

Woody plant phytolith morphology and representation in surface sediments across the Northern Territory, Australia

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ABSTRACT

Phytoliths are a good tool for investigating vegetation change in northern Australia. However, there is a lack of phytolith reference material across the Australian continent, particularly for woody plants. The development of reference material from woody plants is critical to understand regional patterns of phytolith production and preservation. This study analyses phytolith material from 40 woody plants to examine morphological and anatomical variation in phytolith production among Australian plant families. This is paired with phytolith assemblages from nine surface sediment samples to assess the representation and preservation of woody plant phytolith morphotypes. All woody plant species examined produce identifiable phytolith morphotypes, but most morphotypes cannot be differentiated between woody eudicots, monocots, and conifers. However, some woody plant morphotypes do have good potential for taxonomic or anatomical discrimination of plant groups. The analysis of surface sediment phytolith assemblages reveals that not all woody plant morphotypes preserve equally in surface sediments, potentially restricting their ability for taxonomic discrimination. Finally, the relevance of phytolith morphotypes for palaeoecological reconstruction is discussed.

1. Introduction

Despite recent advances at a few key localities (e.g., Marx et al., 2021; Rowe et al., 2022, 2024), little information exists for late Quaternary environmental change in northern Australia. Although pollen and plant macrofossil records are widely used for vegetation reconstructions in temperate south-eastern Australia (e.g., Forbes et al., 2021; Mariani et al., 2022), they do not preserve well in the largely ephemeral conditions of the monsoonal north and arid interior (Horowitz, 1992; Petheram et al., 2008). The few available records from this region are mostly restricted to coastal areas in the far north and are particularly rare in the arid interior, limiting perspectives of terrestrial environmental change (Reeves et al., 2013). Thus, the development of alternative proxy records of vegetation change may provide critical insights into ecosystem structure, function, and composition in this understudied region.

An alternative proxy for reconstructing vegetation change are phytoliths, which are microscopic biogenic silica bodies from plants. Living

plants absorb monosilicic acid (H_2SiO_4) from groundwater, which is eventually deposited as amorphous silica within intracellular and intercellular spaces in plant tissues (Madella and Lancelotti, 2012; Strömberg et al., 2018). This forms opaline silica casts of characteristic shapes (morphotypes) specific to families and below. Phytoliths are released into soils and sediments from the decay of plant material, where they form sedimentary records of past plant communities that are highly robust due to their silica structure (Madella and Lancelotti, 2012; Strömberg et al., 2018). The recognition of phytoliths as an important proxy for palaeoecology and archaeology has only emerged globally in recent years, providing insight into topics such as the origin and domestication of important crops (e.g., Ranere et al., 2009; Zhang et al., 2024), the evolution and expansion of C_4 – dominated grasslands (e.g., Strömberg and McInerney, 2011), and past vegetation and climate dynamics (e.g., Alexandre et al., 1997; Stromberg, 2003; Yost et al., 2021). Moreover, unlike pollen and plant macrofossils, phytoliths tend to preserve better in adverse and rapidly changing environmental conditions, such as those of northern Australia.

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The use of fossil phytolith records for palaeoecology requires the development of local modern reference material from living plants, for accurate identification of phytolith morphology and production. Extensive development of phytolith reference material over the past 20 years has greatly improved knowledge of phytolith morphology across plant families (Strömberg et al., 2018). However, studies of woody plant phytoliths have mostly focused on leaves, with few detailed studies of phytoliths from wood and bark (e.g., Collura and Neumann, 2017; Piperno and McMichael, 2020, 2023). Thus, detailed classifications of woody plant phytolith morphotypes are rare (e.g., Stromberg, 2003), and taxonomic discrimination of woody plants is mostly limited to a broad scale (ICPT, 2019; Piperno, 2006). The development of further reference material from woody plants, across a variety of anatomical contexts, is needed to improve taxonomic discrimination of woody plants.

Comprehensive modern reference material has been developed for many regions worldwide, including Africa (e.g., Collura and Neumann, 2017; Esteban et al., 2017; Novello et al., 2018), south America (e.g., Piperno and McMichael, 2023, 2020; Watling et al., 2020) and east Asia (e.g., Gao et al., 2018; Ge et al., 2020; Liu et al., 2021). However, there is little available phytolith reference material for Australia, where it is limited to grasses and woody plant leaves (Bowdery, 1998; Hart, 1990, 1988; Parr and Watson, 2006; Wallis, 2003). Most of this material was described before the recent standardisation of terminology (Madella et al., 2005; ICPT, 2019), further restricting its application. Although some diagnostic phytolith morphologies have been identified in Australian woody plants (Bowdery, 1998; Hart, 1988; Wallis, 2003), studies from underlying soils and sediments are scarce (e.g., Wallis, 2013) and the potential of these morphotypes as palaeoecological indicators is unclear. This has led to a lack of clarity surrounding phytolith production and preservation in Australian plants and sediments (see Turnbull et al., 2023 for a full review).

To address gaps in woody plant phytolith production and preservation in Australian environments, this study presents modern phytolith reference material from 40 tree and shrub species and underlying surface sediments from northern Australia. Phytolith morphology is described from species collected across the ecological gradient from the northern tropical open woodlands to the arid interior shrublands and

grasslands of the Northern Territory, Australia. Phytolith assemblages recovered from nine underlying surface sediment samples across three climatic zones of this region are presented to test for the preservation of these woody plant morphotypes. Finally, the relevance of these findings for phytolith-based palaeoecological reconstructions are discussed.

2. Environmental setting

The Northern Territory (NT) of Australia covers the central northern portion of the continent, between 129° - 138° E longitude, and from the Timor and Arafura seas around 10° S in the north to the region of South Australia at 26° S latitude (Fig. 1). This region is characterised by strong rainfall seasonality and a latitudinal precipitation gradient, resulting from the Indo-Australian summer monsoon. While the far north coastal region experiences a tropical monsoonal climate with high mean annual precipitation (MAP) of over 1500 mm, rainfall gradually declines southwards to form a semi-arid climate with low MAP (< 300 mm) in the interior south. This precipitation gradient drives strong latitudinal change in vegetation communities, from the *Eucalyptus*-dominated tropical open woodlands of the far north to open shrublands and grasslands across the arid interior (Ma et al., 2013).

The far north region is characterised by Eucalypt open forest and woodlands with a grassy understorey, collectively referred to as tropical savannas (Williams et al., 2017). Canopies are largely dominated by *Eucalyptus miniata*, *E. tetradonta*, and/or *E. tectifica*, with a patchy and mixed subcanopy of trees and shrubs such as *Erythrophleum chlorostachys*, *Buchanania obovata*, *Livistona humilis*, *Petalostigma* species, *Corymbia* spp., *Terminalia* spp., and *Acacia* spp. (Brock, 2022; Ma et al., 2013; Williams et al., 2017). On heavier, water-logged soils, *Melaleuca* forests persist, dominated by species such as *Melaleuca viridiflora*, *M. leucadendra*, *E. camaldulensis*, *Barringtonia acutangula*, *Lophostemon grandiflorus*, and *Acacia auriculiformis* (Brock, 2022). Monsoonal rainforest and thickets are patchily distributed across the far north, featuring trees such as *Ficus* spp., *Antidesma ghesembilla*, *Glochidion* spp., and *Acacia* spp. (Brock, 2022).

Communities transition southwards into semi-arid open woodlands dominated by *Eucalyptus* and/or *Acacia* spp. (Hutley et al., 2011; Williams et al., 2017). Canopies are dominated by *E. tetradonta* and/or

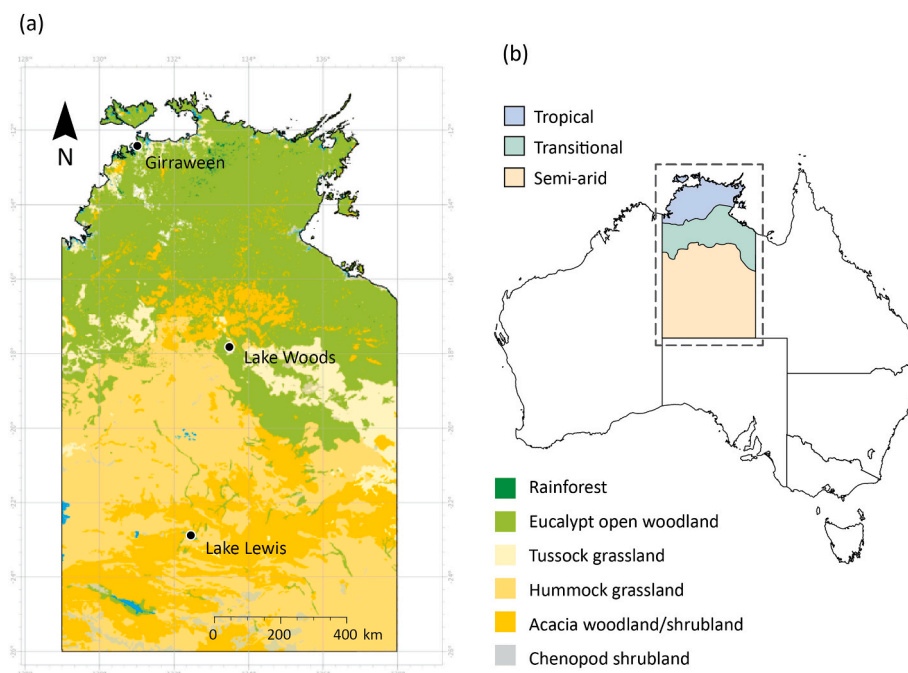


Fig. 1. Maps of Northern Territory region of Australia: (a) Broad bioclimatic zones, and (b) Major vegetation communities and lake sites, modified from the National Vegetation Information System (NVIS) dataset.

E. microtheca, with a mixed understorey of trees and shrubs such as *Lysiphyllum cunninghamii*, *Macropteranthes kekwickii*, *Acacia* spp., *Hakea* spp., and *Corymbia* spp. (Williams et al., 2017). Sparse shrubs of other species may occur scattered throughout communities, including *Eucalyptus* spp., *Macropteranthes kekwickii*, *Erythrophleum chlorostachys*, and *Petalostigma* spp. (Groves, 1994). *Acacia* woodlands dominate on areas of shallow, lateritic soils (Groves, 1994; Williams et al., 2017).

These communities transition into *Acacia*-dominated shrublands and grasslands in the arid interior, with fading dominance of *Eucalyptus* spp. (Ma et al., 2013; Williams et al., 2017). *Acacia* spp., usually *A. aneura*, form monospecific stands across the semi-arid region, interspersed with hummock grasslands of varying shrub cover (Groves, 1994; Ma et al., 2013). Associated shrubs include shrubs include *Eremophila* spp., *Senna* spp., *Callitris glaucophylla*, *Hakea* spp., *Eucalyptus* spp., and other *Acacia* spp. (Groves, 1994).

3. Methods

3.1. Plant specimen processing

Tree and shrub specimens were collected from field locations across the NT. Further species of ecological interest were sampled from the Australian Tropical Herbarium at James Cook University, Cairns Nguma-bada campus. Identification of specimens was carried out to a species level with assistance from the Janet Cosh Herbarium at the University of Wollongong and the John T. Waterhouse Herbarium at the University of New South Wales. A total of 102 samples from 40 woody plant species were analysed (Table 1).

Phytolith extraction from plant material follows a dry-ashing method (Parr et al., 2001). Specimens were sub-sampled into anatomical sections (leaf, stem, bark, seedpod, flower, fruit) and cleaned in an ultrasonic bath with 5% Decon-90 solution. Samples were rinsed and dried before ashing in a furnace at 450 °C for two hours. Samples were transferred to 50 cc tubes, treated with 10% H₂O₂ solution in 5 ml aliquots, and heated to 80 °C in a water bath until the reaction ceased. The remaining material was rinsed and treated with 10% HCl in 2 ml aliquots. Samples were rinsed and transferred with ethanol to small vials for storage.

3.2. Sediment sample processing

Surface sediment samples were collected around three lake sites across the NT: Girraween Lagoon, Lake Woods, and Lake Lewis (Fig. 1). Samples were collected using transects of representative vegetation communities for each region within quadrat perimeters, often 1 × 1 m. Within each quadrat, the tree, shrub, and grass species were recorded, along with ground cover and sediment characteristics. Five pinches of surface sediment were taken within the quadrat perimeters, from each corner and the middle, after covering leaf litter was removed. Three surface sediment samples were selected from each lake site for further analysis, for a total of nine surface sediment samples (Table 2).

Phytolith extraction procedures from sediments follow a heavy liquid flotation method adapted from Lentfer and Boyd (1998) and Zhao and Pearsall (1998). Subsamples of two grams were taken from each bulk sediment sample and sieved through a 125 µm mesh. Samples were transferred to 50 cc tubes and treated with 10% HCl in two ml aliquots. Samples were then treated with 10% H₂O₂ solution in 5 ml aliquots and heated to 80 °C in a water bath until the reaction ceased. Clays were removed by centrifugation in 5% NaPO₃ solution at 2000 rpm for two minutes followed by decantation, repeated until the supernatant was transparent. The supernatant was periodically checked for phytoliths to ensure no sample was lost. Samples were rinsed with deionised water three times between all steps. Samples were then transferred to 15 cc tubes and sodium polytungstate solution (2.3 g/cm³) added to separate phytoliths from remaining silicates. Samples were centrifuged for 10 min at 1000 rpm and the supernatant surface pipetted into clean 15 cc

tubes. Samples were rinsed three times to remove the sodium polytungstate and transferred to small vials for storage using ethanol.

3.3. Counting and analysis

A small amount of each sub-sample was mounted onto a grass slide using Eukitt as a mounting medium. Identification and counting of morphotypes was conducted at 400x magnification using an Olympus Bx51 light microscope. All samples were counted to a minimum of 300 phytoliths, followed by scanning of the entire slide to identify any rare morphotypes.

Where possible, classification of phytolith morphology follows the ICPN 2.0 (ICPT, 2019). For morphotypes not described in this nomenclature, classification closely follows other literature describing woody plant phytoliths (An and Xie, 2022; Collura and Neumann, 2017; Piperno, 2006; Stromberg, 2003). A total of 25 phytolith morphotypes across six categories were identified and described from woody plant samples. Descriptions and occurrence of these morphotypes is presented in Table 3.

4. Results

4.1. Phytoliths from woody plants

Of the 102 samples analysed, 79 were found to produce identifiable phytoliths (Table 1, Plate 1). Leaves from all 40 species contained phytoliths, as well as all bark (12 samples) and fruit (2 samples) examined. However, woody stems, seedpods, and flowers were more variable, with only just over half of these samples containing phytoliths (Table 1).

SPHEROID morphotypes were observed in almost all samples (Fig. 2; Plate 1, 4–7; Table 3). The most common subtype was SPHEROID PSILATE, which were found in 70 samples across 39 species. SPHEROID ORNATE phytoliths were similarly abundant, observed in 62 samples across 39 species. SPHEROID ECHINATE phytoliths were only found in three palm species, making up over 80% of leaf assemblages. SPHEROID NODULAR and IRREGULAR BODY were largely restricted to woody stem and bark samples, in which they were often abundant.

EPIDERMAL phytoliths were similarly widely distributed (Fig. 2; Plate 1, 1–3; Table 3). POLYHEDRAL phytoliths were very common, occurring in 60 samples across 40 species. However, other EPIDERMAL phytoliths were not as widespread or abundant. JIGSAW phytoliths were only observed in two species, making up 31.6% of *Osbeckia australiana* leaves. EPIDERMAL PLATE phytoliths were found in 19 species, and were particularly abundant in the fruit of *Buchanania obovata*. MESOPHYLL SPONGY sheets were observed in the leaves of 12 species, while MESOPHYLL PALISADE sheets were only observed in two species. STOMATA had similarly restricted distributions, with STOMATA SIMPLE types observed in four species and STOMATA CILIATE only in two species.

SCLERENCHYMA and VASCULAR ELEMENT morphotypes were widely distributed in low frequencies (Fig. 2; Plate 1, 9–13; Table 3). SCLEREID PSILATE and FIBRE morphotypes together occurred in 46 samples across 35 species, while TRACHEARY ANNULATE LINEAR morphotypes were observed in 31 samples over 30 species. SCLEREID PITTED were found in five species, making up 17.2% of *Erythrophleum chlorostachys* leaves. TRACHEARY ANNULATE TERMINAL and TRACHEARY PITTED TERMINAL were highly abundant in the leaves of *Acacia* species and were occasionally observed in other species.

HAIR CELL morphotypes were only observed in the leaves of 12 species (Fig. 2, Plate 1, 6–8; Table 3). ACUTE BULBOSUS PSILATE phytoliths were common in all 12 species, while ACUTE BULBOSUS NODULAR and HAIR BASE phytoliths were observed only in the leaves of *Ficus aculeata*.

ELONGATE morphotypes were also relatively common in the samples examined (Fig. 2; Table 3; Plate 1: 17–19). ELONGATE PSILATE phytoliths occurred in 52 samples across 33 species, while ELONGATE

Table 1

Plant type, family, species name and authority, associated vegetation community, anatomical samples, and phytolith production status for 40 tree and shrub species from the Northern Territory, Australia.

Type	Family/subfamily	Species	Community	Anatomy	Production	
Monocot	Arecaceae	<i>Carpentaria acuminata</i> (H. Wendl. & Drude) Becc.	Tropical open woodland	Leaf	Leaf	
		<i>Hydiastele wendlandiana</i> (F.Muell.) H.Wendl. & Drude	Tropical open woodland	Leaf, stem	Leaf, stem	
		<i>Livistona humilis</i> (R.Br.) Mart.	Tropical open woodland	Leaf, fruit, bark	Leaf, fruit, bark	
	Pandaneaceae	<i>Pandanus spiralis</i> R.Br.	Tropical open woodland	Leaf; bark; aerial root	Leaf, bark	
		<i>Pandanus aquaticus</i> F.Muell.	Tropical open woodland	Leaf	Leaf	
	Conifer	Cupressaceae	<i>Callitris glaucophylla</i> Joy Thomps. & L.A.S.Johnson	Semi-arid shrubland	Leaf; stem	Leaf
<i>Callitris intratropica</i> R.T.Baker & H.G.Sm.			Tropical open woodland	Leaf; stem	Leaf	
Eudicot	Myrtaceae	<i>Calytrix exstipulata</i> DC.	Tropical open woodland	Leaf; stem; flower	Leaf, flower	
		<i>Corymbia aparrerinja</i> K.D.Hill & L.A.S. Johnson	Semi-arid shrubland	Leaf; stem; seedpod; bark	Leaf, stem, bark	
		<i>Corymbia terminalis</i> (F. Muell.) K.D.Hill & L.A.S. Johnson	Semi-arid shrubland	Leaf; stem; bark	Leaf, stem, bark	
		<i>Eucalyptus camaldulensis</i> Dehnh.	Semi-arid shrubland	Leaf; stem; seedpod; bark	Leaf, bark	
		<i>Eucalyptus gamophylla</i> F.Muell.	Semi-arid shrubland	Leaf; stem; seedpod	Leaf	
		<i>Eucalyptus microtheca</i> F.Muell.	Semi-arid open woodland	Leaf; stem; seedpod; bark	Leaf, stem, bark	
		<i>Eucalyptus miniata</i> A.Cunn. ex Schauer	Tropical open woodland	Leaf; stem	Leaf, stem	
		<i>Eucalyptus tetradonta</i> F.Muell.	Tropical open woodland	Leaf; stem; bark	Leaf; stem; bark	
		<i>Eucalyptus tectifera</i> F.Muell.	Semi-arid open woodland	Leaf; stem; seedpod	Leaf, stem	
		<i>Lophostemon grandiflorus</i> (Benth.) Peter G. Wilson & J. T.Waterh.	Tropical open woodland	Leaf	Leaf	
		<i>Melaleuca glomerata</i> F.Muell.	Semi-arid shrubland	Leaf; stem; bark	Leaf; stem; bark	
		<i>Melaleuca viridiflora</i> Sol. ex Gaertn.	Tropical open woodland	Leaf; stem; bark	Leaf; stem; bark	
		<i>Melaleuca leucadendra</i> (L.) L.	Tropical open woodland	Leaf; stem	Leaf; stem	
		Fabaceae/ caesalpinoideae	<i>Acacia aneura variant (1)</i> F.Muell. ex Benth.	Semi-arid shrubland	Leaf; stem; flower	Leaf
			<i>Acacia aneura variant (2)</i> F.Muell. ex Benth.	Semi-arid shrubland	Leaf; stem; flower	Leaf; stem; flower
			<i>Acacia auriculiformis</i> A. Cunn. Ex Benth.	Tropical open woodland	Leaf; flower	Leaf
			<i>Acacia colei</i> Maslin & L.A.J. Thomson	Tropical open woodland	Leaf; stem	Leaf; stem
			<i>Acacia kempeana</i> F.Muell.	Semi-arid shrubland	Leaf; stem; flower	Leaf; flower
			<i>Acacia tetragonophylla</i> F.Muell.	Semi-arid shrubland	Leaf; stem; flower; bark	Leaf; stem; bark
			<i>Erythrophleum chlorostachys</i> (F.Muell.) Baill.	Tropical open woodland	Leaf	Leaf
		Fabaceae	<i>Erythrina vespertilio</i> Benth.	Semi-arid shrubland	Leaf; stem	Leaf
			<i>Lysiphyllum cunninghamii</i> (Benth.) de Wit	Semi-arid open woodland	Leaf; stem	Leaf; stem
Proteaceae	<i>Banksia dentata</i> L.F.	Tropical open woodland	Leaf; stem; seedpod; bark; flower	Leaf; seedpod; bark		
	<i>Grevillea pteridifolia</i> Knight	Tropical open woodland	Leaf; stem; flower	Leaf		
	<i>Hakea chordophylla</i> F.Muell.	Semi-arid shrubland	Leaf; stem; seedpod; bark	Leaf; stem; seedpod; bark		
	<i>Hakea divaricata</i> L.A.S. Johnson	Semi-arid shrubland	Leaf; seedpod; flower	Leaf; seedpod		
	<i>Hakea macrocarpa</i> Cunn. ex R.Br.	Semi-arid open woodland	Leaf; stem	Leaf; stem		
Anacardiaceae	<i>Buchanania obovata</i> Engl.	Tropical open woodland	Leaf; stem; flower; fruit	Leaf; flower; fruit		
Combretaceae	<i>Terminalia carpentariae</i> C.T. White	Tropical open woodland	Leaf; stem	Leaf; stem		
Lecythidaceae	<i>Barringtonia acutangula</i> J.R.Forst. & G.Forst.	Tropical open woodland	Leaf; stem	Leaf; stem		
Moraceae	<i>Ficus aculeata</i> A.Cunn. ex Miq.	Tropical open woodland	Leaf	Leaf		
Scrophulariaceae Melastomataceae	<i>Myoporum montanum</i> R.Br.	Semi-arid shrubland	Leaf; stem	Leaf		
	<i>Osbeckia australiana</i> Naudin	Tropical open woodland	Leaf	Leaf		

Table 2

List of surface sediment sample locations, corresponding vegetation communities and major species observed in each plot, from the Northern Territory.

Location	Plot code	Community	Major trees and shrubs
Girraween Lagoon	GL1	Tropical open woodland	<i>Livistona humilis</i> , <i>Pandanus spiralis</i> , <i>Lophostemon grandiflorus</i> , <i>Erythrophleum chlorostachys</i>
	GL2	Tropical open woodland	<i>Eucalyptus miniata</i> , <i>E. tetradonta</i> , <i>Livistona humilis</i>
	GL3	Tropical open woodland	<i>Eucalyptus miniata</i> , <i>E. tetradonta</i> , <i>Erythrophleum chlorostachys</i> , <i>Acacia</i> species
Lake Woods	LW1	Semi-arid open woodland	<i>Eucalyptus microtheca</i> , <i>Acacia</i> species
	LW2	Semi-arid open woodland	<i>Acacia colei</i> , other <i>Acacia</i> species
	LW3	Semi-arid open woodland	<i>Eucalyptus microtheca</i> , <i>Macropteranthes keckwickii</i>
Lake Lewis	LL1	Semi-arid shrubland	<i>Eucalyptus gamophylla</i>
	LL2	Semi-arid shrubland	<i>Melaleuca glomerata</i>
	LL3	Semi-arid shrubland	<i>Hakea chordophylla</i> , <i>Acacia</i> species

Table 3

List of phytolith classes, morphotypes, codes, morphological descriptions, and anatomical and taxonomic derivations for all 25 morphotypes identified from woody plants.

Class	Morphotype	Code	Plate	Morphological description	Anatomical/taxonomic derivation
Epidermal	Polyhedral	POL	1	Tabular body with > 4 straight edges and a smooth or granulate surface, including individuals and intact sheets	Epidermis of woody plants
	Jigsaw	JIG	5	Sinuate body with wavy edges and a smooth surface	Epidermis of woody eudicots and ferns
	Mesophyll	MES_PAL	2	Elliptical, elongated bodies arranged in rows at right angles to the epidermis	Mesophyll of woody plants
	Palisade				
	Mesophyll	MES_SPO	2	Circular or elliptical bodies arranged in honeycomb structures	Mesophyll of woody plants
	Spongy				
	Stomata simple	STO_SIM	3	Silicified stomatal openings with no cilia	Stomata of many plant families
	Stomata ciliate	STO_CIL	4	Silicified stomatal openings with cilia along edges	Stomata of woody eudicots
	Epidermal plate	EPI_PLA		Intact silicified sheet of epidermal phytoliths, excluding polyhedral sheets	Epidermis of many plant families
Hair cell	Irregular body	IRR_BOD	9, 10	Irregularly shaped ellipsoidal or aggregate body, with granulate or nodular surface	Wood and bark of woody plants
	Acute bulbous psilate	ACU_BUL_PSI	8	Lanceolate body with one acute apex and smooth surface	Trichome appendages of leaves, seeds, and fruit in many plant families
	Acute bulbous nodular	ACU_BUL_NOD	7	Lanceolate body with one acute apex and tuberculate projections on surface	Moraceae family in this study, also Ulmaceae and Cannabaceae families
Spheroid	Hair base	ACU_BUL_BAS	6	Flat spherical body with concave area in centre, surrounded by silicified epidermal cells	Epidermis of woody eudicots, only observed in Moraceae in this study
	Spheroid psilate	SPH_PSI	11	Rounded or ellipsoidal body with smooth surface	Epidermis or parenchyma of woody plants
	Spheroid ornate	SPH_ORN	12	Rounded or ellipsoidal body with granulate or rugose surface	Epidermis or parenchyma of woody plants
	Spheroid lobate	SPH_LOB	13	Indented, lobate, or fused rounded body with smooth surface	Epidermis or parenchyma of woody plants
	Spheroid echinate	SPH_ECH	14	Rounded or ellipsoidal body with conical ornamentation	Leaves and fruit of <i>Arecaceae</i> family
Elongate	Spheroid nodular	SPH_NOD	15, 16	Rounded or ellipsoidal with tuberculate or "cauliflower-like" projections	Wood and bark of woody plants
	Elongate psilate	ELO_PSI	17	Linear, elongated body with smooth surface	Many plant families
	Elongate bulbosus	ELO_BUL	18	Linear, elongated body with globular protrusions	Many plant families
Sclerenchyma	Elongate curved	ELO_CUR	19	Curved, elongated body with smooth surface	Many plant families
	Scleireid psilate	SCL_PSI	20	Thin, elongated bodies with a smooth surface. May be variously branched, irregular, S-, Y-, or L- shaped.	Sclerenchyma of woody eudicots
	Scleireid pitted	SCL_PIT	22, 23, 24	Thin, elongated bodies with a baculate, columellate, and/or weakly striate surface. May be variously branched, irregular, S-, Y-, or L- shaped.	Sclerenchyma of woody eudicots, particularly in <i>Caesalpinioideae</i> in this study
	Fibre	FIB	21	Thin, elongated, fibrous bodies.	Sclerenchyma of woody eudicots
Vascular element	Tracheary annulate linear	TRA_ANN_LIN	30	Cylindrical, elongated body with helical ridges perpendicular to long axis	Many plant families
	Tracheary annulate terminal	TRA_ANN_TER	25, 26	Irregular, enlarged body with helical ridges perpendicular to long axis	Woody eudicots, highly abundant in <i>Acacia</i> species
	Tracheary pitted terminal	TRA_PIT_TER	27, 28	Irregular, enlarged body with circular or tuberculate projections on surface	Woody eudicots, highly abundant in <i>Acacia</i> species

BULBOSUS and ELONGATE CURVED together were found in 18 samples.

Detrended correspondence analysis (DCA) was carried out on a matrix of species and phytolith morphotype frequency. The resulting ordination diagram (Fig. 3) features a spread of data across the axes. Conifers and woody eudicots are interspersed across all axes, while woody monocots are distributed on the positive side of axis 1.

4.2. Phytoliths from surface sediments

Phytolith assemblages were recovered from all nine surface sediment samples (Fig. 4). 18 of the 25 phytolith morphotypes from woody plants were identified across these assemblages, as well as an additional seven morphotypes (Supplementary Material, Plate S1). All nine sediment assemblages feature abundant grass silica short cell phytoliths (GSSCPs), which make up 15.2–35.6% of assemblages. The most common morphotypes from woody plants are POLYHEDRAL, SPHEROID PSILATE, and SPHEROID ORNATE.

Some differences in assemblage composition between the three regions are evident (Fig. 4). Tropical open woodland sediments are dominated by SPHEROID PSILATE, SPHEROID ORNATE, and SPHEROID ECHINATE, which together make up 31.5–36.1% of these assemblages. SPHEROID ECHINATE phytoliths are absent from all semi-arid sediments, and SPHEROID PSILATE and SPHEROID ORNATE make

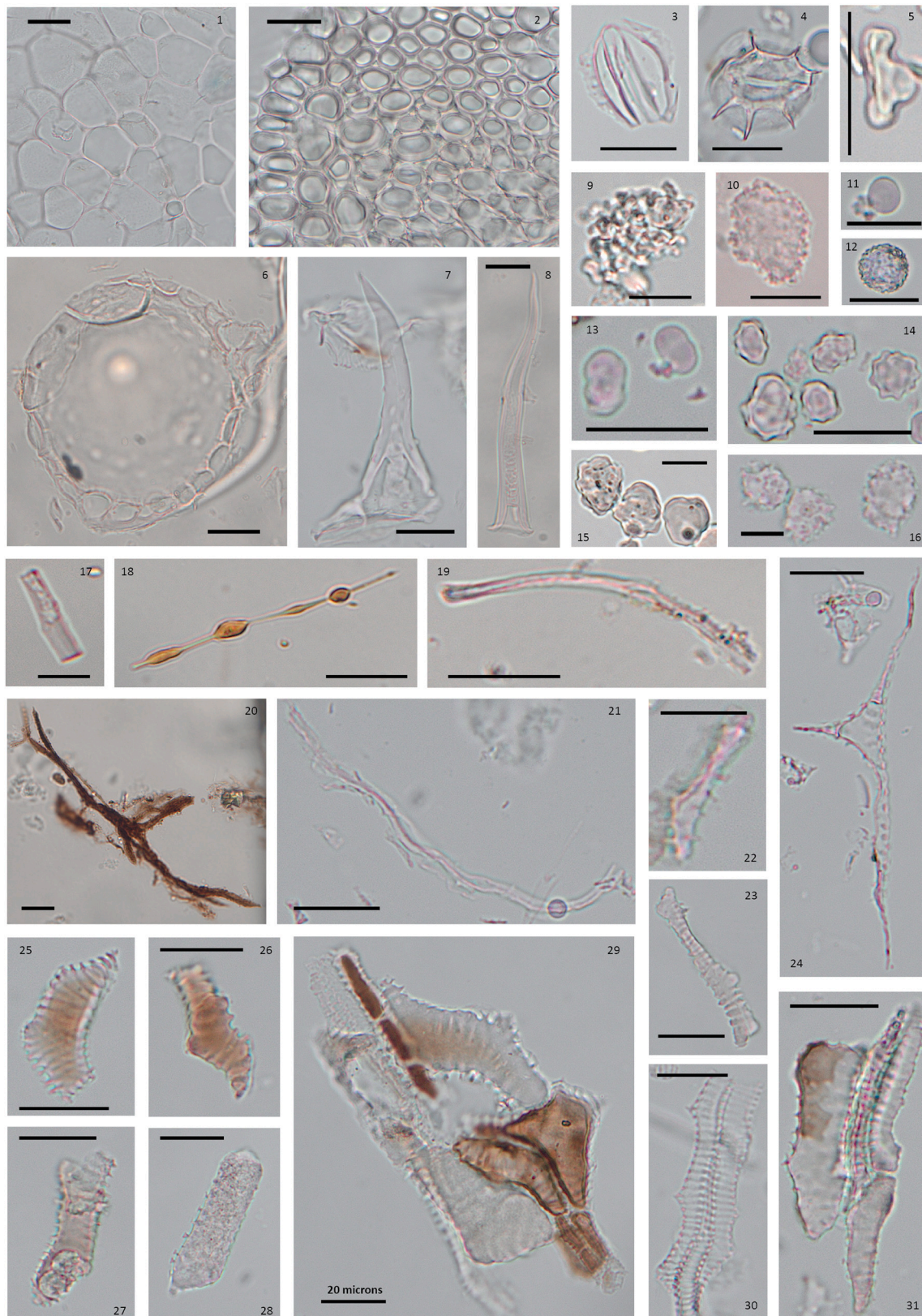


Plate I. Phytolith morphotypes extracted from woody plants of the Northern Territory, Australia (All scale bars: 20 μm). 1: POLYHEDRAL; 2: MESOPHYLL PALISADE and MESOPHYLL SPONGY; 3: STOMATA SIMPLE; 4: STOMATA CILIATE; 5: JIGSAW; 6: HAIR CELL BASE; 7: ACUTE BULBOSUS NODULAR; 8: ACUTE BULBOSUS PSILATE; 9, 10: IRREGULAR BODY; 11: SPHEROID PSILATE; 12: SPHEROID ORNATE; 13: SPHEROID LOBATE; 14: SPHEROID ECHINATE; 15, 16: SPHEROID NODULAR; 17: ELONGATE PSILATE; 18: ELONGATE BULBOSUS; 19: ELONGATE CURVED; 20: SCLEREID PSILATE; 21: FIBRE; 22, 23, 24: SCLEREID PITTED; 25, 26: TRACHEARY ANNULATE TERMINAL; 27, 28: TRACHEARY PITTED TERMINAL; 30: TRACHEARY ANNULATE LINEAR; 29, 31: Intact silicified sheets of VASCULAR ELEMENTS and SCLERENCHYMA, including TRACHEARY ANNULATE TERMINAL, TRACHEARY ANNULATE LINEAR, TRACHEARY PITTED TERMINAL, and SCLEREID PITTED morphotypes.

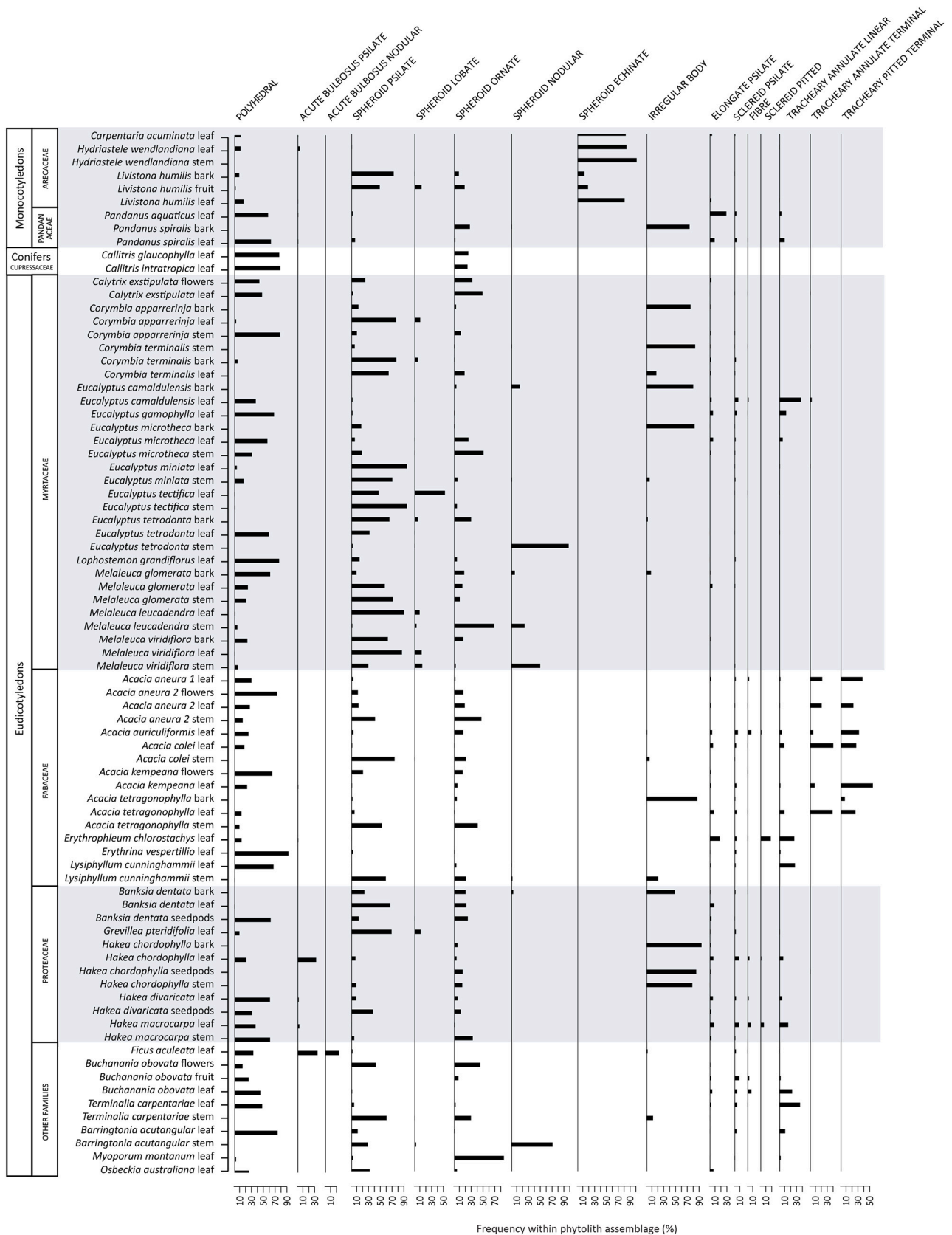


Fig. 2. Frequency (%) of phytolith morphotypes for 79 samples from 40 tree and shrub species from the Northern Territory, Australia.

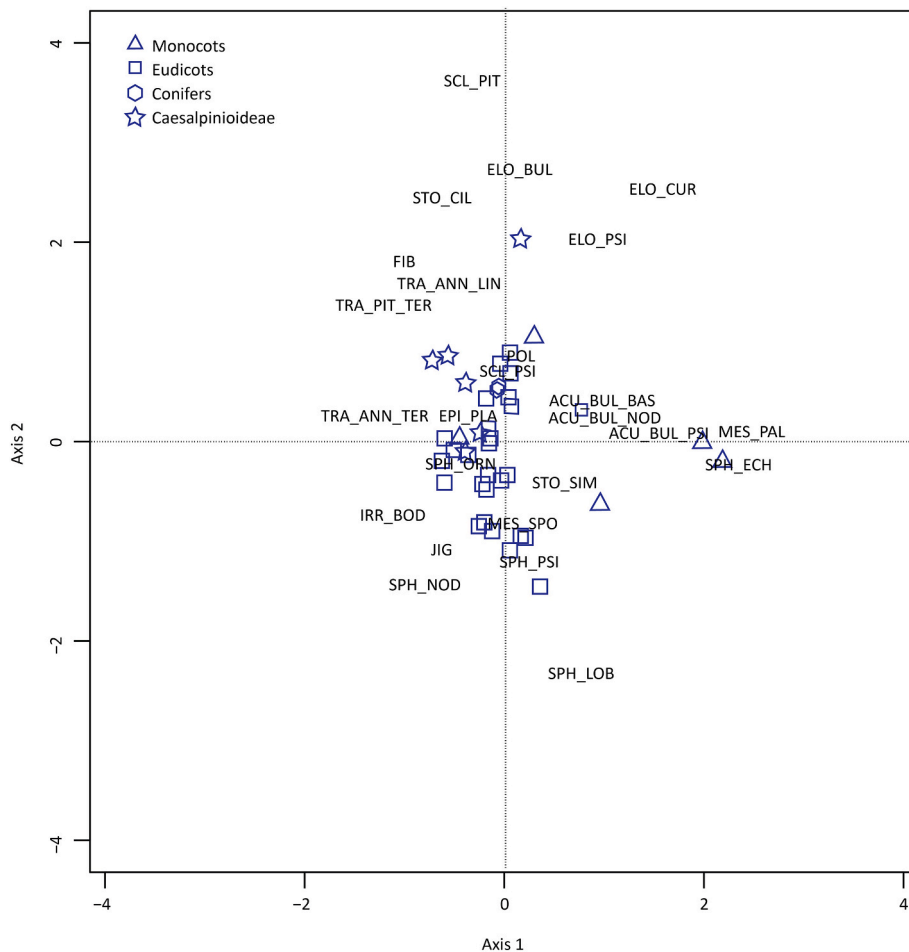


Fig. 3. Detrended correspondence analysis (DCA) of 40 woody plant species and 25 phytolith morphotypes, axis 1 and 2.

up 15.6–25.7% of the semi-arid plots, except for one semi-arid shrubland sample. Semi-arid open woodland sediments are dominated by a combination of SPHEROID PSILATE and POLYHEDRAL morphotypes, with higher frequencies of ACUTE BULBOSUS PSILATE and VASCULAR ELEMENTS. Semi-arid shrubland sediments are similarly dominated by SPHEROID PSILATE and SPHEROID ORNATE and feature higher frequencies of EPIDERMAL PLATE and STOMATA SIMPLE phytoliths.

Representation of woody plant phytolith morphotypes differed between plant and sediment assemblages (Fig. 5). Some morphotypes were found in similar frequencies in both contexts, including SPHEROID PSILATE and SPHEROID ORNATE, SCLEREID PSILATE and FIBRE. EPIDERMAL morphotypes, including POLYHEDRAL, STOMATA SIMPLE, and EPIDERMAL PLATE, were generally poorly represented in sediment assemblages, apart from the semi-arid shrubland sediments. SPHEROID ECHINATE, SPHEROID NODULAR, TRACHEARY ANNULATE TERMINAL, and TRACHEARY PITTED TERMINAL morphotypes were poorly represented in sediment assemblages relative to their abundance in palms, woody material, and *Acacia* species respectively. Contrastingly, ACUTE BULBOSUS PSILATE and ELONGATE PSILATE phytoliths were highly represented in sediment assemblages relative to their frequency in woody plants.

5. Discussion

Tree and shrub phytolith morphotypes display a high degree of redundancy within the dataset (Fig. 2). Most morphotypes observed are broadly associated with arboreal vegetation, including SPHEROID, POLYHEDRAL, and SCLERENCHYMA morphotypes (An and Xie, 2022; Piperno, 2006). Some morphotypes show patterns of taxonomic or

anatomical affiliations within the dataset, which are discussed in Section 5.2 (Table 3; Fig. 2).

5.1. Redundant phytolith morphotypes in woody plants

The most common phytolith morphotypes observed were SPHEROID PSILATE and SPHEROID ORNATE (Table 3; Fig. 2; Plate I: 11–12). These morphotypes were found in all species examined and display no taxonomic or anatomical associations (Fig. 2; Fig. 3). This widespread production aligns with patterns of abundant SPHEROID phytoliths among trees and shrubs across south America, Africa, and east Asia (Collura and Neumann, 2017; Gao et al., 2018; Liu et al., 2021; de Oliveira et al., 2024). SPHEROID PSILATE and/or SPHEROID ORNATE are globally used as broad indicators of arboreal vegetation (Bremond et al., 2005; ICPT, 2019; Madella et al., 2005). The widespread production of these morphotypes in woody plants from northern Australia supports their use as arboreal indicators in this region.

POLYHEDRAL morphotypes were abundantly produced across most plant families and tissues and do not show any taxonomic associations (Fig. 2; Fig. 3; Plate I: 1). This aligns with global patterns, as POLYHEDRAL morphotypes have been observed among monocots, eudicots, gymnosperms, and ferns in south America, southern Africa, and east Asia (de Oliveira et al., 2024; Esteban et al., 2017; Gao et al., 2018; Novello et al., 2018). Comparatively, JIGSAW morphotypes were observed in only two species of woody eudicots (Table 3; Fig. 2; Plate I: 5). Although this morphotype has been observed in many woody eudicot and fern species across the Asia-Pacific region (Kondo et al., 1994; Lentfer, 2003; Ge et al., 2020; Wallis, 2003), the specificity of JIGSAW is unclear. Most EPIDERMAL morphotypes (including POLYHEDRAL and

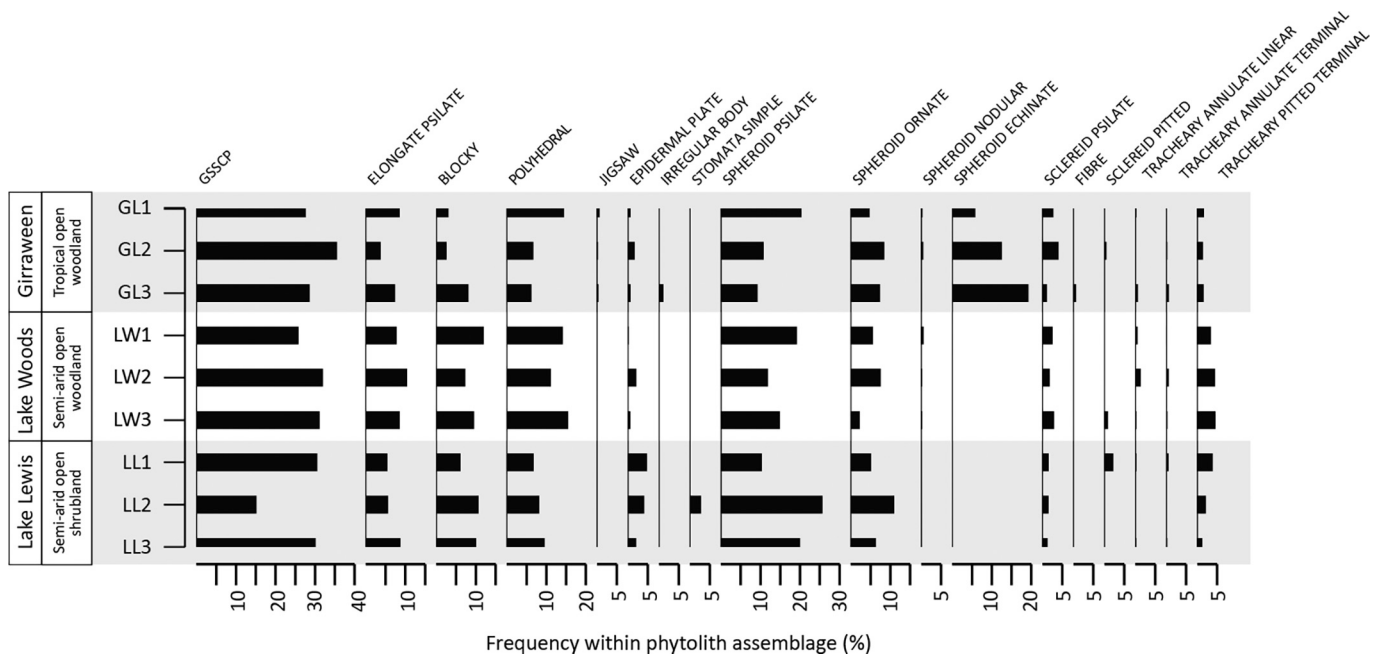


Fig. 4. Frequency (%) of phytolith morphotypes extracted from nine surface sediment samples across the three bioclimatic zones of the Northern Territory, Australia.

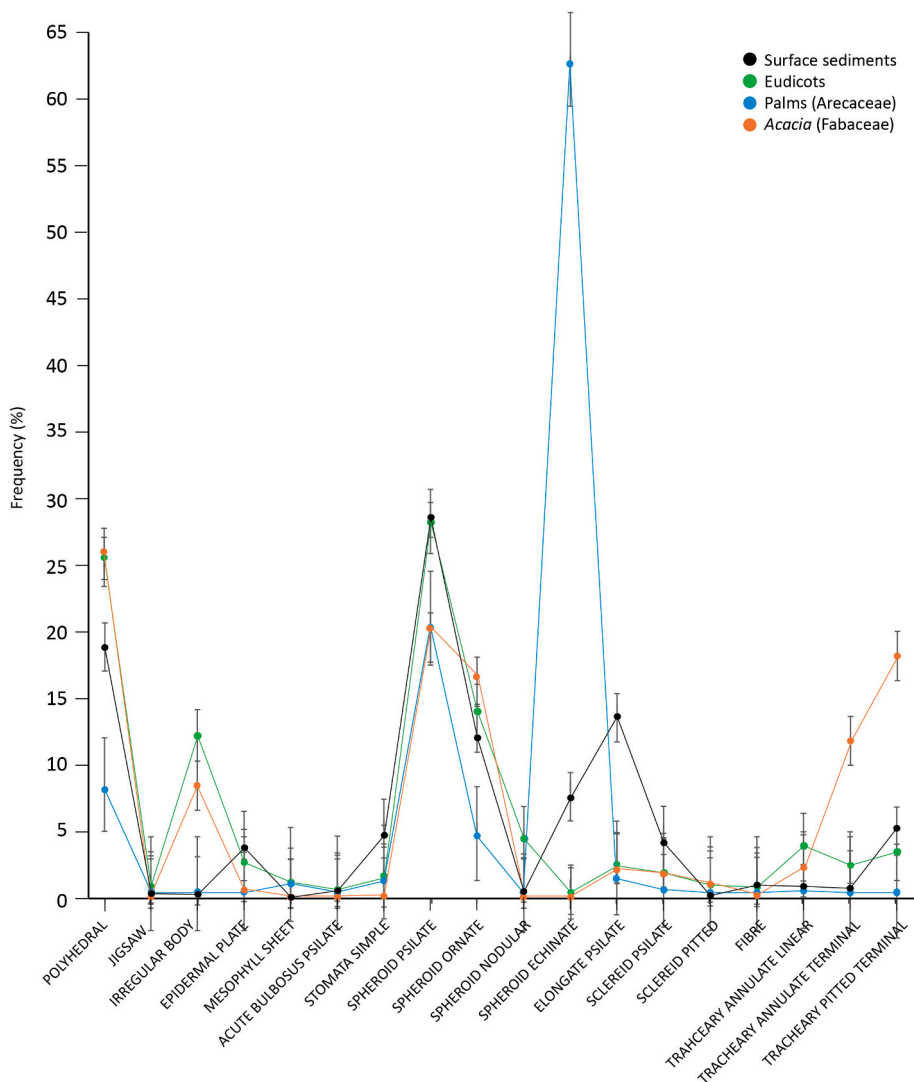


Fig. 5. Average frequency of woody plant phytolith morphotypes in woody plant species and surface sediment assemblages from the Northern Territory, Australia.

JIGSAW) are generally poorly silicified and do not preserve well in sediments (An and Xie, 2022). Because of this, POLYHEDRAL and JIGSAW are not generally used as indicators of any specific vegetation (An and Xie, 2022; Piperno, 2006) and are not useful indicators of woody plants in northern Australia.

SCLERENCHYMA morphotypes were found in most woody eudicot species and were absent or rare in conifers and monocots (Table 3; Fig. 2; Plate I: 20, 21). While SCLEREID PSILATE and FIBRE phytoliths were widely observed in the leaves, fruit, bark, and seeds of woody eudicots in this study, they were not found in conifers and monocots (Fig. 2). There is a broad association of SCLEREID and FIBRE morphotypes with woody eudicots in this study (Fig. 2; Fig. 3) although SCLEREID PITTED morphotypes appear to have a more restricted distribution (See Section 5.2). SCLEREID PSILATE and FIBRE morphotypes are increasingly used as indicators of woody eudicots in Africa, south America, and east Asia (Collura and Neumann, 2017; ICPT, 2019; Ge et al., 2020; Piperno and McMichael, 2020, 2023) and their use as indicators in northern Australia is supported by these results.

TRACHEARY ANNULATE LINEAR morphotypes were observed in many woody eudicots and monocots, usually in low frequencies (Table 3; Fig. 2; Plate I: 30). VASCULAR ELEMENT phytoliths of varying morphology have been observed in many plant families worldwide and are often considered to have low taxonomic relevance. TRACHEARY ANNULATE LINEAR morphotypes show little taxonomic affiliation in this study (Fig. 2; Fig. 3), although TRACHEARY ANNULATE TERMINAL and TRACHEARY PITTED TERMINAL morphotypes may have relevance for taxonomic discrimination among woody eudicots (see Section 5.2) (Collura and Neumann, 2017; Stromberg, 2003; Wallis, 2003). TRACHEARY ANNULATE LINEAR morphotypes do not appear to represent any specific vegetation type in northern Australia, highlighting the importance of detailed morphological systems for woody plant phytoliths.

HAIR CELL morphotypes were commonly observed in the leaves of woody eudicots and palms but were not observed in conifers or other monocots (Table 3; Fig. 2; Plate I: 6–8). ACUTE BULBOSUS PSILATE phytoliths are traditionally associated with grasses (ICPT, 2019) but many studies have noted their abundance in woody plants across the Asia-Pacific region (Kealhofer and Piperno, 1998; Kondo et al., 1994; Lentfer, 2003; Wallis, 2003). The abundant production of ACUTE BULBOSUS PSILATE by woody plants in this study (Fig. 2) confirms that they are not useful indicators of any specific vegetation type in northern Australia.

ELONGATE phytoliths were also widely produced in the leaves of woody eudicots and monocots (Table 3; Fig. 2; Plate I: 17–19). Although ELONGATE morphotypes are commonly associated with grasses, some subtypes (particularly ELONGATE PSILATE) have been observed in woody eudicots (Collura and Neumann, 2017; de Oliveira et al., 2024; Gao et al., 2018; Ge et al., 2020; Liu et al., 2021). Subtypes diagnostic of grass inflorescences (e.g., ELONGATE DENDRITIC) were not observed in woody plant samples (ICPT, 2019). ELONGATE morphotypes observed in woody eudicots have low taxonomic significance, although recent studies suggest that detailed classification may improve taxonomic discrimination in some regions (Piperno and McMichael, 2020, 2023). ELONGATE morphotypes are thus not useful indicators of any specific vegetation type in northern Australia.

5.2. Specific phytolith morphotypes in woody plants

SPHEROID NODULAR and IRREGULAR BODY phytoliths were only commonly observed in wood and bark samples from woody eudicots (Table 3; Fig. 2; Plate I: 9–10, 15–16). The abundance of SPHEROID and IRREGULAR BODY morphotypes within wood and bark tissues is well described globally (Collura and Neumann, 2017; Liu et al., 2021; Piperno and McMichael, 2020, 2023). Such morphologies are usually included within the description of SPHEROID ORNATE (Collura and Neumann, 2017; ICPT, 2019), but some studies differentiate a distinct,

nodular surface texture and/or large, irregular shape in morphotypes from wood and bark (Piperno and McMichael, 2020, 2023). The abundant production of SPHEROID NODULAR and IRREGULAR BODY morphotypes in wood and bark samples suggests that these are useful indicators of woody eudicots in northern Australia.

The production of SPHEROID ECHINATE morphotypes was limited to the Arecaceae (palm) family, in which these phytoliths were abundant (Table 3; Fig. 2; Plate I: 14). SPHEROID ECHINATE phytoliths are widely accepted as global indicators of the palm family (An and Xie, 2022; Alexandre et al., 1997; Piperno, 2006). SPHEROID ECHINATE morphotypes are useful indicators of palms in northern Australia, where they are abundant in tropical savanna communities (Williams et al., 2017). However, some palm lineages in Australia occupy arid or temperate niches; in particular, the origin of *Livistona mariae* in arid central Australia has long been debated (Crisp et al., 2010; Kondo et al., 2012). The application of morphological and morphometric discrimination techniques (e.g., Bowdery, 2015; Brightly et al., 2024; Fenwick et al., 2011) to palm phytoliths may improve taxonomic discrimination and provide insights into palaeoecological topics in Australia.

ACUTE BULBOSUS NODULAR morphotypes were observed only in *Ficus aculeata* (Moraceae) (Table 3; Fig. 2; Plate I: 7). ACUTE BULBOSUS NODULAR phytoliths were previously observed in *Ficus* and *Malaisia* species (Moraceae) and *Trema* species (Cannabaceae, previously Ulmaceae) in northwestern Australia (Wallis, 2003). The Moraceae, Ulmaceae, and Cannabaceae families are known abundant producers of HAIR CELL morphotypes (Collura and Neumann, 2017; Kealhofer and Piperno, 1998). Thus, ACUTE BULBOSUS NODULAR morphotypes are not specific to the Moraceae family but may still be useful for taxonomic discrimination of woody plants. Further examination of reference material from Moraceae, Ulmaceae, and Cannabaceae species is needed to clarify the specificity of this morphotype.

SCLEREID PITTED phytoliths were abundant in *Erythrophleum chlorostachys* (Caesalpinioideae subfamily, Fabaceae family), but also occasionally observed in other species of the Fabaceae and Proteaceae families (Table 3; Fig. 2; Plate I: 22–24). SCLEREID PITTED morphotypes have highly variable morphology, with various types described in a range of woody eudicot families (Collura and Neumann, 2017; Piperno and McMichael, 2020, 2023; Runge, 1999; Stromberg, 2003; Wallis, 2003). In particular, baculate, irregular sclereids have been identified in many *Celtis* species (Collura and Neumann, 2017; Piperno and McMichael, 2023; Wallis, 2003). There is also high morphological similarity between SCLEREID PITTED and VASCULAR ELEMENT morphotypes (Plate I: 22–24), which is widely noted in woody eudicot reference material (Dickau et al., 2013; ICPT, 2019; Runge, 1999; Stromberg, 2003; Wallis, 2003). In particular, overlapping morphologies of SCLEREID PITTED with TRACHEARY PITTED TERMINAL and TRACHEARY ANNULATE TERMINAL complicate differentiation and classification of these morphotypes (Plate I: 22–31). Systematic classifications of VASCULAR ELEMENT and SCLERENCHYMA morphology are limited (e.g., Stromberg, 2003), but are needed to improve morphological and taxonomic discrimination of woody plant phytoliths.

TRACHEARY ANNULATE TERMINAL and TRACHEARY PITTED TERMINAL phytoliths were abundant in the leaves of *Acacia* species (Caesalpinioideae subfamily, Fabaceae family) and rarely observed in other woody eudicots (Table 3; Fig. 2; Plate I: 25–31). Their morphology was variable, with irregular, enlarged shapes and surface ornamentation varying from strongly helical or pitted, to indistinct, granular textures (Plate I: 25–28). These surface textures reflect the degree of lignification of secondary cell walls; it has been suggested that the ratio of pitted to annulate surface textures should increase over time (Esau, 1965; Stromberg, 2003). These morphotypes are sometimes classified as tracheid-sclereid phytoliths due to their similar, irregular morphology (Plate I: 22–31) (Flores-Cruz et al., 2004; Stromberg, 2003; Runge, 1999). These morphologies likely reflect their origin from enlarged, irregularly shaped terminal tracheid elements (Lersten and Curtis, 1994; Luckow, 2002). TRACHEARY ANNULATE TERMINAL and TRACHEARY

PITTED TERMINAL morphotypes were frequently observed silicified within plates alongside TRACHEARY ANNULATE LINEAR and SCLERENCHYMA phytoliths, indicating a shared anatomical derivation (Plate I: 29, 31).

Production of irregular VASCULAR ELEMENT and SCLERENCHYMA phytoliths has been observed among many woody eudicot families (Collura and Neumann, 2017; Kealhofer and Piperno, 1998; Wallis, 2003). However, highly abundant production (as observed in this study) has so far only been noted in Australian *Acacia* species (Bowdery, 1998; Wallis, 2003). Irregular striate and pitted phytoliths equivalent to TRACHEARY ANNULATE TERMINAL and TRACHEARY PITTED TERMINAL have been identified from *Acacia* leaves across northwestern and central Australia (Bowdery, 1998; Wallis, 2003) but were not described in species from eastern Australia by Hart (1988). Similar morphotypes have been observed in sediments across the Asia-Pacific, north America, and Africa, which have been associated with the Caesalpinioideae (Runge, 1999; Strömberg, 2003; Wallis, 2003). Additionally, terminal tracheid features in living plants have been observed in many members of the Caesalpinioideae subfamily (Fabaceae) (Flores-Cruz et al., 2004; Lersten and Curtis, 1994; Luckow, 2002) which *Acacia* have recently been reclassified into (Azani et al., 2017). Thus, TRACHEARY ANNULATE TERMINAL and TRACHEARY PITTED TERMINAL (and possibly related SCLEREID PITTED) morphotypes could be potential indicators of *Acacia* species in northern Australia, but further studies of phytolith production and morphology in closely related species from the Caesalpinioideae subfamily are needed.

5.3. Representation of woody morphotypes in surface sediments

Most of the phytolith morphotypes observed in woody plants were also observed in the surface sediment samples, indicating that vegetation communities are at least broadly represented in sedimentary assemblages (Supplementary Material, Plate S1). Other morphotypes not present in woody plants were also observed in sediment assemblages, some of which can be attributed to grasses (e.g., GSSCP, ELONGATE SINUATE, ELONGATE DENDRITIC, FLABELLATE BULLIFORM) (Boyd et al.; ICPT, 2019) while others cannot be definitively associated with any particular vegetation type (e.g., BLOCKY). Some woody plant phytolith morphotypes were common in all sediment samples, such as SPHEROID PSILATE, SPHEROID ORNATE, and POLYHEDRAL (Fig. 4, Fig. 5). However, not all woody morphotypes are equally represented in surface sediments compared to their frequency in plant tissues (Fig. 5) suggesting environmental and post-depositional influences on assemblage formation and preservation.

Phytoliths are released into soils and surface sediments when plant matter decays, and thus their frequency within sediments is affected by biological factors such as vegetation composition, plant life cycles, and decomposition rates (Strömberg et al., 2018). Resultingly, some phytolith morphotypes are abundant within plant tissues but uncommon in sediment assemblages. The absence of ACUTE BULBOSUS NODULAR and HAIR BASE morphotypes can be attributed to a lack of producing species in the plots examined (Table 1). Poor representation of SPHEROID ECHINATE phytoliths relative to their abundance in palms reflects the composition of local communities (Fig. 5) (Williams et al., 2017). Additionally, poor representation of SPHEROID NODULAR and IRREGULAR BODY phytoliths relative to wood and bark (Fig. 4, Fig. 5) may reflect the slow decomposition of woody material, particularly from *Eucalyptus* species (Garrett et al., 2007; Mackensen et al., 2003). Comparatively, the abundance of redundant morphotypes (e.g., ELONGATE PSILATE, ACUTE BULBOSUS PSILATE) in sediments compared to woody plants is likely due to their widespread production among plant families (Fig. 4, Fig. 5) (Piperno, 2006).

Once deposited into soils and sediments, phytoliths are subject to processes of dispersal and chemical dissolution, which are influenced by sediment geochemistry (e.g., pH, organic matter, trace metals) and water content (Madella and Lancelotti, 2012; Strömberg et al., 2018).

The preservation of individual phytoliths is also highly influenced by morphology, including shape, size, surface texture, and porosity (Cabanes et al., 2011; Liu et al., 2023; Madella and Lancelotti, 2012). Phytoliths with thin, flat, porous morphologies are less resistant to chemical dissolution and may rapidly and preferentially dissolve in soils and sediments (Cabanes et al., 2011; Strömberg et al., 2018). Many woody plant morphotypes, including SPHEROID PSILATE and SPHEROID ORNATE, are represented in similar frequencies between plant and surface sediment assemblages, suggesting they preserve well in sediments (Fig. 5). However many thin, poorly silicified morphotypes are poorly represented in sediment assemblages, including POLYHEDRAL, MESOPHYLL PALISADE, AND MESOPHYLL SPONGY (Fig. 5). Comparatively, EPIDERMAL PLATE and STOMATA SIMPLE were highly represented in semi-arid grassland sediments despite their thin, flat morphologies, which may indicate good preservation of phytolith assemblages in these plots (Fig. 5) (Cabanes et al., 2011; Strömberg et al., 2018).

Despite their abundance in the leaves of *Acacia* species, TRACHEARY ANNULATE TERMINAL and TRACHEARY PITTED TERMINAL morphotypes were uncommon in all sediment samples examined (Fig. 5). TRACHEARY ANNULATE LINEAR phytoliths were also poorly represented (Fig. 5). TRACHEARY ANNULATE and PITTED TERMINAL morphotypes were recovered in the highest frequencies (up to 5.2%) in the semi-arid open woodland sediments, which were collected under juvenile *Acacia* communities (Table 2; Fig. 4). Comparatively, open woodland and semi-arid shrubland sediments without *Acacia* species contained very low frequencies of these morphotypes (1.6–2.2%) (Table 2; Fig. 4). The poor representation of these morphotypes in surface sediments does not reflect the dominance of *Acacia* within the semi-arid landscapes of northern Australia (Groves, 1994; Williams et al., 2017). Previous investigations only rarely (<1%) recovered these morphotypes in surface sediments of northwestern Australia (Fullagar and Wallis, 2012; Wallis, 2013), suggesting these phytoliths may not preserve well in sediments. Further investigation of surface sediment phytolith assemblages underlying *Acacia* communities is needed to better understand the preservation of these morphotypes.

5.4. Taxonomic and palaeoecological relevance of woody plant phytoliths

Phytolith morphotypes from woody plants of northern Australia do not reflect the taxonomic and ecological diversity of the species examined. While some woody plant families produce abundant and specific phytolith morphotypes that align with regional and/or global reference material (see Section 5.2), most families examined did not produce diagnostic morphotypes (Table 1; Fig. 2). Species examined from the Pandanaceae, Cupressaceae, Myrtaceae, Proteaceae, Anacardiaceae, Combretaceae, Lecythidaceae, Scrophulariaceae, and Melastomataceae families produced abundant but redundant phytolith morphotypes, which aligns with global production patterns of these families (Collura and Neumann, 2017; Esteban et al., 2017; Gao et al., 2018; Liu et al., 2021; Piperno, 2006; Piperno and McMichael, 2023; Wallis, 2003; Watling and Iriarte, 2013; Watling et al., 2020). Notably, although specific PAPILLATE morphotypes have been described in some members of the Proteaceae in southern Africa (Esteban et al., 2017; Novello et al., 2018) and eastern Australia (Hart, 1990), these morphotypes were not observed in Proteaceae species from northern Australia in this study.

The production of identifiable phytoliths in all woody plant species, and the recovery of most morphotypes from surface sediments, indicates that broad signals of woody plant communities are preserved in sedimentary phytolith assemblages. Although modern phytolith assemblages may not reflect tree community composition to the same extent as other proxies such as fossil pollen records (Forbes et al., 2021; Mariani et al., 2022), this modern reference material indicates that phytoliths may at least be used for reconstruction of grass-tree ratios through time, as well as the identification of some key taxa (Bremond et al., 2005) in northern Australia. Such broad reconstruction of arboreal taxa using

SPHEROID PSILATE and SPHEROID ORNATE, and palms with SPHEROID ECHINATE, morphotypes is well documented globally (Alexandre et al., 1997; Fenwick et al., 2011; ICPT, 2019; Piperno, 2006). These morphotypes are well represented in surface sediment assemblages in this study (Fig. 5) supporting their use for palaeoecological reconstruction in the study region. This represents a significant advancement in the ability to reconstruct late Quaternary vegetation change in northern Australia, particularly in the arid interior where conditions for preservation of organic matter are unfavourable (Horowitz, 1992; Petheram et al., 2008).

The production of abundant TRACHEARY ANNULATE TERMINAL and TRACHEARY PITTED TERMINAL in *Acacia* species from northern Australia is promising for taxonomic discrimination of woody eudicots. The poor recovery of these morphotypes in surface sediments (Fig. 5) is similar to *Acacia* pollen, which is highly under-represented in fossil pollen assemblages but still used as a palaeoecological indicator (Dodson, 1983; Mariani et al., 2022). Thus, these morphotypes may still be useful indicators of *Acacia* (or Caesalpinioideae) communities in northern Australia, particularly in semi-arid to arid landscapes where they are a dominant arboreal species. These issues of differential production and preservation of phytolith morphotypes (Fig. 4) are similar to those which affect fossil pollen reconstructions, and may be mitigated with the development of regional surface sediment phytolith datasets and corresponding indices (e.g., Aleman et al., 2012; Alexandre et al., 1997; Bremond et al., 2005).

6. Conclusions

Phytolith morphology among woody plant species from northern Australia aligns with global patterns. Although a wide range of phytolith morphologies were observed in woody plant tissues, most morphotypes are redundant. Morphotypes representative of general woody eudicots (SPHEROID PSILATE, SPHEROID ORNATE, SCLERENCHYMA) were identified, as well as specific morphotypes in palms (SPHEROID ECHINATE). Additionally, some potentially specific indicators of woody material (SPHEROID NODULAR, IRREGULAR BODY), Moraceae and related families (ACUTE BULBOSUS NODULAR) and *Acacia* species (TRACHEARY ANNULATE TERMINAL, TRACHEARY PITTED TERMINAL) were identified, but further investigation is needed. Comparison of phytolith morphotypes from woody plants and surface sediments reveals patterns of differential production and preservation but suggests that most woody plant phytolith morphotypes are well represented in surface sediments. Although the taxonomic resolution of most woody plant phytoliths is limited to a broad arboreal signal, phytoliths are a useful proxy for reconstructing past vegetation structure and composition in northern Australia.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2024.105158>.

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