

## RESEARCH ARTICLE

# Soil Building and Capillary Barrier–Enhanced Water Availability Help Explain *Pisonia grandis* and Other Atoll Native's Tolerance for Variable Precipitation Regimes

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## ABSTRACT

*Pisonia grandis*, now threatened, is an important source of soil organic matter on atoll islands and historically composed the dominant canopy of many atoll ecosystems across the Pacific. How the tree manages water to exist across wide precipitation gradients is poorly understood. This study tests the hypotheses that *P. grandis* is using organic-rich soils that develop under their canopy and soil layering where organic soils contact carbonate sands as part of their water management strategy. We analysed the chemical and physical properties of soils from two atolls in the central Pacific Ocean, one wet (Palmyra, USA) and one dry (Nikumaroro, Kiribati). Additionally, we used HYDRUS-1D to simulate vadose zone water dynamics under a range of organic cap thicknesses (0, 14, 30 and 50 cm), precipitation intensities (1, 5 and 10 cm/h) and average precipitation amounts (50, 100, 200 and 400 cm/yr). Laboratory results indicate organic soils are strongly, though not exclusively, associated with *P. grandis*. Water holding capacity increases with soil organic carbon up to about 10% but not beyond that amount. Modelling results indicate significant water retained in organic soils where they overlie coarse carbonate sediments suggesting a capillary barrier development as the plant-mediated organic soil accumulates. Retained soil water extends modelled dry-down times of root-accessible soil by more than 3 weeks. This indicates that capillary barrier-enhanced water availability can help explain how *P. grandis* and other soil-building atoll species can exist across variable precipitation regimes. To our knowledge, this work is the first description of plant-mediated capillary barrier development as a water management strategy.

## 1 | Introduction

Pacific atoll islands are unique ecosystems with closely linked marine and terrestrial environments (McCauley et al. 2012) that occur across wide climatic gradients. Despite being biodiversity 'cool spots' with relatively few endemic species, their biodiversity is essential for sustaining their human populations, who have very little opportunity for modern economic development due to geographic isolation and limited resources

(Thaman 2008). However, historical and current human impacts on atolls make these ecosystems some of the most degraded and threatened in the world (Mueller-Dombois and Fosberg 1998). For example, past industrial copra development and phosphate mining dramatically reduced the extent of native atoll forests and has led to the loss of valuable productive soils (Stone and Robison 2000). Additionally, human-caused climate change is now fundamentally altering climate regimes across the Pacific (Magnan et al. 2022), increasing pressure on these

already struggling ecosystems. Restoration of these forest ecosystems has significant benefits, including increasing carbon sequestration, enhancing seabird habitat and supporting the restoration of culturally important living resources (Longley-Wood et al. 2022; Thaman 2008).

A particularly important restoration target across the Pacific because of its ability to develop soil organic matter (SOM) is the iconic island native tree species *Pisonia grandis* R. Br. (Nyctaginaceae) (Hathaway, McEachern, and Fisher 2011). *P. grandis* has been in decline throughout its range due to increased disturbance from agricultural clearing (T. Walker 1991; Woodroffe and Morrison 2001), increased stress from invasive scale insects (Handler et al. 2007) and encroachment by *Cocos nucifera*, the common coconut palm (Batianoff et al. 2010b; T. Walker 1991). SOM is important in atoll soils because SOM improves soil water storage, reduces root restrictions and acts as the main source and sink of nutrients in the absence of clay and silt, enhancing soil fertility (Stone and Robison 2000). Thus, SOM is critical to soil productivity and plant growth and development across the islands.

*P. grandis* develops SOM through close association with a wide variety of seabirds, which preferentially roost and nest in its canopies. The constant flow of seabird guano mixing with leaf debris beneath the *P. grandis* canopies helps create the distinctive 'Jemo' soils that develop in association with these trees (Fosberg 1954). These soils are typically acidic (typically pH 4–6), highly organic (> 50% OM) and often underlain by a phosphatic hardpan (Fosberg 1953, 1957; T. Walker 1991). The reported depth of 'Jemo' soils varies from a few mm to more than a meter (Batianoff et al. 2010a), and researchers have used the presence of relic sequences of this soil and/or hardpan to infer past locations of *P. grandis* (Fosberg 1994; Shaw 1952; Woodroffe and Morrison 2001). Nutrients associated with 'Jemo' soils are known to be important for *P. grandis* seed germination (Young, McCauley, and Dirzo 2011) and are demonstrably supporting many other parts of atoll island ecosystems, such as manta ray communities in nearby lagoons (McCauley et al. 2012; Young et al. 2010a). *P. grandis*, known as 'cabbage tree' (or te buka in Gilbertese), is also a culturally important source of food and medicine for traditional island communities (Elumalai, Chinna Eswaraiyah, and Rahman 2012). Thus, restoring *P. grandis* on atoll ecosystems can improve not only soil fertility and nutrient cycling but seabird habitats and cultural resources.

One of the roadblocks to the restoration of *P. grandis* is the limited understanding of its freshwater management strategies. *P. grandis* is known to have a water demand comparable to other island tree species (Krauss et al. 2015) yet is found on islands with mean annual precipitation values as low as 50 cm/yr up to as high as 500 cm/yr (Mueller-Dombois and Fosberg 1998). Unlike plants typically found in strand vegetation, *P. grandis* does not tolerate excessive salt exposure (sea spray, overwash, etc.), instead concentrating its growth preferentially in sheltered areas behind stand vegetation (Mueller-Dombois and Fosberg 1998). It also cannot utilize brackish water to meet its water demand (Cole, Gessel, and Held 1961; Mueller-Dombois and Fosberg 1998), a water management strategy employed by a variety of other atoll species. On these atoll islands, freshwater tends to be solely precipitation-derived, and the very high

hydraulic conductivities (50–400 m day<sup>-1</sup>) in the coarse carbonate sands and coral rubble that make up the bulk of atoll islands mean that most freshwater storage is in the freshwater lens at a depth of 1–2 m (Bailey, Jenson, and Olsen 2010). Unlike plants such as *C. nucifera* L., *Heliotropium foertherianum* Diane & Hilger and *Scaevola taccada* Vhal, which have roots deep enough to directly access the freshwater lenses (Carr 2011; R. B. Walker and Gessel 1991), *P. grandis* roots are shallow, with the bulk of the root mass in the top 10 cm of soil (Christophersen 1927; Shaw 1952; T. Walker 1991). How then *P. grandis* can access sufficient freshwater to support its growth is unclear, particularly on dry atolls.

Dating back to 1954, Fosberg hypothesized that the distinctive 'Jemo' soils might also aid the tree in freshwater management (Fosberg 1954), though he did not specify by what mechanism. Given the high amounts of SOM that develop in these soils and the known association between SOM and water holding capacity in sandy soils (Yost and Hartemink 2019), the amount of SOM seems a plausible explanation for increasing water available to *P. grandis*. However, not all soils under *P. grandis* reach high levels of organic enrichment (Woodroffe and Morrison 2001), and in some places, organic soil development under *P. grandis* can be thin or discontinuous (personal observation 2015). An alternative explanation may be that soil layering, not just SOM, is an important factor in controlling the amount of water available to the shallow roots of *P. grandis* (Huang et al. 2011; Naeth, Chanasyk, and Burgers 2011). Thus, the objective of this study is to characterize the influence of both SOM and soil layering on the amount of water available to *P. grandis*. We accomplish these objectives by first characterizing soils from under a variety of tree canopies on two atolls in the central Pacific Ocean, one wet (Palmyra Atoll, ~400 cm/yr) and one dry (Nikumaroro Atoll, ~100 cm/yr), and their water holding capacities at different saturation states. We then use measured soil characteristics to help parameterize a HYDRUS-1D model to investigate the influence of soil layering and soil depth on soil water status. Finally, we model soil water status under different organic cap thicknesses (0, 14, 30 and 50 cm) for four different annual precipitation amounts (50, 100, 200 and 400 cm/yr) and three different rainfall intensities (1, 5 and 10 cm/day), which are representative of the conditions under which *P. grandis* are known to exist (Mueller-Dombois and Fosberg 1998).

## 2 | Methods and Materials

### 2.1 | Study Sites

This work was conducted across two small coral atolls—Palmyra Atoll (5°53'1" N 162°4'42" W) and Nikumaroro Atoll (4°40'32" S 174°31'4" W)—that have similar underlying morphology but strongly different precipitation patterns. Both atolls are formed of coral rubble and sand sourced from the surrounding fringing reef complex and consist of a series of small islets surrounding a central lagoon (although in Palmyra this lagoon was split into two lagoons by a causeway constructed during WWII). Neither has any elevation greater than 2 m above sea level. The total exposed land area of Palmyra Atoll is about 2.5 km<sup>2</sup> (Collen, Garton, and Gardner 2009), whereas for Nikumaroro Atoll, it is approximately 4.3 km<sup>2</sup>, and on both atolls, the land surface

is covered by a mix of native atoll vegetation, including large monospecific stands of *P. grandis* and abandoned *C. nucifera* plantations.

Both atolls currently enjoy high levels of protection (Figure 1). Palmyra is protected as part of the Palmyra Atoll National Wildlife Refuge, managed by the US Fish and Wildlife Service and The Nature Conservancy, and is part of the Pacific Remote Islands Marine National Monument. It has no permanent human residents although there is a well-established research station on the island run by The Nature Conservancy. Nikumaroro Atoll is part of the Phoenix Island Protected Area (PIPA), one of the largest marine reserves in the world, and is part of the Small Island Developing State nation of Kiribati. Nikumaroro is fully uninhabited. Although the research station at Palmyra does use some water (including potable water) in support of research and management activities, this all comes from rainfall collection such that ecohydrological dynamics at both atolls are not influenced by groundwater pumping.

The atolls do have some notable differences. Palmyra was heavily utilized as a military base during WWII; this use included extensive dredging of lagoons, the creation of a large and deep channel into the lagoon, the connection of previous disconnected islets or motus, the creation of a causeway splitting the central lagoon in two and the creation of artificial islets from dredge spoils. In contrast, Nikumaroro atoll, oriented NW–SE, has a nearly intact atoll rim in all but two locations. Access to the atoll and its lagoon is extremely restricted as the atoll is ringed by a wide, shallow, fringing reef complex. However, the most notable difference between the atolls is probably the precipitation differences. The average reported annual rainfall in Palmyra is over 400 cm a year, comparable with other wet islands, particularly those in the western Pacific (Mueller-Dombois and Fosberg 1998). In contrast, PIPA lies at the edge of the Pacific equatorial dry zone, between the Intertropical Convergence Zone (ITCZ) and the South Pacific Convergence Zone (SPCZ). Precipitation is variable and strongly correlated with El Niño, but on average, the area receives 50–100 cm of rain a year depending on the ENSO

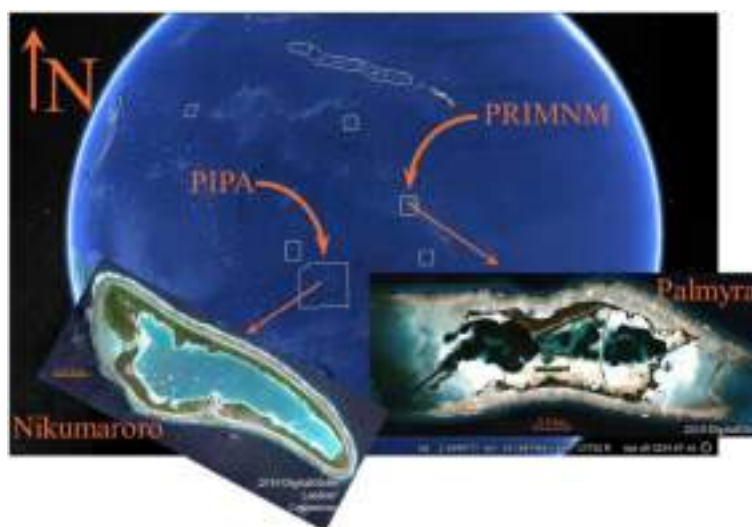
phase (Mueller-Dombois and Fosberg 1998). Nikumaroro is on the western edge of the PIPA and may be on the wetter end of the range but is likely still much drier than Palmyra. However, despite high annual precipitation, even at Palmyra, it is typical for there to be periods of several days to weeks with no rainfall. Given the high hydraulic conductivity of the typical atoll soils (50–400 m day<sup>-1</sup>), these short dry spells would require plants to extract water from the freshwater lens or other water sources (Bailey, Jenson, and Olsen 2010).

## 2.2 | Soil Sampling and Site Characterization

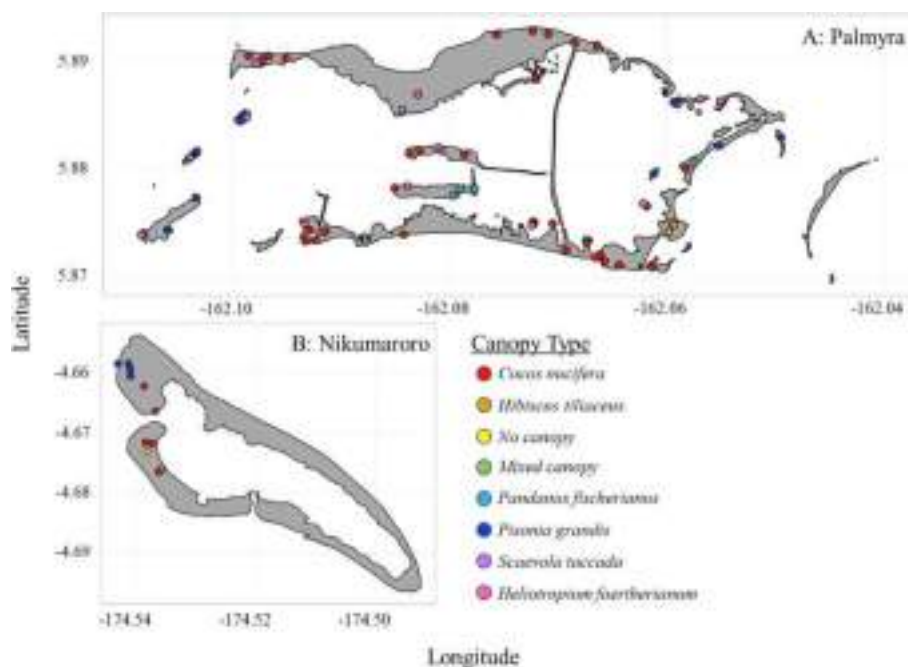
On Palmyra, 72 samples were collected across the atoll in the fall of 2016. Exact sampling locations were chosen based on extensive previous vegetation sampling in the area to encompass soil environments under seven different canopy types (mixed canopy, *P. grandis*, *S. taccada*, *H. foertherianum*, *C. nucifera*, *Pandanus fischerianus* and *Hibiscus tiliaceus*), a range of productivity levels and the entire range of islet sizes (Figure 2). Three of the samples from Palmyra were originally classified as having no canopy cover; however, upon re-examination of site photos, we determined that these samples all had substantial canopy cover within a meter of the sampling location. Due to the likely influence of the nearby canopy cover on the development of soil properties, we reclassified those samples to correspond to the dominant nearby canopy cover type. As a result, there are no ‘no canopy’ samples from Palmyra. Sampling on Nikumaroro was more limited due to time constraints, but included soil samples were collected at 11 sites under three different canopy types (no canopy, *P. grandis* and *C. nucifera*); this sampling was conducted during the summers of 2014 and 2015.

### 2.2.1 | Soil Samples

After removing leaf litter, we collected ~ 600 g soil samples from the upper 20 cm of the surface profile including, where present, the O horizon, as ‘Jemo’ soils (Fosberg 1954) found under *P. grandis* are sometimes classified as a single deep O horizon.



**FIGURE 1** | Location of study atolls. White boxes show the boundaries of the marine protected areas. Palmyra Atoll is part of the Pacific Remote Islands Marine National Monument (PRIMNM), and Nikumaroro is part of the Phoenix Island Protected Area (PIPA).



**FIGURE 2** | Sampling locations on locations on (A) Palmyra Atoll in 2016 and (B) Nikumaroro in 2014 and 2015. Colour coding indicates the dominant canopy type at each sampling location.

Given the very coarse-textured, rocky soil typical of atolls, we used a water-replacement method (Page-Dumroese et al. 2010) to measure soil bulk density, which determines sample volume by lining the sample hole with a thin plastic layer and recording the volume of water needed to fill the hole to the reference surface. Soil samples were then air-dried and returned to the lab for further analysis.

## 2.3 | Laboratory Analyses

Soil samples were sieved and partitioned into greater and less than 2 mm particle size fractions (Staff 2014). The > 2 mm fraction was hand-sorted into organic, inorganic and anthropogenic (clearly human-generated materials such as metal or plastic pieces) classes, whereas the remaining fine earth fraction (<2 mm) was analysed for SOM, soil nutrients, pH and water retention characteristics.

### 2.3.1 | Soil Properties

Subsamples of each soil were sent to Brookside Laboratories Inc. (New Bremen, OH) for comprehensive nutrient analysis using their Standard Soil Assay with Bray 1 (S001PN) and their carbon nitrogen ratio test (S202). Analyses included determinations of carbon–nitrogen ratios, total exchangeable cations, pH, organic matter content and amount of macro (sulfur, phosphorus, calcium, magnesium, potassium, sodium and nitrate nitrogen [and ammonia]) and micro (boron, iron, manganese, copper, zinc and aluminium) nutrients. Additional measures of organic matter and pH were determined in-house for cross-verification purposes. Organic matter characterization followed Dean's (1974) method for the determination of organic matter in carbonate soils, and pH was determined using the saturated paste method

described by the NRCS Soil Survey Manual (Staff 2014). Soil organic carbon (SOC) was calculated using the Van Bemmelen factor of 1.724, where  $SOC = SOM/1.724$  (Van Bemmelen 1890).

To allow us to isolate soil water osmotic potential, soil pore water electrical conductivity ( $EC_{1:5}$ ) was measured using shaking methods described by He et al. (2013) due to limited sample volume. Samples with insufficient headspace due to organic matter expansion were diluted in a 1:5 soil:water ratio before measuring.  $EC_{1:5}$  was converted to  $EC_e$  using a power curve developed for these soils (He et al. 2013).

### 2.3.2 | Soil Water Retention Characteristics

A combination of methods was used to determine the water retention characteristics of these soils. Common values for saturation (SAT, 0 MPa), field capacity (FC,  $-0.033$  MPa) and permanent wilting point (PWP,  $-1.5$  MPa) were used to model soil water retention curves and calculate plant available water.

### 2.3.3 | Saturation

We determined the water content at saturation using an array of Bruckner funnels connected to a Mariotte bottle filled with deionized (DI) water. Sample material was placed in the funnels to a depth of  $\sim 1$  cm of dry material and then was slowly saturated from the bottom via the Mariotte bottle with a head reference above the soil surface. Once completely saturated, the head reference in the Mariotte bottle was dropped to the level of the frit on the bottom of the Bruckner funnels and allowed to drain for 24 h. Samples were then removed from the funnels, weighed, oven-dried for 24 h at  $105^\circ\text{C}$  and then re-weighed. Twenty-five per cent of the samples were dried for

an additional 24 h and then re-weighed to ensure adequacy of drying time. Replicate saturation measurements were made for 7% of the samples. Gravimetric water content was calculated as the difference in mass between the wet and oven-dry samples and converted to volumetric water content using in situ bulk density. Volumetric water content was not determined directly because of significant volume uncertainties associated with the swelling of incompletely decomposed organic matter in highly organic soils.

### 2.3.4 | Field Capacity

Pressure plates were used to determine water retention at  $-0.033$  MPa (Staff 2014) in duplicate when sample volume allowed (37%, 83 total samples).

### 2.3.5 | PWP

The dry end of the water retention curve was characterized using a dewpoint potentiometer (WP4, Meter, Pullman, WA). Oven-dry soils were mixed with triple distilled DI water to prescribed gravimetric water contents and measured to determine soil water potential. Multiple soil slurries were mixed for each sample to ensure several samples were within the  $-1$  MPa to  $-1000$  MPa range. Interpolation of the water content at the PWP ( $-1.5$  MPa) followed methods described by Campbell (2012). Soil matric potential was calculated by subtracting the osmotic potential, estimated as  $0.36 \cdot EC_e$  (Myrold et al. 1981) from each WP4 measurement.

The above water retention measurements were expanded for several representative samples using a Hyprop sensor (Meter, Pullman, WA). Methods followed UMS (UMS GmbH 2015),

except that samples were re-packed into cores using damp  $< 2$  mm soil before saturation. Water retention curves were developed by adding saturation, pressure plate and EC-corrected WP4 data points ( $-0.1$  MPa to  $-300$  MPa) to the Hyprop data (0 to  $-0.1$  MPa) and parameterized using a Mualem–van Genuchten model (van Genuchten 1980). Mualem–van Genuchten values ( $\theta_r$ ,  $\theta_s$ ,  $\alpha$  and  $n$  defined below in Table 1) were determined by fitting curves to laboratory-derived water content and potentials of representative ‘organic’ and ‘mineral’ soils using the SWRC fit (Seki 2007) and Hyprop measurements (UMS GmbH 2015). Both representative soils were from Palmyra and the ‘organic’ soil (DUD-PG1) had a *P. grandis* canopy, whereas the ‘mineral’ soil (KAU-ST2) had a *C. nucifera* canopy.

## 2.4 | Statistical Analysis and Modelling

Soil sample data were examined to determine if the development of SOM differed depending on canopy type or the annual precipitation regime, as represented by the different islands (dry Nikumaroro and wet Palmyra). *C. nucifera* and *P. grandis* were the only canopy types present on both islands, so the initial analysis of SOM was restricted to those canopy types. Before analysis, the data were screened for assumptions (linearity, homogeneity, normality and outliers). One sample was identified as an outlier (using standardized Z-scores) and was removed from the analysis. A  $2 \times 2$  factorial analysis of variants (ANOVA) was analysed on canopy types (*C. nucifera* and *P. grandis*) and islands (Nikumaroro and Palmyra). Independent *t*-tests with a Bonferroni correction were performed to further examine differences in SOM by canopy type on each island.

To assess SOM development under a more diverse suite of canopy types (*C. nucifera*, *H. tiliaceus*, mixed canopy, *P. fischerianus*,

**TABLE 1** | HYDRUS-1D parameter and boundary conditions.

Variable	Unit	Values	Sources
Annual precipitation, <i>AP</i>	cm/yr	50, 100, 200, 400	Mueller-Dombois and Fosberg (1998)
Residual water content, $\theta_r$	$\text{cm}^3 \text{cm}^{-3}$	0	Calculated <sup>a</sup>
Saturated water content, $\theta_s$	$\text{cm}^3 \text{cm}^{-3}$	0.786, 0.511	Calculated <sup>a</sup>
Fitting parameter, $\alpha$	$\text{cm}^{-1}$	0.2832, 0.107	Calculated <sup>a</sup>
Fitting parameter, $n$	(–)	1.191, 1.629	Calculated <sup>a</sup>
Sat. hydraulic conductivity, $K_s$	$\text{cm day}^{-1}$	50, 5000	Bailey, Jenson, and Olsen (2010)
Organic soil depth	cm	0, 14, 30, 50	Batianoff et al. (2010a); Fosberg (1954)
Rooting demand	cm	0–10 cm (100%) 20–50 cm (100% => 0%)	Christophersen (1927)
Evapotranspiration, <i>ET</i>	$\text{cm day}^{-1}$	0.5	Krauss et al. (2015)
Precipitation intensity, <i>PI</i>	$\text{cm day}^{-1}$	1, 5, 10	Krauss et al. (2015)
Precipitation duration, <i>PD</i>	days	0.5	Estimated
Precipitation frequency, <i>PF</i>	days	$PF = AP / (365 \times PI \times PD)$	Calculated

<sup>a</sup>Derived from representative water retention curves.

*P. grandis*, *S. taccada* and *H. foertherianum*), we restricted the analysis to Palmyra only. We analysed the data using a univariate between-subject ANOVA. Before analysis, the data were screened for assumptions (linearity, homogeneity, normality and outliers). Six samples were identified as outliers (using standardized Z-scores) but were not removed from the analysis because we had no indication of issues with the identified samples. An independent *t*-test with Bonferroni correction was used to examine differences between groups.

All statistics were computed in R v4.3.2 (R Development Core Team 2016) using  $\alpha=0.05$  to determine significant differences.

## 2.4.1 | Modelling

Vadose zone hydrology was modelled using HYDRUS-1D (Šimůnek et al. 2008). All model runs consisted of a 200 cm vertical soil column with model discretization at 2 cm and soil hydraulic characteristics parameterized using values from the Mualem–van Genuchten model (van Genuchten 1980) as follows:

$$\theta(h) = \begin{cases} \theta_r + \frac{\theta_s - \theta_r}{[1 + |\alpha h|^n]} m & h < 0 \\ \theta_s & h \geq 0 \end{cases} \quad (1)$$

$$K_{(h)} = K_s S_e^{0.5} \left[ 1 - (1 - S_e^{0.5/m})^m \right]^2 \quad (2)$$

$$m = 1 - \frac{1}{n} \quad n > 1 \quad (3)$$

$$S_e = \frac{\theta - \theta_r}{\theta_s - \theta_r} \quad (4)$$

where  $h$  is the pressure head (cm),  $\theta_r$  is the residual water content ( $\text{cm}^3 \text{cm}^{-3}$ ),  $\theta_s$  the saturated water content ( $\text{cm}^3 \text{cm}^{-3}$ ) and  $\alpha$  and  $n$  are empirical parameters, where  $\alpha$  is related to the air-entry pressure value and  $n$  is related to the pore size distribution.  $K_s$  is saturated hydraulic conductivity ( $\text{cm h}^{-1}$ ), and  $S_e$  is the relative soil saturation.

Mualem–van Genuchten model fitting parameters ( $\theta_r$ ,  $\theta_s$ ,  $\alpha$  and  $n$ ), derived as described above, and other various boundary conditions used to parameterize the HYDRUS-1D model are listed in Table 1.  $K_s$ , which is required for the HYDRUS-1D modelling, was not well constrained during curve fitting to sampled soils and so was estimated from the literature. Fibrous peat, with a  $K_s$  of 50 cm/day, was used as a proxy for the organic soil hydraulic conductivity (Wong, Hashim, and Ali 2009), but the estimate of carbonate sand  $K_s$  of 5000 cm/day came from Bailey, Jensen, and Olsen (2010). Potential root-water uptake in the model is at a maximum between 0 and 10 cm depth for all profiles, which corresponds to the primary rooting depth of *P. grandis* (T. Walker 1991). Below 10 cm soil depth, potential root-water uptake decreases linearly to 50 cm depth in all soil profiles. To minimize the number of model runs precipitation duration was estimated at 0.5 days and held constant for all scenarios. Model

sensitivity analysis was run on each of the individual model parameters to determine which factors had the greatest control over system dynamics.

Model scenarios were run under conditions to capture both the limits of soil water capacity and conditions representative of natural precipitation variation. In the endmember scenarios, fully saturated unlayered single-type (mineral or organic) soil horizons desaturated by internal drainage and ET until water content at the bottom of the main root zone (10 cm) reached equilibrium. In the natural variation scenarios, four different profiles consisting of progressively thicker organic soil caps (0, 14, 30 and 50 cm) were layered over a sand profile to approximate the range of naturally occurring organic soil depths. Beginning soil water conditions were set at FC, and various combinations of rainfall frequency and intensity were applied to the model until starting model conditions were no longer impacting soil water status. Precipitation intervals were determined as a function of total annual precipitation and precipitation intensity, and model precipitation duration was fixed at 0.5 days. Dry-down commenced after a rainfall event, and stable water content at the bottom of the main root zone (10 cm) was taken to be PWP.

## 3 | Results

### 3.1 | Laboratory Analyses

#### 3.1.1 | SOM Content

Soil nutrient data other than SOM and SOC were not relevant to the questions in this paper and so are not presented here but are included for completeness in Appendix S1. A two-way ANOVA was performed to evaluate the effects of the precipitation regime, as represented by islands, and canopy type on SOM. The means and standard deviations for SOM are presented in Table 2. The results indicated no significant main effect for island, ( $F(1, 49) = 1.30$ ,  $p = 0.26$ ,  $\eta^2 = 0.03$ ); a significant main effect for canopy type, ( $F(1, 49) = 34.46$ ,  $p < 0.001$ ,  $\eta^2 = 0.41$ ); and a significant interaction between island and canopy type, ( $F(1, 49) = 4.81$ ,  $p = 0.03$ ,  $\eta^2 = 0.09$ ). Investigating the interaction further, on the dry Nikumaroro, SOM under *P. grandis* canopies was significantly greater than under *C. nucifera* ( $p = 0.003$ ,  $d = 2.97$ ). On wet Palmyra, SOM was also significantly greater under *P. grandis* canopies than under *C. nucifera*, and though the confidence in the difference is greater, the effect is smaller ( $p = < 0.001$ ,  $d = 1.41$ ).

An additional one-way ANOVA was performed to evaluate the relationship between the larger variety of canopy types and

**TABLE 2** | Descriptive statistics for SOM by island and canopy type.

Island	Canopy type	M	SD	N
Nikumaroro	<i>Cocos nucifera</i>	3.97	2.55	5
	<i>Pisonia grandis</i>	35.66	16.04	4
Palmyra	<i>C. nucifera</i>	8.11	5.40	34
	<i>P. grandis</i>	22.56	19.62	10

SOM on Palmyra alone. The ANOVA was significant at the 0.05 level, ( $F(6,65)=3.41$ ,  $p=0.005$ ,  $\eta^2=0.24$ ). An independent  $t$ -test with Bonferroni correction was used to examine differences between groups. As can be seen from the means and SD in Table 3, there were no significant differences between groups except between *C. nucifera* and *P. grandis* ( $p=0.029$ ,  $d=1.54$ ) and between *C. nucifera* and *H. foertherianum* ( $p=0.012$ ,  $d=1.37$ ).

### 3.1.2 | Water Retention

Figure 3 depicts trends in soil water retained at key matric potentials as a function of SOC. For these analyses, we use SOC instead of SOM (Table 3) to align with USDA taxonomic definitions for organic soils as  $>12\%$  SOC (Soil Survey Staff 2022). For all soils, the range of soil water content at saturation is 50%–80%, at FC is 10%–37%, and at PWP is 2%–25%, with a few outliers. At each measured soil water potential, the volumetric water content (VWC) is positively correlated with SOC content until  $\sim 10\%$  SOC at FC and PWP, or  $\sim 20\%$  SOC at SAT, after which additional increases in SOC do not result in greater VWC. Organic soils on average have a higher VWC at saturation than the mineral soils, but only slightly higher water content at FC. However, the available water in soils between FC and PWP is

significantly different ( $t(540)=-9.21$ ,  $p<0.001$ ,  $d=0.94$ ) between the organic soils ( $M=18.19$ ,  $SD=4.71$ ) and the mineral soils ( $M=13.33$ ,  $SD=5.29$ ). Those differences are even more significantly different ( $t(563)=-17.98$ ,  $p<0.001$ ,  $d=1.83$ ) between SAT and PWP in the organic soils ( $M=69.93$ ,  $SD=4.61$ ) and mineral soils ( $M=53.05$ ,  $SD=10.16$ ), which is important to determine given the uncertainty about FC measurements in highly organic soils.

Water retention characteristics of two representative soil samples show the similarities and differences between soil types (Figure 4). In both cases,  $\sim 80\%$  of water is removed from the profile by the time the soil is at FC, and 85% and 94% of the water are lost by PWP for organic and mineral soils, respectively. The mineral soil has a distinct flexure point (air-entry value) in water content that occurs at 1 pF, which is not present in the organic soil, and a less abrupt flexure point at  $\sim 1.5$  pF.

### 3.2 | Modelled Soil Water Potential and Storage

There were a total of 50 unique HYDRUS-1D model runs resulting from the various combinations of soil and model boundary conditions (Table 1). In a pure mineral soil profile, time from FC to no further change at 10cm depth occurred after 9.0 days. In

TABLE 3 | Descriptive statistics for SOM and SOC on Palmyra by canopy type.

Canopy type	M SOM	SD SOM	M SOC	SD SOC	N
<i>Cocos nucifera</i> <sup>a</sup>	8.11	5.40	4.71	3.13	34
<i>Heliotropium foertherianum</i> <sup>a</sup>	27.83	28.18	16.14	16.34	11
<i>Hibiscus tiliaceus</i>	20.04	24.06	11.63	13.95	3
Mixed canopy	9.27	1.12	5.37	0.65	2
<i>Pandanus fischerianus</i>	16.96	11.05	9.84	6.41	8
<i>Pisonia grandis</i> <sup>a</sup>	26.29	22.35	15.25	12.96	11
<i>Scaevola taccada</i>	10.93	4.86	6.34	2.82	3

<sup>a</sup>Canopy types with significant SOM differences.

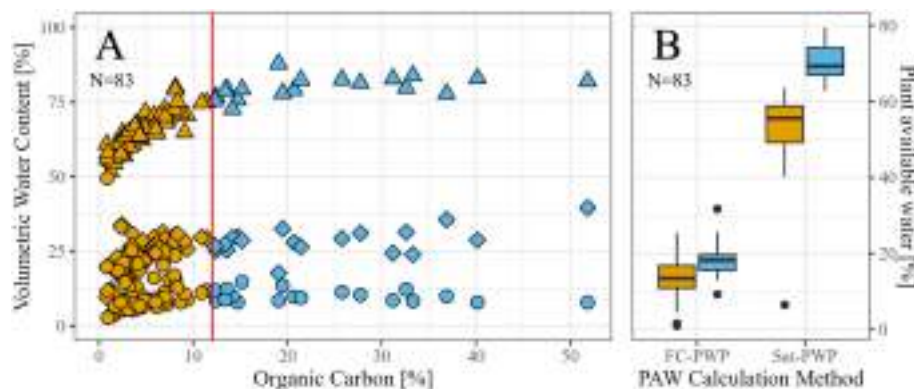
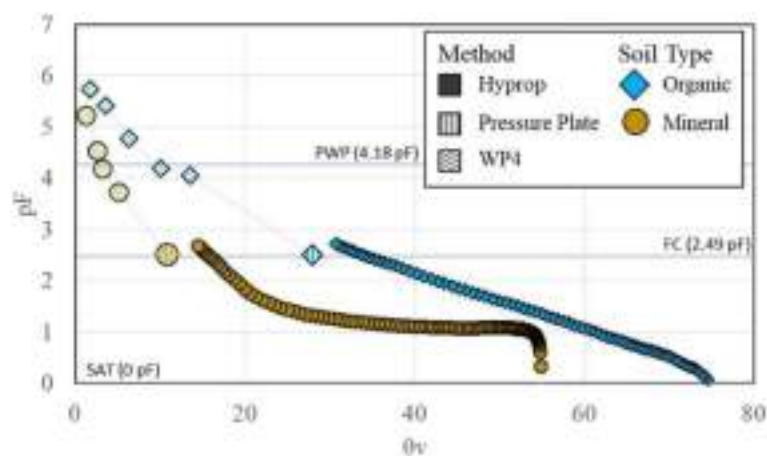
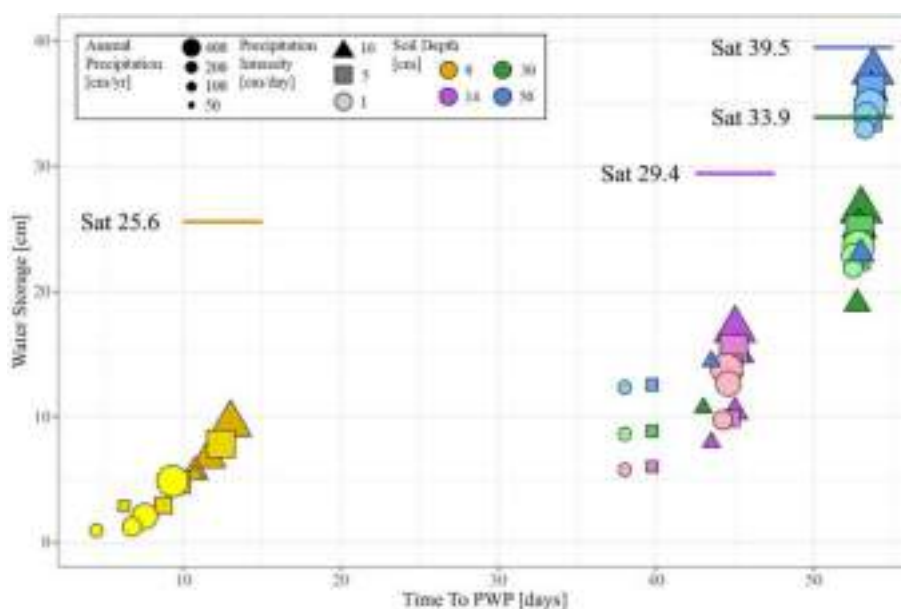


FIGURE 3 | (A) Volumetric water content versus organic carbon percentage of soils at three different saturation states: saturation, 0MPa (triangles); field capacity, 0.03MPa (diamonds); and permanent wilting point, 1.5MPa (circles) for mineral (orange) and organic (blue) soils. The vertical red line at 12% SOC indicates the USDA distinction between organic and mineral soils. (B) Amount of plant-available water in per cent held between FC and PWP and SAT and PWP for mineral (orange) and organic (blue) soils.



**FIGURE 4** | Measured soil water retention data for an organic soil (DUD-PG1) and a mineral (KAU-ST2) soil. Curves combine data from three different methods of measuring soil water content to cover the range of pressures in which plant roots operate. pF is the log of soil water matric potential in hPa.



**FIGURE 5** | Comparison of the amount of water stored in the upper 50 cm of the soil profile and the time until the upper 10 cm (primary rooting zone) of the soil profile reaches the permanent wilting point (PWP). The depth of the organic cap is indicated by marker colours, the intensity of rainfall events is indicated by marker shades, and the annual precipitation for different islands is indicated by marker size. The calculated maximum amount of water stored at saturation for the upper 50 cm of the profile is indicated by horizontal lines in each class. In general, increasing organic cap depth and increasing rainfall intensities result in more water in storage and a longer time to dry down. This pattern holds across the range of annual precipitation.

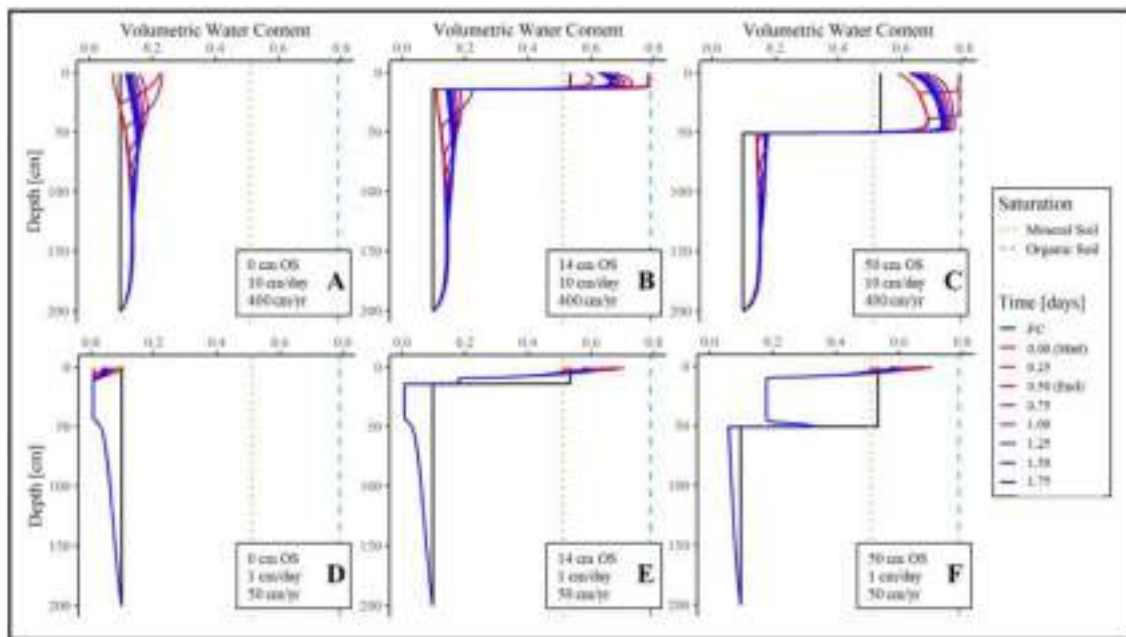
a pure organic soil profile, time from FC to no further change at 10 cm depth occurred after 37.0 days. Increasing the starting soil water status to saturation increased the dry-down time to PWP to 13.5 days for mineral soils and 53.75 days for organic soils, representing a 44% and 45% increase in dry-down time, respectively.

Figure 5 shows soil profile water content in the root zone (0–50 cm) vs. PWP. The four profiles include a pure mineral soil profile and three-layered soil profiles with increasing organic cap thickness (14, 30 and 50 cm), under three different rainfall intensities (low, 1 cm/day; medium, 5 cm/day; and heavy, 10 cm/day) and four different annual precipitation regimes (very dry,

50 cm/yr; dry, 100 cm/yr; wet, 200 cm/yr; and very wet, 400 cm/yr). In general, these modelled results show that for profiles with an organic soil cap overlaying mineral soil, increasing organic soil cap thickness increases time to PWP under all precipitation intensities and all annual precipitation regimes. Water content in the upper 50 cm of the profiles also increases with increasing organic cap thickness, though this is moderated by rainfall frequency and intensity.

In the 0 cm organic soil case (i.e., pure mineral soil–sand), no portion of the profile reaches saturation regardless of rainfall frequency or intensity (Figure 6). In these profiles, only the upper 50 cm ever exceeds FC, except for under medium and





**FIGURE 6** | Volumetric water content of representative soil profiles under 0 cm (A,D), 14 cm (B,E) and 50 cm (C,F) organic caps during and post a precipitation event. Plots A–C represent the wet island extremes, with 400 cm/yr precipitation at 10 cm/h intensity, and plots D–F represent dry island extremes with 50 cm/yr precipitation and 1 cm/h intensity. The black line (FC) indicates the model starting condition, and the coloured lines indicate model timesteps in days. Dotted lines represent maximum saturation for different soil types.

heavy rainfall intensities on very wet islands. In those conditions, the entire lower portion profile remains above FC, whereas the upper 50 cm oscillates between increased water content (max ~45% of SAT) to below FC between precipitation events. The time to PWP in sand ranges from 4.5 to 13 days (Figure 5).

With a 14 cm organic cap, no portion of the cap reaches saturation under low rainfall intensity (Figure 6). At medium and heavy rainfall intensities, the organic cap saturates completely on all islands except the extreme dry islands. On very dry islands, the upper half of the organic cap saturates, but the lower half of the cap remains near PWP. The mineral portion of the profile on dry islands never gets above FC, but on wet and very wet islands, the mineral portion of the profile remains at or above FC except for on wet islands with heavy rainfall intensities when the interval between precipitation events is 9.125 days or greater. Under these conditions, the top 36 cm of the mineral profile drops below FC between rainfall events. The time to dry down with a 14 cm organic cap ranged from 38 to 45 days (see Figure 5).

With a 30 cm organic cap, no portion of the cap reaches saturation under low rainfall intensity. At medium and heavy rainfall intensities on all islands, a fraction of the organic cap saturates, but only under heavy rainfall intensities on wet and very wet islands does the cap saturate completely. The mineral portion of the profile on the very dry islands never gets above FC, but on dry, wet and very wet islands, the mineral portion of the profile remains at or above FC except on dry islands under heavy rainfall intensity when the interval between precipitation events is 18.25 days. The time to dry down with a 30 cm organic cap ranged from 38 to 53 days.

With a 50 cm organic cap (Figure 6), no portion of the cap reaches saturation under low rainfall intensity. At medium and heavy rainfall intensities, a fraction of the organic cap saturates, but not completely. The mineral portion of the profile remains below field capacity on very dry islands, near FC on dry islands and above FC on wet and very wet islands. The time to dry down with a 50 cm organic cap ranges from 38.0 to 53.75 days.

## 4 | Discussion

At our study sites, canopy type is a major control on SOM development. Soils under *P. grandis* accumulate significantly more SOM than soils under *C. nucifera*. This is in line with findings from many other studies of atoll island soils (Christophersen 1927; Fosberg 1954; Niering 1963; T. Walker 1991; Young et al. 2010b) and is generally attributed to higher guano inputs from the close relationship *P. grandis* has with seabirds. Our data show that some of the SOM variability is additionally driven by precipitation regimes. On wet Palmyra, the SOM difference between canopy types was less pronounced than on dry Nikumaroro. This may be partially explained by the small number of samples from Nikumaroro, but SOM in drier conditions is known to decompose more quickly as well (Cotrufo and Lavelle 2022). Given the similarity between these two atolls in terms of temperature, parent material and biodiversity, it may be that in areas without high levels of soil moisture, such as expected under *C. nucifera*, soil bacteria are less constrained, resulting in faster breakdown of SOM.

Our data additionally show that organic soil development is not limited to soils under *P. grandis*. On Palmyra, we found

that *H. foertherianum* also showed significant SOM enrichment relative to soils under *C. nucifera*. The soils under both these canopies had mean SOC above 12% (*P. grandis*, 15.25%; *H. foertherianum*, 16.14%), meeting the USDA definition for organic soils. *H. tiliaceus*, which also developed higher levels of SOM (Table 3), had a SOC average of 11.63%, putting it right on the edge of being an organic soil. There were only three samples from this canopy type; however, additional sampling might help clarify the canopy–SOM relationship for this species. *P. fischerianus* had a surprisingly high average SOC (9.84%) given that it shares the same frond-dominated morphology as *C. nucifera*, which typically limits nesting by seabirds. However, work by Titmus, Arcilla, and Lepczyk (2016) suggests that although *P. fischerianus* tends to host fewer seabird nests than *P. grandis*, it typically hosts more than *C. nucifera*, which could help explain the higher SOC enrichment. *C. nucifera* soils in this study have low SOC which is consistent with previous findings on Palmyra by Young et al. (2010) and is likely due to low utilization by seabirds and slow decomposition of deposited biomass from these trees due to high lignin contents (Abdul Khalil et al. 2006).

The water in these soils varies greatly by composition. As expected, we see an increase in the amount of water stored in organic soils relative to mineral soils. Increases in SOC, up to about 10%, do increase the amount of water retained in atoll soils under different saturation states (Figure 3A). Our results indicate that between FC and PWP, there is ~7% more water retained in organic soils than in mineral soils (Figure 3B), and this amount increases to ~16% when comparing water retained between SAT and PWP. For these systems, plant available water is better characterized as between SAT and PWP than between FC and PWP as our modelling work shows that the water content of the organic soils is often above FC due to slow internal drainage. However, increasing SOC beyond 10% does not result in significant additional water storage at any saturation state (Figure 3A). This result aligns with the findings of Minasny and McBratney (2018).

Importantly, laboratory results do not represent likely field conditions; rather, they represent the minimum possible differences between these two soil types (i.e., comparing saturated condition to saturated condition). In situ conditions play a large role in how much water is available for plant use. For example, hydraulic conductivities of atoll mineral soils are very high ( $5 \times 10^3$  to  $4 \times 10^4 \text{ cm day}^{-1}$ ) (Bailey, Jenson, and Olsen 2010), so they are rarely saturated, even under intense and frequent rainfall ( $10 \text{ cm/h} \times 400 \text{ cm/yr}$ ; Figure 5). Our HYDRUS-1D modelling confirms this and indicates that only limited parts of the profile ever exceed field capacity, and under no combination of our modelled annual precipitation and rainfall intensities do these mineral profiles approach saturated conditions (Figure 6A). The maximum time to PWP in conditions representative of natural precipitation variation was 13 days (Figure 5), with the mineral profile reaching a maximum of ~45% saturation. The time to PWP for a completely saturated mineral profile is 13.5 days, suggesting that water retained in the mineral profile above 45% saturation provides very limited additional time for plants to access soil water if they can do so.

The presence of a layered organic soil cap changes soil water retention in both the mineral and organic soils, increasing plant

available water, especially in the organic cap. The mechanism for this increased water storage in organic caps is the likely formation of a capillary barrier where fine pores of the organic soils meet the coarser textured carbonate sands and rubble (Khire, Benson, and Bosscher 2000). The textural differences between organic and mineral soils in this study support this idea, as do the HYDRUS-1D modelling results. A capillary barrier restricts vertical water movement across this barrier and helps retain water within the organic layer, as has been shown in other layered soil situations (Huang et al. 2011; Naeth, Chanasysk, and Burgers 2011).

In our modelling work, the presence of an organic cap results in anywhere from 2 to 13 times as much water by volume stored in the upper 50 cm of the profile as compared to the same volume of sand. This would substantially increase the water available to *P. grandis* and other soil-building atoll natives, suggesting that the development and layering of these organic soils is an important mechanism for overcoming water limitations. How often those atoll ecosystems experience water limitation depends greatly on their exposure to ENSO phase and proximity to major oceanographic features such as the ITCZ or the SPCZ. For example, between 2011 and 2013 Krauss et al. (2015) found the maximum gap between precipitation events on Palmyra was 12 days, but on Kanton atoll in 2011, which is the closest weather station to Nikumaroro, the month of March had no rainfall accumulation (Bureau of Meteorology n.d.). Our work shows that even thin (14 cm) layers of organic soil can extend water availability upwards of a month, which should be enough to buffer plants and any establishing seedlings with access to the organic cap water resources, from short- to medium-term drought conditions. The development of shallow roots, a characteristic for which *P. grandis* is known, would permit efficient extraction of this stored soil water. This finding supports our hypothesis that soil layering is an important factor in determining the amount of soil water available to *P. grandis*. Assuming *P. grandis* roots can exploit the full depth of the organic layer, this reserve may help explain why *P. grandis* can survive on very dry atolls like [V] Daugo Island, where the estimated annual rainfall was as low as 7 cm per year (Bell 1969).

One unclear thing, particularly on dry islands, is how these organic soils develop in the first place. *P. grandis* are known for their large leaves, brittle parenchyma-rich wood and close association with sea birds (Mueller-Dombois and Fosberg 1998; T. Walker 1991), all of which provide source material for the development of organic-rich soils. However, soils with significant amounts of SOC only occur where the decomposition rate is less than the accumulation rate of the organic matter. Usually, this is associated with environments that limit the microbial breakdown of organic matter. In the tropics, where low temperatures are not a factor, microbial activity is primarily limited by the saturation state of soils. Soils that are too dry will not support the bacterial communities necessary to effectively break down SOM, and soils that are too wet will limit aerobic decomposition. High rates of internal drainage as suggested by very high hydraulic conductivities typically found on tropical atolls (Bailey, Jenson, and Olsen 2009) would normally preclude the accumulation of excess water in the vadose zone. However, this study demonstrates that when organic soils are layered on top of coarse sandy soils, the organic layer

can remain close to saturation, setting up environments conducive to greater accumulations of organic material. Where the organic cap is discontinuous or very thin, due to disturbance or incomplete formation, the organic material is likely prone to oxidation and decomposition.

One mechanism that might increase the water content of thin or discontinuous soils is the development of a phosphatic hardpan known to be associated with *P. grandis* and Jemo soils. Fosberg (1994) describes the formation of this hardpan because of phosphate in seabird guano being mobilized in the acidic environment of *P. grandis* soils and percolating down the soil profile until it neutralizes and precipitates out at the alkaline calcareous surface. Although the hydraulic conductivity of the hardpan is unknown, it is certainly less than underlying carbonate sands and gravels and suggests it could be a restrictive boundary. If this hardpan can develop in small, localized areas, it may help keep the water content of the overlying soil and litter layers high enough to reduce microbial activity and enhance the development of thicker and more continuous organic soil layers. The effects of hardpan were not modelled as part of this study, as they cause model instability when included with hydraulic conductivities close to zero but are an important area for further research.

The presence of capillary barriers may resolve some of the mysteries of atoll soils pointed out by other authors. For example, Shaw (1952) attributes the failure of *P. grandis* forests on Karangbandong island, off Noesa Kambangan on the south coast of Central Java to soil loss. He speculates that seabirds abandoned the trees and islands, and thus, *P. grandis* was failing due to a lack of nutrients supplied by seabird guano in the soil. The work of Young and colleagues (Young, McCauley, and Dirzo 2011; Young et al. 2010a) does suggest that the supply of nutrients could be an issue; however, this work suggests, perhaps more critically, that the loss of soil would result in the loss of water reserves for *P. grandis*. In another example, Deenik and Yost (2006) document soils with high SOC contents associated with historic locations of *P. grandis* across the Marshall Islands but were puzzled that SOC concentrations did not follow the climate gradients as expected (low accumulation where dry, high accumulation where wet). Instead, they find high concentrations of SOC on both wet and dry islands and some low concentrations on wet islands where the soils are heavily altered by humans. This pattern makes sense if the layered soil structure that creates a capillary barrier remains mostly intact on the relatively undisturbed wet and dry islands and if the capillary barrier structure has been destroyed on wet atolls with significantly disturbed soils.

Plant-mediated development of a capillary barrier as a water management strategy, to these authors' knowledge, has not previously been described. The strong association between *P. grandis* and the highly organic Jemo soils suggests *P. grandis* is actively engineering its environment to enhance its access to water. This work also indicates highly organic soils develop in association with other island species, suggesting that this water management strategy may not be unique to *P. grandis*. This strategy has wider ecosystem implications for the development of atoll island soils and tree-species cover across the precipitation gradient. Where *P. grandis* and other organic soil-building species are present, accumulation of SOM is likely to occur at higher rates than is predicted by environmental controls. This

in turn can enhance vegetative cover and support the growth of species that would otherwise be water and nutrient limited. However, if these soil-building species are disturbed or removed, the ecosystem shift, including loss of SOM, tree canopies and changes in species composition, may be large and rapid. This dynamic may help explain the vegetation shifts described by Batianoff et al. (2010b) found in the Coringa-Herald National Nature Reserve, Australia.

Beyond an atoll context, naturally engineered capillary barriers may be more widely present than previously understood. For example, Lichner et al. (2013) found unsaturated hydraulic conductivities up to two orders of magnitude less in biocrusts that develop in dryland ecosystems than in the underlying sand, which would suggest that the development of a capillary barrier is likely occurring. Eldridge et al. (2020), in their synthesis study, found that the presence of biocrusts in dryland ecosystems reduced infiltration and retained more moisture in the uppermost layers of the soil profile, with important implications for dry-land productivity and essential ecosystem services. Although they do not point to an explicit mechanism underlying the water retention, they do find this effect more pronounced when biocrusts were layered over sandy soils than when layered over loam or clay soil, again supporting the idea of the development of a capillary barrier.

## 5 | Conclusions

At our study sites, the presence of organic soils is strongly tied to the type of overstory canopy, in line with the findings of previous authors. Increases in organic content up to about 10% OC enrichment significantly increase the volume of water retained and the duration of water storage within the organic layer, but enrichment beyond ~10% does not lead to further increases. However, the presence of a layered organic soil cap changes soil water retention in both the mineral and organic soils, increasing plant available water, especially in the organic cap. The mechanism for this increased water storage is the likely formation of a capillary barrier. The textural differences between organic and mineral soils in this study support this idea, as do the HYDRUS-1D modelling results.

Our modelling indicates that even in dry conditions a shallow organic cap (14cm) can extend water availability to the tree by more than 3 weeks when compared with pure sand, which helps explain why *P. grandis* is found across such a wide precipitation gradient. This finding supports Fosberg's hypothesis that *P. grandis* is likely utilizing water stored in the Jemo soils that develop under their canopies, and our hypothesis that soil layering is an important factor in determining the amount of available soil water. Additionally, the development of capillary barriers can help explain the accumulation of organic matter in tropical settings and may be a key to understanding previously enigmatic atoll soil and vegetation patterns. This work is the first description of plant-mediated capillary barrier development as a water management strategy to our knowledge.

Although particularly prominent in this case, there may be other examples of this strategy employed both within atoll vegetation communities and in other terrestrial settings. More

investigations of this phenomenon would be helpful to better understand both the mechanics and the impacts of this water management strategy. For example, future studies using stable isotopes could clarify how plants extract water from these capillary barrier water reserves. If *P. grandis* (and other species) are primarily using water from above the capillary barrier for transpiration, we would expect this water, and thus the stems of *P. grandis*, to be enriched with heavy isotopes due to evaporation.

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## 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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### Supporting Information

Additional supporting information can be found online in the Supporting Information section.