Limits of windthrow-driven hillslope sediment flux due to varying storm frequency and intensity

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A B S T R A C T

The uprooting and toppling of trees during storms transports soil, exhumes bedrock, and thus influences the evolution of hillslopes. Given predicted increased storminess due to future climate change, we adopt a forest-gap model (ForGEM) to explore windthrow-driven sediment transport in a Douglas fir forest under increasingly severe wind regimes in order to better assess potential future impacts on soil erosion. Larger trees are more sensitive to wind loading and are therefore preferentially toppled as storm frequency and intensity increase. Because larger trees have larger root-plate volumes and can move large volumes of sediment, increased wind velocities lead to an increase in sediment flux. With increasingly stormier conditions, however, the proportion of large trees dwindles. The net effect of these two countervailing trends is that sediment transport increases as average annual rates of windthrow approach eight trees per hectare, but begins to decline thereafter. Our results highlight the complex relationship between climate and sediment transport, particularly when it is mediated by the biota.

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1. Introduction

Storms consistently cause the most widespread, instantaneous damage to forests across the planet (Stewart, 1986; Quine and Bell, 1998; Arévalo et al., 2000; Ída, 2000; Lässig and Močalov, 2000; Schelhaas et al., 2003) and often result in the uprooting and toppling of trees (Fig. 1A). Known as windthrow or tree throw, this process promotes soil production (Gabet and Mudd, 2010), alters soil development (Schelhaas et al., 2003), affects nutrient cycling (Schaetzl et al., 1989a; Yeakley et al., 2003; Thürg et al., 2005), and impacts forest succession (Putz, 1983; Clinton and Baker, 2000). When occurring on hillsides, windthrow can accelerate soil loss by the removal of trees that stabilize slopes against landsliding (Gerber et al., 2002; Rickli and Graf, 2009) and by the delivery of loose soil to the surface that can be eroded through granular transport (Gabet et al., 2003; Osterkamp et al., 2006; Gallaway et al., 2009; Hughes et al., 2009). The most obvious geomorphic consequence of windthrow is the excavation of pits and the deposition of mounds (Lyford and MacLean, 1966; Putz, 1983; Schaetzl et al., 1989b; Schaetzl, 1990; Schaetzl and Follmer, 1990; Roering et al., 2010), when as much as 10 m³ of soil and rock may be ripped up from the Earth’s surface in root plates (Ray and Nicoll, 1998; Gabet et al., 2003; Gallaway et al., 2009) (Fig. 1B).

Whether windthrow significantly contributes to sediment yield and widespread soil thinning depends upon the manner of its occurrence. Given that neither tree position within a forest (Dyer and Baird, 1997; Greenberg and McNab, 1998; Laurance et al., 1998) nor topography (Nicoll et al., 2005; Gallaway et al., 2009) principally determines the occurrence of windthrow, the process should occur uniformly across a hillside if tree sizes are uniformly distributed and the hillside is uniformly forested (i.e., edges are absent). Under these conditions, sediment flux by windthrow can be expressed as a function of tree characteristics (i.e., root plate volume) and slope (Gabet et al., 2003; Gallaway et al., 2009). In essence, larger trees and steeper slopes will lead to higher sediment fluxes from individual windthrow events. Based upon modeling results of wildfire-induced uprooting and toppling, Gallaway et al. (2009) suggest, however, that the age structure of a forest shifts toward younger and smaller trees as the frequency of tree toppling increases. This effect is enhanced by windthrow as it preferentially selects large trees for removal (Dyer and Baird, 1997; Greenberg and McNab, 1998; Rich et al., 2007) because the force that wind exerts on a tree is proportional to the tree’s frontal area (Mayer, 1989). If storm conditions steadily remove the oldest and largest trees, the resulting shift in age structure may then lead to a reduction in windthrow-driven sediment flux as only smaller trees remain to be uprooted and toppled.
Although some studies have explored the critical role that biota plays in sediment transport (e.g., Gabet et al., 2003), few have quantified sediment flux as a function of ecological parameters such as biomass or forest allometry (e.g., Pelletier et al., 2009; Hancock et al., 2012). In particular, our understanding of how climate signals are transmitted to geomorphic processes via the biota is poor. We are thus left with little ability to predict how sediment fluxes will be affected by climate change in landscapes where bioturbation is an important process (e.g., Gabet and Dunne, 2002). Here, for the first time, we quantify sediment flux as a function of both the characteristics of a population of trees and the climatic forcing leading to their demise via windthrow. By coupling recent advances in numerical modeling of windthrow and forest succession with a windthrow-specific sediment flux equation, we examine how storm-driven variations in rates of windthrow alter sediment flux over centennial timescales. By accounting for the effects of varying climatic conditions on the geomorphic effectiveness of windthrow, our approach may allow for analyses of the sensitivity of many hillslope environments to predicted stormier conditions caused by global shifts in climate (Knutson and Tuleya, 2004; Salathe, 2006; Donat et al., 2010).

2. Model development

2.1. Modeling forest growth dynamics

A numerical analysis of the effect of windthrow on the structure of a forest first requires a model capable of predicting the growth and death of individual trees that would naturally occur in the absence of environmental disturbance. A number of modeling approaches exist for studying such forest dynamics (e.g., Ribbens et al., 1994; Pacala et al., 1996; Purves and Pacala, 2008; Kardol et al., 2010), with perhaps the most widely used and successful of these being forest gap models (Botkin et al., 1972; Shugart and Smith, 1996; Bugmann, 2001). Forest gap models explicitly account for the recruitment, growth, and death of individual trees, with the life history of each tree dependent on prevailing environmental conditions and individual species characteristics (Bugmann, 2001; Shugart, 2002). According to forest gap models, mature trees that are felled create a spatial gap within the forest that allows sunlight to penetrate to the forest floor and the subsequent recruitment of younger trees. In the absence of disturbance and changes in prevailing environmental conditions, this process should eventually produce a temporally stable age-distribution of trees, which can serve as the initial, baseline condition from which windthrow experiments can be conducted. We adopted the approach of forest gap models for our study given that it has been validated for a variety of forest habitats (Bugmann, 2001) and has successfully been incorporated into a range of simulation experiments on forest dynamics (Shugart, 2002). We acknowledge the difficulty of widely employing forest gap models given the requirement of species-dependent empirical relations that govern plant response, but the deterministic nature of these models allows an explicit assessment of the impact of windthrow on forest growth dynamics.

The forest gap model used here was ForGEM (Forest Genetics, Ecology and Management), designed by researchers from Alterra of the Wageningen University & Research Centre in The Netherlands. Details of the structure of the model can be found in Schelhaas et al. (2007), Kramer et al. (2008), and Schelhaas (2008). In essence, tree growth within ForGEM is driven solely by light interception that takes place within 400-m² rectangular cells that make up the spatial extent of the model forest and that is distributed among trees as a function of foliage mass and vertical position (Bugmann, 2001). Light is emitted from directly above and is converted into photosynthates after a formulation by Landsberg and Waring (1997), which sets gross primary production as the product of the absorbed photosynthetically active light-radiation and the total light-radiation that can be absorbed by leaf pigments. This species-specific product must be calibrated using empirical data on seasonal growth and yield. Photosynthates are then allocated within each tree to ensure that the relative distribution of tree components (i.e., stem mass, branches, root mass) is temporally constant. Photosynthates allocated to the stem result in increases in both stem height and diameter, with growth in stem height following a Richards’ growth curve (Richards, 1959), which states that the rate of growth at any point in time is a function of the stem size at that time and the maximum size to which the stem can grow for a given species. Stem height is related to both diameter-at-breast-height and tree volume using species-specific allometric functions derived from yield-table data reported by Jansen et al. (1996). Crown growth is limited by competition with neighboring trees and is considered explicitly using a methodology by Schelhaas et al. (2007). In the absence of physical disturbances (e.g., windthrow), ForGEM predicts tree mortality based on crown competition and age; death by crown competition occurs if the crown of a tree is completely suppressed by its neighbors, and age-related death follows a two-parameter Weibull function. Mortality was calculated monthly, and dead trees are removed from the model forest and assumed to remain on the forest floor. Recruitment of new trees within the resulting forest gaps was accomplished by explicitly modeling seed dispersion and germination. Seedlings were modeled as cohorts within a 25-m² rectangular cell, and self-thinning was simulated using the −3/2-power-law as described by Reineke (1933) and Drew and Flewelling (1979). Once they reached a height of 2 m, the seedlings were then modeled individually and their locations within the model space were recorded.

The forest used in this study consisted solely of Douglas fir (Pseudotsuga menziesii), for which field data exist regarding growth patterns and root structure; these data were used to calibrate the simulation experiments (see below). Douglas fir is a common species...
within many mountainous environments, occurring natively in western North America (Halpern and Spies, 1995) and invasively throughout Europe (Essl, 2005; Vallet et al., 2006). Although growth patterns and sizes are unique to an individual species, the model parameters (e.g., growth rate, root structure, and crown size) used here are generalizable, allowing the results to be compared across environments and particular forest types. We designed our model forest of Douglas fir as a 1-ha forest with an additional 50-wide buffer strip to remove potential edge effects. A 100-m wide strip of open land surrounded the forest plot, necessary for establishing the initial velocity profile of storm-driven winds. Initially, 4000 ten-year old trees were evenly placed within the 1-ha study plot; trees of the same age were placed within the buffer strip at the same density as the 1-ha plot. To generate an uneven-aged model forest, ForGEM was run for a 100-year simulation with trees randomly removed every 10 years. Afterwards, we followed the model set-up of Klein and Jansen (1992) and initially managed the forest by removing trees within each size class to ensure a power-law distribution of tree sizes (scaling exponent of 1.3). After attaining a stable situation, the forest was simulated for another 500 years to remove potential management effects. The resulting forest was then used as the initial, baseline condition for the windthrow experiments.

2.2. Incorporating windthrow into forest growth dynamics

Uprooting and toppling by windthrow will occur if the total turning moment during a storm ($T_m$) exceeds the turning resistance of the root system ($R_{sys}$). $T_m$ can be solved at any tree height $z$ as the sum of the wind-induced drag force ($F_w$) applied over height $z$ and the gravitational force ($F_g$) applied over the horizontal distance ($x$) of wind-induced displacement at height $z$:

$$T_m(z) = 2F_w(z) + x(z)F_g(z).$$  \[1\]

We adopted the approaches of Peltola and Kellomäki (1993) and Peltola et al. (1999) to determine $F_w$ and $F_g$. In particular, $F_w$ was evaluated at height $z$ of the tree as:

$$F_w(z) = \frac{1}{2}C_d\rho A(z)U(z)^2,$$  \[2\]

where $C_d$ is a drag coefficient, $\rho$ is air density, $A(z)$ is the projected area of the tree at height $z$ against the wind, and $U(z)$ is the wind velocity at height $z$. Wind velocity was determined by assuming a logarithmic velocity profile with altitude, in which:

$$U(z) = \frac{U_0}{\kappa} \log \left(\frac{z-L}{z_0}\right),$$  \[3\]

where $U_0$ is the shear velocity equal to the square root of the ratio of the wind-generated shear stress exerted onto the ground surface to $\rho$, $\kappa$ is von Karman’s constant, $L$ is the altitude at which the wind velocity is zero due to the obstruction of the forest, and $z_0$ is the roughness height or altitude increment over which the wind-velocity profile is affected by the forest. We evaluated $F_g$ at height $z$ as the product of the green mass of the tree ($M_g$) and gravitational acceleration. We determined $M_g$ from the state variables of ForGEM, in which stem biomass is distributed over $z$ using stem-form equations and foliage and branch biomass assuming a diamond-shaped crown. The horizontal displacement distance was calculated separately for the crown and stem also after Peltola and Kellomäki (1993) as:

$$x(z) = \frac{F_w(z)U(z)a^2h(3-a)}{6(h^2-3)E} \quad z \geq a$$  \[4\]

$$x(z) = \frac{F_w[(L(z) - b)^3 - a^3(L(z) - b)]}{6E} \quad z < a,$$  \[5\]

where $L(z)$ is the distance from the tree top to $z$, $a$ is the distance from the ground to the crown center, $h$ is the tree height, $E$ is the modulus of elasticity for the stem, $I$ is the area moment of inertia for the stem, and $b$ is the distance between the crown center and the tree top. The total turning moment was then determined by integrating $T(z)$ over the tree’s height, and $R_{sys}$ was determined after Schelhaas (2008) as:

$$R_{sys} = \gamma_1d^2z^2,$$  \[6\]

where $d$ is the stem diameter at breast height, and $\gamma_1$ and $\gamma_2$ are species-specific constants that were determined in the field from the tree-pulling tests of Schooten (1985). Stem breakage was modeled in addition to windthrow following Peltola and Kellomäki (1993), in which breakage occurred once the elastic limit of the stem was exceeded by the stress being exerted onto the stem at breast height ($\sigma_{brk}$), measured as:

$$\sigma_{brk} = \frac{T_m a}{2I}.$$  \[7\]

The preceding equations were used to develop the windthrow model, but with two additional conditions: trees can experience additional loading if hit by fallen trees, and trees in which $h < 5$ m cannot be uprooted or broken, but they can be destroyed by falling trees.

2.3. Model implementation

As explained earlier, an initial forest age structure without storm disturbance was created with ForGEM. This forest structure was then used as the initial condition for nine separate 500-yr simulations based on maximum hourly wind speeds recorded each day at a weather station at Leeuwarden (53°13’ N, 5°46’ E). The Netherlands, for the period between April of 1961 and December of 2005 (data managed by the Dutch Royal Meteorological Institute). Weather at Leeuwarden is typical of temperate maritime climates, with most storms derived from low-pressure systems in the North Atlantic. The frequency and magnitude of storms recorded at Leeuwarden provided a convenient data set that we could manipulate for our windthrow experiments, but it is important to note that Smits et al. (2005) have identified that storminess across The Netherlands has decreased by 5–10% per decade between 1962 and 2002. Nonetheless, given that gusts are primarily responsible for wind damage, the wind speeds were modified by a gust factor after Gardiner et al. (2000). Each of our simulations represents a different wind regime in which the distribution of wind speeds from the Leeuwarden meteorological data were multiplied by a factor ($B$), which was increased from 0 to 4 in increments of 0.5. During the model runs, wind speed from the modified distributions was drawn randomly for each day of the 500-year simulation, with the first 50 years discarded to avoid initialization effects. The simulations recorded the occurrence of every windthrow event as well as the characteristics of the toppled trees (e.g., stem diameter and tree height).

3. Results

Over the 450-yr simulations, the number of trees felled by the wind increased dramatically with storm intensity; 612 trees were toppled when $B = 1$ whereas 3881 trees were toppled when $B = 4$ (Table 1). After allowing 50 years for the model to initialize in order to ensure that forest dynamics could adequately transition from a state of no physical disturbance to one where disturbance regularly occurs, the forest in each simulation was composed of 10,000–60,000 trees, the great majority (>95%) of which consisted of seedlings and young trees (d<10 cm), which resulted in yearly fluctuations by as much as 40,000 trees due to the germination and death of seedlings. The maximum number of trees removed by windthrow in any year was 51.
when \( B = 4 \), but it is important to note that the storm wind speeds (peak of 105 km h \(^{-1} \) when \( B = 4 \)) and durations generated by the model were insufficient to cause blowdown events, defined as occurrences of windthrow that fell large swaths (>1 ha) of forest (Lindemann and Baker, 2001).

Although windthrow had negligible effects on forest structure with respect to seedlings and young trees, the process had discernible effects for larger trees, particularly for those with diameters \( \geq 30 \) cm: as the rate of windthrow increased, the number of trees within this cohort progressively decreased (Fig. 2). The increased rate of windthrow also caused a shift in the population structure of the forest, systematically reducing the presence of large trees from an initial state in which the population structure was similar for each experiment (Fig. 3), though some disturbance was required for the development of large trees through the generation of forest gaps (Schaetzl et al., 1989a). As a consequence, the sizes of felled trees decreased as rates of windthrow increased, but not until the average rate reached 2.4 trees ha \(^{-1} \) yr \(^{-1} \) (when \( B = 1.5 \); Fig. 4). With a slight increase in storm wind speeds (up to \( B = 1.5 \)), the diameter of trees felled by windthrow increased from 41 to 44 cm relative to the present climate (Table 1). In more severe wind regimes, however, the average diameter decreased as windthrow became more common; for example, under the present climate, the windthrow rate was 1.4 trees ha \(^{-1} \) yr \(^{-1} \) and the average trunk diameter of felled trees was 41 cm, but when the windthrow rate reached 8.6 trees ha \(^{-1} \) yr \(^{-1} \), the average diameter dropped to 34 cm. This decline in trunk diameter occurred because windthrow preferentially blows down the largest trees (Dyer and Baird, 1997; Greenberg and McNab, 1998; Rich et al., 2007). As a result, wind toppled large trees faster than they could be replaced by forest growth dynamics. Our results are consistent with field observations that show a reduction in the number of standing large trees after widespread windthrow events (e.g., Arévalo et al., 2000; Lässig and Močalov, 2000; Peterson, 2000).

Windthrow can be considered to have equal probability of occurrence across a hillside if tree sizes are uniformly distributed and the hillside is uniformly forested (Dyer and Baird, 1997; Greenberg and McNab, 1998; Laurance et al., 1998). Some evidence suggests that topography may influence the dimensions of root plates (Gallaway et al., 2009), but we assumed for simplicity that tree size, root plate volume, and windthrow rate are independent of the slope of the model forested-hillside. Considering that uprooted root plates disintegrate relatively quickly, sediment flux \( q_s \) by windthrow can be estimated as:

\[
q_s = \frac{\sum_{i=1}^{N} V_i D_i}{A \Delta t}, \tag{8}
\]

where \( V_i \) is the volume of sediment delivered to the surface by an individual windthrow event \( i \), \( D_i \) is the transport distance of the uprooted sediment across the surface for the event \( i \), \( A \) is the surface area of forest coverage, and \( \Delta t \) is the duration over which windthrow is being assessed (Gabet et al., 2003). To determine \( V_i \), the shape of the root plate was approximated as a half ellipsoid, such that:

\[
V_i = \frac{2}{3} \pi r_i^2 p_i. \tag{9}
\]

where \( r_i \) is the planform radius of the ellipsoid and \( p_i \) is the vertical thickness of the root plate, which can be estimated as one half of \( r_i \). (Schooten, 1985). Schooten (1985) established relationships between \( r \) and \( d \) as well as \( p \) and \( d \) for Douglas fir, which we used to generate an empirical relation between \( V \) and \( d \), similar to that established by Gallaway et al. (2009) (Fig. 5). Wind patterns primarily determine the direction that trees are uprooted and toppled (Schaetzl and Follmer, 1990), but to simplify our estimates of the potential sediment flux by windthrow, we assumed that trees had an equal probability of falling in any direction (or that the prevailing wind direction

---

**Table 1**

<table>
<thead>
<tr>
<th>Wind speed multiplication factor (( B ))</th>
<th>Average wind speed (1x) (km hr (^{-1} ))</th>
<th>Total windthrow events (^a)</th>
<th>Average ( d ) of windthrown tree (1x) (cm) (^b)</th>
<th>Maximum ( d ) of windthrown tree (cm) (^b)</th>
<th>Minimum ( d ) of windthrown tree (cm) (^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>9.4 (1.5)</td>
<td>97</td>
<td>35.3 (5.4)</td>
<td>49.4</td>
<td>26.9</td>
</tr>
<tr>
<td>1.0</td>
<td>19.0 (2.7)</td>
<td>612</td>
<td>40.6 (11.0)</td>
<td>83.5</td>
<td>26.5</td>
</tr>
<tr>
<td>1.5</td>
<td>27.4 (3.8)</td>
<td>1082</td>
<td>44.0 (13.5)</td>
<td>107.1</td>
<td>26.5</td>
</tr>
<tr>
<td>2.0</td>
<td>35.3 (4.8)</td>
<td>1607</td>
<td>42.1 (13.1)</td>
<td>98.8</td>
<td>26.5</td>
</tr>
<tr>
<td>2.5</td>
<td>42.9 (6.5)</td>
<td>2237</td>
<td>40.8 (12.6)</td>
<td>97.1</td>
<td>26.5</td>
</tr>
<tr>
<td>3.0</td>
<td>50.1 (8.0)</td>
<td>2941</td>
<td>38.0 (10.6)</td>
<td>109.1</td>
<td>26.5</td>
</tr>
<tr>
<td>3.5</td>
<td>57.4 (9.6)</td>
<td>3681</td>
<td>35.0 (7.9)</td>
<td>107.7</td>
<td>26.5</td>
</tr>
<tr>
<td>4.0</td>
<td>64.2 (10.7)</td>
<td>3881</td>
<td>34.0 (7.2)</td>
<td>107.8</td>
<td>26.5</td>
</tr>
</tbody>
</table>

\(^a\) Over the 450-year simulations, post-initialization.

\(^b\) Trunk diameter at breast height (\( d \)).
4. Discussion

between storms was random). We acknowledged that such an assumption may lead to underestimates as evidence suggests that trees are more vulnerable to uprooting and toppling by downslope winds (Nicoll et al., 2005). Assuming a linear hillslope, \( D_i \) was determined following Eq. (11) in Gabet et al. (2003), in which:

\[
D_i = \frac{2}{\pi} (r_i + p_i) \sin \theta,
\]

where \( \theta \) is the slope of the hillside in degrees.

Combining the results of the ForGEM simulations with Eqs. (8) and (10) provided novel insights into the interactions of the climate, biota, and sediment transport. Although the rate of windthrow increased as wind regime became more severe, \( q_s \) did not increase accordingly (Fig. 6). Indeed, rates of sediment transport peaked at an average windthrow rate of 8.0 trees ha\(^{-1} \) yr\(^{-1} \) and then began to decline. Because root plate volume is proportional to trunk diameter, the reduction in the sizes of toppled trees in stormier climates led to a decrease in the average volume of sediment displaced during each windthrow event. As demonstrated by the modeling results, the increased frequency of windthrow was not sufficient to compensate for the smaller rootplate volumes.

Although \( q_s \) in any particular forest will be a function of its species composition and local wind regime, our results are comparable to rates measured elsewhere, thus providing an initial test for our model. Empirical studies have found toppling rates ranging from 10\(^{-1} \) trees ha\(^{-1} \) yr\(^{-1} \) for forests in southwest Japan (Naka, 1982) and Michigan, USA (Brewer and Merritt, 1978) to 10\(^{6} \) trees ha\(^{-1} \) yr\(^{-1} \) in southeast Australia (Richards et al., 2011) to 10\(^{4} \) trees ha\(^{-1} \) yr\(^{-1} \) for forests in Poland (Falinski, 1978) and Appalachia, USA (Mills, 1984). Furthermore, our results indicate that peak \( q_s \) should be of order 10\(^{-3} \) m\(^3\) m\(^{-1}\) yr\(^{-1} \), similar to windthrow-influenced fluxes empirically determined in South Island, New Zealand (Hughes et al., 2009), a maple forest of northern Pennsylvania, USA (Gabet et al., 2003), a coniferous forest of northwest Washington, USA (Reid, 1981), and a coniferous forest in southeast Washington, USA (Walther et al., 2009). It is important to note, however, that there are discrepancies between our predictions and some empirical estimates because our model simulates only the delivery of soil to the surface during uprooting and toppling and not the subsequent downslope transport of this sediment by other mechanisms (e.g., rain splash, sheet wash, and rilling). For example, the Holocene sediment fluxes determined by Hughes et al. (2009) in South Island, New Zealand, equalled 22 \times 10^{-4} (\pm 7 \times 10^{-6}) m^3 m^{-1} yr^{-1} for slopes no greater than 16\(^\circ\), over twice the peak flux predicted by the model for similar slopes. Nonetheless, that sediment flux by windthrow may contribute 50% of the total hillslope flux (which integrates all sediment transport mechanisms) highlights the importance of windthrow in instigating and enabling sediment delivery from forested environments.

For environments in which erosion occurs as a linear function of slope, the diffusivity \( (k) \) can be defined as:

\[
k = q_s A (\frac{d^2}{dx^2})^{-1},
\]
where \( z \) represents hillslope elevation and \( x \) represents horizontal distance; \( q_i \) was determined using Eq. (8) and \( \partial z/\partial x \) was determined as the tangent of the downslope angle. Eq. (11) implies that \( k \) does not vary spatially, in effect allowing us to assess the effectiveness of windthrow as a transport process (Fernandes and Dietrich, 1997). Although measures of diffusivity have been established for many environments (e.g., Denny and Goodlett, 1956; Hanks et al., 1985; Martin, 2000; Walther et al., 2009), few studies have identified process-specific values of diffusivity, particularly for those facilitated by the biota (e.g., Gabet, 2000; Gabet et al., 2003; Yoo et al., 2005). Solutions to Eq. (11) indicated that \( k \) increased with rates of windthrow until peaking near 3.5 m\(^2\)kyr\(^{-1}\) once windthrow rates exceeded 8.0 trees ha\(^{-1}\) yr\(^{-1}\), similar to the patterns of \( q_i \) (Fig. 7). The peak \( k \) predicted by the model compares well to empirically derived measurements in forested environments. For example, \( k \) established for a coniferous forest in Washington, USA, equaled 4.8 (±0.7) m\(^2\)kyr\(^{-1}\) (Walther et al., 2009), for a deciduous forest in North Carolina, USA, \( k \) ranged from 7 to 10 m\(^2\)kyr\(^{-1}\) (Jungers et al., 2009); and for a Podocarp and Beech forest in South Island, New Zealand, \( k \) equaled 8.8 (±3.0) m\(^2\)kyr\(^{-1}\) (Walther et al., 2009). These reported estimates of \( k \) integrate all sediment transport operating in the landscape, whereas our diffusivity is for the process of windthrow only. To our knowledge, the only other \( k \) established solely for uprooting and topping was by Gabet et al. (2003), who theoretically determined that an uprooting rate of 4 trees ha\(^{-1}\) yr\(^{-1}\) would generate a diffusivity of 4.8 m\(^2\)kyr\(^{-1}\). That our estimate of peak windthrow diffusivity is of similar magnitude to estimates of whole landscape diffusivity in forested environments further implies the importance of windthrow as a significant contributor to the total sediment flux from forested landscapes.

The results from the model have several important implications. First, sediment yields from windthrow in forested landscapes will increase, albeit nonlinearly, in stormier conditions, with consequences potentially being felt downslope and downstream. For example, if changing storm conditions resulted in a doubling of the windthrow rate from 2 to 4 trees ha\(^{-1}\) yr\(^{-1}\), the rate of sediment delivered from hillslopes due to treethrow would more than double. Second, if the thickness of soils in hilly forested terrain is set by the rooting depth of trees (Gabet and Mudd, 2010; Roering et al., 2010), then a shift toward younger, smaller trees would be accompanied by an overall reduction in soil thickness. Finally, the combination of higher erosion rates and thinner soils will shorten soil residence times (Mudd and Yoo, 2010), leading to younger soils, and thus stimulating higher rates of chemical weathering and potentially increasing the drawdown of atmospheric CO\(_2\) (Gabet and Mudd, 2009).

The importance of forests in stabilizing soil-mantled hillsides from mass wasting has been well documented (e.g., Montgomery et al., 2000; Hales et al., 2009; Rickli and Graf, 2009), and yet empirical evidence exists to suggest that forest expansion can enhance hillslope sediment flux by allowing for increased incidents of windthrow (Osterkamp et al., 2006; Hughes et al., 2009). The reflection of such dualistic effects of forests in the form and evolution of hillslopes is a function of environmental context, as determined by topography and climate. Nonetheless, even where topographic (i.e., landscape curvature and steepness) and climatic (i.e., precipitation) conditions are such that temporal fluctuations in the spatial structure of hillslope vegetation singularly control the mass wasting of soil (Gabet and Dunne, 2002; Roering et al., 2003; Rickli and Graf, 2009), variations in soil thickness driven by changing rates of sediment flux relative to bedrock weathering will directly affect the likelihood of mass wasting (Dietrich et al., 1995), at least in the long term. Uprooting and topping may thus have a two-fold effect on the prevalence of mass wasting across the landscape: promoting its occurrence in the short-term by destabilizing hillslopes, but potentially hindering its occurrence in the long-term by causing widespread thinning of soils by downslope granular transport. Complicating the potential impacts of windthrow on soil thinning is that the presence of pits and mounds may slow rates of granular transport by overland flow as the increased topographic variability may sufficiently interrupt antecedent drainage patterns that route water and sediment down the hillside (Hancock et al., 2012). Windthrow will directly affect soil thickness even if only locally, and the spatial extent of a forest should experience soil turnover by windthrow over centennial timescales. Our modeling results assumed an infinitely thick soil (i.e., transport limited conditions), which prevented any assessment of the dualistic effects of windthrow, indicating a clear direction for improvement of our current efforts.

5. Conclusions

It is difficult to predict how climate changes may affect purely physical sediment transport processes and it is especially difficult in the case of transport processes mediated by the biota. Our results suggest a strongly nonlinear relationship between wind regime, forest growth dynamics, and sediment flux by windthrow. While the rate of windthrow increased with storm intensity, the volume of sediment mobilized by each windthrow event decreased because of the smaller root system of the younger trees, with the net result that sediment flux initially increased but then declined once average rates exceeded 8.0 trees ha\(^{-1}\) yr\(^{-1}\). Peak sediment flux predicted by the model equaled \(-20 \times 10^{-4}\) m\(^3\) m\(^{-1}\) yr\(^{-1}\) at a slope of 30°, and the fluxes predicted by the model are up to half those established in empirical studies that integrate all sediment transport mechanisms, implying the importance of windthrow in instigating sediment flux from forested environments. Sediment diffusivity followed the same pattern as sediment flux, peaking at nearly 3.5 m\(^2\) kyr\(^{-1}\) once windthrow rates exceeded 8.0 trees ha\(^{-1}\) yr\(^{-1}\), comparable to other forested environments. The impacts of windthrow on soil thinning and slope stability remain to be examined, but our results make clear that windthrow is intrinsically limited in directly instigating hillslope sediment flux.

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