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Plant Roots Increase Bacterivorous Nematode Dispersion through Nonuniform Glass-bead Media

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4

5 Title

6 PLANT ROOTS INCREASE BACTERIVOROUS NEMATODE DISPERSION THROUGH
7 NON-UNIFORM GLASS-BEAD MEDIA

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32 Roots increase dispersion through glass beads: *Trap et al.*

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Abstract: Dispersion of bacterivorous nematodes in soil is a crucial ecological process that permits settlement and exploitation of new bacterial-rich patches. Although plant roots, by modifying soil structure, are likely to influence this process, they have so far been neglected. In this study, using an original three-compartment microcosm experimental design and PVC bars to mimic plant roots, we tested the ability of roots to improve the dispersion of bacterivorous nematode populations through two wet, non-uniform granular (glass bead) media imitating contrasting soil textures. We showed that artificial roots increased migration time of bacterivorous nematode populations in the small bead medium, suggesting that plant roots may play an important role in nematode dispersion in fine-textured soils or when soil compaction is high.

Keywords: dispersion; ecology; glass-bead media; migration time; colonization time; plant roots.

48 Bacterivorous nematodes are widely distributed soil organisms involved in key
49 terrestrial ecosystem functions such as soil fertility and plant productivity (Djigal et al., 2004,
50 Irshad et al., 2011, Blanc et al., 2006, Anderson et al., 1978, Ferris et al., 1998, Bonkowski et
51 al., 2009). By releasing nutrients (nitrogen and phosphorus) immobilized in bacterial biomass
52 in the vicinity of plant roots, they largely contribute to soil nutrient availability (Ferris et al.,
53 1998, Anderson et al., 1983) and plant nutrition and growth (Irshad et al., 2012, Bonkowski
54 and Clarholm, 2012, Trap et al., 2015).

55 The positive effects of bacterivorous nematodes on soil and plant functions are
56 conditioned by their ability to move within heterogeneous soils (Griffiths and Caul, 1993).
57 Dispersion of nematodes from one bacterial site to new resource patches is a crucial
58 ecological process facilitating ecosystem functions (Horiuchi et al., 2005, Hassink et al.,
59 1993, Savin et al., 2001, Hassink et al., 1993, Rodger et al., 2004). It is strongly determined
60 by soil conditions such as bulk density (Hunt et al., 2001, Portillo-Aguilar et al., 1999), soil
61 water content (Young et al., 1998) or temperature (Hunt et al., 2001), soil texture and hence
62 porosity (Young et al., 1998, Portillo-Aguilar et al., 1999, Georgis and Poinar, 1983, Prot and
63 Van Gundy, 1981), bacterial species (Rodger et al., 2004, Young et al., 1998), salt gradients
64 (Le Saux and Queneherve, 2002), or soil water run-off (Chabrier et al., 2009).

65 In most experiments, bacteria-nematode effects on soil nutrient availability have been
66 studied in bulk soils and root exudates were mimicked by providing carbon as an energy
67 source for bacteria, usually as glucose (Anderson et al., 1983, Cole et al., 1978, Coleman et
68 al., 1978, Ferris et al., 1997, Ferris et al., 1998). Possible physical influences of roots on
69 nematode dispersal, and the subsequent effects on soil nutrient availability, have thus not been
70 represented. Moreover, in experiments with plants (Bjornlund et al., 2012, Djigal et al., 2004),
71 shifts in both energy supply and porosity induced by roots are confounded, limiting our ability
72 to decipher mechanisms by which roots impact nematode-driven ecological functions. In this

73 study, using an original three-compartment microcosm experimental design, we tested the
74 ability of roots to improve the dispersion of nematodes and their associated bacteria through
75 two wet granular media made from glass beads of different sizes in order to mimic two
76 contrasting soil textures.

77

78 MATERIALS AND METHODS

79

80 The study was conducted in sterile three-compartment 90-mm Petri dishes
81 (compartments labeled A-C). We designed six treatments (Figure 1). The first two treatments
82 corresponded to negative (NC) and positive (PC) controls, respectively. In NC, compartments
83 were not connected (compartments were independent) while in PC and for the four other
84 treatments, short gates (~5 mm width) were opened between compartments A and B and
85 between compartments B and C by melting the plastic walls separating compartments (Figure
86 1). In all treatments, compartments A and C were filled with 10 ml TSB-A (3 g L⁻¹ Tryptic
87 Soy Broth Fluka 22092 and 1% agar w/v supplemented with cholesterol 5 mg L⁻¹). The
88 compartment B was filled with 10 ml TSB-A in NC and PC treatments, whereas in the other
89 four treatments, it was filled with 15 g of non-uniform (polydisperse) glass beads (Abralis,
90 France), either of small size (SB: mean diameter 130 µm, min-max diameters 60-260 µm,
91 porosity 40%), or large size (LB: mean diameter 600 µm, min-max diameters 300-1100 µm,
92 porosity 32%). Bead size was measured using a laser granulometer (Mastersizer APA2000,
93 Malvern Instruments Ltd., United Kingdom) while the distribution of pore size was
94 approximated using the Finney Model (Frost, 1978, Finney, 1970) for uniformly sized
95 (monodisperse) granular media with the average size of beads as the most representative bead
96 size for each medium.

97 Before use, glass beads were acid-washed using HCl 1M, rinsed with sterile deionized
98 water and saturated at 100% of their holding capacity. In two of the glass-bead treatments (5
99 and 6), a flexible PVC bar (2 mm diameter, 4 cm length), previously sterilized in bleach and
100 washed with sterilized deionized water, was used to mimic roots and placed in compartment B
101 (Figure 1). The ends of the PVC bar were inserted through the gates, thus linking
102 compartment A with C (Figure 1). In compartment B, the PVC bar was placed inside the bead
103 medium. This PVC bar was used to test physical effects of roots on nematode dispersion
104 without interfering with carbon supply by rhizodeposition. Each treatment was replicated 5
105 times (30 microcosms).

106 For all microcosms, compartment A was inoculated with 100 µl of fresh gram-positive
107 *Bacillus subtilis* (strain 111b) culture and 15 adult bacterial-feeding nematodes belonging to
108 *Rhabditis* sp., together as a spot dropped from the corner of the compartment at the center of
109 the Petri dish (Figure 1). Bacteria and nematodes for experiments were isolated from an
110 ectomycorrhizal root tip and the soil collected in a maritime pine forest, respectively (Irshad
111 et al., 2011). Nematodes were maintained in our laboratory by transferring individuals onto
112 new TSB-A plates containing *B. subtilis* (Irshad et al., 2011). Nematodes multiplied in the
113 dark at 20 °C. Nematodes used in the inoculation experiments were prepared by removing
114 them from the breeding TSB-A plates by washing the surface with a sterile NaCl solution
115 (1%). They were washed from most *B. subtilis* by centrifugation (1000 rpm, 5 min) and re-
116 suspended in sterile deionized water.

117 Every morning for three weeks, microcosms were carefully inspected using a
118 binocular microscope and the number of individuals in compartment C was counted. We
119 defined the “migration time” as the number of days required to observe one individual
120 (juvenile or adult) in compartment C. We also assessed the “colonization time” as the number
121 of days required for nematodes to exploit the whole compartment C and reach the maximal

122 carrying capacity set at 400 individuals (corresponding to a homogeneous distribution of
123 nematodes in compartment). Means and standard deviation were calculated for each treatment
124 and significant differences were tested using one-way ANOVA and Tukey HSD tests.
125 Normality of residuals was checked using Shapiro test. All tests were computed with the R
126 freeware (R, 2008) and statistical significance was set at $P < 0.05$.

128 RESULTS AND DISCUSSION

129
130 After three weeks of incubation, no nematode was observed in compartment C in the
131 negative control (Figure 2.A), confirming that nematodes were not able to cross the walls
132 separating compartments. In the positive control (PC), around 8 days were required to observe
133 individuals in C while 10 days were required in both large- and small-bead treatments. Our
134 findings are in agreement with those obtained by Wallace (1958) that showed that the pore
135 size in a saturated 75- to 150- μm soil fraction (similar to our small-bead medium) approaches
136 that through which *Heterodera schachtii* larvae are unable to pass. In his study, a maximum
137 of 10% of the nematodes migrated farther than 5 cm from the inoculation site for this soil
138 fraction while ~35% of the population migrated farther than 5 cm in the 150-200 μm fraction.

139 When an artificial root was added across compartment B, the mean migration time
140 decreased to 9 days and 8 days for large and small beads, respectively. The effect of the
141 artificial root on nematode migration time was thus observed for both bead sizes, but the
142 effect was significant for small beads only. By creating macropores (Angers and Caron,
143 1998), roots increased soil porosity for these free organisms and their dispersal rate.
144 Nematodes can also move in the water film formed around the root as a “highway” towards a
145 new site. Here, we did not provide glucose to mimic root exudates because our aim was to
146 discriminate energy supply from physical effects of roots on nematodes. In natural

147 rhizospheres, the presence of root exudates is known to improve soil structure and increase
148 aggregation, especially in clay soils (Angers and Caron, 1998, Bertin et al., 2003). It is
149 possible that in natural conditions, the improving effect of roots on nematode dispersion could
150 be modified by rhizodeposition rate and soil clay content (Hassink et al., 1993).

151 Interestingly, the colonization time of nematode populations growing in C varied
152 according to treatments (Figure 2.B). The lowest values were observed for PC and for small
153 beads with an artificial root (mean ~2.5 days of colonization time) while the highest values
154 were observed for small beads without an artificial root (mean ~4.2 days). Intermediate values
155 were found in large beads, with or without artificial roots. In PC and beads with an artificial
156 root, adults moved easily from A to C. In contrast, for the treatment with small beads and
157 without AR, the first individuals observed in C were juveniles. This pattern can be explained
158 by the diameter of adult nematodes after 14 days of growth oscillating around 35 μm ($n = 30$).
159 Individuals with a diameter superior to ~30 μm were highly constrained by the beads (Figure
160 3). In consequence, in treatments with small beads, only juveniles could move easily from A
161 to C. Several hours and days were thus needed for juveniles to grow in C before becoming
162 adults and reproducing, explaining why colonization was slower.

163 It is important to note that we did not inoculate compartments B and C with *Bacillus*
164 *subtilis* cells. The colonization time of nematode populations was thus based on their ability
165 to transport bacteria (or spores) from compartment A to C. Several studies observed phoretic
166 transport of bacteria by nematodes (Hallmann et al., 1998, Knox et al., 2004, Knox et al.,
167 2003) or defecation of living bacterial cells or spores after their passage through the nematode
168 gut (Laaberki and Dworkin, 2008, Rae et al., 2012). For instance, Laaberki and Dworkin
169 (2008) showed that ingested *B. subtilis* spores were resistant to *Caenorhabditis elegans*
170 digestion. Some studies showed that nematodes can act as vectors of rhizobium (Jatala et al.,
171 1974, Sitaramaiah and Singh, 1975, Horiuchi et al., 2005) or plant pathogenic bacteria

172 (Kroupitski et al., 2015). Once in C, living *B. subtilis* cells or spores attached on nematode
173 cuticles or excreted by nematodes can proliferate rapidly on TSB-A before nematode
174 population growth.

175 In conclusion, this microcosm experiment showed that the presence of small beads
176 severely constrained adult but not juvenile dispersion. An artificial root increased
177 bacterivorous nematode populations and associated-bacterial food dispersion in wet
178 polydisperse media, especially in small-bead media. These results suggested that plant roots
179 can play an important role in assisting nematode dispersion in fine-textured soils or when
180 roots penetrate in compacted soils (Queneherve and Chotte, 1996, Iijima et al., 1991).
181 Nematode effects on nutrient cycling are known to vary according to soil texture (Hassink et
182 al., 1993), but our study suggests that the presence of roots may alleviate the effect of small
183 soil pore size, enhancing local population connection and probably soil nutrient cycling
184 (Clarholm, 1985). Our results also suggested that besides root exudates and active attraction,
185 differences in root architecture among plant species can also explain why nematode
186 population abundance or biomass in plant rhizospheres vary according to plant species
187 (Griffiths, 1990, Horiuchi et al., 2005). Further studies using similar designs could be used to
188 disentangle physical and nutritional impacts of roots on nematode-driven transport of
189 nutrients or organic compounds such as enzymes or pollutants.

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314 Figure 1. Experimental setup with three-compartment Petri dishes used to assess the effect of
315 roots and medium porosity on nematode dispersal and colonization. In all treatments but the
316 negative control (treatment 1), compartments A and C were connected by gates opened
317 through the wall, with or without an artificial root “AR” (2 mm diameter PVC bar) added to
318 cross the compartment B. Compartments A and C were filled with TSB-A (see text for
319 composition). Depending on the treatment, B was filled with TSB-A (treatments 1 and 2) or
320 with small beads (SB) (treatments 3 and 5), or large beads (LB) (treatments 4 and 6) in sterile
321 deionized water. Only compartment A was inoculated with *Bacillus subtilis* and 15 bacterial-
322 feeding adult nematodes belonging to the *Rhabditis* sp., as a spot dropped from the corner of
323 the compartment at the center of the Petri dish (closed circle).

324
325 Figure 2. Migration time (A) and colonization time (B) in days according to treatments. NC:
326 negative control; PC: positive control (white); LB: large beads (light grey); SB: small beads
327 (dark grey); -AR: without artificial root (solid line); +AR: with artificial root (dotted line).
328 Different letters (a and b) indicate significance among treatments according to one-way
329 ANOVA and Tukey HSD post hoc tests ($P < 0.05$, $n = 5$).

330
331 Figure 3. Size distribution of beads (A) and approximation of pore size distribution (B) for
332 small (dotted line) or large (solid line) beads. $P(k)$ is the frequency of the radius (k) of pores.
333 The blue solid line indicates mean nematode diameter size of adults ($n = 30$).





