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Abstract: Most forest soils contain substantial amounts of gravel. However, unlike the more widely known root resource uptake behaviors which respond to resource patches in substrate without gravels, how roots respond to substrate containing different gravel levels is poorly understood. We grew roots in substrates with five gravel levels (0, 10, 20, 30, and 40% of volume) in a subtropical *Schima superba* plantation, determined fine root dynamics and turnover rate with minirhizotrons, measured fine root morphological, architectural, mycorrhizal colonization, chemistry, and mass allocation. The presence of gravel in the substrate delayed the timing of peak root growth. In the substrate with higher gravel content, plants produced more roots in autumn, but there were fewer roots in summer and the roots tended to exhibit lower fine root turnover rate and mycorrhizal colonization, but higher root biomass allocation. The higher root biomass in the substrate with higher gravel content was associated with higher root carbon/nitrogen ratio. Our findings emphasize the complexity of root resource uptake behavior in response to gravel content and suggest that incorporating substrate gravel content into root studies may help to improve the prediction of patch exploitation and nutrient acquisition in stony soils.

Key words: heterogeneous patches, root phenology, root morphology, root architecture, mycorrhizal colonization

1. Introduction

Resources in soil are heterogeneously distributed. Understanding fine root resource uptake strategies in heterogeneous patches is of primary importance for predicting plant growth and adaptation to changing environments (Larson and Funk 2016), and thus, is important for understanding community dynamics and species distribution (Prieto et al. 2015; Valverde-Barrantes et al. 2013).

As plants experience changing environments, they often alter their fine root traits to optimize their resource uptake strategies (Hodge 2004; Liu et al. 2019). In response to nutrient rich patches, the arbuscular mycorrhizal (AM) tree species with thinner roots generally show more sensitive root proliferation by altering root architecture (Chen et al. 2016; Eissenstat et al. 2015; Liu et al. 2015). Ectomycorrhizal (EM) tree species produce more mycorrhizal fungal hyphae and their morphological traits display a lower degree of plasticity in response to nutrient rich patches (Chen et al. 2016; Kou et al. 2015). Across the mycorrhizal types, tree species with thinner root also appear to increase the lifespan of their root system to improve resource acquisition in nutrient rich patches while thicker root species do not (Adams et al. 2013). High water availability increases woody plant's root thickness (Bauerle et al. 2008). Soil moisture limitation increases the root mass fraction and decreases the rates of root elongation and growth, but has little effect on root lifespan (Bauerle et al. 2008; Larson and Funk 2016).

Previous studies that have examined the root resource uptake strategies to resource heterogeneity have typically focused on substrate without stones by manipulating nutrient or water supply. However, many forest soils contain stones as a consequence of the processes involved in soil formation and the underlying bedrock (Parajuli et al. 2017; Zhang et al. 2016). Stones range in size from boulders to fine gravel (down to 2 mm diameter). The presence of gravel would change the volume of space (and thus water and nutrient resources) that is available for roots to explore and the density of obstructions (Semchenko et al. 2008).

Therefore, the root resource uptake strategies in the soil substrate without gravel may not hold true for that in the substrate with gravel (Kulmatiski et al., 2017; Semchenko et al. 2008). For example, substrate with 20% gravel (in volume) was shown to decrease root branching and specific root length, but did not affect the elongation of single roots (Semchenko et al. 2008). However, the effects of gravel on substrate structure and resource availability in volume depend on gravel content. Higher gravel content has been shown to result in more macropore space (Verbist et al. 2009), increased nutrient leaching (Zhang et al. 2016), and the substrate porosity has been shown to initially decrease and then increase with increasing amounts of gravel (Gargiulo et al. 2016). Studies have attempted to investigate effects of gravel contents on fine root biomass or allocation (Du et al. 2017; Jiang et al. 2018). However, the adjustment of key sets of fine root traits such as morphology, architecture, mycorrhizal colonization, and lifespan, and the well documented phenology (Coleman and Aubrey 2018; McCormack et al. 2014), in response to substrate gravel contents, remain poorly known. As a consequence of this, we lack comprehensive understanding of fine root adaption strategies to highly heterogeneous substrates with gravels.

To investigate the multifaceted response of fine root traits in terms of morphological, architectural, mycorrhizal colonization, turnover rate, phenology, and mass allocation to substrate gravel content, we laid out micro-plots with five gravel content levels among tree stems in a subtropical *Schima superba* plantation. Roots grew into the modified substrates without gravel, or substrates containing volumes of 10, 20, 30, and 40% gravel. We expected that absorptive fine roots would improve their attributes to increase resource acquisition with the presence of gravel, since plants are likely to improve their potential capacity to acquire resource when resources are limited (Freschet et al. 2018) and the presence of gravel could decrease space for root growth and thus water and nutrient resources per substrate volume. We specifically hypothesized that substrate with higher gravel content would have greater fine root allocation,

but would not necessarily change the fine root morphology since the high volume of macropores caused by higher gravel content would be easily filled. Substrate with lower gravel content would have lower fine root allocation and thick roots because lower gravel content decrease the substrate porosity and thus more pressure are exerted by the surrounding substrate to pass. Higher gravel content could result in more macropore space and substrate porosity, and higher oxygen availability generally allows for higher mycorrhizal colonization (Saif 1983; Wallace 1987). Therefore, we also hypothesized that fine roots in the substrate with higher gravel content would have higher mycorrhizal colonization.

2. Materials and Methods

2.1. Study site

The experiment was conducted at the Qianyanzhou Ecological Station (26°44'39"N, 115°03'33"E, 102 m a.s.l.) in the Jiangxi Province in southeastern China. The station has a typical subtropical climate. The mean annual temperature is 17.9°C, with a mean daily minimum temperature of 6.4°C in January and a maximum of 28.8°C in July. The mean annual precipitation is 1489 mm, mostly occurring between March and June. The year is divided into four seasons: spring (March - May), summer (June - August), autumn (September - November), and winter (December - February), according to the meteorological definition of the seasons (Trenberth 1983). The soil is classified as Typic Dystrudepts by the USDA system (Wen et al. 2010). Soil profiles on the hillslopes of the Qianyanzhou Ecological Station (204 ha) are highly heterogeneous, with the volumetric contents of gravels ranging from 0 to 37.5%. In 2010, the particle size distribution of gravel was investigated on three stony hillslopes. A pit of 0.5 m × 0.5 m was dug out to a depth of 50 cm in each stony hillslope. All soil materials dug out at five depth increments (0 to 10, 10 to 20, 20 to 30, 30 to 40, and 40 to 50 cm). Then, fine earth (< 2 mm) and gravels (2-10 mm,

10-30 mm, 30-50 mm, and >50 mm) contents were sorted. Gravel volumes of each size were obtained by displacement of water. The particle size distribution of gravel (in volumetric content) was: 0.2-1.0 cm (12%), 1.0-3.0 cm (51%), 3.0-5.0 cm (23%), and >5.0 cm (14%). The gravels in the Qianyanzhou Ecological Station were dominated by fine gravels (2–3 mm), which is similar to that in some areas of French (Cousin et al. 2003), Belgian (Bunte and Poesen 1994), and Niger (Valentin and Casenave 1992).

2.2. Experimental design

In December 2011, the experiment was established on a 30-yr old *S. superba* plantation. The plant spacing of *S. superba* was 200 cm × 200 cm. There were no shrubs under the trees. Few scattered herbs were removed. Soil in this plantation is generally uniform and lacks gravel. The experiment had a completely randomized block design with three replicates. Each block had five 80 cm × 80 cm micro-plots, with each random plot serving as one treatment (Fig. 1). The mean diameter at the breast height in the three blocks were comparable ($F=1.598$, $P=0.211$), with the values of 22.45, 20.01, and 19.14 cm, respectively. The micro-plots were laid out in the center space between trees. Treatments were created with target volumetric gravel contents of 0% (control), 10%, 20%, 30%, and 40%. Micro-plots surrounding trees at different directions (i.e., 45°, 135°, 225°, and 315°) were treated differently with different rates of gravel content, allowing to minimize possible effects of gravel content on tree performance. The particle size distribution of filled gravel is consistent with that of the Qianyanzhou Ecological Station.

To create the treatments, we dug out soil up to 50 cm deep in the micro-plot. One minirhizotron tube and one soil moisture tube (approximately 30 cm apart) were then installed vertically in the center of the micro-plot, up to 100 cm deep. For the micro-plots without gravel, the excavated fine earth was well blended and backfilled based on the pre-tested bulk density and water content. For the micro-plots with

gravel, part of the well-blended excavated fine earth was hand-mixed with gravel in a set proportion and then backfilled. The backfilled procedure was conducted progressively every 10 cm depth to aid the homogeneous distributions of gravel content and fine earth bulk density along the vertical substrate profile. The repacked fresh mass of the fine earth (M_{fe}) in all treatments is calculated:

$$M_{fe} = \rho_{fe} \times V_t \times (1 - V_g) \times (1 + \theta_{fe})$$

where ρ_{fe} is the pre-tested bulk density of fine earth (1.4 g cm^{-3}), V_t is the substrate volume (cm^3), and V_g is the volumetric gravel contents of 0%, 10%, 20%, 30%, and 40%, and θ_{fe} is the water content of fine earth (0.20 g g^{-1}).

2.3. Fine root dynamics

To allow for root development after disturbance, minirhizotron images were first collected in January 2013. We obtained root images monthly using a scanner equipped with an indexing handle (CI-600; CID Inc., Camas, WA, USA). Two panes at 0-20 cm and 20-40 cm depth along each tube were scanned. Images at 20-40 cm depth captured few roots partially because the minirhizotron tubes were installed vertically. Therefore, we focused images from the top 0-20 cm in this study. All images were analyzed with WinRHIZO TRON MF 2005a (Regent Instruments, Quebec City, QC, Canada). We simultaneously monitored substrate moisture and temperature at 0-20 cm depth with a portable soil moisture system (TRIME-PICO-IPH TDR, Germany). The field data collection lasted one year. The most distal root tips that appeared in the field of vision were classified as first order roots, and the higher order roots subtending those tips were classified as second order roots. We focused on the most distal first two order roots, because of their importance in water and nutrient uptake (Liu et al. 2015). The fine root phenology and turnover rate were assessed using the numbers of roots as a result of the small size of the roots (Kou et al. 2019; McCormack et al. 2014). The annual fine root production divided by the average fine root

standing crop yielded the fine root turnover rate. The annual fine root production was the sum of the increments for root number in each month. The average fine root standing crop was the average standing root number of all observation dates.

2.4. Fine root traits

Living roots at a depth of 0-10 cm in each micro-plot were harvested in July 2014 when the living fine root biomass of *S. superba* in control peaked. In order to obtain the intact distal roots, we manually cracked the soil cores inch by inch and picked the living roots directly from the soil. The roots were classified further by root order. The living first two order roots within each micro-plot were carefully hand-washed and separated. The first and second order root pools were weighted and equally divided into three groups.

The first group of roots were oven-dried (60 °C for 72 h) to a constant weight to determine dry mass, and then the first- and second-order roots were combined and finely ground to measure their carbon (C) and nitrogen (N) concentrations using a CN-element analyzer (Elementar VarioMax CN, Mt. Laurel, NJ, USA).

Another group of roots were rinsed and stored at -20°C for morphology and architectural traits measurement. First- and second- order roots were separately analyzed to determine the average root diameter, root total length, volume and root number using a scanner and a WinRhizo visual analysis system (Regent Instruments Inc., Québec, Canada). The specific root length (SRL) was calculated as the root total length divided by its dry mass for each root order. The root tissue density (RTD) was calculated as the ratio of root dry mass to its volume. The root branching intensity (BrIntensity) was calculated as the number of first-order roots divided by the total root length of second-order roots. The root branching ratio (BrRatio) was calculated as the number of first-order roots divided by the number of second-order

166 roots.

167 One part first-order roots were placed into formalin-aceto-alcohol (FAA) solution (90 ml of 50%
168 ethanol, 5 ml of 100% glacial acetic acid, and 5 ml of 37% methanol). Root samples stored in FAA
169 solution were used for the measurement of arbuscular mycorrhizal colonization following Liu et al.
170 (2015). Arbuscular mycorrhizal colonization (AMC) was expressed as the percentage of the roots that
171 were colonized by mycorrhizal fungi.

172 2.5. Soil chemical traits

173 At the same time as the root harvest, four soil cores (0–20 cm) were collected from each micro-plot,
174 composited, and mixed thoroughly. The soil samples were passed through a 2-mm sieve for the nutrient
175 analysis. The dissolved organic carbon (DOC) content of filtered 0.5 M K₂SO₄ extracts from fresh soil
176 was measured with a TOC analyser (Liqui TOC Elementar, Vario Max, Germany). Concentrations of
177 NH₄⁺-N and NO₃⁻-N of filtered 2 M KCl extracts from fresh soil were measured with a flow injection
178 autoanalyser (AutoAnalyzer 3, Bran + Luebbe, Germany). Soil organic carbon (SOC) and total nitrogen
179 (TN) concentrations were measured from air-dried soil using a Vario-Max N/CN elemental analyzer
180 (Elementar Analysensysteme GmbH, Hanau, Germany).

181 2.6. Data analysis

182 To examine whether root traits, substrate moisture, and substrate temperature differed among
183 treatments, we used mixed effects linear models with block as a random effect and treatment as fixed
184 effects, before significant differences were determined by analysis of *t* test or variance (ANOVA). Post
185 hoc group differences were examined with Tukey's test for multiple comparisons. All analyses above
186 were performed using SPSS 17.0 (SPSS Inc., Chicago, IL, USA). A linear or nonlinear regression was

performed to examine the relationships between gravel content and measured soil and root parameters across treatments using SigmaPlot 12.0 (San Jose, CA, USA). The choice of regression model depended on coefficient of determination and model residuals (Aho et al. 2014). Significant and marginally significant were defined as $P < 0.05$ and 0.1 , respectively.

3. Results

3.1. Substrate physical and chemical properties

The annual substrate moisture content at 0-20 cm depth decreased with increasing gravel content (Fig. 2), mainly because the presence of gravel reduced the substrate moisture content in summer and autumn (Fig. 3a). There were no significant changes in annual substrate temperature ($F=0.275$, $P=0.886$) and substrate temperature during each season at the top layer across treatments (Fig. 3b). All the measured soil nutrient concentration per unit of soil mass (SOC, TN, DOC, inorganic nitrogen, nitrate nitrogen, and ammonia nitrogen) did not vary among treatments (Table S1). In the treatments with 30% and 40% gravel, however, the available total nitrogen per substrate volume to plants decreased (Table S2).

3.2. Fine root morphological, architectural, chemical and mycorrhizal traits

Gravel content changed the morphological and mycorrhizal traits of first-order roots and C/N of the first two order roots (Fig. 4), but had no significant effects on the morphological traits of the second-order roots (Table S3). Compared with the substrate without gravel, substrate with 10% gravel had higher root diameter, lower SRL, substrate with 40% gravel had lower AMC, and substrate with 20-30% gravel had similar morphological fine root traits and AMC.

There was no evidence that gravel appearance changed BrIntensity ($F=0.933$, $P=0.483$) or BrRatio ($F=0.561$, $P=0.698$).

3.3. Fine root phenology, production and turnover

The presence of gravel in the substrate delayed the peak of fine root production (Fig. 5). The peak of fine root production occurred in July in substrate without gravel, but in September in substrate with gravel. With an increase in gravel content, plants tended to increase the production of fine roots in autumn, but reduce the production of fine roots in summer (Fig. 6). Across treatments, substrate water content regulated the fine root production pattern more than substrate temperature during the summer and autumn (Table 1). The contrary effects of gravel content on seasonal fine root production in summer and autumn resulted in similar annual fine root production across treatments ($F=0.861$, $P=0.526$).

Fine root turnover rate decreased significantly with increasing gravel content (Fig. 7a). Across treatments, fine root turnover rate was negatively related to annual substrate temperature ($r=-0.636$, $P=0.011$), but not related to annual substrate water content ($r=0.180$, $P=0.522$). The decrease in fine root turnover rate was associated with a reduction in arbuscular mycorrhizal colonization (Fig. 7b).

Increasing gravel content did not change annual fine root production but the decrease in fine root turnover rate was associated with an increase in standing fine root biomass (Fig. 8a), even though the substrate with 10% gravel had similar standing fine root biomass to the control treatment ($t=-1.282$, $P=0.269$). The increase in the standing fine root biomass was associated with an increase of fine root C/N (Fig. 8b), but not with the morphological, architectural and mycorrhizal traits (Table 2).

4. Discussion

We found that fine root resource uptake strategies and dynamics shift along the gradient of gravel contents in the substrate. In our experiment, the response of root system to the presence of gravel was related with a set of changes in root morphological, architectural, chemical, physiological and phenology

traits. Which mechanism involved was dependent on the level of gravel content. More interestingly, the shift of fine root resource uptake strategy caused by gravel presence differed from those shown in response to fertilization and moisture manipulation experiments (Eissenstat et al. 2015; Liu et al. 2015; Wang et al. 2016; Kou et al. 2019). This is because the addition of large amounts of gravel not only could decrease nutrient availability (Table S2) and substrate moisture in volume (Figs. 2, 3), but also may increase air permeability (Gargiulo et al. 2016) and obstructions, and therefore create a more complex habitat than changes in fertilization and soil moisture.

4.1. Effects of gravel on fine root resource uptake strategy

With the presence of 10% gravel content, the root construction response was characterized by adjusting root morphological attributes. Compared with the substrate without gravel, plants constructed thicker root systems with lower SRL in the substrate with 10% gravel content (Fig. 4a, b). This is consistent with our hypothesis. The thick roots increase the ability to penetrate the substrate (Clark et al. 2003), but at the cost of the soil length explored per unit of carbon invested (Lower SRL). Combined with the fact that adding 10% gravel did not change the belowground construction costs of tissue dry mass (indicated by the similar standing fine root biomass and annual fine root production), these results collectively suggest that adding 10% gravel to the substrate did not change belowground carbon investment but decreased the soil length explored per unit of carbon invested.

With the presence of 20-30% gravel content, the plant increased standing fine root biomass (Fig. 8a) rather than adjusting root morphological attributes (Fig. 4). Generally, a more efficient root placement strategy is to allocate more fine roots in resource-rich patches (Bauerle et al. 2008; Liu et al. 2015). We suspect that building more fine roots in the substrate with 20-30% gravel content was a direct result of the macro-pores between gravels which are easily filled because belowground competitive ability was

more closely related to ability to quickly fill a soil volume with roots than the ability to obstruct resource-rich patches (Rajaniemi 2007). It might also be because fine roots of *S. superba* do not self-inhibit root growth by accumulating their own exudates when physical barriers are encountered (Falik et al. 2005; Semchenko et al. 2007). That higher gravel content promoted fine root biomass is consistent with previous field-based findings (Du et al. 2017; Jiang et al. 2018). However, fine root morphology traits in our resource-poor patches with 30% gravel content were similar with control spots that had relatively higher resource availability. This is contrast with water manipulation experiments where drought increased the root mass allocation, but on the other hand increased root diameters and decreased specific root length and thus decreased fine root absorption efficiency (Larson and Funk 2016). In contrast with our study, Semchenko et al. (2008) found that substrate with 20% gravel (in volume) decreased root branching, root mass allocation, and specific root length, where the gravel size was 4 mm. The inconsistent results could be due to the effects of differing sizes of rock fragments, since rock fragment size has been found to affect water infiltration and retention in substrate micro-environments (Katra et al. 2008).

The effects of 40% gravel content on roots were characterized by a reduced mycorrhizal colonization (Fig. 4d) and increasing root biomass (Fig. 8a). This is inconsistent with our second hypothesis. Higher substrate porosity or oxygen availability generally associated with higher AMC (Saif 1983; Wallace 1987), and lower moisture in the field or chronic drought may increase mycorrhizal colonization percentages of roots more often than decreasing it. This is especially likely when a decrease in phosphorous availability accompanies decreased moisture (Augé 2001; Simpson and Daft 1990). Moreover, a study exploring the reliance on mycorrhizal fungi in nutrient addition treatment found that lower nutrient availability increased the mycorrhizal colonization (Liu et al 2015). These previous

findings collectively indicate that a large fraction of gravel should improve the AMC. The unexpected lower AMC in our study may be partially attributed to less propagules of AM fungi per substrate volume, despite levels of AM fungi in soil are not necessarily associated with root colonization levels (Richter et al., 2002). In the substrate with 40% gravel, however, the disadvantage of lower AMC can be compensated by the longer root life spans (as indicated by the lower fine root turnover rate, Fig. 7a) and higher root mass per substrate volume (Fig. 8a).

4.2. Effects of gravel on the fine root dynamics

Fine root dynamics could be mediated by tree size, stem diameter increment, and stand development (Coleman and Aubrey 2018; McCormack et al. 2014). However, our arrangement of the micro-plots precluded these possibilities. The presence of gravel elicited a change of fine root phenology and a decrease of root turnover rate but did not change the annual fine root production. This is inconsistent with the results of a nutrient addition study that reported simultaneous changes in fine root production and turnover (Kou et al. 2019).

Generally, the presence of gravel postponed the peak of fine root production from summer to autumn. In the summer, more gravel led to a lower substrate water content and relatively lower fine root production. In the autumn, more gravel resulted in lower substrate water content but higher relative fine root production (Fig. 6). A reasonable explanation for the contrary effects of gravel content (and therefore substrate water content) on seasonal fine root production could be that high transpiration during the summer (Yang et al. 2017) required plants to invest in more roots to absorb more water. However, in the control treatment without gravel, the substrate water content remained around $0.25 \text{ cm}^3 \text{ cm}^{-3}$ in the summer and autumn. Such long lasting high substrate water content in our study site could inhibit the diffusion of oxygen (Wang et al. 2012) and thus impede the development of roots (Drew 1983).

In our experiment where substrate with different gravel contents were scattered within one stand, the advanced timing of peak root growth in substrate without gravel suggests that plants tend to preemptively access resource-rich patches to limit the fitness of neighbors (Dybzinski et al. 2011). The changes in the timing of peak root growth caused by the presence of gravel might alter the dynamics of aboveground biomass accumulation, since the peak root growth comes at the expense of using carbon for aboveground growth (Radville et al. 2016).

4.3. Association between root proliferation and root trait

The resource uptake behaviors of plant roots for heterogeneously distributed resources are less consistent. In the nutrient-rich patches, root proliferation was observed mainly by altering root architectural traits (Liu et al. 2015) or root morphological traits (Eissenstat et al. 2015; Wang et al. 2016). In our study, however, higher root biomass proliferation in response to the presence of gravel was associated with higher root C/N. Fine roots with higher C/N were shown to live longer because they were less susceptible to herbivory (Withington et al. 2006). Since root longevity was found to be negatively correlated with root maintenance respiration (Eissenstat et al. 2000), our result suggests that the adjustment of root maintenance cost is likely important for root proliferation, and aids in adaption to the presence of gravel in the substrate. Similarly, plant roots were observed to strongly increase biomass allocation and live longer in nutrient-poor patches (Fransen and de Kroon 2001; Kramer-Walter and Laughlin 2017). Also, the increased C/N in living roots could result in a reduction of root litter decomposition rate and an increase in carbon sequestration in the substrate (Cotrufo and Ineson 1995).

Additionally, *S. superba* is a thin root species and its roots are colonized by AM fungi. Root morphology and mycorrhiza types together shape nutrient resource uptake strategies in a patchy environment (Chen et al. 2016). Future studies should examine whether our results also apply to species

with thick absorptive roots and with other types of mycorrhiza (e.g. EM species).

5. Conclusions

Our study provides the first comprehensive picture of the variability of fine-root traits in response to the presence of gravel in substrates. Our findings provide evidence for substantial selective pressures associated with gravel contents on fine-root traits. In substrates without gravel, the fine root allocation biomass tended to be lower, so the finer absorptive roots with higher AMC and SRL were needed to enhance the root's resource absorption efficiency. The presence of gravel in the substrate delayed the timing of peak root growth. Plants produced more roots in the autumn but fewer roots in the summer in the substrate with higher gravel content. Roots in the substrate with higher gravel content tended to exhibit a lower fine root turnover rate, a lower AMC, but a higher root biomass allocation. Moreover, the higher root biomass proliferation in the substrate with higher gravel content was likely associated with the higher root C/N ratio. Since gravel content can significantly affect root traits, descriptions of root resource uptake strategy in stony soils should include the gravel content. While attempting to describe and explain ecosystem functioning and species distribution at larger scales, physiologists should incorporate the substantial root functional trait variation in response to the structural heterogeneity of the soil matrix. Further studies with long-term data collection are needed to investigate the inter-annual variabilities of fine root phenology and turnover in substrates with different levels of gravel content and different gravel sizes.

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465

466 **Table 1** Correlation of percentage of the total annual production (PTAP) against substrate water content (W) and temperature (T) across
467 treatments in the summer and autumn.

	Summer		Autumn	
	r	P	r	P
PTAP vs W	0.881	0.049	-0.832	0.078
PTAP vs T	0.869	0.056	0.306	0.617

468

469

470 **Table 2** Pearson correlation results for the relationships of standing fine root biomass against fine root morphological, architectural, and
471 mycorrhizal traits.

	Diameter		Specific root length		Root tissue density		Root branching ratio	Root branching intensity	Arbuscular mycorrhizal colonization
	1 st order	1 st + 2 nd order	1 st order	1 st + 2 nd order	1 st order	1 st + 2 nd order			
<i>r</i>	0.029	0.055	0.028	0.051	-0.072	-0.154	-0.386	-0.051	-0.161
P	0.918	0.847	0.920	0.858	0.800	0.583	0.155	0.857	0.565

472

473 **Figure captions**

474 Fig.1 A sketch map of the experimental design. 0%, 10%, 20%, 30%, and 40% indicate treatments with 0%, 10%, 20%, 30%, and 40% gravel content, respectively.

475 Fig.2 Effects of gravel content on annual substrate moisture content at 0-20 cm depth.

476 Fig.3 Effects of gravel content on (a) substrate moisture content and (b) substrate temperature during the four seasons. Error bar represents one standard error of the mean.

477 Different letters indicate significant differences between treatments.

478 Fig.4 Differences in (a) root diameter, (b) specific root length, (c) tissue density, (d) arbuscular mycorrhizal colonization of first-order roots, and (e) C/N of the first two order
479 roots. Error bar represents one standard error of the mean. Different letters indicate significant differences between treatments.

480 Fig.5 Effects of gravel content on fine root production phenology. The mean value is shown with the standard error ($\pm$ SE).

481 Fig.6 Effects of gravel content on relative fine root production in the summer and autumn.

482 Fig.7 Significant relationships between (a) gravel content and (b) arbuscular mycorrhizal colonization and turnover rate.

483 Fig.8 Relationships between standing fine root biomass of first two order roots against gravel content and root C/N.

Fig.1

Fig.2

Fig.3

Fig.4

Fig.5

Fig.6

Fig.8