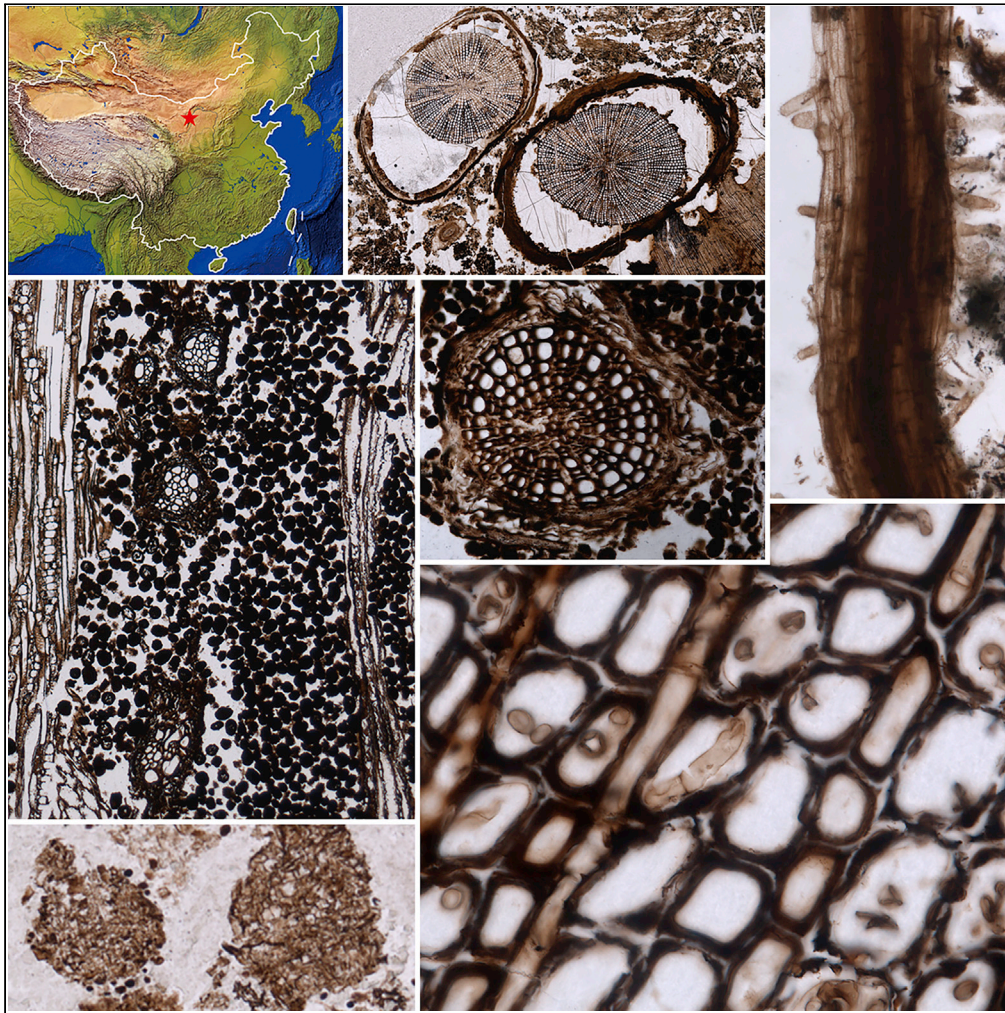**Article**

Nurse logs: A common seedling strategy in the Permian Cathaysian flora

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Highlights

Diverse nurse-log interactions are documented in the Permian Cathaysian flora.

Conifer wood served as substrates for seed plants and sphenopsids at the time.

Arthropods and fungi were crucial for utilization of nurse logs in ancient forests.

Nurse logs probably first occurred in swamps then expanded to various habitats

Article

Nurse logs: A common seedling strategy in the Permian Cathaysian flora

Zhuo Feng,[1,4,*] Xu-Dong Gou,[2] Stephen McLoughlin,[3] Hai-Bo Wei,[1] and Yun Guo[1]

SUMMARY

Nurse logs are common in modern forests from boreal to temperate and tropical ecosystems. However, the evolution of the nurse-log strategy remains elusive because of their rare occurrence in the fossil record. We report seven coniferous nurse logs from lowermost to uppermost Permian strata of northern China that have been colonized by conifer and sphenophyllalean roots. These roots are associated with two types of arthropod coprolites and fungal remains. Our study provides the first glimpse into plant—plant facilitative relationships between late Paleozoic gymnosperms and sphenopsids. Detritivorous arthropods and fungi appear to have been crucial for the utilization of nurse logs in Permian forests. The phylogenetically distant roots demonstrate that nurse-log interaction was a sophisticated seedling strategy in late Paleozoic humid tropical forests, and this approach may have been adopted and developed by a succession of plant groups leading to its wide representation in modern forest ecosystems.

INTRODUCTION

Nurse logs represent a common ecological strategy in modern forest ecosystems, effectively enhancing the regeneration and sustainability of tree species (Sanchez et al., 2009; Fukasawa, 2016). When seeds fall onto decaying tree trunks or stumps, favorable moisture and nutrients on this substrate provide microhabitats for germination and colonization as roots of the seedlings grow throughout the organic substrate (Fisher et al., 2016). However, the origin and evolutionary history of nurse logs remain elusive, given that this particular plant—plant facilitative interaction has been documented rarely in the fossil record (Daugherty, 1963; Fairon-Demaret et al., 2003; Césari et al., 2010; Decombeix et al., 2021; Vera and Loinaze, 2022).

In modern ecosystems, nurse logs are especially common in closed forests of humid habitats (Sanchez et al., 2009; Woods et al., 2021) but also occur in dryland settings (Fagundes et al., 2018). An extreme instance is the conifer-dominated temperate rainforest in the Olympic Peninsula of the USA, in which 88%–97% of new seedlings develop in nurse logs (McKee et al., 1982). Importantly, nurse logs are vital in maintaining diversity within modern forest ecosystems, as they can be colonized disproportionately by small-seeded and wind-dispersed species (Sanchez et al., 2009; Fukasawa, 2016). Despite their ecological importance in modern forests, only six fossil nurse logs from disparate regions and stratigraphic intervals have been reported thus far in the fossil record. These are represented by late Paleozoic (Permian) woods of the paleotemperate *Glossopteris* biome in Argentina and Antarctica (Césari et al., 2010; Decombeix et al., 2021), early Mesozoic (Triassic) conifer logs of the USA (Daugherty, 1963), late Mesozoic (Early Cretaceous) conifers of Patagonia (Vera and Loinaze, 2022), and early Cenozoic (Eocene) temperate to subtropical forest woods of Belgium (Fairon-Demaret et al., 2003). Therefore, the origin and evolutionary history of these specialized plant—plant facilitative relationships remain largely unresolved. Here, we report seven fossil nurse logs from four Permian intervals in the Ordos Basin, northern China (Figures 1 and 2), shedding new light on the early evolution of the nurse-log strategy.

RESULTS

The host plant—root association

One hundred and twenty-three permineralized conifer tree stems were collected from 13 levels within the Shanxi, Lower Shihhotse, Upper Shihhotse, and Sunjiagou formations in the study area (Figure 3). Rootlets were observed penetrating two stems from the Shanxi Formation, three stems from the Lower Shihhotse Formation, and two stems from the Sunjiagou Formation. The root-colonized stems from the Shanxi and

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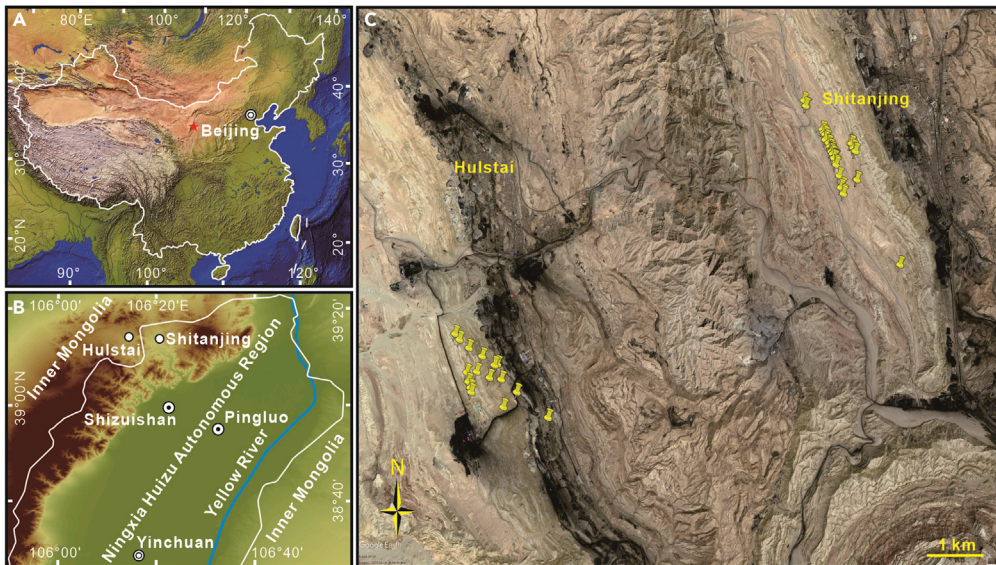https://doi.org/10.1016/j.isci. 2022.105433

Figure 1. Maps of the nurse-log fossil locality in the Ordos Basin of northern China
(A) Map of China, asterisk indicates study area.
(B) Map of study area.
(C) Map of fossil locality; pins indicate occurrence of fossil wood specimens in Hulstai and Shitanjing coal fields.

the Lower Shihhotse formations belong to *Agathoxylon-*, *Plyophyllioxylon-*, and *Protophyllocladoxylon-*type trees (Figures S1–S5). The root-colonized stems from the Sunjiagou Formation are of *Ningxiaites-*type trees, based on their unique arrangement of leaf traces (Figures S6 and S7). Among the seven nurse logs, rootlets penetrate the pith of two stems and the secondary xylem of the other five stems. These protostelic rootlets can be classified readily into two distinctive forms, given their unique anatomical characteristics. The first is consistent with *Amyelon-*type gymnosperm (probably conifer) roots and the second with *Sphenophyllum-*type sphenopsid roots.

Both *Amyelon-* and *Sphenophyllum-*type roots occupy cavities within the roots that are typically 1–5 mm in transverse diameter. Cavity margins are variably sharp (characterized by truncated cell walls) to strongly degraded (characterized by zones, up to 400 μm wide, composed of crushed, diffusely lightened, infilled, or otherwise altered cells (Figures 2A, 2B, and 3G). Roots are irregularly positioned within cavities and no reaction tissue is developed in either the root or host wood. In longitudinal section, the cavities are irregularly tube shaped (Figure 3G). Degraded zones are filled extensively by arthropod coprolites (Figures 2A and 2B) and locally rimmed by tissues containing fungal hyphae (Figure 3L). Thus, such partially degraded host woods provide valuable sources of information on the cryptic diversity and biotic interactions of plants, invertebrates, and fungi in ancient terrestrial ecosystems.

*Amyelon-*type rootlets

The *Amyelon-*type rootlets occur exclusively in two conifer stems from the upper part of the Sunjiagou Formation, including one stem hosting rootlets in the pith and one in the secondary xylem (Figures 3A, S8, and S9). These rootlets are diarch, ranging from 50 μm to 4.5 mm in diameter, and are characterized by an exarch primary xylem and cylindrical or fan-shaped secondary xylem (Figures 3A, S8A, S8B, and S9A–S9D). The primary xylem incorporates annular, helical, and scalariform thickenings on the tracheid walls from the protoxylem to the metaxylem (Figures S9E and S9F). The araucarian-like secondary xylem comprises homocellular rays and tracheids. Uniseriate to triseriate bordered pits are contiguous and arranged alternately on the radial tracheid walls (Figures 3B, S8C, and S8D). Rays are commonly 1–3 cells high in smaller rootlets (Figures S8E and S8F). However, they can be up to fifteen cells high in the secondary xylem periphery of larger rootlets (Figure S8G). Cross-field pitting is of the araucarioid type, with two to seven small bordered pits in each field (Figure S8H). The secondary phloem and periderm are preserved in larger rootlets (Figures S8I and S9F), whereas cortical tissues are present in smaller rootlets (Figures S9E and S9H). A Casparian strip is locally evident in the innermost part of the cortex in smaller rootlets (Figures S9A and
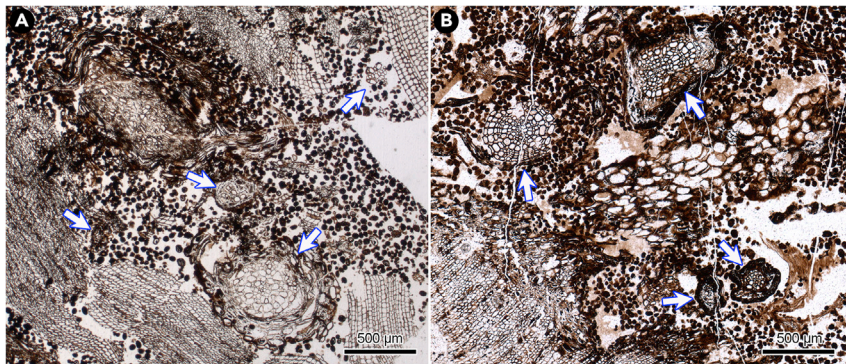
Figure 2. Permian nurse logs from the Ordos Basin of northern China
(A) YKLP20001, from upper Shanxi Formation, showing rootlets (arrows) in the secondary xylem.
(B) YKLP20007, from upper Lower Shihhotse Formation, showing rootlets (arrows) in the pith. See also Figures S1–S14.

S9H). Branching is sparse in large-diameter rootlets (Figure S8J). In contrast, short, unicellular hairs appear on the epidermal cells of small-diameter rootlets (Figures 3C and S9G). These anatomical features allow these rootlets to be assigned to the fossil root genus *Amyelon* (Wan et al., 2019).

Sphenophyllum-type rootlets

Sphenophyllum-type rootlets are preserved penetrating two stems from the upper part of the Shanxi Formation, one stem from the middle part of the Lower Shihhotse Formation, and two stems from the upper part of the same unit, including one stem hosting rootlets in the pith (Figures 3D–3L and S10–S14). These rootlets are diarch or triarch, measuring about 150 µm to 1.2 mm in diameter (Figures S10A–S10L, S13A, S13B, and S14A–S14D). They have an exarch primary xylem with annular, helical, and scalariform thickenings on the tracheid walls from the protoxylem to the metaxylem (Figures S11A, S12C, S12D, S13C, and S14E). The secondary xylem cylinder possesses homocellular rays, tracheids, and small-diameter parenchyma cells (Figure S14G). The secondary xylem tracheids bear either scalariform thickenings or reticulate-bordered pits on the radial walls (Figures 3F, S11C, S11D, and S14F). Rays are commonly one to three cells high (Figure S11E). Each cross-field contains three to six small bordered pits (Figures 3F and S11F). The cortex, secondary phloem, and periderm are positioned peripherally to the vascular strands (Figures S11A, S12E, and S14H). These anatomical features are consistent with assignment to the fossil root of *Sphenophyllum*-type plants (Rößler et al., 2021).

DISCUSSION

Roots have relatively conservative anatomical features compared to stems (Beck, 2010). Thus, in many cases, it is difficult to assess the exact affinities of isolated fossil roots (Decombeix et al., 2021). *Amyelon* is the most common and well-known type of root in the late Paleozoic Euramerican and Cathaysian floral realms (Wang et al., 2003, 2009). This type of root has a rich fossil record and is interpreted to belong primarily to the extinct plant order Cordaitales. However, numerous studies have shown that *Amyelon*-type roots are also commonly associated with non-cordaitalean conifer stems (Rößler et al., 2021). The anatomy of the penetrative *Amyelon*-type rootlets in northern China resembles that of the host plants, and suggests that host and seedling were phylogenetically close to each other. Thus, the fallen conifer trees in the Permian Cathaysian floral realm probably served as nurse logs facilitating the germination of seeds from their own species.

By contrast, the distinctive anatomy of *Sphenophyllum*-type rootlets differs markedly from their conifer host logs. *Sphenophyllum* is a group of articulate, slender, scrambling, vine-like or erect, herbaceous plants belonging to the extinct plant order Sphenophyllales (Galtier and Daviero, 1999). Sphenophyllaleans were groundcover plants or liana-like climbing plants that commonly proliferated in the understory of Carboniferous and Permian forests (Taylor et al., 2009). The occurrence of *Sphenophyllum* rootlets of diverse diameters in the studied nurse logs indicates that the fallen conifer trees also facilitated the germination of spore-producing plants in the Permian Cathaysian floral realm.
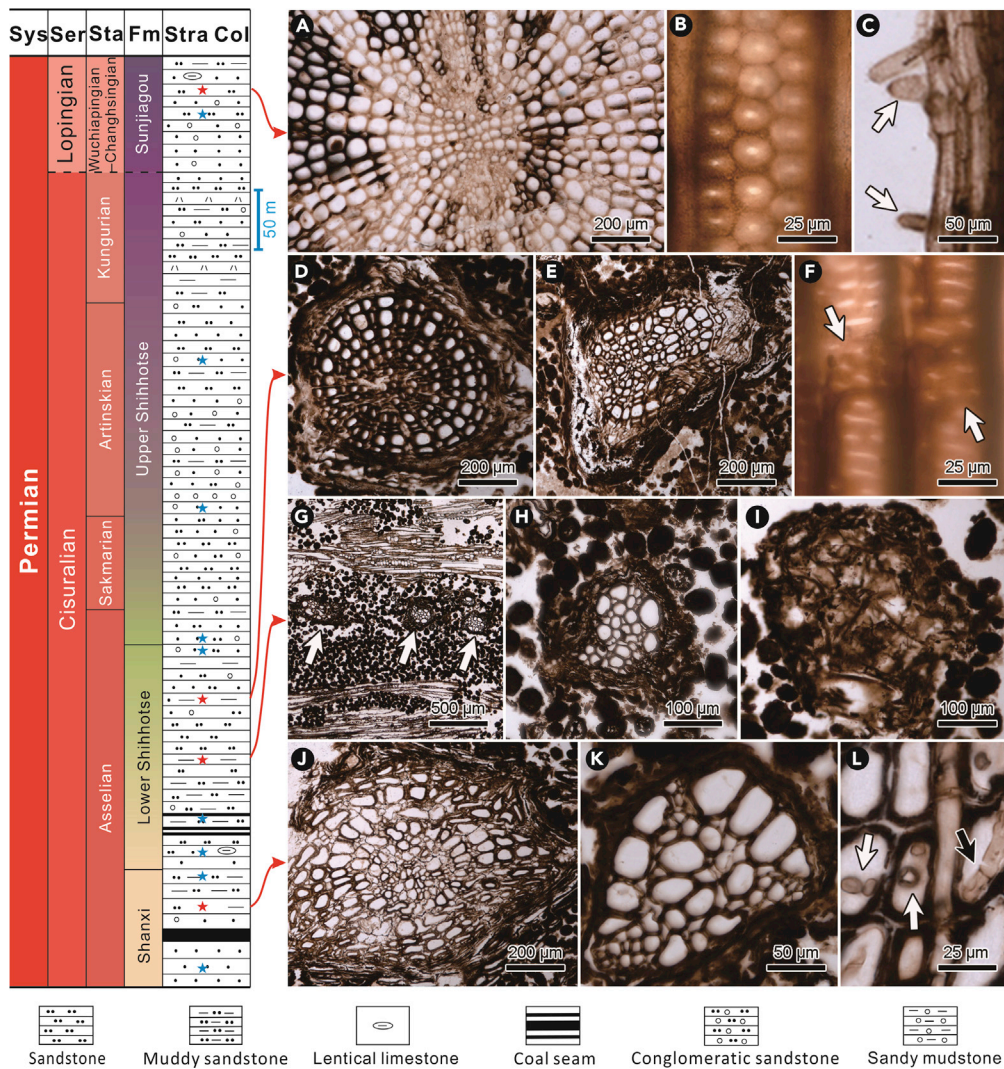
Figure 3. Stratigraphic column showing wood-bearing beds and rootlets in the nurse logs in the Permian Cathaysian flora

Sys, System; Ser, Series; Sta, Stage; Stra Col, Stratigraphic column, asterisks in the stratigraphic column indicate the occurrences of fossil stems. The stage constraints are after Wu et al. (2021).

(A–C) *Amyelon*-type rootlets; YNUPB10151, from upper Sunjiagou Formation.

(A) Cross-section of a rootlet showing diarch stele.

(B), Radial longitudinal section (RLS), showing triseriate bordered pits on the radial tracheid wall.

(C) Root hairs (arrows) on the epidermal cells of a rootlet.

(D–H and J, and K) *Sphenophyllum*-type rootlets; (D, E, J, K) Cross-sections of rootlets, showing diarch and triarch steles.

(F) RLS, arrows indicating bordered pits in cross-fields.

(G) arrows indicating rootlets in the tunnels bored by arthropods.

(H) Higher magnification of (G), showing a rootlet surrounded by small-diameter coprolites that are interpreted to be of oribatid mite origin.

(I) Large-diameter coprolite that is interpreted to be of millipede origin.

(L) Fungal hyphae (arrows) in the lumina of tracheids, black arrow indicates a septate fungal hypha.

(D–F, and I) YKLP20007, upper Lower Shihhotse Formation; (G, H) XS01-01, middle Lower Shihhotse Formation; (J, L) YKLP20001 and (K) YNUPB10149, upper Shanxi Formation. See also Figures S1–S14.

All of the studied rootlets occur in degraded portions of the host wood that contain abundant arthropod coprolites (Figures 3G–3L, S9I, S9J, S10A, S11G–S11L, S12A, S12B, S13A, and S13B), fungal decay features, or fungal hyphae (Figures 3L, S14H, and S14I). These observations demonstrate that the nurse logs had been significantly decomposed by arthropods and fungi before fossilization. The coprolites are typical of those

produced by oribatid mites (Figure 3H) and probable millipedes (Figure 3I), based on their dimensions, shapes, and contents (Feng et al., 2010a, 2015, 2017; Falcon-Lang et al., 2015; Wei et al., 2019). Despite the presence of arthropod coprolites and fungal remains, the exceptional preservation of the Permian nurse log anatomy indicates that these stems were in an early stage of decay. We interpret these stems to have been lying on the ground surface when colonized by new seedlings/sporelings, rather than to have been buried deeply in the sediments. However, the occurrence of rootlets in the pith of the two nurse logs described herein indicates that some stems might have been standing (as nurse stumps) when colonized by the sphenopsids, or as living plants in a host epiphyte relationship. In all cases, prior degradation of the wood by arthropods and fungi appears to have provided conduits that facilitated root penetration of the host axes.

In ancient and modern terrestrial ecosystems, wood-boring detritivores, including oribatid mites, insects, and millipedes, were and remain crucial in regulating nutrient cycling (Jiao et al., 2018; Sagi et al., 2019; Philippe et al., 2022). They accelerate the contribution of organic matter to soils by promoting cellulose and lignin decomposition in wood (Joly et al., 2018; Ma et al., 2019). Thus, they are essential factors in maintaining soil fertility, releasing nutrients, and improving the substrate environment (Pausas and Bond, 2020). Our study indicates that wood-boring detritivores and fungi also played important roles in the functioning of the deep-time terrestrial ecosystems by generating conduits for root growth and releasing nutrients for seedling/sporeling development. The consistent association of wood-boring arthropods and penetrative roots is interpreted to be one of the most important reasons for the nurse-log strategy being relatively common in the Permian conifer forests of northern China.

Previously reported late Paleozoic nurse logs have been identified only from the high-latitude (paleotemperate) Gondwanan floral realm in the Southern Hemisphere dominated by broad-leafed deciduous glossopterid forests (Césari et al., 2010; Decombeix et al., 2021). Three other major floral realms, distributed primarily in the Northern Hemisphere, prevailed in the late Paleozoic: the predominantly humid (sub)tropical Cathaysian and mostly dry (sub)tropical Euramerican floral realms, and the high-latitude humid temperate Angaran floral realm (Feng et al., 2020). Thus far, nurse logs have not been formally documented in any of these Northern Hemisphere late Paleozoic floral realms, although epiphytic relationships that might have persisted on fallen logs have been identified for some gymnosperm—fern—sphenophyte fossil associations from the lowermost Permian of Germany (Rößler, 2021).

Ecologically, the late Paleozoic Gondwanan nurse logs of South America occurred in temperate glossopterid forests that were stressed by both frequent flooding and volcanic disturbances (Césari et al., 2010, 2012). Those identified in Antarctica were adapted to an ever-wet, peat-forming environment (Decombeix et al., 2021). The Mesozoic (Late Triassic) nurse log of southwestern United States was documented from a conifer forest inhabiting a moist overbank environment under a temperate to subtropical paleoclimate (Daugherty, 1963; Jin et al., 2018). The Cretaceous (Aptian) nurse logs from Patagonia derive from a conifer-dominated forest growing in middle latitude temperate climatic settings with strong seasonality and subject to regular volcanic ash falls (Vera and Loinaze, 2022). In contrast, the Cenozoic (Eocene) nurse log from Belgium was reported from a conifer (*Glyptostrobus*) forest that grew in a swampy coastal alluvial floodplain environment under a subtropical paleoclimate (Fairon-Demaret et al., 2003) (Table 1).

The broad-scale paleoclimate was humid to sub-humid in the early Permian, and arid in the late Permian, of northern China (Wu et al., 2021). More specifically, the stratigraphic succession at the fossil locality hosting the studied nurse logs was dominated by swamp and fluvial deposits in the lowermost Permian and well--drained overbank deposits in the uppermost Permian (Feng et al., 2010b). Diverse plant roots have been reported extensively in coal balls from the lower Permian Shanxi Formation of northern China and coal balls from the upper Permian Wangjiazhai Formation in southwestern China (Wang et al., 2009), but the nurse-log phenomenon has not been documented in the Cathaysian floras to date (Wang, 2022; personal communication). Similarly, rootlets intersecting other plant organs, in many cases associated with invertebrate coprolites and fungi, are common in late Paleozoic and early Mesozoic coal balls and siliceous permineralized peats from other regions (Raymond, 1988; McLoughlin, 1992; Decombeix et al., 2009; McLoughlin and Strullu-Derrien, 2016). However, in these cases, the host organs are commonly small, detrital elements that may have been penetrated by rootlets long after their deep incorporation in the peat profile (organosol). Our investigation demonstrates that nurse logs *sensu stricto* were well established in the Permian Cathaysian conifer forests and that the strategy persisted despite significant paleoenvironmental and paleoclimatic changes through the Permian.

Table 1. Comparison of fossil nurse logs

Nurse log	Invaded rootlet	Invaded portion	Habitat	Unit and Age	Locality	References
Ningxiaites sp. 1	*Amyelon*-type	Pith	Subtropical, heterospecific upland forests	Sunjiagou Fm.; late Permian	Shitanjing of Ningxia; China	This paper
Ningxiaites sp. 2	*Amyelon*-type	Secondary xylem	Subtropical, heterospecific upland forests	Sunjiagou Fm.; late Permian	Shitanjing of Ningxia; China	This paper
Plyophyllioxylon hulstaiense Feng, Wang, Liu et Rößler 2012	*Sphenophyllum*-type	Pith	Subtropical, heterospecific upland forests	Lower Shihhotse Fm.; early Permian	Hulstai of Inner Mongolia; China	This paper
Protophyllocladoxylon sp.	*Sphenophyllum*-type	Secondary xylem	Subtropical, heterospecific upland forests	Lower Shihhotse Fm.; early Permian	Hulstai of Inner Mongolia; China	This paper
Agathoxylon sp. 3	*Sphenophyllum*-type	Secondary xylem	Subtropical, heterospecific upland forests	Lower Shihhotse Fm.; early Permian	Hulstai of Inner Mongolia; China	This paper
Agathoxylon sp. 2	*Sphenophyllum*-type	Secondary xylem	Subtropical, heterospecific lowland forests	Shanxi Fm.; early Permian	Hulstai of Inner Mongolia; China	This paper
Agathoxylon sp. 1	*Sphenophyllum*-type	Secondary xylem	Subtropical, heterospecific lowland forests	Shanxi Fm.; early Permian	Hulstai of Inner Mongolia; China	This paper
Cuyoxylon sp.	*Cuyoxylon* sp.	Pith and secondary xylem	High-latitude cool–temperate, lowland swampy monospecific forest	San Ignacio Fm.; latest Carboniferous/earliest Permian	San Juan Province; Argentina	Césari et al. (2010), (2012)
Australoxylon sp.	*Vertebraria* sp.	Secondary xylem	High-latitude cool–temperate, lowland swampy monospecific forest	Buckley Fm.; late Permian	Skaar Ridge, Transantarctic Mountains; Antarctica	Decombeix et al. (2021)
Agathoxylon (*Araucarioxylon*) *arizonicum*	*Araucariorhiza joae*	Hollow center of the stem and secondary xylem	Temperate to subtropical; lowland heterospecific forest	Chinle Fm.; Late Triassic	Petrified Forest National Park, Arizona; USA	Daugherty (1963)
Agathoxylon pseudoparenchymatosum (Gothan) Pujana, Santillana et Marenssi 2014	Undetermined	Secondary xylem	Temperate to warm; mid-latitude heterospecific forest	Punta del Barco Fm.; Early Cretaceous	Santa Cruz Province; Argentina	Vera and Loinaze (2022)
Agathoxylon kellerense (Lucas et Lacey) Pujana, Raffi et Olivero 2017	Undetermined	Secondary xylem	Temperate to warm; mid-latitude heterospecific forest	Punta del Barco Fm.; Early Cretaceous	Santa Cruz Province; Argentina	Vera and Loinaze (2022)
Glyptostroboxylon sp.	*Glyptostroboxylon* sp.	Pith and secondary xylem	Subtropical, monospecific, lowland swampy forest	Tienen Fm.; early Eocene	Hoegaarden, Vlaams-Brabant Province; Belgium	Fairon-Demaret et al. (2003)

Fm. = Formation.

Fossil evidence from the late Paleozoic of Gondwana indicates that glossopterid stems served as nurse logs to conspecific seedlings in mire environments (Césari et al., 2010, 2012; Decombeix et al., 2021). The Mesozoic and Cenozoic nurse logs of the USA and Europe reveal that conifer stems also functioned as hosts to conspecific seedlings in both swampy and moderately dry habitats (Daugherty, 1963; Fairon-Demaret et al., 2003). By contrast, our study reveals that both probable conspecific and interspecific relationships were present in the Permian Cathaysian floral realm and that nurse-log interaction was a sophisticated ecological strategy for seedling survival in the late Paleozoic forests dominated by different gymnosperm groups in separate hemispheres. Although the fossil record is limited at present, a preliminary evolutionary scenario is that: nurse logs developed initially in humid dense-forested habitats in the late Paleozoic, where better access to light and substrates above the water table favored survival of seedlings. Subsequently, this syndrome extended to a broader range of forest types (and plant groups) in both temperate and tropical environments during the Mesozoic and Cenozoic, and has gradually developed into a major regenerative strategy in modern forest ecosystems, even extending into dryland settings.

Limitations of the study

The majority of paleobotanical research is subject to some limitations related to the objects of study. The first limitation is the preservational quality of plant macrofossils. The second limitation concerns the representativeness of data. Both of these factors may influence more accurate taxonomic identification of plant fossils, the assessment of morphological variability of different plant organs, the possibility of whole-plant reconstruction, and, eventually, paleoecological reconstructions.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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  - Data and code availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
  - Materials
- METHOD DETAILS
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  - Specimen imaging and terminology

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2022.105433.

AUTHOR CONTRIBUTIONS

Z.F. designed and led the research. Z.F., X.D.G., H.B.W., and Y.G. conducted fieldwork and prepared fossil specimens. Z.F. photographed specimens, prepared figures, and wrote the initial manuscript. S.M. contributed to writing the text and compared the results with examples from the Southern Hemisphere. All authors participated in the interpretation of the materials and the discussions. All authors read and approved the final article.

DECLARATION OF INTERESTS

The authors declare no conflict of interest.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Fossil specimens, thin sections, cellulose acetate peels	The Palaeobotanical Collections of the Institute of Palaeontology, Yunnan University, China	YKLP20001, YKLP20004, YKLP20007, YNUPB10149, YNUPB10150, YNUPB10151, YNUPB10152
Software and algorithms		
Line drawings were prepared with CorelDRAW 2018 Graphic	Corel Corp.	https://www.coreldraw.com
Post-processing of images were performed with Adobe Photoshop CC 2019	Adobe Inc.	https://www.adobe.com/products/photoshop.html

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Zhuo Feng (zhuofeng@ynu.edu.cn).

Materials availability

Specimens, thin sections, and cellulose acetate peels are housed at the Palaeobotanical Collections of the Institute of Palaeontology, Yunnan University, China. This is a public repository where the specimens are permanently available for research.

Data and code availability

- Data are publicly available as of the date of publication.

- This paper does not report original code.

- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Materials

The fossil specimens used in study are preserved as silica permineralizations with exceptionally well-preserved anatomies, which are listed in the key resources table.

METHOD DETAILS

Locality and geological setting

The fossil nurse log specimens were collected from the Shanxi Formation and Lower Shihhotse Formation in Hulstai Town of Inner Mongolia and the Sunjiagou Formation in the Shitanjing coalfield of Ningxia Huizu Autonomous Region, northern China (Figure 1). Recent high-precision U-Pb age constraints indicate that the Shanxi, Lower Shihhotse, and Upper Shihhotse formations are dated to the Cisuralian, and the Sunjiagou Formation is of Lopingian age (Wu et al., 2021). Tectonically, the study area is located in the western Ordos Basin at the northwestern edge of the North China Block (Cocks and Torsvik, 2013). Diverse, exceptionally well-preserved fossil tree stems form the basis of previous studies detailing the systematics, anatomy, and paleoecology of fossil woods (Feng et al., 2010a, 2010b, 2011, 2012, 2013, 2017, Feng, 2012; Wei et al., 2015, 2019; Yang et al., 2017, 2022). Several fossil-wood taxa have been described previously based on their anatomy, including *Plyophyllioxylon hulstaiense* Feng, Wang, Liu et Rößler 2012 (Feng et al., 2012), *Palaeoginkgoxylon zhoui* Feng, Wang et Rößler 2010 (Feng et al., 2010a), *Shenoxylon mirabile* Feng, Wang et Rößler 2011 (Feng et al., 2011), *Ningxiaites specialis* Feng (2012) (Feng, 2012), and *N. shitanjingensis* Wei et Feng 2019 (Wei et al., 2019). It is noteworthy that the affinities of the trees from

the lower Permian are relatively 'primitive' (plesiomorphic) systematically and are characterized mainly by araucarian type secondary xylem. In contrast, the anatomy of trees in the uppermost Permian Sunjiagou Formation more closely resembles modern conifers in having complex, helically arranged leaf traces (Wei et al., 2015), and in their bark and leaf anatomies (Yang et al., 2017, 2022).

Specimen imaging and terminology

Thin sections and peels were prepared according to the standard method (Hass and Rowe, 1999). Optical examination and photomicrographs were undertaken using a ZEISS AXIO Imager.Z2 transmitted light microscope equipped with a ZEISS Axiocam 512 color digital camera. We follow the anatomical terminology used in previous studies of late Paleozoic roots (Galtier and Daviero, 1999; Wan et al., 2019).