

# Pore structure in detritosphere of soils under switchgrass and restored prairie vegetation community

Jin Ho Lee<sup>1</sup>, Maik Lucas<sup>1</sup>, Andrey K. Guber<sup>1</sup>, and AN Kravchenko<sup>1</sup>

<sup>1</sup>Michigan State University Department of Plant Soil and Microbial Sciences

October 18, 2023

## Abstract

Root detritosphere, i.e., the soil in vicinity of decomposing root residues, plays an important role in soil microbial activity and C sequestration. Pore structure (size distributions and connectivity of soil pores) in the detritosphere serves as a major driver for these processes and, in turn, is influenced by physical characteristics of both soil and roots. This study compared pore structure characteristics in root detritosphere of soils of contrasting texture and mineralogy subjected to >6 years of contrasting vegetation: monoculture switchgrass and polyculture prairie systems. Soil samples were collected from five experimental sites in the US Midwest representing three soil types. Soil texture and mineralogy were measured using hydrometer and X-ray powder diffraction, respectively. The intact cores were scanned with X-ray computed micro-tomography to identify visible soil pores, biopores, and particulate organic matter (POM). We specifically focused on pore structure within the detritosphere around the POM of root origin. Results showed that detritosphere of coarser-textured soils, characterized by high sand and quartz contents, had lower porosity in the vicinity of POM compared to finer-textured soils. POM vicinities in finer soils had high proportions of large (>300  $\mu\text{m}$   $\emptyset$ ) pores, and their pores were better connected than in coarser soils. Lower porosity in outer (>1 mm) parts of detritosphere of switchgrass than of prairie suggested soil compaction by roots, and the effect especially pronounced in coarser soils. The results demonstrated that soil texture and mineralogy played a major, while vegetation a more modest, role in defining the pore structure in root detritosphere.

## 1 INTRODUCTION

Pore structure, i.e., shapes, connectivity, size distributions of soil pores, defines many functions and processes of the soil (Lucas, 2022; Rabot, Wiesmeier, Schlüter, & Vogel, 2018). It regulates availability of  $\text{O}_2$ , water, and nutrients to soil microorganisms and influences processing of soil organics (Bouckaert et al., 2013; Thomsen, Schjøning, Jensen, Kristensen, & Christensen, 1999). Pore connectivity is especially important for providing a suitable habitat for soil-dwelling organisms and enabling microorganisms to access soil organic matter (SOM) (Negassa et al., 2015; Rabbi et al., 2016). Pores of different size ranges have differential effects on the activity and abundance of microorganisms. Specifically, micro-environments associated with higher enzyme activities and greater microbial abundance are found in pores ranging from tens to hundreds  $\mu\text{m}$   $\emptyset$  (Kravchenko et al., 2019; Strong et al., 2004).

Plant roots are a major driver of soil pore formation and a source of SOM (Bodner, Leitner, & Kaul, 2014; Sokol, Kuebbing, Karlsen-Ayala, & Bradford, 2019). After the root senesces, its residues remain in the soil as detritus, and a several millimeters thick region that surrounds these decaying residues is called the detritosphere (Gaillard, Chenu, Recous, & Richard, 1999; Védère, Vieublé Gonod, Pouteau, Girardin, & Chenu, 2020). Soil pore structure within the detritosphere is distinct from that of the bulk soil due to past activity of live roots as well as due to biological and physical changes after roots' senescence. For example, rearrangement of soil particles or micro-aggregates during root growth (Mitchell & Soga, 2005) may lead to an increase in porosity adjacent to the root (Helliwell et al., 2017), while soil compaction can occur near growing roots (Lucas, Schlüter, Vogel, & Vetterlein, 2019a). However, upon root senescence pore spaces can

be partially or completely refilled by soil particles during the decomposition of root residues (Phalempin et al., 2022). Since the detritosphere is a main arena of microbial activity and carbon (C) processing (Kuzyakov & Blagodatskaya, 2015), characteristics of pore structure within detritosphere likely play its special role for the whole soil volume.

Properties of the pore structure in detritosphere depend on a number of factors, including but not limited to: (i) inherent characteristics of soil particles that influence pore formation, such as soil texture and mineralogy; (ii) inherent pore characteristics, i.e., the pore structure within that specific location prior to the root growth within it; (iii) composition of the soil microbial community; (iv) morphological, chemical, and physical characteristics of the roots that generate the detritus.

The structural stability of the detritosphere pores are affected by sand content and abundance of quartz, both known to decrease stability of soil aggregation (Almajmaie, Hardie, Doyle, Birch, & Acuna, 2017; Rivera & Bonilla, 2020), likely due to the large size and low surface area of sand grains as well as the absence of negative charges (Bazzoffi, Mbagwu, & Chukwu, 1995; Six, Elliott, & Paustian, 2000). Moreover, soils dominated by quartz tend to be more easily dispersed than kaolinitic clays due to their lower binding capacity (Buhmann, Rapp, & Laker, 1996; Neaman, Singer, & Stahr, 1999), thus such soils are prone to be easily disaggregated under disruptive forces such as rainfall (Wakindiki & Ben-Hur, 2002).

Inherent soil characteristics affect root growth patterns and thus formation of root-derived pores. Root systems have been shown to grow more extensively in loose than in compact soil (Bengough et al., 2006; Croser, Bengough, & Pritchard, 1999), as well as in an undisturbed soil than in that homogenized by sieving and packing (Phalempin, Lippold, Vetterlein, & Schlüter, 2021b). The roots preferably utilize existing pore spaces, and indeed, the rhizosphere can be more porous than the bulk soil when roots are able to grow into a highly connected pore system (Lucas et al., 2019a). The established soil biopores that have been frequently and continuously used by roots are more likely to be stable due to root exudate and mucilage inputs (Traoré, Groleau-Renaud, Plantureux, Tubeileh, & Boeuf-Tremblay, 2000). Such pores can maintain their structure in detritosphere upon the root senescence and root residue decomposition.

Vegetation type directly affects pore structure via differences in root types and characteristics. For example, presence of coarse root systems increased the volume of  $> 70 \mu\text{m}$   $\emptyset$  pores by 30%, whereas plant species with dense fine root systems generated larger volume of  $< 30 \mu\text{m}$   $\emptyset$  pores (Bodner et al., 2014). Total volumes of soil biopores, i.e., the pores formed by the activity of living organisms such as roots, in  $\emptyset < 0.2 \text{ mm}$  and  $0.2\text{--}0.5 \text{ mm}$  size classes significantly differed among the plant species with different root system characteristics (Lucas, Nguyen, Guber, & Kravchenko, 2022). The differences in pore structure generated by plants with contrasting root systems are expected to be more pronounced in direct vicinity of the roots (Helliwell, Sturrock, Miller, Whalley, & Mooney, 2019), thus, carried later into the properties of the detritosphere. After plant dies, the root residues located in the biopores are decomposed, and the difference in the magnitude of decomposition is likely to be affected by the detritosphere's pore structure. Variations in residue decomposition can result in variations in the size of the gap between the residues and soil particles, potentially leading to further alterations of the pore structure.

While the structure of pores within the rhizosphere under different soil texture and contrasting vegetation has been actively explored (Helliwell et al., 2017; Helliwell et al., 2019; Phalempin et al., 2022, 2021b), very little information is available on pore structure of detritosphere. For example, Helliwell et al. (2017) observed micro-scale structural changes in pores surrounding growing root systems in uniformly packed soils and found increases in porosity at the interface between roots and soil as roots grow into loamy sand and clay loam soils. However, it is still unclear what happens to the pores surrounding roots once the roots die and decomposition begins. As the detritosphere is one of the most important microbial hotspots (Kuzyakov & Blagodatskaya, 2015), the lack of such information in the pore structure limits progress in understanding mechanisms of soil C cycling and sequestration.

The objective of this research was to characterize the pore structure in root detritosphere of the soils of two contrasting vegetation systems: monoculture switchgrass, where root detritus originated from switchgrass

roots, and polyculture restored prairie, where root residues originated from a variety of herbaceous plant species. The two systems have been in place for over 6 years, generating differences in soil C contents (Sanford, 2014; Sprunger & Robertson, 2018), pore structures (Juyal, Guber, Oerther, Quigley, & Kravchenko, 2021), and microbial characteristics (Jesus et al., 2016; Li et al., 2022). We compared pore connectivity and size distribution within the detritosphere of the two systems at five experimental sites representing three soil types with contrasting texture and mineralogy.

## 2 MATERIALS AND METHODS

### 2.1 Experimental design and soil sample collections

Two of the experimental sites used for this study were located in Wisconsin (Oregon and Hancock) and three in Michigan (Lux Arbor, Lake City, and Escanaba), USA. The soils of Oregon, Lux Arbor, and Escanaba sites are Alfisols, and of Hancock and Lake City sites are Entisol and Spodosol, respectively. At each site a randomized complete block design experiment with 3 (Hancock) or 4 (the rest of the sites) replications has been established in 2013. Details on the research sites and soil descriptions have been reported by Kasmerchak and Schaetzl (2018) and Lee et al. (2023).

The two studied vegetation systems were: (1) non-fertilized monoculture switchgrass (*Panicum virgatum* L.; Cave-in-Rock variety); and (2) restored prairie, which consisted of 18 plant species of grasses (including switchgrass), forbs, and legumes. Soil sampling was conducted in 2020 (Oregon site) and 2019 (the other 4 sites). Two types of soil samples were collected from each replicated plot. First, three intact soil cores (5 cm in height and 5 cm  $\emptyset$ ) were collected from 5 to 10 cm depth for X-ray computed micro-tomography ( $\mu$ CT) scanning. Then, the loose soil surrounding the cores was also collected for measurements of soil texture and mineralogy. All samples were stored at 4 °C until scanning and measurements.

### 2.2 Measurements of soil porosity, texture, and mineralogy

Soil porosity was calculated from bulk and particle densities of the collected samples (i.e., total porosity), and texture was determined using the hydrometer method (Gee and Or, 2002) in all replicated plots of all sites. Soil mineralogy composition was measured using X-ray powder diffraction (XRD) carried out at the Illinois State Geological Survey (Champaign, Illinois, USA). Because of the high costs of XRD analyses only three replicated samples from each system in each site were subjected to these measurements. Prior to XRD analyses, the samples were cleaned, dried in a vacuum oven, and ground to  $< 44 \mu\text{m}$ . Then, one subset of the prepared sample was powdered by the McCrone mill (MBP) (McCrone Accessories & Components, Westmont, IL, USA) for quantification of non-clay minerals (quartz, clay, K-feldspar, P-feldspar, calcite, dolomite, siderite, and pyrite/marcasite), and the other was fractionized into  $< 2 \mu\text{m}$  powder for clay minerals (smectite, mica, kaolinite, and chlorite). The prepared two types of powders were then spread on a glass slide and analyzed using a Siemens/Bruker D5000 X-ray Powder Diffraction instrument (Billerica, MA, USA). The JADE software was used to identify percentages of constituents in each powdered sample from XRD patterns.

### 2.3 Soil core scanning and image analysis

Pore structure assessments were performed via X-ray  $\mu$ CT. Soil cores were drained at -28 kPa using a 5-bar pressure plate extractor (Soilmoisture Equipment Corp., Goleta, CA) prior to  $\mu$ CT scanning to remove water from pores  $\emptyset > 10 \mu\text{m}$  and increase the contrast between the solids and air on X-ray  $\mu$ CT images. Then, the cores were scanned using X-ray  $\mu$ CT machine (North Star Imaging, X3000, Rogers, MV, USA) at the Department of Horticulture facility, Michigan State University. The energy settings were 75 kV and 450  $\mu\text{A}$ . The scanning resolution of 18  $\mu\text{m}$  was achieved using the Subpix-mode of the scanner, combining four individual scans shifted half pixel in vertical and horizontal directions. Scanned images of 3014 projections were reconstructed by efX software (North Star, Rogers, MN, USA).

A schematic summary of the steps involved in the image processing for this study is outlined in Figure 1. The image pre-processing was conducted using ImageJ-Fiji software (Schindelin et al., 2012) to remove artifacts and noises. First, to exclude sampling artifacts near the soil core walls, images were centered and

cropped into prisms ( $1500 \times 1500 \times 2240$  pixels corresponded to 2.7 cm in length, 2.7 cm in width, and 4.1 cm height). Then, ‘Remove Background’ tool in Xlib/Beat plugin was used to remove shadowing effects from the images, followed by the removal of ring artifacts on the image’s polar domain using a stripe filter of the Xlib/Beat plugin. After that, a 3D non-local mean filter ( $\sigma = 0.1$ ) implemented in scikit-image (Walt et al., 2014) was used to reduce the noise (Buades, Coll, & Morel, 2011; Darbon, Cunha, Chan, Osher, & Jensen, 2008). The pre-processing steps dropped the resolution of images from 18 to  $36 \mu\text{m}$ .

Root residues, which we will refer to as particulate organic matter (POM), were segmented from the filtered images with Ilastik software, a machine learning-based tool (Berg et al., 2019). A random forest classifier was used on a multi-dimensional feature space of the filtered gray scale images. The classifier was trained using two cores from each combination of different vegetation and sites (20 of total 114 cores) and then applied on entire cores. The training dataset produced out-of-bag error rate estimates less than 1.8% in overall, and all segmented POM images were visually inspected to ensure the accuracy and integrity of the segmentation process. The outcome of POM segmentation was denoised by removing objects smaller than 4 voxels in diameter from the images.

Segmentation of the filtered grayscale images into pore and solid binary images was performed to identify the pores visible at the image resolution, referred further on as image-based pores. For each sample the segmentation threshold was estimated as an ensemble of six segmentation methods (i.e., Otsu, Triangle, Huang, IsoData, Li, and Moments). The global thresholds for the stack of images in each individual core, estimated using the six segmentation methods, were averaged and applied to that stack to separate the solid and air-filled voxels in the images using SimpleITK in Python (Beare, Lowekamp, & Yaniv, 2018; Lucas et al., 2022). Obtained images were used to compute pore size distributions using ‘Local Thickness’ tool, an approach based on the maximum inscribed sphere method (Hildebrand & Rüegsegger, 1997; Vogel, Weller, & Schlüter, 2010).

Biopores were identified as described by (Lucas et al., 2022; Lucas, Schlüter, Vogel, & Vetterlein, 2019b). Specifically, to employ tubular-shaped features of biopores in differentiating them from other irregularly shaped pores, we used the Tubeness plugin in ImageJ-Fiji for shape detection. As rising  $\sigma$ -values significantly increased the computational time, binary images were scaled down to 50% and 20% for Tubeness filtering with  $\sigma$ -values ranging from 1-4 and 2-30, for each scale respectively, with a step size of 1. Gaussian blurring was applied to the entire binary image with varying  $\sigma$ -values in order to efficiently identify biopores of various diameters. The resulting tubular channels were slightly smaller than the root channel itself due to the exclusion of rough surface on biopore walls. Thus, to better capture the actual width of biopores, 3D dilation steps were employed as a postprocessing measure. After combining all elongated objects, misclassified objects were removed (Phalempin, Lippold, Vetterlein, & Schlüter, 2021a). Proportions of biopores in the entire pore system were calculated. After that, proportions of biopores occupied by POM were computed by first calculating the volume of POM located in biopores and then dividing this volume by the entire volume of biopores.

Nine masks corresponding to interval regions nine distances away from the segmented POM (0-0.25, 0.25-0.5, 0.5-1.0, 1.0-1.5, . . . , 3.0-3.5, and 3.5-4.0 mm) were created using 3D distance transform in ImageJ-Fiji. Then, masks of interval regions were applied to the pore-solid segmented image and to the pore size distribution image of the entire sample to calculate the porosities and the size distributions individually for each interval region. Contributions of pores of different size classes to image-based porosity of the distance interval regions were expressed as pore fractions (%). We considered three pore size classes, namely  $36\text{-}150 \mu\text{m}$ ,  $150\text{-}300 \mu\text{m}$ , and  $> 300 \mu\text{m}$   $\emptyset$ . The  $36 \mu\text{m}$   $\emptyset$  corresponded to the smallest pore size that could be reliably detected on the studied images. Pores  $< 150 \mu\text{m}$   $\emptyset$  are known to have especially high microbial activity and strongly contribute to the C processing (Kravchenko & Guber, 2017; Kravchenko et al., 2019; Strong et al., 2004), and pores  $< 300 \mu\text{m}$   $\emptyset$  function as the secondary pathways for water and nutrient supplies to resident microorganisms (Franklin et al., 2021).

A Connectivity tool of BoneJ plugin in the ImageJ-Fiji was used for the pore connectivity calculations: first, Euler numbers ( $\chi$ ) were computed, and the numbers were divided by the total volume of corresponding

regions ( $V$ ) (Odgaard & Gundersen, 1993; Vogel & Roth, 2001):

$$\chi_V = \frac{N-C+H}{V} \quad (1)$$

Where  $N$  is the number of isolated objects,  $C$  is the number of redundant connections or loops, and  $H$  is the number of completely enclosed cavities, which are typically negligible in soil pore system (Lucas, Vetterlein, Vogel, & Schlüter, 2021; Vogel, 2002). The minimum size of the object was  $2 \times 2 \times 2$  voxel. Higher, e.g., positive,  $\chi_V$  values calculated via Eq. (1) correspond to lower connectivity, while lower, e.g., negative, to the higher connectivity. To simplify the presentation of the connectivity data we report the results as negative values of  $\chi_V$ , that is, the high values of  $-\chi_V$  correspond to high connectivity while the low values to the low one.

Since pore connectivity can be affected by the volume of the soil in which it is calculated, we did not assess it at the same distance intervals as those that were used for the image-based porosity and pore size distributions described above. Instead, we only calculated it in immediate vicinity of the residue, i.e., the region of 0-0.25 mm away from the POM, and for the entire soil volume. The resultant two estimates of the connectivity were used for comparisons among the five experimental sites and plant systems.

## 2.4 Statistical analysis

The data were analyzed using SAS 9.4 (SAS Institute Inc., NC, USA) procedures of PROC MIXED and PROC GLIMMIX. Since we did not expect that 6-7 years of disparate vegetation influenced soil texture and mineralogy, the statistical models for texture and mineralogy characteristics included only the fixed effects of the experimental sites. For the other soil properties, the statistical models included the fixed effects of sites, plant systems, and their interaction. Statistical models for analyses of image-based porosity data at different distances from POM additionally included the same fixed effects as the soil properties and individually tested by distance intervals, as the interaction among the sites, plant systems, and distances was significant. All models included the random effects of experimental blocks nested within the sites and, when necessary, the random effects of cores nested within the blocks, plant systems, and sites. The latter were used as an error term for testing the plant system effects. The assumptions of normality and variance homogeneity were assessed using normal probability plots, plots of residuals vs. predicted values, and Levene's tests for equal variances.

Additionally, we grouped the sites into two soil texture classes for comparing pore size distributions and connectivity between finer-textured soils and coarser-textured soils. The first group included Oregon, Lux Arbor, and Escanaba sites, the three soils with  $< 66\%$  sand content, and the second group consisted of Hancock and Lake City sites with  $> 82\%$  sand content (Table 1). Models for analysis of pore size distribution data within each distance interval and of connectivity data within 0-0.25 mm distance and entire image stack included the fixed effects of plant systems, soil groups, and their interaction, and random effects of experimental sites nested within soil groups, blocks nested within the sites, and cores nested within the blocks, plant systems, sites, and groups.

Linear relationships among soil texture variables, mineralogical and clay mineralogy variables, proportions of biopores and POM in biopores, and the distance-based porosities and connectivity were assessed using Pearson's correlation coefficients.

## 3 RESULTS

### 3.1 Soil texture and mineralogy in the studied sites

Sand content varied greatly among the studied sites, with Oregon site having the lowest content at 10% and Lake City having the highest at 87% (Table 1). The silt content was the highest in Oregon at 73% and the lowest in Lake City at 9%, and the site with the highest clay content was also Oregon at 17%. In all five sites, quartz was the dominant mineral (78-92%) with 6-16% of K-feldspars and P-feldspars, and  $< 2\%$  contents of other minerals. Hancock and Lake City had higher contents of quartz and lower contents of K-feldspars and P-feldspars compared to Oregon, Lux Arbor, and Escanaba sites. Mica dominated the clay

fraction of all studied soils (55-67%), while smectite, kaolinite, and chlorite were present at < 20%, and did not differ among the sites.

Quartz was positively correlated with sand content, while silt and clay contents were positively correlated with feldspars, dolomites, and siderites across all studied sites, which (Table S1). Interestingly, contents of smectite and kaolinite were positively correlated with sand contents, while mica was negatively correlated with sand but positively with silt and clay (Table S1).

### 3.2 Bioporosity and POM located within biopores

The soils of Oregon site had the lowest total and image-based porosity, measuring at around 21% and 10% in both plant systems, respectively (Fig. 2A). In soils of Lux Arbor and Escanaba, both types of porosities were higher than those of Oregon. The soils of Hancock and Lake City had the greatest total and image-based porosity, while lower bioporosity than the other three sites (Fig. 2A). There were no significant differences observed in both types of porosities and bioporosities between the two plant systems, with the exception of the bioporosity of Lux Arbor site (Fig. 2A). Proportions of the image-based porosity occupied by biopores were also the greatest in soils of Oregon and Lux Arbor compared to those of Hancock and Lake City soils under both plant systems (Fig. 2C). The significant difference in the proportions occupied by biopores between the two plant systems was found only in Lux Arbor site, where biopores constituted 19% and 24% of the image-based porosities of prairie and switchgrass systems, respectively (Fig. 2C). The proportion of pore space occupied by biopores was negatively correlated with sand content and quartz, while positively correlated to silt, clay and P-feldspar (Table S2).

Neither the two plant systems nor the five studied sites showed significant differences in POM fractions (Fig. 2B). However, proportions of biopores occupied by POM varied among the studied soils (Fig. 2D). In the soils of Hancock and Lake City POM occupied >30% of the bioporosity, while in Oregon and Lux Arbor it was <20% (Fig. 2D). The bioporosity occupied by POM was positively correlated with sand and quartz contents and negatively correlated with silt, clay, K- and P-feldspar contents (Table S2).

### 3.3 Pore structure changes with the distance from POM

Image-based porosity decreased with the distance from the POM surface in all soil cores (Fig. 3). In both systems, at < 0.25 mm distance from POM the image-based porosity tended to be higher in finer-textured soils of Oregon, Lux Arbor, and Escanaba than in the coarser-textured soils of Hancock and Lake City (Fig. 3). These pores are shown as examples in Fig. 4. However, the differences in the porosity among the sites at < 0.25 mm distance faded at 0.25-0.5 mm interval, and upon distance reaching the 0.5-1.0 mm the image-based porosity of Hancock and Lake City exceeded that of the Oregon, Lux Arbor, and Escanaba. The image-based porosities at < 0.25 mm distance were negatively correlated with sand content and quartz, while total image-based porosities were positively correlated with them (Table S4). The total porosities were negatively correlated with silt, clay, and P-feldspar.

The vegetation also affected the imaged-based porosity. From 0.1-1.5 mm distance interval in Hancock and 2.5-3.0 mm in Lake City, the image-based porosity was greater in prairie than that in switchgrass system, while the porosity in switchgrass was numerically greater at <0.25 distance (Fig. 3 and Table S3).

The contribution of the three pore-size classes into the visible porosity changed with the distance from POM. In the region at < 0.25 mm away from the POM, pore group within 36-150  $\mu\text{m}$   $\emptyset$  size range accounted for 4% of the total porosity in finer-textured soils and 11% in coarser-textured soils (Fig. 5). Meanwhile, relatively larger pores (> 300  $\mu\text{m}$   $\emptyset$ ) contributed to 75% and 58% of the porosity in finer- and coarser-textured soil of the same distance region, respectively. The contributions of 36-150  $\mu\text{m}$  pores in both textured groups of soils increased with the distance from POM, while that of the larger pores decreased. Notably, the increases in the fractions of smaller pores were more drastic in coarser-textured soils compared to that in finer-textured soils (Fig. 5). Pores in the coarser soils were mostly represented by finer size pores (36-300  $\mu\text{m}$   $\emptyset$ ) beyond 1.0 mm distance from POM, whereas the finer soils still had 35% and 11 % of the larger pores at 1.0 mm and at 4.0 mm distances from POM, respectively. In coarser-textured soils, prairie system had greater fraction

of smaller size pores within interval regions from 0 to 3.0 mm than that of switchgrass system (Fig. 5C and 5D), while the fractions of such pores did not differ between two systems in finer-textured soils (Fig. 5A and 5B).

In both plant systems, in the immediate vicinity of POM (<0.25 mm away from POM), pore connectivity was greater in finer-textured than in coarser-textured soils. However, when examined across the entire soil volumes, the connectivity was lower in finer-textured than in coarser-textured soils (Fig. 6). The connectivity in the vicinity of POM was negatively correlated with sand, quartz, and smectite contents, while it was positively correlated with silt, clay, and P-feldspar contents (Table S5). However, the total connectivity showed the opposite trend, being positively correlated with sand, quartz, and smectite contents.

## 4 DISCUSSION

The results demonstrated that soil pore structure in the root detritosphere and in the whole soil volumes were affected by both soil texture and plants. Coarser-textured soils had much higher image-based porosity, yet fewer pores of biological origin than finer-textured soils. The biopores of fine-textured soils were numerous and constituted a significantly greater portion of the overall pore space, yet not holding as much remaining POM as those in the coarse-textured soils. Pore-size distributions in detritosphere as well as their spatial distribution trends with distance from the decomposing roots also markedly differed between the finer- and coarser-textured soils. Pores in the immediate vicinity of POM were better connected in finer-textured soils than in coarser-textured soils in both plant systems. While switchgrass soil had more biopores than prairie, its detritosphere pores consisted of relatively large size pores than those of the prairie, especially in coarser-textured soils.

### 4.1 Influences of soil texture on detritosphere pores

The greatest porosities found at < 0.25 mm away from the POM in soils of both plant systems indicated that the vicinity of the POM was mostly air-filled (Fig. 3). This “POM gap” between soil particles and root residues can be explained by incomplete filling of existing pores by roots during their growth and decrease of roots’ volume due to shrinking upon drying and/or their decomposition (De Gryze et al., 2006). Consistent with this explanation, roots of *Agave deserti* were found to shrunk by 34% in 24 days of natural drought in a greenhouse study (North & Nobel, 1997), and transpiration shrank roots of *Lupinus albus* (Koebernick et al. 2018). Decreases in POM volume due to decomposition were both visually observed and quantified using X-ray  $\mu$ CT images of intact soil samples (Juyal et al., 2021; Kim, Guber, Rivers, & Kravchenko, 2020).

Our findings of inherent texture and mineralogy characteristics influencing the contribution of biopores to the overall soil porosities (Fig. 2C and Table 1) were consistent with expectations and previous reports. In relatively sandy soils the biopores formed by roots were partially or completely refilled by sand grains after root decomposition, while in loamy soils the biopores that the roots left behind still maintained their structure (Phalempin et al., 2022). Sand grains have high volume-to-surface area ratios, and quartz on grain surfaces often lacks negative charge (Bazzoffi, Mbagwu, & Chukwu, 1995; Schrader & Zhang, 1997), resulting in low stability of particle arrangements (Almajmaie et al., 2017). Thus, the subsidence and displacement of the dispersed sand grains near decaying POM residues is likely among the reasons for the lower contributions of biopores to overall porosities in coarser-textured soils (Hancock and Lake City sites) compared to that in finer-textured soils (Oregon, Lux Arbor, and Escanaba sites) (Fig. 2C) and for the greater proportions of biopore space occupied by POM (Fig. 2D). The lower pore connectivity near the POM in coarser-textured than in finer-textured soils (Fig. 6) is another outcome of low stability. Finer, i.e., lower sand and quartz contents, soil particles are expected to facilitate maintenance of the structure by pores around POM, as compared to that of pores in coarser-textured soils.

The other two contributors to the observed differences in biopore volumes and in POM presence within the biopores are the inherent differences between coarser- and finer-textured soils in terms of (i) root growth and (ii) root residue decomposition rates. The volume of biopores and their occupation by roots might be overall lower in coarser-textured soils due to poorer root growth conditions (Dodd & Lauenroth, 1997; Sainju, Allen, Lenssen, & Ghimire, 2017). POM in soils with high sand contents might decompose slower

than that in the soils with low sand contents due to lower microbial activity at organo-mineral surfaces of sand grains (Haddix et al., 2020; Kaiser, Mueller, Joergensen, Insam, & Heinemeyer, 1992; Kögel-Knabner et al., 2008). Indeed, a negative correlation between sand contents and microbial biomass C was found across our experimental sites in a parallel study (Lee, Lucas, Guber, Li, & Kravchenko, 2023). Thus, in coarser-textured soils, the size of POM residues might not be decreasing as quickly as in the finer-textured soils, and the region around the POM may not be completely empty yet (Fig. 3). However, if the differences in plant growth and decomposition rates had indeed played a significant role in generating the observed differences in the biopore occupation by POM (Fig. 2D), we would expect to also detect the differences in terms of POM occupation between the two plant systems. Soils of restored prairie have developed higher SOM (Sanford, 2014; Sprunger & Robertson, 2018), thus better plant growth conditions, and much more active and abundant microbial communities (Lange et al., 2015), e.g., significantly higher microbial biomass C (Lee et al., 2023), than those of the monoculture switchgrass. Yet, there were no significant differences between the two systems in terms of POM occupation of the biopores (Fig. 2D) as well as the porosity in the detritosphere at least 1.0 mm away from POM (Table S3), ruling out the importance of these contributors. Thus, we conclude that the loss of structure and collapsing of biopores in coarser-textured soils is the main reason of the observed effects and is likely a wide-spread phenomenon.

Larger proportion of 36-150  $\mu\text{m}$   $\emptyset$  pores in close proximity ( $< 0.25$  mm distance) to POM in coarser-textured soils (Fig. 5) is consistent with lower soil porosity at the same distance (Fig. 3). Sand grains dominating coarser-textured soils can sporadically fill the POM gaps (Phalempin et al., 2022; Schrader & Zhang, 1997), and the filling by the grains may fragment the space of the gaps into finer pores. Indeed, porosities within the  $< 0.25$  mm distance to POM were negatively correlated with sand contents (Table S5). However, coarser-textured soils had larger contribution of such pores in intervals of  $> 0.25$  mm compared to finer-textured soils, showing positive correlations between sand contents and porosities of the entire volume (Table S5). Typically, in such regions beyond the root-influenced zone – areas where root-induced pores are negligible – the porosity tends to increase with higher sand content (Ding, Zhao, Feng, Peng, & Si, 2016; Fan et al., 2021; Nimmo, 2013). Indeed, gaps between sand particles are likely to primarily consist of pores that range between 50-200  $\mu\text{m}$   $\emptyset$  (Bantralexis, Markou, & Zografos, 2023). Therefore, the contrasting contributions of finer pores by distances are an indication of a localized effect ( $\sim 0.25$  mm) of roots on the pore structure, beyond which the porosity was mostly controlled by the soil texture.

#### 4.2 Influences of vegetation on detritosphere pores

The overall influence of the studied plant systems, 5-6 years after their establishment, on the pore characteristics of detritosphere was much lower than that of the inherent soil characteristics, i.e., texture and mineralogy. An important exception was the image-based porosity in remote portions of detritosphere ( $> 1.0$  mm): it tended to be greater in the soils of restored prairie than in those of switchgrass (Fig. 3 and Table S3). Switchgrass roots often reuse existing biopores (Lucas, Santiago, Chen, Guber, & Kravchenko, 2023), and their thick roots were likely responsible for soil compaction and low porosity at  $> 1$  mm distances (Aravena, Berli, Ghezzehei, & Tyler, 2011; Liu, Meng, Huang, Shi, & Wu, 2022). On the contrary, finer and heavily branching roots of many plant species of restored prairie likely promoted formation of finer pore networks throughout the entire detritosphere stabilizing them via root exudates and rhizodeposits (Hairiah, Widiyanto, Suprayogo, & Van Noordwijk, 2020; Smith, Wynn-Thompson, Williams, & Seiler, 2021). We surmise that these very fine roots rapidly decomposed after soil sampling and thus could not be detected as POM in the current study.

### 5 CONCLUSIONS

Soil pore structure both in the entire soil volume and in the root detritosphere was significantly influenced by soil texture and mineralogy. Coarse-textured quartz-rich soils had higher porosity but lower bioporosity than fine-textured soils, as well as greater proportions of biopore spaces occupied by POM. There were clear differences between fine- and coarse-textured soils in spatial patterns of pore size distributions as a function of distance from POM. In the immediate vicinity of POM. Finer-textured soils had higher porosity in close proximity of POM, that is greater POM-gap, consisting mainly of large pores ( $> 300$   $\mu\text{m}$   $\emptyset$ ) as well

as better pore connectivity compared to those of the coarser-textured soils. Despite known differences in the root characteristics of the studied plant systems, i.e., monoculture switchgrass and restored prairie, their impact on detritosphere pore structure was relatively minor. Lack of plant system effect suggests that the observed differences in detritosphere pore structure between finer- and coarser-textured soils are of primarily physical/mineralogical origin, e.g., due to loss of structure and collapsing of biopores in the latter, and the phenomenon present across a wide range (Alfisols, Entisols, and Spodosols) of soil types. The study provides an insight into the relationship among soil texture, mineralogy, and detritosphere pore structure, which serves as an important arena for microbial activity and soil C processing.

## ACKNOWLEDGEMENTS

We would like to thank Michelle Quigley from Michigan State University for conducting X-ray  $\mu$ CT scanning, Martin Pentrak from University of Illinois-Champaign for conducting X-ray powder diffraction, Jenie Gil Lugo and Maxwell Oerther for assistance with sample collection, and the Kellogg Biological Station and Great Lakes Bioenergy Research Center team for agronomic management of the field experiment. This research was funded by the Great Lakes Bioenergy Research Center, U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research under Award Number DE-SC0018409. The work was also supported by the NSF LTER Program (DEB 1027253) at Kellogg Biological Station, by Michigan State University's AgBioResearch, and by NC Regional Multistate Project 1187.

## CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial interest.

## REFERENCES

- Almajmaie, A., Hardie, M., Doyle, R., Birch, C., & Acuna, T. (2017). Influence of soil properties on the aggregate stability of cultivated sandy clay loams. *Journal of Soils and Sediments* , 17 (3), 800–809. <https://doi.org/10.1007/s11368-016-1568-1>
- Aravena, J. E., Berli, M., Ghezzehei, T. A., & Tyler, S. W. (2011). Effects of Root-Induced Compaction on Rhizosphere Hydraulic Properties—X-ray Microtomography Imaging and Numerical Simulations. *Environmental Science & Technology* , 45 (2), 425–431. <https://doi.org/10.1021/es102566j>
- Bantralexis, K. E., Markou, I. N., & Zografos, G. I. (2023). Use of sand pore-size distribution to predict cement suspension groutability. *Developments in the Built Environment* , 14 , 100138. <https://doi.org/10.1016/j.dibe.2023.100138>
- Bazzoffi, P., Mbagwu, J. S. C., & Chukwu. W. I. E. (1995). Statistical models for predicting aggregate stability from intrinsic soil components. *International Agrophysics* , 9 .
- Beare, R., Lowekamp, B., & Yaniv, Z. (2018). Image Segmentation, Registration and Characterization in R with SimpleITK. *Journal of Statistical Software* , 86 , 8. <https://doi.org/10.18637/jss.v086.i08>
- Bengough, A. G., Bransby, M. F., Hans, J., McKenna, S. J., Roberts, T. J., & Valentine, T. A. (2006). Root responses to soil physical conditions; growth dynamics from field to cell. *Journal of Experimental Botany* , 57 (2), 437–447. <https://doi.org/10.1093/jxb/erj003>
- Berg, S., Kutra, D., Kroeger, T., Straehle, C. N., Kausler, B. X., Haubold, C., ... Kreshuk, A. (2019). ilastik: Interactive machine learning for (bio)image analysis. *Nature Methods* , 16 (12), 1226–1232. <https://doi.org/10.1038/s41592-019-0582-9>
- Bodner, G., Leitner, D., & Kaul, H.-P. (2014). Coarse and fine root plants affect pore size distributions differently. *Plant and Soil* , 380 (1–2), 133–151. <https://doi.org/10.1007/s11104-014-2079-8>
- Bouckaert, L., Sleutel, S., Van Loo, D., Brabant, L., Cnudde, V., Van Hoorebeke, L., & De Neve, S. (2013). Carbon mineralisation and pore size classes in undisturbed soil cores. *Soil Research* , 51 (1), 14–22. <https://doi.org/10.1071/SR12116>

- Buades, A., Coll, B., & Morel, J.-M. (2011). Non-Local Means Denoising. *Image Processing On Line* , 1 , 208–212. [https://doi.org/10.5201/ipol.2011.bcm\\_nlm](https://doi.org/10.5201/ipol.2011.bcm_nlm)
- Buhmann, C., Rapp, I., & Laker, M. (1996). Differences in mineral ratios between disaggregated and original clay fractions in some South African soils as affected by amendments. *Soil Research* ,34 (6), 909. <https://doi.org/10.1071/SR9960909>
- Croser, C., Bengough, A. G., & Pritchard, J. (1999). The effect of mechanical impedance on root growth in pea (*Pisum sativum*). I. Rates of cell flux, mitosis, and strain during recovery. *Physiologia Plantarum* , 107 (3), 277–286. <https://doi.org/10.1034/j.1399-3054.1999.100304.x>
- Darbon, J., Cunha, A., Chan, T. F., Osher, S., & Jensen, G. J. (2008). Fast nonlocal filtering applied to electron cryomicroscopy. *2008 5th IEEE International Symposium on Biomedical Imaging: From Nano to Macro* , 1331–1334. Paris, France: IEEE. <https://doi.org/10.1109/ISBI.2008.4541250>
- De Gryze, S., Jassogne, L., Six, J., Bossuyt, H., Wevers, M., & Merckx, R. (2006). Pore structure changes during decomposition of fresh residue: X-ray tomography analyses. *Geoderma* , 134 (1), 82–96. <https://doi.org/10.1016/j.geoderma.2005.09.002>
- Ding, D., Zhao, Y., Feng, H., Peng, X., & Si, B. (2016). Using the double-exponential water retention equation to determine how soil pore-size distribution is linked to soil texture. (National Agricultural Library).
- Dodd, M. B., & Lauenroth, W. K. (1997). The influence of soil texture on the soil water dynamics and vegetation structure of a shortgrass steppe ecosystem. *Plant Ecology* , 133 (1), 13–28. <https://doi.org/10.1023/A:1009759421640>
- Fan, Z., Hu, C., Zhu, Q., Jia, Y., Zuo, D., & Duan, Z. (2021). Three-dimensional pore characteristics and permeability properties of calcareous sand with different particle sizes. *Bulletin of Engineering Geology and the Environment* , 80 (3), 2659–2670. <https://doi.org/10.1007/s10064-020-02078-1>
- Franklin, S. M., Kravchenko, A. N., Vargas, R., Vasilas, B., Fuhrmann, J. J., & Jin, Y. (2021). The unexplored role of preferential flow in soil carbon dynamics. *Soil Biology and Biochemistry* , 161 , 108398. <https://doi.org/10.1016/j.soilbio.2021.108398>
- Gaillard, V., Chenu, C., Recous, S., & Richard, G. (1999). Carbon, nitrogen and microbial gradients induced by plant residues decomposing in soil. *European Journal of Soil Science* , 50 (4), 567–578. <https://doi.org/10.1046/j.1365-2389.1999.00266.x>
- Gee, G. W., & Or, D. (2002). 2.4 Particle-Size Analysis. In *Methods of Soil Analysis* (pp. 255–293). John Wiley & Sons, Ltd. <https://doi.org/10.2136/sssabookser5.4.c12>
- Haddix, M. L., Gregorich, E. G., Helgason, B. L., Janzen, H., Ellert, B. H., & Francesca Cotrufo, M. (2020). Climate, carbon content, and soil texture control the independent formation and persistence of particulate and mineral-associated organic matter in soil. *Geoderma* ,363 , 114160. <https://doi.org/10.1016/j.geoderma.2019.114160>
- Hairiah, K., Widiyanto, W., Suprayogo, D., & Van Noordwijk, M. (2020). Tree Roots Anchoring and Binding Soil: Reducing Landslide Risk in Indonesian Agroforestry. *Land* , 9 (8), 256. <https://doi.org/10.3390/land9080256>
- Helliwell, J. R., Sturrock, C. J., Mairhofer, S., Craigon, J., Ashton, R. W., Miller, A. J., ... Mooney, S. J. (2017). The emergent rhizosphere: Imaging the development of the porous architecture at the root-soil interface. *Scientific Reports* , 7 (1), 14875. <https://doi.org/10.1038/s41598-017-14904-w>
- Helliwell, Jon R., Sturrock, C. J., Miller, A. J., Whalley, W. R., & Mooney, S. J. (2019). The role of plant species and soil condition in the structural development of the rhizosphere. *Plant, Cell & Environment* , 42 (6), 1974–1986. <https://doi.org/10.1111/pce.13529>

- Hildebrand, T., & Rügsegger, P. (1997). A new method for the model-independent assessment of thickness in three-dimensional images. *Journal of Microscopy* , 185 (1), 67–75. <https://doi.org/10.1046/j.1365-2818.1997.1340694.x>
- Jarvis, N. J. (2007). A review of non-equilibrium water flow and solute transport in soil macropores: Principles, controlling factors and consequences for water quality. *European Journal of Soil Science* , 58 (3), 523–546. <https://doi.org/10.1111/j.1365-2389.2007.00915.x>
- Jesus, E. da C., Liang, C., Quensen, J. F., Susilawati, E., Jackson, R. D., Balsler, T. C., & Tiedje, J. M. (2016). Influence of corn, switchgrass, and prairie cropping systems on soil microbial communities in the upper Midwest of the United States. *GCB Bioenergy* , 8 (2), 481–494. <https://doi.org/10.1111/gcbb.12289>
- Juyal, A., Guber, A., Oerther, M., Quigley, M., & Kravchenko, A. N. (2021). Pore architecture and particulate organic matter in soils under monoculture switchgrass and restored prairie in contrasting topography. *Scientific Reports* , 11 (1), 21998. <https://doi.org/10.1038/s41598-021-01533-7>
- Kaiser, E. A., Mueller, T., Joergensen, R. G., Insam, H., & Heinemeyer, O. (1992). Evaluation of methods to estimate the soil microbial biomass and the relationship with soil texture and organic matter. *Soil Biology and Biochemistry* , 24 (7), 675–683. [https://doi.org/10.1016/0038-0717\(92\)90046-Z](https://doi.org/10.1016/0038-0717(92)90046-Z)
- Kasmerchak, C. S., & Schaetzl, R. (2018). *Soils of the GLBRC Marginal Land Experiment (MLE) Sites* . <https://doi.org/10.5281/ZENODO.2578238>
- Kim, K., Guber, A. K., Rivers, M., & Kravchenko, A. N. (2020). Contribution of decomposing plant roots to N<sub>2</sub>O emissions by water absorption. *Geoderma* , 375 , 114506. <https://doi.org/10.1016/j.geoderma.2020.114506>
- Koebnick, N., Schluter, S., Blaser, S. R. G. A., & Vetterlein, D. (2018). Root-soil contact dynamics of *Vicia faba* in sand. *Plant and Soil* , 431 (1), 417–431. <https://doi.org/10.1007/s11104-018-3769-4>
- Kogel-Knabner, I., Guggenberger, G., Kleber, M., Kandeler, E., Kalbitz, K., Scheu, S., ... Leinweber, P. (2008). Organo-mineral associations in temperate soils: Integrating biology, mineralogy, and organic matter chemistry. *Journal of Plant Nutrition and Soil Science* , 171 (1), 61–82. <https://doi.org/10.1002/jpln.200700048>
- Kravchenko, A. N., Guber, A. K., Razavi, B. S., Koestel, J., Blagodatskaya, E. V., & Kuzyakov, Y. (2019). Spatial patterns of extracellular enzymes: Combining X-ray computed micro-tomography and 2D zymography. *Soil Biology and Biochemistry* , 135 , 411–419. <https://doi.org/10.1016/j.soilbio.2019.06.002>
- Kravchenko, A. N., Guber, A. K., Razavi, B. S., Koestel, J., Quigley, M. Y., Robertson, G. P., & Kuzyakov, Y. (2019). Microbial spatial footprint as a driver of soil carbon stabilization. *Nature Communications* , 10 (1), 3121. <https://doi.org/10.1038/s41467-019-11057-4>
- Kravchenko, A. N., & Guber, A. K. (2017). Soil pores and their contributions to soil carbon processes. *Geoderma* , 287 , 31–39. <https://doi.org/10.1016/j.geoderma.2016.06.027>
- Kuzyakov, Y., & Blagodatskaya, E. (2015). Microbial hotspots and hot moments in soil: Concept & review. *Soil Biology and Biochemistry* , 83 , 184–199. <https://doi.org/10.1016/j.soilbio.2015.01.025>
- Lange, M., Eisenhauer, N., Sierra, C. A., Bessler, H., Engels, C., Griffiths, R. I., ... Gleixner, G. (2015). Plant diversity increases soil microbial activity and soil carbon storage. *Nature Communications* , 6 (1), 6707. <https://doi.org/10.1038/ncomms7707>
- Lee, J. H., Lucas, M., Guber, A. K., Li, X., & Kravchenko, A. N. (2023). Interactions among soil texture, pore structure, and labile carbon influence soil carbon gains. *Geoderma* , 439 , 116675. <https://doi.org/10.1016/j.geoderma.2023.116675>
- Li, X., Petipas, R. H., Antoch, A. A., Liu, Y., Stel, H. V., Bell-Dereske, L., ... Friesen, M. L. (2022). Switchgrass cropping systems affect soil carbon and nitrogen and microbial diversity and activity on marginal

lands. *GCB Bioenergy* , 14 (8), 918–940. <https://doi.org/10.1111/gcbb.12949>

Liu, Y.-F., Meng, L.-C., Huang, Z., Shi, Z.-H., & Wu, G.-L. (2022). Contribution of fine roots mechanical property of Poaceae grasses to soil erosion resistance on the Loess Plateau. *Geoderma* , 426 , 116122. <https://doi.org/10.1016/j.geoderma.2022.116122>

Lucas, M. (2022). Perspectives from the Fritz-Scheffer Awardee 2020—The mutual interactions between roots and soil structure and how these affect rhizosphere processes #. *Journal of Plant Nutrition and Soil Science* , 185 (1), 8–18. <https://doi.org/10.1002/jpln.202100385>

Lucas, M., Nguyen, L. T. T., Guber, A., & Kravchenko, A. N. (2022). Cover crop influence on pore size distribution and biopore dynamics: Enumerating root and soil faunal effects. *Frontiers in Plant Science* , 13 , 928569. <https://doi.org/10.3389/fpls.2022.928569>

Lucas, M., Santiago, J. P., Chen, J., Guber, A., & Kravchenko, A. N. (2023). The soil pore structure encountered by roots affects plant-derived carbon inputs and fate. *New Phytologist* , 240 (2), 515–528. <https://doi.org/10.1111/nph.19159>

Lucas, M., Schluter, S., Vogel, H.-J., & Vetterlein, D. (2019a). Roots compact the surrounding soil depending on the structures they encounter. *Scientific Reports* , 9 (1), 16236. <https://doi.org/10.1038/s41598-019-52665-w>

Lucas, M., Schluter, S., Vogel, H.-J., & Vetterlein, D. (2019b). Soil structure formation along an agricultural chronosequence. *Geoderma* , 350 , 61–72. <https://doi.org/10.1016/j.geoderma.2019.04.041>

Lucas, M., Vetterlein, D., Vogel, H.-J., & Schluter, S. (2021). Revealing pore connectivity across scales and resolutions with X-ray CT. (National Agricultural Library).

Mitchell, J. K., & Soga, K. (2005). Fundamentals of Soil Behavior. In *Fundamentals of Soil Behavior* . John Wiley and Sons, Inc.

Neaman, A., Singer, A., & Stahr, K. (1999). Clay mineralogy as affecting disaggregation in some palygorskite containing soils of the Jordan and Bet-She'an Valleys. *Soil Research* , 37 (5), 913. <https://doi.org/10.1071/SR98118>

Negassa, W. C., Guber, A. K., Kravchenko, A. N., Marsh, T. L., Hildebrandt, B., & Rivers, M. L. (2015). Properties of Soil Pore Space Regulate Pathways of Plant Residue Decomposition and Community Structure of Associated Bacteria. *PLOS ONE* , 10 (4), e0123999. <https://doi.org/10.1371/journal.pone.0123999>

Nimmo, J. R. (2013). Porosity and Pore Size Distribution. In *Reference Module in Earth Systems and Environmental Sciences* (p. B9780124095489052659). Elsevier. <https://doi.org/10.1016/B978-0-12-409548-9.05265-9>

North, G. B., & Nobel, P. S. (1997). Root–soil contact for the desert succulent *Agave deserti* in wet and drying soil. *The New Phytologist* , 135 (1), 21–29. <https://doi.org/10.1046/j.1469-8137.1997.00620.x>

Odgaard, A., & Gundersen, H. J. G. (1993). Quantification of connectivity in cancellous bone, with special emphasis on 3-D reconstructions. *Bone* , 14 (2), 173–182. [https://doi.org/10.1016/8756-3282\(93\)90245-6](https://doi.org/10.1016/8756-3282(93)90245-6)

Phalempin, M., Landl, M., Wu, G.-M., Schnepf, A., Vetterlein, D., & Schluter, S. (2022). Maize root-induced biopores do not influence root growth of subsequently grown maize plants in well aerated, fertilized and repacked soil columns. *Soil and Tillage Research* , 221 , 105398. <https://doi.org/10.1016/j.still.2022.105398>

Phalempin, M., Lippold, E., Vetterlein, D., & Schluter, S. (2021a). An improved method for the segmentation of roots from X-ray computed tomography 3D images: Routine v.2. *Plant Methods* , 17 (1), 39. <https://doi.org/10.1186/s13007-021-00735-4>

Phalempin, M., Lippold, E., Vetterlein, D., & Schluter, S. (2021b). Soil texture and structure heterogeneity predominantly governs bulk density gradients around roots. *Vadose Zone Journal* , 20 (5).

<https://doi.org/10.1002/vzj2.20147>

Rabbi, S. M. F., Daniel, H., Lockwood, P. V., Macdonald, C., Pereg, L., Tighe, M., ... Young, I. M. (2016). Physical soil architectural traits are functionally linked to carbon decomposition and bacterial diversity. *Scientific Reports* , 6 (1), 33012. <https://doi.org/10.1038/srep33012>

Rabot, E., Wiesmeier, M., Schluter, S., & Vogel, H.-J. (2018). Soil structure as an indicator of soil functions: A review. *Geoderma* , 314 , 122–137. <https://doi.org/10.1016/j.geoderma.2017.11.009>

Rivera, J. I., & Bonilla, C. A. (2020). Predicting soil aggregate stability using readily available soil properties and machine learning techniques. *CATENA* , 187 , 104408. <https://doi.org/10.1016/j.catena.2019.104408>

Sainju, U. M., Allen, B. L., Lenssen, A. W., & Ghimire, R. P. (2017). Root biomass, root/shoot ratio, and soil water content under perennial grasses with different nitrogen rates. *Field Crops Research* , 210 , 183–191. <https://doi.org/10.1016/j.fcr.2017.05.029>

Sanford, G. R. (2014). Perennial Grasslands Are Essential for Long Term SOC Storage in the Mollisols of the North Central USA. In A. E. Hartemink & K. McSweeney (Eds.), *Soil Carbon* (pp. 281–288). Cham: Springer International Publishing. [https://doi.org/10.1007/978-3-319-04084-4\\_29](https://doi.org/10.1007/978-3-319-04084-4_29)

Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., ... Cardona, A. (2012). Fiji: An open-source platform for biological-image analysis. *Nature Methods* , 9 (7), 676–682. <https://doi.org/10.1038/nmeth.2019>

Schrader, S., & Zhang, H. (1997). Earthworm casting: Stabilization or destabilization of soil structure? *Soil Biology and Biochemistry* , 29 (3), 469–475. [https://doi.org/10.1016/S0038-0717\(96\)00103-4](https://doi.org/10.1016/S0038-0717(96)00103-4)

Six, J., Elliott, E. T., & Paustian, K. (2000). Soil Structure and Soil Organic Matter II. A Normalized Stability Index and the Effect of Mineralogy. *Soil Science Society of America Journal* , 64 (3), 1042–1049. <https://doi.org/10.2136/sssaj2000.6431042x>

Smith, D. J., Wynn-Thompson, T. M., Williams, M. A., & Seiler, J. R. (2021). Do roots bind soil? Comparing the physical and biological role of plant roots in fluvial streambank erosion: A mini-JET study. *Geomorphology* , 375 , 107523. <https://doi.org/10.1016/j.geomorph.2020.107523>

Sokol, N. W., Kuebbing, S. E., Karlsen-Ayala, E., & Bradford, M. A. (2019). Evidence for the primacy of living root inputs, not root or shoot litter, in forming soil organic carbon. *New Phytologist* , 221 (1), 233–246. <https://doi.org/10.1111/nph.15361>

Sprunger, C. D., & Robertson, G. P. (2018). Early accumulation of active fraction soil carbon in newly established cellulosic biofuel systems. *Geoderma* , 318 , 42–51. <https://doi.org/10.1016/j.geoderma.2017.11.040>

Strong, D. T., Wever, H. D., Merckx, R., & Recous, S. (2004). Spatial location of carbon decomposition in the soil pore system: Spatial location of carbon decomposition. *European Journal of Soil Science* , 55 (4), 739–750. <https://doi.org/10.1111/j.1365-2389.2004.00639.x>

Thomsen, I. K., Schjonning, P., Jensen, B., Kristensen, K., & Christensen, B. T. (1999). Turnover of organic matter in differently textured soils: II. Microbial activity as influenced by soil water regimes. *Geoderma* , 89 (3), 199–218. [https://doi.org/10.1016/S0016-7061\(98\)00084-6](https://doi.org/10.1016/S0016-7061(98)00084-6)

Traore, O., Groleau-Renaud, V., Plantureux, S., Tubeileh, A., & Boeuf-Tremblay, V. (2000). Effect of root mucilage and modelled root exudates on soil structure. *European Journal of Soil Science* , 51 (4), 575–581. <https://doi.org/10.1111/j.1365-2389.2000.00348.x>

Vedere, C., Vieuble Gonod, L., Pouteau, V., Girardin, C., & Chenu, C. (2020). Spatial and temporal evolution of detritusphere hotspots at different soil moistures. *Soil Biology and Biochemistry* , 150 , 107975. <https://doi.org/10.1016/j.soilbio.2020.107975>

Vogel, H.-J. (2002). Topological Characterization of Porous Media. In K. Mecke & D. Stoyan (Eds.), *Morphology of Condensed Matter: Physics and Geometry of Spatially Complex Systems* (pp. 75–92). Berlin, Heidelberg: Springer. [https://doi.org/10.1007/3-540-45782-8\\_3](https://doi.org/10.1007/3-540-45782-8_3)

Vogel, H.-J., & Roth, K. (2001). Quantitative morphology and network representation of soil pore structure. *Advances in Water Resources* , 24 (3–4), 233–242. [https://doi.org/10.1016/S0309-1708\(00\)00055-5](https://doi.org/10.1016/S0309-1708(00)00055-5)

Vogel, H.-J., Weller, U., & Schluter, S. (2010). Quantification of soil structure based on Minkowski functions. *Computers & Geosciences* ,36 (10), 1236–1245. <https://doi.org/10.1016/j.cageo.2010.03.007>

Wakindiki, I. I. C., & Ben-Hur, M. (2002). Soil Mineralogy and Texture Effects on Crust Micro-morphology, Infiltration, and Erosion. *Soil Science Society of America Journal* , 66 (3), 897–905. <https://doi.org/10.2136/sssaj2002.8970>

Walt, S. van der, Schonberger, J. L., Nunez-Iglesias, J., Boulogne, F., Warner, J. D., Yager, N., . . . Yu, T. (2014). scikit-image: Image processing in Python. *PeerJ* , 2 , e453. <https://doi.org/10.7717/peerj.453>

### Hosted file

LDD\_Figures\_Lee.docx available at <https://authorea.com/users/674794/articles/672989-pore-structure-in-detritosphere-of-soils-under-switchgrass-and-restored-prairie-vegetation-community>

### Hosted file

LDD\_Tables\_Lee.docx available at <https://authorea.com/users/674794/articles/672989-pore-structure-in-detritosphere-of-soils-under-switchgrass-and-restored-prairie-vegetation-community>