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BOOK REVIEW

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Fossil soils: trace fossils of ecosystems on land and windows on the context of evolution

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Abstract

This is a review of *Soil Grown Tall: The Epic Saga of Life from Earth*, by Gregory J. Retallack. In this book, Retallack shows how soils and life have coevolved over the last 3.5 billion years, and what soils tell us about the environments in which various terrestrial organisms have evolved and flourished. A theme of the book is the Proserpina Principle: producers consume CO_2, consumers exhale it, and alternating dominance of producers and consumers alternates global warming and cooling, while keeping temperature within life-permitting limits.

Keywords: Ancient life on land, Ediacaran biota, Evolution of grassland, Evolutionary innovations affecting climate, Fossil soils, Gaia hypothesis, Global climate change, Mass extinctions, Origin of life in soil, "Proserpina Principle"

Book details

Title:	Soil Grown Tall: The Epic Saga of Life From Earth,
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Book review

Fossil soils and their remnants fascinated Gregory Retallack ever since he was a child. He pursued this interest as a student, postdoctoral researcher and professor of geology at the University of Oregon. He has published on topics ranging from the evolution of grassland, global climate change, and mass extinctions to Martian soils, and has sparked great controversy. *Soils of the Past* (Retallack 2019a) is a scholarly summary of his work. *Soil Grown Tall*, reviewed here, is a shorter summary intended for a wider audience. It is not the "easy night's read" promised on the back cover, but it is clear, readable, and well worth taking the time to read.

The book's stated aim is to look "backward into deep time to develop an appreciation of the coevolution of life and soil over the ages that followed life's origin" (p. 1). This book does devote much attention to how soils and the ecosystems they supported shaped each other's evolution. Its primary thrust, however, is how fossil soils reveal the environments in which different terrestrial organisms evolved and amplify our understanding of how certain ecosystems evolved. Some of his inferences from fossil soils provoked bitter controversy and overturned deeply rooted beliefs.

After stating the book's aim the first chapter recounts how he got interested in fossil soils in Sydney, Australia, as a child, his graduate education, and his career in the United States. He ends it by proposing the "Proserpina Principle," the alternating dominance of carbon consuming primary producers and carbon dioxide producing consumers, as a lens for viewing ecosystem evolution as revealed in fossil soils.

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The second chapter presents the basic structure of a typical forest soil, with an ‘A layer’ of mixed litter and mineral grains above a ‘B layer’ largely dominated by clay and a C layer of weathered rock or sediment. Next he introduces a variety of soils: desert soils (aridisols), swamp soils (histosols) full of peat, grassland soils (mollisols), fertile forest soils (alfisols), infertile forest soils (ultisols and sandy spodosols), deeply weathered tropical forest soils (ultisols) and many others. He shows that soils vary with climate and vegetation, but are little affected by bedrock. The first two chapters reveal Retallack’s fine feel for landscapes and his love of madcap adventure, which have led him to spectacular landscapes and novel soils. His feel for landscape lends power to his studies of fossil soils and to the summary he has written of his life’s work. What can we learn from fossil soils?

Retallack’s first example of the interplay between soil and biota is that between soils and past human civilization. His clearest example is that between soils and human culture in ancient Greece. Immigrant farmers deforested the Peloponnesus for agriculture ~3000 BC, triggering massive mud flows and depopulation by 2000 BC. Forest returned as did another alfisol, less thick than the first, allowing renewed agriculture that supported Mycenaean civilization. Again, agriculture wore out the soil, causing chaos, depopulation and a prolonged dark age that allowed forest to return and soil to recover. Renewed agriculture supported the flowering of classic Greek civilization ~500 BC. Overexploitation ruined the soil by Plato’s time, and Greek civilization only survived by importing grain from what is now Ukraine. That civilization breeds hierarchy that breeds social injustice that leads to overexploitation of the environment is an old story, foreshadowed in Isaiah 5: 8–10.

Retallack then discusses how sequences of fossil soils reveal how global climate change affected human evolution. In Europe, Cromagnons, *Homo sapiens*, from the south displaced *H. neanderthalensis* during a brief global warming 40,000 years ago (p. 51). An interglacial global warming 130,000 years ago may have enabled African races of *H. sapiens* to replace *H. heidelbergensis* and *H. antecessor* in Europe (p. 54). In east Africa, an earlier warm period 1.2 million years ago caused woodland to replace wooded grassland, where *H. habilis* lived and desert scrub, where *Australopithecus boisei* lived, enabling the larger-brained *H. erectus* to replace both and spread all through Eurasia (pp. 55–59). Previous spells of hominin diversification were terminated by global warming, which made habitat more uniform and allowed only one species to replace them (p. 60). Haile-Selassie (2021) worked out the history of hominin evolution, but paleosols revealed the ecological setting of this evolution.

Next, Retallack explains how grazers, not climate change, drove the evolution of grassland. Grasslands found a new way of dealing with grazers: growing at their bases, not their tips, which allowed them to maintain grazer populations dense enough to exclude trees (McNaughton 1985). Grasslands transform soils, forming small, soft, fertile clods, grassland soils’ distinguishing feature. Grasslands cool the climate by burying carbon. The layers of fossil soils in the South Dakota badlands reveal the origin of bunch grasslands and grazers with teeth that can sustain wear from the silica grit in grass blades (pp. 76–79). The layers of fossil soils of the NW Nebraska badlands record the evolution 19 million years ago of short-sod grasslands, more effective grazers, and pack-hunting predators that forced grazers to form herds (pp. 79–81). Sod grasslands yield soils with yet smaller clods that distinguish them from bunch grassland soils. Finally, tall sod grassland, powered by C_4 photosynthesis, superior to the normal C_3 photosynthesis at low atmospheric CO_2 levels, evolved simultaneously in various parts of the world 7 million years ago (p. 83: see also Brown et al. 2011). C_4 photosynthesis increases the proportion of ^{13}C in soil and grazer bones, allowing the detection of tall sod grassland soils. McNaughton (1985) showed that the interaction between grazers and grasslands was remarkably mutualistic, but Retallack shows that grazers drove grassland evolution.

After explaining how fossil soils helped show that the collision of a 10 km-wide bolide with gypsum beds in Yucatan caused a mass extinction (ch. 6), a dramatic but familiar story (Schulte et al. 2010), Retallack turns to the origin of flowering plants (angiosperms). Like Jud and Hickey (2013) and Jud (2015), he thinks that the first angiosperms were small, weedy herbs of thin soils frequently disturbed by floods or storms (p. 105). Early angiosperms had inconspicuous flowers (p. 105): Retallack (p. 104) ascribes their initial success to the lack of delay between pollination and fertilization that afflicts ferns, horsetails and gymnosperms. Later, when angiosperm forests occupied floodplains, their litter fertilized the soil and favored the conversion of CO_2 into carbonic acid, which enhanced soil weathering (p. 112). Both carbon consumption and carbon burial reversed the trend to global warming induced by the dominance of animals during the first half of the Cretaceous.

Retallack says nothing about how animal pollinators later enabled a diverse set of fast-growing flowering trees whose litter fertilized the soil to replace a less diverse set of slower-growing wind-pollinated conifers whose pesticide-crammed litter poisoned the soil (Leigh 2010). This omission is serious, for animal pollination and seed dispersal allows seedlings to escape their parents’ specialized pests rather than use growth-slowing defenses against them (Leigh 2010). He is silent about how the fourfold increase in flowering plant vein density 100 million years ago enabled much higher photosynthetic capacity in their leaves and increased rainfall by increased transpiration (Boyce et al. 2009; Boyce and Lee 2010). Finally, he touts a 45 million year-old Oregon forest (then in a tropical climate) as the first flowering tropical rainforest, ignoring the 57 million year-old Colombian rainforest described by Wing et al. (2009).

Next, Retallack explains what soils dinosaur bones are found in or near reveal about the types of places they lived in (cf Retallack 1997). In the Jurassic, 153 million years ago, dinosaurs were the largest land animals. Huge, long-necked sauropods lived and left footprints in clayey alfisols where the depth of calcium nodules suggest rainfall of 600–900 mm rainfall per year and traces of stout roots and rare permineralized seeds and shoots indicate coniferous forest (p. 119). This era of animal dominance was a time of global warming, when forests extended to the poles, although polar forests had strong growth rings (p. 122).

Before the age of dinosaurs, a massive extinction 252 million years ago eliminated > 90% of the earth's species and killed nearly all the earth's trees. There were no coals for 6 million years. A depauperate vegetation of quillworts (*Isoetes*) and conifers tolerant of infertile soils replaced the diverse Permian tropical forests (pp. 125, 131, 132). What happened? Post-extinction soils at an Antarctic site lasted only a few thousand years but were deeply weathered and nutrient depleted, suggesting truly intense heat (pp. 133–5). Changes in the proportion of the isotope ^{13}C in fossil soils worldwide signal huge increases in the greenhouse gases CO_2 and methane. Oxidizing methane and dead plant matter cut the atmosphere's oxygen content to 12%, killing the world's trees by depriving their roots of oxygen. The largest lava eruption in the last half billion years, which pierced thick coal beds, caused this catastrophe (pp. 136–141).

Before the extinction, trees evolved, transforming soils. The earliest fossil trees occur in 370 million year-old reworked sandstone and pond shales, interbedded with thick, fertile alfisol-like soils riddled with abundant tree root traces denoting forest (pp. 148–9). The first swamp forests appeared 360, the first forest on deeply weathered oxisol, 305 million years ago (pp. 152–4). Lacking wood decomposers, forests stored carbon in their wood, swamp forests in peat that became coal. Tree roots enhanced weathering, which consumes carbon. The less CO_2 in the atmosphere, the more stomates per unit area of leaf a plant needs to acquire CO_2 for photosynthesis (McElwain and Chaloner 1996). The decrease in stomatal density starting 350 million years ago shows that carbon consumption drove atmospheric CO_2 down to premodern levels, causing glaciation in the Carboniferous and Permian (p. 156). The first lignin-decomposers, white rot fungi, evolved ~ 296 million years ago, sharply reducing carbon burial (Floudas et al. 2012). These fungi evolved in time to help oxidize the trees killed by the oxygen shortage 252 million years ago.

In 1983, Retallack's knowledge of fossil soils enabled him to recognize the earliest traces of land animals yet known (p. 160). A Pennsylvanian soil, 444 million years old, had burrows like those of millipedes. This clay-rich soil's calcareous nodules signaled a dry-climate aridisol, otherwise depleted in calcium, magnesium and sodium, clearly a soil, not a sea-floor deposit. A bilaterally symmetric animal made the burrows. No land millipedes this old have yet been found (p. 162), but molecular evidence suggests that millipedes appeared on land late in the Cambrian (Rota-Stabelli et al. 2013). Millipedes eat dead vegetable matter. Lenton et al. (2012) ascribed the global cooling during the Ordovician, that caused glaciation, to the greening of the land. Cambrian and Ordovician soils contain abundant liverwort-like spores (p. 164). Retallack (2019b) finally found 460 million year-old fossil liverworts, hornworts, mosses, lichens, and mycorrhizae in Tennessee (p. 164): nonvascular plants had indeed colonized the land.

Knowledge of fossil soils also enabled Retallack to show that a set of late pre-Cambrian (Ediacaran) organisms, long considered macroscopic marine animals, were terrestrial. This idea bred intense resistance, hence this chapter's close, careful reasoning and signs of irritation at poor opposing arguments. Others already saw that none of these "animals" had mouth, gut or anus (p. 172) or the cell structure (p. 175) of animals. Some supposedly soft-bodied exemplars left impressions 5 mm deep in the sandstone, under 6 km of rock, that they were buried in (p. 171). They were as tough as lichens and hardly more compressible than tree trunks (p. 174). Like glomeromycotan fungi, they contained cholesterol; like green algae, they contained stigmasterol (p. 183). Some were preserved with internal structure resembling a mass of fungal hyphae and dark spots on the outside, perhaps the remains of algae (p. 176). Moreover, the spread of these organisms was associated with global cooling and glaciation, which lichens that photosynthesize and enhance weathering would cause (pp. 183–4).

Next, Retallack shows how the "great oxidation event" 2.4 billion years ago affected soils. He compares thick, clayey, deeply weathered, well-drained soils ranging in age from 800 to 2460 million years ago, with evidence of photosynthetic microbe activity. Before the great oxidation, the atmosphere's oxygen content was 0.03%. Soils younger than 2.4 billion years contained reddish oxidized iron; older soils contained greenish unoxidized iron. One well-oxidized 2.2 billion year-old soil contained fossils ~ 1 mm long resembling modern *Geosiphon*, a glomeromycotan bladder-shaped fungus harboring cyanobacteria. If they are indeed fungi, our idea of when complex multicellular life evolved would need radical revision. A 3.1 billion year old soil harbored photosynthetic sulphur bacteria, methane-generating microbes and other bacteria, as did other soils up to 3.5 billion years old. Life of some form lived on land for most of the earth's history.

He next discusses "soils" on Venus and Mars, which never had life, and Mars. Under a stony layer at a site on Mars is a clayey fossil soil 3.7 billion years old with abundant sulphate resembling 3.1 billion year-old desert soil on earth (p. 213), suggesting life was present on Mars while it still had an atmosphere and braided rivers of running water. If so, life died out when Mars lost its atmosphere and liquid water. "Soils" of Venus and the moon have no clay. On the other hand, Ceres, a planetesimal 1000 km in diameter, has clayey, carbonaceous soil whose carbon compounds include sugars and amino acids. How this soil came to be is mysterious.

In Retallack's penultimate chapter, he argues that life evolved in soil. First, he justly dismisses two other explanations. The first asserts that lightning strikes through an anaerobic atmosphere of CO_2 or ammonia on a lake or sea transformed it into an organic soup propitious for life's origin by producing dissolved amino acids, sugars &c (p. 228, cf Miller 1953). This soup, however, would always be too dilute for these compounds to form building blocks of life. The second asserts that life evolved in volcanic vents, where reaction of vented fluids with oxygenated seawater provides an energy subsidy supporting abundant life. This subsidy, however, depends on oxygenated seawater. Then Retallack (pp. 228–233) sketches steps by which life could evolve in soil, starting with developing clays propitious for life's origin.

Another possibility, however, is that life began in alkaline vents several kilometers from the zone of volcanic vents. In these vents, alkaline water, 60° to 90 °C, pH ~ 10, replete with hydrogen, met cooler water, pH ~ 7, replete with dissolved CO_2 and ferrous (unoxidized) iron in a mass of minute cells with semipermeable walls of FeS studded with catalytic lumps iron, sulphur and nickel. This setting still hosts a series of reactions forming methane from H_2 and CO_2, an abiotic prototype of the acetyl coenzyme A pathway by which anaerobic microbes now combine H_2 and CO_2 to make organic compounds and release energy (Lane 2015, pp. 131–133). Many of the FeS walls separate fluids differing greatly in acidity (Lane 2015, p. 134), generating a proton motive force analogous to that used by all archaea and bacteria to generate adenine triphosphate from adenine biphosphate (Mitchell 1961). No other setting provides an energy subsidy, prototypes for the two main ways anaerobic microbes harness it, and a setting where compounds generated by the energy subsidy may accumulate and react with each other (Martin et al. 2008; Lane 2015).

In the final chapter, Retallack first summarizes his Proserpina Principle: producers consume CO_2, cooling the planet; consumers exhale CO_2, warming it. Producers and consumers alternate dominance, cooling and warming the planet by turns. Soils help drive this alternation. More atmospheric CO_2 promotes global warmth, which spreads soils like oxisols, ultisols and mollisols that support high plant productivity, which then cools the planet. Global cold spreads desert and tundra soils that support such low productivity that volcanic outgassing can restore the atmosphere's CO_2 content (pp. 242–3). Organisms also play a role: trees weather soil which, like their photosynthesis, promotes global cooling as in the Devonian and Carboniferous. Wood decay organisms like white rot fungi (evolved 296 million years ago, Floudas et al. 2012) and termites (evolved 230 million years ago, p. 235) turn wood into CO_2, promoting global warming. Yet this alternation of dominance kept temperature within livable bounds, slowly cooling the plant by drastically reducing atmospheric CO_2 as the sun warmed (p. 246). Without life, the earth would have warmed by 50 °C during the last 4 billion years (p. 184).

To explain this temperature stability, Lovelock (1979, 1988) proposed that the biosphere was a superorganism (like a termite colony) regulating temperature and other conditions to be favorable to life (the Gaia hypothesis, p. 239). The Proserpina Principle's temperature regulation by alternating overshoots contradicts this hypothesis (p. 247). Nevertheless, life's story is not that of a zero-sum war of all against all, but a progressive expansion of ways of life, complexity, productivity, interdependence and mutualism (Vermeij 2011, 2013; Leigh and Ziegler 2019).

How did this expansion happen? Organisms change the environment, often for their own benefit, for example, by increasing their control over the cycles of elements essential to life—carbon, nitrogen, phosphorus, oxygen, and water (Vermeij 2011, pp. 199, 202). The most effective and enduring competitors benefit their resources, enhancing their availability by indirect feedback loops, thereby stabilizing their ecosystems (Vermeij 2013, pp. 8, 9). A top competitor must perform many functions. Cooperation, as in honeybee or termite colonies with complex division of labor, and other forms of interdependence can be effective ways of enhancing these varied abilities (Vermeij 2011, p. 197). The diversity and productivity of modern ecosystems accordingly depend on mutualisms such as those between plants and soil microbes—mycorrhizae, nitrogen-fixing bacteria and soil-weathering agents.

Retallack's book is well stuffed with insights and ideas, some quite startling. The drone bass is what fossil soils tell us about the ecological stage where the evolutionary play revealed by fossils is played. The evolution of grasslands is revealed mainly by their distinctive fossil soils. Understanding how fossil soils worked helped show that grazers, not global cooling from the rise of the Himalayas, drove grassland evolution. Ability to recognize fossil soils enabled him to see that certain Ordovician burrows were in soil, not seafloor sediment, showing that bilaterian animals were then living on land. This same ability enabled him to see that Ediacaran organisms were terrestrial, probably lichens. The storm caused by this idea has yet to end. Another theme is the Proserpina Principle, the alternate dominance of plants and animals, alternating global cooling and warming, thanks largely to how global climate affects the world's spectrum of soils. Yet, this alternation stabilizes climate over the long run. Indeed, organisms have made earthly habitats more and more propitious to life, showing that life is not a zero-sum war of all against all (Vermeij 2013, p. 8). Like other geologists with a long-term perspective on evolution, he takes the Gaia hypothesis seriously, abstracting its truth from the fictitious superorganism. This is quite a mix of achievements for one book.

The book shines with a sense of the beauty of landscape, which has served Retallack well. The book is full of well-chosen reminiscences, which lend life to the narrative. He is fond of ancient goddesses, a fondness which served him well in Greece (Retallack 2008) but is merely distracting in his final chapter. The book is clearly written, well illustrated, and well produced. Springer has priced it extremely reasonably, and deserves to benefit by a large sale.

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