Root Annual Ring Characteristics of Perennial Herbs in the Loess Plateau (Postprint)

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Abstract

Perennial herbaceous ring data are important indicators reflecting the growth status of herbaceous species and have been applied to studies on interannual growth dynamics, life history strategies, and climate response sensitivity of herbaceous species; however, such research has not received sufficient attention on the Loess Plateau. Root ring samples of 16 perennial herbaceous species were collected from different locations on the Loess Plateau, ring structures were identified through analysis of root anatomical structure, and the variation characteristics of ring width and vessel size with age in these species were analyzed. The results demonstrated that among the surveyed samples, 14 herbaceous species (87.5%) possessed clearly identifiable ring structures, with an average age of approximately 7 years; herbaceous ring width exhibited a continuous decreasing trend with age, which was primarily caused by intensifying water stress with age. The vessel diameter (hydraulic conductivity) of natural herbaceous species exhibited a continuous increasing trend with age, indicating sustainable growth; the hydraulic conductivity of artificial herbaceous species exhibited a continuous decreasing trend with age, with growth tending to decline; whereas Limonium bicolor, distributed from the northern margin of the Loess Plateau to semi-desert regions, showed a trend of hydraulic conductivity first increasing and then decreasing with age, demonstrating a trade-off strategy between hydraulic efficiency and safety. This study elucidates the dendrochronological value of perennial herbs on the Loess Plateau and their life history strategies under stressed habitat conditions, which can provide a scientific basis for the ecological restoration of grassland vegetation on the Loess Plateau.

Full Text

Preamble

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Growth Increment Patterns in Roots of Perennial Forbs in the Loess Plateau, China

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Abstract

Perennial herb chronology data serve as important indicators of herbaceous species growth status and have been applied in studies examining interannual growth dynamics and climate response sensitivity. However, such research has not received sufficient attention in the Loess Plateau region. We collected root samples from multiple sites across the Loess Plateau, identified annual ring structures through root anatomical analysis, and examined how ring width and vessel size change with age in these species. Our results demonstrate that most sampled herbaceous species (87.5%) exhibit clearly identifiable annual ring structures, with an average age of approximately seven years. Ring width shows a consistent decreasing trend with age across species, primarily attributed to intensifying water stress over time. Native forb species exhibit increasing vessel diameter with age, indicating sustainable growth through enhanced hydraulic conductivity. In contrast, planted forb species show decreasing hydraulic capacity with age, suggesting progressive growth decline. *Limonium bicolor*, distributed along the northern margin of the Loess Plateau in semi-desert regions, displays an initial increase followed by a decrease in hydraulic capacity, representing a trade-off strategy between water transport efficiency and safety. This study elucidates the dendrochronological value of perennial herbs in the Loess Plateau and their life history strategies under stressful environmental conditions, providing a scientific basis for ecological restoration of grassland vegetation in this region.

Keywords: Perennial forbs; Main root anatomy; Annual rings; Life history strategy; Loess Plateau

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Introduction

As global climate change intensifies its impacts on natural ecosystems and human society, research on regional-scale vegetation growth responses to climate variability and extreme events has attracted increasing attention [1-2]. Tree-ring materials, with their wide distribution and clear environmental signals, have become a primary source for investigating vegetation-climate responses [3-4], enabling regional climate reconstructions [5-7], assessments of spatial heterogeneity in climate responses [8], and documentation of drought-induced growth inhibition from modern warming [9-10]. However, most dendrochronological studies have focused on woody species (trees and shrubs) [8,11], with perennial herbaceous species receiving limited attention [12].

Emerging research demonstrates that perennial herbs in temperate, boreal, and Mediterranean regions of the Northern Hemisphere develop secondary anatomical structures in their roots, forming large vessels early in the growing season and smaller vessels later, thereby creating distinguishable annual ring structures [13-14]. The climatological and ecological value of herb chronologies is gaining recognition. For example, von Arx et al. [15] used perennial herb chronologies to examine altitudinal variation in plant life history strategies in northwestern U.S. mountains, finding that high-altitude plants adopt more conservative strategies. Dietz and von Arx [12] documented synchronous growth fluctuations in perennial herbs across North America and Europe linked to El Niño events. Olano et al. [16] analyzed growth and anatomical vessel structure along elevation gradients in Mediterranean perennial herbs. Zhang [17] and Liu and Zhang [18] explored the dendroclimatological potential of perennial herbs in Inner Mongolian grasslands, finding that most species produce recognizable annual rings with consistent interannual patterns containing reliable temperature and precipitation signals.

The Loess Plateau, the world' s largest loess deposition region, represents an ecologically fragile area with severe soil erosion and a key region for soil conservation in China [20-21]. To combat escalating soil erosion, large-scale revegetation programs have substantially improved vegetation cover [22]. While tree-ring studies in the Loess Plateau have primarily focused on climate responses in forested nature reserves (e.g., Luyashan [23-24], Liupanshan [25], Kongtongshan [26]) and shrub species in desert-grassland transition zones [27-29], the dendrochronological value of perennial herbs remains unexplored. This study represents the first large-scale collection of perennial herb root samples across precipitation gradients in the Loess Plateau, aiming to elucidate the dendrochronological potential of herb rings and provide a scientific foundation for studying grassland ecosystem responses to climate change.

1. Study Area Overview

The Loess Plateau, located in the middle and upper reaches of the Yellow River in China, extends from Taihang Mountains in the east to Riyue Mountain in Qinghai Province in the west, and from the Great Wall in the north to the Qinling Mountains in the south. The region has a warm temperate continental monsoon climate, transitioning from arid to semi-arid and semi-humid conditions from northwest to southeast. Mean annual temperature ranges from 8.6°C in the northwest to 14.3°C in the southeast, with average precipitation of 300–800 mm and elevations of 1500–2000 m. Soil types include aeolian sandy soil, loessial soil, dark loessial soil, and cinnamon soil. Vegetation zones progress from desert-steppe to typical steppe and forest-steppe [31]. Long-term human disturbance and improper land use have caused severe soil erosion and soil degradation [32]. Since implementing vegetation restoration and the Grain-for-Green program, vegetation coverage has markedly improved, and Yellow River sediment load has decreased [21].

[Figure 1: see original paper] Location of 13 study sites of perennial forb species sampled across the Loess Plateau, China

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2. Methods

2.1 Sample Collection

We established 13 sampling sites along an east-west precipitation gradient (approximately 280 mm, from 300 mm at Yanchi Hui' anbu in the west to 580 mm at Yicheng Longhua in the east). At each site, we selected perennial herb species with distinct taproots (monocots with fibrous, non-lignified roots were excluded). Main roots were sectioned with a blade, and samples were fixed in FAA solution (70% ethanol:formalin:acetic acid = 9:0.5:0.5) [33] and stored in a portable refrigerator.

2.2 Sample Processing

Samples underwent paraffin sectioning pretreatment including dehydration, clearing, and embedding. Dehydration involved sequential immersion in ethanol solutions of increasing concentration (70%, 80%, 85%, 95%, 100%). Clearing used xylene to replace ethanol in tissues. Samples were then repeatedly infiltrated with paraffin wax and embedded [34].

2.3 Data Processing

Cross-sections approximately 10–15 m thick were cut using a rotary microtome, mounted on slides, and stained with safranin-fast green to differentiate xylem from non-xylem tissues [33]. Digital microscopy enabled clear identification of ring characteristics [12]. Anatomical images were stitched to create complete

ring images using image processing software. Ring structures and maximum vessel diameters were measured annually using IMAGE TOOLS software. Each sample was measured along four radial directions; when ring counts differed among directions, the mean value was used as the final ring width sequence [12]. If directional variation occurred, the average of maximum and minimum ages was used to estimate longevity [15,17].

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3. Results

3.1 Perennial Herb Ring Structure Characteristics

We collected ring data from 16 perennial herb species across the Loess Plateau. Fabaceae was most represented (7 species), followed by Rosaceae (5 species). Other families included Zygophyllaceae, Plumbaginaceae, Boraginaceae, Umbelliferae, and Euphorbiaceae. Based on vessel size, density, and ray divergence patterns, all collected species exhibited ring structures, with 14 species (87.5%) showing clear, distinguishable rings.

Site characteristics of perennial forb species sampled in the Loess Plateau, China

Secondary xylem structure of 16 perennial forb species in the Loess Plateau

Age frequency distribution showed a right-skewed normal pattern, with moderate ages (4–8 years) most common and younger/older ages less frequent. Mean age was approximately 7 years, with *Medicago sativa* being oldest (14 years) and *Lespedeza davurica* and *Bupleurum chinense* youngest (2 years).

3.2 Ring Width Trends with Age

Most species showed decreasing ring width with age. *Potentilla discolor*, *P. recta*, *Cynoglossum divaricatum*, and *Limonium bicolor* exhibited the most pronounced declines, followed by *P. chinensis* and *P. multicaulis*. *P. anserina*, *Sophora flavescens*, and *Astragalus melilotoides* showed relatively flat trends. Notably, *Speranskia tuberculata* showed increasing ring width with age, while *Glycyrrhiza uralensis* showed only slight decline, representing different growth strategies.

3.3 Vessel Size Trends with Age

Vessel diameter changes with age fell into three patterns: (1) Continuous increase in native species (*Potentilla* spp., *Cynoglossum divaricatum*), indicating enhanced hydraulic efficiency to meet increasing water demands with sustained growth [45-46]; (2) Continuous decrease in planted species (*Medicago sativa*, *Sophora flavescens*, *Glycyrrhiza uralensis*), indicating hydraulic failure and growth decline due to soil desiccation from deep root water extraction [47-48]; and (3) Initial increase followed by decrease in *Limonium bicolor* from semi-desert regions, representing a trade-off between hydraulic efficiency and safety under extreme drought.

[Figure 2: see original paper] Patterns of growth rings in secondary root xylem for perennial forb species in the Loess Plateau (1)

[Figure 3: see original paper] Patterns of growth rings in secondary root xylem for perennial forb species in the Loess Plateau (2)

[Figure 4: see original paper] Age structure characteristics of perennial forb species in the Loess Plateau

[Figure 5: see original paper] Changing trend of growth rings with age for perennial forb species in the Loess Plateau

[Figure 6: see original paper] Changing trend of vessel size with age for perennial forb species in the Loess Plateau

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4. Discussion

4.1 Environmental Stress Effects on Herb Growth

The high proportion (87.5%) of ring-forming species and relatively old ages in our Loess Plateau samples exceed those reported for central Europe (60-75%) [12], North America (66%) [13], and Europe [14]. This reflects more stressful growing conditions in the Loess Plateau, where water availability is the primary growth-limiting factor. Studies show drought stress (measured by PDSI) explains 43% of vegetation NPP variation [43]. Combined with severe soil erosion that depletes surface nutrients (soil organic carbon density is only one-third the national average [40]), these conditions favor ring formation and longevity [41-42].

4.2 Growth Rate Trends in the Loess Plateau

The predominant pattern of decreasing ring width with age reflects intensifying water stress and nutrient limitation as plants age. Early rapid growth maximizes resource capture and establishment, while developed root systems store nutrients and enhance stress resistance [15]. However, as plants age, soil moisture and nutrients decline, inter- and intraspecific competition intensifies, and reproductive allocation increases at the expense of vegetative growth [34]. Climate data from 52 meteorological stations confirm a significant shift around 1985 toward warmer, drier conditions—temperature increased sharply while precipitation declined [37,44]. This warming-drying trend strengthens water stress constraints on herb growth, contributing to the observed age-related growth decline.

4.3 Hydraulic Efficiency Trends

Larger vessel diameters generally confer greater water transport capacity and hydraulic conductivity [43]. The three observed patterns reflect different life his-

tory strategies: (1) Native species increase vessel diameter to enhance hydraulic efficiency and sustain growth; (2) Planted species decrease vessel diameter due to soil desiccation, leading to hydraulic failure and growth decline; (3) *Limonium bicolor* exhibits a safety-efficiency trade-off, reducing vessel diameter in later life stages to avoid cavitation risk in extremely dry, sandy soils, while compensating through increased root:leaf ratios [59-60].

4.4 Comparison with Inner Mongolia Studies

Liu and Zhang [17,18] studied perennial herbs in Duolun grassland, Inner Mongolia, finding only 66% had clear rings and that ring width increased with age due to warming-wetting trends. In contrast, our Loess Plateau study shows 87.5% ring formation with decreasing ring width, reflecting more arid conditions and intensifying drought stress. The contrasting hydraulic strategies between regions highlight how climate gradients shape herb life history adaptations.

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5. Conclusion

This study analyzed root rings from 16 perennial herb species in the Loess Plateau, finding that most produce clearly identifiable annual rings with relatively old ages, demonstrating significant dendroecological and dendroclimatological potential. Ring width decreases with age, primarily due to intensifying water stress and increased reproductive allocation. Hydraulic capacity shows three patterns: increasing in native species (sustainable growth), decreasing in planted species (growth decline), and trade-off strategies in semi-desert species like *Limonium bicolor*. These findings provide scientific guidance for grassland vegetation restoration in the Loess Plateau.

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Note: Figure translations are in progress. See original paper for figures.