

Hydrologic regulation of plant rooting depth

Ying Fan^{a,1}, Gonzalo Miguez-Macho^b, Esteban G. Jobbágy^c, Robert B. Jackson^{d,e,f}, and Carlos Otero-Casal^b

^aDepartment of Earth and Planetary Sciences, Rutgers University, New Brunswick, NJ 08854; ^bNon-Linear Physics Group, Faculty of Physics, Universidade de Santiago de Compostela, E-15782 Santiago de Compostela, Galicia, Spain; ^cGrupo de Estudios Ambientales-Instituto de Matemática Aplicada San Luis, Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de San Luis, D5700HHW San Luis, Argentina; ^dDepartment of Earth System Science, Stanford University, Stanford, CA 94305; ^eWoods Institute for the Environment, Stanford University, Stanford, CA 94305; and ^fPrecourt Institute for Energy, Stanford University, Stanford, CA 94305

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Plant rooting depth affects ecosystem resilience to environmental stress such as drought. Deep roots connect deep soil/groundwater to the atmosphere, thus influencing the hydrologic cycle and climate. Deep roots enhance bedrock weathering, thus regulating the long-term carbon cycle. However, we know little about how deep roots go and why. Here, we present a global synthesis of 2,200 root observations of >1,000 species along biotic (life form, genus) and abiotic (precipitation, soil, drainage) gradients. Results reveal strong sensitivities of rooting depth to local soil water profiles determined by precipitation infiltration depth from the top (reflecting climate and soil), and groundwater table depth from below (reflecting topography-driven land drainage). In well-drained uplands, rooting depth follows infiltration depth; in waterlogged lowlands, roots stay shallow, avoiding oxygen stress below the water table; in between, high productivity and drought can send roots many meters down to the groundwater capillary fringe. This framework explains the contrasting rooting depths observed under the same climate for the same species but at distinct topographic positions. We assess the global significance of these hydrologic mechanisms by estimating root water-uptake depths using an inverse model, based on observed productivity and atmosphere, at 30" (~1-km) global grids to capture the topography critical to soil hydrology. The resulting patterns of plant rooting depth bear a strong topographic and hydrologic signature at landscape to global scales. They underscore a fundamental plant-water feedback pathway that may be critical to understanding plant-mediated global change.

plant rooting depth | soil hydrology | global change biology | infiltration depth | water table depth

Plant rooting depth is a sensitive parameter in Earth system models for understanding past and predicting future global change (1–3) because it is a basic plant functional trait determining ecosystem resilience (4–6), plant biogeography (7, 8), pedogenesis (9, 10), and long-term carbon cycle (1, 10, 11). Unlike their aboveground counterparts, roots are difficult to observe, and basic knowledge such as their vertical extent remains limited, hindering mechanistic understanding and prediction of plant-mediated global change. Observation syntheses in the 1990s (12–14) revealed widely varying rooting depths (0.3–68 m; *SI Appendix, Fig. S1*) and broad associations with biome types; roots are shallow in boreal biomes on thinly thawed soils; roots of annual crops start from seeds each season reaching only shallow depths; and deep roots are found in arid, semiarid, and season-arid climates. In fact, a key finding from past syntheses is that both the shallowest and the deepest roots are found in dry biomes (3, 15). Because biomes are closely associated with climate, subclimate-scale factors likely explain the large within-biome spread. Candidates include species and age, but the same species/age displayed contrasting rooting depths in monoculture crops and plantations (16, 17), because roots are highly adaptive to local soil environments (18).

A frequently evoked subclimate-scale environmental factor is soil water status. Near the surface, coarse-grained soils with low water holding capacity allow deep infiltration encouraging deep roots (19–21); at the base, waterlogging and associated oxygen stress in topographic depressions inhibit deep roots (16, 17, 22,

23). Thus, variations in local soil water profile, driven by infiltration above and drainage below, are known causes for rooting depth variations (12). While climate and soil regulate infiltration, topography drives drainage; water flows toward topographic depressions creating shallow water tables in the latter. This is why the water table depth (WTD) reflects local topography as much as or more than regional climate (*SI Appendix, Fig. S2*); one finds deep and shallow water tables under most climates (24).

We hypothesize that along a topographic gradient, root–water relation shifts systematically (Fig. 1); on excessively drained uplands (position 1), the water table is deep or absent and rooting depth is limited to infiltration depth/frequency (25) (example in *SI Appendix, Fig. S3B*). At a lower position 2, roots may sense groundwater capillary rise; in climates with dry seasons, dimorphic roots (*SI Appendix, Fig. S3C*) are observed, with a shallow cluster using rain and a deep cluster using groundwater in dry seasons (26–28). At position 3, infiltration meets capillary rise and water is not limiting. At position 4, seasonal waterlogging limits roots to the oxygenated soils above the water table (*SI Appendix, Fig. S3D*); shallow or aerial roots are common in lowland forests (12, 29, 30). At position 5, permanent waterlogging selects wetland species insensitive to WTD.

To test this hypothesis, we compiled rooting depth observations (*SI Appendix* and *Dataset S1*), recording local drainage conditions neglected in earlier syntheses. The 2,200 observations (Fig. 2) represent >1,000 species under a range of climate, soil, and drainage conditions. Rooting depth varied from <0.01 to >70 m

Significance

Knowledge of plant rooting depth is critical to understanding plant-mediated global change. Earth system models are highly sensitive to this particular parameter with large consequences for modeled plant productivity, water–energy–carbon exchange between the land and the atmosphere, and silicate weathering regulating multimillion-year-timescale carbon cycle. However, we know little about how deep roots go and why. Accidental discoveries of >70-m-deep roots in wells and >20-m-deep roots in caves offer glimpses of the enormous plasticity of root response to its environment, but the drivers and the global significance of such deep roots are not clear. Through observations and modeling, we demonstrate that soil hydrology is a globally prevalent force driving landscape to global patterns of plant rooting depth.

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¹To whom correspondence should be addressed. Email: yingfan@eps.rutgers.edu.

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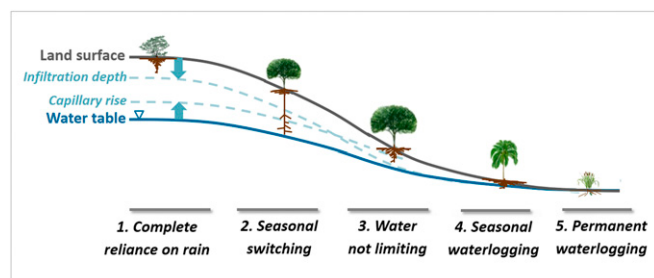


Fig. 1. Schematic of soil water profiles along a drainage gradient, wetted from above by rain infiltration and from below by groundwater capillary rise, with a dry gap that diminishes downslope. Along this gradient, plant rooting depths vary systematically (see text). *SI Appendix, Fig. S3* gives examples of published root images at different drainage positions.

with a distribution peak at 1 m. Because the deepest roots were discovered accidentally, they are likely undersampled.

We plot (log) rooting depth (Fig. 3) vs. several potential drivers (*SI Appendix, Table S1*). A wide range of rooting depths are observed at any given annual rainfall (Fig. 3*A*) and soil texture (Fig. 3*B*). Many roots penetrated soil concretions (27, 28) or into bedrock fractures (31–34) (Fig. 3*C*, below 1:1 line). Across growth forms (Fig. 3*D*), shallow roots are found in small, annual herbs and deep roots in large, broadleaf trees. Among the 30 best-observed genera (Fig. 3*E*), shallower roots occur in wetland, desert, and boreal taxa and deeper roots in those of warm-dry regions. The wide spread within a growth form or genera suggests large plasticity in root response to local environments.

Drainage, quantified by WTD, emerged as a strong environmental factor (Fig. 3*F*). On one hand, it restricts roots to the oxygenated soils above the water table (above 1:1 line); points below are attributable to water table rise/fall outpacing root response, temporary perched saturation, or wetland plants insensitive to waterlogging. On the other hand, the presence of a water table can draw roots deeper to tap its capillary rise; roots terminating in the capillary fringe and root elongation following a declining water table are observed in laboratories and the field (27, 35). Points far above the 1:1 line are from upland plants disconnected from deep groundwater. These two functions of the

water table, pushing roots shallower to avoid oxygen stress, and pulling them deeper to tap the capillary rise, result in a narrower range of rooting depth at a given WTD.

This groundwater push–pull is illustrated in an unintended experiment: the 46 mature trees of 37 species planted as windbreaks in eastern Nebraska (36). The sites have similar rainfall (~735 mm/y) and soil (silt loam), but WTD varied (1–25 m) (*SI Appendix, Fig. S4 A and B*). The same species displayed contrasting rooting depths (*SI Appendix, Fig. S4 C and D, and E and F*) but all terminating near the water table. Plotting rooting depth vs. WTD (*SI Appendix, Fig. S5*) reveals three distinct root–WTD relations: roots independent of WTD, roots tapping groundwater (pulled deeper), and roots restricted by WTD (pushed shallower). Here, the climate and soil varied little, bringing out the WTD influence.

An important question is the relative control of genetic vs. environmental factors. Besides the Nebraska example, we plot the six most-observed genera (named in Fig. 3*E*) against mean annual rainfall (*SI Appendix, Fig. S6, Top*) and WTD (*Bottom*). The latter better explains the spread, as reported in many single-species studies [e.g., spruce (16) and maize (17)].

These results point to land drainage as a powerful environmental axis at the subclimate scale, a main distinction of this study from past syntheses and modeling that evoked climate and soil as primary abiotic drivers (3, 13, 20). We suggest that drainage gradient be considered along with climate and soil gradients to fully describe the soil water conditions for roots. Such an attempt is made in Fig. 4; from *Top* to *Bottom* is rainfall gradient driving regional-scale but episodic infiltration events (top wetting); from *Left* to *Right* is drainage gradient driving local-scale but more stable water-oxygen status (bottom wetting). Increasing rainfall (*Top* to *Bottom*) wets a deeper profile. Deteriorating drainage (*Right* to *Left*) increases groundwater access but also oxygen stress. At any point in the landscape, the soil water profile reflects both wetting mechanisms, with a dry gap that diminishes toward wetter climates or lower grounds. For example, in an arid climate on uplands (case 1), shallow infiltration leads to shallow rooting (25). Downslope (case 2), occasional deep infiltration (35) leads roots across the dry gap (25, 26). This explains why both the shallowest (case 1) and deepest (case 2) roots are found in dry climates; the polarizing root behavior reflects the polarizing soil hydrology with and without groundwater access (15,

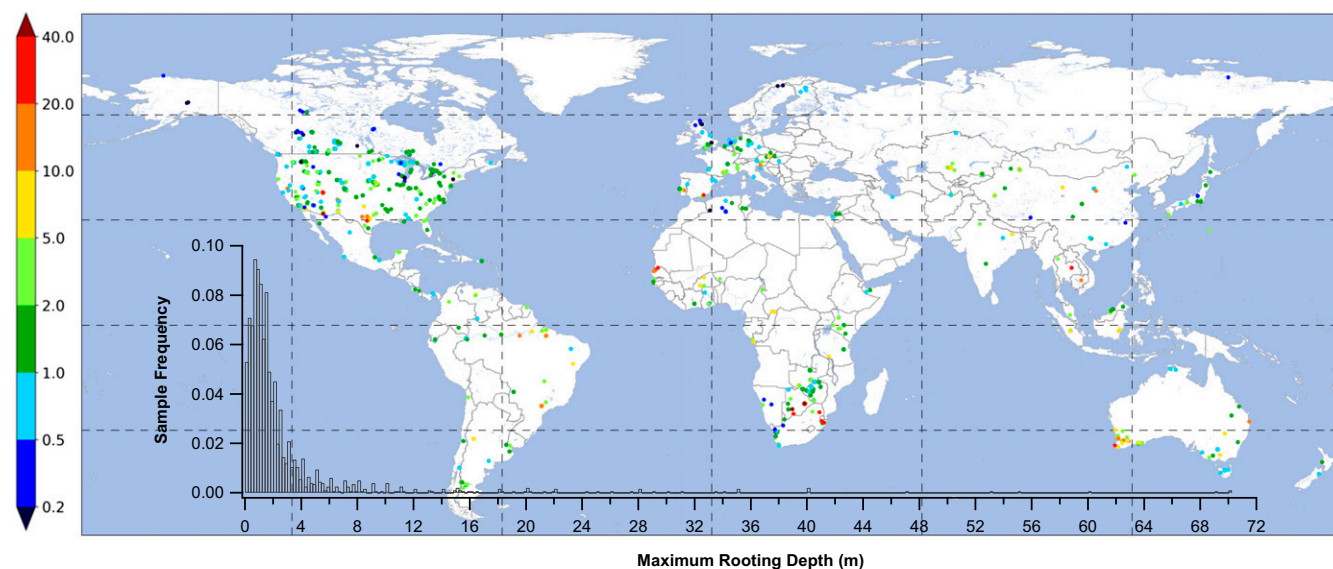
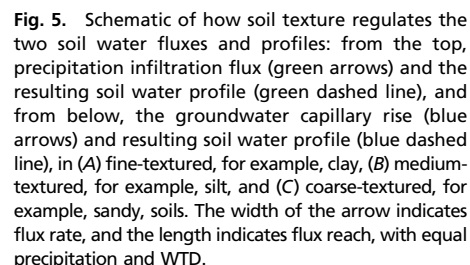


Fig. 2. Maximum observed rooting depth (in meters). Points overlap due to multiple samples in a small area. The deepest root is shown at sites with multiple samples. *Inset* gives frequency distribution (0.2-m bin width).

Fig. 4. A hydrologic framework for interpreting plant rooting depth along the climate gradient (vertical axis) defining regional patterns in infiltration depth and frequency, and land drainage gradient (horizontal axis) defining local patterns in groundwater accessibility and oxygen stress. See text for discussions of the cases.

The distribution of maximum uptake depth from the inverse model (Fig. 6) suggests a much higher occurrence of very shallow (especially northern continents) and very deep (especially southern continents) uptake than observed (bars). It may be that current field sampling of roots is biased toward moderate climates, and that it may have stopped too soon in seasonal and arid climates (6, 42, 43), missing a vital part of the plant that may

The insights gained here are highly relevant to Earth System Modeling, an essential tool for understanding past and predicting future global change that regulates and is regulated by land plants. Current models prescribe rooting depth according to plant functional types, and neglect landscape-scale topography and the resulting hydrologic convergence from high to low grounds, a fundamental hydrologic process that creates a strongly articulated, fine-scaled spatial structure in water availability regardless of the climate (24, 44). Here, we demonstrate that this hydrologic structure is a potent force in shaping plant rooting depths, a biological response that may further differentiate plant–water relations from uplands to lowlands. The adaptive ability of plant roots to reach deep soil and groundwater has important consequences for the hydrologic cycle and regional climate through land–atmosphere interactions, and it may have expanded the hydrologic habitats for



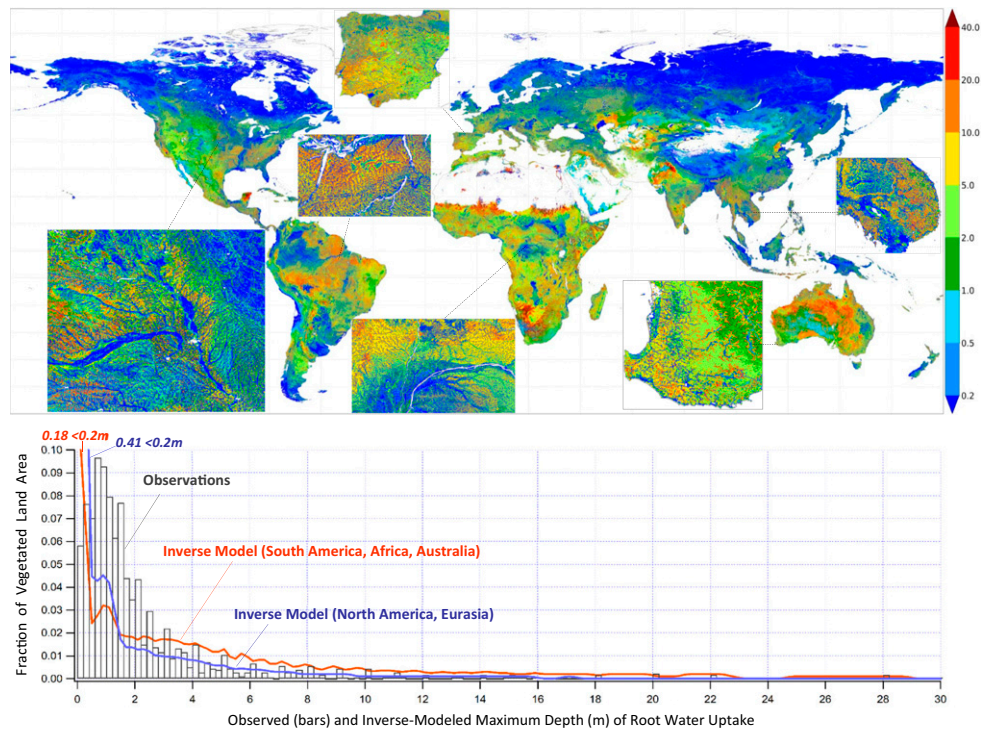


Fig. 6. Inverse-model results of 10-y mean maximum depth (in meters) of root water uptake (*Upper*). *Insets* reveal strong local topographic influence. The frequency distribution (*Lower*, 0.2-m bin width), over vegetated surface only, suggests large model–observation discrepancy, which may imply observation bias (undersampling of very shallow and very deep roots). The oscillations in the model distribution are due to soil water uptake crossing discrete soil layers.

land plants by allowing them to survive water-stressed periods. Therefore, accounting for landscape-scale topography, the resulting hydrology, and the consequent plant root–water interactions in

Earth System Models may enable critical mechanistic pathways in these models for exploring and predicting global change that are strongly mediated by land plants.

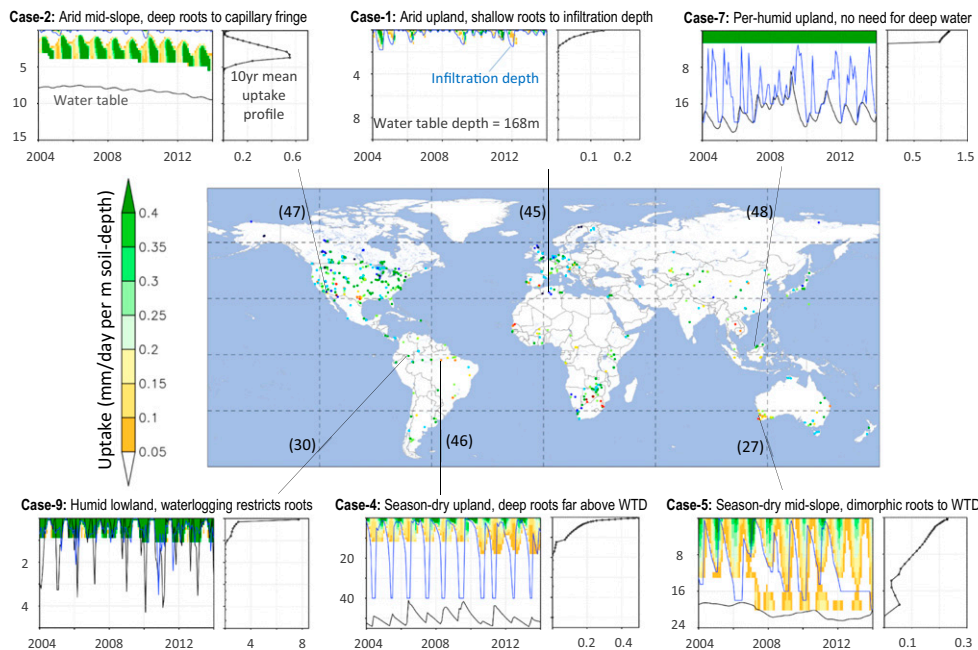


Fig. 7. Modeled uptake profiles at six grid cells with rooting depth observations (27, 30, 45–48), corresponding to six cases in the conceptual model of Fig. 4. The colored panels plot monthly root water uptake (in millimeters per day per meter soil depth) over the 10 y of simulation, at different soil depth (in meters), with monthly mean infiltration depth (blue line) WTD (gray line). The 10-y mean uptake profile is shown to the *Right*. The map at *Center* is a reduced version of Fig. 2. The model exhibits the same behavior as observations under different climate/drainage combinations. In the desert, observations are of single plants not detectable by satellites, so model results of a nearby grid are shown, which have higher leaf area index and thus deeper uptake than observed.

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