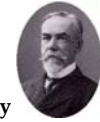




# Root rhizosphere carbon deposition

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## OBJECTIVES

- Quantify carbon associated with border cell release and with exudation from the growth zone of the root.
- Integrate the fine scale of the plant processes with the larger scale of the soil profile.

## BACKGROUND

As they grow, plant roots release organic C to the soil. The root tips, including root caps, meristems and elongation zones (Fig. 1), secrete sugars and organic acids as well as more complicated compounds such as phytosiderophores (see Jaeger *et al.* 1999). Mucilage containing high molecular weight polysaccharides, particularly polyuronic acids, is produced copiously by root caps and cortical cells (Guinel and McCully 1987). These C sources sustain the rich microflora of the rhizosphere.

Another source of C is provided by border cells, formed as part of the root cap and released from the exterior of the cap to live freely in the soil for a time. As many as 3,000 cells can be released when a root cap is immersed in water for one minute (Hawes and Pueppke 1986; Guinel and McCully 1987; Fig. 1). Recent quantitative studies have shown that roots of maize seedlings have thousands of border cells at any given time (Iijima *et al.*, 2004). Estimates suggest that a root tip may provide a pulse of 0.1 g of fixed C to the rhizosphere of the growth zone when it grows from an unsaturated into a saturated soil stratum.

To understand the rhizosphere of the root tip, the time dependent classical models of flux across the root surface must be extended to include convection resulting from root displacement during growth (Kim *et al.* 1999; Nichol and Silk 2001). On a larger scale, for an understanding of C sequestration, the complex spatial patterns of transport within the growth zone must be studied with characterization of the propagation of the growth zones relative to the soil structure.

## ACKNOWLEDGEMENTS

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## METHODS

### Root cap cell sloughing

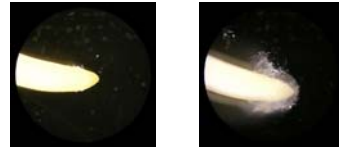
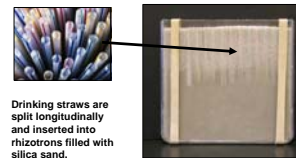


Figure 1. Before wetting (left) and after wetting (right).

Seeds are germinated and grown for a few days in rhizotrons filled with sand. Seedlings are removed, and 1 cm of the root from the tip is excised. The tip is placed in a 5 ml centrifuge tube with 0.5 ml of Tween solution and sonicated for 1 min. After root removal and addition of a drop of toluidine blue stain, the tube is shaken for 30 min. 0.4 ml of contents of the tube are placed on a Sedgewick Rafter counter under a compound microscope for counting of border cells.

### Rhizosphere substrate collection



Drinking straws are split longitudinally and inserted into rhizotrons filled with silica sand.

Figure 2. Rhizotron set-up

Pregerminated seeds are positioned above the rhizosphere cylinders (straws) in prepared rhizotrons (Fig. 2) and the radicle is inserted into the top of the cylinder. The radicle is allowed to grow for 2-5 days through the rhizosphere cylinder. The rhizosphere cylinder is then removed and divided into rhizosphere volumes of interest. That volume plus the root is removed and placed into a vial with a small volume of deionized water. The sample is sonicated to free any loose border cells; the root is removed; and the sample is dried for C analysis.

### Growth analysis in stationary reference frame



Figure 3. Time lapse root growth experimental setup

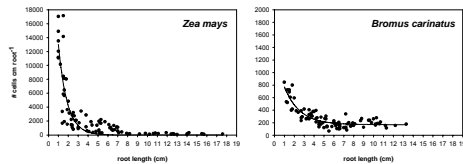
*Zea mays* seeds are germinated and grown in a rhizotron until the seminal root reaches a length of 3 to 8 cm. The seedlings are then gently withdrawn from the substrate, and the root tip ends marked (rapidograph).

The seedlings are re-inserted into the channels of the rhizotron and are placed in the time-lapse growth chamber. A camera (Nikon Coolpix 5000) is mounted on the frame inside the growth chamber with the intervalometer (Harbortronics DigiSnap 2000) attached, set to take pictures at 5 minute intervals.

Photography continues undisturbed for 2-3 days. The images are then downloaded onto a computer, where they can be processed and digitized and the data used to plot root growth trajectories.

## PRELIMINARY RESULTS

### Influence of root age on number of root cap cells sloughed



Figures 4 (l) and 5 (r). Number of root cap cells sloughed versus root length for *Zea mays* and *Bromus carinatus* seedlings. n=80.

Short (young) roots slough the most cap cells. In both *Zea mays* and *Bromus carinatus*, the number of cells sloughed declines with root length to a constant value when roots reach 4 cm long.

### C content in soil of potbound annual and perennial grasses

Species	Common name	Native/Invasive/Exotic	Annual/Perennial	mg belowground C contributed to sand per g of sand sloughed cells & exudates	
				Mean ± StdErr	Mean ± StdErr
Silica sand control				36.98	
<i>Nassella pulchra</i>	Purple needle grass	Native	Perennial	34.34 ± 1.06	24.01 ± 6.39
<i>Bromus carinatus</i>	California brome	Native	Perennial	42.26 ± 3.83	58.34 ± 7.99
<i>Vulpia microstachya</i>	Small fescue	Native	Annual	40.81 ± 1.29	35.21 ± 10.79
<i>Aegilops triuncialis</i>	Barbed goatgrass	Invasive	Annual	43.99 ± 3.28	35.79 ± 8.61
<i>Lolium multiflorum</i>	Italian ryegrass	Invasive	Annual	47.25 ± 2.26	34.37 ± 7.07
<i>Bromus diandrus</i>	Ripgut brome	Invasive	Annual	46.36 ± 2.00	38.48 ± 6.84
<i>Bromus hordebaccus</i>	Soft chess	Invasive	Annual	47.97 ± 3.10	25.09 ± 1.79
<i>Poa trivialis</i>	Corn	Exotic	Annual	37.99 ± 3.77	12.76 ± 4.04

Figure 6. Rhizosphere C accumulation and deposition in soil surrounding root systems of invasive annual and native annual and perennial grasses from California. Mean ± StdErr, n=3.

Species had similar amounts of rhizosphere C accumulation in the form of sloughed cells & exudates. Rhizosphere C deposition varied between 12.75 and 58.34 mg C g<sup>-1</sup> root for the 37 day growth period.

### Spatial patterns of rhizosphere C exuded by *Zea mays* root tips

Rhizosphere volume relative to the root tip	mg belowground C contributed to sand per g of sand sloughed cells & exudates	
	Mean ± StdErr	Mean ± StdErr
Silica sand control	13.94	
3 mm in front	24.01 ± 2.11	
3 mm behind	41.21 ± 1.07	6.28 ± 0.98
2-3 mm behind	22.27 ± 1.85	1.19 ± 0.23

Figure 7. Rhizosphere C deposition of regions of *Zea mays* seedling roots. Mean ± Std Err, n=3

Highest C accumulation occurred in sand surrounding the apical 3 mm. Lower levels of C accumulation were found in the rhizosphere behind and in front of the root cap. Lower levels of C behind the root tip suggest border cells and exudates are very labile in sand.

### Growth trajectories



See movie

## FUTURE GOALS

### Effects of environmental variation

Because our methods involve extracting with aqueous solutions, our preliminary results represent the C deposition associated with soil flooding. Methods need to be developed to analyze the C released by root tips in soils at field capacity.

The good reproducibility of our preliminary results suggests we will be able to quantify the effects of environmental variation on the carbon deposition from the root. We hope to assess the effects of soil wetting (from rainfall or irrigation) and anthropogenic copper deposition (from mine sites, automobile traffic, and pesticide application) on the carbon flows from root to soil.

### Computational Model

Several computational models have analyzed root-rhizosphere interactions. These models range in size scale from the organ level (Kim *et al.* studying rhizosphere pH) to the field scale (Molina *et al.* studying C-N interactions). We hope to integrate our results on border cell sloughing, C exudation, and root growth analysis to move from a physiology-based model at the organ scale to seasonal root development models on the field scale.