

# Optical coherence tomography imaging of plant root growth in soil

**Curtis J. Larimer,  Elizabeth H. Denis, Jonathan D. Suter,  
James J. Moran**

Complex interactions between roots and soil provide the nutrients and physical support required for robust plant growth. Yet, visualizing the root–soil interface is challenged by soil’s opaque scattering characteristics. Herein, we describe methods for using optical coherence tomography (OCT) to provide non-destructive 3D and cross-sectional root imaging not available with traditional bright-field microscopy. OCT is regularly used for bioimaging, especially in ophthalmology, where it can detect retinal abnormalities. Prior use of OCT in plant biology has focused on surface defects of above-ground tissues, predominantly in food crops. Our results show OCT is also viable for detailed, *in situ* study of living plant roots. Using OCT for direct observations of root growth in soil can help elucidate key interactions between root morphology and various components of the soil environment including soil structure, microbial communities, and nutrient patches. Better understanding of these interactions can guide efforts to improve plant nutrient acquisition from soil to increase agricultural efficiency as well as better understand drivers of plant growth in natural systems.

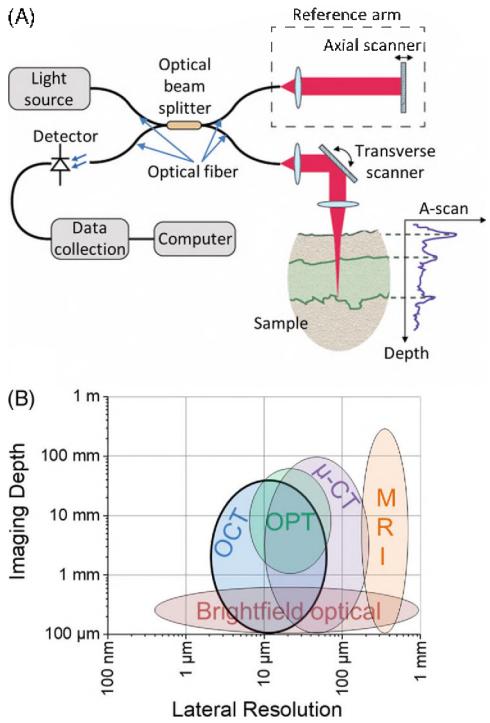
## 1. INTRODUCTION

Soil is highly heterogeneous due to interacting geochemical, biological, and physical processes, which can create strong nutrient gradients at pore-sized (roughly millimeter, mm) or smaller scales [1]. Roots must navigate this complex environment to efficiently extract needed nutrients to support plant growth. Previous work has demonstrated morphological adaptation of roots, highlighted by larger rates of root branching to focus plant investment in regions of soil with higher nutritional value to the plant [2]. Other work demonstrates a link between the formation of root hairs and a plant's interaction with and ability to harvest nutrients from soil [3]. Additionally, a suite of nutrient exchange processes can be facilitated by symbiotic interactions between plant roots and fungi, which effectively extend the spatial reach of nutrient collection from soil well beyond the root boundary itself [4,5]. Examining the complex coordination of these nutrient acquisition strategies is crucial to establishing a holistic understanding of nutrient exchange between soil and plants and may form a foundation for enriching these processes to improve agricultural or natural plant growth [6]. Each of the above processes can be visually observed (with magnification), but high-throughput tools for detailed, three-dimensional

tracking of these physical interactions during root growth are largely lacking.

The principal challenge is that soil itself can obscure *in situ* root system visualization. To avoid this issue, plants are sometimes grown in liquid culture, surfaces of agar or paper, or in transparent gel growth media that can enable visualization but may not be representative of the 3D nature of growth in the natural environments (i.e., soil) and may restrict analysis of larger plants [7–10]. Imaging techniques such as x-ray micro-focus computed tomography (x-ray  $\mu$ CT) and synchrotron tomography (SR-CT) can enable imaging directly within soil, but both have limitations. X-ray  $\mu$ CT functions on the nanometer (nm) to decimeter (dm) scale but has limited sample throughput, and the resulting long scan times can negatively impact soil biota and are thus not truly non-destructive to the holistic root–soil system [9]. Synchrotron tomography [nm to centimeter (cm) scale], is limited by sample size, throughput, expense, and accessibility, and it is not transportable to the field [10,11].

Optical coherence tomography (OCT), often described as an “optical ultrasound,” offers a potential solution for non-destructive imaging and tomography of roots. OCT is a commonly applied technique for studying the morphology



**Fig. 1.** (A) Major components and functions of an optical coherence tomography (OCT) imaging system are laid out as a Michelson interferometer. Light from a broadband source is split by an optical beam splitter and sent to both a reference arm and sample arm. Recombined light creates interference that is observed at a photodetector. Raw spectra are converted to 3D images. (B) OCT has a combination of lateral resolution and imaging depth that is not available with other root imaging methods (e.g., optical projection tomography [OPT] [25,26], micro-computed tomography [ $\mu$ -CT] [27,28], magnetic resonance imaging [MRI] [29], and bright-field optical microscopy).

and changes in human skin [12], retina [13], veins and arteries, and other soft tissues [14,15]. Functionally, OCT uses interferometry to record the optical path of photons reflected from the layers of soft tissues. A near-infrared laser light source scans over the surface of a sample to produce depth-resolved cross sections, which can be assembled into a full 3D tomogram. Figure 1(A) shows the major optical components of an OCT system.

OCT imaging systems can achieve spatial resolution of approximately 2–4  $\mu$ m (lateral resolution is restricted by the optical diffraction limit and lateral sampling rate, while the axial resolution is inversely proportional to the bandwidth of the light source), and depths of up to 10 mm can be resolved [14,16], which gives it a unique combination of lateral resolution and imaging depth when compared to other root imaging techniques [as shown in Fig. 1(B)]. OCT imaging is also relatively fast (scans can take from 10 s to 5 min depending on settings) and non-destructive (the laser light source is relatively low power). In terms of plant biology, OCT has been demonstrated for imaging of subsurface layers of fruits, seeds, and plant leaves [17–20], stomata [21], and leaf defects that result from the stresses associated with environmental pollutants [22], drought [23], and disease [24]. Despite this previous work, OCT has

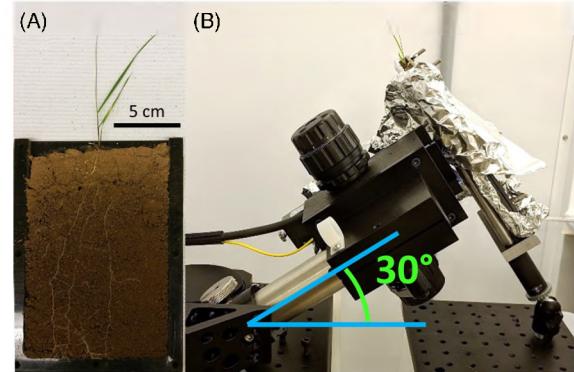
not been used to study root systems in soil, likely owing to the difficulty of imaging in a highly scattering medium.

In this paper, we describe application of OCT imaging to the study of roots, including those grown in soil. First, we present a traditional use of OCT to monitor the emergence of roots from germinating seeds through air. Then we describe the custom growing and imaging conditions that are needed to achieve high-quality images in the challenging soil medium. As OCT imaging is non-destructive, roots were imaged at regular intervals while growing through soil, and the resulting series of images enabled estimation of the growth rate of the root tip and several root hairs. In the future, we envision continued use of these methods to better understand root systems and their interaction with the soil and symbiotic species such as fungi and bacteria.

## 2. METHODS

### A. Plants, Soil, and Growth Conditions

Seeds (*Panicum virgatum* L., PI 469228, switchgrass, variety Cave-in-Rock, provided from the USDA National Plant Germplasm System) were germinated on a layer of wet Kimwipes in a petri dish. Images were collected from germinating seeds every 3 h for several days in order to capture the time at which roots emerged. A subset of the germinated seedlings were planted in rhizoboxes (black high-density polyethylene, 15 cm  $\times$  20 cm  $\times$  1 cm) filled with soil (4 mm sieved) from the Kellogg Biological Station, Michigan, USA [Fig. 2(A)]. Rhizoboxes were placed in a Conviron walk-in growth chamber at an approximately 45 deg angle relative to horizontal to encourage root growth along a side transparent panel to optimize imaging of the root. Climate controlled conditions were 16 h of light at 22°C and 60% relative humidity and 8 hrs of dark at 18°C and 50% relative humidity. The plant grew in the chamber for 21 days. The side section of the rhizobox was removed and replaced with a transparent plexiglass panel. Sections of this clear panel not targeted for imaging were covered in aluminum foil to protect the soil and roots from ambient light exposure.



**Fig. 2.** (A) Photo of a switchgrass plant grown in a rhizobox. (B) Photo of the imaging setup showing the imaging end of the OCT system pointing up to the right at an angle of approximately 30° above horizontal. The imager sits  $\sim$ 3 mm from the surface of the rhizobox, which is covered in aluminum foil to block light from reaching roots during the experiment.

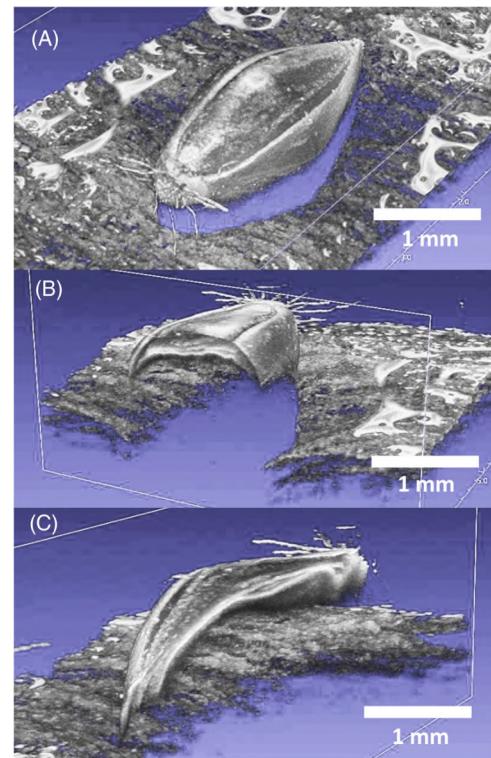
## 128 B. OCT Imaging Setup

129 Imaging was performed with a spectral domain OCT instrument system (Ganymede Model 210C1, ThorLabs, Newton, NJ). The laser light source has a center wavelength of 930 nm and was scanned at 36 kHz. A scanning lens (model OCT-LK3-BB) with  $\sim$ 25 mm working distance, 8  $\mu$ m lateral resolution, and 2.9  $\mu$ m axial resolution was used. Maximal scanning areas of 130 10 mm by 10 mm were explored, but we generally used smaller 131 areas of between 2 to 7 mm lateral distance to minimize scanning 132 time and resulting file sizes. ThorLabs ThorImage OCT 133 4.4 software was used to collect and process raw data into 3D 134 tomograms. The software performs a fast Fourier transform of 135 the raw spectral data and then takes the absolute value of the 136 complex data to produce A-scans (i.e., the image intensity of 137 each axial column in the field of view). For processing, three 138 A-scans were averaged, and spectral shaping was applied. The 139 averaged A-scan data for the full field were stored in decibels 140 (dB), which was computed by taking the base-10 logarithm 141 and multiplying by 20. A Hann apodization window was 142 chosen to reduce imaging artifacts, and quadratic dispersion 143 compensation was applied to reduce axial blurring. A grayscale 144 color map was applied to the dB values of the 3D image using 145 a dynamic range that was selected to filter out speckle in the air 146 around samples.

147 Typically, OCT imaging systems are set up like traditional 148 microscopes, with the imaging lens pointing down at a sample. 149 However, as described above, plants were grown in rhizoboxes 150 [see Fig. 2(A)] placed at an angle to encourage growth of the 151 root against the transparent panel on one side of the box. For 152 this research, a custom stand was built to accommodate imaging 153 at adjustable angles, including pointing up at approximately 154 30° relative to horizontal [as shown in Fig. 2(B)]. The angle and 155 pitch of the rhizobox was also made adjustable using a ball joint 156 to facilitate aligning the sample perpendicular to the imager. 157 Suitable imaging areas of seeds and roots were selected, and the 158 imaging system was focused. A single imaging scan typically 159 took 30–120 s to acquire, depending on the size of the field 160 of view.

161 Time series image collection was enabled by using built-in 162 scheduling features of the ThorImage software, and our applied 163 collection intervals ranged from 15 min to 3 h for periods up to 164 6 days. The software was typically set to automatically collect 165 data for 24–48 h, after which time we would archive collected 166 data and reset the system for continued data collection. In 167 several cases (especially for germinating seeds), images were 168 collected over several days before roots began to emerge. Data 169 that was collected was periodically moved to an external storage 170 device to avoid exhausting the memory of the computer system. 171 Image focus was adjusted as necessary at the start of each series of 172 data collection.

173 Imaging roots and soil in proximity to a transparent panel 174 resulted in a bright plane artifact in each image. Reflections of 175 this plane above or below the primary root imaging data were 176 eliminated by choosing a panel with thickness (approximately 177 3 mm) greater than the imaging depth. Using a thinner panel 178 would result in multiple planar artifacts that could not easily 179 be filtered because they would overlap the data of interest. The 180 bright plane was removed using the clipping feature of the 181 182 183 184 185

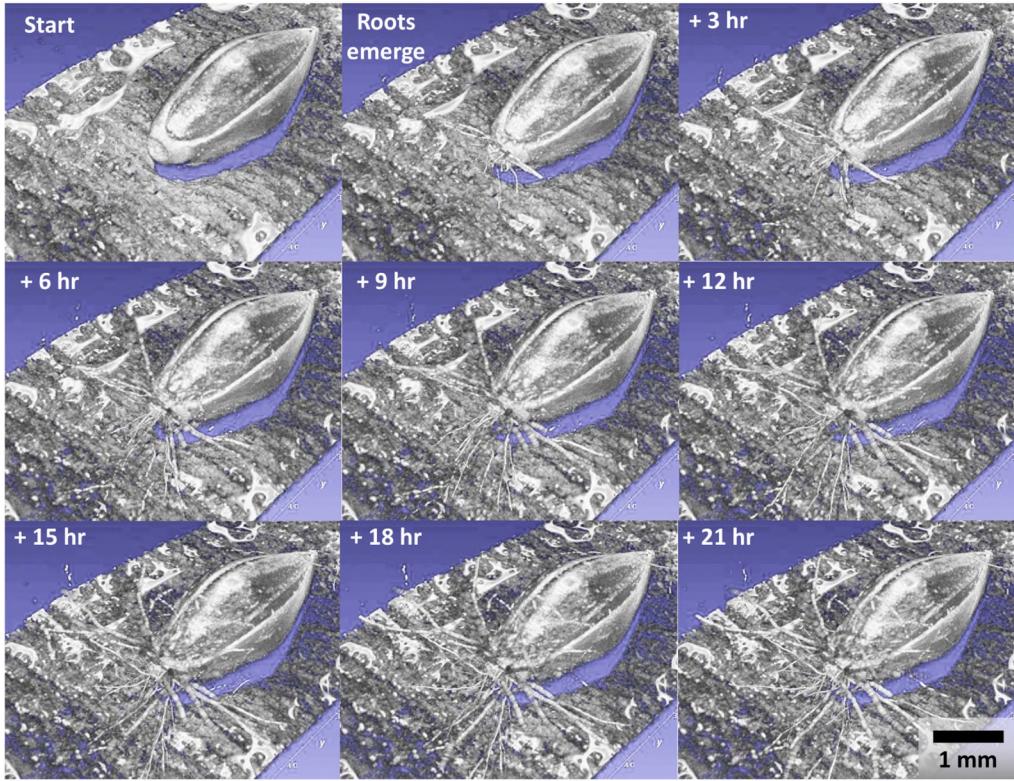


**Fig. 3.** (A) OCT image of a switchgrass seed on a wet paper towel at the time of root emergence. Cross sections of the image shown in A across the (B) width of the seed and the (C) length of the seed show the depth imaging capability. Scales are indicated by the bar in each image.

186 ThorImage software. As much as possible, identical clip settings 187 were used for all images in a time series. Subtle shifts in the 188 sample relative to the imager occasionally resulted in a change 189 in the location of the viewing window in the image. Clipping 190 was adjusted to accommodate these shifts. Images were exported 191 from the ThorImage software as jpg images. Clipping was also 192 used to generate cross sections, such as in Figs. 3 and 8.

193 Exported images were subsequently processed using Adobe 194 Photoshop CC 2019. Brightness and contrast were adjusted 195 uniformly for all images in Figs. 3, 4, and 8(B) and 8(C). 196 Visualizations of the time series were also created using this 197 software. [Visualization 1](#), [Visualization 2](#), [Visualization 3](#), 198 [Visualization 4](#), [Visualization 5](#), and [Visualization 6](#) were made 199 from animated files exported from the ThorImage software.

200 The Tracker Video Analysis and Modeling tool, an open 201 source software (available at [physlets.org/tracker](http://physlets.org/tracker)), was used to 202 track the movement of a main root tip and two root hairs growing 203 through soil. The software takes a video of the time series as 204 input. The location of the tip of the root was selected manually 205 by advancing the video “frame-by-frame” through each image 206 in the time series. The distance the tip moved between images 207 was automatically calculated by entering the image’s scale. The 208 Tracker software then used these distances and the time elapsed 209 between images to calculate growth rate in millimeters per hour 210 (mm/hr). The path that the root tip followed was also tracked 211 to create a trace of movement. Data were plotted, and trend 212 analysis was performed using graphing and analysis software 213 (Origin 2019a).



**Fig. 4.** Time series of OCT images of a switchgrass seed show the emergence of roots over 21 hrs. Scale is indicated by the bar in the lower right image.

### 3. RESULTS AND DISCUSSION

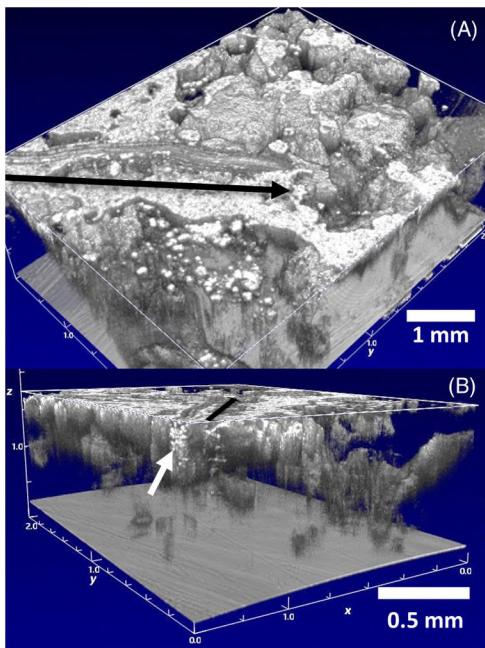
The first objective of this research was to ascertain the degree to which OCT could resolve the fine details of root structures and to establish procedures needed to perform time series imaging of roots within soil. We germinated switchgrass seeds on a wet paper towel to encourage germination while allowing for unobscured sample imaging. The seed was imaged every 3 hrs to enable tracking of root emergence and elongation from the seed. Figure 3 shows 3D images of the seed at the first time point after roots appeared (see also [Visualization 1](#), which shows a rotating view of the same data), and the complementary horizontal and lengthwise cross-section images reveal some internal structures in the seed. The images clearly show fine roots emerging from the seed and branching out into the surrounding medium. The “shadow” effect visible under the seed in this image highlights one potential limitation of OCT, in that the method prevents collection of data from the surface under the seed because light cannot pass through the seed to reach structures underneath. Some artifacts of water in the paper towel are also visible around the seed. The presence of water in and around plant roots may influence OCT imaging because water can create a reflective surface and can also absorb near-IR light.

Figure 4 and [Visualization 2](#) show time series of root growth from a germinating seed over time, which helps highlight the non-destructive nature of OCT. The panels of Fig. 4 show the first 21 hrs of a 39 hr observation period. The images clearly show lengthening and thickening of nascent roots, which radiate from the seed tip. Near the end of the observational window,

many of the roots extend beyond the focal plane of the imaging system, leading to image blurring and other artifacts. This blurring highlights the need to ensure the sample is within suitable imaging boundaries to ensure the efficacy of quantitative measurements (e.g., root diameter), because root dimensions may appear to vary with the level of blurring.

Results of a separate experiment where two seeds were placed next to each other are shown in [Visualization 3](#). The observation period was 69 h. Interestingly, this set of images also shows emergence of the thicker primary root in addition to a large collection of fine root hairs. The time series also shows one of the seeds being lifted towards the top of the imaging field near the end of the experiment. These experiments show it is possible to observe root growth over extended time periods (>72 h) using OCT.

After completing simple experiments with germinating seeds, we attempted imaging of roots in soil. Two conditions were created to enable imaging in this challenging medium. First, the roots were grown in an angled rhizobox, which encouraged growth in contact with a transparent imaging window. This would allow direct imaging of the root with a surrounding matrix of soil. Second, the imaging window was thick enough to avoid reflective artifacts in the depth region that was most of interest. Figure 5 shows an angled perspective of a switchgrass root growing in soil and a cross section of the root as it enters the field of view. Black arrows indicate the direction of root growth, and a series of hourly images (Fig. 6) shows the progression of root growth over 9 h. [Visualization 4](#) shows the same growth with images every 15 min. The series clearly show the root pushing through the soil. Closer inspection (clearly seen in



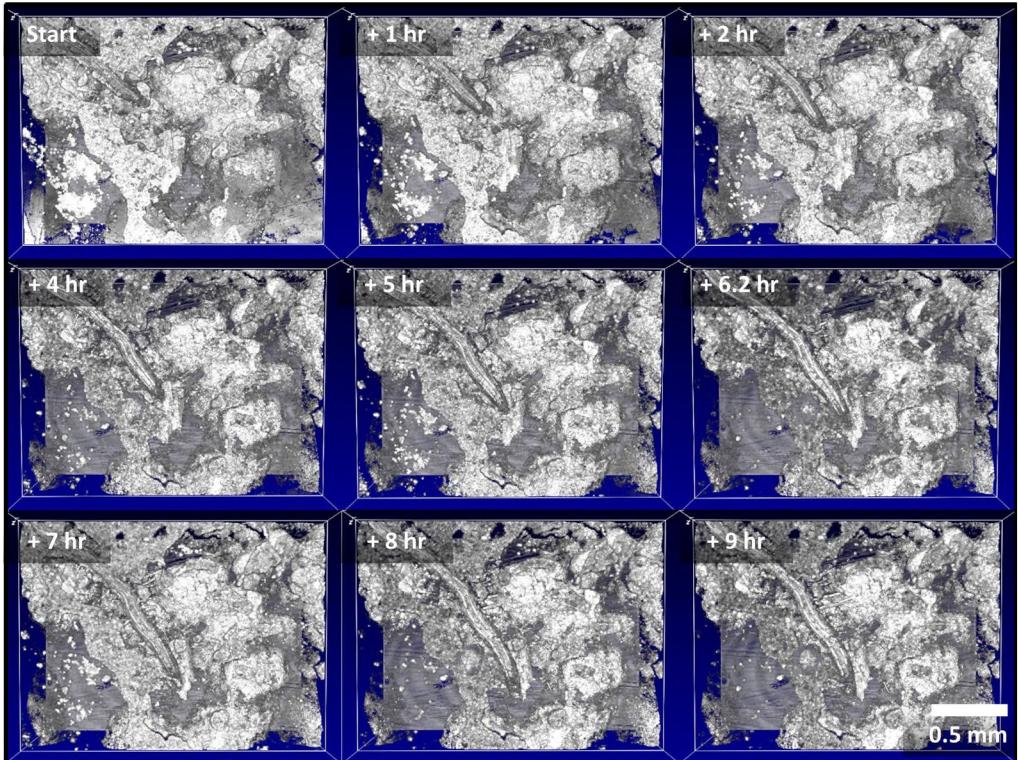
**Fig. 5.** OCT image of a switchgrass root in soil shown (A) from above and (B) from the side. The black arrow in A indicates the direction of growth of the root, which is directly above the arrow. The white arrow in B shows where the root is cross-sectioned at the edge of image.

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Visualization 4) also reveals the emergence of root hairs from  
the sides of the main root. Visualization 5 shows images taken  
in a separate experiment over a time period of 44 hrs. Both sets

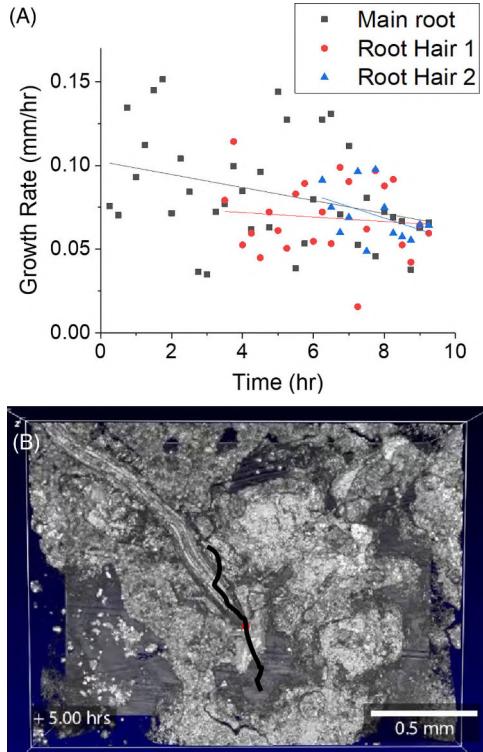
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of images show that OCT can be used to observe root growth  
in soil.

The images shown in Fig. 6 and [Visualization 4](#) were further analyzed using tracker software to measure root growth rate, and the results are shown in Fig. 7. The growth rates of the primary root and two root hairs were measured by tracing the movement of the tips through the series of images. Figure 7 shows a trace of the path that the root tip follows overlaid on one of the images in the middle of the observed period. The root does not grow in a straight line as seen by the black trace in Fig. 7(B) and appears to be influenced by obstruction by soil mineral particulates. One period between 5 and 8 hrs in [Visualization 4](#) shows the root pushing particulate material out of its path; the root changes direction and moves the particulate out of the way as it grows. Growth rate ranged from 0.02 to 0.15 mm/hr, which is of a similar order (a fraction of a mm/hr) but potentially slower than those observed in switchgrass by Mann *et al.* [30], likely owing to the constrained geometry of the rhizobox in which our plants were grown (in comparison to field grown plants). The average growth rate of the main root was  $0.08 \pm 0.03$  mm/hr. The average growth rates of the two measured root hairs were both  $0.07 \pm 0.02$  mm/hr. Linear trend lines in Fig. 7(A) show that the growth rate appears to be declining for all three roots over the observed period. Root growth rates are known to respond to environmental conditions, and diurnal cycling or slight changes in conditions may have initiated the observed shift.

The above figures demonstrate OCT applicability to observing plant roots in soil. OCT is also suitable for imaging other parts of the plant [18–22]. Figure 8 and Vis. 6 show images of switchgrass stem, leaf, and seeds. The images can show the surface layer and a few subsurface layers of cells in the plant stem

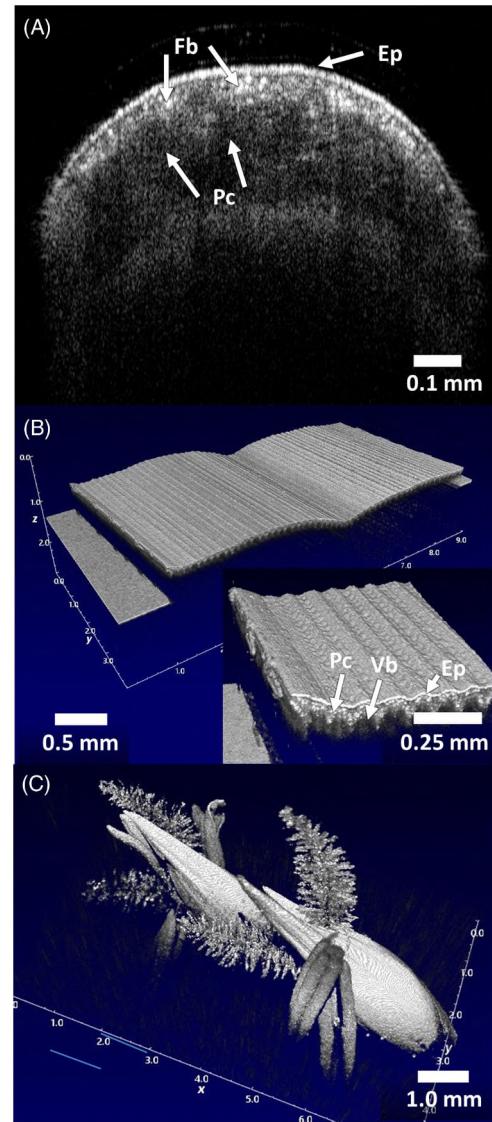


**Fig. 6.** Series of OCT images showing switchgrass root growth over 9 hrs. Scale is shown at lower right.



**Fig. 7.** (A) Plot of growth rates from the primary root (black square) and two root hairs (orange dot and blue triangle) as measured from the images shown in Fig. 6 and [Visualization 4](#). Linear trend lines for each series are shown in the corresponding color. (B) An image midway through the observed time period with a trace of the path of the root tip shown in black.

306 and leaf tissues. The stem and leaf cross sections clearly show the  
 307 stem and leaf cross sections clearly show the epidermal cells (Ep). Fiber bundles (Fb),  
 308 vascular bundles (Vb), and parenchyma cells (Pc) are noticeably less defined, especially  
 309 as the depth below the surface of the plant increases. Notably,  
 310 Fig. 8C shows the plant's stamen and stigma extending from  
 311 the seed pod floret. The pollen-producing stamen appears as a  
 312 grouping of linear filaments. Four feather-like plumed stigma  
 313 are visible in this image, and it is possible to distinguish each of  
 314 the fine hairs of stigma within the focal range of the microscope.  
 315 The rightmost stigma has clear details since it is better focused  
 316 than the leftmost stigma, which likely fell below the optimal  
 317 focal plane. Imaging of stomata on the leaf was attempted but  
 318 not clearly resolved with the available imaging system. Future  
 319 work focused on stomata imaging would require either a higher-  
 320 resolution lens or to focus on plants with larger stomata. These  
 321 images, along with root system images, demonstrate how OCT  
 322 imaging can contribute to holistic observation of a developing  
 323 plant. A challenge of analyzing time series OCT data is that  
 324 current OCT analysis software does not have the capability to  
 325 merge and align data from multiple time points. The images  
 326 and video visualizations presented in this manuscript were  
 327 constructed from static 2D captures of the 3D data. It would be  
 328 more interesting and informative to align and integrate 3D time  
 329 series data so it can be visually explored.



**Fig. 8.** (A) OCT cross section of a switchgrass stem with labels for the epidermis (Ep), fiber bundles (Fb), and parenchyma cells (Pc). (B) 3D surface image of switchgrass leaf with a magnified inset of the leaf's edge. The magnified inset has labels for the epidermis (Ep), parenchyma cells (Pc), and vascular bundles (Vb). (C) 3D image of a group of switchgrass seeds with the stamen and stigma. Scales are indicated by a bar in each image.

#### 4. CONCLUSION

This work presented a new method of imaging plant roots in the challenging conditions of natural soil. The 3D images of roots may help to elucidate their interaction with heterogeneously distributed nutrients and other organisms in the soil. Growing the plants in an angled rhizobox with a thick imaging window facilitated OCT root imaging by ensuring growth against the surface of the window. OCT imaging with other rhizobox configurations may be possible, but it is likely that fewer roots will be optimally placed. The key advantages of OCT imaging are (1) a unique combination of lateral resolution and imaging depth, (2) non-destructive incident light that does not require use of contrast agents, and (3) relatively fast data acquisition in

343 a compact benchtop system. The key limitations include the  
344 shadow effect, where features become hidden below thick or  
345 opaque surface features and distortion that can result from a lens  
346 effect in the first layer of cells. A requirement for a long-term  
347 time series is a computer with enough memory to store many  
348 multi-gigabyte files. We found that the memory available on  
349 our system limited either the imaging interval or the recording  
350 period, and the system had to be reset for long data-collection  
351 periods. OCT can become a valuable tool for a variety of plant  
352 studies. For instance, the non-destructive nature of OCT can  
353 be leveraged to help elucidate morphological root responses to  
354 environmental perturbations, including those associated with  
355 desiccation stress, pathogen exposure, competition between  
356 neighboring plants, or bioturbation by various macrofauna.  
357 The high spatial resolution of OCT will also permit analysis  
358 of the fine-scale interactions between roots and soil microbial  
359 hotspots or associations with fungi or bacteria-induced nodules.  
360 Finally, we reiterate that OCT is completely non-destructive  
361 and does not require any addition of contrasting agents or other  
362 exogenous material. Thus, OCT may be employed as a preliminary  
363 screening technique whereby the resulting highly resolved  
364 images can be used to direct the timing or spatial location of  
365 sample collection for a suite of omics, culturing, or further  
366 refined imaging techniques.

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