Forest Ecology and Management 393 (2017) 40–51

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Pit-mound microrelief in forest soils: Review of implications for water retention and hydrologic modelling

Martin Valtera [a,*], Randall J. Schaetzl [b]

[a] Department of Forest Ecology, Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Lidická 25/27, 602 00 Brno, Czech Republic
[b] Department of Geography, Environment, and Spatial Sciences, 673 Auditorium Rd, Michigan State University, East Lansing, MI 48823, USA

ARTICLE INFO

Article history:
Received 8 November 2016
Received in revised form 24 February 2017
Accepted 27 February 2017

Keywords:
Tree uprooting
Microtopography
Runoff
Sustainable management
Climate change
Drought mitigation

ABSTRACT

Forest ecosystems are known for their capacity to retain and redistribute water. Nevertheless, even in some forested watersheds, prolonged or intense rainfall events often exceed the retention threshold of the system, generating accelerated runoff. Surface microrelief is an important attribute of forest ecosystems that often act to mediate potential runoff. In most natural forests, the soil surface is typically unevenly broken with pit and mound microrelief, formed by both historical and recent tree uprooting events. In managed forests, however, tree uprooting is traditionally seen as undesirable. The systematic repression of this process may lead to gradual loss of microrelief. To date, little attention has been paid to the impacts of the pit-mound microrelief, or its absence, on forest hydrology. Restoration of naturally undulating microrelief in managed forests can help to accentuate water retention and mitigate runoff, while reducing drought stress and reinforcing forest productivity and resilience.

This paper summarizes the literature and presents insights on the effects of tree uprooting on the microrelief of forest soils and forest hydrology, focusing on its consequences to water retention, tree water supply, and forest health. Furthermore, we explore the mechanisms and possible consequences of the long-term repression of these processes in intensively managed forests, with implications for forest management and further research.

Contents

* Corresponding author.
E-mail address: martin.valtera@vukoz.cz (M. Valtera).

http://dx.doi.org/10.1016/j.foreco.2017.02.048
0378-1127/

1. Introduction

Various forecasts of climate change foresee the continuing rise in the incidence of hydrological extremes such as floods and prolonged droughts, which may cause an increased hazard to terrestrial ecosystems, global water resources, production, and human society (Allen et al., 2010; Ciscar et al., 2014; Dai, 2011). The main factors to be concerned with are (i) decreased effectivity of water retention on the land, particularly in urban and agricultural soils, therefore (ii) increased heating, especially over the land surfaces with limited evaporation (Bates et al., 2008; Dai, 2011; Jung et al., 2010), which in turn may result in (iii) more intense precipitation events in cooler (usually upland and forest) areas (Pielke, 2001). These aspects will result in increased demands on forest ecosystems for water retention and mediation.

Soils and vegetation play a crucial role in terrestrial water cycling, as they intercept, retain, store and recycle water. In forest ecosystems, vegetation intercepts precipitation, lessening runoff and accentuating infiltration and groundwater recharge. Indeed, forests are recognized as the most effective runoff retarders and water recyclers from among all terrestrial ecosystems (Archer et al., 2013; Makarieva et al., 2013). However, even in forested catchments, a prolonged or intense rainfall (or rapid period of snowmelt) often exceeds the retention threshold of the system, generating accelerated runoff (Tromp-van Meerveld and McDonnell, 2006).

Surface microrelief, a common feature in most forests, is an important component of slope hydrology (Frei and Fleckenstein, 2014; Kishné et al., 2014; Thompson et al., 2010; van der Ploeg et al., 2012). The soil surface in forests is characterized by microtopographic irregularities formed by various natural processes and/or by human activities. In natural forests, the soil surface is typically unevenly broken with paired pits and mounds, formed by both historical and recent tree uprooting events. The impacts of this type of microrelief, with its indirect impacts on soil formation and forest ecology, have been studied since the first half of the last century (Beatty and Stone, 1986; Denny and Goodlett, 1956; Lutz, 1940; Lyford and MacLean, 1966; Stephens, 1956). Several comprehensive reviews have been dedicated to the mechanisms of soil disturbance and the various ecological and pedological impacts of tree uprooting (Schaetzl et al., 1990; Schaetzl et al., 1989a,b; Šamonil et al., 2010a). However, no study to date has quantified, or reviewed the effects of these types of pits and mounds on forest hydrology. This paper addresses that deficit by summarizing the pertinent literature and bringing together new insights on the effects of tree uprooting on the microrelief of forest soils and hydrology. We choose to focus on the consequences of surface microrelief to water retention, tree water supply, and forest health. Furthermore, we explore the mechanisms and possible consequences of the long-term repression of these processes in intensively managed forests. We hope that this study will initiate further research on the importance of soil-surface microrelief formed by tree uprooting on forest hydrology. Such work might include future direct hydrological measurements and experimental verifications of some of the processes outlined in this paper, and wider inventories of the treethrow pits and mounds in forests, thereby enabling quantifications of their contribution to the hydrology of these types of watersheds.

2. Hydrological function of forests

Forest ecosystems are an essential component in the terrestrial water cycle. Their high capacity to retain and redistribute water is usually attributed to: (i) the high specific area of the aboveground biomass (Myneni et al., 2002); (ii) the presence of a litter mat (Stuart and Edwards, 2006), and macropores, which retain moisture and reduce the potential negative effects of soil freezing on infiltration (Isard and Schaetzl, 1995; Lin et al., 2008; Stuart and Edwards, 2006); (iii) the deep penetration of forest soils by roots and the formation of highly permeable root channels (Jost et al., 2012); and (iv) water uptake by trees (Nadezhdina et al., 2010). Much of the precipitation impacting forest ecosystems is captured at the vegetation-atmosphere interface (interception), and only slowly delivered to the soil surface. Here, it is eventually allowed to infiltrate into the soil, where it is further utilized by plants or stored in the deeper groundwater reservoirs (Lin et al., 2008). Moreover, comparatively high evapotranspiration rates in most forest ecosystems increase atmospheric humidity locally, and substantially reduce or moderate air and soil temperatures (Pokorný, 2001). Thus, the effect of water retention in forests is crucial not only for their own water supply, but also for the water budget of the larger ecosystem (Makarieva et al., 2013). Therefore, the joint management of forests and water resources has become one of the leading environmental and economic issues of both global and local policy makers (Bates et al., 2008; European Commission, 2013), and in hydrological research (Rewald et al., 2011; Vose et al., 2011).

Forest structure and composition, as well as soil properties, are important synthetic factors of soil moisture and runoff dynamics in forest ecosystems, and significantly influence their ability to protect the lower parts of watershed against floods during extreme hydrological events (Hümann et al., 2011; Jost et al., 2012). Nonetheless, most studies on soil water dynamics in forests have focused on the effects of the aboveground structures of the forest stand (Schume et al., 2004; Vertessy et al., 2001), or the belowground structures in soil and tree-root systems (Lin et al., 2008; Nadezhdina et al., 2010). Other key physiographic attributes that control soil water dynamics are topographic features (Bachmair and Weiler, 2012; Lin et al., 2008; Yeakley et al., 1998), including soil surface microrelief (Frei and Fleckenstein, 2014; Martin et al., 2008; Thompson et al., 2010; van der Ploeg et al., 2012), which is the focus of this discussion.

3. Microrelief in forest soils

3.1. Types and factors of soil surface microrelief

Surface microrelief (here considered at the scale of decimeters to meters) in forests is formed by natural processes and/or by human activities. The most common anthropogenic causes of forest-soil microrelief formation are the wakes after mechanical soil preparation, traces of axles, scratches after skidding, or excavations along forest roads. Although some exceptions exist (see Hupy and Schaetzl, 2008), all of the most common anthropogenic elements of soil microrelief in forests have a linear character, hence serving as potential water-discharge accelerating structures (unless they run parallel to the contour; Schüler, 2006). Other forms (either natural or artificial) of microrelief in forest soils include trenches, rills, or other forms of microrelief, all of which act as water-discharge agents, and are outside the scope of this paper.

Moreover, soil surface microrelief in forests can form in many other natural ways, mostly generating point features that do not promote concentrated runoff. Beyond some site-specific, less obvious, or easily-erodible microrelief features formed by soil fauna (Gabet et al., 2003; Richards et al., 2011; Wilkinson et al., 2009), and substrate- or climate-specific microrelief formed by various physical forces, such as wind accumulation, argilliturbation (e.g., gilgai microrelief; Kishné et al., 2014), or cryoturbation (e.g., frost heaving and patterned ground), surface microrelief in forests is

Fig. 1. (A) A rootball (ca 2.5 m^3) and associated pit formed by a recently uprooted beech tree in the Boubín virgin forest, Czech Republic; (B) A pit-mound pair (ca 2.0 m wide × 2.5 m long) formed by tree uprooting in the Červík experimental basin, Czech Republic; (C) A large, broad depression formed by recently uprooted spruce tree, currently infilled by water after a period of rain; P. Šamonil provides scale, poking a spade into the pit, to the point of maximum depth; Boubín virgin forest; (D) Water ponding in a treethrow pit near a treethrow mound, formed by a rotational treefall. Photos A–C by MV, photo D by RJS.

Fig. 2. Pit-mound microrelief in northern Wisconsin, US, which remains preserved after deforestation and years of pasturing. Photo by RJS.

primarily formed by the biomechanical effects of trees (see Schaetzl and Thompson, 2015 for a comprehensive review).

The most common, but usually less apparent, biomechanical effect of trees on soil surface microrelief is the displacement of soil and rocks by root and bole growth, and the subsequent infilling of stump holes after decay (Hoffman and Anderson, 2013; Phillips and Marion, 2006). Forests also have significant stabilizing functions against soil erosion, thus indirectly influencing some geomorphic processes, and the resulting microrelief (Pawlik, 2013). However, regarding spatial scale and frequency, the most widespread and most obvious natural process that forms microrelief in forest soils is tree uprooting (Gabet et al., 2003; Roering et al., 2010; Schaetzl et al., 1989b; Šamonil et al., 2010a).

3.2. The pit-mound microrelief by tree uprooting

Uprooted trees often heave a rootball with its embedded soil material, leaving a pit at the original-tree microsite (Fig. 1A). The volume of displaced soil mass by tree uprooting can range up to 5.6 m^3 (Pawlik, 2013). After collapse of the rootball, as the roots decay, the detached soil mass typically subsides into an irregular mound (Fig. 1B). Some of the soil in the rootball usually slumps or washes onto the former surface, where it buries preexisting soils (Schaetzl, 1986; Šamonil et al., 2013); some of the soil may fall and wash back into the pit (Schaetzl et al., 1990; Šamonil et al., 2015). The resulting pit and mound features may remain clearly identifiable on the ground for hundreds or even thousands of years after the uprooting event (Schaetzl and Follmer, 1990; Šamonil et al., 2013), sometimes visible long after deforestation (Embleton-Hamann, 2004; Fig. 2). Depending on the natural conditions and disturbance history of the forest, pits and mounds may occupy up to 90% of the soil surface (Šamonil et al., 2010a), making the role of pit-mound microtopography in generating surface roughness and influencing runoff potentially very significant (Martin et al., 2008; Phillips et al., 2017).

The physical dimensions (e.g., length, width, and depth or height) of treethrow pits and mounds largely depends on the dimensions of the uprooted tree and its roots (Phillips et al., 2017; Richards et al., 2011; Sobhani et al., 2014), the age of the treethrow pit-mound (Šamonil et al., 2010b, 2013, 2015), and the types and rates of the associated erosion-sedimentation processes (Schaetzl and Follmer, 1990). For example, Sobhani et al. (2014) found that the areas of pits and mounds formed by a recently uprooted tree followed a power-law dependence on tree diameter. The vertical dimensions of treethrow pits and mounds substantially change over time as the mound subsides and the pit infills by litter and sediment transport, so the relative steepness of both pits and mounds can be used as proxies of their age (Šamonil et al., 2009).

The dimensions of a treethrow pit, relative to the paired mound, have long been known to depend on slope inclination and tree-fall direction (Beatty and Stone, 1986; Norman et al., 1995), as well as on tree species and root architecture (Beatty and Stone, 1986; Bobrovsky and Loiko, 2016), and on the intensity and types of erosion–sedimentation processes. Thus, these relationships can be highly site-specific (see Pawlik et al., 2016a). For example, on gentle slopes, more of the soil volume upheaved by uprooting wastes backward, off the mound as the rootball collapses (Norman et al., 1995). This leads to decreased volumes of the resulting pit. On steeper slopes, by comparison, most trees fall downslope and hence, more of the soil in the root plate falls onto the preexisting soil surface, and not into the pit itself (Beatty and Stone, 1986; Schaetzl, 1986). As a result, pits are proportionately larger, and of key hydrological importance – they are often upslope of mounds.

4. The hydrology of treethrow pits and mounds

Many hydrological studies highlight the role of soil surface microrelief in rainfall partitioning between infiltration and runoff (Frei and Fleckenstein, 2014; Kishné et al., 2014; van der Ploeg et al., 2012). Thompson et al. (2010) estimated that pit and mound microrelief on sloping surfaces may increase the proportion of rainfall that infiltrates by 20–200%, when compared to a reference "smooth" slope. However, there are several aspects of forest soils and of the soil properties within pit and mound microsites formed by tree uprooting that can substantially differentiate the hydrological effects from the model example by Thompson et al. (2010), or from the hummocky microsites in other environments, such as wetlands with shallow groundwater system (Frei and Fleckenstein, 2014; Kishné et al., 2014; van der Ploeg et al., 2012). Unfortunately, comparable studies on the hydrological processes in the soils within treethrow pit-mounds are lacking, with the exception of a study by Embleton-Hamann (2004) on carbonate bedrock.

4.1. Treethrow pits

Unlike the conceptual approach of surface runoff used by Thompson et al. (2010), in most upland forests, lateral subsurface flow is the dominant runoff-producing mechanism (Lin et al., 2008; Tromp-van Meerveld and McDonnell, 2006). Tree uprooting may disturb soil to a considerable depth, and depressions formed by uprooting can effectively disrupt both surface runoff and subsurface flow, allowing for ponding and surface water storage in pits (Fig. 1C). Treethrow pits may so substantially collect (and thus, focus) runoff and snowmelt waters from surrounding areas that they facilitate spatially focused infiltration into deeper soil layers (Embleton-Hamann, 2004; Schaetzl, 1990; Table 1). Eluvial horizon funnels and tongues in the soils beneath pits are clear evidence of this type of focused flow (Schaetzl, 1986; Schaetzl et al., 1990; Šamonil et al., 2013, 2015). Moreover, in older pits with well-developed soil profiles, subsurface flow might pass below the pit base without surface recharge, leaving a relatively dry topsoil downslope (usually beneath the mound interface), as visible in Figs. 3–5 in Pawlik and Kasprzak (2015). In less permeable soils, seasonal, or even long-term perching of water can occur in pits, leading to gleying in soils below (Bobrovsky and Loiko, 2016). However, where old roots remain in pits (e.g., Fig. 10 in Bobrovsky and Loiko, 2016), the macropores that form after their decomposition can serve as channels for preferential flow, enhancing the infiltration rate much above background levels (Jost et al., 2012). In a karst landscape, Embleton-Hamann (2004) observed that some treethrow pits, like sinkholes, concentrate precipitated water, and deepen in time by secondary dissolution of the carbonate rock. A similar sinkhole effect of treethrow pits on runoff infiltration on a forested slope was expected in a model by Phillips et al. (2017) even in a non-karst landscape.

4.2. Treethrow mounds

Within treethrow mounds, soil material is typically loose, with low bulk densities. Hence soils here are more permeable than within undisturbed microsites nearby (Lutz, 1940; Meyers and McSweeney, 1995; Schaetzl, 1990). This characteristic may contribute to both enhanced infiltration within mounds, and increase the potential water retention capacity of the soils there (Table 1).

Patterns of infiltration or water flux through mounds will strongly depend on local soil properties (Kodešová et al., 2009), and on soil horizontation patterns that may have resulted from the previous soil disturbance and subsidence. Various types of uprooting may lead to different patterns in the resulting soils

Table 1
Overview of the hydrological effects of pit-mound microrelief in forest soils.

Hydrological process	Pit-mound impact/effects	Comments
Infiltration	Increased infiltration potential in mounds due to higher permeabilities, but may be offset by less-developed litter mat or by rocks at the surface; increased but highly focused infiltration in pits	Depends on rate of influx of precipitation vs infiltration capacities of pit and mound soils. Nonetheless, pits focus infiltration, whereas mounds often do the opposite.
Focused flow/percolation, and groundwater recharge	Increased within (older) pits, various within mounds	Depends on soil architecture at the pit and mound bases. Facilitated along eluvial tongues, organic funnels, and root channels
Ponded (depression) storage	Increased in pits where permeability is low, due to concentration of runoff	Depends on the hydraulic conductivity of the soil comprising pit bottom, the precipitation intensity, and the catchment area of each pit
Runoff	Locally, may be accelerated due to steeper slopes of surface microrelief, but over larger scales is retarded due to retention in pits, redirection into deeper soil layers, and changes to overall slope flowlines	Subsurface flow is the most common runoff process on forested slopes. Overland flow occurs rarely or highly localized in most forests; usually only after extreme rainfall events and on less permeable soils
Snow accumulation[a]	Reduced on mounds, increased in pits	Depends on the amount of blowing and drifting, which acts to increase the snowpack variability across pit vs mound microsites
Snowmelt[a]	Increased spatial and temporal variability	Temperatures are more variable on mounds, and more stable in pits, as compared to undisturbed areas, leading to increased spatial variation in snowmelt
Soil freezing and freeze-thaw cyclicity [a]	More intense in mounds, less intense in pits, with impacts on soil structure	Thicker litter and snowpacks in pits lead to more stable temperatures and less freeze-thaw cycles there; the opposite situation is present on mounds
Soil moisture	Higher in pits, lower in mounds	Mounds are often sites of runoff and more intense evaporation, pits have more runin and are more protected from evaporation by thick litter mat
Watershed discharge	Reduction, mitigation of hydrological extremes, contribute to more balanced seasonal course	May be reduced temporally (direct effect; water retention), or in total (indirect effect; higher utilization by plants)

[a] A regionally (climatically) dependent process.

(Beatty and Stone, 1986; Schaetzl et al., 1989b, 1990). As the water infiltrating through the mound reaches the level of the underlying (buried) soil surface, it may either continue to infiltrate, or be compartmentalized into lateral subsurface flow. The latter alternative is more likely in mounds that completely overturn an undisturbed original-soil profile, although this is relatively rare and may occur only on steep slopes (Schaetzl, 1986). Nonetheless, complete soil inversion may lead to mounds that creep and elongate downslope (Norman et al., 1995), further increasing its surface area available for infiltration. However, the root ball of the uprooted tree usually flips ± parallel to the soil surface, and then subsides either partially (hinge-type uprooting) or almost entirely (rotational-type uprooting) over the pit and the flipped root ball. Therefore, both the mound and the soil beneath a mound have usually mixed or contorted horizontation (Lyford and MacLean, 1966; Norman et al., 1995; Schaetzl, 1990; Šamonil et al., 2015), which cannot predictably impede infiltration patterns. Alternatively, some mounds may also consist of less-weathered material from deeper soil layers, leaving a higher amount of rock clasts at the surface, which can impede erosion (Small et al., 1990), but which may also partially inhibit infiltration and generate additional runoff. Much of this is site (mound)-specific. Although occasional runoff from mounds may cause localized soil erosion (Schaetzl and Follmer, 1990; Šamonil et al., 2015), this type of runoff typically spans from decimeters to a few meters, and does not lead to losses of water from the forest system via surface flow (Phillips et al., 2017); unless soil surface in the area was exposed to further disturbance, e.g. fire (Martin et al., 2008). Instead, it generally only facilitates subtle and short-distance translocation of sediment across the soil surface.

4.3. Pit-mound hydrology in time

The hydrological characteristics of treethrow pit-mounds may substantially change over time due to (i) accumulation of organic matter in pits (Šamonil et al., 2008; Fig. 4 in Bobrovsky and Loiko, 2016), which usually accentuates infiltration, and (ii) subsequent, often divergent soil evolution at the mound, pit, and undisturbed microsites (Schaetzl, 1990; Šamonil et al., 2015), which can affect the soil's saturated and unsaturated hydraulic conductivities. For example, with increasing age, the upper part of the mineral soil in a pit is usually either increasingly enriched by organic matter (Šamonil et al., 2010b), or transformed into an eluvial horizon (Šamonil et al., 2013, 2015), both of which may enhance infiltration rates. In contrast to the relatively slow post-disturbance pedogenesis at mounds (Šamonil et al., 2015), the intense pedogenic processes in pits often lead to formation of distinct, either organic-rich or eluvial funnels that document the paths of intense infiltration and focused flow. Therefore, older pits may be increasingly more effective in accepting infiltrating water, despite their overall decline in size; see Figs. 2 and 3 in Schaetzl (1986), Fig. 1 in Schaetzl (1990), Appendix 1 in Šamonil et al. (2010b), Figs. 5–7 in Šamonil et al. (2015), Fig. 4 in Šamonil et al. (2016). Nevertheless, as far as we know, these hydrologic processes in treethrow pits have never been directly measured or experimentally verified, except the study by Embleton-Hamann (2004) on carbonate bedrock.

5. Pits and mounds in forest hydrology

Treethrow pits and mounds are reliable indicators of forest disturbance dynamics (Lenart et al., 2010; Šamonil et al., 2009). The hydrological impacts of treethrow pits and mounds have been mostly inferred, based largely on their morphologies (Schaetzl et al., 1990; Small et al., 1990; Schaetzl, 1990; Bobrovskii, 2008; Šamonil et al., 2010a,b; Šamonil et al., 2015). However, the basic hydrological characteristics recognized in the pit and mound microsites (Bobrovsky and Loiko, 2016; Embleton-Hamann, 2004; Kooch et al., 2014; Lutz, 1940; Nachtergale et al., 2002; Phillips et al., 2008; Schaetzl, 1990; Simon et al., 2011; Šamonil et al.,

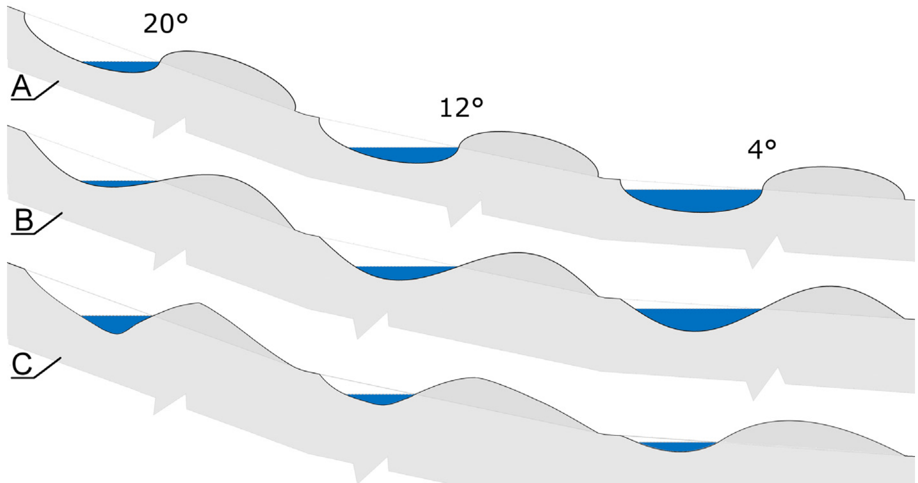

Fig. 3. Illustration of three different slope transects through treethrow pit-mound pairs as positioned at slopes with inclinations of 20°, 12°, and 4°. (A) Simplified pit-mound pairs, approximated by a half-ellipsoid, as commonly used in sediment-transport calculations (e.g., Pawlik et al., 2013; Šamonil et al., 2016); (B) More idealized, naturally-undulating microrelief constructed by a sinusoid function (Thompson et al., 2010) and applied in pit-mound approximations; (C) Examples of real pit-mound pairs, i.e., the silhouettes of real profiles redrawn after Šamonil et al. (2015). The fill within the treethrow pits illustrates their potential depression storage capacities (DSC).

2015; Ulanova, 2000) have not been extrapolated to wider spatial scales, to predict the overall impacts of the pit-mound microrelief on the hydrology of forested watersheds.

5.1. Modelling pit-mound surfaces

Although the volumes of treethrow pits and mounds have been reported for various forest biomes (Gallaway et al., 2009; Norman et al., 1995; Pawlik et al., 2016a; Richards et al., 2011; Šamonil et al., 2016), cumulative quantification and/or comparisons of pit-mound volumes are rare (Pawlik et al., 2013; Phillips et al., 2017) and have focused primarily on sediment transport by tree uprooting. However, the volume of a pit is a key physical attribute to understanding its role in forest hydrology. Pit-mound dimensions, patterns and densities should be some of the better documented hydrologic attributes of the forest surface, with regard to its ability to retain water and delay runoff (see Section 4).

Much confusion exists regarding the volumetric modelling of pit-mound features. The most widely used approximation of treethrow pit-mound volumes is the half-ellipsoid model (Norman et al., 1995). However, this model forces pits/mounds to pass perpendicularly to a plane, which is seemingly not natural. This is most obvious on the sloping sides of mounds, particularly at the lower-side of a mound and the front-side of a pit that contravene common erosion-sedimentation processes (Fig. 3). Consequently, the volume of a pit or mound as calculated from its depth/height, width, and length would be substantially overestimated. This discrepancy may imply potential bias in volume estimations in some earlier studies (Norman et al., 1995; Gallaway et al., 2009; Pawlik et al., 2013, 2016a; Šamonil et al., 2016). A significant overestimation of pit volumes calculated by the half-ellipsoid model has already been reported for several recently uprooted trees (Richards et al., 2011).

A sinusoidal function has also been widely used as a model for the study of naturally undulating microrelief (Thompson et al., 2010). A sinusoid-based model has a potential to construct a more realistic approximation of treethrow pit and mound dimensions (Fig. 3). In such a case, the pit-mound length will represent the wavelength, while pit-depth and mound-height the amplitude of the sinusoid function (Thompson et al., 2010). Nevertheless, unlike the idealized sinusoidal microrelief, real treethrow mounds on slopes are naturally more extended in the downslope direction (Norman et al., 1995), while pits are increasingly skewed upslope. Thus, even the sinusoid model cannot perfectly reflect the natural asymmetry of real pit/mound profiles, especially on steep slopes (Fig. 3). Leaving aside the effect of pit and mound asymmetries on their volume estimates, mound volumes on slopes or across landscapes are usually lower than pit volumes (Norman et al., 1995; Pawlik et al., 2013). Therefore, the paired pits and mounds should be rather measured and modelled separately. Nevertheless, even separate modelling of pits and mounds using any of the models would not properly deal with some specific features, such as the sickle or ring-shaped pits occasionally formed by rotational treefalls (Beatty and Stone, 1986; Fig. 1D).

One of the most promising approaches in modelling pit-mound microrelief is the implementation of high-resolution 3D data, e.g., from terrestrial laser scanning (e.g., Martin et al., 2008). Such a 3D model of a forested slope, including detailed pit-mound microrelief, could be further used for evaluating various hydrological parameters of pit-mound surfaces (e.g., their contribution to overall surface roughness, or the depression storage capacity), as well as for direct hydrological modelling (e.g., Frei and Fleckenstein, 2014; Kishné et al., 2014).

5.2. Hydrology of pit-mound surfaces

The effect of treethrow pits and mounds on the hydrology of forested watersheds will strongly depend on their (i) abundance (Section 3.1), (ii) physical dimensions (Section 3.2), and (iii) soil characteristics (Section 4), as well as (iv) on the overall slope settings (e.g., on steeper slopes, more water could potentially runoff into, or run out of, pits). A modelling example by Thompson et al. (2010) simulated infiltration and runoff generation after exposition to various rainfall scenarios at idealized slopes with pit-mound microrelief, on millimeter to centimeter scales. After considering the expected hydrological effects of treethrow pits and mounds (Section 4), and the overall hydrology of forest soils (Lin et al., 2008; Tromp-van Meerveld and McDonnell, 2006), the modified conceptual scenario after Thompson et al. (2010) may look as follows: (1) Up to some threshold, water will infiltrate and partially run off through subsurface flow that may concentrate and sink into pits without surface ponding. (2) After exceeding the infiltration capacity of pits, water may pond in pits, further delaying runoff from the immediate catchment of each pit. Here, the depression storage capacity (DSC) of a pit will represent the volume of water that can be ponded. (3) After exceeding both the infiltration capacity and the DSC of a pit, e.g., after an extreme rainfall event or on clayey soils with low hydraulic conductivities, the water may spill over the rim of the pit. This may lead either to surface runoff or re-infiltration, with possible subsequent retention in another pit downslope. As mentioned above, slope inclination may have a positive effect on the pit volume (Section 3) and hence, its potential for runoff interception, while in turn affects the proportion of the pit volume available for depression storage. This may be critical for the retention threshold of the system during rainfall or spring thaw events, while less important for snow accumulation.

The negative dependence of DSC on slope inclination may substantially increase in soils with shallow profiles. For example, on steep slopes a shallow pit may have a DSC of <10% of its volume, whereas a deeper pit of the same volume may still store water in a substantial part of its volume. This depth-dependence in relative DSC will also have substantial impact on water retention; Thompson et al. (2010) found that increasing the amplitude of simulated pit-mound microrelief significantly increased the proportion of rainfall infiltration on a modelled slope. Therefore, deeper pits would be always more effective in water retention on slopes than would a larger number of more shallow pits of equal cumulative volume.

In well drained soils with large infiltration rates and hydraulic conductivities in pits (Section 4.1), and under relatively less intense rainfall, it is possible the DSCs of pits may be seldom utilized (e.g., Phillips et al., 2017). However, on steeper slopes that are generally more prone to increased runoff and to shallow subsurface flow (Lin et al., 2008, 2006), surface ponding may be more common and hence, the importance of DSC for the potential of a pit to intercept runoff and generate focused infiltration may substantially increase (Fig. 1C). A similar positive effect of pit-mound microrelief can also be expected on poorly-drained soils with low hydraulic conductivities, where water ponding in pits may substantially prolong the time available for infiltration (e.g., Kishné et al., 2014; Fig. 1D).

Pit-mound microrelief almost always increases surface roughness at the hillslope or watershed scale (Fig. 2). Generally, the presence of microrelief may result in substantial time delay in runoff generation either due to depression storage (e.g., Frei and Fleckenstein, 2014), or flowlines routing (e.g., van der Ploeg et al., 2012) (Table 1). Thus, when compared to a reference slope without pits and mounds, the mean flowline length for both surface and subsurface runoff may significantly increase, either laterally, vertically, or both. Here, higher numbers of smaller pits and mounds would be more effective in generating surface roughness, than would a smaller number of larger ones of equal cumulative volumes. Flowlines routing through pit-mound microrelief could even be increasingly important for runoff retardation at relatively flat surfaces (van der Ploeg et al., 2012; Fig. 1D).

Fig. 4. Dense regeneration of beech saplings under a spruce snag atop a treethrow mound in the Žofín virgin forest, Czech Republic. Photo by MV.

5.3. Pit-mound moisture patterns and tree-water supply

Pits and mounds formed by tree uprooting may substantially increase the fine-scale variability in soil water contents in both horizontal and vertical directions (see Pawlik and Kasprzak, 2015), which can in turn affect other aspects of forest ecology. For example, in humid areas of temperate, boreal, and tropical forests, elevated and well-drained treethrow mounds generally represent highly favorable microsites for tree regeneration (Lutz, 1940; Lyford and MacLean, 1966; Putz, 1983; Šamonil et al., 2016; Šebková et al., 2012; Fig. 4). In contrast, pits formed by tree uprooting are microsites of increased accumulation of undecomposed organic matter and (sometimes) snow, and almost always provide for wetter soil conditions (Kooch et al., 2014; Nachtergale et al., 2002; Schaetzl, 1990; Šamonil et al., 2008), resulting in comparatively poorer sites for successful seed germination and sapling establishment (Lyford and MacLean, 1966; Simon et al., 2011; see Schaetzl et al., 1989a for a more comprehensive review). However, this general relationship has other far reaching consequences, which have not been mentioned in the literature. For example, a tree in the proximity of a pit (most likely a tree on the adjacent mound) may benefit from the pit by using it as a strategic source of moisture and nutrients (Table 1), while simultaneously avoiding the potential ponding or prolonged wetness of the pit site proper. This ecological advantage would enable higher rates of growth of trees near pits, especially during dry periods and in well-drained soils. Thus, many trees growing on mounds may combine favorable physical conditions of mounds with the hydrological benefit of the nearby pit.

The competitive advantage of mound microsites might be larger and persist even longer than previously assumed. This mechanism would result in even higher occupation of mounds for large trees, as observed e.g. for *Acer saccharum* in Šamonil et al. (2016) or for *Fagus sylvatica* in Šebková et al. (2012). The same positive feedback can also apply on pit microsites in some specific environments, and for tree species that preferably locate in pits (e.g., Henry and Swan, 1974; Peterson and Pickett, 1990). Nevertheless, the nonrandom distribution of trees within pits, mounds and undisturbed microsites may further modify the overall hydrological effect of treethrow pit-mounds, due to the redistribution of precipitation associated with stemflow and throughfall, which is specific for various tree species (Bialkowski and Buttle, 2015; Nikodem et al., 2013).

Mounds and pits can also serve as important seasonal microhabitats for many species of soil fauna (Table 1). As noted, for example, by Beatty and Stone (1986, p. 547): "*Depending on the time of year, earthworms may selectively concentrate in mound, pit, or undisturbed microsite*". Kooch et al. (2014) found significantly higher earthworm abundances in treethrow pits, when compared to both mounds and undisturbed microsites. Although some studies (e.g., Nachtergale et al., 2002) report negative correlations between tree uprooting and earthworm biomass, this relationship may have resulted because earthworms are more abundant in older pits (Kooch et al., 2015). Also, in forest soils, the burrowing activity of earthworms provides a strong positive feedback on soil porosity and infiltration rates (Schütz et al., 2008).

Finally, uprooting dynamics may also influence local soil and regolith depths (Gabet and Mudd, 2010; Pawlik et al., 2016b;

Fig. 5. Examples of uprooted spruce trees in (A) managed and (B) natural forests; the arrows represent ca. 0.6 m scale. The reduction of the new-formed, and the old microrelief of forest soils by (C) the cleanup of uprooted trees after logging and (D) heavy machinery, is shown respectively. A and D photos are from Šumava Mts., B is from the Razula reserve, and C is from the Červík experimental basin, all in Czech Republic. All photos by MV.

Phillips et al., 2008), thereby increasing the potential water retention capacity of the soil profile. All these processes may positively contribute to water recharge into forest soils, and its availability for subsequent tree uptake (Table 1).

Thus, in a forest ecosystem the occurrence or absence of tree uprooting events, and the microrelief they create, may directly and indirectly affect soil moisture, tree-water supply, production, and the overall resilience of the forest stand.

6. The smoothed microrelief in managed forests

In managed forests, tree uprooting is traditionally seen as undesirable to timber production due to its negative impacts on wood quality, and increased logging (recovery) costs (see Schaetzl et al., 1989b). Therefore, forest managers are highly motivated to secure mechanical stability of forest stands by prudent thinning and felling practices (e.g., Alexander, 1964; Schelhaas, 2008). Thus, most trees are harvested standing. In contrast, Šamonil et al. (2014) found that one third of trees in a natural beech-dominated forest died uprooted. Moreover, not only the frequencies but the volumes of tree uprooting may be lower in managed forests due to the limited occurrence of larger trees that are more prone to uprooting (Mezei et al., 2014), and which could disturb much larger volumes of soil (Sobhani et al., 2014; Phillips et al., 2017). Consequently, intensive forest management not only reduces the number of uprooted trees, but also the areas and volumes of the resultant pits and mounds (Fig. 5A and B). Furthermore, occasionally the newly formed microrelief by tree uprooting is eliminated by logging operations, often as the rootball is returned to its original position (either intentionally using a winch, or spontaneously after cutting the stem; Fig. 5C). In addition, many of the technologies used in forestry also directly contribute to the reduction of preexisting microrelief, such as heavy machines operating in the forest interior (Fig. 5D), or site preparation practices at clearings.

Fig. 6. Reduced microrelief in an intensively managed forest in the Pekelský potok experimental basin, Czech Republic. Photo by MV.

As already discussed in Section 3.2, treethrow pits and mounds may remain visible for hundreds or even thousands of years (Schaetzl and Follmer, 1990; Šamonil et al., 2013). However, these examples of extreme pit-mound pair ages have developed when large trees are uprooted, and their longevity is influenced by reduced local erosion rates (Schaetzl and Follmer, 1990; Šamonil et al., 2013). This is usually not the case of intensively managed forests, where the erosion processes are indirectly intensified by human activities that damage the litter and undergrowth vegetation (Hartanto et al., 2003). Furthermore, on some less stable landforms and/or steeper slopes, the leveling of pit-mound microrelief may be much more intense, and often takes less than a century, even in an unmanaged forest (Šamonil et al., 2010b). In managed forests, the systematic repression or elimination of the processes that form microrelief in forest soils may lead to a gradual leveling of the preserved pits and mounds, and substantial smoothing of microrelief (Fig. 6).

Although lowered microrelief in forests is undoubtedly more convenient for logging, hauling, and other forestry operations, these modifications of forest surfaces may have far reaching consequences to the forest's hydrological function, resilience, and production. Moreover, Šamonil et al. (2010b) found that the absence of tree uprooting in a managed forest also may lead to substantial changes in soil evolution in only a few centuries. Following the global industrial intensification of forestry in the last three centuries, this type of cumulative impact of forest management on forest soils has become increasingly important. From a long-term perspective, this continual and, over the horizon of a human life, hardly noticeable trend in managed forests may have significant long-term effects on their hydrology, such as decreased efficiency of infiltration, accelerated runoff, and more synchronized melting of snow, thereby providing lower protection against runoff, soil erosion, and floods. The negative feedback to forest management may involve weakened resilience of trees to drought and pests.

7. Implications for practice and further research

"*Forestry practices that preserve natural ecosystem processes are likely to be more effective in maintaining forests' biodiversity and natural resilience against climate change.*" (Jonsson et al., 2015)

Potential negative impacts of reduced microsite diversity on forest ecology, in the absence of tree uprooting, can be partially inferred from previously published studies (Beatty, 1984; Flinn, 2007; Jonsson and Esseen, 1990; Miller et al., 2002; Schaetzl et al., 1989a; Ulanova, 2000; von Oheimb et al., 2006). However, the effects of smoothed or reduced microrelief on water retention and tree-water supply in forests has neither been quantified nor discussed in the literature. The absence of relevant data also limits our ability to quantify the degree of microrelief reduction in managed forests, as well as the direct and indirect effects of this phenomenon in the hydrological functioning of forest ecosystems.

Hydrologists may wish to experimentally quantify the impact of pit-mound microrelief on soil water retention and runoff retardation, under both exceptional and typical hydrological conditions. Moreover, the effect of pit-mound microrelief on forest hydrology and runoff generation should be evaluated in different topographic and geologic settings, so as to determine the most critical areas for water retention.

Microrelief formed by tree uprooting should be simultaneously inventoried in both managed and natural forests at different slope inclinations (Norman et al., 1995; Šamonil et al., 2016) and topographic settings (Cremeans and Kalisz, 1988), and on various substrates (Valtera et al., 2015). Comparisons of these data would help understand the differences in microrelief in managed forests vis a vis their natural (potential) state. Such data would be highly useful for the restoration management or formation of microrelief in forest soils to identify sites where: (i) pit-mound microrelief has considerably lower residence times, or (ii) uprooting has a lower probability to occur, and/or (iii) uprooting rarely forms pit/mound microsites (Norman et al., 1995).

The preferences of pit-mound microsites for seed germination and tree growth (Simon et al., 2011; Šamonil et al., 2016; Šebková et al., 2012) should be considered in afforestation, thinning, and other silvicultural practices (Fig. 6). However, forest managers should also pay attention to specific environments and tree species that may have inverse preferences to pit and/or mound microsites (Schaetzl et al., 1989a; Peterson and Pickett, 1990).

For hydrological modelling at both the slope and watershed scale, the physical attributes of pit-mound features should be transformed into relevant quantitative indices that would reflect their contributions to slope hydrology (Barnes et al., 2014; Le and Kumar, 2014). The most widely used half-ellipsoid physical model for treethrow pit-mounds (Norman et al., 1995) should be replaced by a more realistic model, or by high-resolution 3D data of forested surfaces (e.g., Martin et al., 2008) for possible application in both microrelief and hydrological modelling (Frei and Fleckenstein, 2014; Kishné et al., 2014). This change would allow for a suitable basis for forest management to ameliorate the hydrological function of managed forests, and would support the resilience of forest ecosystems to ongoing climate change (Bates et al., 2008; European Commission, 2013; Vose et al., 2011). However, any management practices "employing" natural processes to ameliorate forest ecosystem functions should also take into account all other desired forest functions.

8. Conclusions

The potential impacts of smoothed microrelief in forest ecosystem functioning can be partially inferred from already published studies. Well-developed pit-mound microrelief in forests mediates runoff into watercourses and enhances overall water quality, soil water retention, and groundwater recharge. Moreover, more effective retention of water due to pit-mound microrelief may enable higher availability of moisture for nearby trees, enhancing their resilience and growth.

In intensively managed forests, the gradual leveling of old, and the absence of newly formed, pits and mounds can lead to gradual smoothing of microrelief. This loss of microrelief differentiation over large forested watersheds may allow more uniform melting of snow across the soil surface, decrease water retention in forest soils, and impair the long-term availability of water for trees. Water would drain faster to streams, such that an intense or prolonged rainfall may more likely cause floods, reinforcing drought stress during subsequent dry periods. Together, these processes may significantly weaken the production and resilience of forest ecosystems. From a long-term perspective, the decreased efficiency in rainwater harvesting in forests may have negative impacts not only on their own water supply, but also on the water regime of the basin. This would become increasingly important with the increasing frequency of extreme hydrological events expected in the most accepted scenarios of future climate change.

Further hydrological analyses using high-resolution 3D data of forest surfaces, perhaps coupled with direct field experiments, would give a more realistic picture of how the natural pit-mound microrelief in forest soils affects water retention and hydrology. Hydrologists should experimentally measure and quantify the real impact of pit-mound microrelief on soil water retention and runoff retardation.

Further research is also needed to quantify the differences between the microrelief of intensively managed forests, as compared to their natural (potential) state. Determination of the most critical areas for potential restoration of naturally undulated microrelief in forest soils should be based on detailed monitoring and comparisons with reference natural forests under similar topographical, geological and pedological conditions, and should take into account different biomechanical impacts of various tree species, as well as other desired functions of the forest, including its accessibility and safety for humans.

Funding

This work was supported by an institutional subsidy (VUKOZ-IP-00027073).

Acknowledgements

We appreciate previous contributing discussions on this issue, including a field excursion on experimental basins, with Zora Lachmanová, and further Martin Šanda, Miroslav Tesař and Jiří Pavlásek. We thank two anonymous reviewers, whose comments substantially improved the quality of the paper, and Pavel Šamonil for his critical comments on an early version of the manuscript. We also thank Tomáš Vrška for consultation on forest management, and Martin Krůček for consultation on modeling. The authors declare no conflict of interest.

References

Alexander, R.R., 1964. Minimizing windfall around clear cuttings in spruce-fir forests. For. Sci. 10, 130–142.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg(Ted), E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, JH., Allard, G., Running, SW., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684. http://dx.doi.org/10.1016/j.foreco.2009.09.001.

Archer, N.A.L., Bonell, M., Coles, N., MacDonald, A.M., Auton, C.A., Stevenson, R., 2013. Soil characteristics and landcover relationships on soil hydraulic conductivity at a hillslope scale: a view towards local flood management. J. Hydrol. 497, 208–222. http://dx.doi.org/10.1016/j.jhydrol.2013.05.043.

Bachmair, S., Weiler, M., 2012. Hillslope characteristics as controls of subsurface flow variability. Hydrol. Earth Syst. Sci. 16, 3699–3715. http://dx.doi.org/10.5194/hess-16-3699-2012.

Barnes, R., Lehman, C., Mulla, D., 2014. Priority-flood: an optimal depression-filling and watershed-labeling algorithm for digital elevation models. Comput. Geosci. 62, 117–127. http://dx.doi.org/10.1016/j.cageo.2013.04.024.

Bates, B.C., Kundzewicz, Z.W., Wu, S., Palutikof, J.P., 2008. Climate Change and Water, Technical Paper of the Intergovernmental Panel on Climate Change. IPCC Secretariat, Geneva.

Beatty, S.W., 1984. Influence of microtopography and canopy species on spatial patterns of forest understory vegetation. Ecology 65, 1406–1419.

Beatty, S.W., Stone, E.L., 1986. The variety of soil microsites created by tree falls. Can. J. For. Res. 16, 539–548. http://dx.doi.org/10.1139/x86-094.

Bialkowski, R., Buttle, J.M., 2015. Stemflow and throughfall contributions to soil water recharge under trees with differing branch architectures. Hydrol. Process. 29, 4068–4082. http://dx.doi.org/10.1002/hyp.10463.

Bobrovskii, M.V., 2008. The role of windfall pedoturbations in the formation of forest soil profiles. Eurasian Soil Sci. 41, 1366–1370. http://dx.doi.org/10.1134/S1064229308130036.

Bobrovsky, M., Loiko, S., 2016. Patterns of pedoturbation by tree uprooting in forest soils. Russ. J. Ecosyst. Ecol. 1, 1–22. http://dx.doi.org/10.21685/2500-0578-2016-1-3.

Ciscar, J.C., Feyen, L., Soria, A., Lavalle, C., Raes, F., Perry, M., Nemry, F., Demirel, H., Rozsai, M., Dosio, A., Donatelli, M., Srivastava, A., Fumagalli, D., Niemeyer, S., Shrestha, S., Ciaian, P., Himics, M., Van Doorslaer, B., Barrios, S., Ibáñez, N., Forzieri, G., Rojas, R., Bianchi, A., Dowling, P., Camia, A., Libertà, G., San Miguel, J., de Rigo, D., Caudullo, G., Barredo, J., Paci, D., Pycroft, J., Saveyn, B., Van Regemorter, D., Revesz, T., Vandyck, T., Vrontisi, Z., Baranzelli, C., Vandecasteele, I., Batista e Silva, F., Ibarreta, D., 2014. Climate Impacts in Europe: The JRC PESETA II Project, JRC Scientific and Policy Reports, EUR 26586EN. http://dx.doi.org/10.2791/7409.

Cremeans, D.W., Kalisz, P.J., 1988. Distribution and characteristics of windthrow microtopography on the Cumberland Plateau of Kentucky. Soil Sci. Soc. Am. J. 52, 816–821. http://dx.doi.org/10.2136/sssaj1988.03615995005200030039x.

Dai, A., 2011. Drought under global warming: a review. Wiley Interdiscip. Rev. Clim. Chang. 2, 45–65. http://dx.doi.org/10.1002/wcc.81.

Denny, C.S., Goodlett, J.C., 1956. Microrelief resulting from fallen trees. In: Denny, C. S. (Ed.), Surficial Geology and Geomorfology of Potter County, Pennsylvania. pp. 59–66.

Embleton-Hamann, C., 2004. Processes responsible for the development of a pit and mound microrelief. Catena 57, 175–188. http://dx.doi.org/10.1016/j.catena.2003.10.017.

European Commission, 2013. A new EU Forest Strategy: for forests and the forest-based sector. Commun. from Comm. to Eur. Parliam. Counc. Eur. Econ. Soc. Comm. Comm. Reg. COM (2013) 659.

Flinn, K.M., 2007. Microsite-limited recruitment controls fern colonization of post-agricultural forests. Ecology 88, 3103–3114. http://dx.doi.org/10.1890/06-2124.1.

Frei, S., Fleckenstein, J.H., 2014. Representing effects of micro-topography on runoff generation and sub-surface flow patterns by using superficial rill/depression storage height variations. Environ. Model. Softw. 52, 5–18. http://dx.doi.org/10.1016/j.envsoft.2013.10.007.

Gabet, E.J., Mudd, S.M., 2010. Bedrock erosion by root fracture and tree throw: a coupled biogeomorphic model to explore the humped soil production function and the persistence of hillslope soils. J. Geophys. Res. Earth Surf. 115, 1–14. http://dx.doi.org/10.1029/2009JF001526.

Gabet, E.J., Reichman, O.J., Seabloom, E.W., 2003. The effects of bioturbation on soil processes and sediment transport. Annu. Rev. Earth Planet. Sci. 31, 249–273. http://dx.doi.org/10.1146/annurev.earth.31.100901.141314.

Gallaway, J.M., Martin, Y.E., Johnson, E.A., 2009. Sediment transport due to tree root throw: integrating tree population dynamics, wildfire and geomorphic response. Earth Planet. Sci. Lett. 1269, 1255–1269. http://dx.doi.org/10.1002/esp.1813.

Hartanto, H., Prabhu, R., Widayat, A.S., Asdak, C., 2003. Factors affecting runoff and soil erosion: plot-level soil loss monitoring for assessing sustainability of forest management. For. Ecol. Manage. 180, 361–374. http://dx.doi.org/10.1016/S0378-1127(02)00656-4.

Henry, J.D.D., Swan, J.M.a.M.a., 1974. Reconstructing forest history from live and dead plant material – An approach to the study of forest succession in Southwest New Hampshire. Ecology 55, 772–783. http://dx.doi.org/10.2307/1934413.

Hoffman, B.S.S., Anderson, R.S., 2013. Tree root mounds and their role in transporting soil on forested landscapes. Earth Surf. Process. Landforms 722, 711–722. http://dx.doi.org/10.1002/esp.3470.

Hümann, M., Schüler, G., Müller, C., Schneider, R., Johst, M., Caspari, T., 2011. Identification of runoff processes – the impact of different forest types and soil properties on runoff formation and floods. J. Hydrol. 409, 637–649. http://dx.doi.org/10.1016/j.jhydrol.2011.08.067.

Hupy, J.P., Schaetzl, R.J., 2008. Soil development on the WWI battlefield of Verdun, France. Geoderma 145, 37–49. http://dx.doi.org/10.1016/j.geoderma.2008.01.024.

Isard, S.A., Schaetzl, R.J., 1995. Estimating soil temperatures and frost in the lake effect snowbelt region, Michigan, USA. Cold Reg. Sci. Technol. 23, 317–332. http://dx.doi.org/10.1016/0165-232X(94)00020-X.

Jonsson, B.G., Esseen, P.-A., 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. J. Ecol. 78, 924–936. http://dx.doi.org/10.2307/2260943.

Jonsson, B.G., Pe'er, G., Svoboda, M., 2015. Forests: not just timber plantations. Nature 521, 32. http://dx.doi.org/10.1038/521032b.

Jost, G., Schume, H., Hager, H., Markart, G., Kohl, B., 2012. A hillslope scale comparison of tree species influence on soil moisture dynamics and runoff processes during intense rainfall. J. Hydrol. 420–421, 112–124. http://dx.doi.org/10.1016/j.jhydrol.2011.11.057.

Jung, M., Reichstein, M., Ciais, P., Seneviratne, S.I., Sheffield, J., Goulden, M.L., Bonan, G., Cescatti, A., Chen, J., de Jeu, R., et al., 2010. Recent decline in the global land evapotranspiration trend due to limited moisture supply. Nature 467, 951–954. http://dx.doi.org/10.1038/nature09396.

Kishné, A.S., Morgan, C.L.S., Neely, H.L., 2014. How much surface water can gilgai microtopography capture? J. Hydrol. 513, 256–261. http://dx.doi.org/10.1016/j.jhydrol.2014.03.053.

Kodešová, R., Vignozzi, N., Rohošková, M., Hájková, T., Kočárek, M., Pagliai, M., Kozák, J., Šimůnek, J., 2009. Impact of varying soil structure on transport processes in different diagnostic horizons of three soil types. J. Contam. Hydrol. 104, 107–125. http://dx.doi.org/10.1016/j.jconhyd.2008.10.008.

Kooch, Y., Darabi, S.M., Hosseini, S.M., 2015. Effects of pits and mounds following windthrow events on soil features and greenhouse gas fluxes in a temperate forest. Pedosphere 25, 853–867. http://dx.doi.org/10.1016/S1002-0160(15)30066-7.

Kooch, Y., Zaccone, C., Lamersdorf, N.P., Tonon, G., 2014. Pit and mound influence on soil features in an oriental beech (fagus orientalis lipsky) forest. Eur. J. For. Res. 133, 347–354. http://dx.doi.org/10.1007/s10342-013-0766-2.

Le, P.V.V., Kumar, P., 2014. Power law scaling of topographic depressions and their hydrologic connectivity. Geophys. Res. Lett. 41, 1553–1559. http://dx.doi.org/10.1002/2013GL059114.

Lenart, M.T., Falk, D.A., Scatena, F.N., Osterkamp, W.R., 2010. Estimating soil turnover rate from tree uprooting during hurricanes in Puerto Rico. For. Ecol. Manage. 259, 1076–1084. http://dx.doi.org/10.1016/j.foreco.2009.12.014.

Lin, H., Brooks, E., McDanie, P., Boll, J., 2008. Hydropedology and surface/subsurface runoff processes. In: Anderson, M.G. (Ed.), Encyclopedia of Hydrological Sciences. John Wiley & Sons Ltd, pp. 1–25. http://dx.doi.org/10.1002/0470848944.hsa306.

Lin, H.S., Kogelmann, W., Walker, C., Bruns, M.a., 2006. Soil moisture patterns in a forested catchment: a hydropedological perspective. Geoderma 131, 345–368. http://dx.doi.org/10.1016/j.geoderma.2005.03.013.

Lutz, H.J., 1940. Disturbance of forest soil resulting from the uprooting of trees. Yale Univ. Sch. For. Bull. 45, 37.

Lyford, W.H., MacLean, D.W., 1966. Mound and pit microrelief in relation to soil disturbance and tree distribution in New Brunswick, Canada. Harvard For. Pap. 15, 1–18.

Makarieva, A.M., Gorshkov, V.G., Li, B.-L., 2013. Revisiting forest impact on atmospheric water vapor transport and precipitation. Theor. Appl. Climatol. 111, 79–96. http://dx.doi.org/10.1007/s00704-012-0643-9.

Martin, Y., Valeo, C., Tait, M., 2008. Centimetre-scale digital representations of terrain and impacts on depression storage and runoff. Catena 75, 223–233. http://dx.doi.org/10.1016/j.catena.2008.07.005.

Meyers, N.L., McSweeney, K., 1995. Influence of treethrow on soil properties in Northern Wisconsin. Soil Sci. Soc. Am. J. 59, 871–876. http://dx.doi.org/10.2136/sssaj1995.03615995005900030035x.

Mezei, P., Grodzki, W., Blaženec, M., Jakuš, R., 2014. Factors influencing the wind–bark beetles' disturbance system in the course of an Ips typographus outbreak in the Tatra Mountains. For. Ecol. Manage. 312, 67–77. http://dx.doi.org/10.1016/j.foreco.2013.10.020.

Miller, T.F., Mladenoff, D.J., Clayton, M.K., 2002. Old-growth northern hardwood forests: spatial autocorrelation and pattern of understory vegetation. Ecol. Monogr. 72, 487–503. http://dx.doi.org/10.1890/0012-9615(2002) 072[0487:OGNHFS]2.0.CO;2.

Myneni, R.B., Hoffman, S., Knyazikhin, Y., Privette, J.L., Glassy, J., Tian, Y., Wang, Y., Song, X., Zhang, Y., Smith, G.R., Lotsch, a., Friedl, M., Morisette, J.T., Votava, P., Nemani, RR., Running, SW., 2002. Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. Rem. Sens. Environ. 83, 214–231. http://dx.doi.org/10.1016/S0034-4257(02)00074-3.

Nadezhdina, N., David, T.S., David, J.S., Ferreira, M.I., Dohnal, M., Tesař, M., Gartner, K., Leitgeb, E., Nadezhdin, V., Cermak, J., Jimenez, M.S., Morales, D., 2010. Trees never rest: the multiple facets of hxydraulic redistribution. Ecohydrology 3, 431–444. http://dx.doi.org/10.1002/eco.148.

Nachtergale, L., Ghekiere, K., De Schrijver, A., Muys, B., Luyssaert, S., Lust, N., 2002. Earthworm biomass and species diversity in windthrow sites of a temperate lowland forest. Pedobiologia (Jena) 46, 440–451. http://dx.doi.org/10.1078/0031-4056-00151.

Nikodem, A., Kodešová, R., Bubeníčková, L., 2013. Simulation of the influence of rainfall redistribution in spruce and beech forest on the leaching of Al and SO4 2- from forest soils. J. Hydrol. Hydromech. 61, 39–49. http://dx.doi.org/10.2478/johh-2013-0006.

Norman, S.A., Schaetzl, R.J., Small, T.W., 1995. Effects of slope angle on mass movement by tree uprooting. Geomorphology 14, 19–27. http://dx.doi.org/10.1016/0169-555X(95)00016-X.

Pawlik, Ł., 2013. The role of trees in the geomorphic system of forested hillslopes – a review. Earth-Sci. Rev. 126, 250–265. http://dx.doi.org/10.1016/j.earscirev.2013.08.007.

Pawlik, Ł., Kasprzak, M., 2015. Electrical resistivity tomography (ERT) of pit-and-mound microrelief, Mt Rogowa Kopa case study, the Stołowe Mountains, SW Poland. Landf. Anal. 29, 41–47. http://dx.doi.org/10.12657/landfana.029.006.

Pawlik, Ł., Migoń, P., Owczarek, P., Kacprzak, A., 2013. Surface processes and interactions with forest vegetation on a steep mudstone slope, Stołowe Mountains, SW Poland. Catena 109, 203–216. http://dx.doi.org/10.1016/j.catena.2013.03.011.

Pawlik, Ł., Migoń, P., Szymanowski, M., 2016a. Local- and regional-scale biomorphodynamics due to tree uprooting in semi-natural and managed montane forests of the Sudetes Mountains. Central Europe. Earth Surf. Process. Landforms 41, 1250–1265. http://dx.doi.org/10.1002/esp.3950.

Pawlik, Ł., Phillips, J.D., Šamonil, P., 2016b. Roots, rock, and regolith: Biomechanical and biochemical weathering by trees and its impact on hillslopes—a critical literature review. Earth-Sci. Rev. 159, 142–159. http://dx.doi.org/10.1016/j.earscirev.2016.06.002.

Peterson, C.J., Pickett, S.T.A., 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. J. Veg. Sci. 1, 657–662. http://dx.doi.org/10.2307/3235572.

Phillips, J.D., Marion, D.A., 2006. Biomechanical effects of trees on soil and regolith: beyond treethrow. Ann. Assoc. Am. Geogr. 96, 233–247. http://dx.doi.org/10.1111/j.1467-8306.2006.00476.x.

Phillips, J.D., Marion, D.A., Turkington, A.V., 2008. Pedologic and geomorphic impacts of a tornado blowdown event in a mixed pine-hardwood forest. Catena 75, 278–287. http://dx.doi.org/10.1016/j.catena.2008.07.004.

Phillips, J.D., Šamonil, P., Pawlik, Ł., Trochta, J., Daněk, P., 2017. Domination of hillslope denudation by tree uprooting in an old-growth forest. Geomorphology 276, 27–36. http://dx.doi.org/10.1016/j.geomorph.2016.10.006.

Pielke, R.A., 2001. Influence of the spatial distribution of vegetation and soils on the predictions of cumulus convective rainfall. Rev. Geophys. 39, 151–177. http://dx.doi.org/10.1029/1999RG000072.

Pokorný, J., 2001. Dissipation of solar energy in landscape — controlled by management of water and vegetation. Renew. Energy 24, 641–645. http://dx.doi.org/10.1016/S0960-1481(01)00050-7.

Putz, F.E., 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. Ecology 64, 1069–1074. http://dx.doi.org/10.2307/1937815.

Rewald, B., Michopoulos, P., Dalsgaard, L., Jones, D.L., Godbold, D.L., 2011. Hydrological effects on below ground processes in temperate and Mediterranean forests. In: Bredemeier, M., Cohen, S., Godbold, D.L., Lode, E., Pichler, V., Schleppi, P. (Eds.), Forest Management and the Water Cycle, Ecological Studies. Springer, Netherlands, Dordrecht, pp. 5–29. http://dx.doi.org/10.1007/978-90-481-9834-4_2.

Richards, P.J., Hohenthal, J.M., Humphreys, G.S., 2011. Bioturbation on a south-east Australian hillslope: estimating contributions to soil flux. Earth Surf. Process. Landforms 36, 1240–1253. http://dx.doi.org/10.1002/esp.2149.

Roering, J.J., Marshall, J., Booth, A.M., Mort, M., Jin, Q., 2010. Evidence for biotic controls on topography and soil production. Earth Planet. Sci. Lett. 298, 183–190. http://dx.doi.org/10.1016/j.epsl.2010.07.040.

Schaetzl, R.J., 1986. Complete soil profile inversion by tree uprooting. Phys. Geogr. 7, 181–189.

Schaetzl, R.J., 1990. Effects of treethrow microtopography on the characteristics and genesis of Spodosols, Michigan, USA. Catena 17, 111–126. http://dx.doi.org/10.1016/0341-8162(90)90002-U.

Schaetzl, R.J., Burns, S.F., Johnson, D.L., Small, T.W., 1989a. Tree uprooting: review of impacts on forest ecology. Vegetatio 79, 165–176. http://dx.doi.org/10.1007/BF00044908.

Schaetzl, R.J., Burns, S.F., Smal, T.W., Johnson, D.L., 1990. Tree uprooting: review of types and patterns of soil disturbance. Phys. Geogr. 11, 277–291.

Schaetzl, R.J., Follmer, L.R., 1990. Longevity of threethrow microtopography: implications for mass wasting. Geomorphology 3, 113–123. http://dx.doi.org/10.1016/0169-555X(90)90040-W.

Schaetzl, R.J., Johnson, D.L., Burns, S.F., Small, T.W., 1989b. Tree uprooting: review of terminology, process, and environmental implications. Can. J. For. Res. 19, 1–11. http://dx.doi.org/10.1139/x89-001.

Schaetzl, R.J., Thompson, M.L., 2015. Soils: Genesis and Geomorphology. Cambridge University Press.

Schelhaas, M.J., 2008. The wind stability of different silvicultural systems for Douglas-fir in the Netherlands: a model-based approach. Forestry 81, 399–414. http://dx.doi.org/10.1093/forestry/cpn028.

Schüler, G., 2006. Identification of flood-generating forest areas and forestry measures for water retention. J. For. Snow Landsc. Res. 80, 99–114.

Schume, H., Jost, G., Hager, H., 2004. Soil water depletion and recharge patterns in mixed and pure forest stands of European beech and Norway spruce. J. Hydrol. 289, 258–274. http://dx.doi.org/10.1016/j.jhydrol.2003.11.036.

Schütz, K., Nagel, P., Dill, A., Scheu, S., 2008. Structure and functioning of earthworm communities in woodland flooding systems used for drinking water production. Appl. Soil Ecol. 39, 342–351. http://dx.doi.org/10.1016/j.apsoil.2008.02.002.

Simon, A., Gratzer, G., Sieghardt, M., 2011. The influence of windthrow microsites on tree regeneration and establishment in an old growth mountain forest. For. Ecol. Manage. 262, 1289–1297. http://dx.doi.org/10.1016/j.foreco.2011.06.028.

Small, T.W., Schaetzl, R.J., Brixie, J.M., 1990. Redistribution and mixing of soil gravels by tree uprooting. Prof. Geogr. 42, 445–457. http://dx.doi.org/10.1111/j.0033-0124.1990.00445.x.

Sobhani, V.M., Barrett, M., Peterson, C.J., 2014. Robust prediction of treefall pit and mound sizes from tree size across 10 forest blowdowns in Eastern North America. Ecosystems 17, 837–850. http://dx.doi.org/10.1007/s10021-014-9762-8.

Stephens, E.P., 1956. The uprooting of trees: a forest process. Soil Sci. Soc. Am. J. 20, 113–116. http://dx.doi.org/10.2136/sssaj1956.03615995002000010029x.

Stuart, G.W., Edwards, P.J., 2006. Concepts about forests and water. North. J. Appl. For. 23, 11–19.

Šamonil, P., Antolík, L., Svoboda, M., Adam, D., 2009. Dynamics of windthrow events in a natural fir-beech forest in the Carpathian mountains. For. Ecol. Manage. 257, 1148–1156. http://dx.doi.org/10.1016/j.foreco.2008.11.024.

Šamonil, P., Daněk, P., Schaetzl, R.J., Vašíčková, I., Valtera, M., 2015. Soil mixing and genesis as affected by tree uprooting in three temperate forests. Eur. J. Soil Sci. 66, 589–603. http://dx.doi.org/10.1111/ejss.12245.

Šamonil, P., Král, K., Douda, J., Šebková, B., 2008. Variability in forest floor at different spatial scales in a natural forest in the Carpathians: effect of windthrows and mesorelief. Can. J. For. Res. 38, 2256–2606. http://dx.doi.org/10.1139/X08-100.

Šamonil, P., Král, K., Hort, L., 2010a. The role of tree uprooting in soil formation: a critical literature review. Geoderma 157, 65–79. http://dx.doi.org/10.1016/j.geoderma.2010.03.018.

Šamonil, P., Schaetzl, R.J., Valtera, M., Goliáš, V., Baldrian, P., Vašíčková, I., Adam, D., Janík, D., Hort, L., 2013. Crossdating of disturbances by tree uprooting: Can treethrow microtopography persist for 6000years? For. Ecol. Manage. 307, 123–135. http://dx.doi.org/10.1016/j.foreco.2013.06.045.

Šamonil, P., Tejnecký, V., Borůvka, L., Šebková, B., Janík, D., Šebek, O., 2010b. The role of tree uprooting in Cambisol development. Geoderma 159, 83–98. http://dx.doi.org/10.1016/j.geoderma.2010.06.020.

Šamonil, P., Valtera, M., Schaetzl, R.J., Adam, D., Vašíčková, I., Daněk, P., Janík, D., Tejnecký, V., 2016. Impacts of old, comparatively stable, treethrow microtopography on soils and forest dynamics in the northern hardwoods of Michigan, USA. Catena 140, 55–65. http://dx.doi.org/10.1016/j.catena.2016.01.006.

Šamonil, P., Vašíčková, I., Daněk, P., Janík, D., Adam, D., 2014. Disturbances can control fine-scale pedodiversity in old-growth forests: is the soil evolution theory disturbed as well? Biogeosciences 11, 5889–5905. http://dx.doi.org/10.5194/bg-11-5889-2014.

Šebková, B., Šamonil, P., Valtera, M., Adam, D., Janík, D., 2012. Interaction between tree species populations and windthrow dynamics in natural beech-dominated forest, Czech Republic. For. Ecol. Manage. 280, 9–19. http://dx.doi.org/10.1016/j.foreco.2012.05.030.

Thompson, S.E., Katul, G.G., Porporato, A., 2010. Role of microtopography in rainfall-runoff partitioning: An analysis using idealized geometry. Water Resour. Res. 46, W07520.1-W07520.11. http://dx.doi.org/10.1029/2009WR008835.

Tromp-van Meerveld, H.J., McDonnell, J.J., 2006. Threshold relations in subsurface stormflow: 1. A 147-storm analysis of the Panola hillslope. Water Resour. Res. 42, W02410. http://dx.doi.org/10.1029/2004WR003778.

Ulanova, N., 2000. The effects of windthrow on forests at different spatial scales: a review. For. Ecol. Manage. 135, 155–167. http://dx.doi.org/10.1016/S0378-1127(00)00307-8.

Valtera, M., Šamonil, P., Svoboda, M., Janda, P., 2015. Effects of topography and forest stand dynamics on soil morphology in three natural Picea abies mountain forests. Plant Soil. 392, 57–69. http://dx.doi.org/10.1007/s11104-015-2442-4.

van der Ploeg, M.J., Appels, W.M., Cirkel, D.G., Oosterwoud, M.R., Witte, J.-P.M., van der Zee, S.E.a.T.M., 2012. Microtopography as a driving mechanism for ecohydrological processes in shallow groundwater systems. Vadose Zo. J. 11. http://dx.doi.org/10.2136/vzj2011.0098.

Vertessy, R.A., Watson, F.G.R., O'Sullivan, S.K., 2001. Factors determining relations between stand age and catchment water balance in mountain ash forests. For. Ecol. Manage. 143, 13–26. http://dx.doi.org/10.1016/S0378-1127(00)00501-6.

von Oheimb, G., Friedel, A., Bertsch, A., Härdtle, W., 2006. The effects of windthrow on plant species richness in a Central European beech forest. Plant Ecol. 191, 47–65. http://dx.doi.org/10.1007/s11258-006-9213-5.

Vose, J.M., Sun, G., Ford, C.R., Bredemeier, M., Otsuki, K., Wei, X., Zhang, Z., Zhang, L., 2011. Forest ecohydrological research in the 21st century: what are the critical needs? Ecohydrology 4, 146–158. http://dx.doi.org/10.1002/eco.193.

Wilkinson, M.T., Richards, P.J., Humphreys, G.S., 2009. Breaking ground: pedological, geological, and ecological implications of soil bioturbation. Earth-Sci. Rev. 97, 257–272. http://dx.doi.org/10.1016/j.earscirev.2009.09.005.

Yeakley, J.A., Swank, W.T., Swift, L.W., Hornberger, G.M., Shugart, H.H., 1998. Soil moisture gradients and controls on a southern Appalachian hillslope from drought through recharge. Hydrol. Earth Syst. Sci. 2, 41–49.