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Terrestrial surface stabilisation by modern analogues of the earliest land plants: A multi-dimensional imaging study

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Abstract

The evolution of the first plant-based terrestrial ecosystems in the early Palaeozoic had a profound effect on the development of soils, the architecture of sedimentary systems, and shifts in global biogeochemical cycles. In part, this was due to the evolution of complex below-ground (root-like) anchorage systems in plants, which expanded and promoted plant–mineral interactions, weathering, and resulting surface sediment stabilisation. However, little is understood about how these micro-scale processes occurred, because of a lack of in situ plant fossils in sedimentary rocks/palaeosols that exhibit these interactions. Some modern plants (e.g., liverworts, mosses, lycophytes) share key features with the earliest land plants; these include uni- or multicellular rhizoid-like anchorage systems or simple roots, and the ability to develop below-ground networks through prostrate axes, and intimate associations with fungi, making them suitable analogues. Here, we investigated cryptogamic ground covers in Iceland and New Zealand to better understand these interactions, and how they initiate the sediment stabilisation process. We employed multi-dimensional and multi-scale imaging, including scanning electron microscopy (SEM) and X-ray Computed Tomography (μCT) of non-vascular liverworts (Haplomitriopsida and complex thalloids) and mosses, with additional imaging of vascular lycopods. We find that plants interact with their substrate in multiple ways, including: (1) through the development of extensive surface coverings as mats; (2) entrapment of sediment grains within and between networks of rhizoids; (3) grain entwining and adherence by rhizoids, through mucilage secretions, biofilm-like envelopment of thalli on surface grains; and (4) through grain entrapment within upright 'leafy' structures. Significantly, μCT imaging allows us to ascertain that rhizoids are the main method for entrapment and stabilisation of soil grains in the thalloid liverworts. This information provides us with details of how the earliest land plants may have significantly influenced early Palaeozoic sedimentary system architectures, promoted in situ weathering and proto-soil development, and how these interactions diversified over time with the evolution of new plant organ systems. Further, this study highlights the importance of cryptogamic organisms in the early stages of sediment stabilisation and soil formation today.

1 | INTRODUCTION

When the earliest plants (embryophytes) evolved on land in the early Palaeozoic, probably sometime between ~500 and 480 million years ago (Morris et al., 2018; Puttick et al., 2018; Strother & Foster, 2021), they are thought to have had an influential effect on the stabilisation of sediment surfaces. This terrestrial vegetation not only led to a shift in the architecture of sedimentary (fluvial) systems (Gibling & Davies, 2012; Gibling et al., 2014; Ielpi et al., 2022) but also promoted in situ biologically mediated weathering (Mitchell et al., 2019), proto-soil development (Mitchell et al., 2021a), and increased muddy sediments in continental settings (Bruckner et al., 2021; McMahon & Davies, 2018). Larger scale shifts in global biogeochemical cycles (Elbert et al., 2012; Mills et al., 2018; Porada et al., 2014), and drawdown of atmospheric CO_2 (Berner, 1998; Lenton et al., 2012; Lenton & Daines, 2017) are also thought to be the result of expanding terrestrial biospheres.

The earliest land plants were non-vascular and small statured (Edwards et al., 2021a; Kenrick & Strullu-Derrien, 2014; Strullu-Derrien et al., 2018), and progressively evolved to more extensive coverings as trees and forests by the middle Devonian (~385 Ma; Stein et al., 2020). The pre-vascular and earliest plant-based biotas are mostly comparable to modern cryptogamic ground covers (CGCs) (Kenrick et al., 2012; Mitchell et al., 2016, 2021a), which are variable communities composed of bryophytes (liverworts, hornworts, mosses), lichens, algae, fungi, and bacteria. Although uncertainties remain on how evolutionary ancient some of these lineages are, some, e.g., the liverworts have a lengthy fossil record (Hernick et al., 2008) and the relevance of modern bryophytes has been supported by recent phylogenetic and molecular clock analyses (de Sousa et al., 2019; Harris et al., 2020; Leebens-Mack et al., 2019; Morris et al., 2018; Puttick et al., 2018) (Figure 1). Crucially, modern liverworts (and hornworts) share morphological features with the early land plants, as evidenced from fossils in the exceptionally preserved 407 Ma Rhynie chert; these features include unicellular rhizoids (Duckett et al., 2014; Jones & Dolan, 2012; Kenrick & Strullu-Derrien, 2014) and symbiotic associations with microbes (Figure 1b). Specifically, some Rhynie chert plants and many modern liverworts and hornworts form mutualistic symbiotic associations with soil fungi (Desiro et al., 2013; Duckett et al., 2006; Field et al., 2015; Humphreys et al., 2010; Rimington et al., 2018; Strullu-Derrien et al., 2014, 2018). Cyanobacterial endophytes are ubiquitous in hornworts while in liverworts they are restricted to the Blasiales (Adams & Duggan, 2008), however they are extremely rare in the Rhynie chert (Strullu-Derrien, 2018). While early land plants (cryptophytes; Edwards et al., 2015, 2021a) were mostly axial/erect, leafless, and rhizomatous (Edwards et al., 2014; Strullu-Derrien et al., 2018), there are some fossilised remains suggestive of thalloid

plants from the Silurian and Early Devonian (Edwards et al., 2021a; Tomescu & Rothwell, 2006). Moreover, both early- (*Blasia* and *Lunularia*, Galloway et al., 2017) and later diverging (*Marchantia*, Crandall-Stotler et al., 2009) genera secrete the polysaccharide xyloglucan from their rhizoids. Xyloglucan released from plant rhizoids and roots has been shown to be an effective soil particle aggregator and, given its occurrence in extant liverworts, it has been suggested that xyloglucan released from the rhizoids/rhizoid-like structures of the earliest land plants may have had a similar role, aiding the formation of primeval soils (Galloway et al., 2017). Consequently, the exudates and anchorage structures of modern bryophytes make them highly suitable analogues for understanding how early land plants contributed to the stabilisation of sedimentary surfaces at the scale of micrometres to centimetres.

We investigated CGCs growing on loose regolith sediments in a variety of settings from Iceland and New Zealand. We applied 2D and 3D imaging through scanning electron microscopy (SEM) and X-ray computed tomography (μCT), respectively, to determine how sediment grains become stabilised by CGC organisms. By understanding these processes in modern CGC plants, our aim was to infer how the earliest embryophytes stabilised loose surface sediments, leading to promotion of plant–mineral interactions, in situ weathering, proto-soil development, and the likely impact on the architecture (and mudrock content) of fluvial sedimentary systems in deep time.

2 | MATERIALS AND METHODS

2.1 | Fieldwork, organisms, and biological sample preparation

CGC proto-soils were collected in various forms (as cores, clumps, and sections) from various sites in Iceland and New Zealand, including glacial moraine, volcaniclastic regolith, and lava flows (see Table S1 for further information). Cores measuring 25×80 mm at their largest were extracted using a cork borer and placed in plastic vials, and clumps were collected at random to obtain larger soil surface areas. Plants were fixed with 10% formalin, which was added for preservation and to prevent desiccation. The liverworts studied include *Treubia lacunosa*, *Haplomitrium gibbsiae*, and *Lunularia cruciata* from New Zealand, and *Blasia pusilla* from Iceland. Mosses studied include *Polytrichum alpinium* and *Racomitrium lanuginosum*, both from Iceland. We also collected some *Lycopodium* specimens from Iceland. Sites were selected based on (a) the presence of early diverging land plants (Figure 1), and (b) substrate, including loose volcaniclastic regolith which represents virgin 'primeval' terrains, being devoid of vascular plants, and whose formation can be accurately
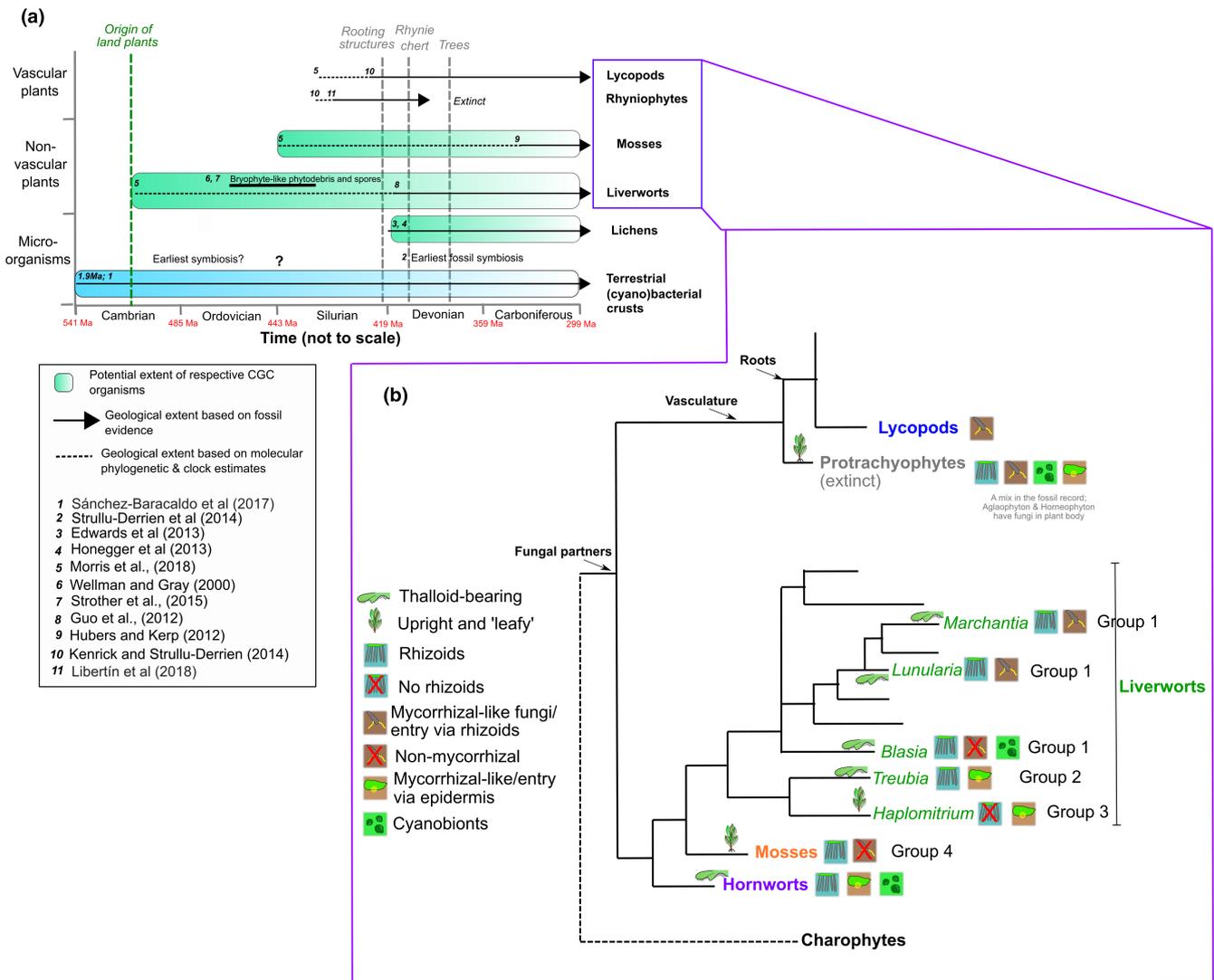
FIGURE 1 (a) Summary chart highlighting the evolution of different CGC elements from contrasting molecular, phylogenetic and fossil dating methods. (b) Schematic land plant phylogeny of modern terrestrial organisms, focussing on the bryophytes (and specific liverwort genera) studied in this work. Key features (and lack of features) summarised graphically in different plant groups and liverwort genera. Groups correspond to different groups, based on morphology and other features, that are assigned in this work. (a) adapted from Mitchell et al., 2021a, (b) adapted from Field & Pressel, 2018.

dated from geologically recent effusive eruptions. Sample preparation and analyses were carried out in the Imaging and Analysis Centre (IAC) at The Natural History Museum, London (UK).

Some cores and soil clumps were imaged as they were collected, but in some cases plants were removed to enable clearer imaging of their ventral surface using scanning electron microscopy (SEM). The removed plants were put through an alcohol series and critically point dried. Critical point drying (CPD) dehydrates biological tissue and replaces the water with liquid CO_2. When the temperature is raised above 35°C, the liquid CO_2 becomes vapour, keeping the biological morphology and ultrastructure intact. This allows biological tissues to be studied in an SEM (or other imaging instrumentation under vacuum) without desiccation and collapse, which would likely occur with simple air drying. The plant is first put through an alcohol (ethanol) series of varying concentration percentages (between 30%

and 100%) to gradually remove water from the plant. Following this, the plant is placed inside the critical point dryer; ethanol is added to the chamber, followed by liquid CO_2, and after 30s the mixture is vented from the chamber. This cycle is repeated six times. Lastly, the sample is heated to 39°C and the pressure set to the critical point of 75 BAR. Following this, the sample may be removed.

2.2 | Scanning electron microscopy (SEM)

Plant specimens were affixed to carbon sticky pads and mounted upside down (with ventral surface facing upwards) on standard stubs for SEM imaging, without coating, using a FEI Quanta 650 FEG SEM and a Zeiss Leo 1455 variable pressure SEM. Variable conditions were used depending on the sample in both secondary electron (SE)

and backscatter detector (BSD) modes. Low pressure BSD mode (on the Leo) was used for those samples that had not been critically point dried, and high pressure SE mode (on the Quanta) was used for those specimens that had been critically point dried (see Table S2 for further information relating to specific imaging configuration on both instruments). We also studied thin sections, which were prepared via a standard method of vacuum impregnation and cut to ~30 μm thickness. Thin sections were fixed to sample holders with copper tape to prevent charging, were without cover slips, and were uncoated.

2.3 | X-ray computed tomography (μCT)

μCT was employed to visualise the 2D and 3D structure of proto-soil cores, clumps and plants non-destructively using a Nikon Metrology HMX ST 225 μCT scanner with a tungsten reflection target. Variable scanning conditions were used for each sample (summarised in Table S2). Voxel (3D pixel) sizes ranged between 15 and 38 μm. A copper filter was sometimes used to pre-harden the beam and remove unwanted lower energy X-rays. Other parameters, including the number of projections collected (3142), the μA (180), the exposure time (708 ms), and the frames per projection (1), were consistent for all scans. Average scan time was ~35 min. Scans were reconstructed into 3D tomographic datasets as .tiff stacks using CT Pro

Software (Nikon Metrology) and were rendered using Drishti v2.5 (Limaye, 2012) and ORS Dragonfly software to reveal 3D and 2D (X, Y, Z axes) views (see Table S2). In some cases, liverwort thalli were digitally segmented, 3D thickness surface meshes were applied, and imaging analysis was undertaken using ORS Dragonfly software v 2020.1. No staining agents (e.g., iodine) were used, and the fixation of soil and plant material with 10% formalin, together with short scan times, aided in prevention of plant desiccation (and movement) during scanning.

3 | RESULTS

3.1 | Methods of stabilisation

Our results show that there are many macro-to-nanoscale (cm–μm) ways in which cryptogamic plants interact with sediment/soil surfaces leading to stabilisation, and that this varies depending on the morphology and features associated with the different plants; these are summarised in Table 1. We have divided our observations into numerous groups based on the morphology and relevant features of the different organisms; this includes plants bearing a thallus, rhizoids, and which secrete xyloglucan (from their rhizoids exemplified here by the liverworts *Lunularia* and *Blasia*; group 1); plants

TABLE 1 Summary of the stabilisation methods observed in different cryptogamic organisms

Stabilisation method	Plants and organisms studied					
	Treubia lacunosa	*Haplomitrium gibbsiae*	*Lunularia cruciata*	*Blasia pusilla*	*Foliose lichens*	*Racomitrium, Polytrichum*
Appressed surface ground covers	🔵	N/A – upright growth	🔵	🔵	🔵	N/A – upright growth
Upright surface ground covers	N/A – Thallus bearing	🔵	N/A – Thallus bearing	N/A – Thallus bearing	🔵	🔵
Rhizoid entrapment	🔵	N/A – No rhizoids	🔵	🔵	N/A – No rhizoids	🔵
Rhizoid adhering/static	🔵	N/A – No rhizoids	🔵	🔵	N/A – No rhizoids	🔵
Mucilage/secretion Sticking to plant	🔵	🔵	🟡	🔵	🔵	🟡
Sticking/lodged in cells	🔵	🔵	🟡	🟡	🟡	🟡
Trapped in upright 'leafy' structure	Not leafy	🔵	Not leafy	Not leafy	Not leafy	🔵

Note: Blue circles represent features observed in this study, orange circle represent features not observed directly in this study but known to be present from the literature.

bearing a thallus, rhizoids, and which secrete other mucilage (directly from the thallus exemplified here in the liverwort *Treubia*; group 2); plants with erect habit, lacking rhizoids, and bearing a subterranean axes, with mucilage secretion (from the subterranean axes exemplified here in the liverwort *Haplomitrium*; group 3); and plants with an erect habit and bearing multicellular rhizoids (exemplified here by the mosses *Polytrichum* and *Racomitrium*; group 4).

3.1.1 | Group 1: plants bearing a thallus, rhizoids, and which secrete xyloglucan from their rhizoids (e.g., *Lunularia*, *Blasia*)

CGCs dominated by thalloid organisms (i.e., liverworts) form closely packed surface coverings (Figure 2a), but these are generally localised only forming patches of up to 1 m². Thalloid liverworts do not share the upright growing habit of other CGC plants such as mosses; they are by and large appressed to the ground surface and envelop sediment surfaces as dense mats (Figure 2a,b). The appressed nature of the liverworts thalli allows them to grow over each other, forming an extra layer of surface protection and stabilisation, while their unicellular rhizoids penetrate the substrate surface (e.g., Figure 2b). A closer examination of *Lunularia* in 2D reveals finer grained minerals trapped within rhizoid networks directly beneath the thalli and grains adhering directly to rhizoids (Figure 2c). Similar rhizoid stabilisation processes were observed in the other thalloid liverwort, *Blasia*, where minerals are held in place along the thalli midrib (Figure 2d), presumably mostly by rhizoids adhering to and entwining grains (Figures 2e,f), and possibly also by other adhesive mechanisms such as xyloglucan secretions (e.g., Figure 2d). Other microbes (potentially
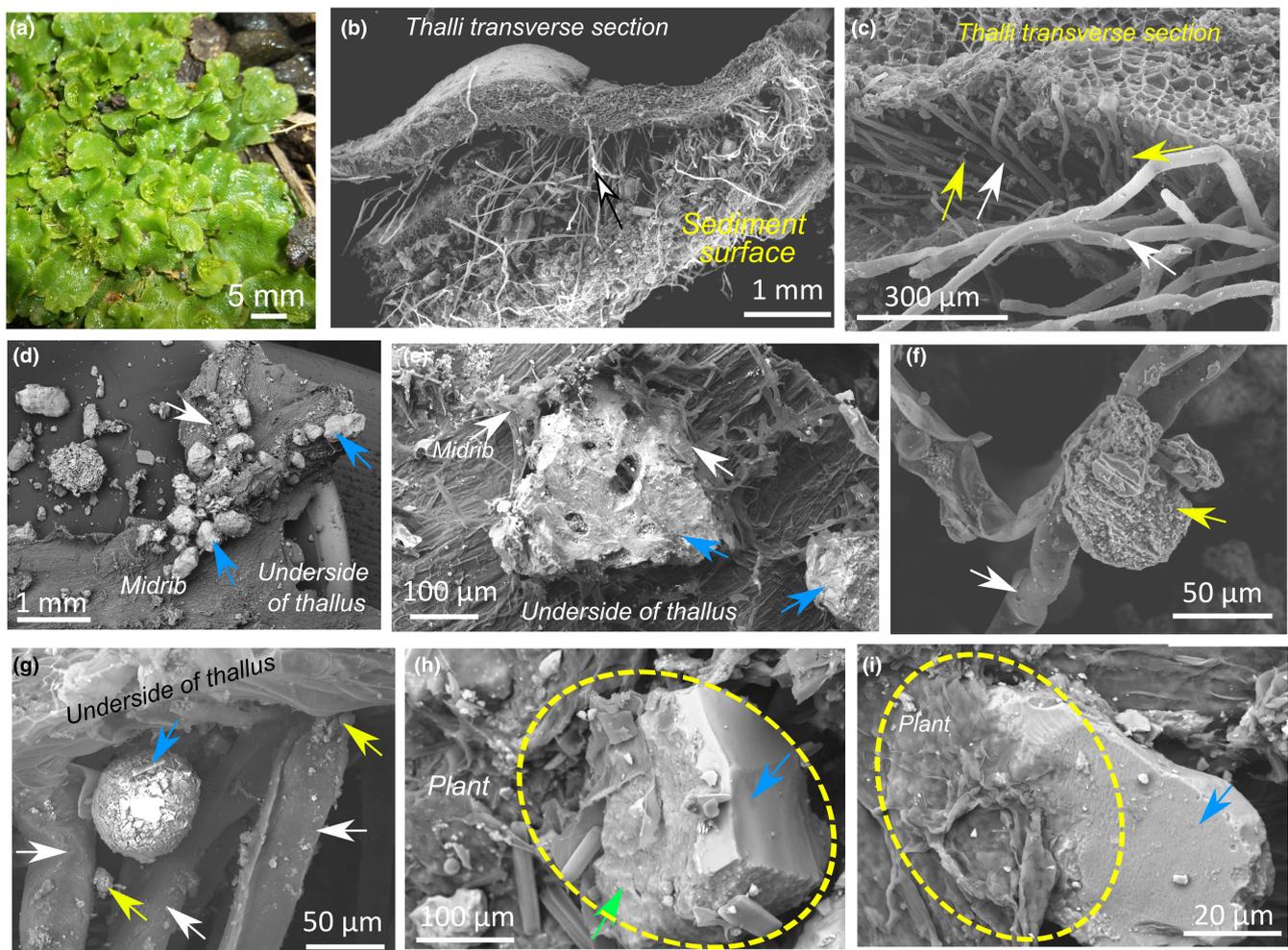

FIGURE 2 Field image (a) and scanning electron micrographs (b–i) showing substrate interactions in liverworts bearing a thallus, rhizoids, and secreting xyloglucan; (group 1) *Lunularia* (a–c), and *Blasia* (d–i). (a) Field image of overlapping thalli forming encrusting mats over the sediment surface. (b) Transverse section of a thallus showing mass of rhizoids extending into the sediment/soil surface. (c) Soil material trapped within rhizoids directly beneath the thallus; examples of pegged rhizoids (upper; directly beneath the thalli) and smooth rhizoids (lower, larger rhizoids). (d) Soil/sediment grains trapped within rhizoids along the midrib of the midrib on the ventral surface of a thallus; grain dissolution shown in (e, f) Soil clump and grain adhering to and within rhizoid(s). (g) Sediment clumps adhering to the ventral surface of thallus and within rhizoids. (h, i) Thalli appear to hold grains in place with the assistance of biofilms. White arrow = rhizoids, blue arrow = soil/sediment material held in place by rhizoids, yellow arrow = grains stuck to rhizoids, green arrow = other organisms likely contributing to adhesion, yellow circle = probable biofilm holding grain to thalli.
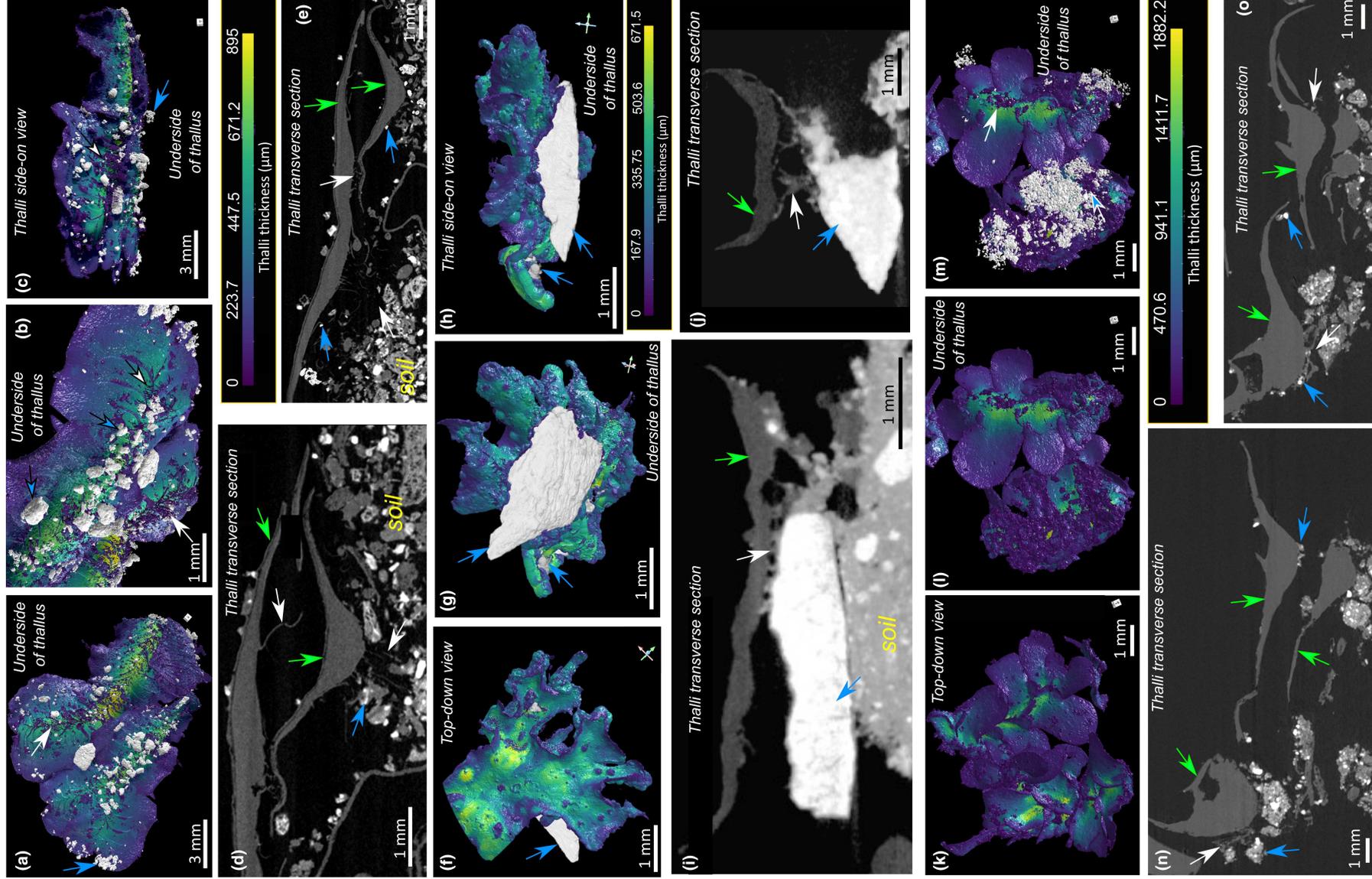
FIGURE 3 Examples of sediment/soil surface stabilisation by plant rhizoids from 3D imaging (μCT) in plants bearing a thallus, rhizoids, and with xyloglucan secretion from rhizoids (group 1) or non-xyloglucan exudates from the thallus (group 2). (a–e) *Lunularia* (thalloid liverwort; group 1), (f–j) *Blasia* (thalloid liverwort; group 1), (k–o) *Treubia* (liverwort; group 2). (a–c) 3D thickness maps of thalli; visualising the thalli by this method enables clear variations in thallus thickness, with the thickest region usually found along the midrib (yellow colour). Soil grains (white) adhering to specific locations of the thalli ventral surface, mostly concentrated along the thicker midrib. Rhizoids visible as purple-coloured thin strands. (d, e) 2D sections of thalli showing rhizoids and clumps of soil/sediment trapped within them at various locations along the thalli. (f–h) 3D thickness maps of thalli showing the envelopment of a soil surface grain. (i, j) 2D sections of thalli showing rhizoids attaching to soil surface grain. (k–m) 3D thickness maps of thalli. (l, m) underside of thalli without (l) and with (m) grains that are held in place by rhizoids (grains white in colour). (n, o) 2D sections showing soil material adhering to the ventral surface of thalli within rhizoid clumps, mostly along the midrib. White arrow = rhizoids, blue arrow = soil/sediment material held in place by rhizoids, green arrows = plants and surface organisms. 3D videos as Videos S3–S7 complement this figure.

forming biofilms) and thalli encrustation may also play a part, since *Blasia* thalli appear to adhere directly to and encrust some grains, holding them in place (Figures 2h,i).

3D imaging from μCT brings an additional perspective to visualising the interaction between plant and sediment. Thallus thickness maps of *Lunularia* again reveal accumulation of grains within the rhizoids along the thicker ventral midrib (Figure 3a–c, Video S1), and 2D digital slices show rhizoid grain augmentation of the top few mm of the soil surface, while thalli grow over and encrust over one another (Figures 3d,e and 4a–e, Video S2). *Lunularia* thalli and rhizoids have the ability to trap, adhere to, and stabilise grains ranging in size from 1.6 to 7.8 mm^3 in the top 20 mm of the soil surface (Figure 4e,g). Similarly, thallus thickness maps of *Blasia* illustrate how thalli drape and encrust over large, singular soil surface grains holding them in place (Figure 3f–h, Video S3), while 2D slice views show that rhizoids are instrumental in attachment to the grain surface (Figure 3i,j, Video S4).

3.1.2 | Group 2: plants bearing a thallus, rhizoids, and secrete other mucilage directly from the thallus (e.g., *Treubia*)

3D visualisation of a *Treubia* thallus reveals thickness variations and the locations of grains which are held in place by rhizoids (Figures 3k–m and 4f–h, Videos S5 and S6), mostly along the thicker midrib. This observation is confirmed by visualisation of transverse sections of individual slices, where grains and mineralogical material aggregate mostly within the tufts of rhizoids along the midrib, but sometimes on other areas (Figure 3n,o, Video S7). *Treubia* thalli and rhizoids have the ability to adhere to and stabilise grains in the top 30 mm of the soil surface (Figure 4f–h), the majority of these being around 23 μm from the top of the thalli. SEM imaging supports the μCT data and indicates that rhizoids are able to hold sedimentary and mineralogical material in place at the soil surface. *Treubia* produces tufts of short rhizoids along its midrib (Figure 5a–c) which hold mineralogical material close to the thallus ventral surface, often accumulating only along the midrib (Figure 5d). *Treubia* also develops quite extensive mats of rhizoids which interact with the sediment surface (Figure 5c). Accumulations of mineralogical material and sediment are observed adhering to both the rhizoid tips (Figure 5e) and along their lengths (Figure 5f), likely held there by exudates and potentially static forces, respectively. It is also common to find numerous (usually finer) grains

adhering directly to areas of the thallus not associated with rhizoids (Figure 5g–j), most likely due to mucilage secretions through pores (Figure 5h) onto which the grains adhere. Static forces and possibly microorganisms and microbial biofilms present on the surface of thalli may also play a role in grain adhesion (Figure 5g–j).

3.1.3 | Group 3: plants with erect habit, lacking rhizoids, and bearing a subterranean axis with mucilage secretion from the subterranean axes (e.g., *Haplomitrium*)

μCT imaging shows that *Haplomitrium* CGC (and CGC other plants) encrust the soil surface, with the upright morphology of the *Haplomitrium* gametophytes (Figure 6a) and a system of rhizoidless subterranean axes (Figure 6b) clearly visible in the μCT images. The latter penetrates the soil surface to a depth of ~4 mm. SEM images of a whole plant of *Haplomitrium* (Figure 6c–g) shows that the plant has mineral grains adhering to different structures, including the subterranean axis (Figure 6d), the aerial axis (Figure 6e–g), and the leaves (Figure 6f). The grains likely adhere to the subterranean axis by mucilage secreted by these, while on the aerial axis some grains appear to be lodged between cells (Figure 6g), with others adhering to the leaves or trapped between them (Figure 6f).

3.1.4 | Group 4: plants with erect habit and bearing multicellular rhizoids (e.g., *Polytrichum* and *Racomitrium* mosses)

Moss-dominated CGCs often cover extensive areas are present in a variety of different habitats and can develop surface covers of closely packed branching axes of variable structure and morphology (Figure 7a,b). Although their thickness varies, they usually consist of thick cushions, comprising large proportions of buried axes, rhizoids and organic material (Figure 7a,b). Large quantities of mineral grains aggregate and become easily trapped within the above ground leafy stems (Figure 7c), and closely adhere to below-ground rhizoids both at their tip and along their lengths (Figure 7d,e). μCT imaging further illustrates the large proportion of mineral grains which become entrapped within the above-ground portion of a moss dominated CGC (Figure 7f–j) and how these tend to be of higher density (i.e., brighter) than those associated with below ground structures (Figure 7f, Video S10).
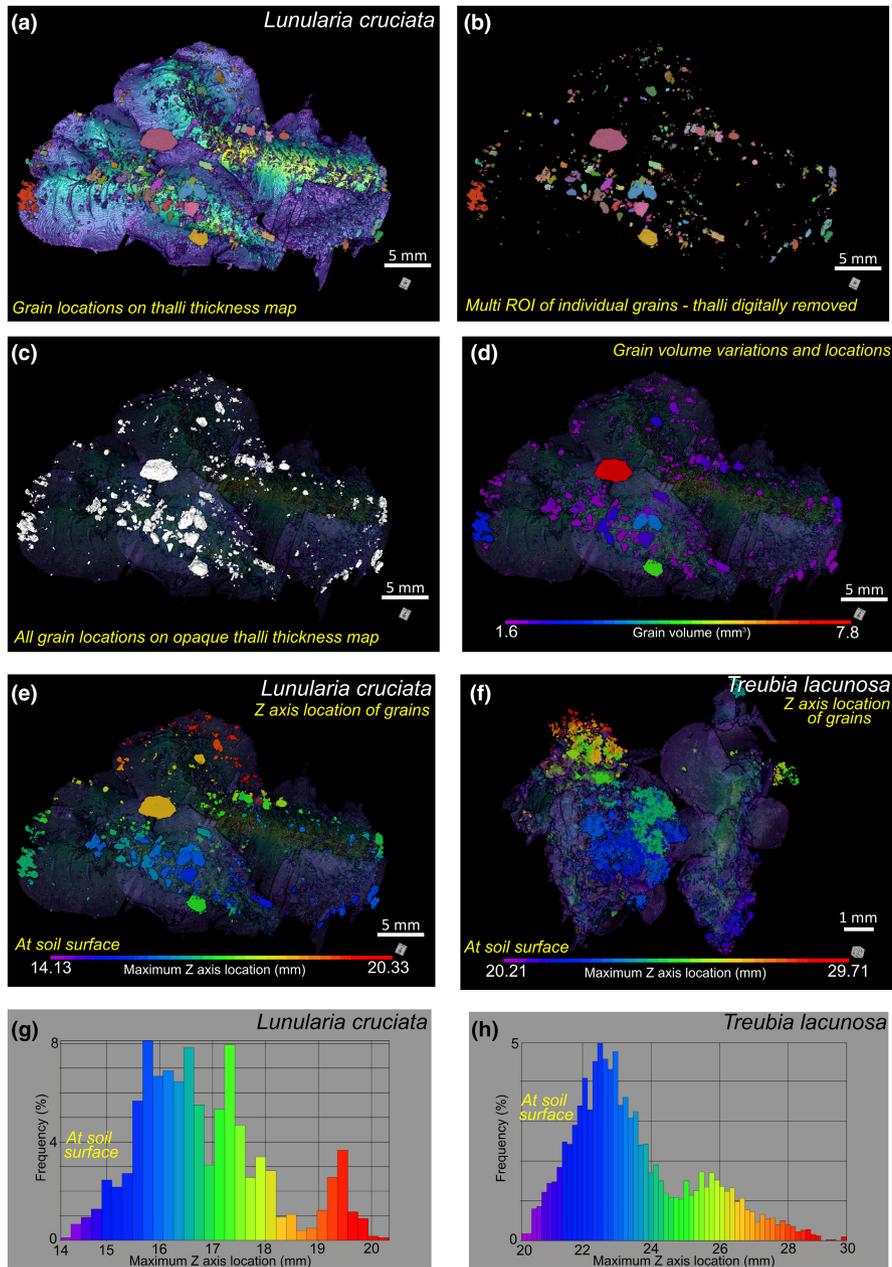
FIGURE 4 µCT analysis of entrapped grains in *Lunularia* (a–e, g) and *Treubia* (f, h) thalloid liverworts. (a) Ventral surface of a thallus showing the location of entrapped grains. Thalli thickness is the same as that in Figure 3a. (b) Same view as a, with thalli digitally removed and individual grains coloured differently as a Multi ROI (region of interest). (c) All grains coloured the same on thallus (d) Volume analysis of grains attached to thallus. (e, f) Maximum Z axis location of grains on thalli in *Lunularia* (e) and *Treubia* (f); the Z axis measures the grain location from the top of the scanned volume (i.e., above the top surface of the thalli) to the bottom of the scanned volume (i.e., within the soil core). (g, h) Corresponding frequency histograms complementing (e and f) detailing the proportion of grains in different locations in the Z axis.

4 | DISCUSSION

4.1 | Early proto-soil formation: the importance of scale

The results presented here provide new insights into how the earliest land plants might have contributed towards aggregation and

3D reconstruction provides additional insights on moss interactions with grains, showing that moss (*Polytrichum*) rhizoids are able to extend through cracks in a soil grain, albeit with no indication of whether the crack preceded rhizoid growth or was caused by it (Figure 8a–c, Video S8). Further, the subterranean rhizoid structure of *Lycopodium* can be digitally segmented in 3D from µCT, detailing the below-ground structure and interaction with soil grains (Figure 8d,e, Video S9).

stabilisation of mineral grains on loose regolith-like terrestrial surfaces with the subsequent potential to initiate weathering and proto-soil development. The organisms involved are all small, ranging in size from fungal hyphae measuring a few micrometres in diameter to plants a few centimetres in size. The effective forces and mechanisms at play are proportional to the scale of the organisms. Based on our analyses of modern analogous systems, these include entrapment of sediment grains within and between tufts of rhizoids, grain entwining and direct adhesion by rhizoids, secretions by plants, biofilm-like envelopment of thalli on surface grains, and grain entrapment within upright leafy structures. These interactions result in the development of thin, generally weakly structured proto-soils (Mitchell et al., 2016, 2021a). However, the growth form of the plants appears to influence the type of interactions and therefore on soil development, as well as the potential interactions (Mitchell et al., 2021a). Thalloid plants tend to grow laterally, encrusting surfaces, whereas some forms of erect and axial plants that grow vertically can result in deeper, organic rich profiles

FIGURE 5 Examples of sediment/soil surface stabilisation by plant rhizoids and other filamentous structures acquired via SEM for *Treubia* (thallus and rhizoid bearing with mucilage secretions; group 2) from the thallus. (a, b) Transverse view through a thallus showing location of rhizoids on the midrib and soil material held in place between the rhizoids. (c) Dense 'mats' of rhizoids extend from the ventral side of the thalli and are in contact with the soil/sediment surface. (d) Accumulation of soil surface material along the thalli midrib where rhizoids are located. (e) Soil clump adhering to the tip of a rhizoid. (f) Soil mineral material adhering to various points along a rhizoid. (g–j) Various soil, mineral and grain material stuck to the underside of a thalli. Some of these may be held in place by secretions/mucilage from pores. Examples of numerous other soil-dwelling organisms are indicated including fungal hyphae (g, i), diatoms (g, i), bacterial filaments/chains (h, j), and bacterial rods (h, green circle). White arrow = rhizoids, blue arrow = soil/sediment material held in place by rhizoids, yellow arrow = grains stuck to rhizoids, green arrow and circle = other organisms stuck to/inhabiting plant surface.
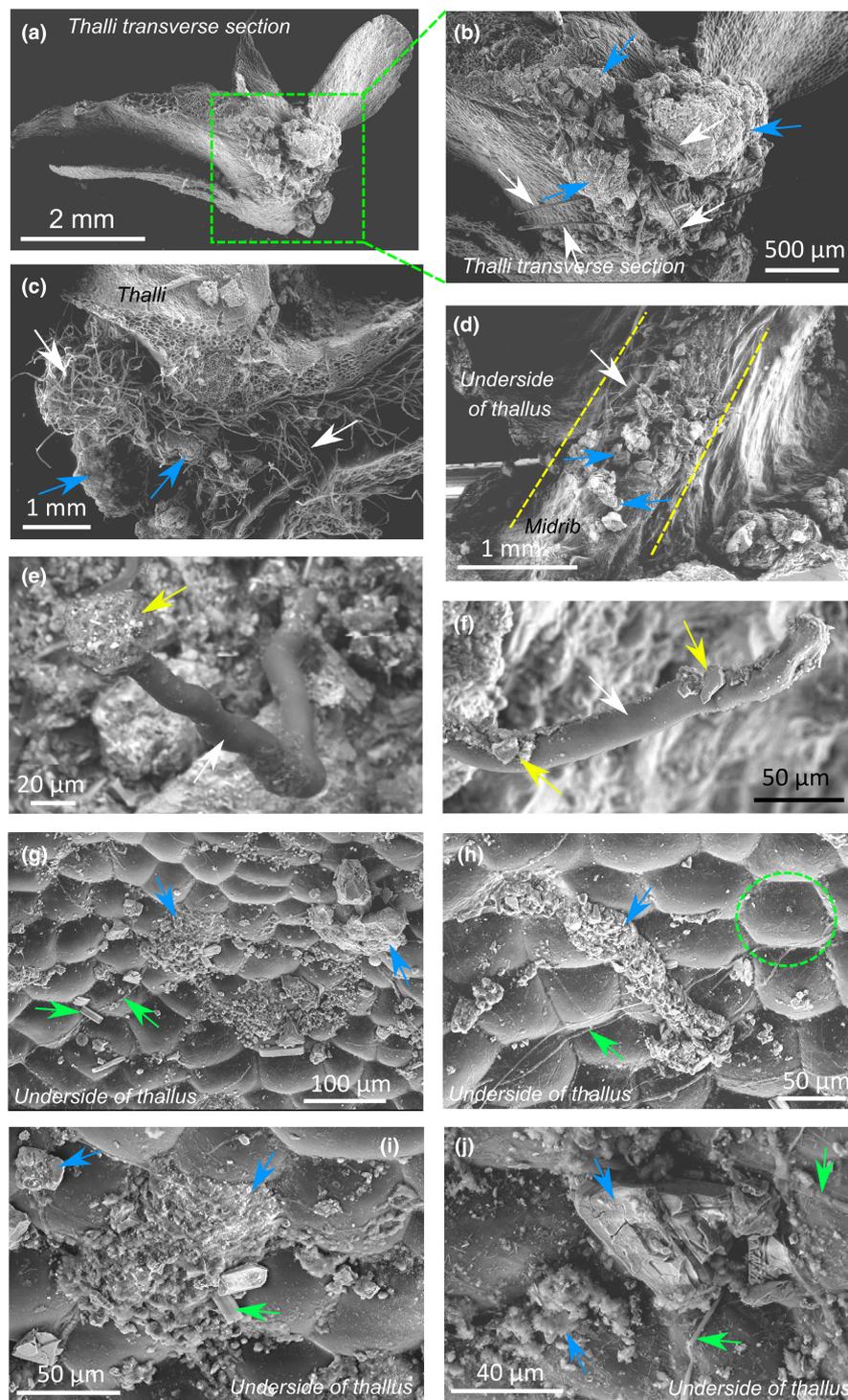
(Mitchell, Strullu-Derrien, et al., 2021). Combining the observations presented here with collective knowledge and previous knowledge of fossils, it appears that anchorage systems (rhizoids, subterranean axes, rooting structures), plant–microbe associations, and secretions by plants (Galloway et al., 2017) were the most probable influential micro-scale features involved in stabilisation by early plants. It is also likely that different the combinations of these in different plant groups (our groups 1–4) affect stabilisation differently. Studying these plant features and traits, with comparison to fossil record, can shed light on potential mechanisms of sediment stabilisation and soil formation in

deep time, with a view to better understand how these small-scale processes accrue to influence larger scale environmental change and processes.

4.1.1 | Anchorage systems, rhizoids, and rooting-structures

A key feature of both liverworts and mosses are rhizoids, with the notable exceptions of *Haplomitrium* (see Figure 6) and *Takakia*, the
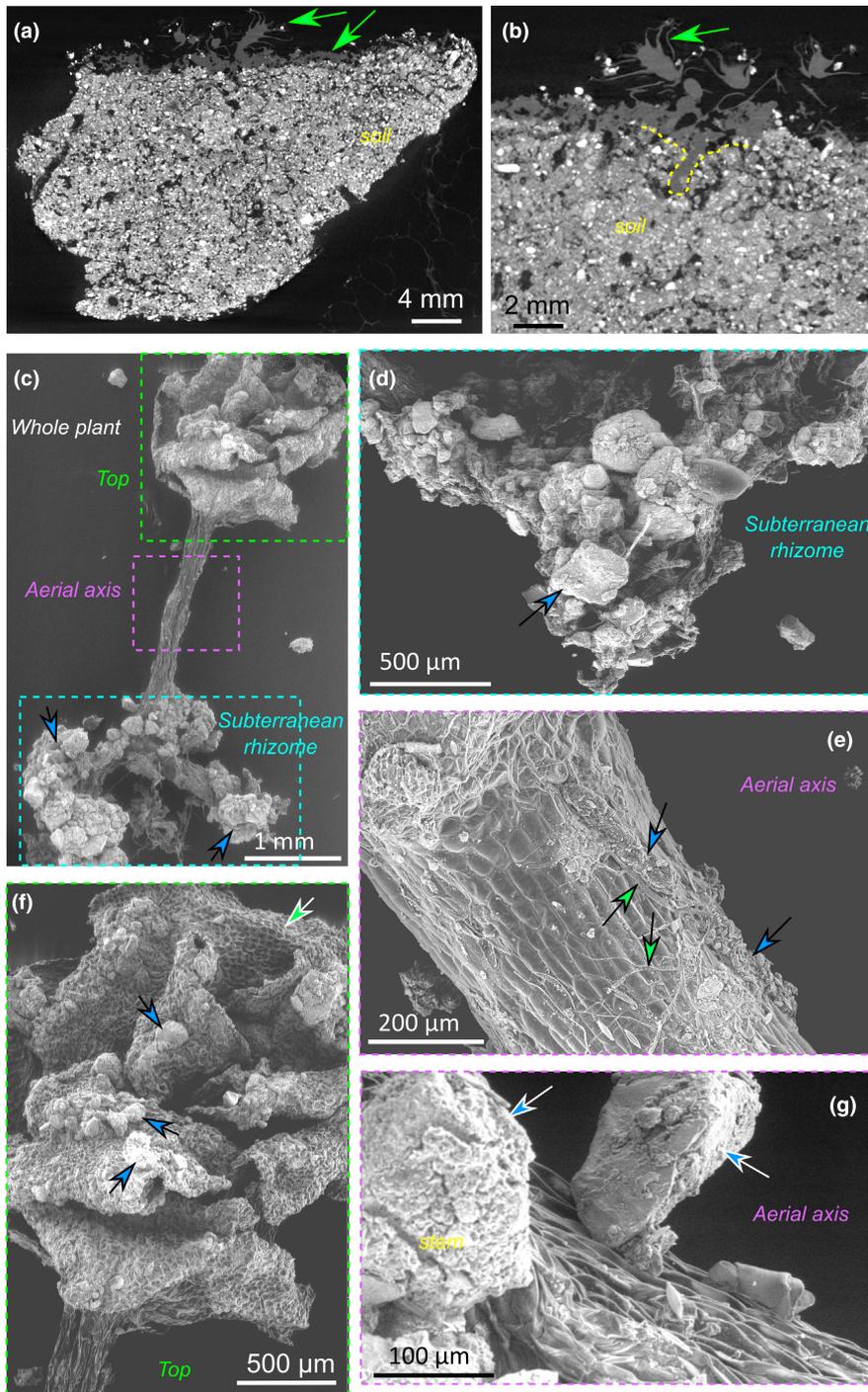
FIGURE 6 Examples of sediment stabilisation in *Haplomitrium* (plant with erect habit, bearing a subterranean axis, erect habit, and with mucilage secretion—group 3). (a, b) 2D Y axes slices through μCT data showing the in situ growth habit (darker greys represent organic material). (a) A CGC 'crust' colonising a loose sediment surface. (b) Zoomed in view of *Haplomitrium* on soil surface, with subterranean axis also visible (outlined by yellow dashed border). (c–g) SEM images of various parts of the *Haplomitrium* gametophyte. (c) SEM image of the whole plant; coloured boxes represent zoomed in views of specific areas of the plant (subterranean axis, aerial axis, and top). (d) mineral and soil grain accumulation around the subterranean axis. (e, g) zoomed in views of the aerial axis of *Haplomitrium* showing soil material stuck to the aerial axis and those that appear to be wedged in between cells. Additional soil dwelling organisms also highlighted in (e) (filamentous structures likely fungal hyphae and bacteria). (f) Mineral grains trapped within the leafy upright structure. Blue arrow = Soil grains held in place by plant, Green arrow = plant/organic material.

earliest divergent taxa of liverworts and mosses, respectively, which are characterised by rhizoidless underground rhizomatous axes (Renzaglia et al., 2018). All rhizoids consist of elongate, tip-growing cells that function in water acquisition and also play a role in anchorage and in sediment stabilisation. However, there are considerable structural differences between the rhizoids of mosses and liverworts. There are structural differences even within liverworts, where some complex thalloids develop two types of rhizoids: larger smooth rhizoids grow at right angles to the thallus and provide anchorage to the sediment surface, and thinner pegged rhizoids run parallel to the thallus and function as an external water conducting

system (Duckett et al., 2014; e.g., *Lunularia*, see Figure 3l). Such differences demonstrate the complex nature of some anchorage systems and lead to different mechanisms for sediment grains entrapment.

We observed that dense rhizoid mats and tufts radiating from the ventral surface of liverwort thalli interact in complex ways with the sediment surface. Rhizoid tufts can hold sediment grains of variable sizes within their structure and in close proximity to the ventral surfaces of thalli, predominantly along the thallus midrib (particularly larger grains), from which the rhizoid tufts extend (e.g., see *Lunularia* in Figures 2–4). Grains can also become trapped by

FIGURE 7 Examples of plants with an erect habit and multicellular rhizoids (e.g., the mosses *Racomitrium* and *Polytrichum*). (a) Close-up view of a mixed moss and lichen CGC dominated by the moss *Polytrichum alpinum*. (b) Cross section through a thick moss cushion growing on loose regolith. (c) mineral grains trapped within moss leaves of *Racomitrium*. (d, e) Soil/sediment grains held in place on a moss aerial axis and further grains stuck to rhizoids. (f) Y axis 2D slice through CT data showing the surface of a moss soil; high density mineral grains are shown trapped within upright moss 'leaves'. (g) Soil mineral grains trapped within moss 'leaves' (SEM thin section image). (h–j) Three views of the same moss core showing the complete soil profile in 3D, highlighting the different components; green = plant material, brown = finer grained soil minerals, red = high density soil grains. White arrow = rhizoids, blue arrow = soil/sediment material held in place by rhizoids, yellow arrow = grains stuck to rhizoids, red arrow = filamentous structures (likely fungi) holding sediment/soil material in place.
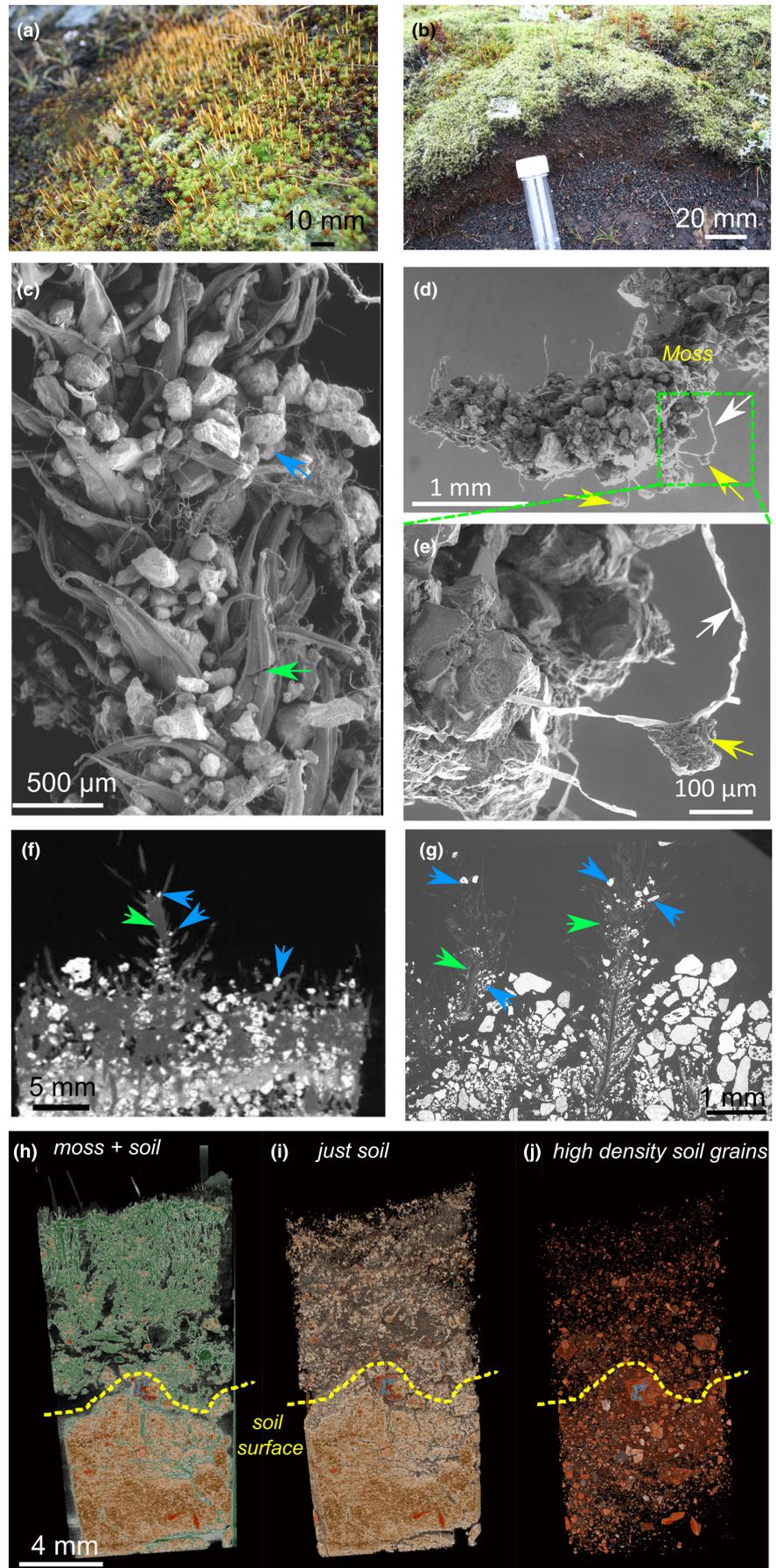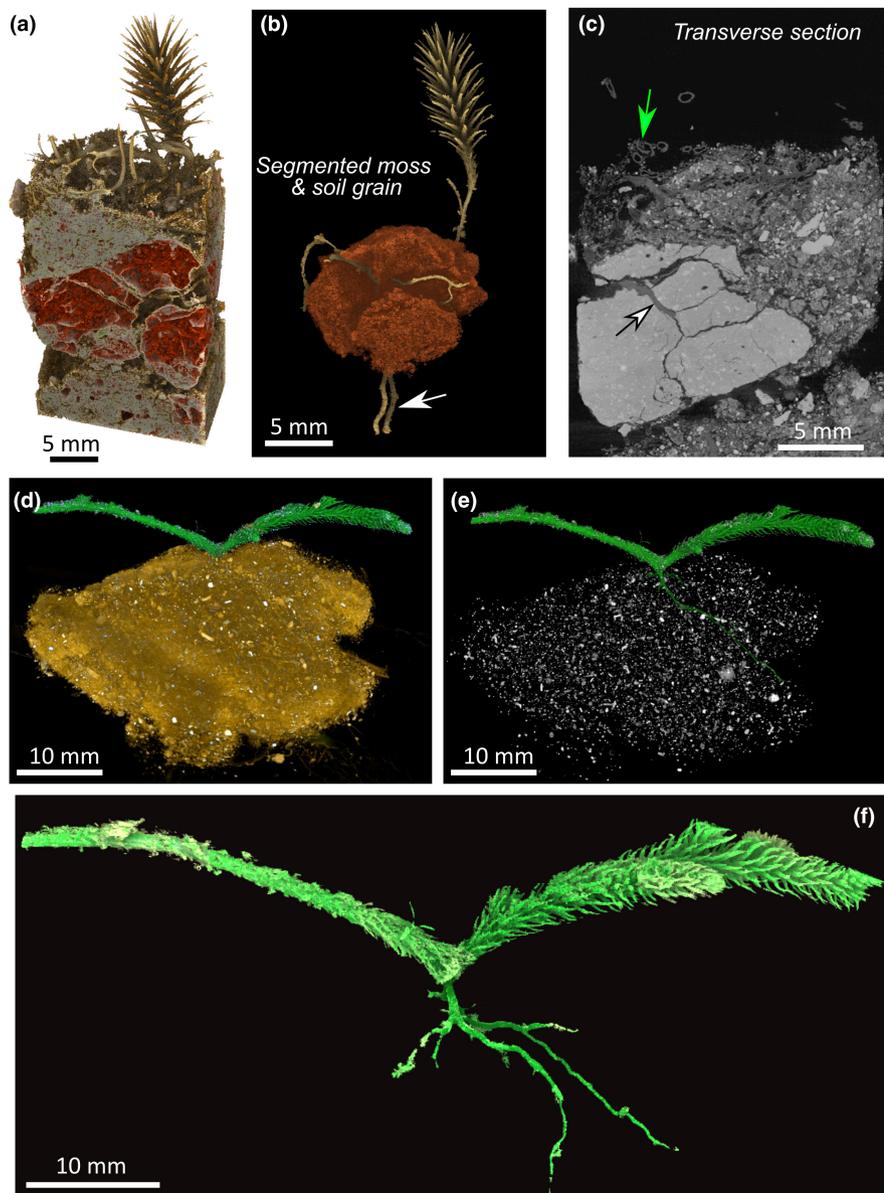
FIGURE 8 (a, b) 3D reconstruction of *Polytrichum* moss rhizoids growing through a soil grain, and (d–f) 3D reconstruction of *Lycopodium* and its subterranean rhizoids. (c) 2D digital section view of *Polytrichum* stem growing within the soil grain crack. (e) Soil digitally removed showing only high density soil grains, while in (f) all soil has been digitally removed. White arrow = rhizoids, green arrows = plants and surface organisms. 3D videos as Videos S8 and S9 complement this figure.

adherence to individual rhizoids through physically entwining at the rhizoid tip, through xyloglucan secretion (Galloway et al., 2017), and potentially by electrostatic forces. Moss rhizoids are significantly different, being multicellular structures that typically arise from the aerial axis where they can form greatly entangled tufts that bind sediment grains and organic materials. They are generally smooth but can have papillose surfaces, and are much narrower than the unicellular rhizoids of liverworts, typically measuring 20 μm in diameter. Moss rhizoid systems growing through soils branch extensively, with the sometimes thigmotropic (Pressel & Duckett, 2009) furthest ramifications only 3–5 μm diameter, which is a similar size to soil-dwelling fungal hyphae, indicating that moss rhizoids may also play a role in nutrient acquisition and potentially explaining the lack of fungal symbiosis in them (Field et al., 2015). It has been suggested that the release of a non-cellulosic polysaccharide adhesive by rhizoid tips may also contribute to their attachment to the substrate (Jones & Dolan, 2012; Odu, 1989 and literature therein).

Rhizoid 'stickiness' is crucial for their adhesion to solid substrates, and there are variations in function even between different mosses. For example, *Racomitrium lanuginosum* does not produce new shoots from deep within the substrate; it has relatively few rhizoids, and because of that soil grains become trapped mainly in the upright leafy stems. On the other hand, *Polytrichum* sp. produces underground rhizomes with numerous rhizoids, increasing the probability that often-forming rope-like structures which increase the likelihood of grains adhering to them. Grains also become trapped in both the living above ground upright leafy stems and in the buried portions. We have also shown here that moss rhizoids, in *Polytrichum* at least, are capable of growing through grains, which will inevitably contribute to mineral destruction and soil development (Figure 8). This physical destruction is in addition to chemical dissolution through from the release of organic acids, shown to be an effective weathering facilitator (Lenton et al., 2012). Therefore, in addition to aggregating

sediments, moss rhizoids can potentially aid in soil development through mineral grain destruction.

Fossils and sedimentary structures provide direct evidence that rhizoid-based rooting systems evolved in early plants before the evolution of roots (Hillier et al., 2008; Jones & Dolan, 2012; Kenrick & Strullu-Derrien, 2014). The best fossil examples come from the exceptionally preserved 407 Ma Rhynie chert. These plants had erect and axial rather than thalloid growth, and in all but one species, non-septate (i.e., unicellular) rhizoids developed in dense tufts from bulbous or creeping prostrate axes in contact with thin sediment/proto-soil surfaces (Edwards, 2004). *Nothia aphylla* had a branched rhizome with a distinct ventral ridge of rhizoids (Kerp et al., 2001), analogous to the thallus midrib of complex thalloid liverworts. *Nothia* is thought to have been a geophyte, with a persistent rhizomatous system growing within a shallow sandy sediment substrate containing plant remains. The aerial parts might have been short-lived, and the rhizomatous pattern of growth enabled large colonies of *Nothia* to develop (Daviero-Gomez et al., 2005). The rhizomes of two other Rhynie species (*Ventarura lyonii* and *Trichopherophyton teuchansii*) are also thought to have grown within the substrate sediment layer because rhizoids developed on all of their surfaces (Edwards, 2004). By contrast, in the plant *Aglaophyton majus*, rhizoids developed locally where prostrate axes made contact with the substrate surface. The upper surface of these axes have stomata, further supporting the idea that they were surficial rather than subterranean (Edwards, 2004). Rhizoids developed on one side of the axes interpreted as rhizomes in *Rhynia gwynne-vaughanii* as well as ectopically on aerial axes where they arose from small mounds of tissue, the so-called hemispherical projections. *Horneophyton lignieri* differs from these other species in the tuberous shape of the axis, a corm, in contact with the substrate sediment. Numerous rhizoids developed from its lower surface (Strullu-Derrien et al., 2014). In the Rhynie chert plants, rhizoids typically measure 20–30 μm in diameter but they vary greatly in length, being shortest in *Trichopherophyton* (<250 μm) and *Ventarura* (<450 μm), and very elongate in *Horneophyton* (>2000 μm). The earliest fossil rhizoids therefore resemble the simple, robust, non-septate rhizoids of modern liverworts rather than the septate rhizoids with ramification of decreasing diameters of mosses. It is likely that functionally, and in the ways that they interacted physically with the substrate, they were closer too.

The earliest evidence of rooting systems comes from stem-group lycopods in the Drepanophycales. Their development and anatomy were recently characterised in detail in exceptional well-preserved specimens of *Asteroxylon mackiei* (Hetherington et al., 2021; Hetherington & Dolan, 2018), which is the only plant in the Rhynie chert known to possess root-like organs. Although these early roots differed in some key anatomical and developmental respects to those of modern lycopods they represent a step change in the manner in which plants interact with their substrates. The evolution of specialised geotropic axes opened up a new means of anchorage and interaction with the substrate, but came later than the early divergent rhizoid-bearing plants.

4.1.2 | Symbiosis

We did not specifically investigate fungal symbioses here, because fungal hyphae fall below the limit of resolution of our 3D imaging methods and are likely obstructed from view in our 2D SEM imaging. However, considerations of these are pertinent in the context of early divergent land plant interactions with their substrate. Today, mutualistic symbioses (mycorrhizae) develop between the roots of most plants and soil fungi in the Dykaria (Ascomycota and Basidiomycota) and Mucoromycota (Mucoromycotina and Glomeromycotina); these plant–fungal mutualisms play crucial roles in the acquisition of key elements required in the host plant metabolism (e.g., nitrogen, phosphorus) (Smith & Read, 2008). Some extant, early divergent bryophytes (thalloid liverworts, hornworts) and spore-producing vascular plants (lycopods, ferns) (Figure 1) develop mycorrhizal or mycorrhizal-like associations (when true roots are lacking) with members of the early divergent fungal sub-phyla Mucoromycotina and Glomeromycotina (or Glomeromycota) (Field et al., 2016; Rimington et al., 2015, 2020), a relationship that extends back more than 400 million years (Berbee et al., 2020; Strullu-Derrien et al., 2014, 2018). With the possible exception of *Nothia aphylla* (Krings et al., 2007a, 2007b), rhizoids are not known to be involved in the mycorrhizal-like associations of the Rhynie chert plants and in the earliest diverging Haplomitriopsida liverworts (i.e., the fungus-free rhizoids in *Treubia* and the absence of rhizoids in *Haplomitrium*), whilst they are the conduits for fungal entry in all other liverwort-fungal associations (Duckett et al., 2006; Read et al., 2000), suggesting that Haplomitriopsida fungal relationships were established before the evolution of rhizoids. The notion that mycorrhizal-like symbioses evolved during the early colonisation of the land by plants is consistent with their global abundance in the soil today, their broad phylogenetic distribution, and recent evidence acquired from plant and fungal genomes (Berbee et al., 2020). There is also direct evidence of mycorrhizal-like associations in the fossil record. The earliest geological evidence again comes from the Rhynie chert. Both the sporophyte and gametophyte of *Aglaophyton majus* formed associations with a fungus attributed to the Glomeromycota (Remy et al., 1994; Strullu-derrien et al., 2014; Taylor et al., 2005) and, like in *Treubia*, its rhizoids were fungus free indicating an alternate route for colonisation. Mycorrhizal-like endophytes were documented in *Nothia aphylla* (Krings et al., 2007a, 2007b), and here rhizoids are thought to have been the route of infection. Recently, a mycorrhizal-like association with Mucoromycotina was documented in the plant *Horneophyton lignieri* (Strullu-Derrien et al., 2014). In both *Nothia* and *Horneophyton*, fungal colonisation consisted of intra- and intercellular phases, as typical of *Treubia* (Pressel et al., 2010). Mycorrhizal associations were therefore present in early terrestrial ecosystems where they probably played a crucial role in plant colonisation during primary succession, which often begins under conditions of nutrient impoverishment (Smith & Read, 2008). The fungal structures observed in the fossil plants represent the end points of a much larger mycelial network that extended into the soil far beyond the rhizomes and rhizoids of the host plant (Smith & Read, 2008). This relationship

likely made a profound contribution to plant–soil interactions and the formation of proto-soils leading to aggregation and stabilisation of sediment surfaces and the promotion of in situ biologically mediated weathering (Mitchell et al., 2019, 2021b). Fungal hyphae and their interactions with plant cells fall below the limit of resolution of the 3D imaging methods that we employed here, but it might be possible in the future to resolve structures of this scale using a correlative microscopy approach utilising nanotomography and FIB-SEM (e.g., Mitchell et al., 2021b).

4.1.3 | Appressed thalli, secretions and mucilage

Dense surface coverings, or mats, are formed by the moss elements of CGCs and consist of up to 80 mm thick aggregated mixtures of buried organic material with photosynthetic leafy parts emerging at the surface. Thalloid organisms form much more localised surface coverings where individual thalli grow over one another, forming additional surficial layers that can contribute to sediment protection and stabilisation.

In the results presented here, the appressed nature of the liverwort thalli means sediment grains can be stabilised by the surface envelopment of thalli, entrapment between cells, and by mucopolysaccharide secretions (i.e., mucilage), in addition to rhizoid interactions. Some bryophytes have the ability to adhere to solid objects through the secretion from their rhizoids of a sticky and viscous sulphated mucopolysaccharide (Odu, 1989), while some liverworts (*Haplomitrium*), devoid of a thallus and instead having an erect structure, must rely on a subterranean axes and mucilage secretions for anchorage because of a lack of rhizoids. In *Lunularia* and *Treubia*, while most grains are entrapped by rhizoids where the thalli (midribs) touch the soil surface, we were able to visualise a smaller number of other grains that are held in place in other areas of the thalli, probably by mucilage secretions. This will vary between xyloglucans secreted from rhizoids for *Lunularia* and *Blasia*, and thalli mucilage for *Treubia*. Mucilages are carbohydrates that are involved in the absorption and retention of water. Most mosses and liverworts produce mucilage from slime papillae (Renzaglia et al., 2000); in rare cases, very large quantities of mucilage are produced from clefts in the thallus (*Treubia*) or by underground axes (*Haplomitrium*) (Carafa et al., 2003; Duckett et al., 2006; Renzaglia et al., 2007). Mucilage produced in this way, in addition to conferring a measure of protection against desiccation, could have contributed towards the aggregation of sediment grains in early soils. The basal thalloid liverworts *Blasia* and *Lunularia* secrete the polysaccharide xyloglucan which acts as an efficient soil particle aggregator at the modern day (Galloway et al., 2017), likely also making it an important method of stabilisation in the geologic past. Ligrone et al. (2012) inferred that the last common ancestor of present-day land plants was leafless, had an axial/erect growth form, and bore unicellular rhizoids and mucilage papillae. All these features have been observed in well-preserved early fossil land plants, with the exception of mucilage

papillae. Documentation of mucilage papillae or mucilage production within the tissue systems of fossils is challenging but could be envisaged under exceptional conditions of preservation. Papillate epidermal cells have been documented in several plants from the Rhynie chert (Edwards, 2004; Lyon and Edwards, 1991), and these might have had a secretory function. Thus, secretions and mucilage were likely an important method of substrate stabilisation in early land plants contributing to the formation of thin proto-soils.

4.2 | Landscape evolution with the evolution of land plants

The ways in which modern biological soil crusts and cryptogamic ground covers enhance resistance of surface run-off and erosion, while also promoting dust capture, are well understood (Belnap, 2003; Gao et al., 2016; Williams et al., 2012). However, unequivocally recognising structures of these types in the rock record (see Davies et al., 2020), quantifying their influence on rates of weathering, distinguishing between the effect of rhizoid-like and root-like anchorage systems, and elucidating different influence of plant body plan variations, can be challenging. In many instances, the likely effects of plant influence can be identified in otherwise unfossiliferous rocks, by comparison between strata dating to before the evolution of land plants (Davies et al., 2020), but evidence of 'smoking guns' is rare, often because even in situ plants are often parautochtonous and there is a paucity of records of small standing fossil plants in situ. Where palaeosols developed under larger vascular plants, weathering effects similar to those in modern soils can be recognised as well as evidence of rooting systems (Driese et al., 2021). For smaller statured plants, one potential way forward is to identify and characterise vegetation-induced sedimentary structures (VISS) in the rock record, where indirect effects of sediment accumulation and erosion can also be inferred (Davies et al., 2021; Rygel et al., 2004). Another approach is to identify micro-to-nanoscale biologically mediated weathering features (BWFs) that are present in potential proto-soil like substrates (Mitchell et al., 2019). The recognition of such features in the sedimentary record could provide an indicator of the presence of proto-soil forming communities, and lends value to studying and characterising these features in modern analogues at various scales.

When plants first colonised the land they had a profound influence on fluvial environments, recorded as a frequency distribution shift from sedimentary facies suggestive of a global preponderance of braided fluvial systems to a record containing greater evidence for meandering deposition (Davies & Gibling, 2010). An upsurge in alluvial mudrock also occurs, with explanations for this trend considering that mud production (from weathering) and retention (from binding, baffling and organically induced flocculation and settling) would have been important drivers (Davies & McMahon, 2021; McMahon & Davies, 2018; Zeichner et al., 2021; McMahon et al., *submitted*). However, it is less clear how different types of terrestrial

communities influenced the scale of this weathering and landscape evolution, particularly by smaller statured plants (Edwards et al., 2015; Quirk et al., 2015).

Results presented here provide an indication that micro-scale processes can contribute to sediment stabilisation and soil formation in diminutive communities; such phenomena would have been wholly novel Earth surface processes in the early Palaeozoic (Figure 9). Both thalloid and erect/axial plants can hold sediment grains in place through dense surface coverings, rhizoid interactions, secretions, and envelopments, suggesting that whatever the morphology of the earliest land plants, they had many methods at their disposal for anchorage and sediment interactions. Indeed, our results show that plants with different features (i.e., groups 1–4) all have slight variations in the way that they colonise and stabilise sediment surfaces, which will have evolved at different time periods. The hierarchical nature of organisms and population dynamics (Post, 2019) means that these localised interactions and processes would have scaled up to landscape and continental levels, and the precise nature of this scaling could in future be approached through a study of weathering in modern cryptogamic ground cover communities.

Plants first colonised the land during the early Palaeozoic (Figure 1). Evidence for the nature and evolution of this early vegetation comes from the fossil record and also indirectly from the plant tree of life. Calibrated molecular phylogenetic trees indicate that the last common ancestor of living land plants evolved between 515–482 million years ago, but the stem-group could extend into the Neoproterozoic (Ediacaran) (Morris et al., 2018; Puttick et al., 2018). This precedes the earliest fossil evidence from cryptospores, which first appeared about 480 Ma (Strother & Foster, 2021) and diversified through the Ordovician and Silurian (Strother et al., 2015; Wellman & Strother, 2015). The earliest unequivocal plant macrofossil remains are documented at about 430 Ma (Libertín et al., 2018). The discrepancy in timing seen among calibrated phylogenetic trees, spores, and macrofossil has been widely discussed (Strother & Foster, 2021), and may in part reflect a taphonomic bias favouring the larger vascular plants (Kenrick et al., 2012). The growth forms of the earliest land plants therefore remain somewhat speculative. There is some evidence of thalloid communities associated with cyanobacterial mats in a braided fluvial system at 440 Ma (Tomescu et al., 2008; Tomescu & Rothwell, 2006). Direct evidence of the cryptospore-producing plants comes from Late Silurian and Early Devonian fossils preserved as charcoal (Edwards et al., 2014; Edwards, Morris, Axe, Duckett, et al., 2021; Edwards, Morris, Axe, Taylor, et al., 2021). These are predominantly axial fossils with rarer associated thalloid remains. The plants were diminutive, with axes measuring less than 1 mm in diameter and height probably not exceeding a centimetre or two. It seems likely that rhizoid based systems preceded the evolution of simple roots and therefore that the earliest plants interacted with and stabilised substrates in a similar manner to modern liverworts in groups 1–3, including the entrapment, sticking and entwining of sedimentary grains within rhizoid bundles, grain aggregation due to xyloglucan, mucilage, and other

secretions, and the biofilm-like encrusting of thalli or axial rhizomatous systems over surfaces creating a protective layer that reduced erosion. While rhizoids are known to have existed in early land plants in the geologic past, it seems likely that some may have been devoid of rhizoids and had subterranean axes, akin to modern *Haplomitrium*, and may have relied on secretions for their main form of stabilisation. Thalloid, lichen-like associations are also known from rocks of the Lower Devonian (Honegger, Axe, & Edwards, 2013; Honegger, Edwards, & Axe, 2013; Lücking & Nelsen, 2018), further reinforcing the potential importance of encrusting growth forms. These plants and the associated organisms would have formed relatively thin proto-soils, mostly devoid of organic material with thin, surface organic layers (Mitchell et al., 2021a).

The earliest fossils with rooting systems that have been reconstructed in some detail come from the Early Devonian and these are either rhizoid-based systems in plants of axial growth form (Kenrick & Strullu-Derrien, 2014) or shallow root-like systems in small herbaceous lycopods (Hetherington & Dolan, 2018; Matsunaga and Tomescu 2016, 2017). By the Middle Devonian, tree-like growth forms with wood and extensive rooting systems were evolving independently in several major clades of plants (Berry & Marshall, 2015; Morris et al., 2015; Stein et al., 2007, 2012, 2020; Xu et al., 2017). With the evolution of roots in the vascular plants the influence of vegetation on sedimentary systems starts to become apparent. By 407 Ma, the average proportion of mudrock in alluvial successions globally is 15.4% of total stratigraphic thickness, compared with 1.3% in earlier units (McMahon & Davies, 2018). Additionally small meandering channels had become globally abundant (Gibling & Davies, 2012) likely not only initiated by more widespread land plants but also with an increased number of cohesive muddy substrates. Proto-soils would probably also have been more organic-rich (Mitchell et al., 2021a), and more buried organic matter likely changed sediment properties leading to improved cohesiveness (Davies et al., 2021), with multicellular rhizoids able to stabilise and adhere to soil mineral grains, akin to group 4 in this study. With the evolution of vascular plants with 'true' root systems there was a marked shift in sedimentary architecture towards channelled sand-bed rivers, meandering rivers, and muddy floodplains (the average proportion of mudrock in alluvial successions is 29.9% for formations deposited after the Early Devonian evolution of rooting; Gibling & Davies, 2012; McMahon & Davies, 2018).

The nature of early terrestrial communities therefore changed significantly from the Cambrian through to the Devonian, with the greatest changes happening in the plant morphology. Plants increased in size by several orders of magnitude and developed specialised organ systems including stems, leaves and roots. These changes would have influenced the ways that they interacted with their substrates and therefore their broader impacts on sedimentary systems. In terms of rock weathering, this might simply reflect a change in rate. However, it may be that a threshold in plant size, and the shifts in associated features (rhizoids, appressed vs upright, secretions), needed to be reached to influence the shape and flow of river systems.
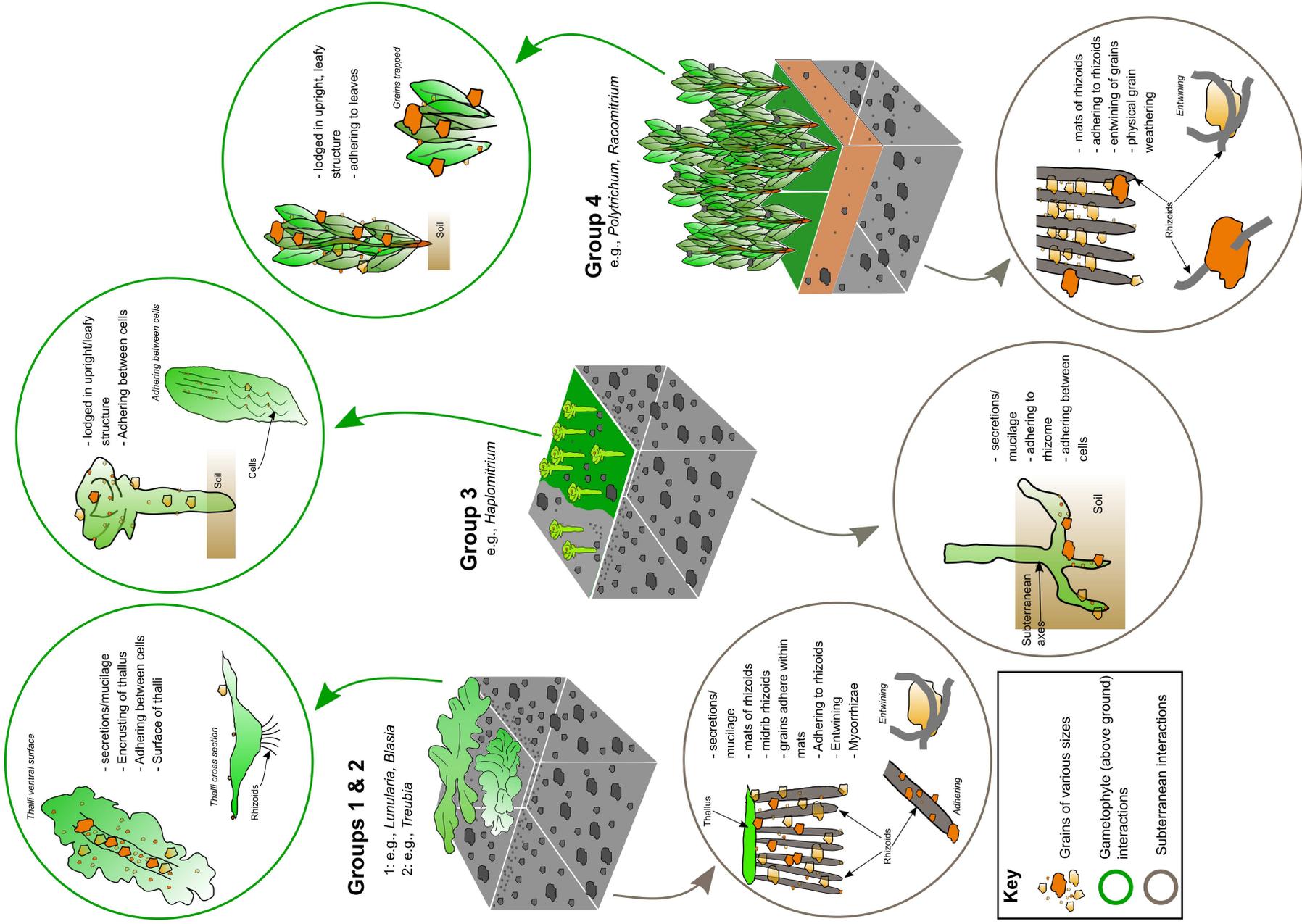
FIGURE 9 Summary diagram highlighting the above ground (gametophyte) and subterranean interactions with substrate mineral grains in groups 1–4 organisms.

5 | CONCLUSIONS

The organisms involved in proto-soil formation from the Cambrian through the Silurian were all small, ranging in size from fungal hyphae measuring micrometres in diameter to plants a few centimetres in size. The effective forces and mechanisms at play were proportional to the scale of the organisms. Based on our analysis of modern analogous systems, these include electrostatic forces, secretion of mucilage, entrapment of matter on the substrate by thalli and rhizoids, and the entrapment of grains by leaves. Together, these resulted in the development of thin, generally weakly structured proto-soils. The growth form of the plant also influences soil development. Thalloid plants tend to grow laterally, encrusting surfaces, whereas some forms of axial plant that grow vertically can result in deeper, organic rich profiles. The earliest anchorage systems in plants were composed of unicellular rhizoids like those of modern liverworts, hornworts, and the gametophytes of lycopods, ferns, and horsetails. These developed from rhizomatous axes or possibly thalloid growth forms. The plants formed symbiotic associations with other organisms, notably fungi, that facilitated the colonisation of new substrates. Moss-like growth forms were not an element of early terrestrial plant ecosystems. The evolution of vascular plants with well-developed rooting systems is known to have had a significant influence on the nature of sedimentary systems and the shape and flow of rivers. The small-scale features described here provide a framework to understand the effect that early diverging plants of various morphologies had on Earth system processes in the early Palaeozoic.

CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest from any of the authors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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