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Micromechanics of root development in soil

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Our understanding of how roots 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 refresh our views on root growth in heterogeneous environments.

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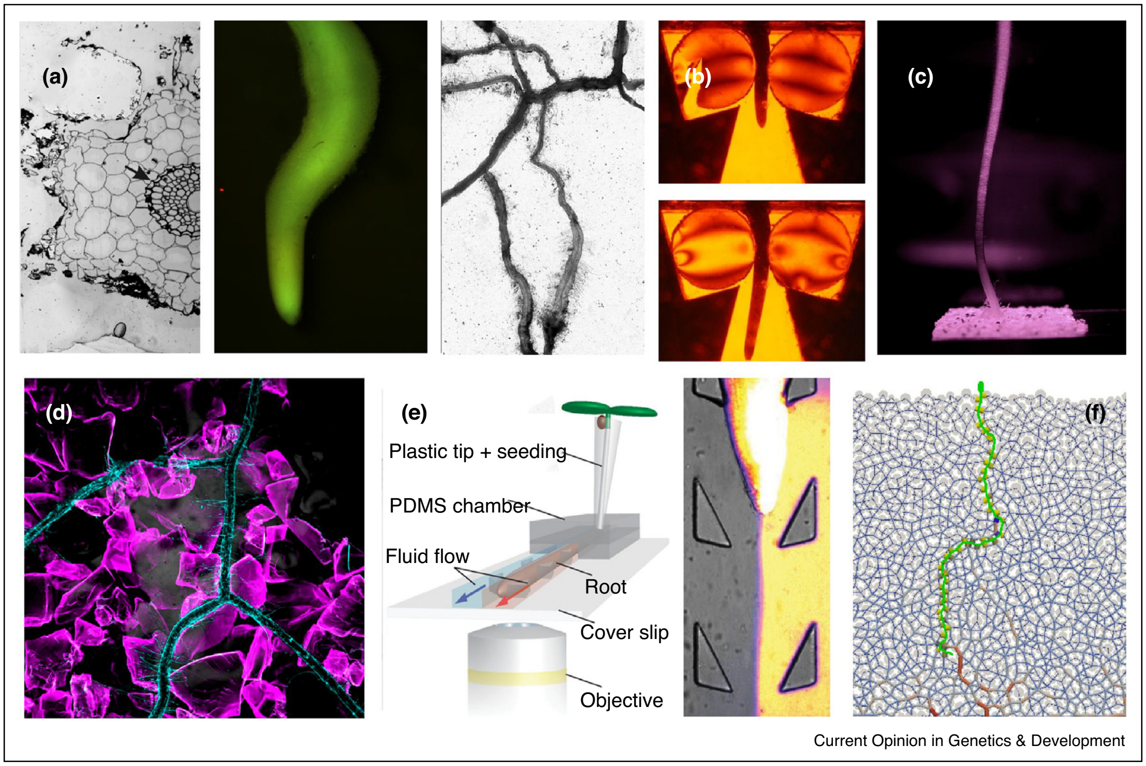
Current knowledge of the biomechanics of root growth in soil is largely based on the extensive work of plant biophysicists from the second half of the 20th century [1–3]. The view was that both roots and soil must be considered as continua so that the description of root soil interactions can be achieved with continuous mathematical functions of macroscopic variables such as Young's modulus of root tissue, soil penetration stress, and pore water pressure [4]. Mechanics and physiology then provide a suitable framework to understand what influences root elongation in soil. The energy required to deform the root and surrounding soil, which originates from the photosynthetic chemical energy accumulated within the tissues, is converted into turgor pressure and mechanical energy [5]. Turgor pressure then overcome the resistance from cell wall to stretching, the resistance to movement of water across membranes, and the resistance to the displacement of the soil around the root [6].

This classical view of root–soil biomechanics has been central to identify the biophysical factors limiting growth in soil, but it is now challenged to predict morphologies and developmental patterns observed in natural conditions (Figure 1). If roots were to experience homogeneous mechanical stress from the soil, one would expect turgor pressure and Lockhart equation [1] to predict accurately growth arrest in soil. This is not the case and discrepancies remain between common measures of turgor pressure (in the order of 1 MPa [7]) and the levels of mechanical stresses at which growth is arrested (>5 MPa [8]). Classical mechanics of continua is ill-equipped to explain the links between soil heterogeneity and stochasticity of plant development. The root tissue itself is heterogeneous and cell types have different roles in facilitating growth and penetration. Anchoring the base of the root for example, is necessary for cell elongation to produce apical movement and deformation of the soil [9•]. The root cap and its associated border cells have also a fundamental role in reducing friction from the bulk soil. It was shown recently that wheat genotypes with sharper root tips are more efficient at soil penetration [10•].

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). Kolb *et al.* [11••] 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) [12]. Soils also contain objects that are too large and or too rigid for a root to deform and displace, for example when roots grow in contact with stones, in cracks or in pores [13,14]. Growth forces cannot displace the obstacle and the root usually combines tropic responses and mechanical buckling to avoid the obstacle (Box 1B) [15]. The behaviour of roots growing in soils with particles of intermediate sizes is more challenging to understand. A root can displace individual particles from the soil, but the forces exerted by each of the particles can also influence the course of root development (Box 1C).

Figure 1



Growing roots interact mechanically with soil particles during growth. These interactions influence the morphology of the root, and the dynamics of development of the root system. **(a)** Irregular growth of cortex cells is observed in hard or compacted soil [(left, 69)]. Resistance from the soil particles causes root diameter to increase and the root tip to buckle and bend towards the path of least resistance (middle, lentils roots grown at 2 MPa confining pressure). At the scale of the root system, interactions causes growth trajectories to be stochastic as observed here on *Anthyllis vulneraria* grown on landslide soils (image courtesy Loïc Pagès). Technological developments now allow precise characterisation of mechanical interactions between a root and the growth substrate. These include for example, **(b)** photoelastic discs for measurement of growth forces in soil pores [56] (images courtesy Evelyne Kolb), **(c)** root growing on a cantilever sensor for measuring growth forces [59•], **(d)** transparent soil substrates that provide the physical structure of soil with the ability to carry out 3D live imaging [50••], **(e)** dual flow microfluidic systems with microscale both physical and chemical heterogeneity [68••] and **(f)** discrete element modelling for testing root responses to interactions with granular media [28•] (image courtesy Mahmoud Fakih).

Although such growth environments are common for fine roots or due to the presence of aggregate and sand particles, growth patterns in such conditions are not well understood. How frequently does a root deflect from their growth trajectory? What are the magnitude of deflections? How does the distribution of particle forces modify the growth trajectory?

Understanding the forces acting on a root during the elongation requires detailed knowledge of the physics of granular media. Granular media are assemblages of particles held by frictional and repulsive forces from adjacent particles. The forces holding particles together form chain-like networks that propagate at the contact points between neighbouring particles [16]. Because particles are disordered or have various sizes and shapes, large variations in magnitude and direction of particle forces arise [16,17]. Early theoretical work based on dry and static monodisperse particles showed that distribution of contact forces vary greatly and the overall force distribution follows an exponential decline [18,19••]. Particles dynamics is better understood too. Contact forces in granular media propagate through complex waves [20] with appearance of macroscopic phenomenon such as clogging and arching, where particles spontaneously organise as vaults [21]. Solid, liquid and even gaseous phases may be observed in granular media depending on the external forces applied upon them [22]. Findngs have been facilitated by powerful techniques and hardware now available to examine theories in conditions that are nearly identical to experiments. 3D templates of the pore geometry together with description of the root and anatomical details can be obtained [23,24], 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