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1 **Micromechanics of root development in soil**

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3

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10 Keywords: plant roots, particle, granular media, biomechanics

11

12

13 **Abstract**

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

21 **Main text**

22 Current knowledge of the biomechanics of plant root growth in soil is largely based on the extensive
23 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="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" 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="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" 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="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" 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-

76 275</pages><volume>8</volume><number>2</number><dates><year>1965</year></dates><isbn>
77 0022-5193</isbn><urls></urls></record></Cite></EndNote>} to predict accurately growth arrest in
78 soil. This is not the case and large discrepancies remain between measured turgor pressure (in the
79 order of 1MPa { ADDIN EN.CITE
80 <EndNote><Cite><Author>Clark</Author><Year>1996</Year><RecNum>231</RecNum><DisplayTex
81 t>[7]</DisplayText><record><rec-number>231</rec-number><foreign-keys><key app="EN" db-
82 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512664911">231</key></foreign-
83 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Clark,
84 LJ</author><author>Whalley, WR</author><author>Dexter, AR</author><author>Barraclough,
85 PB</author><author>Leigh, RA</author></authors></contributors><titles><title>Complete
86 mechanical impedance increases the turgor of cells in the apex of pea roots</title><secondary-
87 title>Plant, Cell & Environment</secondary-title></titles><periodical><full-title>Plant, Cell
88 & Environment</full-title></periodical><pages>1099-
89 1102</pages><volume>19</volume><number>9</number><dates><year>1996</year></dates><isb
90 n>1365-3040</isbn><urls></urls></record></Cite></EndNote>}) and the levels of mechanical
91 stresses at which growth is arrested (>5MPa { ADDIN EN.CITE
92 <EndNote><Cite><Author>Bengough</Author><Year>1991</Year><RecNum>224</RecNum><Displ
93 ayText>[8]</DisplayText><record><rec-number>224</rec-number><foreign-keys><key app="EN"
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95 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Bengough,
96 AG</author><author>Mullins, CE</author></authors></contributors><titles><title>Penetrometer
97 resistance, root penetration resistance and root elongation rate in two sandy loam
98 soils</title><secondary-title>Plant and Soil</secondary-title></titles><periodical><full-title>Plant
99 and Soil</full-title></periodical><pages>59-
100 66</pages><volume>131</volume><number>1</number><dates><year>1991</year></dates><isbn
101 >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"
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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-
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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="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" 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-
127 title></periodical><pages>2289-

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

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ext>Kolb, et al. [11]</DisplayText><record><rec-number>199</rec-number><foreign-keys><key
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timestamp="1512484212">199</key></foreign-keys><ref-type name="Journal Article">17</ref-
type><contributors><authors><author>Kolb, Evelyne</author><author>Legue,
Valérie</author><author>Bogeat-Triboulot, Marie-

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
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AG</author></authors></contributors><titles><title>Stress field developed by root growth:
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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"
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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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173 Num>235</RecNum><record><rec-number>235</rec-number><foreign-keys><key app="EN" db-
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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 &
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"

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190 Simon</author></authors></contributors><titles><title>The exploring root—root growth responses

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192 biology</secondary-title></titles><periodical><full-title>Current opinion in plant biology</full-

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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-
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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"
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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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233 packs</title><secondary-title>Science</secondary-title></titles><periodical><full-
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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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244 h</author><author>Majumdar, Satya</author><author>Narayan,
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249 s></urls></record></Cite><Cite><Author>Hurley</Author><Year>2016</Year><RecNum>251</Rec-
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252 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Hurley,
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-
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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-
262 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" timestamp="1511963947">61</key><key
263 app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-
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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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-
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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><DisplayText>
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288 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" timestamp="1512485408">202</key></foreign-
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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><DisplayText>
301 ext>[23,24]</DisplayText><record><rec-number>203</rec-number><foreign-keys><key app="EN"
302 db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" 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</RecNu
 m><record><rec-number>69</rec-number><foreign-keys><key app="EN" db-
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 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="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" 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="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" 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="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" 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="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" 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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375 Despite recent experimental and theoretical breakthroughs, granular matter physics has not
376 transformed our understanding of the mechanics of root growth. Many current limitations are due to
377 our lack of understanding of how roots respond to complex mechanical signals, and particularly how
378 competition between multiple mechanical stimuli affects root responses. Cellular mechanisms
379 involved in the response to physical obstacles have not been fully characterised, but a growing number
380 of studies are now revealing the signalling and regulatory mechanisms involved in plant responses to
381 mechanical force. Research in animal sciences have identified a multitude of proteins which binding
382 domains are modified by mechanical forces { ADDIN EN.CITE
383 <EndNote><Cite><Author>Iskratsch</Author><Year>2014</Year><RecNum>269</RecNum><Display
384 Text>[29]</DisplayText><record><rec-number>269</rec-number><foreign-keys><key app="EN" db-
385 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" timestamp="1519223480">269</key></foreign-
386 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Iskratsch,
387 Thomas</author><author>Wolfenson, Haguy</author><author>Sheetz, Michael

388 P</author></authors></contributors><titles><title>Appreciating force and shape—the rise of
389 mechanotransduction in cell biology</title><secondary-title>Nature Reviews Molecular Cell
390 Biology</secondary-title></titles><periodical><full-title>Nature Reviews Molecular Cell Biology</full-
391 title></periodical><pages>825</pages><volume>15</volume><number>12</number><dates><year
392 >2014</year></dates><isbn>1471-0080</isbn><urls></urls></record></Cite></EndNote>} and their
393 discovery in plants may follow. Large families of mechanosensitive ion channels have been identify in
394 plants { ADDIN EN.CITE
395 <EndNote><Cite><Author>Hamilton</Author><Year>2015</Year><RecNum>240</RecNum><Displa
396 yText>[30]</DisplayText><record><rec-number>240</rec-number><foreign-keys><key app="EN"
397 db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" timestamp="1512938828">240</key></foreign-
398 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Hamilton,
399 Eric S</author><author>Schlegel, Angela M</author><author>Haswell, Elizabeth
400 S</author></authors></contributors><titles><title>United in diversity: mechanosensitive ion
401 channels in plants</title><secondary-title>Annual Review of Plant Biology</secondary-
402 title></titles><periodical><full-title>Annual review of plant biology</full-
403 title></periodical><pages>113-
404 137</pages><volume>66</volume><dates><year>2015</year></dates><isbn>1543-
405 5008</isbn><urls></urls></record></Cite></EndNote>}, with for example MCA calcium
406 mechanosensitive channels being linked to growth response to hard gel layers { ADDIN EN.CITE
407 <EndNote><Cite><Author>Nakagawa</Author><Year>2007</Year><RecNum>268</RecNum><Displ
408 ayText>[31]</DisplayText><record><rec-number>268</rec-number><foreign-keys><key app="EN"
409 db-id="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" timestamp="1519213479">268</key></foreign-
410 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Nakagawa,
411 Yuko</author><author>Katagiri, Takeshi</author><author>Shinozaki, Kazuo</author><author>Qi,
412 Zhi</author><author>Tatsumi, Hitoshi</author><author>Furuichi,
413 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

466 1BJ,UK.</auth-address><titles><title>The Application of Contrast Media for In Vivo Feature
467 Enhancement in X-Ray Computed Tomography of Soil-Grown Plant Roots</title><secondary-
468 title>Microscopy and Microanalysis</secondary-title></titles><periodical><full-title>Microscopy and
469 Microanalysis</full-title></periodical><pages>538-
470 552</pages><volume>23</volume><number>3</number><edition>2017/03/23</edition><keyword
471 s><keyword>X-ray computed tomography</keyword><keyword>contrast
472 agents</keyword><keyword>imaging</keyword><keyword>plant
473 roots</keyword></keywords><dates><year>2017</year><pub-dates><date>Jun</date></pub-
474 dates></dates><isbn>1435-8115 (Electronic)1431-9276 (Linking)</isbn><accession-
475 num>28320487</accession-num><urls><related-
476 urls><url>https://www.ncbi.nlm.nih.gov/pubmed/28320487</url></related-urls></urls><electronic-
477 resource-num>10.1017/S1431927617000319</electronic-resource-
478 num></record></Cite></EndNote>}. Root hairs can be resolved using synchrotron sources with
479 resolution of up to 5µm and at temporal resolution sufficient for tracking particle movement due to
480 root growth { ADDIN EN.CITE
481 <EndNote><Cite><Author>Keyes</Author><Year>2017</Year><RecNum>223</RecNum><DisplayTe
482 xt>[37]</DisplayText><record><rec-number>223</rec-number><foreign-keys><key app="EN" db-
483 id="w99ddwvpas9ff5epww0vw5ratpx5azrxstez" timestamp="1512646619">223</key></foreign-
484 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Keyes,
485 SD</author><author>Cooper, Laura</author><author>Duncan, S</author><author>Koebernick,
486 N</author><author>Fletcher, DM McKay</author><author>Scotson, CP</author><author>Van
487 Veelen, Arjen</author><author>Sinclair, Ian</author><author>Roose,
488 Tiina</author></authors></contributors><titles><title>Measurement of micro-scale soil
489 deformation around roots using four-dimensional synchrotron tomography and image
490 correlation</title><secondary-title>Journal of The Royal Society Interface</secondary-
491 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="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" 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="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" 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="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" 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="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" 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>Huisken,
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>Huisken,
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="w99ddwvpas9ff5epww0vw5ratpx5azrxstz" 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
602 X</author></authors></contributors><titles><title>New live screening of plant-nematode
603 interactions in the rhizosphere</title><secondary-title>Scientific Reports</secondary-
604 title></titles><periodical><full-title>Scientific reports</full-
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><
613 DisplayText>[53]</DisplayText><record><rec-number>242</rec-number><foreign-keys><key
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617 Pawel</author><author>Wightman, Raymond</author><author>Milani,
618 Pascale</author><author>Berquand, Alexandre</author><author>Boudaoud,
619 Arezki</author><author>Hamant, Olivier</author><author>Jönsson,
620 Henrik</author><author>Meyerowitz, Elliot
621 M</author></authors></contributors><titles><title>Subcellular and supracellular mechanical stress

622 prescribes cytoskeleton behavior in Arabidopsis cotyledon pavement cells</title><secondary-

623 title>Elife</secondary-title></titles><periodical><full-title>Elife</full-

624 title></periodical><pages>e01967</pages><volume>3</volume><dates><year>2014</year></dates

625 ><isbn>2050-084X</isbn><urls></urls></record></Cite></EndNote>}, whilst optical trapping has

626 been used to apply small localised forces { ADDIN EN.CITE

627 <EndNote><Cite><Author>Mártonfalvi</Author><Year>2017</Year><RecNum>215</RecNum><Disp

628 layText>[54]</DisplayText><record><rec-number>215</rec-number><foreign-keys><key app="EN"

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630 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Mártonfalvi,

631 Zsolt</author><author>Bianco, Pasquale</author><author>Naftz,

632 Katalin</author><author>Ferenczy, György G</author><author>Kellermayer,

633 Miklós</author></authors></contributors><titles><title>Force generation by titin

634 folding</title><secondary-title>Protein Science</secondary-title></titles><periodical><full-

635 title>Protein Science</full-title></periodical><dates><year>2017</year></dates><isbn>1469-

636 896X</isbn><urls></urls></record></Cite></EndNote>}. Photoelastic materials have been central to

637 establishing the nature of the chains of forces and how they propagate within a granular medium {

638 ADDIN EN.CITE

639 <EndNote><Cite><Author>Tordesillas</Author><Year>2014</Year><RecNum>26</RecNum><Display

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643 type><contributors><authors><author>Tordesillas, A.</author><author>Steer, C. A.

644 H.</author><author>Walker, D. M.</author></authors></contributors><titles><title>Force chain and

645 contact cycle evolution in a dense granular material under shallow penetration</title><secondary-

646 title>Nonlinear Processes in Geophysics</secondary-title></titles><periodical><full-title>Nonlinear

647 Processes in Geophysics</full-title></periodical><pages>505-

648 519</pages><volume>21</volume><number>2</number><section>505</section><dates><year>2014

649 </year></dates><isbn>1607-7946</isbn><urls></urls><electronic-resource-num>10.5194/npg-21-
650 505-2014</electronic-resource-num></record></Cite></EndNote>}. { ADDIN EN.CITE <EndNote><Cite
651 AuthorYear="1"><Author>Kolb</Author><Year>2012</Year><RecNum>40</RecNum><DisplayText>
652 Kolb, et al. [56]</DisplayText><record><rec-number>40</rec-number><foreign-keys><key app="EN"
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654 app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-
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
658 Soil</secondary-title></titles><periodical><full-title>Plant and Soil</full-
659 title></periodical><pages>19-35</pages><volume>360</volume><number>1-
660 2</number><section>19</section><dates><year>2012</year></dates><isbn>0032-079X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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667 name="Journal Article">17</ref-type><contributors><authors><author>Wendell,
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-
671 title></titles><periodical><full-title>Experimental Mechanics</full-title></periodical><pages>945-
672 949</pages><volume>52</volume><number>7</number><section>945</section><dates><year>20
673 11</year></dates><isbn>0014-48511741-2765</isbn><urls></urls><electronic-resource-

675 num>10.1007/s11340-011-9569-x</electronic-resource-num></record></Cite></EndNote>} have
676 successfully created a granular medium using a photo elastic media where maximum growth forces
677 and avoidance mechanisms could be observed (Figure 1B). New cantilever-based optical sensors {
678 ADDIN EN.CITE { ADDIN EN.CITE.DATA }} have also been developed to measure simultaneously growth
679 forces generated by a root and three-dimensional strain rate in responses to changes in external forces
680 applied to the root. { ADDIN EN.CITE { ADDIN EN.CITE.DATA }} for example, obtained stereoscopic data
681 to decompose root response to axial mechanical forces into different phases (Figure 1C). Hydrogels
682 can also be combined with fluorescent dyes and light sheet imaging to reconstruct interparticle forces
683 within the granular medium { ADDIN EN.CITE
684 <EndNote><Cite><Author>Brodu</Author><Year>2015</Year><RecNum>15</RecNum><DisplayText>
685 t>[60]</DisplayText><record><rec-number>15</rec-number><foreign-keys><key app="EN" db-
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687 app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-
688 type><contributors><authors><author>Brodu, N.</author><author>Dijksman, J.
689 A.</author><author>Behringer, R. P.</author></authors></contributors><auth-address>1]
690 Department of Physics, Duke University, Physics Building, Science Drive, Box 90305, Durham, North
691 Carolina 27708, USA [2] Institut National de Recherche en Informatique et en Automatique, Bordeaux
692 Sud-Ouest, 200 avenue de la Vieille Tour, 33405 Talence, France.1] Department of Physics, Duke
693 University, Physics Building, Science Drive, Box 90305, Durham, North Carolina 27708, USA [2]
694 Laboratory of Physical Chemistry and Colloid Science, Wageningen University, PO Box 8038, 6700EK
695 Wageningen, The Netherlands.Department of Physics, Duke University, Physics Building,
696 Science Drive, Box 90305, Durham, North Carolina 27708, USA.</auth-
697 address><titles><title>Spanning the scales of granular materials through microscopic force
698 imaging</title><secondary-title>Nature Communication</secondary-title></titles><periodical><full-
699 title>Nature Communication</full-
700 title></periodical><pages>6361</pages><volume>6</volume><edition>2015/03/06</edition><date

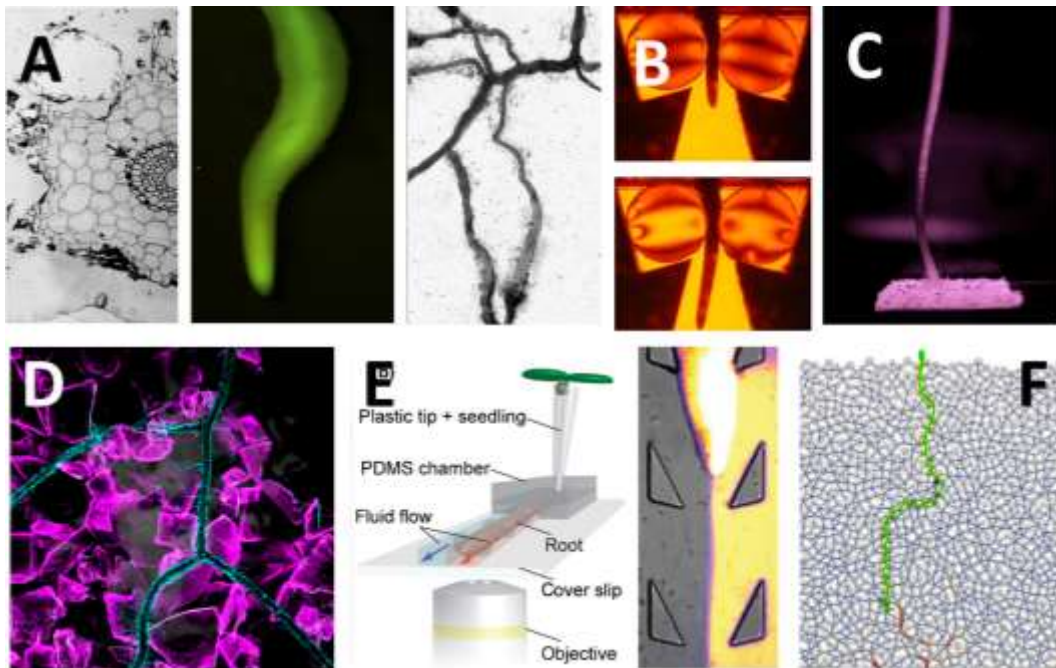
701 s><year>2015</year><pub-dates><date>Mar 5</date></pub-dates></dates><isbn>2041-1723
702 (Electronic)2041-1723 (Linking)</isbn><accession-num>25739968</accession-
703 num><urls><related-urls><url>https://www.ncbi.nlm.nih.gov/pubmed/25739968</url></related-
704 urls></urls><custom2>PMC4366509</custom2><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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713 type><contributors><authors><author>Downie, H.</author><author>Holden,
714 N.</author><author>Otten, W.</author><author>Spiers, A. J.</author><author>Valentine, T.
715 A.</author><author>Dupuy, L. X.</author></authors></contributors><auth-address>The James
716 Hutton Institute, Invergowrie, Dundee, United Kingdom.</auth-address><titles><title>Transparent
717 soil for imaging the rhizosphere</title><secondary-title>PLoS One</secondary-
718 title></titles><periodical><full-title>PLoS One</full-
719 title></periodical><pages>e44276</pages><volume>7</volume><number>9</number><edition>20
720 12/09/18</edition><keywords><keyword>Bacteria/metabolism</keyword><keyword>Humans</ke
721 yword><keyword>Imaging, Three-Dimensional/*methods</keyword><keyword>Microscopy,
722 Confocal</keyword><keyword>Plant Roots/growth &
723 development/microbiology</keyword><keyword>Refractometry</keyword><keyword>*Rhizospher
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729 urls></urls><custom2>PMC3439476</custom2><electronic-resource-
730 num>10.1371/journal.pone.0044276</electronic-resource-num></record></Cite></EndNote>}. The
731 media reproduces the physical and chemical properties of soil through control of the distribution of
732 sizes and surface chemistry of the particles (Figure 1D). Because the particles are made of
733 fluoropolymers that have refractive index close to water, only small adjustment of refractive indices,
734 usually by adding a colloid to the nutrient solution, allows light to travel without refraction through
735 the substrate. Microfluidics techniques have also progressed significantly and are becoming suitable
736 to live and high resolution microscopy of roots and microbes { ADDIN EN.CITE { ADDIN EN.CITE.DATA
737 }}. Microfluidics allows precise and repeatable control of liquids and this could be used, for example,
738 to control water tension and particle cohesion in soil during live experiments. The range of materials
739 and fabrication techniques has been considerably expanded with the use of 3D printing { ADDIN
740 EN.CITE
741 <EndNote><Cite><Author>Kitson</Author><Year>2012</Year><RecNum>216</RecNum><DisplayTe
742 xt>[63]</DisplayText><record><rec-number>216</rec-number><foreign-keys><key app="EN" db-
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744 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>Kitson, Philip
745 J</author><author>Rosnes, Mali H</author><author>Sans, Victor</author><author>Dragone,
746 Vincenza</author><author>Cronin,
747 Leroy</author></authors></contributors><titles><title>Configurable 3D-Printed millifluidic and
748 microfluidic 'lab on a chip' reactionware devices</title><secondary-title>Lab on a Chip</secondary-
749 title></titles><periodical><full-title>Lab on a Chip</full-title></periodical><pages>3267-
750 3271</pages><volume>12</volume><number>18</number><dates><year>2012</year></dates><u
751 rls></urls></record></Cite></EndNote>}, photo lithography { ADDIN EN.CITE
752 <EndNote><Cite><Author>Yanagisawa</Author><Year>2017</Year><RecNum>252</RecNum><Disp

753 layText>[64]</DisplayText><record><rec-number>252</rec-number><foreign-keys><key app="EN"
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756 Naoki</author><author>Sugimoto, Nagisa</author><author>Arata,
757 Hideyuki</author><author>Higashiyama, Tetsuya</author><author>Sato,
758 Yoshikatsu</author></authors></contributors><titles><title>Capability of tip-growing plant cells to
759 penetrate into extremely narrow gaps</title><secondary-title>Scientific Reports</secondary-
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762 2017</year></dates><isbn>2045-2322</isbn><urls></urls></record></Cite></EndNote>}, etching
763 technics { ADDIN EN.CITE
764 <EndNote><Cite><Author>Anderson</Author><Year>2000</Year><RecNum>217</RecNum><Displa
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768 Janelle R</author><author>Chiu, Daniel T</author><author>Wu,
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770 M</author></authors></contributors><titles><title>Fabrication of microfluidic systems in poly
771 (dimethylsiloxane)</title><secondary-title>Electrophoresis</secondary-
772 title></titles><periodical><full-title>Electrophoresis</full-title></periodical><pages>27-
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776 xt>[66,67]</DisplayText><record><rec-number>218</rec-number><foreign-keys><key app="EN" db-
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779 Steven L</author><author>MacDonald, Michael P</author><author>Dholakia,
780 Kishan</author><author>Krauss, Thomas F</author></authors></contributors><titles><title>All-
781 optical control of microfluidic components using form birefringence</title><secondary-title>Nature
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790 Christophe</author><author>Miller, Oliver J</author><author>Taly,
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792 Abdeslam</author><author>Frenz, Lucas</author><author>Rick,
793 Christian</author><author>Samuels, Michael L</author><author>Hutchison, J
794 Brian</author><author>Agresti, Jeremy
795 J</author></authors></contributors><titles><title>Fluorescence-activated droplet sorting (FADS):
796 efficient microfluidic cell sorting based on enzymatic activity</title><secondary-title>Lab on a
797 Chip</secondary-title></titles><periodical><full-title>Lab on a Chip</full-
798 title></periodical><pages>1850-
799 1858</pages><volume>9</volume><number>13</number><dates><year>2009</year></dates><url
800 s></urls></record></Cite></EndNote>}. It has been possible, for example, to produce chambers with
801 physical heterogeneity, physical barriers and chemical gradients, with direct applications to root and
802 soil studies { ADDIN EN.CITE { ADDIN EN.CITE.DATA } } .
803 The scientific community is better equipped than ever to make observations on the micromechanics
804 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

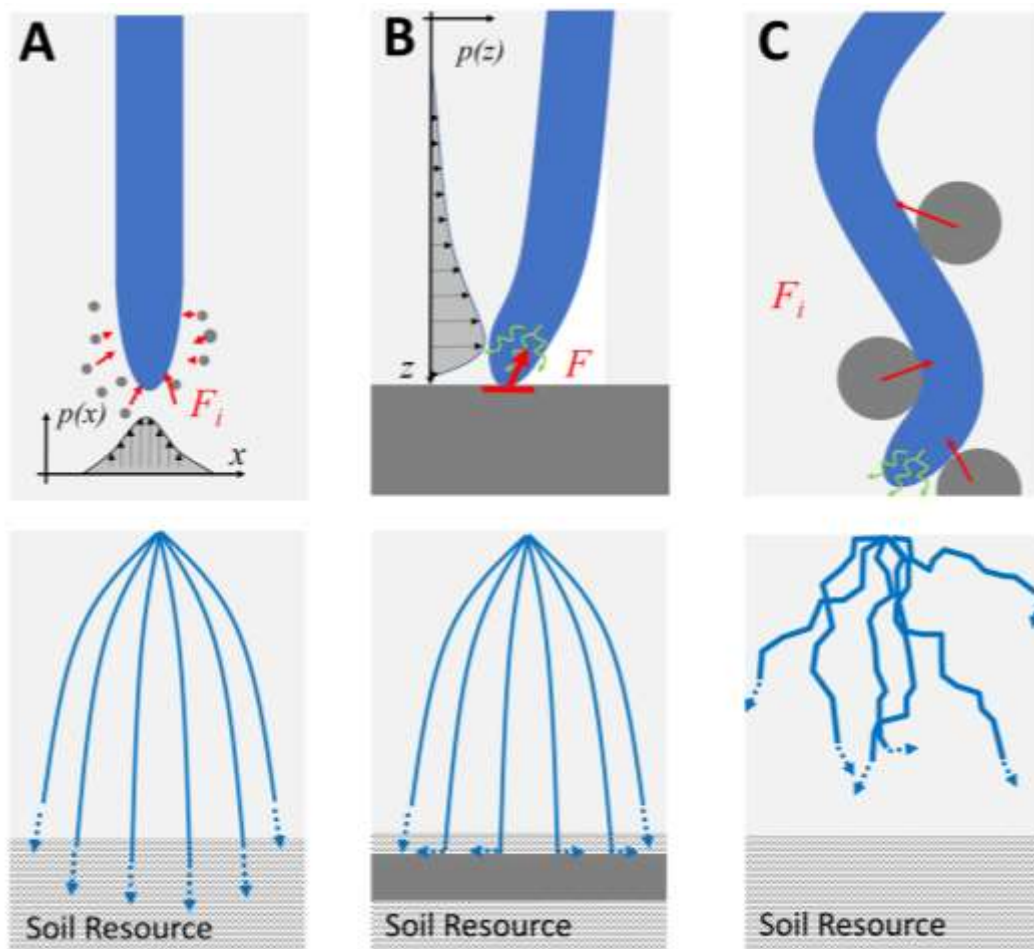
819 Figure 1: Growing roots interact mechanically with soil particles during growth. These interactions
 820 influence the morphology of the root, and the dynamics of development of the root system. A)
 821 Irregular growth of cortex cells is observed in hard or compacted soil { ADDIN EN.CITE
 822 <EndNote><Cite><Author>Lipiec</Author><Year>2012</Year><RecNum>243</RecNum><Prefix>left
 823 ` , </Prefix><DisplayText>[left, 69]</DisplayText><record><rec-number>243</rec-number><foreign-
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 825 type><contributors><authors><author>Lipiec, Jerzy</author><author>Horn,
 826 Rainer</author><author>Pietrusiewicz, Jacek</author><author>Siczek,
 827 Anna</author></authors></contributors><titles><title>Effects of soil compaction on root elongation
 828 and anatomy of different cereal plant species</title><secondary-title>Soil and Tillage
 829 Research</secondary-title></titles><periodical><full-title>Soil and Tillage Research</full-
 830 title></periodical><pages>74-
 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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843 app="ENWeb" db-id="">0</key></foreign-keys><ref-type name="Journal Article">17</ref-
844 type><contributors><authors><author>Kolb, Evelyne</author><author>Hartmann,
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
847 Soil</secondary-title></titles><periodical><full-title>Plant and Soil</full-
848 title></periodical><pages>19-35</pages><volume>360</volume><number>1-
849 2</number><section>19</section><dates><year>2012</year></dates><isbn>0032-079X1573-
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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858 keys><ref-type name="Journal Article">17</ref-type><contributors><authors><author>O'Callaghan,
859 Felicity E </author><author>Braga, Roberto A </author><author>Neilson,

860 Roy</author><author>MacFarlane, Stuart A </author><author>Dupuy, Lionel
861 X</author></authors></contributors><titles><title>New live screening of plant-nematode
862 interactions in the rhizosphere</title><secondary-title>Scientific Reports</secondary-
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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-
869 id="w99ddwvpa9ff5epww0vw5ratpx5azrxstex" timestamp="1518642710">261</key></foreign-
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871 Claire E</author><author>Shrivastava, Jagriti</author><author>Brugman,
872 Rik</author><author>Heinzelmann, Elisa</author><author>Swaay,
873 Dirk</author><author>Grossmann, Guido</author></authors></contributors><titles><title>Dual-
874 flow-RootChip reveals local adaptations of roots towards environmental asymmetry at the
875 physiological and genetic levels</title><secondary-title>New Phytologist</secondary-
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877 1369</pages><volume>217</volume><number>3</number><dates><year>2018</year></dates><is
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
880 <EndNote><Cite><Author>Fakih</Author><Year>2017</Year><RecNum>270</RecNum><DisplayTex
881 t>[28]</DisplayText><record><rec-number>270</rec-number><foreign-keys><key app="EN" db-
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884 type><contributors><authors><author>Fakih, Mahmoud</author><author>Delenne, Jean
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886 Thierry</author></authors></contributors><title><title>Modeling root growth in granular soils:
 887 effects of root stiffness and packing fraction</title><secondary-title>EPJ Web of
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895 *Box 1: Root primary growth is a local process where elongation of tissues is taking place at the root*
 896 *tip. Soil heterogeneity influences strongly how the tissue elongates and deforms (top), and local*
 897 *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
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 917 1058</pages><volume>67</volume><number>4</number><dates><year>2016</year></dates><isbn
 918 n>0022-0957</isbn><urls></urls></record></Cite></EndNote>}. The growth velocity E ($\text{cm}\cdot\text{d}^{-1}$) 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.

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

$$928 \quad \partial_n \rho = 0.$$

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

932 (C) Intermediate cases are more problematic to analyse. Roots are in contact with particles which
933 apply forces of varying magnitudes and orientation. Although the root may overcome these forces, a
934 single particle may be able to deflect the growth trajectory. Since particles have inhomogeneous
935 distribution, root deflection occurs is stochastic. Mathematically, the phenomenon can be described by
936 a convection, where the growth velocity $e < E$ ($\text{cm} \cdot \text{d}^{-1}$) and the rate of change in root angle due to
937 gravitropism g (d^{-1}) and random fluctuations define the dynamics:

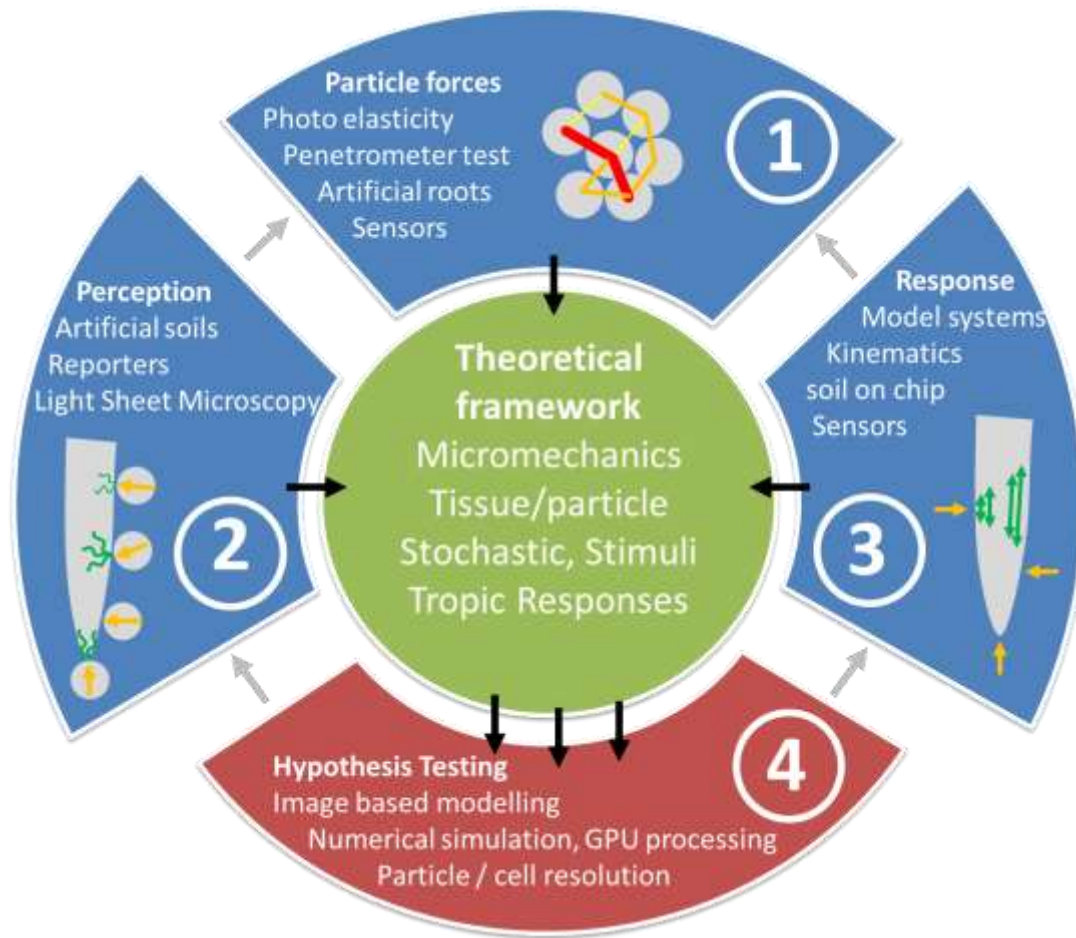
$$938 \quad \partial_t \rho + \nabla \cdot \mathbf{F} + \partial_\theta (g\rho + D\partial_\theta \rho) = 0,$$

939 $g\rho + D\partial_\theta \rho$ the angular flux of roots. The parameter D is the angular diffusion coefficient. Because D
940 relates to the probability of roots to be deflected by a particle, and the magnitude of such deflection,
941 there is a direct link between micro-mechanics of root particle interactions and the morphology of the
942 root system. Diffusive growth makes root trajectories irregular, and limits the expansion of the root
943 system, even when the elongation rate is not affected. Mathematical analysis of equation 3 reveals
944 the conditions for which transitions from convective growth to diffusive growth occur, i.e. for Peclet
945 number $Pe = \frac{g}{D} \ll 1$.

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950 Figure 2: Dissecting the complexity of root particles mechanical interactions requires an elaborate

951 research strategy. (1) First step is to better understand the nature of the forces applied to a root. This

952 can be achieved, using photo elastic beads, imaging, or developing artificial roots equipped with

953 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
969 <EndNote><Cite><Author>Perfect</Author><Year>1990</Year><RecNum>249</RecNum><DisplayT
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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).

1000

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1005 ANR-10-LABX- 001-01).

1006

1007 **Publication Highlight**

1008 9. Bengough AG, Loades K, McKenzie BM: **Root hairs aid soil penetration by anchoring the root**
1009 **surface to pore walls.** *Journal of Experimental Botany* 2016, **67**:1071-1078.

1010 This paper demonstrates that penetration of granular media uses root hair cells to anchor the base of
1011 the root while the tip of the root is moving and expanding. The study provides experimental
1012 evidence that root microscopic traits play an important role in mechanical interactions with the
1013 granular media.

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1015 10. Colombi T, Kirchgessner N, Walter A, Keller T: **Root tip shape governs root elongation rate under**
1016 **increased soil strength.** *Plant Physiology* 2017, **174**:2289-2301.

1017 This study illustrates the role of the morphology of the root tip in the penetration of hard soil. The
1018 angle of the root tip, more than the diameter itself, is found to be the trait that segregates for ability
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1021 11. Kolb E, Legue V, Bogeat-Triboulot M-B: **Physical root-soil interactions.** *Physical Biology* 2017,
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1023 This paper provides an overview of the physics of root soil interactions. The study classify the main
1024 biomechanical processes of growth, namely axial elongation, thickening and reorientation, and it
1025 details the basic principles that control their magnitude and occurrence in a soil.

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1028 **granular materials**. *Physical Review Letters* 2016, **117**:098005.

1029 **This paper provides a clear and concise introductions to current understanding of granular matter**
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1050 This paper exposes state of the art approaches to track plant growth and particle movement in soil.
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1088 This study explores the development of root inspired robotic devices to penetrate soil. The device
1089 embark various sensors (touch, humidity, accelerometer). Although the work targets soil monitoring
1090 and exploration, similar devices could be used to obtain data on the nature of the force experienced
1091 by roots during growth.

1092

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