



Roots, rock, and regolith: Biomechanical and biochemical weathering by trees and its impact on hillslopes—A critical literature review



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ABSTRACT

The role of trees and forests as a critical component of the biosphere and critical zone, and of the Earth system more generally, is widely appreciated. Less known and acknowledged are the geomorphological functions of tree roots, although their importance has been widely referred to in soil studies, paleopedology, and paleobotany. Tree roots and their impact on weathering processes and soil production were incorporated in the *Devonian plant hypothesis* and tree root casts served as a key evidence of recognition of past soils in geology, sedimentology, and paleopedology. However, knowledge of biomechanical and biochemical weathering induced by vascular plant roots (mainly trees) has been rarely utilized in geomorphic studies. Biogeomorphic and pedologic studies in recent decades have highlighted the importance of tree uprooting, in which roots play a primary role, in soil development, regolith disturbance and bedrock mining. Other important functions of roots were also recognized, e.g., soil displacement by growing roots, infilling of stump holes and root cavities, root groove development, direct and indirect effects taking place in the rhizosphere and mycorrhizosphere (mainly biochemical weathering of minerals, support by microbial communities and symbiotic fungi), and changes in porosity, permeability, and hydrology of soils in the root zone. However, further studies are urgently needed because many aspects of biochemical and biomechanical weathering are not well understood. This is especially true with respect to taxa-specific impacts. Variations in root architectures, edaphic settings, ecological relationships, and geographic ranges result in substantially different biogeomorphic impacts of different tree species. Additionally, the same species in different environmental settings may have different effects.

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1. Introduction

Trees interact with their environment in complex ways, and this phenomenon has been a subject of interest for more than a century. While much of this work was motivated by interests in silviculture, agriculture, and forest ecology, we focus here on Earth science perspectives. As early as the late 19th century, the attention of forest soil scientists and geologists was focused on their most hidden part—tree roots. It was hypothesized that roots “(...) *act substantially like subsoil plows*” (Shaler, 1892; p. 271). After a century of research, Earth scientists concluded, for instance, that “*root growth and animal burrowing disrupt bedrock that is weathered but structurally intact, creating a loose material free to move downslope.*” (Dietrich and Perron, 2006; p. 412). Both statements are important and address the same issue but from different points of view: 1) soil or regolith and 2) hillslope evolution. Soil geomorphology and biogeomorphology made an attempt to combine these points of view while focusing on scale differences of phenomena involved in the process of soil/regolith and landscape evolution. For instance, soil mixing and various forms of disrupted horizonation are common features observed in soils, described for instance in the Charles Darwin’s last, “worm” book (Darwin, 1881; Johnson and Schaetzl, 2015) and early forest soil reports (e.g. Lutz and Griswold, 1939). From the hillslope perspective, disturbances induced by trees through their root systems often contribute to downslope movement of weathering products and soil material and thus act as factors of hillslope morphodynamics. These are common issues in soil and geomorphic studies but they are frequently omitted in biological analysis (Pregitzer, 2008; Hodge and Berta, 2009).

In this context, we ask whether the present state of geomorphic knowledge allows us to formulate any clear statement about weathering induced by growing tree roots. Yatsu’s (1988) treatise on weathering doubted the process is possible at all (see also Pawlik, 2013). This paper seeks to identify the effects of tree roots on rock weathering and assesses their general importance at the global scale. If the process of the physical and chemical weathering induced by tree roots is significant, it should have far-reaching consequences for geomorphic systems (e.g. modulating sediment flux and balance). Because interactions between biotic and abiotic environmental factors are increasingly incorporated in geologic and geomorphic studies, the answer to the abovementioned question should be a valuable contribution to such disciplines as biogeomorphology (Viles, 1988; Viles et al., 2008; Corenblit et al., 2011), ecogeomorphology (Hupp and Osterkamp, 2013), geoecology (Trofimov and Kurilenko, 2015), and geobiology (Brantley et al., 2011).

Additionally, past views on trees and their role in environmental evolution and functioning are highly contrasting and can be a source of unclear messages (e.g. Yatsu, 1988). First, we have to distinguish a variety of disciplines that study or incorporate into their own analysis knowledge on the roles, functioning and physical, chemical and biological effects of roots. Equally important is the scale of analyses and the level of generalization of the key functions of tree roots.

Geomorphologists and engineers have generally viewed trees and their root systems as a factor of hillslope and river bank stabilization, with retarding effects on erosion and mass wasting processes (e.g., Gilbert, 1880; Jahn, 1989; O’Loughlin, 2005; Steinacher et al., 2009; Buma and Johnson, 2015). However, if we take into account

another biomechanical process—tree uprooting—the problem becomes even more complex (Schaetzl et al., 1989a, 1989b; Phillips et al., 2015; Šamonil et al., 2010; Finke et al., 2013; Pawlik, 2013; Pawlik et al., 2013, 2016). Recently, some authors point to a dualistic function of trees after taking into account their long-lasting effect on soils during their undisturbed growing and sudden biotransport of material and disruption of regolith during uprooting (Almond et al., 2008; Hughes et al., 2009). The geomorphic efficacy of uprooting is closely related to root properties, and this factor has been raised to the rank of a phenomenon modulating the evolution of landscapes (Gabet and Mudd, 2010; Roering et al., 2010). Uprooting, an example of proisotropic pedoturbation, can cause soil transport, biomechanical weathering, and both upbuilding or reduction of soil thickness and is considered a predominantly regressive pathway of soil development (Johnson and Watson-Stegner, 1987; Johnson et al., 1987; Amundson et al., 2015).

In this paper, we try to focus on a fundamental function of trees—rock weathering by expanding tree root systems (Johnson, 1993). We will review literature about tree roots acting as a biogeomorphological force driving processes within the boundary zone between regolith and bedrock, a part of the Critical Zone (Amundson et al., 2007; Lin, 2010; Brantley et al., 2011). Additionally, we will explore tree roots/bedrock/regolith interactions and their mutual dependences.

2. Early views on the role of plants in geomorphic and soil processes

In the history of geomorphological research, trees have been analyzed in a variety of environmental contexts and spatio-temporal scales. Traditionally, forest communities are considered as one of the vascular plant formations that effectively minimize erosional processes and support hillslope and river bank stability over short- and long-time periods. They also effectively contribute to soil strength, reducing probability of shallow landsliding (O’Loughlin, 2005; Marston, 2010).

However, from the beginning of geological and geomorphological studies, researchers pointed to more than one critical function of plants. For instance, Gilbert (1880, p. 95) observed that “*Plants often pry apart rocks by the growth of their roots (...)*” but also that “*(...) the general effect of vegetation is to retard erosion (...)*” (p. 99). This observation was supported by Merrill (1906), who agreed that “*both plants and animals aid to some extent in the work of rock disintegration*” (p. 180). The author noticed that “*roots, (...), serve to enlarge the rifts (...)*” and this process facilitates access of rain water, leading to farther rock deterioration (p. 180).

Proof of early attention to apparent effects of roots on bedrock weathering can be found in impressive descriptions and drawings presenting tree roots physically disrupting places they occupied. For instance, Stephens (1843) described an elm tree growing on an ancient wall where “*(...) fibres crept into cracks and crevices, and became shoots and branches, which, as the trunk rose, in struggling to rise with it, unsettled and overturned the wall, and still grew, carrying up large stones fast locked in their embraces (...)*” (p. 392–395) (Fig. 1).

A far more detailed early theory of soil production by root activity was given by geologist Nathaniel Shaler (1892) in his influential “*The origin and nature of soils.*” He found the following root–rock interactions (Fig. 2):

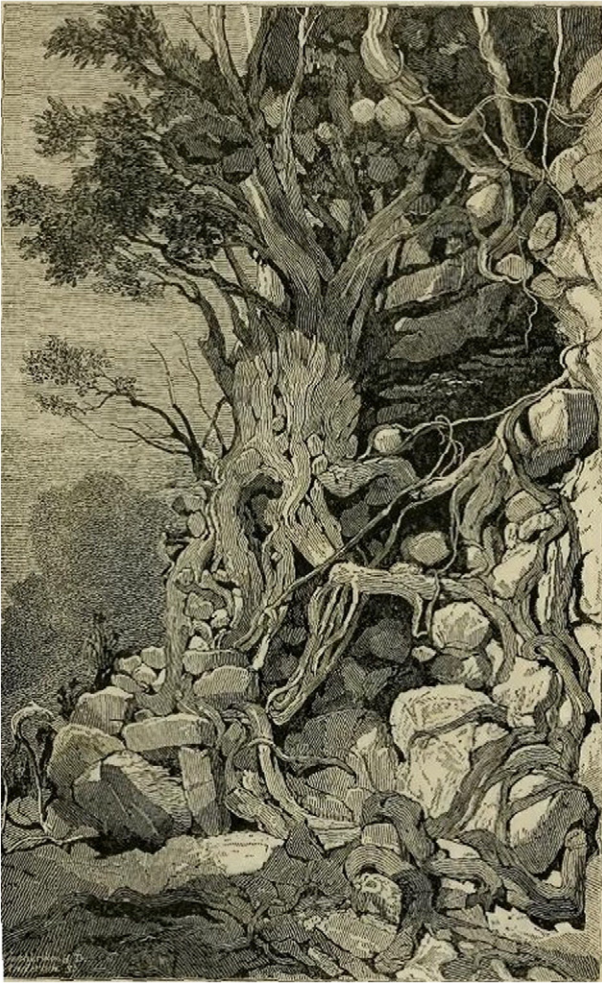


Fig. 1. Root deterioration of an ancient wall, the Malayan ruins at Kabah, Mexico (Stephens, 1843; p. 393; see also Viles, 1988; p. 337).

1. during their growth, roots push the soil outward and may “exercise a powerful wedging action”;
2. many generations of large roots of forest trees and the movement during their growth may “grind the particles of soil against each other”;
3. roots penetrate crevices and grow in them, disrupting the rock mass;
4. “small roots penetrate fissures and break up the decayed portion of the mass” and this process promotes chemical weathering;
5. initial roots “break up the rock and open its structure,” leaving easier access for the next roots.

A similar view of root growth processes and influence on soils was recognized by Shaler's student, William Morris Davis, who hypothesized that trees can contribute to soil creep (Davis, 1899; see also King and Schumm, 1980) (Fig. 3). The idea was reiterated recently, but based on the additional assumption that growing tree roots push the soil upward, so that after root decay, the mass is displaced downslope (Gabet et al., 2003; Field and Little, 2009). Together with other biologically induced diffusive hillslope processes (e.g. tree uprooting, animal burrowing), it has been included in a concept of biogenic creep (Lehre, 1987; Wilkinson et al., 2009) and biological saltation (Biro, 1966). Hypothetically, due to multiple tree-uprooting events (repeated soil turnover), soil transport (creep-like soil material movement) might have appeared even on completely flat surfaces (!) (see Gabet et al., 2003). Additionally, the direction of tree uprooting events in relation to topography can even cause upslope soil movement (Šamonil et al., 2016).

3. Biology of tree roots

3.1. Functions of tree roots

Considering biomechanical effects of tree roots and their geomorphic significance, we first have to see them from biological perspective. “Trees, like all plants growing in the wild, must solve a host of problems using their root systems” (Pregitzer, 2008), and this fundamental issue has important consequences for soil and regolith properties. Trees belong to phanerophyte plant life-form (Raunkjær, 1934) and thus their bodies are adapted to face extreme meteorological conditions. They need to withstand periods of drought as well as very low temperatures, competition with other tree species, injuries from animals, other falling trees, lightning, etc. There is no doubt root systems play a major role in overcoming these stress factors and/or recovery after a disturbance. Along with this general function, root systems (Kramer and Boyer, 1995; Little and Field, 2003; Pregitzer, 2008; Hodge and Berta, 2009):

1. anchor trees to a substrate (although roots of many tree species do not develop stabilizing reaction wood and thick walls of latewood unless exposed to light, Fayle, 1976; Schweingruber, 2007);
2. store nonstructural carbohydrates (simple sugars, starch, and fructans) and use them as a source of the energy;
3. transport the soil solution both up and down (water solution can move in any direction in the plant–soil continuum through a process called hydraulic redistribution, which means the passive conduits of roots and stems move water towards the lowest water potential, Nadezhdina et al., 2010), and transport water and other compounds;
4. fix atmospheric nitrogen, together with their associated symbiotic bacteria and fungi (nitrogen-fixing and rhizobial bacteria), an essential nutrient required for growth.

Thanks to the firm anchorage, trees can contribute functions 2–4 (above). And this “system” makes “plants geochemical pumps that remove bio-essential elements from the soil solution...” (Anderson et al., 2007; p. 327). Nutrients and other elements are protected against faster removal from the soil and regolith in humid regions by their pumping and cycling in active root zone (Lucas, 2001), which in some cases can even cause changes in mineral composition of soil (Lucas et al., 1993). If deepening of gradually leached soil horizons, such as eluvial podzolic horizons, cross the depth of active tree roots, the following pedogenesis can hardly be reversible (e.g. Šamonil et al., 2016). Although upwards direction of solution is prevailing in plant–soil continuum, all directions of solution movement are possible (Nadezhdina et al., 2010). This function is genetically controlled, but it is also modulated by water and nutrient availability, as well as substrate and soil properties. Simply speaking: external morphology of roots is related to their environment (Zwieniecki and Newton, 1995).

3.2. Types of tree roots and root system dynamics

Roots are multicellular organs characterized by gravitropic response, endogenous branching root hairs, and a protective root cap (Kenrick and Strullu-Derrien, 2014). Due to gravitropism (geotropism), roots grow downward and anchor to the soil, regolith, and/or bedrock, providing stability essential for further growth. Some trees develop quickly growing taproots that may reach depths of 10–30 m (Stone and Kalisz, 1991). When stable, plants through root systems can further control secular soil production and processes. Anchoring to a substrate is a domain of woody tree roots (Fig. 4). Non-woody roots are short-lived (up to a year) and are responsible for nutrient and water uptake. In a broader context, three main categories of roots can be distinguished (Hodge and Berta, 2009):

1. primary roots which can be a starting point for a single-axis root system or taproot system, with dominant vertical growth due to gravitropism (Fig. 4);

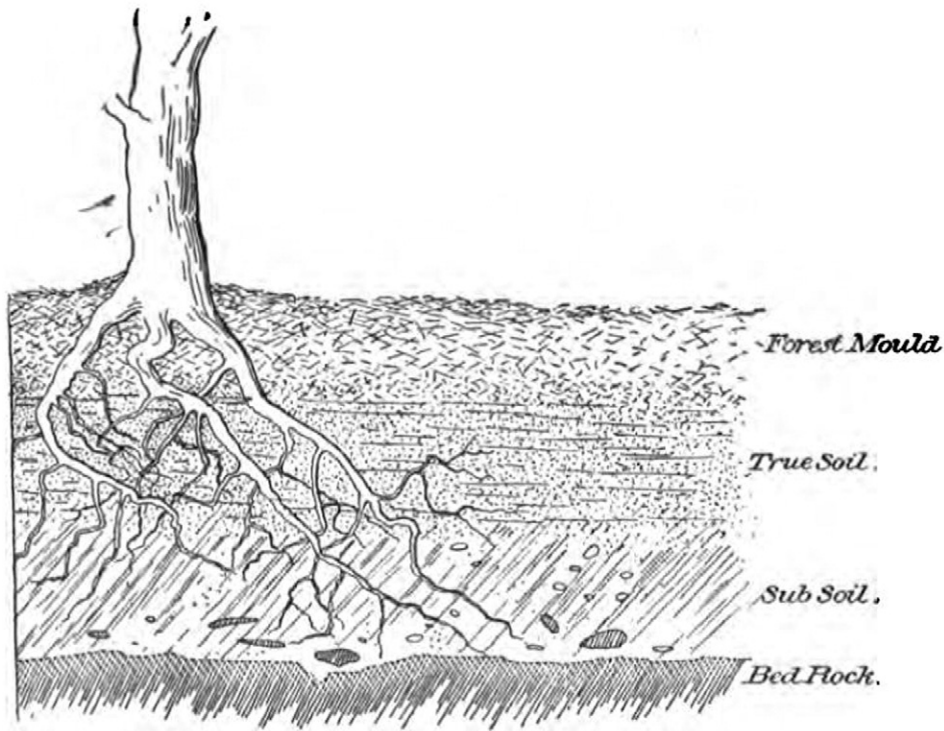


Fig. 7.—Effect of roots of trees on the formation of soil.

Fig. 2. Nathaniel Shaler's view on soil properties influenced by tree roots (Shaler, 1892; p. 270).

2. nodal (or adventitious) roots differentiate from organs other than roots (e.g. rhizomes, stems, etc., for instance, the Banyan tree *Ficus benghalensis* with 3300 aerial roots, Kolkata, India);
3. lateral roots which originate from the branching of a parent axis.

Root hairs play a key role in nutrient uptake because they increase the total root surface area and shorten the distance that ions and water must cover to reach root surfaces. Transport is facilitated by the fact that root hairs can penetrate small pores (>5–20 μm), not available

for roots, and also because they develop in a great number from 20 to 500 cm⁻² of root surface on roots of trees (Kramer and Boyer, 1995).

Traditional views of Earth scientists on root system dynamics were mainly through a prism of observed microscale morphological changes, past or present, for instance, forms of root plates of fallen trees, tree throw mounds, stone rings in places of completely decomposed tree stumps (Phillips and Marion, 2006), and, when fossilized, “tree root casts” (Mossa and Schumacher, 1993). However, this evidence was also frequently neglected or, if documented, wrongly interpreted as,

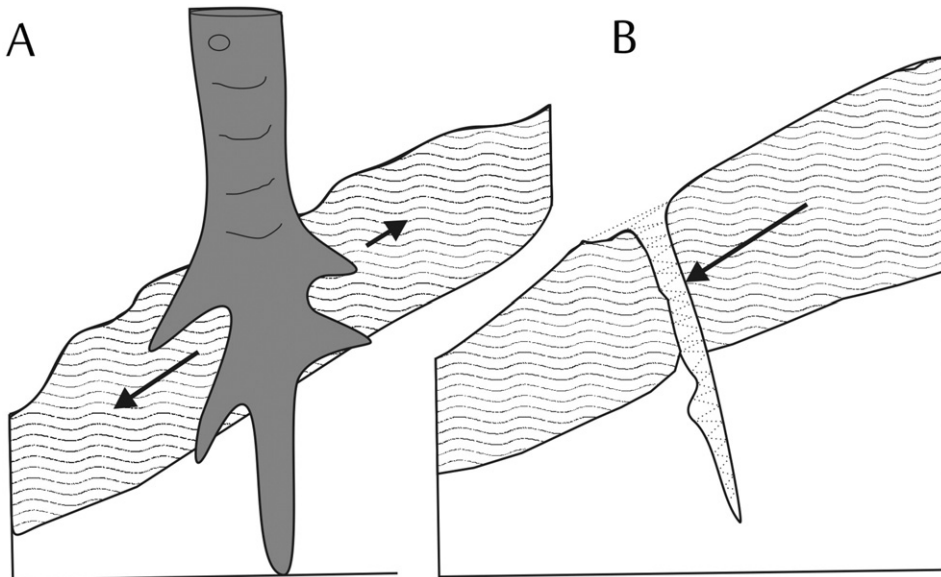


Fig. 3. One of the possible processes involved in soil creep as explained by William Morris Davis (King and Schumm, 1980). Original figure's caption: “Soil creep produced by growth of tree roots. A) During growth, soil is forced downhill. B) During decay, soil from uphill moves into the cavity (from a blackboard sketch).”

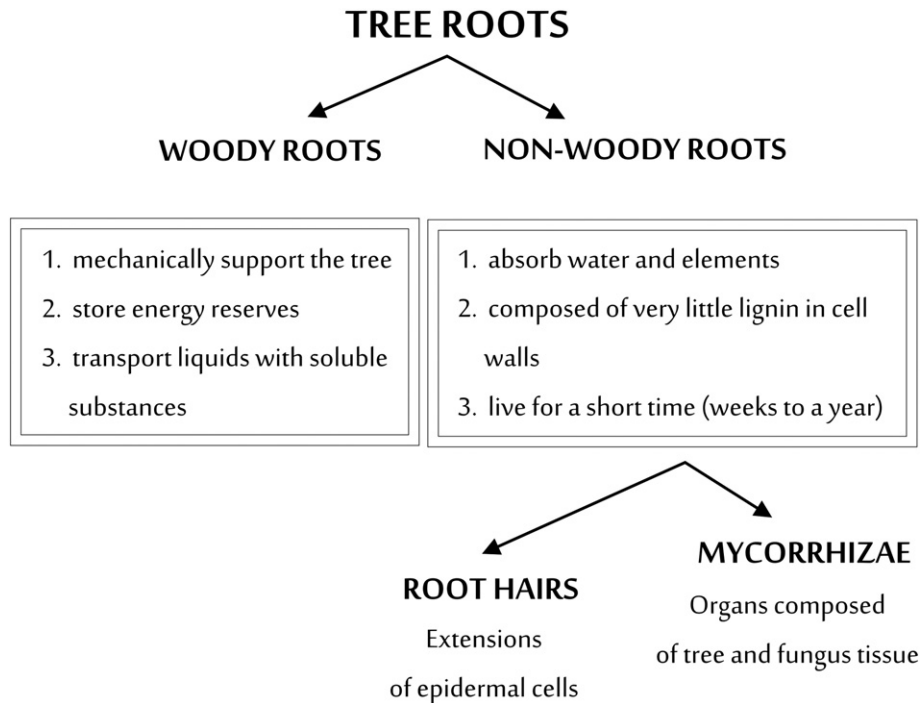


Fig. 4. Main types of tree roots.

for example, an effect of karst or frost processes (e.g. [Embleton-Hamann, 2004](#)). Obviously, the study of the root system development and its consequences on the above and belowground ecosystems is a natural subject of analysis for biologists and this knowledge is a prerequisite for understanding trees influence on geomorphic systems. Biologists refer to root system dynamics as changes in the main properties of the root system architecture (shape and structure) but also anatomical differentiation of roots on the level of individual cells. Hence root system dynamics may include ([Hodge and Berta, 2009](#)):

1. development of new main axes (primary or adventitious);
2. branching—the development of lateral and adventitious roots that represent adaptive response for resource availability or the need to secure anchorage ([Atkinson et al., 2014](#));
3. axial growth—involves two properties of a root, its length and trajectory, which contribute to the dynamic colonization of new soil zones. It occurs from the distal end (root tip) by cell division resulting in root elongation. The root axial growth and its trajectory is forced by a sort of tropism (e.g. gravitropism, hydrotropism, P tropisms, etc.), and it is believed that the root cap plays a major role in this phenomenon by sensing different stimulants. Another interesting property of axial growth is return of root tips to their original direction of growth after passing around obstacles, a behavior known as exotropism ([Kramer and Boyer, 1995](#)).
4. radial growth—can be responsible for increased axial transport properties (particularly axial hydraulic conductivity), increased mechanical strength and anchorage, storage capacity and protection against predation, drought, or pathogens.
5. root senescence and decay—root mortality and turnover are important processes in the development and function of root systems, particularly in perennial plants. Replacement of decaying roots by more efficient new ones (i.e. root turnover) may account for c. 30% of global terrestrial net primary production ([Kramer and Boyer, 1995](#); [Jackson et al., 1997](#); [Hodge and Berta, 2009](#)).

Root system dynamics is also greatly influenced by channels left by decayed old roots ([Stone and Kalisz, 1991](#); [Phillips and Marion, 2005](#)). Using these channels, new roots enter the soil which physical properties, mainly bulk density and water permeability, due to the past

development of tree roots, are significantly improved. Another positive feedback can be created by earthworm activity. Earthworms form channels that provide pathways for root growth, and, as in the case of root channels, they improve aeration and increase the infiltration of water. These two positive feedbacks contradict the opinion that tree roots can be uniformly distributed ([Kramer and Boyer, 1995](#)).

External processes which act upon a tree can also stimulate changes in root anatomy and structure, or influence development of new roots. Geomorphic processes play a special role here and two such cases include 1) burial of tree stems by, for instance, flood or aeolian sediments or debris flow material ([Sigafos, 1964](#); [Alestalo, 1971](#); [Strunk, 1997](#)), and 2) exposure of tree roots by e.g. erosion or shallow landsliding ([Gärtner, 2007](#)). In the first instance, adventitious roots develop directly from buried tree stem. They can appear in several sequences (layers), one above another, indicating subsequent burial episodes. When the burial is sufficiently deep, the original root systems die, and their functions are replaced by secondary adventitious roots ([Alestalo, 1971](#), p. 45). Because development of adventitious roots after burial can be immediate (in spruces) or delayed up to 5 years (other species), their identification is a well-established dating tool in dendrogeomorphology ([Gärtner and Heinrich, 2013](#); [Stoffel et al., 2013](#)). Exposed tree roots are also frequently used as dating technique because during gradual exposition, anatomical changes occur and are similar to those recorded in stems or branches and they are easily detected ([Hitz et al., 2008](#); [Stoffel et al., 2013](#); [Wrońska-Wałach, 2014](#)). In both cases, roots and/or their structural and anatomical changes serve as very precise geoindicators ([Schroder, 2010](#)).

3.3. Rhizosphere—A niche of high microbial activity

When analyzing root system dynamics, we cannot omit the rhizosphere (from Greek “rhizo” meaning “root” and Greek “sphaira”; the term defined by Lorenz Hiltner in 1904 ([Hartmann et al., 2008](#))), the space, a niche of high microbial activity, cylindrical in shape, around actively growing roots which contain the volume of soil that is influenced by root activity ([Yatsu, 1988](#); [Gobran et al., 1998](#); [Little et al., 2004](#); [Gregory, 2006](#); [Amundson et al., 2007](#); [Hodge and Berta, 2009](#); [Lambers et al., 2009](#); [Sokolova, 2011, 2015](#); [McNear, 2013](#)). The

rhizosphere supports microorganisms' growth (e.g. 10^9 bacteria population in 1 g of rhizosphere soil; Yatsu (1988)) and thus stimulates biochemical processes in the root zone (Kramer and Boyer, 1995; Little and Field, 2003). This narrow space is thought to extend up to >10–20 mm from the root surface and it is generally limited to interactions from 1) millimeter scale of microbial populations and immobile nutrients to 2) tens of millimeter scale for volatile compounds and gases released from roots (Gregory, 2006, 2010; Sokolova, 2011).

Rhizospheric processes include (Gregory, 2006):

1. rhizodeposition—C compounds released from living roots into the soil (Lambers et al., 2009), e.g., exudation of low-molecular-weight (LMW) organic acids and enzymes which influence the release of nutrients; and release of gases, e.g., CO_2 (Gobran et al., 1998; see Yatsu, 1988, p. 368, for a complete list of organic compounds in root exudates);
2. enhanced chemical weathering by LMW organic acids.

Probably the first exhaustive description of biochemical interactions taking place in the rhizosphere in an Earth science textbook was by Yatsu (1988). Before, as he noted, geology and geomorphology books rarely referred to the importance of rhizospheric processes in weathering. Since Yatsu (1988) scientists have described in detail rhizosphere effects on the mineral stability and alteration, soil solution composition and nutrients availability, soil formation processes (pedogenesis), and the biogeochemistry of elements that could be either beneficial or toxic to themselves or other soil biota (Hinsinger et al., 2006; Collignon et al., 2011; McGahan et al., 2014; Rahimzadeh et al., 2015). Lambers et al. (2009) considered rhizosphere processes in the long run of evolutionary perspective to be a central to biogeochemical cycles, soil formation, and Earth history.

3.4. Mycorrhizosphere and mycorrhizal “rock-eating” fungi

Mycorrhiza is a sort of symbiosis between plant roots and fungi (also “fungus-root,” from Greek “myco” meaning “fungi” and “Rhiza” meaning “root” (Alizadeh, 2011)) and is based on a network of fungal hyphae penetrating the surrounding soil, regolith, and bedrock but also extending into the host plant in a form growing into intercellular spaces (ectomycorrhizal) or directly entering to the root cortex and cells (endomycorrhiza) (Bornyasz et al., 2005; Lehto and Zwiazek, 2011; McNear, 2013).

Mycorrhizal fungi play additional roles in nutrient and water acquisition, a mechanism present in almost all terrestrial ecosystems (Jongmans et al., 1997; Witty et al., 2003; Hodge and Berta, 2009; Lambers et al., 2009; Van der Heijden et al., 2015). Sometimes mycorrhizas are associated with chemical weathering of primary minerals such as feldspars and hornblendes (Jongmans et al., 1997) and are even considered as the most important soil fungi type in terms of mineral weathering and dissolution of insoluble metal compounds (Burford et al., 2003). A similar process has been postulated by Van Breemen et al. (2000a, 2000b) who concluded that the mycorrhizal “rock-eating” fungi may contribute to the formation of bleached E horizons of Albic Podzols (WRB, 2014) through local dissolution of Al silicates by strongly complexing LMW organic acids at their hyphal tips causing creation of micropores in soils.

Mycorrhizal fungi develop at least three ways of direct co-existence with plant roots; with the most important synergetic effects occurring within the rhizosphere (Sokolova, 2011). Soil fungi can live 1) inside the cortex (the outermost layer of a root), 2) on the surface of the root, or 3) around the epidermal cells, i.e., a single-layer of cells covering roots. However, an additional mode of, e.g., nitrate and phosphate acquisition by mycorrhizas, is developed through the hyphae of these fungi that grow out from the roots into the soil (Van der Heijden et al., 2015).

Four main types of mycorrhizal fungi can be distinguished: 1) arbuscular mycorrhiza (AM), 2) ectomycorrhizal (EM), 3) orchid, and 4) ericoid mycorrhiza (Table 1).

The ectomycorrhizal (EM) hyphae living in a symbiosis with the roots of trees (e.g. *Quercus* or *Pinus*) can penetrate weathered granitic bedrock and stimulate microcline and biotite weathering (Van Breemen et al., 2000a, 2000b). In addition to increasing weathering, EM hyphae contribute to transport of Al in soils which can intensify pedogenesis, especially podzolisation (van Scholl et al., 2008). As a result, EM could support formation of so called “basket” or “egg cup” podzols under tree trunks (Bloomfield, 1953; Schaetzl, 1990), but EM participation on this process has not been proved so far. The so-called ectomycorrhizosphere acts as an effective medium for water transportation to the main roots (Witty et al., 2003; Sokolova, 2011). In this context, it is important to mention that some plants with thick roots rely on mycorrhizal fungi to a much greater extent than plants with fine roots (Van der Heijden et al., 2015). For instance, in boreal forests, even if composed of only a few tree species, the diversity of EM fungi can be high and reach several hundreds of fungal species coexisting in a single forest. Mycorrhizas are frequently interconnected in space and can be shared between neighboring trees and plant species (e.g., Ingleby et al., 2007). As many as 6000 plant species form associations with EM fungi (mainly trees), but this number is greatly overwhelmed when arbuscular mycorrhiza (AM) is concerned. AM are hosted by c. 200,000 plant species (Van der Heijden et al., 2015); however the direct weathering impact on minerals is far less known and sometimes doubted when compared to EM fungi (Taylor et al., 2009) (Table 1). However, one exception is AM in symbiosis with *Thuja occidentalis*, which can result in surface etch pitting of feldspars. This effect is far greater than AM and EM in the case of other trees. Here, it is supposed that a large amount of LMW organic acids are taken from its litter (Taylor et al., 2009).

4. Biological weathering

Biological weathering has a long history of study and its general meaning and functions are widely recognized. Most commonly it is understood as a set of processes by which biota (microorganisms, animals, and higher plants) and their decomposition products alter chemically or physically parent rock or regolith (Yatsu, 1988; p. 285; Burford et al., 2003; p. 1128; Field and Little, 2009; Brantley et al., 2011; p. 4). It is, however, also difficult to distinguish between the effects of purely physical, chemical, and biological weathering (Dixon, 2004) because they frequently act synergistically.

Full evaluation of weathering effects induced by trees requires a distinction between biochemical (bioweathering) and biomechanical weathering, and both must be considered on several levels of spatio-temporal scales motivated by 1) ecosystem parameters (e.g. climate, geology), 2) disturbance regime of a site, 3) genetically and environmentally stimulated properties of trees (e.g. longevity, root system type), 4) rhizospheric processes, and 5) type of mycorrhizal association (symbiosis). These “natural frames” of biological weathering caused by trees and tree roots starts with tree germination and continue as direct and indirect effects through the entire life span of the tree. Indirect effects are also detectable long after the tree death and can stimulate further changes in soils and regolith (root channels, infilled tree stumps, pit-mound relief, etc.).

4.1. Biomechanical weathering of bedrock

Biomechanics is a description of biological systems such as humans, animals, plants, organs, and cells from mechanistic point of view (Hatze, 1974). In geomorphology and soil science terms such as “biomechanical processes,” “biomechanical effects,” and “biomechanical weathering” are already in use (Johnson, 1993; Phillips and Marion, 2006; Phillips et al., 2008a, 2008b; Šamonil et al., 2010; Pawlik, 2013), and they

Table 1
Mycorrhizal fungi types (Landeweert et al., 2001; Brundrett, 2002; Taylor et al., 2009; Van der Heijden et al., 2015).

Name	Abbreviation	Estimated appearance in associations with all plant species	Number of plant species forming associations with mycorrhizal fungi	Geological history (first appearance)	Chemical weathering effects
<i>Indirect effects on weathering</i>					
Arbuscular mycorrhiza (vascular-arbuscular mycorrhizas)	AM (VAM)	74–80%	200,000	450–460 million years ago	1. Secretion of organic acids or chelators needed for mineral dissolution has not been proven. 2. Indirect effects through glomalin (the compound which increases soil quality, retention of water, and by promoting soil particle aggregation decrease soil erosion)
<i>Direct effects on weathering</i>					
Ectomycorrhizal	EM (ECM)	2–3%	6000 (e.g. pines, beeches, oaks, birches and alders)	135–220 million years ago	1. LMW exudates; the most important for weathering are oxalates and citrates. 2. EMs bacteria produce siderophores; strong Fe chelator.
<i>Not considered in this paper</i>					
Orchid mycorrhiza	–	9%	20,000–35,000	?	–
Ericoid mycorrhiza	–	1%	3900	80 million years ago	–

normally refer to the ability of living organisms to physically change soils, regolith, and bedrock. Biomechanical processes are commonly associated with soil mixing and bioturbations (including faunal turbations and floral turbations), rock fracturing and wedging, and sometimes with biotransport. They are normally analyzed at the scale of pedon or bigger, but in biogeomorphology and zoogeomorphology, the scale is largely dependent on the size of the engineering organism itself and its abundance (e.g. individual tree, ants, termites, pocket gophers, etc.).

Biomechanical interactions between tree roots and bedrock are more obvious when growing roots encounter gaps in or weaker portion of the rock: e.g., elongated fissures, chemically altered joints, etc. When weathered, the bedrock zone can be entered through fractures as quickly as 2–3 years; the time documented for *P. ponderosa* on <1 m deep soil (Witty et al., 2003; p. 398). However, does the story continue? Are growing and expanding tree roots opening joints and cracks in fresh or weakly weathered bedrock? If yes, in what conditions; under the soil cover, within joints in rock outcrops?

Here we refer specifically to the widening of joints or rock partings by the radial pressure of root growth, resulting in the splitting of rock masses. This mechanism is far from obvious, mainly due to the monitoring constraints, and sometimes doubted (Yatsu, 1988). Even so, several observations have been already made which pointed to such possibility (Little and Field, 2003), and tree roots can frequently be observed growing in bedrock joints that appear to have been widened. For instance, Little and Field (2003) speculated on bedrock breaking along small cracks caused by growing plant roots. Root and trunk growth is clearly capable of displacing even large rock fragments where the roots can grow under or along the rock (e.g., Phillips and Marion, 2006), but the tensile strength of most unweathered rock greatly exceeds the radial pressure than growing roots can achieve. Maximum radial pressures of root growth range from 0.51 to 0.9 MPa (Bennie, 1991; Lambers et al., 2008), while the tensile strength of crustal rocks ranges from 1 to 25 MPa (Yatsu, 1988; Selby, 1993). Pores in rocks are frequently too small (<100 µm) for roots to enter (Zwieniecki and Newton, 1995). It has been found that sometimes roots are concentrated as mats within fractures (Witty et al., 2003). Larger (woody) roots, while growing in rock fissures, adopt morphologically to such unfavorable conditions developing flattened cortex (Zwieniecki and Newton, 1995; Gregory, 2006).

Several observations exist which suggest that roots enhance rock weathering, but that this is controlled by rock body properties, mainly the existing network of joints, cracks, and fissures (Zwieniecki and Newton, 1995; Little and Field, 2003; Phillips et al., 2008a; Phillips,

2016a). Additionally, the process of biomechanical reworking of discontinuities in bedrock is not a standalone mechanism, and if it exists, is largely accompanied by biochemical effects of rhizospheric and mycorrhizal processes (see Sections 3.3 and 3.4). However, both processes have been rarely studied. Newly exposed rock surfaces can be quickly (within a few years) covered by vegetation and, for instance, tree roots, root hairs, and fungal hyphae preferably exploit open joints (Phillips et al., 2008a). Similar opportunistic behavior is known for microorganisms and mycorrhizal fungi which penetrate (or create) micro-spaces on and within mineral grains (crystals) (Burford et al., 2003) through

1. penetration by fungal hyphae (along crystal planes);
2. burrowing and tunneling of minerals in consequence of organic acids and chelators impact produced by mycorrhizas, fungal hyphae, and rhizospheric microbes.

Once roots have entered rock via a joint or crack, biochemical weathering is enhanced by moisture fluxes along the root, root respiration, LMW acid production, and rhizosphere processes. Although root growth pressure cannot break up intact, unweathered rock, via radial growth roots tend to fill partings widened by biochemical weathering, thus keeping moisture and rhizosphere processes in contact with the rock.

One important contribution on biomechanical weathering comes from botanists who studied limestone cliffs and documented numerous cases of rock fragments detached from the cliff by expanding roots of *Taxus baccata* (Jackson and Sheldon, 1949). Tree roots used discontinuities and softer, more weathered, parts of limestone, and their action contributed to the cliff recession. This may be the only example of a study devoted to biomechanical weathering caused by tree roots. We are not aware of other similar research, and undoubtedly, further investigation is needed on different types of bedrock and under impact of different tree species.

Tree throw dynamics briefly mentioned above are the most important biomechanical processes in forest ecosystems. Approximately a quarter or even a third of all trees are uprooted at the end of their life cycle in temperate old-growth forests (Šamonil et al., 2013). Although the role of tree uprooting in soil formation on the pedon scale was repeatedly extensively reviewed (Schaeztl et al., 1989a, 1989b; Ulanova, 2000; Šamonil et al., 2010; Pawlik, 2013), its effect on the landscape scale as well as implications to biogeomorphology and long-term forest ecosystem dynamics is still unclear. Where tree roots are in contact with the bedrock, uprooting can locally intensify weathering and deepening

of soils by “mining” bedrock fragments (Phillips et al., 2008b, 2015; Roering et al., 2010; Pawlik et al., 2013, 2016). Geophysical measurement by ground-penetrating radar in beech-dominated old-growth forest in the Czech Republic supported this idea also on stand scale (Šamonil et al. unpublished). Although soil mixing or soil profile inversion (Schaeztl, 1986; Butler and Malanson, 1990; Šamonil et al., 2015) by uprooting clearly locally resets pedogenesis on a pedon scale, long-term soil development on landscape scale in areas occupied by tree throws could be more advanced than in less disturbed areas because of changing weathering and leaching rates in soils (Šamonil et al., 2014, 2015).

4.2. Biochemical weathering

Biochemical weathering (bioweathering) is a biotically mediated chemical weathering process of rocks and minerals (Burford et al., 2003; Fei et al., 2014). It is believed that this type of weathering is more important than mechanical degradation for several reasons. For instance, microorganisms (e.g. bacteria, fungi) are widespread, can survive under the most extreme conditions (e.g. hot springs, cold deserts), and are very opportunistic, inhabiting niches that are hardly available for other organisms (rock cracks and fissures) (Burford et al., 2003). Examples of such organisms include endoliths, which colonize micro-discontinuities in rocks (chasmoliths and cryptoendoliths) and even bore into the interior of rocks (euendoliths) (Friedmann, 1980; Blackhurst et al., 2005). In far more hospitable conditions, under the soil cover, the hyphae of fungi associated with tree roots penetrate soil pores smaller than 5–20 μm , normally unavailable for root hairs (Taylor et al., 2009). Hence, it is a very effective way by which plant roots, relying on the fungal hyphae, expand the space available for biochemical weathering.

Effects of biochemical weathering include changes in mineral crystals microtopography by pitting and etching on their surfaces, and even complete dissolution of mineral grains (Burford et al., 2003). Many examples of pores, 3–10 μm in width, were found in feldspars and hornblendes in podzol E soil horizons and granitic bedrock (under *Pinus sylvestris* and *Picea abies*). It is believed that they were formed by mycorrhizal or saprotrophic fungi (Jongmans et al., 1997).

Buurman and Jongmans (2002, 2005), for example, complemented existing fulvate, proto-imogolite, and fulvatebicarbonate theories of podzolization describing mobilization, transport, and precipitation of organo-metallic-silicate complexes by biological activity of tree roots. They found predominance of root-derived organic matter in some Podzols and concluded that the root activity and decay can play a crucial role in Podzol development, i.e., deepening of transition between eluvial E and illuvial Bhs horizons. Significant amounts of root-derived organic matter in Podzols was formerly observed by De Coninck (1980). Skjemstad et al. (1992) highlighted effects of root exudates in podsolization rather than the effect of root decay. Podzolization seems to be narrowly connected with microbial activity. According to Lundstrom et al. (1995) and Buurman and Jongmans (2002, 2005), the removal of metals by dissolved organic carbon in originating eluvial E horizon is followed by microbial decay of formerly accumulated organic matter no longer protected by Al and Fe complexes. Microbial activity can drive gradual deepening of Podzols in time. Abrupt deepening of Podzols in space on the finest spatial scale of decimeters or meters can be linked to, apart from preferential water flow, decomposition of organic material accumulated within tree throw pits or decomposition of uprooted, sometimes buried trunks (Schaeztl et al., 1989a; Šamonil et al., 2010, 2015).

Plants, their mycorrhizal fungi, and microbes living in the rhizosphere are able to contribute to chemical weathering phenomena through the following mechanisms (Taylor et al., 2009):

1. exudation of reactive species (e.g. H^+) and LMW organic chelators (e.g. oxalate, citrate, and malate, which are the strongest chelators

of trivalent metals such as Al^{3+} and Fe^{3+} , Landeweert et al., 2001) (also known as “rock-eating fungi,” Jongmans et al., 1997; Van Breemen et al., 2000a, 2000b):

- a. organic acids enhance chemical weathering of mainly mafic minerals (e.g. amphibole, pyroxene) (Drever, 1994);
 - b. mycorrhizal hyphae penetrate aluminosilicate minerals through complex solution of organic acids;
 - c. carbon-rich exudates support large communities of rhizospheric bacteria and fungi which actively accelerate weathering of minerals (Landeweert et al., 2001);
2. increased pCO_2 (partial CO_2) of soil solution due to plant respiration (resulting in decreased pH);
 3. organic matter decomposition products increase concentration of high molecular weight (HMW) organic acids and LMW organic chelators in the soil solution;
 4. evapotranspiration, which stirs “the water cycle engine” bearing base cations and other nutrients to plants;
 5. stabilization of the soil body which allows undisturbed activity of roots and their mycorrhizas.

Organic acids are released through root tips; however, weathering of soil minerals is also enhanced by fungi hyphae (mycelium) which grow from the root tips, enclose mineral particles, and penetrate mineral interlayer spaces (Landeweert et al., 2001). EM fungi hyphae develop additional organs, called rhizomorphs, which elongate root tips into the soil by as much as 10 cm (Taylor et al., 2009). Also, EM act as biosensors and they can distinguish different grain sizes and mineralogies (Leake et al., 2008) suggesting EM ability for selective rock weathering. All these properties make mycorrhizal fungi associated with tree roots a very effective system of chemical alteration of rocks and minerals.

4.2.1. Indirect effects on biochemical weathering

Direct effects of root and rhizospheres, and the associated microbial communities on weathering, are often important, such as production of organic acids, chelation, and activities of endolithic microbes. Many important direct effects are described above, associated with biochemical weathering in the root zone. However, indirect effects on weathering may also be important.

Trees can affect soils, regolith, and bedrock through their indirect input of water, organic matter, and bioconstructions in places presently or previously occupied by roots. After tree roots find their way through substrate into the fractured bedrock, they commence to play a role of transmission pathways for moisture, nutrients, microorganisms, and heat. This is especially important in very shallow and immature soils where tree roots penetrate only slightly weathered bedrock (Schwinning, 2013). Because of these factors, roots are a key agent of further soil development.

Bioconstructions include rhizoliths, which are structures formed around or in places occupied by the root when root tissue is substituted by precipitated mineral compounds, e.g., calcium (Goudie, 1996; Lipar and Webb, 2015). Rhizoliths include root moulds (tubular voids), casts (filled root moulds), tubules (cemented cylinders around root moulds), rhizcretions (mineral accumulation around roots, Kindle, 1925), and root petrifications (when plant tissue is replaced by mineral matter). Recognition of rhizoliths, casts, tubules, and root petrifications including also biogenic calcretes are an important tool in paleobotanical and paleopedological studies, for example, in stratigraphic correlations and interpretations (see Retallack, 2001; Stein et al., 2012; Brlek et al., 2014).

Roots influence soil porosity and permeability by pushing the soil vertically and horizontally as they develop and find their way through the soil and explore new nutrient and water resources, which can result in so called root mounds on surface (Phillips and Marion, 2006; Hoffman and Anderson, 2014). Agitation of plants, particularly trees, during the storms, which promotes root movement in soils can be

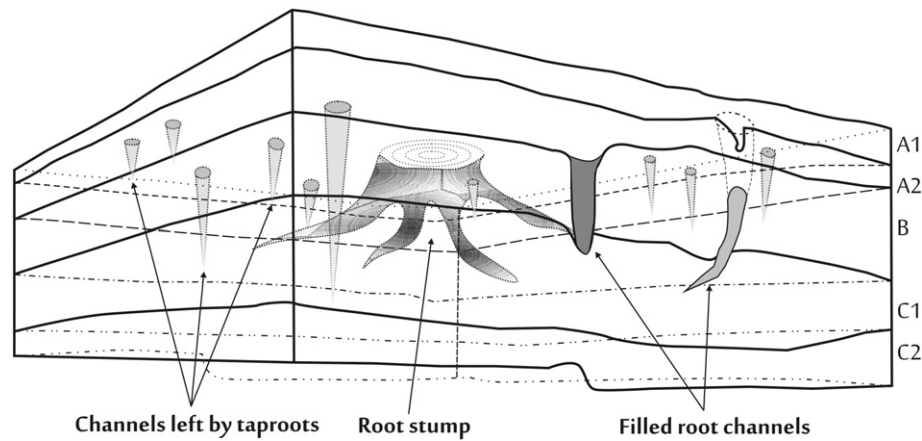


Fig. 5. A hypothetical imprint left in soil by growing and decayed plant roots which influence permeability and hydrological connectivity with lower soil horizons and bedrock (the figure based on Gaiser, 1952, p. 63; modified).

seen as another agent significantly influencing physical soil properties (Gabet et al., 2003). When roots decay, they leave root channels that are then used as pathways for free water movement (Gaiser, 1952) (Fig. 5). Some influences caused by roots of various size can be similar to effects made by burrowing animals in terms of soil founalturbation and transport, and water and nutrient regimes. It has been suggested that vertical channels might be interconnected by lateral channels forming far more complex systems of water transmittance in soil (Gaiser, 1952). It is evident in very porous immature soils developed in karst areas (Martin, 2006; Phillips, 2016a). Such conditions inevitably influence the presence of rhizospheres (Schwinning, 2013).

Root grooves are weathering features directly associated with coarse roots. Grooves develop along living roots in contact with rock due to chemical weathering associated with moisture moving along the root, respiration, and transpiration by the root, organic acids, and associated effects of microbes (Wall and Wilford, 1966; Sweeting, 1973; Bull and Laverty, 1982; Trudgill, 1985; Taborosi, 2002). Such features may be an initial point of self-reinforcing mechanisms of further rock dissolution, especially in carbonate rocks, where these features are most common (Phillips, 2016a). Existing root grooves act as pathways of rapid rain water percolation. These spaces are a subject of enlargement and can be repeatedly occupied by future generations of roots.

4.3. Other effects: Mass displacement, stump infilling

Tree uprooting and the resulting pit-mound microtopography, and effects on soil hydrology, have traditionally been considered the main biomechanical effects of trees on soil. However, at least two other effects are significant: mass displacement by trunk and root growth, and infilling of cavities associated with decomposed or burnt stumps. Although tree uprooting was repeatedly found to be the most important biomechanical process driven by trees in temperate forests (in terms of volume of moved soil material), infilling of decomposed tree stumps is even more frequent.

Root biomass is generally proportional to above-ground biomass, so large trees comprise a significant amount of soil mass and volume, particularly in the upper soil layers. The ability of radial pressure of wood growth to displace mass is indicated by the displacement of rock fragments up to boulder size (and, in urban settings, pavements). Thus, even where no uprooting occurs, trees perform a significant amount of bioturbation (Lutz and Griswold, 1939; Lutz, 1958; Phillips and Marion, 2006; Wilkinson et al., 2009; Hoffman and Anderson, 2014).

Trees that die (or are cut) without uprooting leave surface depressions when the stumps eventually decompose or burn. In beech-dominated old-growth forest between 60 and 80% of trees are broken at the end of life cycle (Šamonil et al., 2013). The depressions may fill

with material slumping or eroding from the surrounding soil, sediment-transported downslope, organic litter, or a combination. This stump infilling process has significant impacts on soil spatial variability and hillslope mass fluxes but has been studied in detail in only a few cases (Phillips and Marion, 2006; Shouse and Phillips, accepted for publication).

5. Tree roots as ecosystem engineering

Ecosystem engineering reflects effects of organisms on the abiotic environment where organisms have disproportionate impacts relative to their numbers or size, and where the effects influence habitat, resource availability, or mass and energy fluxes (Jones et al., 1994, 1997; Jones, 2012). When ecosystem engineering organisms influence selective pressure, it constitutes niche construction (Odling-Smee et al., 2003; Matthews et al., 2014). Ecosystem engineering and niche construction indicate reciprocal effects of trees and geomorphic processes on each other, and in the latter case raise the possibility of coevolution (Phillips, 2016b). Binkley and Giardina (1998) specifically related tree root influences on soil and water chemistry, surface erosion and deposition, and soil mixing and bioturbation to various levels of interaction, from indirect one-way influences to coevolution.

As discussed above, tree roots have substantial impact on weathering and regolith formation, some of which result in conversion of bedrock to regolith, or local deepening/thickening of regolith. These effects include

1. penetration of joints, fractures, and bedding planes (hereafter just joints, for brevity) in both weathered and unweathered bedrock;
2. roots in rock joints facilitate chemical weathering via moisture flux along roots and root channels, root and rhizosphere respiration, formation of organic acids, and hosting of microbial and other biotic activity;
3. radial pressure of root growth widens joints, and maintains biological contact with the interior joint surfaces;
4. adhesion of roots to rock via root hairs and mycorrhizae and the encompassing of rock fragments by roots allows for loosening of joint blocks during tree shaking by wind, and bedrock “mining” by tree uprooting.

These deepening effects can be considered biogeomorphic ecosystem engineering because they increase the habitat size and suitability for trees and other organisms that require or benefit from thicker soil. Root-rock interactions are only beginning to be understood from geomorphological and hydrological perspectives. However, in general, roots grow into or through fractured rock to access water, and in some cases, there appear to be ecological advantages to the plant strategy of

accessing rock fissures relative to soil (Schwinning, 2010). Trees vary greatly in their general root architecture, typical rooting depths, and phenotypic plasticity in adapting to different substrate conditions (Stone and Kalisz, 1991). Soil deepening is probably followed by releasing of relationship between local soil depth and individual tree species occurrence.

Soil and regolith thickness is an important factor in habitat suitability for deep-rooted plants and a number of soil fauna. There is therefore evidence of positive feedback between local soil deepening by trees and reoccupation of these locally deeper patches after tree mortality (Phillips, 2008, 2009a; Shouse and Phillips, accepted for publication). In karst landscapes, weathering-related feedback relationships linked to ecosystem engineering by tree roots are described by Crowther

(1987), Sustersic et al. (2009), Schwinning (2010), Estrada-Medina et al. (2013), and Nie et al. (2014). In general, these involve geomorphically controlled or influenced edaphic effects (e.g., topography, microclimate, substrate) on vegetation. These result in varying vegetation patterns in relation to karst landforms, and these differing plant communities (and associated microbial communities) result in differential dissolution, which feeds back to the landforms. Ecosystem engineering by trees, particularly with respect to weathering and regolith deepening, is discussed in the context of niche construction and related concepts by Binkley and Giardina (1998), Phillips (2009a, b, 2015, 2016b), and Verboom and Pate (2013). In general, these studies suggest that biogeomorphic ecosystem engineering by trees is common. Niche construction is more difficult to prove, but there are clear

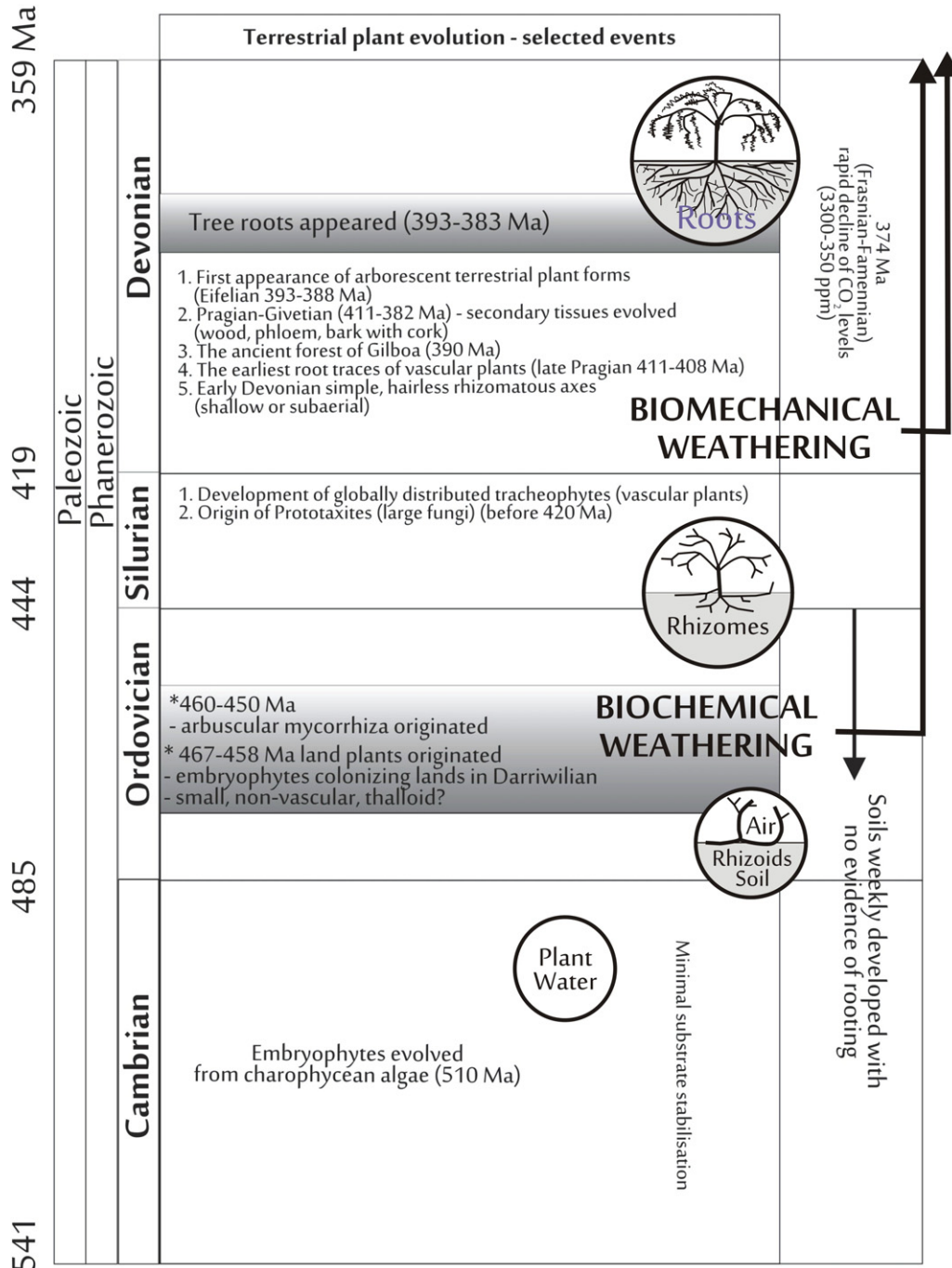


Fig. 6. The main paleobotanical events considering the evolution of plants and plant roots (authors' compilations based on Kenrick and Crane, 1997; Algeo and Scheckler, 1998; Raven and Edwards, 2001; Stein et al., 2012; Kenrick and Strullu-Derrien, 2014). Imaginations of rhizoids, rhizomes and roots taken from Brundrett (2002).

examples in some cases. Coevolution and extended composite phenotypes associated with tree–soil–landform interactions is even more difficult to prove, but strong circumstantial evidence exists. Despite the limited evidence for taxa-specific eco-evolutionary dynamics, general evidence of coevolution of vascular plants, trees, and forests on the one hand, and regoliths on the other, is clear, as outlined in the next section.

6. Tree roots and global environmental changes

6.1. Early evolution of terrestrial plant roots

The land plants (embryophytes) may have originated in the Middle Ordovician 470–450 Ma, but these were small, non-vascular, and morphologically undifferentiated in terms of their roots, stems, and leaves (Kenrick and Crane, 1997; Algeo and Scheckler, 1998; Kenrick and Strullu-Derrien, 2014). The evolution of roots, as organs of different anatomical structure, physiological functions and tropism (gravitropism) than shoots, followed the advance of vascular plants in the Late Silurian and Early Devonian, but was delayed by 15 million years (during the Pragian 411–408 Ma, Algeo and Scheckler (1998), or Emsian 408–393 Ma; Raven and Edwards, 2001) after the first appearance of tracheophytes (vascular plants) (Retallack, 2001; Raven and Edwards, 2001). The phylogenetic context of terrestrialization during Paleozoic times was described by Gerrienne et al. (2016). Roots probably evolved from rhizomes (subterranean stems) of vascular plants in the Early Devonian and root hairs may have developed from rhizoids of early plants to improve plant soil connectivity and nutrient flow (Kenrick and Crane, 1997; Brundrett, 2002). Underground rhizome systems developed in response to different environmental requirements to optimize nutrient uptake, allow mycorrhizal fungi coevolution, and provide mechanical support for plant stability. In more advanced stages, some rhizomes became thinner and longer to provide better connectivity with soil mass and increase absorption of solutes (Brundrett, 2002). Similar needs were probably supported by symbiotic mycorrhizal fungi evolving since the Middle Ordovician 460–450 Ma (Kenrick and Strullu-Derrien, 2014). The early roots were short (<20 cm in the Eifelian–Givetian, 393–383 Ma; but see also Elick et al. (1998) for the evidence of roots nearly 1 m deep from the Emsian stage 408–393 Ma) but extended to 80–100 cm in the Frasnian–Famennian stage 383–360 Ma (Algeo and Scheckler, 1998). The expanding root sizes were commonly correlated with changes in weathering rates and processes (Algeo et al., 1995; Algeo and Scheckler, 1998).

6.2. The rise of trees and global environmental changes

We have no doubt trees are a key component of the global environment. They modulate global greenhouse effects, control water cycling, and strongly influence erosion and accumulation (e.g. Allen et al., 2010; Neill et al., 2005). Additionally, from the present perspective, tree roots are most frequently seen as a factor of soil stabilization. Those functions of trees have been acknowledged for decades. However, on a global scale, processes attributed to land plant roots are increasingly viewed as a key driving factor of climate change since the Devonian (Le Hir et al., 2011; Doughty et al., 2014). Prior to the Devonian, the soils, if developed at all, were probably shallow, originated by soil microbes (Retallack, 2001). Trees, together with other tracheophytes, were able to change global environments and were even considered as a force accelerating the Late Devonian mass extinction (Algeo et al., 1995). The so-called “Devonian plant hypothesis” (Algeo et al., 1995; Algeo and Scheckler, 1998) has been built mainly on the most important attributes of trees, i.e. growth of deep root systems and physical and chemical changes taking place in their root zone, accelerating weathering processes, atmospheric carbon binding in soils and climate cooling (Algeo and Scheckler, 1998; Beerling and Berner, 2005).

It is commonly acknowledged that vascular plants, and most importantly deep-rooted trees, enhanced silicate mineral weathering, lowering of atmospheric CO₂, and global climate changes in the Devonian (Algeo and Scheckler, 1998; Berner, 1998; Algeo et al., 2001; Goudie and Viles, 2012). The Devonian period was a time of evolution, diversification, and spatial redistribution of vascular plants, and trees may have performed a key role in these changes. As vascular plants developed root-like structures and, later, true root systems, allowed plant stabilization, and enhanced their ability to extract moisture and nutrients from the soil and regolith. Erwin (2008) argues that the gradual evolution of root systems and organisms themselves has been accompanied by increasing role of ecosystem engineering in terrestrial systems since the early Phanerozoic times. Positive feedbacks through environmentally arranged selection have affected macroevolutionary patterns and diversity. They have not only persisted but even reinforced over geologic time.

From the evolutionary perspective, a key phase was development of vascular tissue; water-conducting cells (tracheids) in the Late Silurian to Early Devonian (Kenrick and Crane, 1997), and secondary tissues (wood and phloem, between the Pragian and the Givetian) which allowed arborescence (tree-sized stature) (Algeo and Scheckler, 1998) (Fig. 6). Trees evolved independently in several major groups (Kenrick and Crane, 1997) by the Middle Devonian 398–385 Ma (Stein et al., 2012), and wider distribution of tree-sized plants was possible after they developed the seed habit in the Famennian, between 372 and 360 Ma (Algeo et al., 1995, 2001). By the end of the Devonian, stem diameter of tree-like plants increased logarithmically from 3 mm to 1.5 m and their height from a few cm up to ≈30 m in the Givetian 388–383 Ma (Algeo and Scheckler, 1998; Algeo et al., 2001; Beerling and Berner, 2005).

Rooting depth is positively correlated with the tree size and this led to the conclusion that larger vascular plants through their roots systems were more effective in soil production (Algeo and Scheckler, 1998). This assumption supports consideration of trees as a key factor of changes in the Devonian (but see Goddérís et al., 2014, for additional explanation).

Millions of years of evolution of microbes and lower plants undoubtedly had significant influence on rock weathering processes. Without a soil mantle, even immature, thin, and chemically only weakly altered, rhizospheric processes could be only minimally active, and the role of soil as an important medium of plant development is thought to be a key factor of global changes (Retallack, 1997; Amundson et al., 2015). However, pre-Devonian proto-soils are thought to be formed by microbial communities with minimal or without active role of early roots (Algeo and Scheckler, 1998; Retallack, 2001) and the early land plants with shallow anchorage systems (if any) may have been far less effective (>10-fold) in mineral weathering than trees which evolved later

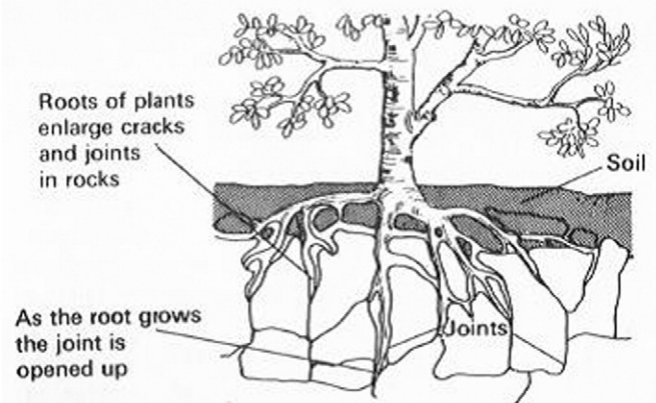


Fig. 7. Potential local biomechanical effects of growing tree roots on bedrock (from Bunnett, 1965).

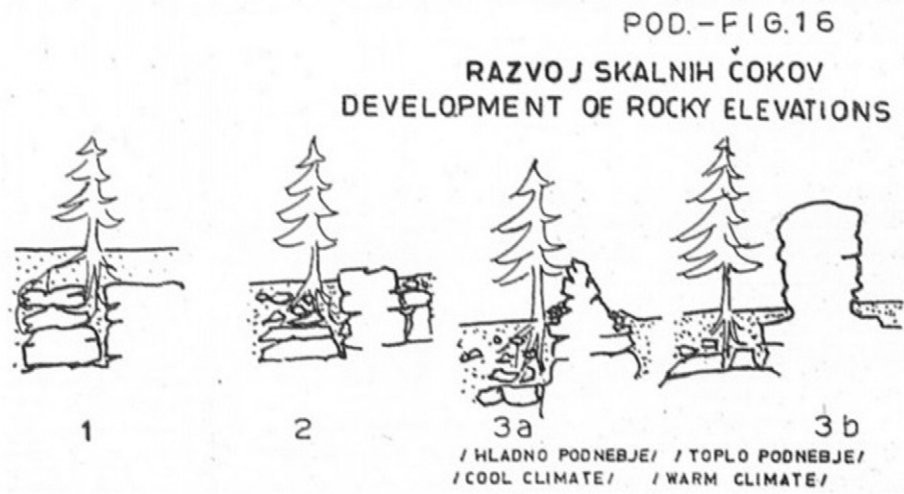


Fig. 8. Conceptual model of tors development under tree cover (from Gams, 1966, see also Pitty, 1971).

(Quirk et al., 2015). Retallack (1997) argued that at the end of the Silurian rhizosphere were “impressively dense and deep.” In the light of the present results (see Sections 3.3 and 4.2), we cannot neglect the ability of rhizospheric processes to chemically change minerals and rocks. The same applies to mycorrhizal fungi but with two important differences. First, mycorrhizas (mycorrhizosphere) have a wider spatial redistribution than rhizospheres, and second, they appeared much earlier, in the Ordovician (AM fungi) (Brundrett, 2002).

Deep-rooted trees and their rhizospheres lead to the following effects (Lambers et al., 2009):

1. mechanical deterioration of rocks and subsequent changes in water cycle;
2. carbon input into regolith, soil horizon development, and positive influence on microorganisms in the rhizosphere;
3. chemical changes in the rhizosphere, e.g. pH lowering due to cation uptake by roots (Doughty et al., 2014); “rhizoturbations” sensu Algeo and Scheckler (1998).

Many authors attribute more effective chemical weathering to mycorrhizal fungi (Pagani et al., 2009; Doughty et al., 2014; Morris et al.,

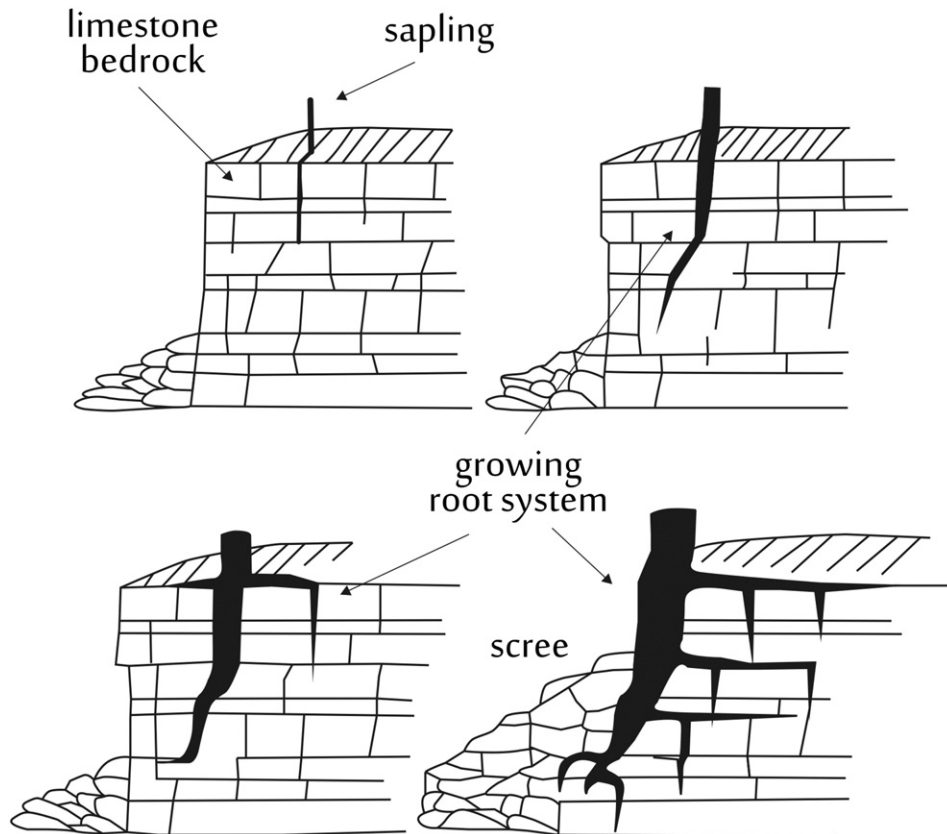


Fig. 9. Rock cliff development under biomechanical impact of growing tree roots (modified after Jackson and Sheldon, 1949).

2015; Quirk et al., 2015). They also point to mechanical breakdown of minerals, creating more surface for chemical action (mineral dissolution).

Also, on the global scale, intensive chemical weathering on lands would lead to much greater nutrient loads of rivers that could enhance marine production and led to anoxic events in the Late Devonian (Algeo and Scheckler, 1998; Taylor et al., 2009).

6.3. Root–bedrock interactions and landscape evolution

There is a positive feedback between soil and regolith stabilization caused by plants and weathering processes induced by their roots. Vegetation is an important factor in the theory of soil science and hillslope and fluvial geomorphology (e.g. Schatzl and Thompson, 2015). Tree roots, because of their various functions described in the previous sections, may modulate local and regional relief when appropriate spatial and temporal scale is reached. For instance, soil stabilization function was a key surficial effect by the Devonian, when a shift from sheet-braided style rivers to meandering rivers may have been a consequence of the important innovation by plants of deep root systems (Davies and Gibling, 2010). In river valleys, they caused valley-sides and river bank stabilization, but after colonizing uplands, the primary effect of vascular

plants was biomechanical and biochemical weathering of bedrock; the assumption underpinning the *Devonian plant hypothesis*.

Modification of landscapes takes place through secular processes of soil production under tree cover, with bioturbations and lateral soil and regolith transport in a form of tree uprooting frequently engaged (Gabet and Mudd, 2010; Roering et al., 2010). During uprooting, trees are able to uplift in their root systems even larger fragments of fractured bedrock (Phillips et al., 2008b; Pawlik et al., 2013), and Lutz (1960) observed movement of rock fragments of 4 tons due to tree throw. This is an additional mechanism of biomechanical weathering and biotransport that is commonly not taken into account in general statements about soil production in the past. Other biomechanical processes associated with vegetation as an important geomorphic factor were also frequently omitted in theories of landscape evolution (Johnson, 2002; Phillips, 2009b). These are not gradual effects operating over millennial timescales, but sudden changes of forest floor microtopography (for instance, effects of tree uprooting). The process which takes a moment can leave microtopographical imprints in the form of pit-and-mound microrelief which may last for several thousand years (Šamonil et al., 2013). Longevity of tree throw pit-mound microtopography as well as erosional effects of uprooting processes are highly dependent on soil texture. We can generally conclude that the increasing amount of coarse



Fig. 10. Examples of biomechanical effects of tree roots (all photographs: authors): 1A and 1B—chinkapin oak (*Quercus muehlenbergii*), limestone; 1C—American sycamore (*Platanus occidentalis*); 2A and 2C—European beech (*Fagus sylvatica*), limestone; 2B—European hornbeam (*Carpinus betulus*), shale; 3A and 3C—Norway spruce (*Picea abies*), mudstone; 3B—Norway spruce (*Picea abies*), sandstone.



Fig. 11. Angkor Temple in Cambodia overgrown by large trees of *Ficus* sp. (upper photographs were taken in 2012 by Sigita Sabaliauskaite, lower photographs were taken in 2004 by Vít Zoufalý; all photographs are used with permission of the Authors).

sand and gravels in soils promotes longevity of these features and decreases their erosional potential (Šamonil et al., 2010, 2016).

Direct fracturing of bedrock by growing tree roots has been postulated in the past and accompanied by descriptive figures and impressive pictures of split rocks (Fig. 7). However, in such assumptions, at least two facts have to be considered: 1) roots tend to concentrate into top soil horizon, 2) biochemical processes probably act first and after that available space is occupied by enlarging tree roots.

An interesting example of long-term landscape evolution comes from the Dinaric and Alpine karst area of Slovenia (Gams, 1966). The author found higher rates of dissolution of carbonate substrate under trees and this caused spatial differentiation of tors development, first in subterranean conditions, under soil mantle, and lately, when soil cover was removed, as subaerial forms (Fig. 8) (see also Pitty, 1971, for explanation). Somewhat similar positive feedback has been found in Northern Limestone Alps, in Austria, but as an effect of another process. In this study area, tree uprooting event was followed by intensified dissolution within tree throw pit on limestone leading to surprising enlargement (deepening and widening) of this post-disturbance microtopographical form (Embleton-Hamann, 2004).

Another example of slow changes in rock properties caused by roots comes from volcanic rocks of arid Baha California, Mexico, colonized by different species of cacti (Bashan et al., 2002). The authors argued that plants in such extreme arid conditions were able to enhanced soil production by breaking up small and large rocks within the time period of several years. However, also in this case, the process of mechanical deterioration of rocks was not exhaustively documented and evidently physical changes were accompanied by biochemical action taking place in the root zones of cacti and a wild fig tree (Puente et al., 2004).

Jackson and Sheldon (1949) were probably the first researchers who pointed to an importance of mechanical action of tree roots and its contribution to limestone cliff recession (Fig. 9). However, they did not consider the impact of this process in a wider landscape scale. When extrapolated on a regional scale, we hypothesize that the process of biomechanical fracturing of rock fragments from the cliff face can be significant and play primary role in cliff development. We do not know other studies, except Jackson and Sheldon (1949) contribution, to support the hypothesis; however, our own observations from Arkansas and Kentucky (USA), Carpathians and Sumava Mts. (both in the Czech Republic) and Sudetes and Gorce Mts. (Poland) prove that biomechanical weathering of rock walls caused by tree roots should be taken into account in geomorphic analysis of weathering and landscape evolution (Fig. 10).



Fig. 12. Uprooted tree with bricks in a root plate. The tree was growing on the wall of an abandoned old house in the Table Mts., SW Poland. During uprooting event, it caused damage of the wall. (Photo: Ł. Pawlik).

7. Biodeterioration—Invasive roots and damage caused to infrastructure and buildings

Much basic information on tree roots behavior and their ability to weather bedrock can be drawn from their observations in artificial environments. Tree roots frequently damage urban underground infrastructure or historical buildings (e.g. Caneva et al., 2009). This is called *biodeterioration*, i.e., the process of biotic attack when an undesirable change in the properties of a material is caused by the activity of organisms (Hueck, 1968; after Yatsu, 1988, p. 348). This definition applies also to other organisms.

Numerous examples from around the world bring evidence of serious damage caused by tree roots with the most striking examples of Angkor Temple in Cambodia and many others (Fig. 11).

The most important biomechanical effects caused by roots in the built environment include (Perry, 1982; Almeida et al., 1994; Kumar and Kumar, 1999; Allsopp et al., 2004)

1. growth and radial thickening of roots along existing weak zones between blocks and bricks (Fig. 12);
2. in clay soils roots may decrease moisture and cause soil shrinkage leading to damage to the foundation of nearby buildings;
3. roots may penetrate and block drains and water supply pipes.

8. Conceptual model of tree roots interactions with rocks and regolith

Living functions of tree roots and their evidently opportunistic behavior, which supports tree growth and species long-term existence

even in the most inhospitable environment or after a severe disturbance, have geomorphic significance at spatio-temporal scales from mineral to biosphere. Conversely, geomorphic processes (hillslope instability, erosion, mass movements) can modulate tree and root growth or influence development of new tree stems and roots. Tree roots influence biological weathering in a complex way, thus we propose a conceptual model encompassing major agents of this fundamental geomorphic process. In general, the model indicates that tree roots through their growth, activity, and persistence directly and indirectly influence biological weathering, playing a significant part in soil production and landscape denudation (Fig. 13).

9. Conclusions, knowledge gaps, and future studies

Biological weathering by tree roots, the main subject of this paper, is considered as a set of cascading processes with changing direct and indirect effects along a life cycle of vascular and non-vascular roots and rhizoids, accompanied by rhizospheric processes and mycorrhizal associations. Tree roots are an important element of biogeomorphic systems and their paleogeographical meaning has been widely recognized and incorporated in the *Devonian plant hypothesis*. However, a full appreciation of geomorphic processes associated with tree roots is still constrained by the lack of their thorough understanding and, in consequence, cannot be fully incorporated into models of different geomorphic systems and soil evolution. While biological and ecological functions of tree roots have been exhaustively studied and their theory applied in other closely related analyses, the functions of tree roots have been rarely recognized in geomorphic studies, and normally limited to the two fundamental effects: hillslope and river bank stabilization, and

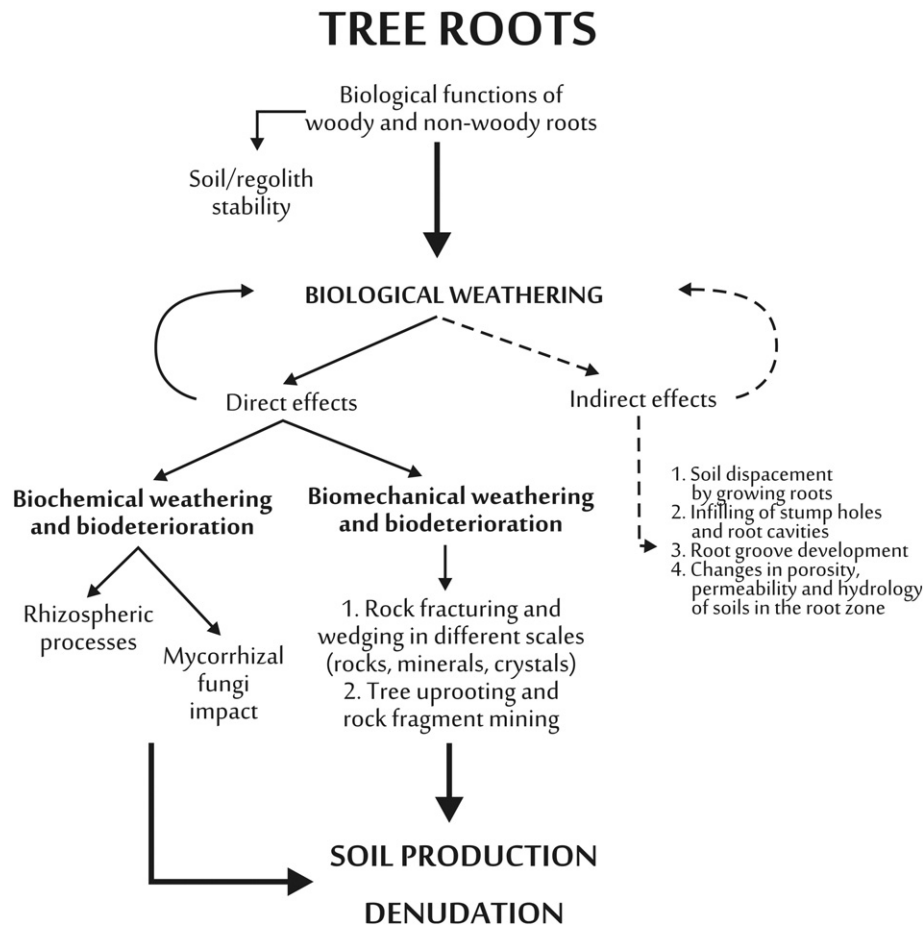


Fig. 13. Conceptual model of biological weathering caused by tree roots and its direct and indirect effects on soil production and denudation. Dashed arrows indicate biological weathering *sensu lato*.

protection against erosion. Increasingly, tree uprooting has been well studied and incorporated in the theory of soil evolution and biogeomorphic studies. However, this is not the only process induced by tree roots and there exist several issues which need research attention. These include

1. effectiveness and rates of biomechanical weathering (rock fracturing and root wedging) of bedrock of different geologic substrates caused by different tree species;
2. soil displacement by growing tree roots and its importance for soil biotransport and sediment flux in a short- and long-term perspective not only on local scale but also on scale of the landscape;
3. timeframes and effectiveness of biochemical weathering in the rhizosphere and mycorrhizosphere and most importantly a significance of this process for geomorphology, biogeomorphology, and eco-evolution dynamics;
4. further studies on tree uprooting in different environmental conditions and vegetation types or even biomes (the relevant studies are nearly absent from tropical forests);
5. further studies on root development, decay, and root stump infilling in different environmental conditions;
6. recognition of tree root disturbances and their influences as ecosystem engineering;
7. taxa-specific studies of biogeomorphic effects;
8. changes in structure of mutual tree–soil interactions due to human interventions in the landscape; and
9. the role of other organisms, particularly fungi and bacteria in tree–soil interactions and ecosystem engineering by trees.

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