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Published in:
Current Opinion in Genetics & Development

DOI:
[10.1016/j.gde.2018.03.007](https://doi.org/10.1016/j.gde.2018.03.007)

Publication date:
2018

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Document Version
Peer reviewed version

[Link to publication in Discovery Research Portal](#)

Citation for published version (APA):
Dupuy, L. X., Mimault , M., Patko, D., Ladmiral, V., Ameduri, B., MacDonald, M. P., & Ptashnyk, M. (2018). Micromechanics of root development in soil. *Current Opinion in Genetics & Development*, 51, 18-25.
<https://doi.org/10.1016/j.gde.2018.03.007>

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Micromechanics of root development in soil

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Keywords: plant roots, particle, granular media, biomechanics

Abstract

Our understanding of how root develop in soil may be at the eve of significant transformations. The formidable expansion of imaging technologies enables live observations of the rhizosphere micro-pore architecture at unprecedented resolution. Granular matter physics provides ways to understand the microscopic fluctuations of forces in soils, and the increasing knowledge of plant mechanobiology may shed new lights on how roots perceive soil heterogeneity. This opinion paper exposes how recent scientific achievements may contribute to design a new theory for root growth in heterogeneous environments.

Main text

Current knowledge of the biomechanics of plant root growth in soil is largely based on the extensive work of plant biophysicists from the second half of the 20th century { ADDIN EN.CITE { ADDIN

24 EN.CITE.DATA }} . The view was that both roots and soil must be considered as continua so that the
25 description of root soil interactions can be achieved with continuous mathematical functions of
26 macroscopic variables such as Young's modulus of root tissue, soil penetration stress, and pore water
27 pressure { ADDIN EN.CITE
28 <EndNote><Cite><Author>Abdalla</Author><Year>1969</Year><RecNum>232</RecNum><DisplayText>
29 <[4]</DisplayText><record><rec-number>232</rec-number><foreign-keys><key app="EN" db-
30 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512665632">232</key></foreign-
31 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Abdalla,
32 AM</author><author>Hettiaratchi, DRP</author><author>Reece,
33 AR</author></authors></contributors><titles><title>The mechanics of root growth in granular
34 media</title><secondary-title>Journal of Agricultural Engineering Research</secondary-
35 title></titles><periodical><full-title>Journal of Agricultural Engineering Research</full-
36 title></periodical><pages>236-
37 248</pages><volume>14</volume><number>3</number><dates><year>1969</year></dates><isbn
38 >0021-8634</isbn><urls></urls></record></Cite></EndNote>}. Classical concepts from mechanics
39 and physiology then provide a suitable framework to understand factors controlling tissue growth in
40 its natural environment. The energy required to deform the root and surrounding soil, which
41 originates from the photosynthetic chemical energy accumulated within the tissues, is converted into
42 turgor pressure and mechanical energy { ADDIN EN.CITE
43 <EndNote><Cite><Author>Silk</Author><Year>1980</Year><RecNum>229</RecNum><DisplayText
44 >[5]</DisplayText><record><rec-number>229</rec-number><foreign-keys><key app="EN" db-
45 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512664575">229</key></foreign-
46 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Silk, W.
47 K.</author><author>Wagner, K.</author></authors></contributors><titles><title>Growth-
48 sustaining water potential distributions in the primary corn root. a non compartmented continuum
49 model</title><secondary-title>Plant Physiology</secondary-title></titles><periodical><full-

50 title>Plant Physiology</full-title></periodical><pages>859-
51 863</pages><volume>66</volume><number>5</number><dates><year>1980</year></dates><isbn
52 >1532-2548</isbn><urls></urls></record></Cite></EndNote>}. Turgor pressure then overcome the
53 resistance from cell wall to stretching, the resistance to movement of water across membranes, and
54 the resistance to the displacement of the soil around the root { ADDIN EN.CITE
55 <EndNote><Cite><Author>Dexter</Author><Year>1987</Year><RecNum>226</RecNum><DisplayT
56 ext>[6]</DisplayText><record><rec-number>226</rec-number><foreign-keys><key app="EN" db-
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58 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Dexter,
59 AR</author></authors></contributors><titles><title>Mechanics of root growth</title><secondary-
60 title>Plant and soil</secondary-title></titles><periodical><full-title>Plant and Soil</full-
61 title></periodical><pages>303-
62 312</pages><volume>98</volume><number>3</number><dates><year>1987</year></dates><isbn
63 >0032-079X</isbn><urls></urls></record></Cite></EndNote>}.
64 This classical view of root-soil biomechanics has been central to identify the biophysical factors limiting
65 growth in soil, but it is now challenged to predict morphologies and developmental patterns observed
66 in natural conditions (Figure 1). If roots were to experience homogeneous mechanical stress from the
67 soil, one would expect turgor pressure and Lockhart equation { ADDIN EN.CITE
68 <EndNote><Cite><Author>Lockhart</Author><Year>1965</Year><RecNum>185</RecNum><Display
69 Text>[1]</DisplayText><record><rec-number>185</rec-number><foreign-keys><key app="EN" db-
70 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512051649">185</key></foreign-
71 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Lockhart,
72 James A</author></authors></contributors><titles><title>An analysis of irreversible plant cell
73 elongation</title><secondary-title>Journal of Theoretical Biology</secondary-
74 title></titles><periodical><full-title>Journal of theoretical biology</full-
75 title></periodical><pages>264-

275</pages><volume>8</volume><number>2</number><dates><year>1965</year></dates><isbn>
0022-5193</isbn><urls></urls></record></Cite></EndNote>} to predict accurately growth arrest in
soil. This is not the case and large discrepancies remain between measured turgor pressure (in the
order of 1MPa { ADDIN EN.CITE
<EndNote><Cite><Author>Clark</Author><Year>1996</Year><RecNum>231</RecNum><DisplayTex
t>[7]</DisplayText><record><rec-number>231</rec-number><foreign-keys><key app="EN" db-
id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512664911">231</key></foreign-
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LJ</author><author>Whalley, WR</author><author>Dexter, AR</author><author>Barracough,
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mechanical impedance increases the turgor of cells in the apex of pea roots</title><secondary-
title>Plant, Cell & Environment</secondary-title></titles><periodical><full-title>Plant, Cell
& Environment</full-title></periodical><pages>1099-
1102</pages><volume>19</volume><number>9</number><dates><year>1996</year></dates><isb
n>1365-3040</isbn><urls></urls></record></Cite></EndNote>}} and the levels of mechanical
stresses at which growth is arrested (>5MPa { ADDIN EN.CITE
<EndNote><Cite><Author>Bengough</Author><Year>1991</Year><RecNum>224</RecNum><Displ
ayText>[8]</DisplayText><record><rec-number>224</rec-number><foreign-keys><key app="EN"
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keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Bengough,
AG</author><author>Mullins, CE</author></authors></contributors><titles><title>Penetrometer
resistance, root penetration resistance and root elongation rate in two sandy loam
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and Soil</full-title></periodical><pages>59-
66</pages><volume>131</volume><number>1</number><dates><year>1991</year></dates><isbn
>0032-079X</isbn><urls></urls></record></Cite></EndNote>}}). Classical mechanics of continua is ill-

102 equipped to explain the links between soil heterogeneity and stochasticity of plant development. The
 103 root tissue itself is heterogeneous and cell types have different roles in facilitating growth and
 104 penetration. Anchoring the base of the root for example, is necessary for cell elongation to produce
 105 apical movement and deformation of the soil { ADDIN EN.CITE
 106 <EndNote><Cite><Author>Bengough</Author><Year>2016</Year><RecNum>225</RecNum><Displ
 107 ayText>[9]</DisplayText><record><rec-number>225</rec-number><foreign-keys><key app="EN"
 108 db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstex" timestamp="1512663688">225</key></foreign-
 109 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Bengough, A
 110 Glyn</author><author>Loades, Kenneth</author><author>McKenzie, Blair
 111 M</author></authors></contributors><titles><title>Root hairs aid soil penetration by anchoring the
 112 root surface to pore walls</title><secondary-title>Journal of Experimental Botany</secondary-
 113 title></titles><periodical><full-title>Journal of experimental botany</full-
 114 title></periodical><pages>1071-
 115 1078</pages><volume>67</volume><number>4</number><dates><year>2016</year></dates><isb
 116 n>0022-0957</isbn><urls></urls></record></Cite></EndNote>}. The root cap and its associated
 117 border cells have also a fundamental role in reducing friction from the bulk soil. It was shown recently
 118 that wheat genotypes with sharper root tips are more efficient at soil penetration { ADDIN EN.CITE
 119 <EndNote><Cite><Author>Colombi</Author><Year>2017</Year><RecNum>230</RecNum><Display
 120 Text>[10]</DisplayText><record><rec-number>230</rec-number><foreign-keys><key app="EN" db-
 121 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstex" timestamp="1512664744">230</key></foreign-
 122 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Colombi,
 123 Tino</author><author>Kirchgessner, Norbert</author><author>Walter,
 124 Achim</author><author>Keller, Thomas</author></authors></contributors><titles><title>Root tip
 125 shape governs root elongation rate under increased soil strength</title><secondary-title>Plant
 126 Physiology</secondary-title></titles><periodical><full-title>Plant Physiology</full-
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2301</pages><volume>174</volume><number>4</number><dates><year>2017</year></dates><is
bn>0032-0889</isbn><urls></urls></record></Cite></EndNote>}.
To establish a biomechanical framework that accounts for the complexity of root interactions with the
granular medium, one must capture the microscopic nature of particle forces and the collective action
they have on root tissues (Figure 1A). { ADDIN EN.CITE <EndNote><Cite
AuthorYear="1"><Author>Evelyne</Author><Year>2017</Year><RecNum>199</RecNum><DisplayT
ext>Kolb, et al. [11]</DisplayText><record><rec-number>199</rec-number><foreign-keys><key
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Béatrice</author></authors></contributors><titles><title>Physical root-soil
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title></periodical><pages>065004</pages><volume>14</volume><dates><year>2017</year></dat
es><isbn>1478-3975</isbn><urls></urls></record></Cite></EndNote>} proposed to categorise the
nature of root mechanical responses to soil based on the scale of the soil heterogeneities. When the
medium is composed of small particles, individual variations in the force required to move them are
not perceived by the root. The behaviour of roots and soil can be homogenised, and classical
continuum mechanics usually applies (Box 1A) { ADDIN EN.CITE
<EndNote><Cite><Author>Faure</Author><Year>1994</Year><RecNum>233</RecNum><DisplayTe
xt>[12]</DisplayText><record><rec-number>233</rec-number><foreign-keys><key app="EN" db-
id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512665757">233</key></foreign-
keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Faure,
AG</author></authors></contributors><titles><title>Stress field developed by root growth:
theoretical approach</title><secondary-title>Journal of Agricultural Engineering

154 Research</secondary-title></titles><periodical><full-title>Journal of Agricultural Engineering
 155 Research</full-title></periodical><pages>53-
 156 67</pages><volume>58</volume><number>1</number><dates><year>1994</year></dates><isbn>
 157 0021-8634</isbn><urls></urls></record></Cite></EndNote>}. Soils also contain objects that are too
 158 large and or too rigid for a root to deform and displace, for example when roots grow in contact with
 159 stones, in cracks or pores { ADDIN EN.CITE
 160 <EndNote><Cite><Author>Jackson</Author><Year>1999</Year><RecNum>234</RecNum><DisplayT
 161 ext>[13,14]</DisplayText><record><rec-number>234</rec-number><foreign-keys><key app="EN"
 162 db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512725012">234</key></foreign-
 163 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Jackson,
 164 RB</author><author>Moore, LA</author><author>Hoffmann, WwA</author><author>Pockman,
 165 WT</author><author>Linder, CR</author></authors></contributors><titles><title>Ecosystem
 166 rooting depth determined with caves and DNA</title><secondary-title>Proceedings of the National
 167 Academy of Sciences of the United States of America</secondary-title></titles><periodical><full-
 168 title>Proceedings of the National Academy of Sciences of the United States of America</full-
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 171 isbn>0027-
 172 8424</isbn><urls></urls></record></Cite><Cite><Author>White</Author><Year>2010</Year><Rec
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 174 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512725591">235</key></foreign-
 175 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>White,
 176 Rosemary G</author><author>Kirkegaard, John
 177 A</author></authors></contributors><titles><title>The distribution and abundance of wheat roots
 178 in a dense, structured subsoil—implications for water uptake</title><secondary-title>Plant, Cell & Environment</secondary-title></titles><periodical><full-title>Plant, Cell & Environment</full-
 179 Environment</secondary-title></titles><periodical><full-title>Plant, Cell & Environment</full-

180 title</periodical><pages>133-
181 148</pages><volume>33</volume><number>2</number><dates><year>2010</year></dates><isbn
182 >1365-3040</isbn><urls></urls></record></Cite></EndNote>}. Growth forces cannot displace the
183 obstacle and the root usually combines tropic responses and mechanical buckling to avoid the obstacle
184 (Box 1B) { ADDIN EN.CITE
185 <EndNote><Cite><Author>Monshausen</Author><Year>2009</Year><RecNum>200</RecNum><Dis
186 playText>[15]</DisplayText><record><rec-number>200</rec-number><foreign-keys><key app="EN"
187 db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstex" timestamp="1512484654">200</key></foreign-
188 keys><ref-type name="Journal Article">17</ref-
189 type><contributors><authors><author>Monshausen, Gabriele B</author><author>Gilroy,
190 Simon</author></authors></contributors><titles><title>The exploring root—root growth responses
191 to local environmental conditions</title><secondary-title>Current opinion in plant
192 biology</secondary-title></titles><periodical><full-title>Current opinion in plant biology</full-
193 title></periodical><pages>766-
194 772</pages><volume>12</volume><number>6</number><dates><year>2009</year></dates><isbn
195 >1369-5266</isbn><urls></urls></record></Cite></EndNote>}. The behaviour of roots growing in
196 soils with particles of intermediate sizes is more challenging to understand. A root can displace
197 individual particles from the soil, but the forces exerted by each of the particles can also influence the
198 course of root development (Box 1C). Although such growth environments are common for fine roots
199 or due to the presence of aggregate and sand particles, growth patterns in such conditions are not
200 well understood. How frequently does a root deflect from their growth trajectory? What are the
201 magnitude of deflections? How does the distribution of particle forces modify the growth trajectory?
202 Understanding the forces acting on a root during the elongation requires detailed knowledge of the
203 physics of granular media. Granular media are assemblages of particles held by frictional and repulsive
204 forces from adjacent particles. The forces holding particles together form chain-like networks that
205 propagate at the contact points between neighbouring particles { ADDIN EN.CITE

206 <EndNote><Cite><Author>Mueth</Author><Year>1998</Year><RecNum>236</RecNum><DisplayT
207 ext>[16]</DisplayText><record><rec-number>236</rec-number><foreign-keys><key app="EN" db-
208 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512726253">236</key></foreign-
209 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Mueth,
210 Daniel M</author><author>Jaeger, Heinrich M</author><author>Nagel, Sidney
211 R</author></authors></contributors><titles><title>Force distribution in a granular
212 medium</title><secondary-title>Physical Review E</secondary-title></titles><periodical><full-
213 title>Physical Review E</full-title></periodical><pages>3164-
214 3169</pages><volume>57</volume><number>3</number><dates><year>1998</year></dates><url
215 s></urls></record></Cite></EndNote>}. Because particles are disordered or have various sizes and
216 shapes, large variations in magnitude and direction of particle forces arise { ADDIN EN.CITE
217 <EndNote><Cite><Author>Mueth</Author><Year>1998</Year><RecNum>236</RecNum><DisplayT
218 ext>[16,17]</DisplayText><record><rec-number>236</rec-number><foreign-keys><key app="EN"
219 db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512726253">236</key></foreign-
220 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Mueth,
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222 R</author></authors></contributors><titles><title>Force distribution in a granular
223 medium</title><secondary-title>Physical Review E</secondary-title></titles><periodical><full-
224 title>Physical Review E</full-title></periodical><pages>3164-
225 3169</pages><volume>57</volume><number>3</number><dates><year>1998</year></dates><url
226 s></urls></record></Cite><Cite><Author>Liu</Author><Year>1995</Year><RecNum>237</RecNum
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231 DA</author><author>Coppersmith, SN</author><author>Majumdar,

232 Satya</author></authors></contributors><titles><title>Force fluctuations in bead
 233 packs</title><secondary-title>Science</secondary-title></titles><periodical><full-
 234 title>Science</full-title></periodical><pages>513-
 235 515</pages><volume>269</volume><number>5223</number><dates><year>1995</year></dates>
 236 <isbn>0036-8075</isbn><urls></urls></record></Cite></EndNote>}. Early theoretical work based on
 237 dry and static monodisperse particles showed that distribution of contact forces vary greatly and the
 238 overall force distribution follows an exponential decline { ADDIN EN.CITE
 239 <EndNote><Cite><Author>Coppersmith</Author><Year>1996</Year><RecNum>186</RecNum><Dis-
 240 playText>[18,19]</DisplayText><record><rec-number>186</rec-number><foreign-keys><key
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 242 timestamp="1512053975">186</key></foreign-keys><ref-type name="Journal Article">17</ref-
 243 type><contributors><authors><author>Coppersmith, SN</author><author>Liu, C-
 244 h</author><author>Majumdar, Satya</author><author>Narayan,
 245 Onuttom</author><author>Witten, TA</author></authors></contributors><titles><title>Model for
 246 force fluctuations in bead packs</title><secondary-title>Physical Review E</secondary-
 247 title></titles><periodical><full-title>Physical Review E</full-title></periodical><pages>4673-
 248 4685</pages><volume>53</volume><number>5</number><dates><year>1996</year></dates><url
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 253 RC</author><author>Hall, SA</author><author>Andrade, JE</author><author>Wright,
 254 J</author></authors></contributors><titles><title>Quantifying interparticle forces and
 255 heterogeneity in 3D granular materials</title><secondary-title>Physical Review Letters</secondary-
 256 title></titles><periodical><full-title>Physical Review Letters</full-
 257 title></periodical><pages>098005</pages><volume>117</volume><number>9</number><dates><

258 year>2016</year></dates><urls></urls></record></Cite></EndNote>}. Particles dynamics is better
 259 understood too. Contact forces in granular media propagate through complex waves { ADDIN EN.CITE
 260 <EndNote><Cite><Author>Zhang</Author><Year>2017</Year><RecNum>61</RecNum><DisplayTex
 261 t>[20]</DisplayText><record><rec-number>61</rec-number><foreign-keys><key app="EN" db-
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 264 type><contributors><authors><author>Zhang, Lingran</author><author>Lambert,
 265 Stéphane</author><author>Nicot,
 266 François</author></authors></contributors><titles><title>Discrete dynamic modelling of the
 267 mechanical behaviour of a granular soil</title><secondary-title>International Journal of Impact
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 269 Engineering</full-title></periodical><pages>76-
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 271 >0734743X</isbn><urls></urls><electronic-resource-
 272 num>10.1016/j.ijimpeng.2017.01.009</electronic-resource-num></record></Cite></EndNote>}
 273 with appearance of macroscopic phenomenon such as clogging and arching, where particles
 274 spontaneously organise as vaults { ADDIN EN.CITE
 275 <EndNote><Cite><Author>Aranson</Author><Year>2006</Year><RecNum>191</RecNum><Display
 276 Text>[21]</DisplayText><record><rec-number>191</rec-number><foreign-keys><key app="EN" db-
 277 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" timestamp="1512054913">191</key></foreign-
 278 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Aranson,
 279 Igor S</author><author>Tsimring, Lev S</author></authors></contributors><titles><title>Patterns
 280 and collective behavior in granular media: Theoretical concepts</title><secondary-title>Reviews of
 281 Modern Physics</secondary-title></titles><periodical><full-title>Reviews of modern physics</full-
 282 title></periodical><pages>641-
 283 692</pages><volume>78</volume><number>2</number><dates><year>2006</year></dates><urls

284 ></urls></record></Cite></EndNote>}. Solid, liquid and even gaseous phases may be observed in
285 granular media depending on the external forces applied upon them { ADDIN EN.CITE
286 <EndNote><Cite><Author>Gnoli</Author><Year>2016</Year><RecNum>202</RecNum><DisplayTex
287 t>[22]</DisplayText><record><rec-number>202</rec-number><foreign-keys><key app="EN" db-
288 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512485408">202</key></foreign-
289 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Gnoli,
290 Andrea</author><author>Lasanta, Antonio</author><author>Sarracino,
291 Alessandro</author><author>Puglisi,
292 Andrea</author></authors></contributors><titles><title>Unified rheology of vibro-fluidized dry
293 granular media: From slow dense flows to fast gas-like regimes</title><secondary-title>Scientific
294 Reports</secondary-title></titles><periodical><full-title>Scientific reports</full-
295 title></periodical><pages>38604</pages><volume>6</volume><dates><year>2016</year></dates>
296 <urls></urls></record></Cite></EndNote>}. Indeed, powerful techniques and hardware are available
297 to examine theories in conditions that are nearly identical to experiments. 3D templates of the pore
298 geometry together with description of the root and anatomical details can be obtained { ADDIN
299 EN.CITE
300 <EndNote><Cite><Author>Richard</Author><Year>2003</Year><RecNum>203</RecNum><DisplayT
301 ext>[23,24]</DisplayText><record><rec-number>203</rec-number><foreign-keys><key app="EN"
302 db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512485734">203</key></foreign-
303 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Richard,
304 Patrick</author><author>Philippe, Pierre</author><author>Barbe,
305 Fabrice</author><author>Bourlès, Stéphane</author><author>Thibault,
306 Xavier</author><author>Bideau, Daniel</author></authors></contributors><titles><title>Analysis
307 by x-ray microtomography of a granular packing undergoing compaction</title><secondary-
308 title>Physical Review E</secondary-title></titles><periodical><full-title>Physical Review E</full-
309 title></periodical><pages>020301-

1</pages><volume>68</volume><number>2</number><dates><year>2003</year></dates><urls></urls></record></Cite><Cite><Author>Vlahinić</Author><Year>2013</Year><RecNum>69</RecNum><record><rec-number>69</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1511963981">69</key><key app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Vlahinić, Ivan</author><author>Andò, Edward</author><author>Viggiani, Gioacchino</author><author>Andrade, José E.</author></authors></contributors><titles><title>Towards a more accurate characterization of granular media: extracting quantitative descriptors from tomographic images</title><secondary-title>Granular Matter</secondary-title></titles><periodical><full-title>Granular Matter</full-title></periodical><pages>9-21</pages><volume>16</volume><number>1</number><section>9</section><dates><year>2013</year></dates><isbn>1434-5021
1434-7636</isbn><urls></urls><electronic-resource-num>10.1007/s10035-013-0460-6</electronic-resource-num></record></Cite></EndNote>}, and there are efficient computational techniques that exploit the power of Graphical Processing Unit to simulate roots and soil at the particle and cell resolution. Discrete Element Modelling (DEM) for example uses Newton's second law to describe the motion of millions of interacting particles { ADDIN EN.CITE <EndNote><Cite><Author>Guo</Author><Year>2015</Year><RecNum>51</RecNum><DisplayText>[25,26]</DisplayText><record><rec-number>51</rec-number><foreign-keys><key app="EN" db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1511963873">51</key><key app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Guo, Yu</author><author>Curtis, Jennifer Sinclair</author></authors></contributors><titles><title>Discrete Element Method Simulations for Complex Granular Flows</title><secondary-title>Annual Review of Fluid Mechanics</secondary-title></titles><periodical><full-title>Annual Review of Fluid Mechanics</full-

336 title</periodical><pages>21-
 337 46</pages><volume>47</volume><number>1</number><section>21</section><dates><year>2015
 338 </year></dates><isbn>0066-4189
1545-4479</isbn><urls></urls><electronic-resource-
 339 num>10.1146/annurev-fluid-010814-014644</electronic-resource-
 340 num></record></Cite><Cite><Author>Nicot</Author><Year>2017</Year><RecNum>220</RecNum>
 341 <record><rec-number>220</rec-number><foreign-keys><key app="EN" db-
 342 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512646059">220</key></foreign-
 343 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Nicot,
 344 François</author><author>Xiong, Hao</author><author>Wautier,
 345 Antoine</author><author>Lerbet, Jean</author><author>Darve,
 346 Félix</author></authors></contributors><titles><title>Force chain collapse as grain column buckling
 347 in granular materials</title><secondary-title>Granular Matter</secondary-
 348 title></titles><periodical><full-title>Granular Matter</full-
 349 title></periodical><pages>18</pages><volume>19</volume><number>2</number><dates><year>2
 350 017</year></dates><isbn>1434-5021</isbn><urls></urls></record></Cite></EndNote>}. The
 351 models reproduce closely experimental observations, even in the case of biologically complex systems
 352 with detailed quantification of the force distribution surrounding growing roots { ADDIN EN.CITE
 353 <EndNote><Cite><Author>Bourrier</Author><Year>2013</Year><RecNum>222</RecNum><Display
 354 Text>[27,28]</DisplayText><record><rec-number>222</rec-number><foreign-keys><key app="EN"
 355 db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512646513">222</key></foreign-
 356 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Bourrier,
 357 Franck</author><author>Kneib, François</author><author>Chareyre,
 358 Bruno</author><author>Fourcaud,
 359 Thierry</author></authors></contributors><titles><title>Discrete modeling of granular soils
 360 reinforcement by plant roots</title><secondary-title>Ecological Engineering</secondary-
 361 title></titles><periodical><full-title>Ecological Engineering</full-title></periodical><pages>646-

362 657</pages><volume>61</volume><dates><year>2013</year></dates><isbn>0925-
363 8574</isbn><urls></urls></record></Cite><Cite><Author>akih</Author><Year>2017</Year><RecNu
364 m>270</RecNum><record><rec-number>270</rec-number><foreign-keys><key app="EN" db-
365 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1520156221">270</key></foreign-
366 keys><ref-type name="Conference Proceedings">10</ref-
367 type><contributors><authors><author>Fakih, Mahmoud</author><author>Delenne, Jean
368 Yves</author><author>Radjai, Farhang</author><author>Fourcaud,
369 Thierry</author></authors></contributors><titles><title>Modeling root growth in granular soils:
370 effects of root stiffness and packing fraction</title><secondary-title>EPJ Web of
371 Conferences</secondary-title></titles><periodical><full-title>EPJ Web of Conferences</full-
372 title></periodical><pages>14013</pages><volume>140</volume><dates><year>2017</year></dat
373 es><publisher>EDP Sciences</publisher><isbn>2100-
374 014X</isbn><urls></urls></record></Cite></EndNote>}.
375
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Despite recent experimental and theoretical breakthroughs, granular matter physics has not
transformed our understanding of the mechanics of root growth. Many current limitations are due to
our lack of understanding of how roots respond to complex mechanical signals, and particularly how
competition between multiple mechanical stimuli affects root responses. Cellular mechanisms
involved in the response to physical obstacles have not been fully characterised, but a growing number
of studies are now revealing the signalling and regulatory mechanisms involved in plant responses to
mechanical force. Research in animal sciences have identified a multitude of proteins which binding
domains are modified by mechanical forces { ADDIN EN.CITE
<EndNote><Cite><Author>Iskratsch</Author><Year>2014</Year><RecNum>269</RecNum><Display
Text>[29]</DisplayText><record><rec-number>269</rec-number><foreign-keys><key app="EN" db-
id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1519223480">269</key></foreign-
keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Iskratsch,
Thomas</author><author>Wolfenson, Haguy</author><author>Sheetz, Michael

P</author></authors></contributors><titles><title>Appreciating force and shape—the rise of
 mechanotransduction in cell biology</title><secondary-title>Nature Reviews Molecular Cell
 Biology</secondary-title></titles><periodical><full-title>Nature Reviews Molecular Cell Biology</full-
 title></periodical><pages>825</pages><volume>15</volume><number>12</number><dates><year
 >2014</year></dates><isbn>1471-0080</isbn><urls></urls></record></Cite></EndNote>} and their
 discovery in plants may follow. Large families of mechanosensitive ion channels have been identify in
 plants { ADDIN EN.CITE
 <EndNote><Cite><Author>Hamilton</Author><Year>2015</Year><RecNum>240</RecNum><Displa
 yText>[30]</DisplayText><record><rec-number>240</rec-number><foreign-keys><key app="EN"
 db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" timestamp="1512938828">240</key></foreign-
 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Hamilton,
 Eric S</author><author>Schlegel, Angela M</author><author>Haswell, Elizabeth
 S</author></authors></contributors><titles><title>United in diversity: mechanosensitive ion
 channels in plants</title><secondary-title>Annual Review of Plant Biology</secondary-
 title></titles><periodical><full-title>Annual review of plant biology</full-
 title></periodical><pages>113-
 137</pages><volume>66</volume><dates><year>2015</year></dates><isbn>1543-
 5008</isbn><urls></urls></record></Cite></EndNote>}, with for example MCA calcium
 mechanosensitive channels being linked to growth response to hard gel layers { ADDIN EN.CITE
 <EndNote><Cite><Author>Nakagawa</Author><Year>2007</Year><RecNum>268</RecNum><Displ
 ayText>[31]</DisplayText><record><rec-number>268</rec-number><foreign-keys><key app="EN"
 db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" timestamp="1519213479">268</key></foreign-
 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Nakagawa,
 Yuko</author><author>Katagiri, Takeshi</author><author>Shinozaki, Kazuo</author><author>Qi,
 Zhi</author><author>Tatsumi, Hitoshi</author><author>Furuichi,
 Takuya</author><author>Kishigami, Akio</author><author>Sokabe,

414 Masahiro</author><author>Kojima, Itaru</author><author>Sato,
 415 Shusei</author></authors></contributors><titles><title>Arabidopsis plasma membrane protein
 416 crucial for Ca²⁺ influx and touch sensing in roots</title><secondary-title>Proceedings of the National
 417 Academy of Sciences</secondary-title></titles><periodical><full-title>Proceedings of the National
 418 Academy of Sciences</full-title></periodical><pages>3639-
 419 3644</pages><volume>104</volume><number>9</number><dates><year>2007</year></dates><is-
 420 bn>0027-8424</isbn><urls></urls></record></Cite></EndNote>}. Adaptation to mechanical forces
 421 are also well characterised, including the changes in cell division patterns, growth direction, cell
 422 differentiation and gene expression { ADDIN EN.CITE
 423 <EndNote><Cite><Author>Mirabet</Author><Year>2011</Year><RecNum>262</RecNum><Display
 424 Text>[32]</DisplayText><record><rec-number>262</rec-number><foreign-keys><key app="EN" db-
 425 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1518712800">262</key></foreign-
 426 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Mirabet,
 427 Vincent</author><author>Das, Pradeep</author><author>Boudaoud,
 428 Arezki</author><author>Hamant, Olivier</author></authors></contributors><titles><title>The role
 429 of mechanical forces in plant morphogenesis</title><secondary-title>Annual review of plant
 430 biology</secondary-title></titles><periodical><full-title>Annual review of plant biology</full-
 431 title></periodical><pages>365-
 432 385</pages><volume>62</volume><dates><year>2011</year></dates><isbn>1543-
 433 5008</isbn><urls></urls></record></Cite></EndNote>}
 434 A main difficulty, however, is to understand the nature of the mechanical signals perceived from the
 435 soil particles surrounding plant roots. It is central to develop capabilities to study not only the forces
 436 and displacement produced in the root soil system, but also the biological responses due to
 437 mechanical interactions with soil particles. Unfortunately, experimenting with natural soils is
 438 challenging because of its opacity. Rhizotron systems have been an extremely powerful tool to study
 439 root growth { ADDIN EN.CITE { ADDIN EN.CITE.DATA }}, glass interfaces introduce strong border effects

440 and observations of biomechanical processes are often biased. X-ray imaging allows visualisation of
441 interactions between roots and soil particles *in situ* in high resolution { ADDIN EN.CITE
442 <EndNote><Cite><Author>Mooney</Author><Year>2012</Year><RecNum>238</RecNum><Display
443 Text>[35]</DisplayText><record><rec-number>238</rec-number><foreign-keys><key app="EN" db-
444 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512727537">238</key></foreign-
445 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Mooney,
446 Sacha J</author><author>Pridmore, Tony P</author><author>Helliwell,
447 Jonathan</author><author>Bennett, Malcolm
448 J</author></authors></contributors><titles><title>Developing X-ray computed tomography to non-
449 invasively image 3-D root systems architecture in soil</title><secondary-title>Plant and
450 soil</secondary-title></titles><periodical><full-title>Plant and Soil</full-
451 title></periodical><pages>1-22</pages><volume>352</volume><number>1-
452 2</number><dates><year>2012</year></dates><isbn>0032-
453 079X</isbn><urls></urls></record></Cite></EndNote>}. The technique allows time-lapse imaging for
454 several weeks of growth. Improved images can be obtained with the application of contrasting agents.
455 For example, iodine perfused into plant leaves revealed the vascular structures of the roots and
456 rhizobial nodules { ADDIN EN.CITE
457 <EndNote><Cite><Author>Keyes</Author><Year>2017</Year><RecNum>125</RecNum><DisplayTe
458 xt>[36]</DisplayText><record><rec-number>125</rec-number><foreign-keys><key app="EN" db-
459 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1511964225">125</key><key
460 app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-
461 type><contributors><authors><author>Keyes, S. D.</author><author>Gostling, N.
462 J.</author><author>Cheung, J. H.</author><author>Roose, T.</author><author>Sinclair,
463 I.</author><author>Marchant, A.</author></authors></contributors><auth-address>2The Faculty
464 of Engineering and the Environment,The University of Southampton,Southampton,SO17
465 1BJ,UK.
1The Centre for Biological Sciences,The University of Southampton,Southampton,SO17

1BJ,UK.</auth-address><titles><title>The Application of Contrast Media for In Vivo Feature
Enhancement in X-Ray Computed Tomography of Soil-Grown Plant Roots</title><secondary-
title>Microscopy and Microanalysis</secondary-title></titles><periodical><full-title>Microscopy and
Microanalysis</full-title></periodical><pages>538-
552</pages><volume>23</volume><number>3</number><edition>2017/03/23</edition><keyword
s><keyword>X-ray computed tomography</keyword><keyword>contrast
agents</keyword><keyword>imaging</keyword><keyword>plant
roots</keyword></keywords><dates><year>2017</year><pub-dates><date>Jun</date></pub-
dates></dates><isbn>1435-8115 (Electronic)
1431-9276 (Linking)</isbn><accession-
num>28320487</accession-num><urls><related-
urls><url>https://www.ncbi.nlm.nih.gov/pubmed/28320487</url></related-urls></urls><electronic-
resource-num>10.1017/S1431927617000319</electronic-resource-
num></record></Cite></EndNote>}. Root hairs can be resolved using synchrotron sources with
resolution of up to 5µm and at temporal resolution sufficient for tracking particle movement due to
root growth { ADDIN EN.CITE
<EndNote><Cite><Author>Keyes</Author><Year>2017</Year><RecNum>223</RecNum><DisplayTe
xt>[37]</DisplayText><record><rec-number>223</rec-number><foreign-keys><key app="EN" db-
id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512646619">223</key></foreign-
keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Keyes,
SD</author><author>Cooper, Laura</author><author>Duncan, S</author><author>Koebernick,
N</author><author>Fletcher, DM McKay</author><author>Scotson, CP</author><author>Van
Veelen, Arjen</author><author>Sinclair, Ian</author><author>Roose,
Tiina</author></authors></contributors><titles><title>Measurement of micro-scale soil
deformation around roots using four-dimensional synchrotron tomography and image
correlation</title><secondary-title>Journal of The Royal Society Interface</secondary-
title></titles><periodical><full-title>Journal of The Royal Society Interface</full-

492 title</periodical><pages>20170560</pages><volume>14</volume><number>136</number><date
493 s><year>2017</year></dates><isbn>1742-5689</isbn><urls></urls></record></Cite></EndNote>}.
494 However, X-ray is an ionising radiation that affects biological processes especially meristematic
495 regions where high cell division rates occurs { ADDIN EN.CITE <EndNote><Cite><Author>De
496 Micco</Author><Year>2011</Year><RecNum>239</RecNum><DisplayText>[38]</DisplayText><rec
497 ord><rec-number>239</rec-number><foreign-keys><key app="EN" db-
498 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512729900">239</key></foreign-
499 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>De Micco,
500 Veronica</author><author>Arena, Carmen</author><author>Pignalosa,
501 Diana</author><author>Durante, Marco</author></authors></contributors><titles><title>Effects of
502 sparsely and densely ionizing radiation on plants</title><secondary-title>Radiation and
503 Environmental Biophysics</secondary-title></titles><periodical><full-title>Radiation and
504 Environmental Biophysics</full-title></periodical><pages>1-
505 19</pages><volume>50</volume><number>1</number><dates><year>2011</year></dates><isbn>
506 0301-634X</isbn><urls></urls></record></Cite></EndNote>}, and despite the increase in
507 resolutions, details of the inner cellular processes and biochemical activity have remained invisible {
508 ADDIN EN.CITE { ADDIN EN.CITE.DATA }}.

509 Optics and microscopy in the visible range have thus remained the preferred approach to make
510 observation of the biology and mechanics of the root. Confocal Laser Scanning Microscopes (CLSM)
511 have provided the first live images of root-particle interaction in high resolution with details available
512 on contact with particle surface, anatomical features at cell resolution and gene expression { ADDIN
513 EN.CITE { ADDIN EN.CITE.DATA }}. FRET imaging now allows tension sensors to record molecular forces
514 at the piconewton scale { ADDIN EN.CITE
515 <EndNote><Cite><Author>Cost</Author><Year>2015</Year><RecNum>263</RecNum><DisplayText
516 >[43]</DisplayText><record><rec-number>263</rec-number><foreign-keys><key app="EN" db-
517 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1518798628">263</key></foreign-

518 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Cost, Anna-
 519 Lena</author><author>Ringer, Pia</author><author>Chrostek-Grashoff,
 520 Anna</author><author>Grashoff, Carsten</author></authors></contributors><titles><title>How to
 521 measure molecular forces in cells: a guide to evaluating genetically-encoded FRET-based tension
 522 sensors</title><secondary-title>Cellular and molecular bioengineering</secondary-
 523 title></titles><periodical><full-title>Cellular and molecular bioengineering</full-
 524 title></periodical><pages>96-
 525 105</pages><volume>8</volume><number>1</number><dates><year>2015</year></dates><isbn>
 526 1865-5025</isbn><urls></urls></record></Cite></EndNote>}. However, CLSM has proved limited for
 527 long observations due to photo toxicity and photo bleaching. Because of the confined environment of
 528 the microscope, it has also remained limited to small plant samples. The field is now turning to
 529 different types of microscopes. Light Sheet Microscopy (LSM), in particular, has drastically reduced
 530 the light doses to the samples { ADDIN EN.CITE
 531 <EndNote><Cite><Author>Reynaud</Author><Year>2008</Year><RecNum>155</RecNum><Display
 532 Text>[44]</DisplayText><record><rec-number>155</rec-number><foreign-keys><key app="EN" db-
 533 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512050719">155</key><key
 534 app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-
 535 type><contributors><authors><author>Reynaud, E. G.</author><author>Krzic,
 536 U.</author><author>Greger, K.</author><author>Stelzer, E.
 537 H.</author></authors></contributors><auth-address>Cell Biology and Biophysics Unit, European
 538 Molecular Biology Laboratory (EMBL), Meyerhofstrasse 1, D-69117 Heidelberg, Germany.</auth-
 539 address><titles><title>Light sheet-based fluorescence microscopy: more dimensions, more photons,
 540 and less photodamage</title><secondary-title>HFSP Journal</secondary-
 541 title></titles><periodical><full-title>HFSP journal</full-title></periodical><pages>266-
 542 75</pages><volume>2</volume><number>5</number><edition>2009/05/01</edition><dates><ye
 543 ar>2008</year><pub-dates><date>Oct</date></pub-dates></dates><isbn>1955-2068

544 (Print)
1955-205X (Linking)</isbn><accession-num>19404438</accession-num><urls><related-
 545 urls><url>https://www.ncbi.nlm.nih.gov/pubmed/19404438</url></related-
 546 urls></urls><custom2>PMC2639947</custom2><electronic-resource-
 547 num>10.2976/1.2974980</electronic-resource-num></record></Cite></EndNote>}. Illumination of
 548 the sample is planar and achieved orthogonal to the detection so that 2D images are generated
 549 instantaneously often using the new generation of scientific-CMOS cameras. By taking a whole 2D
 550 section in one "shot", volume scanning is accelerated, enabling small and fast developmental events
 551 to be tracked during development. The technique has considerably advanced our ability to observe
 552 living organisms both live and *in situ* with, for example, the ability to track cell growth, movement and
 553 divisions of entire embryos { ADDIN EN.CITE
 554 <EndNote><Cite><Author>Rozbicki</Author><Year>2015</Year><RecNum>250</RecNum><Display
 555 Text>[45]</DisplayText><record><rec-number>250</rec-number><foreign-keys><key app="EN" db-
 556 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1513156281">250</key></foreign-
 557 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Rozbicki,
 558 Emil</author><author>Chuai, Manli</author><author>Karjalainen, Antti I</author><author>Song,
 559 Feifei</author><author>Sang, Helen M</author><author>Martin, René</author><author>Knölker,
 560 Hans-Joachim</author><author>MacDonald, Michael P</author><author>Weijer, Cornelis
 561 J</author></authors></contributors><titles><title>Myosin II-mediated cell shape changes and cell
 562 intercalation contribute to primitive streak formation</title><secondary-title>Nature Cell
 563 Biology</secondary-title></titles><periodical><full-title>Nature cell biology</full-
 564 title></periodical><pages>397</pages><volume>17</volume><number>4</number><dates><year>
 565 2015</year></dates><urls></urls></record></Cite></EndNote>} or capturing the beating of a living
 566 heart { ADDIN EN.CITE
 567 <EndNote><Cite><Author>Mickoleit</Author><Year>2014</Year><RecNum>213</RecNum><Displa
 568 yText>[46]</DisplayText><record><rec-number>213</rec-number><foreign-keys><key app="EN"
 569 db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512555423">213</key></foreign-

570 keys<ref-type name="Journal Article">17</ref-type><contributors><authors><author>Mickoleit,
 571 Michaela</author><author>Schmid, Benjamin</author><author>Weber,
 572 Michael</author><author>Fahrbach, Florian O</author><author>Hombach,
 573 Sonja</author><author>Reischauer, Sven</author><author>Huiskens,
 574 Jan</author></authors></contributors><titles><title>High-resolution reconstruction of the beating
 575 zebrafish heart</title><secondary-title>Nature Methods</secondary-title></titles><periodical><full-
 576 title>Nature methods</full-title></periodical><pages>919-
 577 922</pages><volume>11</volume><number>9</number><dates><year>2014</year></dates><isbn
 578 >1548-7091</isbn><urls></urls></record></Cite></EndNote>}. Because axial resolution in light sheet
 579 systems is not dependent upon high numerical aperture imaging objectives, they allow larger fields of
 580 view and can easily accommodate microcosms and instruments for maintaining healthy growth
 581 conditions { ADDIN EN.CITE
 582 <EndNote><Cite><Author>Reynaud</Author><Year>2015</Year><RecNum>214</RecNum><Display
 583 Text>[47]</DisplayText><record><rec-number>214</rec-number><foreign-keys><key app="EN" db-
 584 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1512555979">214</key></foreign-
 585 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Reynaud,
 586 Emmanuel G</author><author>Peychl, Jan</author><author>Huiskens,
 587 Jan</author><author>Tomancak, Pavel</author></authors></contributors><titles><title>Guide to
 588 light-sheet microscopy for adventurous biologists</title><secondary-title>Nature
 589 Methods</secondary-title></titles><periodical><full-title>Nature methods</full-
 590 title></periodical><pages>30-
 591 34</pages><volume>12</volume><number>1</number><dates><year>2015</year></dates><isbn>
 592 1548-7091</isbn><urls></urls></record></Cite></EndNote>}. Details of the morphology and
 593 anatomy of tissues can be obtained without the use of markers { ADDIN EN.CITE { ADDIN EN.CITE.DATA
 594 }} and recently dynamic light scattering (biospeckle) has been used to enhance image contrast { ADDIN
 595 EN.CITE

596 <EndNote><Cite><Author>O'Callaghan</Author><Year>2018</Year><RecNum>247</RecNum><Dis
 597 playText>[50]</DisplayText><record><rec-number>247</rec-number><foreign-keys><key app="EN"
 598 db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstsz" timestamp="1513086523">247</key></foreign-
 599 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>O'Callaghan,
 600 Felicity E </author><author>Braga, Roberto A </author><author>Neilson,
 601 Roy</author><author>MacFarlane, Stuart A </author><author>Dupuy, Lionel
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 603 interactions in the rhizosphere</title><secondary-title>Scientific Reports</secondary-
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 605 title></periodical><pages>1440</pages><volume>8</volume><dates><year>2018</year></dates><
 606 urls></urls></record></Cite></EndNote>}. Light sheet imaging has also been used in granular matter
 607 physics for a long time, although its application to root and soil is just emerging { ADDIN EN.CITE {
 608 ADDIN EN.CITE.DATA }}.
 609 Optics and microscopy also provides many ways to control and measure mechanical forces. Laser
 610 ablation for example, has long been used to understand the distribution of forces within a tissue {
 611 ADDIN EN.CITE
 612 <EndNote><Cite><Author>Sampathkumar</Author><Year>2014</Year><RecNum>242</RecNum><
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 618 Pascale</author><author>Berquand, Alexandre</author><author>Boudaoud,
 619 Arezki</author><author>Hamant, Olivier</author><author>Jönsson,
 620 Henrik</author><author>Meyerowitz, Elliot
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><isbn>2050-084X</isbn><urls></urls></record></Cite></EndNote>}, whilst optical trapping has
been used to apply small localised forces { ADDIN EN.CITE
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title>Protein Science</full-title></periodical><dates><year>2017</year></dates><isbn>1469-
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establishing the nature of the chains of forces and how they propagate within a granular medium {
ADDIN EN.CITE
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 650 505-2014</electronic-resource-num></record></Cite></EndNote>}. { ADDIN EN.CITE <EndNote><Cite
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 655 type><contributors><authors><author>Kolb, Evelyne</author><author>Hartmann,
 656 Christian</author><author>Genet, Patricia</author></authors></contributors><titles><title>Radial
 657 force development during root growth measured by photoelasticity</title><secondary-title>Plant and
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1573-
 661 5036</isbn><urls></urls><electronic-resource-num>10.1007/s11104-012-1316-2</electronic-
 662 resource-num></record></Cite></EndNote>} used photoelasticity to characterise the forces created
 663 by root growth within a pore, and { ADDIN EN.CITE <EndNote><Cite
 664 AuthorYear="1"><Author>Wendell</Author><Year>2011</Year><RecNum>36</RecNum><DisplayT
 665 ext>Wendell, et al. [57]</DisplayText><record><rec-number>36</rec-number><foreign-keys><key
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 668 D.M.</author><author>Luginbuhl, K.</author><author>Guerrero, J.</author><author>Hosoi,
 669 A.E.</author></authors></contributors><titles><title>Experimental Investigation of Plant Root
 670 Growth Through Granular Substrates</title><secondary-title>Experimental Mechanics</secondary-
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 672 949</pages><volume>52</volume><number>7</number><section>945</section><dates><year>20
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num>10.1007/s11340-011-9569-x</electronic-resource-num></record></Cite></EndNote> } have
 successfully created a granular medium using a photo elastic media where maximum growth forces
 and avoidance mechanisms could be observed (Figure 1B). New cantilever-based optical sensors {
 ADDIN EN.CITE { ADDIN EN.CITE.DATA }} have also been developed to measure simultaneously growth
 forces generated by a root and three-dimensional strain rate in responses to changes in external forces
 applied to the root. { ADDIN EN.CITE { ADDIN EN.CITE.DATA }} for example, obtained stereoscopic data
 to decompose root response to axial mechanical forces into different phases (Figure 1C). Hydrogels
 can also be combined with fluorescent dyes and light sheet imaging to reconstruct interparticle forces
 within the granular medium { ADDIN EN.CITE
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 Department of Physics, Duke University, Physics Building, Science Drive, Box 90305, Durham, North
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 Sud-Ouest, 200 avenue de la Vieille Tour, 33405 Talence, France.
1] Department of Physics, Duke
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 Laboratory of Physical Chemistry and Colloid Science, Wageningen University, PO Box 8038, 6700EK
 Wageningen, The Netherlands.
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 704 urls></urls><custom2>PMC4366509</custom2><electronic-resource-
 705 num>10.1038/ncomms7361</electronic-resource-num></record></Cite></EndNote>}.
 706 Techniques for mimicking soil physical conditions under a microscope are also emerging rapidly.
 707 Transparent artificial media based on fluoropolymers that can mimic soil properties have been
 708 developed { ADDIN EN.CITE
 709 <EndNote><Cite><Author>Downie</Author><Year>2012</Year><RecNum>126</RecNum><DisplayT
 710 ext>[42]</DisplayText><record><rec-number>126</rec-number><foreign-keys><key app="EN" db-
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 723 development/microbiology</keyword><keyword>Refractometry</keyword><keyword>*Rhizospher
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 urls></urls><custom2>PMC3439476</custom2><electronic-resource-
 num>10.1371/journal.pone.0044276</electronic-resource-num></record></Cite></EndNote>}. The
 media reproduces the physical and chemical properties of soil through control of the distribution of
 sizes and surface chemistry of the particles (Figure 1D). Because the particles are made of
 fluoropolymers that have refractive index close to water, only small adjustment of refractive indices,
 usually by adding a colloid to the nutrient solution, allows light to travel without refraction through
 the substrate. Microfluidics techniques have also progressed significantly and are becoming suitable
 to live and high resolution microscopy of roots and microbes { ADDIN EN.CITE { ADDIN EN.CITE.DATA
 }}. Microfluidics allows precise and repeatable control of liquids and this could be used, for example,
 to control water tension and particle cohesion in soil during live experiments. The range of materials
 and fabrication techniques has been considerably expanded with the use of 3D printing { ADDIN
 EN.CITE
 <EndNote><Cite><Author>Kitson</Author><Year>2012</Year><RecNum>216</RecNum><DisplayTe
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 1858</pages><volume>9</volume><number>13</number><dates><year>2009</year></dates><url
 s></urls></record></Cite></EndNote>}. It has been possible, for example, to produce chambers with
 physical heterogeneity, physical barriers and chemical gradients, with direct applications to root and
 soil studies { ADDIN EN.CITE { ADDIN EN.CITE.DATA } } .
 The scientific community is better equipped than ever to make observations on the micromechanics
 of root development in soil. Experimental systems provide soil-like growth conditions and allow for

805 observations, measurements and data generation with precision, accuracy and resolution. How then
806 to transform the amount of information available to us into scientific breakthrough? The complexity
807 of the root-particle interactions is a major challenge. At each growth step, a root is in contact with a
808 new arrangement of particles that apply forces of varying magnitudes and orientations. Because there
809 are countless numbers of possible arrangements, the forces applied on roots cannot be
810 experimentally controlled. Measurements of granular forces *in situ* is required (Figure 2.1), and
811 granular media physicist have achieved such measurements. There are now great opportunities to
812 combine current knowledge of soil micromechanics with mechanobiology and propose a mechanistic
813 framework that account for sensing and response to micro-scale heterogeneity (Figure 2.2). New
814 theories must be developed to embrace stochasticity and explain responses to multiple mechanical
815 stimuli (Figure 2.3-4). Major challenges remain, but a recent look at the literature indicates our
816 thinking is evolving in the right way.

818

819 Figure 1: Growing roots interact mechanically with soil particles during growth. These interactions
 820 influence the morphology of the root, and the dynamics of development of the root system. A)
 821 Irregular growth of cortex cells is observed in hard or compacted soil { ADDIN EN.CITE
 822 <EndNote><Cite><Author>Lipiec</Author><Year>2012</Year><RecNum>243</RecNum><Prefix>left
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 831 81</pages><volume>121</volume><dates><year>2012</year></dates><isbn>0167-
 832 1987</isbn><urls></urls></record></Cite></EndNote>}. Resistance from the soil particles causes

834 root diameter to increase and the root tip to buckle and bend towards the path of least resistance
835 (middle, lentils roots grown at 2MPa confining pressure). At the scale of the root system, interactions
836 causes growth trajectories to be stochastic as observed here on *Anthyllis vulneraria* grown on landslide
837 soils (image courtesy Loïc Pagès). Technological developments now allow precise characterisation of
838 mechanical interactions between a root and the growth substrate. These include for example, B)
839 photoelastic discs for measurement of growth forces in soil pores { ADDIN EN.CITE
840 <EndNote><Cite><Author>Kolb</Author><Year>2012</Year><RecNum>40</RecNum><DisplayText>
841 [56]</DisplayText><record><rec-number>40</rec-number><foreign-keys><key app="EN" db-
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845 Christian</author><author>Genet, Patricia</author></authors></contributors><titles><title>Radial
846 force development during root growth measured by photoelasticity</title><secondary-title>Plant and
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849 2</number><section>19</section><dates><year>2012</year></dates><isbn>0032-079X
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850 5036</isbn><urls></urls><electronic-resource-num>10.1007/s11104-012-1316-2</electronic-
851 resource-num></record></Cite></EndNote>} (images courtesy Evelyne Kolb), C) root growing on a
852 cantilever sensor for measuring growth forces { ADDIN EN.CITE { ADDIN EN.CITE.DATA }}, D)
853 transparent soil substrates that provide the physical structure of soil with the ability to carry out 3D
854 live imaging { ADDIN EN.CITE
855 <EndNote><Cite><Author>O'Callaghan</Author><Year>2018</Year><RecNum>247</RecNum><Dis
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 864 title></periodical><pages>1440</pages><volume>8</volume><dates><year>2018</year></dates><
 865 urls></urls></record></Cite></EndNote>}, E) Dual flow microfluidic systems with microscale both
 866 physical and nutrient heterogeneity { ADDIN EN.CITE
 867 <EndNote><Cite><Author>Stanley</Author><Year>2018</Year><RecNum>261</RecNum><DisplayT
 868 ext>[68]</DisplayText><record><rec-number>261</rec-number><foreign-keys><key app="EN" db-
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 875 physiological and genetic levels</title><secondary-title>New Phytologist</secondary-
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 878 bn>1469-8137</isbn><urls></urls></record></Cite></EndNote>} and F) discrete element modelling
 879 for testing root responses to interactions with granular media { ADDIN EN.CITE
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 884 type><contributors><authors><author>Fakih, Mahmoud</author><author>Delenne, Jean
 885 Yves</author><author>Radjai, Farhang</author><author>Fourcaud,

Thierry

effects of root stiffness and packing fraction

Conferences

title

pages14013

volume140

dates

year2017

publisherEDP Sciences

isbn2100-014X

(image courtesy Mahmoud Fakih).

Box 1: Root primary growth is a local process where elongation of tissues is taking place at the root tip. Soil heterogeneity influences strongly how the tissue elongates and deforms (top), and local interactions taking place at the tip can have drastic effects on the morphology and development of the

898 whole root system, and the resources available to the plant (bottom). Mathematical modelling
899 provides a useful framework to explain how heterogeneity can affect the morphology of the root
900 system.

901 (A) When roots grow in soil particles which representative volume is small compared to the diameter
902 of the roots, the action of the particles can be averaged (top). In such conditions, it is unlikely for a
903 plant to perceive the fluctuations of forces from individual particles. If the mechanical resistance of the
904 soil is not limiting, root trajectories follow smooth streamlines (bottom). Mathematically, this
905 phenomenon has been described as the convection of root tips (density ρ) { ADDIN EN.CITE
906 <EndNote><Cite><Author>Kalogiros</Author><Year>2016</Year><RecNum>241</RecNum><Display
907 Text>[70]</DisplayText><record><rec-number>241</rec-number><foreign-keys><key app="EN" db-
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909 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Kalogiros,
910 Dimitris I</author><author>Adu, Michael O</author><author>White, Philip
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917 1058</pages><volume>67</volume><number>4</number><dates><year>2016</year></dates><isb
918 n>0022-0957</isbn><urls></urls></record></Cite></EndNote>}. The growth velocity E (cm.d^{-1}) and
919 the rate of change in root angle due to gravitropism g (d^{-1}) define the growth of the root system:

920
$$\partial_t \rho + \nabla \cdot \mathbf{F} + \partial_\theta g \rho = 0,$$

921 with $\mathbf{F} = \rho E (\cos(\theta) + \sin(\theta))$ is the spatial flux of root tips and $g \rho$ is the angular flux of roots. In this
922 case, growth and resource acquisition is optimal.

(B) When soil elements cannot be displaced, in the case of stones and rock for example, the root adopts avoidance behaviours. Optimal growth is not affected and remains similar to (A), until the obstacle is reached. Heterogeneities in this case define the boundaries within which convective growth is taking place. Using the same mathematical framework, presence of such boundaries can be modelled through boundary conditions, for example

$$\partial_n \rho = 0.$$

Large scale soil heterogeneities can be problematic because they may restrain access to pools of resources, e.g. deep water, even though the root growth in most parts of the soil domain is unaffected. They may also form paths of least growth resistance, for example in the case of pores and cracks.

(C) Intermediate cases are more problematic to analyse. Roots are in contact with particles which apply forces of varying magnitudes and orientation. Although the root may overcome these forces, a single particle may be able to deflect the growth trajectory. Since particles have inhomogeneous distribution, root deflection occurs stochastically. Mathematically, the phenomenon can be described by a convection, where the growth velocity v (cm.d⁻¹) and the rate of change in root angle due to gravitropism g (d⁻¹) and random fluctuations define the dynamics:

$$\partial_t \rho + \nabla \cdot \mathbf{F} + \partial_\theta (g\rho + D\partial_\theta \rho) = 0,$$

$g\rho + D\partial_\theta \rho$ the angular flux of roots. The parameter D is the angular diffusion coefficient. Because D relates to the probability of roots to be deflected by a particle, and the magnitude of such deflection, there is a direct link between micro-mechanics of root particle interactions and the morphology of the root system. Diffusive growth makes root trajectories irregular, and limits the expansion of the root system, even when the elongation rate is not affected. Mathematical analysis of equation 3 reveals the conditions for which transitions from convective growth to diffusive growth occur, i.e. for Peclet number $Pe = \frac{g}{D} \ll 1$.

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Figure 2: Dissecting the complexity of root particles mechanical interactions requires an elaborate research strategy. (1) First step is to better understand the nature of the forces applied to a root. This can be achieved, using photo elastic beads, imaging, or developing artificial roots equipped with sensors

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962 plant-inspired robot with soft differential bending capabilities</title><secondary-title>Bioinspiration
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 966 ear>2016</year></dates><isbn>1748-3190</isbn><urls></urls></record></Cite></EndNote>}, but
 967 also by revisiting older techniques, for example by analysing micro penetrometer test and exploit force
 968 fluctuations { ADDIN EN.CITE
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 977 271</pages><volume>16</volume><number>3</number><dates><year>1990</year></dates><isbn
 978 >0167-1987</isbn><urls></urls></record></Cite></EndNote>}. (2) In the second step, it is essential
 979 to characterise how these forces (orange arrows) are perceived by plant roots. This could be achieved
 980 using e.g. modern LSM microscopes, artificial soils, calcium or FRET tension sensors to inform on the
 981 perception of forces induced by heterogeneous media { ADDIN EN.CITE
 982 <EndNote><Cite><Author>Monshausen</Author><Year>2012</Year><RecNum>254</RecNum><Dis
 983 playText>[73]</DisplayText><record><rec-number>254</rec-number><foreign-keys><key app="EN"
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991 682</pages><volume>15</volume><number>6</number><dates><year>2012</year></dates><isbn
992 >1369-5266</isbn><urls></urls></record></Cite></EndNote>}. (3) Finally, the mechanism of
993 response to complex distribution of forces must be characterised. In this case, responses can be
994 studied on simplified systems where position and magnitude of forces can be controlled accurately,
995 using lab-on-chip device and more traditional developmental biology approaches. Experiments and
996 data can then be used to formulate and test new concepts and biomechanical theories (black arrows).
997 Computational models can test biomechanical theories in most realistic conditions using latest
998 technologies, e.g. particle based simulations and computer hardware (4) and influence the design of
999 new experiments (grey arrows).

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Acknowledgements

This work was supported by the consolidator fellowship from the European Research Council ERC SENSOILS-647857. We also thank the colleagues from the RoSoM project for inspiring discussions on root biomechanics and discrete element modelling (Agropolis Fondation ID 1202-073; LabexAgro: ANR-10-LABX- 001-01).

Publication Highlight

9. Bengough AG, Loades K, McKenzie BM: **Root hairs aid soil penetration by anchoring the root surface to pore walls.** *Journal of Experimental Botany* 2016, **67**:1071-1078.

This paper demonstrates that penetration of granular media uses root hair cells to anchor the base of the root while the tip of the root is moving and expanding. The study provides experimental evidence that root microscopic traits play an important role in mechanical interactions with the granular media.

10. Colombi T, Kirchgessner N, Walter A, Keller T: **Root tip shape governs root elongation rate under increased soil strength.** *Plant Physiology* 2017, **174**:2289-2301.

This study illustrates the role of the morphology of the root tip in the penetration of hard soil. The angle of the root tip, more than the diameter itself, is found to be the trait that segregates for ability to overcome mechanical resistance from soil in a set of wheat genotypes.

11. Kolb E, Legue V, Bogeat-Triboulot M-B: **Physical root-soil interactions.** *Physical Biology* 2017, **14**:065004.

This paper provides an overview of the physics of root soil interactions. The study classifies the main biomechanical processes of growth, namely axial elongation, thickening and reorientation, and it details the basic principles that control their magnitude and occurrence in a soil.

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1027 19. Hurley R, Hall S, Andrade J, Wright J: **Quantifying interparticle forces and heterogeneity in 3D**
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1038 work also presents interesting preliminary results showing factors that contribute to the stability of
1039 root trajectories and the nature of particle forces that develop in response to growth.

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1041 30. Hamilton ES, Schlegel AM, Haswell ES: **United in diversity: mechanosensitive ion channels in**
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1046 37. Keyes S, Cooper L, Duncan S, Koebernick N, Fletcher DM, Scotson C, Van Veelen A, Sinclair I,
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This paper exposes state of the art approaches to track plant growth and particle movement in soil. The study combines synchrotron based X-Ray tomography with image correlation to estimate soil displacement around the root.

44. Reynaud EG, Peychl J, Huisken J, Tomancak P: **Guide to light-sheet microscopy for adventurous biologists**. *Nature Methods* 2015, **12**:30-34.

This is an introduction to light-sheet microscopy for beginners. It covers aspects related to basic principles, existing commercial device, and data generation and handling process.

50. O'Callaghan FE, Braga RA, Neilson R, MacFarlane SA, Dupuy LX: **New live screening of plant-nematode interactions in the rhizosphere**. *Scientific Reports* 2018, **8**:1440

This study demonstrates the use of transparent soil and light sheet microscopy to study root-particle-nematode interactions. The paper combines dynamic speckle and light sheet imaging to enhance the contrast of microscopic worms without the need for fluorescent labelling.

59. Bizet F, Bengough AG, Hummel I, Bogeat-Triboulot MB, Dupuy LX: **3D deformation field in growing plant roots reveals both mechanical and biological responses to axial mechanical forces**. *Journal of Experimental Botany* 2016, **67**:5605-5614.

This study presents the development of cantilever based mechanical sensor to assess growth forces of a root on an obstacle simultaneously with quantification of the elongation of the root tissue. The study uses stereoscopic reconstruction to determine growth responses in 3 dimensions.

60. Brodu N, Dijksman JA, Behringer RP: **Spanning the scales of granular materials through microscopic force imaging**. *Nature Communication* 2015, **6**:6361.

This study demonstrates how measurement of particle forces can be achieved in a light sheet imaging set up. The experimental system consists of deformable beads in a refractive index matched

solution. The reconstruction of the deformed shape of particles is then used to determine inter-particle forces in the granular media.

68. Stanley CE, Shrivastava J, Brugman R, Heinzelmann E, Swaay D, Grossmann G: **Dual-flow-RootChip reveals local adaptations of roots towards environmental asymmetry at the physiological and genetic levels.** *New Phytologist* 2018, **217**:1357-1369

This paper exposes the development of microfluidic devices that mimic soil heterogeneity. The study shows how asymmetric phosphate distribution affects growth response of root hairs.

72. Sadeghi A, Mondini A, Del Dottore E, Mattoli V, Beccai L, Taccola S, Lucarotti C, Totaro M, Mazzolai B: **A plant-inspired robot with soft differential bending capabilities.** *Bioinspiration & biomimetics* 2016, **12**:015001.

This study explores the development of root inspired robotic devices to penetrate soil. The device embeds various sensors (touch, humidity, accelerometer). Although the work targets soil monitoring and exploration, similar devices could be used to obtain data on the nature of the force experienced by roots during growth.

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