**Core Ideas:**

- Models for bacterial colonization of root tips require root growth kinematics.
- Rates of root elongation and bacterial attachment affect exposure to root exudates.
- Microbial attachment to roots contributes to dispersal of microbes in soil.
- The root cap may play a role in the maintenance of bacteria at the tip.

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# Mechanisms of Early Microbial Establishment on Growing Root Surfaces

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Microbial activity in the soil surrounding plant roots contributes to nutrient bioavailability, crop growth, and soil biodiversity and fertility. Colonization of the rhizosphere and the rhizoplane in particular requires early establishment on root surfaces where sources of nutrients are abundant. In this study, we investigated the physical interactions taking place between bacteria and the root surface when a root tip enters unexplored regions of soil. We developed a theoretical framework that generalizes the prevailing approaches for describing root growth kinematics and bacterial growth and adhesion on root surfaces. We found that the root elongation rate, bacterial attachment rate, and root cap carrying capacity are key traits for successful establishment. Models also indicate that chemotaxis is more important for radial transport and adhesion than for longitudinal movement of bacteria. Controls on bacterial attachment are required for both efficient root colonization and subsequent dispersal of bacteria in soil. The findings of this study help to understand the establishment of the structure and composition of microbial communities in soil.

The thin layer of soil affected by plant root activity is termed the *rhizosphere*. Microbial processes within the rhizosphere are important to plant growth but also contribute to soil biodiversity and soil quality (Banfield et al., 1999; Wardle, 2006), yet the formation of microbial communities within the rhizosphere, from the time a root tip penetrates the bulk soil until maturity of the root tissues, remains poorly understood. It has been observed, for example, that the abundance and composition of bacterial communities around the root change as a function of the distance from the root tip, soil type, and plant species (Marschner et al., 2001). The abundance of bacteria at the root tip is sometimes reported to be higher than in the region basal to the elongating zone (Fig. 1A; Jaeger et al., 1999; Watt et al., 2006a), then increases to reach a peak in the region of lateral root initiation (Jaeger et al., 1999), although other studies have reported the absence of bacteria at the root tip (Lugtenberg et al., 2001). The structure of bacterial communities may also vary markedly along the root (Gochnauer et al., 1989; Yang and Crowley, 2000), although some investigators have found bacterial richness to be independent of the location on the root axis (Baudoin et al., 2002).

What mechanisms explain such diverse microbial activity in the rhizosphere? This question has attracted much interest from the scientific community (Bulgarelli et al., 2012; Lugtenberg et al., 2001), but basic knowledge of the mechanisms to answer them has not yet emerged. How can bacterial colonies establish themselves along moving root tips on a growing root tissue? A priori, one would expect the mechanisms for motility or adhesion to dominate the formation of a microbial population along the root. But could bacteria be recruited from the local environment and remain for only short periods of time in contact with the root tip? Then the bacterial growth rate and ability to exploit C deposits such as mucilage or organic acid from the root must be factors for successful colonization of the rhizosphere.

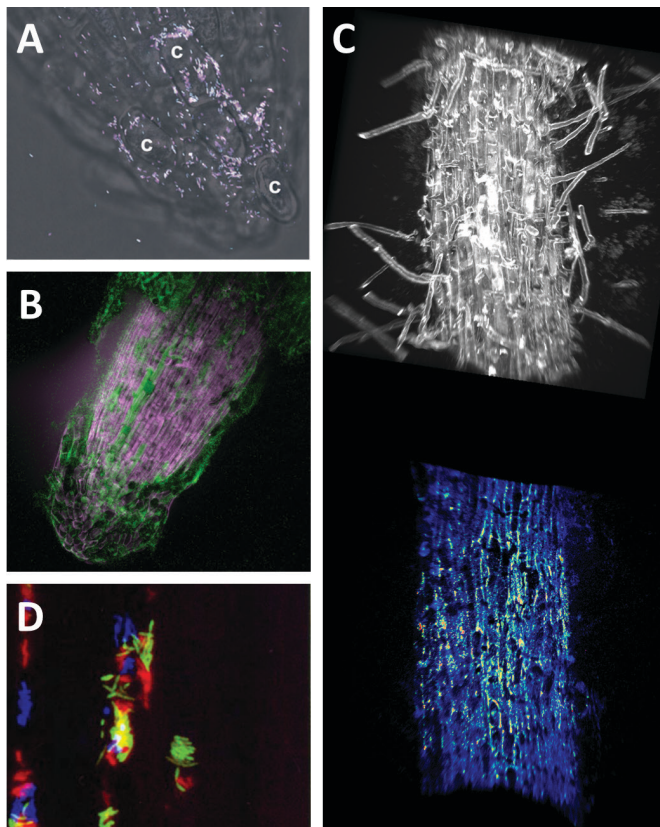


Fig. 1. Spatial distribution of bacteria on root tissues observed using fluorescent microscopy: (A) *Pseudomonas* sp. (purple dots) grown on agar plates were shown to accumulate on the cap of wheat roots (from Watt et al., 2006a). (B) *Pseudomonas* sp. (green clusters) grown in transparent soils have been observed in root cap cells (Downie et al., 2014). (C) Bacteria usually colonize nutrient-rich microsites such as intercellular junctions. Here, a confocal laser scanning microscopy three-dimensional image of lettuce root (calcofluor stained, image at the top) and the matching distribution of *Pseudomonas* sp. distribution on the root surface show a high cell concentration at cell junctions (green fluorescent protein labeled, image on the bottom). (D) Bacteria attaching on a root surface proliferate rapidly and form microcolonies and biofilms. Here, identical strains of *Pseudomonas fluorescens* expressing different fluorescent proteins are grown on tomato (*Solanum lycopersicum* L.) plants. After 5 d of growth, microcolonies of identical colors are formed, which indicates that proliferation on the root surface is a key for utilization of root-derived nutrients (Bloemberg et al., 2000).

Bacteria must colonize roots early to exploit nutrient-rich habitats along the root (e.g., intercellular junctions; Fig. 1B) and exclude other organisms from the habitat (Fig. 1C). Unfortunately, the way newly divided root cells are colonized by bacteria remains unknown. Observations of the formation of the rhizosphere microbiome during root development are lacking because the root tip is moving and in expansion when it enters unexplored regions of the soil. The meristem exhibits cell divisions and a low cell elongation rate, whereas more proximal regions of the root growth zone are characterized by an increase in the elongation rate and a reduced or negligible cell division rate (Erickson and Sax, 1956; Federici et al., 2012; Silk and Erickson, 1979). These processes induce large variations in the relative root–soil velocity and in the

number of intercellular junctions available at root surfaces, both of which affect opportunities for bacteria to adhere and proliferate on C-rich root surfaces. Existing models have revealed many aspects of rhizosphere functioning, but they are limited in their ability to describe bacterial establishment on root tips because they do not account for root growth kinematics (Darrah, 1991b; Muci et al., 2012; Scott et al., 1995).

This study developed a new theoretical framework to analyze cell flows along moving and elongating root tips. In this framework, bacterial growth kinetics, root development, cell movement, and cell adhesion are expressed in both moving and stationary reference frames to describe transient and stationary flow of root and bacterial cells relative to stationary soil particles (Silk, 2002; Watt et al., 2006b). We constructed a model based on experimental data from the literature. We then used the model to identify the factors that contribute to the formation of microbial populations along the root tip.

## Material and Methods

### The Moving Reference Frame

The moving reference frame is a one-dimensional, root-centered coordinate system where the origin is placed at the tip of the root (Erickson and Sax, 1956). In this coordinate system, a position along the root axis is noted  $x$ , and it measures the distance from the root tip. Root cells move with velocity  $v(x)$  that increases with  $x$  to a maximum value  $V_{\max}$  at the base of the growth zone;  $V_{\max}$  equals the root elongation rate. In this moving reference frame, fixed points in the soil move at the constant velocity  $V_{\max}$ , and the velocity of fixed points relative to the root surface is  $V_{\max} - v$  (Silk, 2002; Walter et al., 2009). Bacteria attached on the surface of the root have the same velocity as root cells at this point. The advantage to the root-centered coordinate system is that variables associated with the root tip and its rhizosphere often exhibit a steady or quasi-steady pattern (see the supplementary material for additional details).

The study presented here focused on the growth of bacteria at the root tip. Other sources of nutrients from the soil or from mature parts of the root tissue, e.g., exudation at the site of lateral root initiation, were not considered in the model. Therefore the model describes the fraction of soil bacteria that benefit and grow directly from nutrients exuded from the root tip. We also assumed that C is the limiting element for growth, and both nutrients and bacterial abundance are represented by their C mass ( $\mu\text{g}$ ). By convention, uppercase letters are used for model parameters. Variables and functions are lowercase. Greek letters are used for dependent variables and Latin letters for functions and independent variables. All quantities in the model are expressed and calculated in centimeters, micrograms, and hours. To facilitate comparison with the literature, however, graphics are presented with distances expressed

in millimeters and bacterial abundance as the number of cells.

The modeled system consists of the following dependent variables (Fig. 2A):  $\alpha$  ( $\mu\text{g cm}^{-3}$ ) is the density of bacterial cells attached at an interface between the root and the rhizosphere;  $\beta$  is the density of free-moving microbial cells ( $\mu\text{g cm}^{-3}$ ); and  $\gamma$  is the total soluble C concentration around the root ( $\mu\text{g cm}^{-3}$ ). To keep the model to its simple form and facilitate mathematical analysis, the radial distribution of root and bacterial cells is modeled using compartments of fixed cross-sectional area. We define the cross-sectional area  $C_a$  and  $C_f$  occupied by attached and free-moving bacteria, respectively, while  $C_r$  defines the cross-section of the root and is assumed to be free of bacteria. Therefore,  $C_a\alpha$  and  $C_f\beta$  are the linear density ( $\mu\text{g cm}^{-1}$ ) of attached and free-moving microbial cells, and  $\int_{dL} C_a\alpha dx$  and  $\int_{dL} C_f\beta dx$  are the total amount of bacteria ( $\mu\text{g}$ ) in a segment of length  $dL$  of attached and free-moving bacteria, respectively.

### Root Exudation

Root exudation is modeled as a C production rate  $s$  ( $\mu\text{g cm}^{-1} \text{h}^{-1}$ ) that declines exponentially with the distance from the root tip:

$$s = S_{\max} \bar{s}(x) \quad [1]$$

where

$$\bar{s}(x) = \exp\left(\frac{-x}{L}\right)$$

is the C production function so that its maximum is 1 at the root tip, and  $L$  is the length scale of the exudation profile, chosen to match the length of the root growth zone (1 cm). The exponential decline in the C production rate mirrors the commonly accepted view that exudation is maximum at regions where root growth occurs (Darwent et al., 2003).

The model needs also to account for enzymatic degradation, gasification, mineralization, or other forms of interactions with the soil particles and losses to the environment (Jones, 1998). A C decay rate  $p$  ( $\mu\text{g cm}^{-1} \text{h}^{-1}$ ) is therefore introduced:

$$p = -P\gamma \quad [2]$$

where  $P$  is the C decay rate coefficient.

### Bacterial Growth Kinetics

Bacterial growth (Fig. 2B) is modeled using the concept of specific growth rate. The specific growth rate  $g$  ( $\text{h}^{-1}$ ) represents the relative

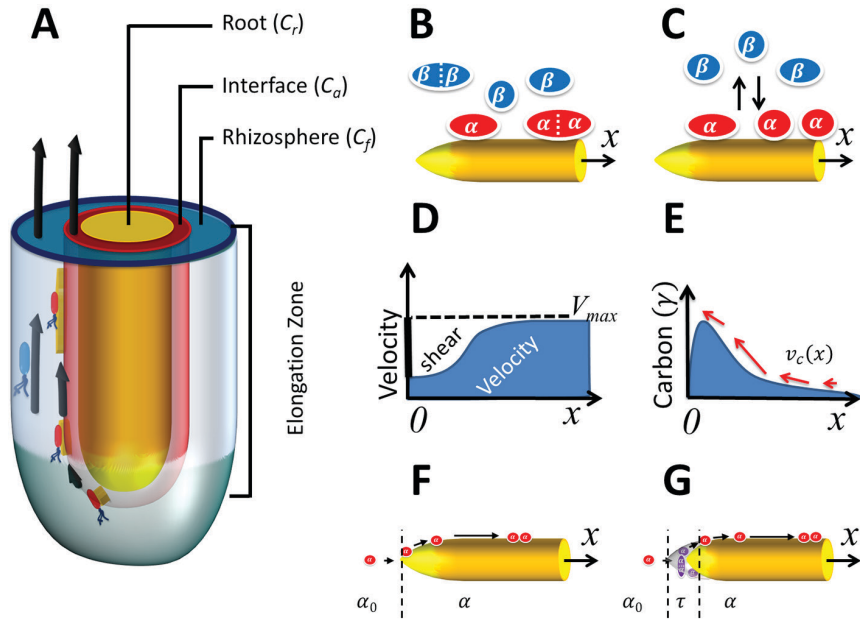


Fig. 2. Model of microbial establishment on growing root surfaces: (A) The root–soil domain consists of compartments: the root compartment where exudates are produced with cross-section  $C_r$ , the interface compartment where bacteria attach to the root with cross-section  $C_a$ , and the rhizosphere compartment where bacteria can move freely with cross-section  $C_f$ . The model for microbial establishment on the root surface is in a one-dimensional setting ( $x$  coordinate) and consists of four submodels: (B) a Monod growth kinetics model for both attached bacteria ( $\alpha$ ) and free-moving bacteria ( $\beta$ ), (C) an attachment model, (D) a root elongation model defined as the elongation rate ( $V_{\max}$ ) and the length of the elongation zone ( $L$ ), and (E) a model for cell transport including dispersion and chemotaxis ( $v_c$ ). The effect of the root cap was modeled by adding a bacterial carrying capacity at the tip. (F) When the root cap does not provide a carrying capacity, soil bacteria initially at concentration  $\alpha_0$  can attach on elongating root cells and move away from the tip at the velocity of the root cells. (G) When the root cap provides a carrying capacity, the flux of bacteria released from the root cap becomes a function of the bacterial density in the root cap,  $\tau$ .

increase in the population biomass per unit of time. It is thought to be dependent on the available C (Tindall et al., 2008). Here, it is expressed as a Monod kinetics following parameters derived by Darrah (1991b):

$$g = G_{\max} \frac{\gamma}{\gamma + K} - M \quad [3]$$

where  $G_{\max}$  is the maximum growth rate of bacteria,  $M$  is the mortality rate, and  $K$  is the affinity constant for microbial growth. The growth rates for attached and free-moving bacteria are therefore determined as  $\alpha g$  and  $\beta g$ , respectively.

### Bacteria and Carbon Fluxes along the Root

The concentrations of either attached or free-moving bacteria are all defined in the moving reference frame centered at the root tip. When bacterial cells are attached to the surface of the root, they have the same velocity as root cells at the attachment site. The velocity  $v$  varies as a function of  $x$ , with maximum velocity  $V_{\max}$  observed in mature cells beyond the growth zone:

$$v = V_{\max} \bar{v} \quad [4]$$

where  $\bar{v}$  defines a normalized velocity  $v$  such that its maximum value is 1; it is modeled using an exponential function:

$$\bar{v}(x) = 1 - \Theta \exp\left(\frac{-x^2}{W}\right)$$

The residual cell velocity at the root tip is  $V_{\max}(1 - \Theta)$ . For internal cells,  $\Theta$  equals 1 so that the cell wall at position  $x = 0$  is not moving in the moving reference frame. For bacterial cells and root cells at the surface (e.g., the root cap and epidermis), movement at the very tip is not zero due to, for example, friction at the root–soil interface and sloughing of root cap cells. The variable  $W$  determines the size of the elongation zone so that  $v \approx V_{\max}$  when  $x > L$ . This function is used for all  $x \in \mathbb{R}$ . For positive  $x$  values,  $v$  represents the movement of root and attached bacterial cells accelerating as they move away from the root tip. For negative  $x$  values,  $v$  represents the movement of bacterial cells decelerating as they approach the root tip and attach to root cells.

The convective flux of attached bacteria,  $J_{\text{attach}}$  ( $\mu\text{g cm}^{-2} \text{h}^{-1}$ ), resulting from root elongation can therefore be determined as

$$J_{\text{attach}} = \alpha v \quad [5]$$

Free bacteria that are immobile in the soil have a constant velocity  $V_{\max}$  in the moving reference frame, where  $V_{\max}$  is the velocity of the root tip in the global reference frame. The flux of these cells,  $J_{\text{free}}$  ( $\mu\text{g cm}^{-2} \text{h}^{-1}$ ), would therefore be equal to  $\beta V_{\max}$ . Free bacteria in the soil, however, are usually mobile, with transport due to dispersion and chemotaxis. The flux of free-moving bacteria can therefore be generalized to

$$J_{\text{free}} = \beta V_{\max} + \beta \chi \partial_x \gamma - D \partial_x \beta \quad [6]$$

where  $\chi \partial_x \gamma$  is the microbial chemotactic velocity as defined in the Keller–Segel model (Tindall et al., 2008), and  $D \partial_x \beta$  is the diffusive flux due to the dispersion of bacteria.

The C exuded from the roots is deposited in the soil surrounding the roots and therefore remains fixed in the global reference frame. Fluxes of C exudates,  $J_{\text{carbon}}$  ( $\mu\text{g cm}^{-2} \text{h}^{-1}$ ), can therefore be defined following similar principles:

$$J_{\text{carbon}} = V_{\max} \gamma - E \partial_x \gamma \quad [7]$$

where the first term describes the convection of exudates due to root growth and the second term describes exudate diffusion in the soil.

## Radial Mobility and Attachment of Bacteria to the Root Surface

The model for dynamic bacterial attachment and detachment (Fig. 2C) is adapted from the Langmuir adsorption model proposed and

validated experimentally by Shimshick and Hebert (1979). The model describes the rate at which bacteria attach and detach from the root surface. The net bacterial attachment rate  $a$  ( $\mu\text{g cm}^{-3} \text{h}^{-1}$ ) is expressed as the difference between the rate at which bacteria from the soil solution attach and the rate at which bacteria on the surface detach:

$$a = \text{attachment rate} - \text{detachment rate}$$

The attachment rate is proportional to the amount of free-moving bacteria  $\beta$  and the amount of free binding sites  $(N - \alpha)$ , where  $N$  is the total amount of binding sites on the surface. The detachment rate is directly proportional to the concentration of attached bacteria  $\alpha$  on the root surface. The net attachment rate is therefore determined as

$$a = AB\beta(N - \alpha) - B\alpha \quad [8]$$

where  $A$  and  $B$  are parameters of the Langmuir adsorption model;  $A$  controls the proportion of free vs. attached bacteria at equilibrium, and  $B$  determines the rate at which equilibrium is achieved. Although the Langmuir adsorption model does not represent radial movements of adsorbates explicitly, it has proved to be extremely powerful to predict chemical reactions on surfaces (Del Bubba et al., 2003). Radial movement of bacteria is represented implicitly through the attachment rate parameter  $B$ . Bacteria with a larger  $B$  move faster toward the surface of the root than bacteria with a lower  $B$ .

## Equations for the Dynamics of Bacterial Cells at the Root Tip

The model for the dynamics of bacteria along the root tip is derived from Eq. [1–8] using the principle of mass conservation. The conservation principle states that the change with time in the mass of C in a portion of root or soil of length  $dL$  results from the mass of C entering and leaving  $dL$  at the boundaries of the segment and the mass of C being produced or lost, e.g., through exudation or leaching. It is expressed mathematically as

$$\left\{ \begin{array}{l} \partial_t \int_{dL} C_a \alpha dx + C_a \Delta J_{\text{attach}} = \int_{dL} C_a g \alpha dx + \int_{dL} C_a a dx \\ \partial_t \int_{dL} C_f \beta dx + C_f \Delta J_{\text{free}} = \int_{dL} C_f g \beta dx - \int_{dL} C_a a dx \\ \partial_t \int_{dL} (C_a + C_f) \gamma dx + (C_a + C_f) \Delta J_{\text{carbon}} = \\ \quad \int_{dL} (C_a + C_f) s dx - \int_{dL} (C_a + C_f) P \gamma dx \\ \quad - \int_{dL} C_a g \alpha dx - \int_{dL} C_f g \beta dx \end{array} \right. \quad [9]$$

The first, second, and third equations describe the dynamics of attached bacteria, free-moving bacteria, and C exudates, respectively;  $\Delta J$  represents the net influx of C through (Fig. 2D–2E) the element  $dL$  so that  $\Delta J = J(x + dL) - J(x)$ . Continuity equations can then be obtained by dividing each equation by the cross-section

of the compartment,  $C_a$ ,  $C_f$  and  $C_a + C_f$  for attached, free-moving, and exudates, respectively, and applying the divergence theorem:

$$\begin{cases} \partial_t \alpha + \partial_x (v\alpha) = g\alpha + a \\ \partial_t \beta + \partial_x [(V_{\max} + \chi \partial_x \gamma)\beta - D\partial_x \beta] = g\beta - \frac{C_a}{C_f} a \\ \partial_t \gamma + \partial_x (V_{\max} \gamma - E\partial_x \gamma) = \\ s - P\gamma - \frac{C_a}{C_a + C_f} g\alpha - \frac{C_f}{C_a + C_f} g\beta \end{cases} \quad [10]$$

Each equation expresses that the change with time ( $\partial_t$ ) of  $C$  from bacteria and from the root exudates in a unit domain is a function of the net flux of  $C$  moving into and out of the unit domain, the increase in bacterial density due to growth ( $g\alpha$  and  $g\beta$  for attached and free-moving bacteria, respectively), attachment–detachment ( $C_a a$ ), the increase in  $C$  due to exudation ( $S_{\max} s$ ), and the removal of  $C$  due to growth ( $-g\alpha$  and  $-g\beta$  for attached and free-moving bacteria, respectively) or loss from the rhizosphere ( $P\gamma$ ). It is useful also to express this equation in a nondimensional form (see the supplemental material) to outline the mechanisms underlying the growth of bacteria along the root. The following nondimensional equations are obtained:

$$\begin{cases} \partial_t \alpha + \partial_x (v\alpha) = \\ K^* \left( \frac{\gamma}{\gamma+1} - Y^* \right) \alpha + \beta (N^* - \alpha) - B^* \alpha \\ \partial_t \beta + \partial_x (\beta + C^* \gamma \beta - D^* \partial_x \beta) = \\ K^* \left( \frac{\gamma}{\gamma+1} - Y^* \right) \beta - \beta (N^* - \alpha) + B^* \alpha \\ \partial_t \gamma + \partial_x (\gamma - E^* \partial_x \gamma) = \\ S^* s - R^* \left( \frac{\gamma}{\gamma+1} - Y^* \right) (\alpha + \beta) - P^* \gamma \end{cases} \quad [11]$$

To understand the factors that dominate bacterial colonization on the root surface, three of the coefficients of Eq. [11] must be examined. First,  $C^*$  is the nondimensional chemotactic coefficient, expressed as

$$C^* = \frac{K\chi}{V_{\max} L}$$

For chemotaxis to dominate over the advection induced by the elongation of the root,  $C^*$  must be much larger than 1. The variables  $D^*$  and  $E^*$  are the nondimensional bacterial dispersion and  $C$  diffusion coefficients:

$$D^* = \frac{D}{V_{\max} L}, \quad E^* = \frac{E}{V_{\max} L}$$

and their reciprocal is recognizable as the Péclet number (Kim et al., 1999).

For diffusion of exudates or dispersion of microbes to dominate over advection,  $D^*$  and  $E^*$  must also exceed  $V_{\max} L$  by an order of magnitude. Non-dimensional analysis, therefore, reveals the factors that dominate the transport of microbes around the root tip.

## Initial and Boundary Conditions

Solutions to Eq. [10] are obtained on a finite domain  $\Omega$  of length  $2\Lambda$  and centered on 0 at the position of the root tip, i.e.,  $\Omega = [-\Lambda, \Lambda]$ . The right-hand side of the domain ( $x > 0$ ) is occupied by the root, while the left-hand side of the domain ( $x < 0$ ) consists of the unexplored region of the bulk soil. The distance between the root tip and the boundaries of the domain  $\Lambda$  is fixed to a value large enough so that border effects can be neglected.

We consider the case where microbes from the soil are recruited to colonize the root surface. Therefore, initial conditions on this domain consist of a root domain free of the microbial species of interest (Fig. 2F). Exudate concentration is also zero, although by the time microbes reach the root tip, the  $C$  concentration around the root is already established. At the left-hand side of the domain ( $x = -\Lambda$ ), in front of the root tip, an influx of bacteria is imposed by a Dirichlet boundary condition, and on the right-hand side of the domain ( $x = \Lambda$ ), a Neumann boundary condition is used:

for  $x = -\Lambda$

$$\alpha = \alpha_0, \quad \beta = \beta_0, \quad \gamma = 0$$

for  $x = \Lambda$

$$\partial_x \alpha = 0, \quad \partial_x \beta = 0, \quad \partial_x \gamma(\Lambda) = 0 \quad [12]$$

If there are no bacteria,  $\alpha_0 = 0$  and  $\beta_0 = 0$ . If the soil contains bacteria,  $\alpha_0 > 0$  and  $\beta_0 > 0$ . We have also investigated the role of the root cap as a potential reservoir for bacteria (Fig. 2G). In this case,  $\alpha_0 = 0$ ,  $\beta_0 = 0$ , and the domain consists only of the region of the soil occupied by the root  $\Omega = [0, \Lambda]$ , and boundary conditions are imposed on the left-hand side:

$$\alpha(0) = \frac{\tau^2}{\tau_0}, \quad \beta(0) = 0, \quad \gamma(0) = 0 \quad [13]$$

with  $\tau$  representing the concentration of microbes in the root cap, for which the evolution can be described using an ordinary differential equation:

$$\partial_t \tau = g\tau + V_{\max} \beta_0 - V_{\max} (1 - \theta) \frac{\tau^2}{\tau_0} \quad [14]$$

The first term,  $g\tau$ , is the  $C$ -dependent growth of bacteria on the root cap, the term  $V_{\max} \beta_0$  is the net flux of bacteria from the soil to the root cap, and  $V_{\max} (1 - \theta) \tau^2 / \tau_0$  is the efflux of bacteria from the root cap to the rhizosphere. The root cap is therefore modeled

as a boundary condition that is acting as a reservoir of bacteria. The simplest possible nonlinear assumption therefore is that the release of bacteria from this reservoir and to the rhizosphere is a quadratic function of the concentration of microbes in the root cap.

## Model Parameters

The cross-section of the bacterial compartments  $C_a$  and  $C_f$  are based on typical values measured on cereal roots, with a root diameter of 0.05 cm, a root–soil interface of 11  $\mu\text{m}$  (Watt et al., 2006a). The cross-section of the rhizosphere was defined with a radius of 0.2 cm, a value that corresponds to the zone of influence of some exudates such as citrate (Tinker and Nye, 2000). The size of the elongation zone  $L$  was chosen as 1 cm, and the size of the domain  $2\Lambda = 8L$ . The root tip velocity  $V_{\max}$  was chosen as 0.1  $\text{cm h}^{-1}$ , and the residual cell velocity parameter  $\Theta$  was chosen so that the residual cell velocity,  $V_{\max}(1 - \Theta)$ , is 0.01  $\text{cm h}^{-1}$ , and the elongation zone parameter  $W = 0.2 \text{ cm}^2$ . The maximum exudation rate  $S_{\max}$  was chosen to match experimental observations that rhizosphere exudates reach a concentration in the rhizosphere of about 100  $\mu\text{g cm}^{-3}$  with a half-life of a few hours (Jones et al., 2004). A value of 35  $\mu\text{g cm}^{-1} \text{ h}^{-1}$  was used. The maximum growth rate of bacteria  $G_{\max} = 0.165 \text{ h}^{-1}$  and  $K = 70 \mu\text{g cm}^{-3}$ . The mortality rate  $M = 0.012 \text{ h}^{-1}$ . Parameters of the bacterial attachment model were derived from Shimshick and Hebert (1979), with  $A = 3 \times 10^{-4} \text{ cm}^3 \mu\text{g}^{-1}$ ,  $B = 0.01 \text{ h}^{-1}$ , and  $N = 1.5 \times 10^5 \mu\text{g cm}^{-3}$  (see the supplemental material). The chemotactic parameter  $\chi$  ( $1.5 \times 10^{-6} \text{ cm}^5 \mu\text{g}^{-1} \text{ h}^{-1}$ ) was determined based on the assumption that the maximum bacterial velocity in soil does not exceed 0.06  $\text{cm h}^{-1}$  following the observations of Bashan (1986). The estimation of diffusion coefficients in soil for bacteria and exudates are extremely variable (Darrah, 1991a) and depend strongly on the soil water content (Ebrahimi and Or, 2014; Roose et al., 2001). We used diffusion coefficient values ( $10^{-5} \text{ cm}^2 \text{ h}^{-1}$ ) that are at the higher end of the spectrum of diffusion of a solute in soil (Roose et al., 2001; Sung et al., 2006). The degradation rate for the soluble C was chosen to be equivalent to a half-life of 4 h ( $P = 0.17$ ).

## Numerical Simulations

Numerical solutions of the model were obtained using the smoothed particle hydrodynamics method (SPH). Similarly to most numerical methods, the SPH provides estimations for the solutions of partial differential equations through a discretization of space and time. In the SPH method, however, the quantity of bacteria is represented as a finite set of weighted particles, whose position and weight evolve through time. Interpolation is then used to derive a smooth solution to the equation using kernel-based density estimation (Monaghan, 1992). In a system where advection is the dominant process, the method has the advantage of representing changes in the bacterial density as a combination of two factors: bacterial growth factors (increased weight of particle) and kinematics factors, i.e., the accumulation of the bacteria due to adhesion and changes in velocity (density of particles). The SPH model was implemented in Python using the scientific library

Numpy, and a graphical interface was constructed to operate the model interactively. Software and source code can be downloaded at <http://www.archiroot.org.uk>. Mathematical details on the derivation of the model and the application of SPH are provided in the supplemental material. To test the accuracy of the new solver, steady-state solutions of Eq. [10] were obtained using a high-resolution ordinary differential equation (ODE) software. The steady-state system contains only spatial derivatives, and solutions can be obtained using classic ODE solvers. The outputs of the SPH models were tested at steady state against solutions obtained using a Runge–Kutta ODE solver (function `ode45` in Matlab). See the supplemental material for details on numerical techniques.

Numerical simulations were used to analyze the mechanisms of establishment of bacteria along the root surface. The model was simulated with parameters obtained from the literature as described above. Simulations consisted of the equivalent of 10 d of growth so that, at the end of the simulation, steady state had been achieved. The model outputs were used to dissect the different transient phases during which the system was brought from the non-colonized state to the colonized state. In particular, the model was used to determine bacterial density, particle weight (growth accumulation) and particle density (growth dilution), the attachment rate, and the mean time spent in the growth zone.

Also, the effect of root and bacterial traits was tested by running a sensitivity analysis of four key parameters, the elongation rate ( $V_{\max}$ ), the attachment rate ( $B$ ), the size of the elongation zone ( $L$ ), and the chemotactic parameter ( $\chi$ ). Parameters were modified in the range of 50 to 150% of the mean bibliographic value. The bacterial distribution at steady state on the immobile region of the root was then recorded and the maximum bacterial density was used as a quantitative indicator to assess the sensitivity of root colonization to the associated mechanism.

Finally, simulations were performed to analyze the factors that explain the maintenance of bacteria in the absence of external sources of bacteria. Simulation consisted of varying the factors that can explain the maintenance or extinction of bacteria, e.g., root cap carrying capacity and chemotactic coefficient, to identify the values at which the root cap becomes permanently colonized by bacteria.

## Results

### Nondimensional Analysis of Bacterial Movement

The analysis of the nondimensional model in Eq. [11] revealed the number  $C^* = K\chi/V_{\max}L$  that characterizes the importance of chemotaxis in the transport of bacteria in the system. Model parameters for which  $C^*$  is  $\gg 1$  represent systems where chemotaxis dominates over convective transport due to root elongation.

With the parameters obtained from the literature, the order of magnitude for  $C^*$  is  $10^{-3}$ , which indicates that the role of chemotaxis in the axial movement of the bacteria is not significant, and transport of bacteria due to root elongation controls the flow of bacteria along the root. A significant contribution of chemotaxis in the transport of bacteria along the root would be expected for non-growing roots or roots growing more slowly than  $10^{-4}$  mm  $h^{-1}$  with a growth zone of 1 cm.

The dimensionless number  $D^* = D/V_{\max}L$  in Eq. [11] (inverse of the Péclet number), characterizes the importance of dispersion in the transport of bacteria in the system. Model parameters for which  $D^*$  is  $\gg 1$  represent systems where diffusion dominates over convective transport due to root elongation. With the parameters obtained from the literature, the order of magnitude for  $D^*$  is  $10^{-4}$ , which indicates that the role of diffusion in the axial movement of bacteria is not significant, and the transport of bacteria due to root elongation controls the flow of bacteria along the root. A significant contribution of dispersion in the transport of bacteria along the root would be expected when  $D^*$  exceeds 1. This occurs when the root is growing more slowly than  $10^{-5}$  mm  $h^{-1}$ .

This result confirms that it is a valid assumption to consider the root tip as a one-dimensional structure because the advection of cells parallel to the root's axis is the dominant form of transport. On mature roots, however, where tissues are immobile, dispersion and/or chemotaxis are dominant in the microbial transport process. In this case, different models will be required so that microbial distribution and movement normal to the root surface can be represented explicitly.

### Attachment Improves Early Colonization of the Root Tip

Attachment of bacteria on the root tip in the model is characterized by an initial deceleration of bacterial cells during which the bacterial cell velocity is adjusted to match the velocity of the root cells. Once attached, bacterial cells move slowly with their attachment site away from the root tip and can stay longer periods of time (40 h) in the region where maximum root exudation occurs (Fig. 3A and 3B). In the zone of root elongation, however, the root tissue is “stretched” and the density of bacteria is “diluted.” A local maximum in bacterial density is therefore observed at the root tip where bacteria accumulate due to deceleration shortly before much dilution takes place. Attached bacteria have access to larger quantities of C from the root and grow at a faster rate because of the availability of exudate (Fig. 3B; Supplemental Video S1). Bacterial growth supported by root

exudates can reduce the dilution process in the root elongation zone but not remove it completely. Bacteria that do not attach to the root surface are displaced at a constant velocity  $V_{\max}$  from the root tip. They exit the basal region of the root growth zone within 10 h and grow less than attached bacteria because less C is available to them during this time.

The dynamic process of bacterial attachment and detachment on root surfaces provides great flexibility for rhizosphere bacteria to maximize the acquisition of C from the root. Without attachment–detachment, the number of bacterial cells is determined solely by the number of bacteria directly in the path of the root tip. Cells then grow at a rate determined by the availability of C exuded by the root (Fig. 4A). When bacteria from the rhizosphere can attach to and detach from the root surface, the amount of bacteria reaching the root surface increases at the root tip because its surface is sparsely populated. This increases the density of attached bacteria at the root tip but has little effect on the density of free-moving bacteria in the rhizosphere (Fig. 4B; Supplemental Video S2). The strategy is beneficial to bacteria because they acquire more C from the root than if they were not able to attach (Fig. 4C).

The root tip provides a finite number of permanent binding sites to bacteria. Many of these sites are available at the root tip because the bacterial density is low. The root surface is therefore a net acceptor of bacterial cells from the rhizosphere. However, the density of attached bacteria on mature portions of the root reaches a point where the number of bacteria on the root surface exceeds the number of permanent binding sites on the root ( $N$ ), and the epidermis becomes a net donor of bacterial cells that contributes

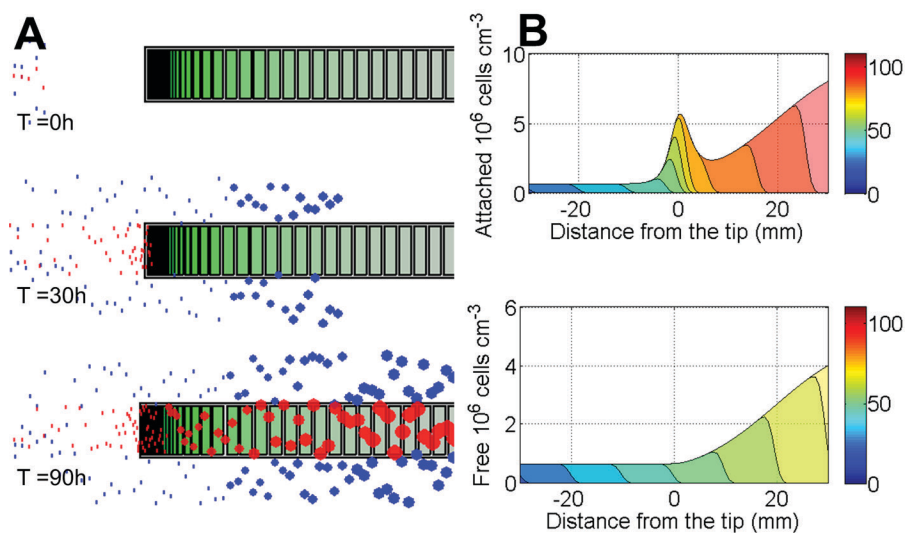


Fig. 3. The smooth particle hydrodynamic approach: (A) Simulation of root colonization at 0, 30, and 90 h of growth. Bacteria that are on the path ( $\alpha$ , pink dots,  $x < 0$ ) to intercept the root become attached ( $\alpha$ ,  $x \geq 0$ ), move slowly away from the tip, and accumulate at the tip (red circles), while free bacteria ( $\beta$ , blue circles) move away from the tip at constant velocity. (B) Superposed bacteria density distribution for attached and free-moving bacteria. The color (blue = 0 h to red = 150 h) indicates the time elapsed from the start of the experiment.

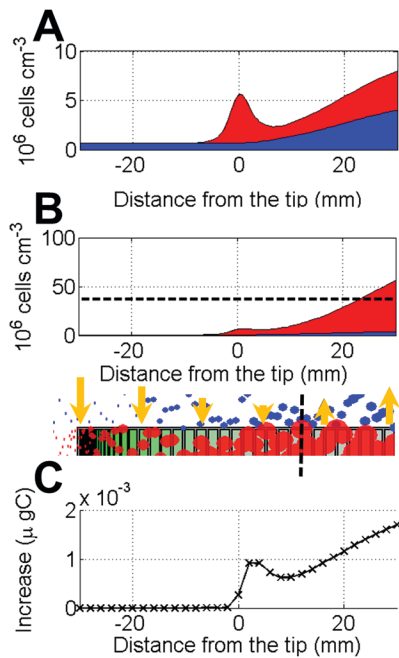


Fig. 4. Dynamic attachment and detachment is a bidirectional process that increases bacterial biomass at the root tip: (A) Attached (top red) and free (bottom blue) bacteria density at steady state in the absence of dynamic attachment or detachment. (B) Attached (top red) and free (bottom blue) bacteria density at steady state where dynamic attachment and detachment occurs. A sharp increase of attached bacteria can be observed (note the difference in scales between A and B). At the root tip, attachment is contributing to populating binding sites on the root surface. On older portions of the root, the root surface is saturated with the bacteria and becomes a donor of bacteria to the rhizosphere. When the density of the attached bacteria reaches the carrying capacity (dashed line), detachment becomes dominant and contributes to replenishment of the rhizosphere. (C) The difference between predicted total bacteria with dynamic attachment–detachment and predicted total bacteria without dynamic attachment–detachment.

to the fast replenishment and dispersion of the bacteria in the rhizosphere (Fig. 4B). At this stage, attached bacteria will have been transported as far as 2.3 cm from the root tip before being dispersed in the rhizosphere.

### Root and Bacterial Traits Have Varying Influences on Bacterial Colonization of the Surface of the Root Tip

Root exudation, bacterial growth rate, motility, the presence of fimbriae, and the ability to attach on the root surface are among the root colonization factors that have been studied the most in the literature (Lugtenberg et al., 2001). In this study, we found that a 50% increase in the attachment–detachment rate results in an increase in bacterial density of about a third. The effect of the length of the exudation zone is quantitatively similar because it also affects the length of time during which a bacterium is exposed to high levels of C. The velocity of the root tip is the parameter that has the largest effect on the bacterial abundance on the root surface. A 10-fold increase in bacterial density was observed in

response to a 50% decrease in root tip velocity. This was due essentially to the fact that bacteria move slowly away from the root tip and benefit from larger pools of exudates. The vigor of bacterial growth is also an important factor. A 50% increase in  $G_{\max}$  and  $G$  induced a 60% increase in bacterial abundance along the root.

We found that a 50% increase of the chemotactic parameter  $\chi$  induced a change of about 10% of the abundance of the attached bacteria. For a rhizosphere bacterium to be able to match the speed of the elongation rate and maintain at the root tip, a threshold value for the chemotactic parameter  $\chi$  must be exceeded. In our simulations, values above  $8 \times 10^{-4} \text{ cm}^5 \mu\text{g}^{-1} \text{ h}^{-1}$  were required. However, simulations of free-moving bacteria with high  $\chi$  values did not produce patterns that have been reported in the literature (Fig. 5A; Supplemental Video S4). Because chemotactic velocity increases with bacterial density, the velocity of the first bacteria coming in contact with the root tip is initially too small to match that of the root tip. However, after about 60 to 80 h spent in contact with the root tip, the bacterial population attains a critical size and starts to progress toward the root tip (Fig. 5B). A sharp bacterial front is then formed. The formation of this front is similar to shock waves formed by supersonic booms. Bacteria behind the root tip can exceed the velocity of the root tip to catch up with bacteria from the soil in front of the root, and an accumulation of bacteria at the front of the root is formed. At steady state, the front is placed in the elongation zone and corresponds to the peak C concentration.

### The Carrying Capacity of the Root Cap May Explain Bacterial Maintenance at the Root Tip

When the root cap is not able to hold bacteria (Eq. [12]), a root tip exposed to bacteria for a short period of time becomes sterile after 140 h. This is explained by the fact that bacteria bind to cells that move progressively away from the root tip (Fig. 6A; Supplemental Video S3). In the presence of a nonlinear carrying capacity at the root tip (Eq. [13–14]), the behavior of the model is modified significantly. First, because the bacteria are held in the root cap, they stay longer at the root tip and this causes an increased abundance of bacteria at the root tip (Fig. 6B; Supplemental Video S3). Also, because the root cap retains bacteria, the population is maintained along the root in the absence of external sources of bacteria from the bulk soil. It is important to note that for the bacterial population to be maintained at the root tip, the carrying capacity, defined here as the net detachment rate of bacteria from the root cap, must be a nonlinear function of the bacterial density. From Eq. [14], it can be concluded that the only steady state with a non-zero bacterial density in the root cap with no external sources of bacteria is obtained when  $g\tau - V_{\max}(1 - \theta)\tau^2/\tau_0 = 0$ , i.e.,  $\tau = g\tau_0/V_{\max}(1 - \theta)$ . However, such equilibrium is not mathematically possible from Eq. [14] if the carrying capacity of the root cap is linearly related to the bacterial density at the root tip. Therefore, if the flow of bacteria originating from the root cap is proportional to the



quantity accumulated, the root tip will become free of bacteria, similar to the case where no root cap is modeled.

## Discussion

### A New Framework to Understand Microbial Colonization on Carbon-Rich Growing Root Surfaces

The study of microbial activity in the rhizosphere has become an important field of research. Rhizosphere bacteria are associated with numerous soil processes. They facilitate the access of nutrients to plants (Subbarao et al., 2009), promote plant growth, and protect them from pathogens (Dekkers et al., 2000). Previous models of the rhizosphere have provided great insights into the factors controlling the growth and proliferation of bacteria at root–soil interfaces. Pioneering work from Newman and Watson (1977) proposed the first comprehensive model of microbial population dynamics showing the change in the abundance of microorganisms in relation to distance from the root surface. The model combined the growth rate of microorganisms in relation to the production of C from the root surface and its diffusion in the soil solution. Since then, various developments of the theory have been proposed, including the addition of different types of C sources from the root (Darrah, 1991b) and different species of bacteria (Zelenev et al., 2005). Models have also investigated more detailed aspects of bacterial mobility in soil (Ebrahimi and Or, 2014) or competition between bacteria (Faybishenko and Molz, 2013).

However, root tissues are in first contact with soil bacteria at the apex, where new cells are produced through cell division and pushed through the bulk soil by the elongation of maturing tissues from more proximal regions of the root. The root growth zone is particularly active in nutrient uptake (Silk and Bogeat-Triboulot, 2014), and we expect it to be particularly sensitive to microbial activity. Furthermore, mature tissues that are fixed in the soil have been moving and have been exposed to bulk soil bacteria for many hours before becoming immobile (Kim et al., 1999; Silk, 2002; Watt et al., 2006b). Key questions, therefore, are how bacteria from the bulk soil are recruited in the initial stages of the

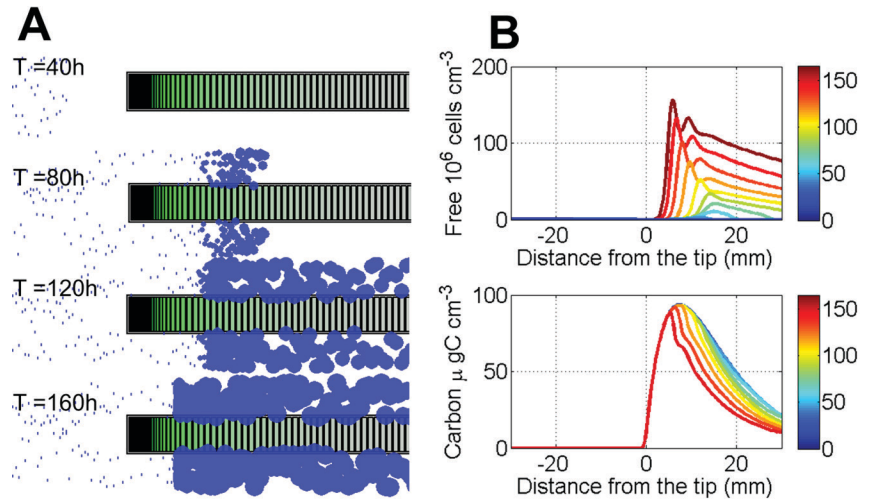


Fig. 5. Simulation of colonization of the root tip induced by chemotactic transport of bacteria: (A) At low concentration, the velocity of soil bacteria cannot exceed that of the root tip. However, after about 60 to 80 h, the bacterial population attains a critical size and progresses toward the root tip. (B) A discontinuous bacterial front is formed and its profile is similar to a supersonic boom: the flow of bacteria moving toward the root tip on the right is allowed to move faster than the front. Soil bacteria entering the front from the left cannot escape it because the high density of bacteria in the front stimulates a chemotactic response to the C gradient. At steady state, the front is placed in the elongation zone and corresponds to the peak of C density. The color key indicates time from the start of the experiment in hours.

formation of the root, and how this impacts the structure and composition of the microbial population during the life span of a root. It is clear that the ability to move, attach, and feed on root exudates are essential traits to colonize growing roots (Lugtenberg et al.,

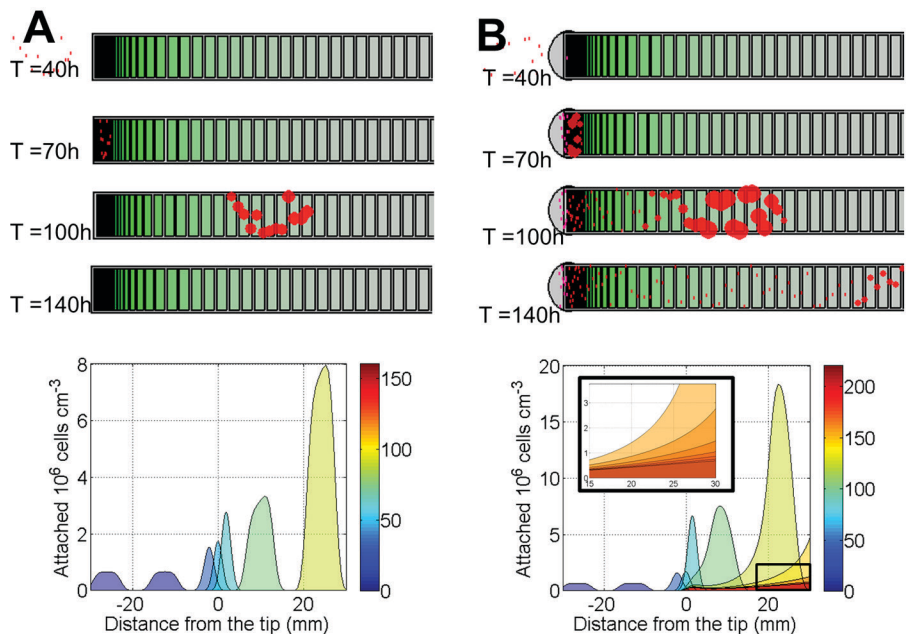


Fig. 6. A carrying capacity is required in the root cap for maintenance of bacteria at the root tip: (A) simulation of a root growing through a patch of rhizosphere bacteria without root cap carrying capacity, and (B) simulation of a root growing through a patch of rhizosphere bacteria with root cap carrying capacity. In the presence of the root cap carrying capacity, bacteria are able to maintain permanently at the root tip. The color key indicates the time elapsed from the start of the experiment in hours.

2001), but mathematical frameworks to understand the interactions among these different processes have been lacking.

In this study, we developed a mathematical framework to carry out such analyses. The theory combines mechanisms for root growth, elongation, and exudation with mechanisms to describe microbial proliferation, mobility, and attachment both in the soil and at the surface of the root. The nondimensional analysis of the model revealed that at the root tip, the advection of bacterial cells due to root elongation dominates over chemotaxis and dispersion of bacteria. The colonization of the root tip can therefore be represented as a one-dimensional process, and model predictions using this approach were in good agreement with experimental observations from the literature. In particular, the model could predict the macroscopic patterns of bacterial density along the root in rhizosphere bacteria (Humphris et al., 2005) but also explained the accumulation of bacteria in the root tip as observed at the microscopic scale (Watt et al., 2006a, 2006b).

There is also great potential to extend the theory to discover the mechanisms that underlie diversity in the rhizosphere. Roots exude a multitude of organic compounds whose fate in the soil varies based on parameters such as diffusion and mineralization rates, molar mass, charge, and sorption–desorption rates on the soil particles (Dennis et al., 2010; Jones, 1998; Jones et al., 2004). Experiments have shown that a very broad range of microbial species benefit from diverse root exudates (Barea et al., 2005), and future models could investigate mechanisms such as cooperation, antagonism, and mutualism among various functional types. Finally, the model could also be improved to represent the geometry of the rhizosphere in greater detail. For example, the root could be considered as a radially symmetric structure or even modeled as a full three-dimensional structure so that movement perpendicular to the root surface or fluxes of border cells can be described explicitly. New experimental observations will be essential to such theoretical development so that model complexity is built on more accurate measurements.

### **Mobility as a Mechanism for Fast Attachment on the Root Tip**

Adhesion of bacteria on root surfaces is a complex multistage process. First, bacteria must get near the surface of a root through passive (Brownian) motion or active (chemotactic) transport. Once at the surface of the root, a bacterium can either be repulsed by electrostatic Coulomb forces, attracted by van der Waals forces, or bound by specialized structures such as fimbriae and flagella. The strength of attachment is then determined by surface charges, cell size, and the ionic strength of the soil solution (Rossez et al., 2014). At this stage, detachment of bacteria is still frequent (Zhao et al., 2013), but minutes after reversible attachment, bacteria can synthesize extracellular polymers and form biofilms so that adhesion at the root surface becomes strong and irreversible (Berry and Armitage, 2008).

Because contact with the root surface is required before attachment, the ability of bacteria to navigate from the bulk soil to the surface of the root is essential. The velocity of bacteria in solution can exceed that of some root tips (Saragosti et al., 2011), and the role of chemotaxis on root colonization was demonstrated in experiments with mutants affected in their chemotactic functions (de Weert et al., 2002). However, maintenance at the tip cannot be explained solely by chemotaxis. The radial movement of bacteria from the soil to the root surface, captured in this study by the attachment parameter  $B$ , was shown to have a strong effect on the abundance of bacteria along the root. It is not possible for bacteria to match the speed of the root tip in the soil, however, because soil water usually does not allow a fast traveling speed for bacteria (Bashan, 1986). The analysis of the model also showed that the chemotactic parameter would need to exceed its reasonable value by three orders of magnitude, and such a setting would produce (unrealistic) sharp fronts of bacteria.

We hypothesize, therefore, that bacterial motility contributes essentially to proximal attachment on root surfaces, and a multitude of biophysical factors are likely to affect this process. First, the soil pore network structure and availability of a flow path toward the root surface will influence bacterial attachment to the root surface. It has been shown, for example, that lateral movement of bacteria in soil is linearly correlated to soil water content (Bashan, 1986), and theoretical studies by Ebrahimi and Or (2014) indicated that the decline of bacterial mobility with water content is exponential. Harder and more compacted soils reduce the root elongation rate and increase bacterial exposure to exudates and growth rates (Humphris et al., 2005). Genotypes with more slowly growing roots maintain much larger bacterial densities on the tip, and this is also predicted accurately by the model presented here and supported by empirical studies in the literature (Humphris et al., 2005; Watt et al., 2003, 2006b). A large fraction of bacterial movement could potentially be induced by mass flows linked to root water uptake and the rearrangement of soil particles during root penetration.

### **Root Cap May Allow Maintenance of Colonization at the Root Tip**

Bacterial mobility and attachment are required for efficient root colonization, but they are not sufficient for maintenance at the root tip because the flow of root cells drives attached bacterial cells away from the tip. To maintain bacterial colonies at the tip of roots in sterile soil (Simons et al., 1996), the root cap must have some form of carrying capacity (Fig. 1A). This is clear from the model outputs (Fig. 6). In the absence of a nonlinear rule for cell attachment on the root cap, bacteria are unable to maintain at the tip because they would have to bind to root cells that are either sloughed off or displaced from the tip through cell expansion.

The root cap must therefore provide a different type of habitat for bacteria than epidermis cells, with cavities and channels for

microbes to accumulate. This is evident, for example, in images of *Arabidopsis* roots obtained by confocal microscopy by Fan et al. (2011), where the sloughing of root cap cells is extremely limited. Similar observations were made on wheat (*Triticum aestivum* L.) (Fig. 1A; Watt et al., 2006a). A few studies, however, could not detect major bacteria colonization at the tip (Chin-A-Woeng et al., 1997; Foster and Rovira, 1976). Experiments involving the removal of the root cap (Humphris et al., 2005) have also reported an increase in bacterial density at the macroscopic scale, probably stimulated by the reduction in the elongation rate and changes in the exudation pattern. It is likely that the functioning of the root cap and the nature of the habitats available to bacteria at the root surface depend on both bacterial and plant species and the root developmental stage. In this case, the model for bacterial carrying capacity proposed in Eq. [14] may not represent the range of patterns observed experimentally. Species such as maize (*Zea mays* L.) exhibit rapid root cap cell turnover and mucilage production (Bengough and McKenzie, 1997) and may prevent permanent accumulation of bacteria or even act as a repellent due to a diverging flow of border cells and mucilage. Species such as *Arabidopsis* with limited or no cell turnover in the root cap may act as a reservoir for bacterial cells that, in turn, fuels the colonization of the remaining parts of the root.

## A General Model for the Colonization of the Root Tip by Bacteria Can Explain Observations in the Literature

Early colonization of the root tip is fundamental to the establishment of plant–bacteria interactions because the tip is the site where new root tissues are being formed, and this provides opportunities for bacteria to exploit nutrient-rich habitats along the root. Based on the behavior of our model and analysis of the literature, it is possible therefore to formulate a general model for the colonization of the root tip by bacteria (Fig. 7). Sterile root tips get in contact with soil bacteria, and some cells attach to the root surface. The root cap may have intercellular space and/or low cell turnover, allowing it to constitute a reservoir of bacterial cells. In other species, more intense sloughing may prevent bacteria from colonizing the root cap. Free-moving bacteria or root-cap bacteria flow along the root away from the root tip. The abundance of bacteria on root surfaces increases because of the attachment and growth of bacteria supported by exudation. After a certain time, the carrying capacity of mature roots is exceeded, detachment from the root exceeds attachment, and bacterial cells are released into the rhizosphere (Fig. 7). Attachment is therefore an essential trait for microbe dispersal in soil because it allows bacteria to travel macroscale distances fast and with limited energy expense.

## Conclusion

The root tip is a complex target for microorganisms. The theoretical framework presented here elucidates how bacteria use the resources available at the root tip to grow and disperse in the soil.

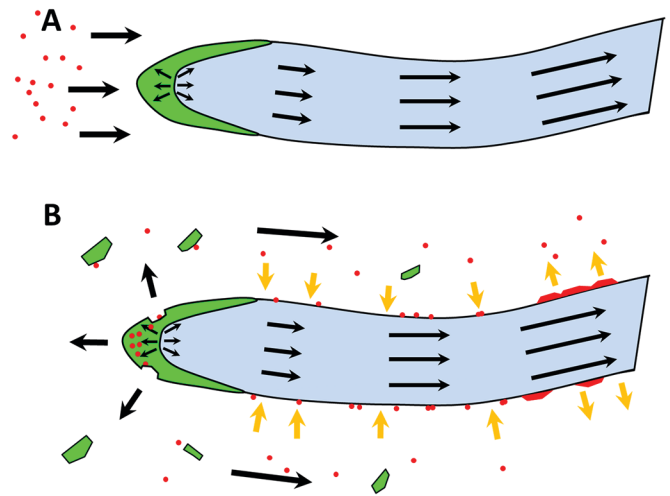


Fig. 7. General model for bacterial maintenance at the root tip: A root first contacts soil bacteria, and some bacterial cells attach to the root surface (yellow arrows). In some species, intercellular space between root cap cells (in green) may provide habitats to bacterial cells that can constitute a reservoir of bacterial cells. During root growth, the root cap is sloughed off (black arrows), releasing border cells (in green) but also bacterial cells into the soil solution (red). Attachment–detachment of bacteria on the surface of the root leads to the buildup of microcolonies (red patches) that exploit available exudates. At a certain distance from the tip, bacteria exceed the binding capacity of root surfaces. The net attachment–detachment flux is then reversed and bacterial cells are released and dispersed in different regions of the soil.

This theoretical framework is mechanistic, explains observations reported in the literature, and predicts the patterns of bacterial distribution in the rhizosphere. The challenge now is to find ways to observe and quantify bacterial cells live and in situ so that the theory can be refined and expanded based on new observations.

## Variables and Parameters

$a$	Net bacterial attachment rate, $\mu\text{g cm}^{-3} \text{h}^{-1}$
$A$	Langmuir coefficient for equilibrium proportions, $\text{cm}^3 \mu\text{g}^{-1}$
$B$	Langmuir coefficient for rate of equilibration, $\text{h}^{-1}$
$C_a$	cross-sectional area of the zone of attached bacteria, $\text{cm}^2$
$C_f$	cross-sectional area of the zone of free bacteria, $\text{cm}^2$
$D$	dispersion coefficient for bacteria, $\text{cm}^2 \text{h}^{-1}$
$E$	diffusion coefficient for C exudates, $\text{cm}^2 \text{h}^{-1}$
$G$	relative growth rate of bacteria, $\text{h}^{-1}$
$J_{\text{attach}}$	convective flux of attached bacteria, $\mu\text{g cm}^{-2} \text{h}^{-1}$
$J_{\text{carbon}}$	convective flux of C, $\mu\text{g cm}^{-2} \text{h}^{-1}$
$J_{\text{free}}$	convective flux of free bacteria, $\mu\text{g cm}^{-2} \text{h}^{-1}$
$K$	affinity constant for microbial growth, $\mu\text{g cm}^{-3}$
$L$	scale length of root exudation zone, cm
$M$	mortality rate, $\mu\text{g cm}^{-3}$
$N$	amount of binding sites on the surface, $\mu\text{g cm}^{-3}$
$P$	C decay rate coefficient, $\text{h}^{-1}$
$S_{\text{max}}$	C release rate of root, $\mu\text{g cm}^{-1} \text{h}^{-1}$
$v(x)$	velocity of displacement from root tip, $\text{cm h}^{-1}$
$V_{\text{max}}$	elongation rate of root, $\text{cm h}^{-1}$

$W$	scale for length of growth zone, $\text{cm}^2$
$x$	distance from root tip, $\text{cm}$
$\alpha$	density of bacterial cells attached at an interface between the root and the rhizosphere, $\mu\text{g cm}^{-3}$
$\beta$	density of free moving microbial cells, $\mu\text{g cm}^{-3}$
$\gamma$	total C concentration around the root, $\mu\text{g cm}^{-3}$
$\Theta$	“residual velocity” parameter to root surface cells
$\tau$	bacterial concentration in the root cap, $\mu\text{g cm}^{-3}$
$\chi$	chemotaxis coefficient for bacteria (from Keller–Segel model), $\text{cm}^5 \mu\text{g}^{-1} \text{h}^{-1}$

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