	0.7633	0.1272
PSR*WUE	11	11	0.0008**	0.0224*	0.0011**	0.0048**	0.0079**	0.6510
Leaf size*PSR*WUE	11	11	<.0001*	<.0001*	0.1177	0.9468	0.0196*	0.0139*

Nparm: The number of parameters associated with this effect; DF: The degree of freedom for the effect test; Prob > ChiSq: The probability of obtaining a greater chi-square value (not shown) if the specified model fits no better than the model that includes only an intercept. Significant differences were set at p < 0.05 (*) and p < 0.01 (**), respectively.

correlation with PSR (r = 0.270, p <0.05) and WUE (r = 0.300, p < 0.05) during most time of a day (Table 4).

Leaf nutrition

Nutrient analysis of scion leaves showed variability in most leaf nutrients but no significant differences across the 12 rootstocks, except for zinc (Zn) and boron (B) (Table 5). The rootstock 'Riverside' exhibited the highest Zn content (45.95 ppm), while 'Peruque' had the lowest Zn content (27.59 ppm). Similarly, 'Major' contained the highest B content (180.63 ppm), and 'Frutoso' had the lowest (108.40 ppm). Rootstock origin had minimal impact on nutrient content, except for potassium (K), magnesium (Mg), and boron (B). Northern rootstocks had the highest K and B levels but the lowest Mg, while western rootstocks showed the opposite trend (Table 6). These findings demonstrate the role of rootstocks in nutrient uptake and distribution within the scion.

Soil microbial community

The microbial diversity in the roots and rhizosphere soil was examined for two rootstocks: one of the tallest (87MX5-1.7) and one of the shortest ('Peruque') (Figure 1). The composition of microbial communities varied significantly between the two rootstocks.



'Peruque', a northern rootstock, exhibited a higher abundance of ectomycorrhizal fungi (e.g., *Inocybe* and *Russula*), which decompose organic matter and cycling nutrients, particularly phosphorus. In contrast, the southern provenance 87MX5-1.7 showed elevated levels of nitrogen-fixing bacteria (*Bradyrhizobium*) and phosphorus-absorbing fungi (*Tuber*) (Table 7).

Discussion

The results from this trial evaluating the impact of 12 rootstocks on the 'USDA-ARS-Pawnee' scion cultivar provide valuable insights into the role of rootstock provenance in shaping key physiological traits and growth parameters in pecan trees. Several significant trends emerged across different rootstocks, highlighting the importance of selecting the right rootstock to optimize growth, health, and productivity in the pecan orchards. The findings further highlight the pivotal role of rootstock origin in influencing various aspects of tree physiology, including budbreak timing, tree size, leaf development, nutrient uptake, photosynthesis, leaf retention, and soil microbial diversity.

Influence of rootstock on budbreak timing

Budbreak timing is a crucial phenological trait in pecan trees that influences the overall growth cycle and potential for damage from late-season frost (Grauke et al., 1992). In this study, the timing of budbreak in the 'USDA-ARS-Pawnee' scion was significantly affected by the rootstock, with a range of 1–4 days difference observed across the four years of the study. Northern rootstocks, such as 'Peruque', exhibited later budbreak time compared to southern and eastern rootstocks. This aligns with the natural adaptation of northern provenances to colder climates, where delayed budbreak can serve as a protective mechanism against TABLE 5 Nutrient composition (%) in scion leaves across 12 different rootstocks in a replicated testing orchard (average data in 2018 and 2022).

		Panance P								К		Zn				Са				Mg					
Rootstock	Provenance	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level
Elliott	Eastern	2.2791	0.1531	0.0685	a	0.1463	0.0090	0.0040	a	0.6654	0.0691	0.0309	a	0.0034	0.0008	0.0003	ab	2.2948	0.4382	0.1960	a	0.5886	0.1247	0.0558	a
Moore	Eastern	2.2529	0.1811	0.0810	a	0.1348	0.0077	0.0035	а	0.7324	0.0735	0.0329	a	0.0036	0.0008	0.0004	ab	2.5514	0.2239	0.1001	а	0.5604	0.0719	0.0322	а
Giles	Northern	2.2716	0.0966	0.0432	a	0.1475	0.0148	0.0066	a	0.7502	0.0553	0.0247	a	0.0035	0.0003	0.0001	ab	2.6725	0.1305	0.0584	a	0.5658	0.0636	0.0285	a
Major	Northern	2.2159	0.1048	0.0469	a	0.1400	0.0102	0.0046	a	0.7251	0.0731	0.0327	a	0.0034	0.0009	0.0004	ab	2.5710	0.1787	0.0799	a	0.4830	0.0535	0.0239	a
Peruque	Northern	2.2423	0.1871	0.0837	a	0.1518	0.0156	0.0070	a	0.8301	0.1347	0.0603	a	0.0028	0.0005	0.0002	b	2.2212	0.0410	0.0183	a	0.5288	0.0791	0.0354	a
Posey	Northern	2.3170	0.0755	0.0337	a	0.1495	0.0123	0.0055	a	0.7700	0.0909	0.0407	a	0.0035	0.0010	0.0005	ab	2.3745	0.1996	0.0893	a	0.5627	0.1283	0.0574	a
87MX1-2.2	Southern	2.2564	0.1111	0.0497	a	0.1471	0.0074	0.0033	a	0.6973	0.0828	0.0370	a	0.0036	0.0010	0.0004	ab	2.3878	0.2390	0.1069	a	0.6218	0.1024	0.0458	a
87MX5-1.7	Southern	2.1563	0.1626	0.0727	a	0.1452	0.0203	0.0091	a	0.7091	0.0764	0.0341	a	0.0029	0.0004	0.0002	ab	2.5735	0.2758	0.1234	a	0.5688	0.0592	0.0265	а
Frutoso	Southern	2.1380	0.1140	0.0510	a	0.1463	0.0036	0.0016	а	0.7277	0.0865	0.0387	а	0.0034	0.0004	0.0002	ab	2.3803	0.1772	0.0792	а	0.5681	0.0494	0.0221	a
Riverside	Western	2.2335	0.1493	0.0668	a	0.1537	0.0246	0.0110	а	0.6726	0.0513	0.0229	a	0.0046	0.0014	0.0006	а	2.4446	0.4162	0.1861	а	0.5891	0.1052	0.0470	a
San Felipe	Western	2.1794	0.1340	0.0599	a	0.1365	0.0079	0.0035	а	0.6796	0.0896	0.0401	a	0.0032	0.0005	0.0002	ab	2.3938	0.2637	0.1179	а	0.6649	0.0880	0.0393	a
VC1-68	Western	2.3532	0.1547	0.0692	a	0.1505	0.0067	0.0030	a	0.6964	0.0442	0.0198	a	0.0033	0.0011	0.0005	ab	2.2185	0.2133	0.0954	a	0.6420	0.0469	0.0210	a
			1	Na				Fe			1	Cu	1			Mn				S				В	
Rootstock	Provenance	Mean	Std Dev	Na Std Err Mean	Level	Mean	Std Dev	Fe Std Err Mean	Level	Mean	Std Dev	Cu Std Err Mean	Level	Mean	Std Dev	Mn Std Err Mean	Level	Mean	Std Dev	S Std Err Mean	Level	Mean	Std Dev	B Std Err Mean	Level
Rootstock Elliott	Provenance Eastern	Mean 0.0132	Std Dev 0.0054	Na Std Err Mean 0.0024	Level	Mean 0.0064	Std Dev 0.0000	Fe Std Err Mean 0.0002	Level	Mean 0.0009	Std Dev 0.0001	Cu Std Err Mean 0.0000	Level	Mean 0.0562	Std Dev 0.0214	Mn Std Err Mean 0.0096	Level	Mean 0.3114	Std Dev 0.0149	S Std Err Mean 0.0067	Level	Mean 0.0144	Std Dev 0.0009	B Std Err Mean 0.0004	Level
Rootstock Elliott Moore	Provenance Eastern Eastern	Mean 0.0132 0.0117	Std Dev 0.0054 0.0029	Na Std Err Mean 0.0024 0.0013	Level a a	Mean 0.0064 0.0088	Std Dev 0.0000	Fe Std Err Mean 0.0002	Level a a	Mean 0.0009 0.0014	Std Dev 0.0001 0.0009	Cu Std Err Mean 0.0000	Level a a	Mean 0.0562 0.0592	Std Dev 0.0214 0.0095	Mn Std Err Mean 0.0096 0.0042	Level a a	Mean 0.3114 0.3095	Std Dev 0.0149 0.0162	S Std Err Mean 0.0067 0.0073	Level a a	Mean 0.0144 0.0158	Std Dev 0.0009 0.0031	B Std Err Mean 0.0004	Level abc abc
Rootstock Elliott Moore Giles	Provenance Eastern Eastern Northern	Mean 0.0132 0.0117 0.0120	Std Dev 0.0054 0.0029 0.0031	Na Std Err Mean 0.0024 0.0013 0.0014	Level a a a	Mean 0.0064 0.0088 0.0063	Std Dev 0.0000 0.0000	Fe Std Err Mean 0.0002 0.0020 0.0003	Level a a a	Mean 0.0009 0.0014 0.0011	Std Dev 0.0001 0.0009 0.0001	Cu Std Err Mean 0.0000 0.0004 0.0000	Level a a a	Mean 0.0562 0.0592 0.0628	Std Dev 0.0214 0.0095 0.0133 0.0133	Mn Std Err Mean 0.0096 0.0042 0.0060	Level a a a	Mean 0.3114 0.3095 0.3211	Std Dev 0.0149 0.0162 0.0286	S Std Err Mean 0.0067 0.0073 0.0128	Level a a a	Mean 0.0144 0.0158 0.0164	Std Dev 0.0009 0.0031 0.0024	B Std Err Mean 0.0004 0.0014	Level abc abc ab
Rootstock Elliott Moore Giles Major	Provenance Eastern Eastern Northern Northern	Mean 0.0132 0.0117 0.0120 0.0141	Std Dev 0.0054 0.0029 0.0031 0.0030	Na Std Err Mean 0.0024 0.0013 0.0014 0.0013	Level a a a a	Mean 0.0064 0.0088 0.0063 0.0080	Std Dev 0.0000 0.0000 0.0000 0.0000 0.0000	Fe Std Err Mean 0.0002 0.0020 0.0003 0.0012	Level a a a a	Mean 0.0009 0.0014 0.0011	Std Dev 0.0001 0.0009 0.0001 0.0001	Cu Std Err Mean 0.0000 0.0004 0.0000	Level a a a a	Mean 0.0562 0.0592 0.0628 0.0469	Std Dev 0.0214 0.0095 0.0133 0.0086	Mn Std Err Mean 0.0096 0.0042 0.0060 0.0039	Level a a a a	Mean 0.3114 0.3095 0.3211 0.2834	Std Dev 0.0149 0.0162 0.0286 0.0164	S Std Err Mean 0.0067 0.0073 0.0128 0.0073	Level a a a a	Mean 0.0144 0.0158 0.0164 0.0181	Std Dev 0.0009 0.0031 0.0024 0.0023	B Std Err Mean 0.0004 0.0014 0.0011 0.0010	Level abc abc ab ab
Rootstock Elliott Moore Giles Major Peruque	Provenance Eastern Eastern Northern Northern Northern	Mean 0.0132 0.0117 0.0120 0.0141 0.0147	Std Dev 0.0054 0.0029 0.0031 0.0030 0.0053	Na Std Err Mean 0.0024 0.0013 0.0014 0.0013 0.0024	Level a a a a a	Mean 0.0064 0.0088 0.0063 0.0080 0.0106	Std Dev 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000	Fe Std Err Mean 0.0002 0.0003 0.0003 0.0012 0.0018	Level a a a a a	Mean 0.0009 0.0014 0.0011 0.0009 0.0010	Std Dev 0.0001 0.0009 0.0001 0.0001 0.0001	Cu Std Err Mean 0.0000 0.0004 0.0000 0.0000	Level a a a a a	Mean 0.0562 0.0592 0.0628 0.0469 0.0451	Std Dev 0.0214 0.0095 0.0133 0.0086 0.0140	Mn Std Err Mean 0.0096 0.0042 0.0060 0.0039 0.0063	Level a a a a a	Mean 0.3114 0.3095 0.3211 0.2834 0.2931	Std Dev 0.0149 0.0162 0.0286 0.0164	S Std Err Mean 0.0067 0.0073 0.0128 0.0073 0.0105	Level a a a a a	Mean 0.0144 0.0158 0.0164 0.0181 0.0159	Std Dev 0.0009 0.0031 0.0024 0.0023 0.0028 0.0028	B Std Err Mean 0.0004 0.0014 0.0011 0.0010 0.0013	Level abc abc ab ab ab
Rootstock Elliott Moore Giles Major Peruque Posey	Provenance Eastern Eastern Northern Northern Northern Northern	Mean 0.0132 0.0117 0.0120 0.0141 0.0147 0.0229	Std Dev 0.0054 0.0029 0.0031 0.0030 0.0053 0.0307	Na Std Err Mean 0.0024 0.0013 0.0014 0.0013 0.0024 0.0137	Level a a a a a a a	Mean 0.0064 0.0088 0.0063 0.0080 0.0106 0.0073	Std Dev 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000	Fe Std Err Mean 0.0002 0.0020 0.0013 0.0018 0.0010	Level a a a a a a a	Mean 0.0009 0.0014 0.0011 0.0009 0.0010 0.0010	Std Dev 0.0001 0.0009 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001	Cu Std Err Mean 0.0000 0.0000 0.0000 0.0000	Level a a a a a a a	Mean 0.0562 0.0592 0.0628 0.0469 0.0451 0.0531	Std Dev 0.0214 0.0095 0.0133 0.0086 0.0140	Mn Std Err Mean 0.0096 0.0042 0.0060 0.003 0.0063 0.0060	Level a a a a a a	Mean 0.3114 0.3095 0.3211 0.2834 0.2931 0.2974	Std Dev 0.0149 0.0162 0.0286 0.0164 0.0235 0.0048	S Std Err Mean 0.0067 0.0073 0.0128 0.0073 0.0105 0.0021	Level a a a a a a a	Mean 0.0144 0.0158 0.0164 0.0181 0.0159 0.0152	Std Dev 0.0009 0.0031 0.0023 0.0023 0.0028 0.0039	B Std Err Mean 0.0004 0.0014 0.0011 0.0013 0.0018	Level abc abc ab ab abc abc
Rootstock Elliott Moore Giles Major Peruque Posey 87MX1-2.2	Provenance Eastern Eastern Northern Northern Northern Southern	Mean 0.0132 0.0117 0.0120 0.0141 0.0147 0.0229 0.0194	Std Dev 0.0054 0.0029 0.0031 0.0030 0.0053 0.0307 0.0132	Na Std Err Mean 0.0024 0.0013 0.0014 0.0013 0.0024 0.0137 0.0059	Level a a a a a a a a a	Mean 0.0064 0.0088 0.0063 0.0080 0.0106 0.0073 0.0073	Std Dev 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000	Fe Std Err Mean 0.0002 0.0003 0.0013 0.0012 0.0010 0.0008	Level a a a a a a a a a a a	Mean 0.0009 0.0014 0.0011 0.0009 0.0010 0.0010 0.0011	Std Dev 0.0001 0.0009 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001	Cu Std Err Mean 0.0000 0.0000 0.0000 0.0000 0.0000	Level a a a a a a a a a a	Mean 0.0562 0.0592 0.0628 0.0469 0.0451 0.0531 0.0531	Std Dev 0.0214 0.0095 0.0133 0.0086 0.0140 0.0135 0.0098	Mn Std Err Mean 0.0096 0.0042 0.0060 0.0039 0.0063 0.0060 0.0044	Level a a a a a a a a a	Mean 0.3114 0.3095 0.3211 0.2834 0.2931 0.2974 0.3138	Std Dev 0.0149 0.0162 0.0286 0.0164 0.0235 0.0048 0.00248 0.0248	S Std Err Mean 0.0067 0.0073 0.0128 0.0073 0.0105 0.0021 0.0111	Level a a a a a a a a a a a	Mean 0.0144 0.0158 0.0164 0.0181 0.0159 0.0152 0.0147	Std Dev 0.0009 0.0031 0.0024 0.0023 0.0028 0.0028 0.0029 0.0029	B Std Err Mean 0.0004 0.0011 0.0010 0.0013 0.0018 0.0009	Level abc ab ab ab abc abc abc
Rootstock Elliott Moore Giles Major Peruque Posey 87MX1-2.2 87MX1-2.7	Provenance Eastern Eastern Northern Northern Northern Southern Southern	Mean 0.0132 0.0117 0.0120 0.0141 0.0147 0.0229 0.0194 0.0136	Std Dev 0.0054 0.0029 0.0031 0.0030 0.0053 0.0132 0.0053	Na Std Err Mean 0.0024 0.0013 0.0014 0.0013 0.0024 0.0137 0.0059 0.0024	Level a a a a a a a a a a a	Mean 0.0064 0.0088 0.0063 0.0080 0.0106 0.0073 0.0073 0.0073	Std Dev 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000	Fe Std Err Mean 0.0002 0.0003 0.0012 0.0018 0.0018 0.0008	Level a a a a a a a a a a a a	Mean 0.0009 0.0014 0.0011 0.0009 0.0010 0.0010 0.0011 0.0011	Std Dev 0.0001 0.0009 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001	Cu Std Err Mean 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000	Level a a a a a a a a a a a a	Mean 0.0562 0.0592 0.0628 0.0469 0.0451 0.0531 0.0491 0.0462	Std Dev 0.0214 0.0095 0.0133 0.0086 0.0140 0.0135 0.0098 0.0113	Mn Std Err Mean 0.0096 0.0042 0.0063 0.0063 0.0064 0.0044 0.0050	Level a a a a a a a a a a a	Mean 0.3114 0.3095 0.3211 0.2834 0.2931 0.2974 0.3138 0.2991	Std Dev 0.0149 0.0162 0.0286 0.0164 0.0235 0.0048 0.0248	S Std Err Mean 0.0067 0.0073 0.0128 0.0073 0.0105 0.0021 0.0111 0.0051	Level a a a a a a a a a a a a	Mean 0.0144 0.0158 0.0164 0.0181 0.0159 0.0152 0.0147 0.0140	Std Dev 0.0009 0.0031 0.0024 0.0023 0.0028 0.0028 0.0029 0.0020 0.0020	B Std C.0.0014 C.0.0014 C.0.0010 C.0.0010 C.0.0018 C.0.0009 C.0.0007	Level abc abc ab ab abc abc abc abc
Rootstock Elliott Moore Giles Major Peruque Posey 87MX1-2.2 87MX5-1.7 Frutoso	Provenance Eastern Eastern Northern Northern Northern Southern Southern Southern	Mean 0.0132 0.0117 0.0120 0.0141 0.0147 0.0229 0.0194 0.0136 0.0185	Std Dev 0.0054 0.0029 0.0031 0.0030 0.0053 0.0307 0.0132 0.0053 0.0053	Na Std Err Mean 0.0024 0.0013 0.0014 0.0013 0.0024 0.0137 0.0024 0.0137 0.0059 0.0024	Level a a a a a a a a a a a a a a	Mean 0.0064 0.0088 0.0063 0.0080 0.0106 0.0073 0.0073 0.0078 0.0066	Std Dev 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000	Fe Std Err Mean 0.0002 0.0020 0.0012 0.0018 0.0018 0.0003 0.0003 0.0004 0.0005 0.0005 0.0007 0.0002	Level a a a a a a a a a a a a a	Mean 0.0009 0.0014 0.0011 0.0009 0.0010 0.0010 0.0011 0.0010 0.0009	Std Dev 0.0001 0.0009 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001	Cu Std Err Mean 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000	Level a a a a a a a a a a a a a	Mean 0.0562 0.0592 0.0628 0.0469 0.0451 0.0531 0.0462 0.0462	Std Dev 0.0214 0.0095 0.0133 0.0086 0.0140 0.0135 0.0098 0.0113 0.0093	Mn Std Err Mean 0.0096 0.0042 0.0043 0.0063 0.0064 0.0044 0.0050	Level a a a a a a a a a a a a a a	Mean 0.3114 0.3095 0.3211 0.2834 0.2931 0.2974 0.3138 0.2991 0.2991	Std Dev 0.0149 0.0162 0.0286 0.0164 0.0235 0.0048 0.0248 0.0115 0.0100	S Std Err Mean 0.0067 0.0073 0.0128 0.0073 0.0105 0.0021 0.0111 0.0051 0.0045	Level a a a a a a a a a a a a a	Mean 0.0144 0.0158 0.0164 0.0181 0.0159 0.0152 0.0147 0.0140 0.0108	Std Dev 0.0009 0.0031 0.0024 0.0023 0.0028 0.0028 0.0029 0.0020 0.0021 0.0020 0.0017 0.0016	B 2 Std 2 0.0004 0 0.0014 0 0.0013 0 0.0013 0 0.0003 0 0.0007 0 0.0007	Level abc ab ab ab ab abc abc abc c
Rootstock Elliott Moore Giles Major Peruque Posey 87MX1-2.2 87MX1-2.2 87MX5-1.7 Frutoso Riverside	Provenance Eastern Eastern Northern Northern Northern Southern Southern Southern Southern Western	Mean 0.0132 0.0117 0.0120 0.0141 0.0147 0.0229 0.0194 0.0136 0.0185 0.0153	Std Dev 0.0054 0.0029 0.0031 0.0030 0.0053 0.0132 0.0053 0.0053 0.0053	Na Std Err Mean 0.0024 0.0013 0.0014 0.0013 0.0024 0.0137 0.0059 0.0024 0.0059 0.0024 0.0011 0.0011	Level a a a a a a a a a a a a a a a a	Mean 0.0064 0.0088 0.0063 0.0080 0.0106 0.0073 0.0073 0.0073 0.0078 0.0066 0.0062	Std Dev 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000	Fe Std Err Mean 0.0002 0.0003 0.0012 0.0012 0.0013 0.0003 0.0003 0.0002 0.0002	Level a a a a a a a a a a a a a	Mean 0.0009 0.0014 0.0011 0.0009 0.0010 0.0010 0.0010 0.0010 0.0009 0.0009	Std Dev 0.0001 0.0009 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001	Cu Std Err Mean 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000	Level a a a a a a a a a a a a a a a	Mean 0.0562 0.0592 0.0628 0.0469 0.0451 0.0531 0.0491 0.0462 0.0512 0.0512	Std Dev 0.0214 0.0095 0.0133 0.0086 0.0140 0.0135 0.0098 0.0113 0.0093 0.0175	Mn Std Err Mean 0.0096 0.0042 0.0042 0.0039 0.0063 0.0064 0.0054 0.0042 0.0042	Level a a a a a a a a a a a a a a a a	Mean 0.3114 0.3095 0.3211 0.2834 0.2931 0.2974 0.3138 0.2991 0.2979 0.3102	Std Dev 0.0149 0.0162 0.0286 0.0164 0.0235 0.0048 0.0248 0.0248 0.0115 0.0100	S Std Err Mean 0.0067 0.0073 0.0128 0.0073 0.0105 0.0021 0.0011 0.0051 0.0045 0.0170	Level a a a a a a a a a a a a a	Mean 0.0144 0.0158 0.0164 0.0181 0.0159 0.0152 0.0147 0.0140 0.0108 0.0124	Std Dev 0.0009 0.0031 0.0023 0.0023 0.0023 0.0023 0.0020 0.0020 0.0021 0.0020 0.0016 0.0030	B Std Err Mean 0.0004 0.0014 0.0011 0.0013 0.0013 0.0007 0.0007 0.00014	Level abc abc ab ab abc abc abc abc c bc
Rootstock Elliott Moore Giles Major Peruque Posey 87MX1-2.2 87MX1-2.2 87MX5-1.7 Frutoso Riverside San Felipe	Provenance Eastern Eastern Northern Northern Northern Southern Southern Southern Western Western	Mean 0.0132 0.0117 0.0120 0.0141 0.0147 0.0229 0.0194 0.0136 0.0153 0.01153	Std Dev 0.0054 0.0029 0.0031 0.0030 0.0053 0.0132 0.0053 0.0025 0.0023 0.0036	Na Std Err Mean 0.0024 0.0013 0.0014 0.0013 0.0024 0.0039 0.0024 0.0024 0.0011 0.0010 0.0016	Level a a a a a a a a a a a a a a a a a a	Mean 0.0064 0.0088 0.0063 0.0080 0.0106 0.0073 0.0073 0.0073 0.0078 0.0066 0.0062 0.0082	Std Dev 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000	Fe Std Err Mean 0.0002 0.0020 0.0018 0.0018 0.0008 0.0008 0.0002 0.0003 0.0004 0.0004 0.0004 0.0018	Level a a a a a a a a a a a a a	Mean 0.0009 0.0014 0.0011 0.0009 0.0010 0.0010 0.0010 0.0010 0.0010 0.0009 0.0010 0.0009 0.0010 0.0009	Std 0.0001 0.0009 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001 0.0001	Cu Std Err Mean 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000 0.0000	Level a a a a a a a a a a a a a a a a a a a	Mean 0.0562 0.0592 0.0628 0.0451 0.0451 0.0451 0.0491 0.0462 0.0512 0.0486 0.0517	Std Dev 0.0214 0.0095 0.0133 0.0086 0.0140 0.0135 0.0098 0.0113 0.0093 0.0175 0.0185	Mn Std Err Mean 0.0096 0.0042 0.0043 0.0063 0.0064 0.0044 0.0054 0.0054 0.0054 0.0054 0.0054 0.0054 0.0054 0.0054 0.0054 0.0054 0.0054 0.0054	Level a a a a a a a a a a a a a a a a a a a	Mean 0.3114 0.3095 0.3211 0.2834 0.2931 0.2974 0.3138 0.2991 0.3192 0.3102 0.3986	Std Dev 0.0149 0.0162 0.0286 0.0164 0.0235 0.0048 0.0248 0.0115 0.0100 0.0379 0.0168	S Std Err Mean 0.0067 0.0073 0.0128 0.0073 0.0105 0.00111 0.00111 0.0051 0.0045 0.0170	Level a a a a a a a a a a a a a	Mean 0.0144 0.0158 0.0164 0.0181 0.0159 0.0152 0.0147 0.0147 0.0108 0.0124 0.0124	Std Dev 0.0009 0.0031 0.0024 0.0023 0.0028 0.0029 0.0020 0.0017 0.0016 0.0030 0.0030	B Std C.0.0014 C.0.0014 C.0.0014 C.0.0014 C.0.0013 C.0.0007 C.0.0007 C.0.0014 C.0.0014	Level abc abc ab ab abc abc abc abc c bc

The highest and lowest values in each element were outlined in red and blue, respectively. Comparisons for all pairs were conducted using Tukey-Kramer HSD, with levels not connected by the same letter considered significantly different (p = 0.05).

	Ν									· · · · · · · · · · · · · · · · · · ·				7.0											
																			Ca				Mg		
Provenance	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level	Mean	Std Dev	Std Err Mean	Level	
Eastern	2.2660	0.1587	0.0502	a	0.1406	0.0100	0.0032	a	0.6989	0.0759	0.0240	ab	0.0035	0.0007	0.0002	a	2.4231	0.3548	0.1122	a	0.5745	0.0971	0.0307	ab	
Northern	2.2617	0.1197	0.0268	a	0.1472	0.0131	0.0029	a	0.7689	0.0944	0.0211	a	0.0033	0.0007	0.0002	a	2.4598	0.2261	0.0506	a	0.5351	0.0861	0.0192	b	
Southern	2.1836	0.1330	0.0343	a	0.1462	0.0117	0.0030	a	0.7114	0.0770	0.0199	ab	0.0033	0.0007	0.0002	a	2.4472	0.2357	0.0609	a	0.5862	0.0733	0.0189	ab	
Western	2.2554	0.1549	0.0400	a	0.1469	0.0162	0.0042	a	0.6829	0.0609	0.0157	b	0.0037	0.0012	0.0003	a	2.3523	0.3040	0.0785	a	0.6320	0.0841	0.0217	a	
											Cu				Mn										
Provenance	Mean	Std Dev	Na Std Err Mean	Level	Mean	Std Dev	Fe Std Err Mean	Level	Mean	Std Dev	Cu Std Err Mean	Level	Mean	Std Dev	Mn Std Err Mean	Level	Mean	Std Dev	S Std Err Mean	Level	Mean	Std Dev	B Std Err Mean	Level	
Provenance Eastern	Mean 0.0125	Std Dev 0.0042	Na Std Err Mean 0.0013	Level	Mean 0.0076	Std Dev 0.0033	Fe Std Err Mean 0.0010	Level	Mean 0.0012	Std Dev 0.0007	Cu Std Err Mean 0.0002	Level	Mean 0.0577	Std Dev 0.0157	Mn Std Err Mean 0.0050	Level	Mean 0.3105	Std Dev 0.0147	S Std Err Mean 0.0047	Level	Mean 0.0151	Std Dev 0.0022	B Std Err Mean 0.0007	Level	
Provenance Eastern Northern	Mean 0.0125 0.0159	Std Dev 0.0042 0.0150	Na Std Err Mean 0.0013 0.0034	Level a a	Mean 0.0076 0.0080	Std Dev 0.0033 0.0030	Fe Std Err Mean 0.0010 0.0007	Level a a	Mean 0.0012 0.0010	Std Dev 0.0007 0.0001	Cu Std Err Mean 0.0002 0.0000	Level a a	Mean 0.0577 0.0520	Std Dev 0.0157 0.0135	Mn Std Err Mean 0.0050 0.0030	Level a a	Mean 0.3105 0.2987	Std Dev 0.0147 0.0235	S Std Err Mean 0.0047 0.0053	Level a a	Mean 0.0151 0.0164	Std Dev 0.0022 0.0029	B Std Err Mean 0.0007 0.0006	Level ab a	
Provenance Eastern Northern Southern	Mean 0.0125 0.0159 0.0172	Std Dev 0.0042 0.0150 0.0082 0.0082	Na Std Err Mean 0.0013 0.0034 0.0021	Level a a a	Mean 0.0076 0.0080 0.0072	Std Dev 0.0033 0.0030 0.0014 0.0014	Fe Std Err Mean 0.0010 0.0007 0.0004	Level a a a	Mean 0.0012 0.0010 0.0010	Std Dev 0.0007 0.0001	Cu Std Err Mean 0.0002 0.0000	Level a a a	Mean 0.0577 0.0520 0.0488	Std Dev 0.0157 0.0135 0.0097	Mn Std Err Mean 0.0050 0.0030 0.0025	Level a a a	Mean 0.3105 0.2987 0.3036	Std Dev 0.0147 0.0235 0.0173	S Std Err Mean 0.0047 0.0053 0.0045	Level a a a	Mean 0.0151 0.0164 0.0132	Std Dev 0.0022 0.0029 0.0024 0.0024	B Std Err Mean 0.0007 0.0006	Level ab a b	

Comparisons for all pairs using Tukey-Kramer HSD. Levels not connected by same letter are significantly different at p = 0.05.

TABLE 7 Microbial richness in the root and rhizosphere soils of a southern (87MX5-1.7) and a northern ('Peruque') pecan rootstock.

Corresto	Catagory	Dala	8	37MX5-1.7_	R		Peruque_R		8	37MX5-1.7_	S	Peruque_S			
Genus	Category	Role	Mean	Std error	Level	Mean	Std error	Level	Mean	Std error	Level	Mean	Std error	Level	
Bradyrhizobium	Bacteria	Nitrogen fixation	4.7680	1.9060	a	1.1690	0.8180	b	0.2450	0.0430	b	0.2400	0.0790	b	
Tuber	Ectomycorrhizal fungus	Nutrient cycling	45.1950	8.7750	a	0.4600	0.3200	b	6.7520	2.8000	Ь	1.1330	1.1200	b	
Inocybe	Ectomycorrhizal fungus	Phosphorus absorption	0.6130	0.5620	с	2.1850	0.8360	Ь	23.5790	13.7920	a	27.1620	13.6080	a	
Russula	Ectomycorrhizal fungus	Decomposing organic matter	1.7830	1.7400	с	31.6520	11.1830	а	9.3270	9.2790	b	13.6100	3.6090	b	
Ilyonectria	Plant pathotrogh fungus	Causing root rot and canker diseases	0.9460	0.2310	а	0.2500	0.2200	b	0.0900	0.0027	b	0.1470	0.0130	b	
Lectera	Plant pathotrogh fungus	Causing leaf spot or branch dieback	0.0670	0.0600	b	0.0230	0.0230	b	0.7110	0.0540	a	0.0830	0.0540	b	

The rhizosphere soil and root samples were taken following the previous protocol in Ren et al. (2024). Comparisons for all pairs using Tukey-Kramer HSD. Levels not connected by same letter are significantly different at p = 0.05. Comparisons for all pairs using Tukey-Kramer HSD. Levels not connected by same letter are significantly different at p = 0.05.

frost damage (Smith et al., 2001; Wood and Reilly, 2001; Kaur et al., 2024). Conversely, eastern and southern rootstocks showed earlier budbreak, likely due to their adaptation to milder climates with longer growing seasons (Grauke et al., 1992, 2003).

This difference in budbreak timing also suggests that northern rootstocks may have an advantage in regions where early frosts are a concern, while eastern rootstocks could perform better in areas with a longer frost-free period. These findings are consistent with previous studies showing that budbreak is influenced by the rootstock's climatic adaptation, with early budbreak increasing the risk of frost damage in some regions (Fallah et al., 2022; Grauke et al., 1992; Wood and Reilly, 2001). Moreover, the lack of significant differences in budbreak timing between southern and western rootstocks suggests that these rootstocks may be more similar in their physiological responses to climate variables, such as temperature and day length (Grauke et al., 1992).

Tree size and growth performance

Tree size, including parameters such as plant height, trunk diameter, and canopy width, serves as a critical indicator of tree vigor and productivity. The results from this study indicate that southern rootstocks, particularly those of Mexican (southern) provenance, generally resulted in superior tree growth compared to northern rootstocks. Among the southern rootstocks, 87MX1-2.2 exhibited the most vigorous growth, leading to significant increases in scion plant height, trunk diameter, and canopy width. These findings are consistent with the well-established notion that Mexican pecan rootstocks, which have evolved in regions with hot and dry climates, tend to confer enhanced growth vigor, especially in terms of root development and nutrient uptake (Brown et al., 1994; Mir et al., 2023; Valverdi et al., 2021).

In contrast, northern rootstocks, such as 'Peruque', resulted in smaller trees, likely due to their adaptation to colder climates where growth is naturally more limited. This may also reflect differences in the rootstock's ability to access and utilize soil nutrients, particularly in warmer climates, where higher nutrient availability promotes faster growth. We measured the common nutrient contents in soil samples taken annually at depths of 6 inches and 12 inches and found no significant difference (p = 0.05; data not shown), indicating that soil nutrient levels were consistent across all rootstocks. Interestingly, rootstocks from the eastern and western regions showed intermediate performance, suggesting that these rootstocks might be better suited for regions with moderate climatic conditions, offering balanced growth characteristics that could be beneficial in more variable environments.

The growth advantages associated with southern rootstocks have practical implications for orchard management strategies aimed at maximizing tree size and canopy development before tree maturity. Larger trees are often associated with higher nut production, greater canopy coverage for improved pest and disease management, and better overall orchard performance (Westwood et al., 1973; Caruso et al., 2020; Valverdi et al., 2021). These results suggest that pecan growers in warmer climates may benefit from selecting Mexican rootstocks to improve orchard productivity (Wang et al., 2025b).

Leaf size and growth conditions

Leaf size is an important trait that can serve as an indirect indicator of a plant's overall physiological condition, including its capacity for photosynthesis and environmental adaptation. Leaflet size is influenced by a variety of factors, including genetic traits, environmental conditions, and the efficiency of the photosynthetic apparatus (Salazar et al., 2019; Sun et al., 2020; Ferdous et al., 2023; Kawai et al., 2023). Larger leaves, particularly in the early stages of growth, may indicate better photosynthetic capacity, which could contribute to improved tree growth. The results of this study showed significant variation in leaflet size across the evaluated rootstocks, with 'Posey' exhibiting the largest leaflets and 'San Felipe' the smallest. While these differences were not statistically significant, the observed trend suggests that rootstock provenance may influence leaf size. Additionally, larger leaves showed the higher photosynthesis rate and water use efficiency (Table 4). The lack of statistical significance, however, indicates that other factors such as soil conditions and environmental stresses may have a greater impact on leaf size than the rootstock origin alone. Generally, rootstocks from eastern and northern regions were associated with larger leaflets compared to those from southern and western regions.

The variation in leaf size observed in this study likely reflects genetic differences among the rootstocks, with northern and eastern provenances potentially having more robust leaf growth characteristics. The differences may ultimately affect the tree's ability to capture light and produce energy, potentially impacting overall tree health and nut production in the long term. Nevertheless, further research is needed to better understand the direct impact of leaf size on yield and quality.

Leaf retention and environmental adaptation

Leaf retention is an important physiological trait, particularly due to its implications for tree energy conservation during the dormant season (Zhao et al., 2023; Koundinya et al., 2023). The results indicated that rootstock origin did not significantly influence leaf retention during the first two weeks of November. However, northern and eastern provenances tended to retain more leaves compared to southern and western rootstocks. This pattern suggests that northern rootstocks, which are adapted to more temperate climates, may have a greater capacity for leaf retention, potentially conserving energy and prolonging photosynthesis before leaf falls.

The trend observed in this study is consistent with previous research indicating that leaf retention can vary depending on environmental factors, such as temperature, light, and moisture availability (Steinparzer et al., 2023; Lv et al., 2024). For instance, rootstocks from cooler climates may retain leaves longer, which could help the tree absorb more sunlight and store energy for the winter months. Conversely, southern and western rootstocks may shed their leaves earlier as a response to hot and dry conditions.

Despite these trends, the lack of statistically significant variation suggests that leaf retention may not be a primary factor influencing tree performance in this study. However, in regions with less favorable growing conditions, such as late-season droughts or early frosts, retaining more foliage on the canopy before frosts could potentially provide an advantage in optimizing photosynthetic activity during the late-growing season (Mickelbart and Arpaia, 2002; Marquard, 1987).

Leaf photosynthesis and water use efficiency

Photosynthesis is a vital process for tree growth, and its efficiency can be influenced by both genetic and environmental factors. In this study, photosynthetic rates (PSR) and water use efficiency (WUE) were measured for the same scion cultivar grafted onto each of the 12 rootstocks. Two rootstocks - 'Giles' (northern provenance) and 'VC1-68' (western provenance) - showed the highest PSR and WUE, indicating their superior efficiency in utilizing water and converting it into energy through photosynthesis. This is particularly important as higher WUE is often associated with better drought tolerance and improved growth in arid conditions (Mickelbart and Arpaia, 2002; Marquard, 1987; Fallahi et al., 2001).

In contrast, 'Elliott', a rootstock commonly used in southeastern and southern regions, showed high or at least a moderate PSR and WUE compared to other rootstocks during most period of the day. However, at 5 p.m., when PSR and WUE peaked, 'Elliott' exhibited the lowest values, suggesting that it may not be optimal for maximizing photosynthetic efficiency in certain environments, especially in south Texas. In addition, these findings carry practical implications, as optimizing photosynthesis and WUE is crucial for increasing overall tree productivity, particularly in areas prone to drought or water stress.

The results highlight the potential for selecting rootstocks based on their photosynthetic efficiency and WUE, particularly in areas where water availability is a limiting factor for tree growth. Growers in areas with unpredictable rainfall or prolonged droughts might benefit from selecting rootstocks like 'Giles' or VC1–68 to maximize photosynthetic performance and ensure better water utilization.

Leaf nutrient composition and rootstock influence

Nutrient content in the leaves of pecan trees is critical factor influencing overall tree health and productivity. This study found that most leaf nutrients showed no significant differences across the 12 rootstocks, except for Zinc (Zn) and Boron (B). 'Riverside' exhibited the highest Zn content, while 'Peruque' had the lowest, 'Major' had the highest B content, whereas 'Frutoso' showed the lowest levels. Notably, differences in nutrient content were generally not associated with rootstock origin, except for Potassium (K), Magnesium (Mg), and Boron (B).

Rootstocks play a significant role in shaping leaf nutrient composition, as the availability of these nutrients is essential for tree health, growth, and productivity. Zn deficiency is common and frequently limits productivity in commercial pecan orchards, especially those established in soils with low Zn availability (Fenn et al., 1990; Ojeda-Barrios et al., 2012; Sparks and Payne, 1982). Poor zinc uptake requires multiple foliar application per year (Cruz-Alvarez et al., 2024; Liu et al., 2021; Ojeda-Barrios et al., 2012; Smith et al., 2022; Walworth et al., 2006). Rootstocks with higher levels of Zn and B may offer advantages such as enhanced enzyme activity, improved disease resistance, and more efficient nutrient cycling (Smith et al., 2022; Barone et al., 1998; Fallahi et al., 2001; Amiri et al., 2014). Conversely, variations in K and Mg content, which were higher in northern rootstocks and lower in western rootstocks, could have important implications for nutrient management in pecan orchards. For instance, higher K content in northern rootstocks may improve the tree's ability to tolerate stress, while lower Mg content in southern rootstocks could negatively impact photosynthetic efficiency and plant growth.

Soil microbial community and rootstock effects

This study investigated the influence of rootstocks on soil microbial diversity within the roots and the rhizosphere. The findings revealed that a northern rootstock, 'Peruque', exhibited a higher relative abundance of ectomycorrhizal fungi, such as *Inocybe* and *Russula*. These fungi are critical for decomposing organic matter and facilitating phosphorus cycling. In contrast, the southern provenance, 87MX5-1.7, demonstrated elevated levels of nitrogen-fixing bacteria, such as *Bradyrhizobium*, and fungi like Tuber, which are actively involved in nutrient absorption, particularly phosphorus. These distinct microbial communities play a crucial role in improving soil fertility and supporting plant growth by enhancing nutrient uptake and creating a balanced soil ecosystem (Ren et al., 2023, 2024).

The findings emphasize the potential of rootstocks to influence soil health by shaping microbial community. Rootstocks originating from different geographical regions appear to foster unique microbial populations that may be beneficial for nutrient cycling and overall tree performance. Understanding these interactions offers valuable insights for orchard managers, aiding in the selection of rootstocks that not only promote tree growth but also enhance soil fertility and long-term orchard sustainability (Palma et al., 2018).

Conclusions

This study underscores the significant influence of rootstock provenance on the growth and physiological traits of 'USDA-ARS-Pawnee' pecan trees. Based on four years of data (2020–2023), results revealed that northern rootstocks delayed budbreak (resulting in longer Julian days) and slowed tree growth, which may be beneficial in regions prone to early-season frost risks. In contrast, southern rootstocks (excluding Frutoso) promoted earlier budbreak (shorter Julian days) and enhanced tree growth, making them ideal for warmer climates where tree vigor is critical for productivity. Western and eastern rootstocks showed varying effects, reflecting region-specific adaptations. Northern rootstocks, such as 'Peruque' and 'Giles,' were associated with higher concentrations of essential nutrients like zinc and boron, which could enhance tree health and stress resilience. Additionally, they exhibited higher photosynthetic rates, suggesting greater efficiency in energy conversion under specific environmental conditions. Southern rootstock displayed superior growth metrics, potentially due to their capacity to foster robust root development and nutrient uptake.

This study also highlights the role of rootstocks in influencing soil microbial diversity. Northern rootstocks fostered greater populations of ectomycorrhizal fungi, while southern rootstocks supported higher levels of nitrogen-fixing bacteria. These microbial communities contribute to nutrient cycling and soil health, which are essential for sustainable orchard management. Overall, these findings provide practical guidance for selecting rootstocks tailored to specific environmental conditions, enhancing tree growth, productivity, and soil health in pecan orchards. Key choices include 'Giles' and 'Peruque' for northern regions, 'VC1-68' and 'Riverside' for western areas, and 'Elliott' for the southeastern United States and beyond. Future research should explore the long-term effects of rootstock-scion interactions on nut yield and quality while investigating the genetic and physiological mechanisms underlying these variations to refine rootstock selection for diverse growing regions.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

XW: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing. KK: Conceptualization, Data curation, Writing – review & editing. WC: Writing – review & editing. AH: Writing – review & editing. BT: Data curation, Writing – review & editing. TX: Formal Analysis, Validation, Writing – review & editing. LZ: Formal Analysis, Validation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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