A comparative study of soil disturbance from uprooted trees, and mound and pit decay in Puerto Rico and Colorado

A COMPARATIVE STUDY OF SOIL DISTURBANCE FROM UPROOTED TREES, AND MOUND AND PIT DECAY IN PUERTO RICO AND COLORADO

by

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and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy

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Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

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DEDICATION

To my husband, Robert Joel Segal, whose loving support during this process was crucial and appreciated. Thank you, Bob.

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ABSTRACT

The toppling of trees forms mounds of disturbed sediment and pits from which the mound removes sediment, rocks, and organic matter. Sites of uprooted trees in Puerto Rico and Colorado were examined (1) to compare areas and volumes of mounds and pits relative to tree size, (2) to compare areas and volumes of mounds and pits formed during catastrophic events at the landscape scale, and (3) to consider decay of mounds and pits after formation. For a given basal area, the analyses found no difference among sites in area and volume of freshly formed individual mounds and pits. For landscape-level catastrophic uprooting, the percent of toppled trees in a plot can explain 85% and 87% of the areas and volumes, respectively, of the quantity of soil uplifted. Exponential decay coefficients developed by monitoring mound/pit complexes indicate that mounds and pits at the humid tropical site in Puerto Rico decay in about 74% and 57% of the time, respectively, of mounds and pits at a temperate Colorado site. Decay coefficients developed for the Colorado site indicate that mounds and pits are reduced to 10% of their original volume within 30 and 78 years, respectively. Coefficients for Puerto Rico suggest that a similar reduction in volume requires 17 years, whereas pits generally fill within a decade.

INTRODUCTION TO THE DISSERTATION

The study of mound and pit microtopography has interested geomorphologists and soil scientists for more than half a century (Lutz, 1940; Stephens, 1956; Denny and Goodlet, 1956; Lyford and MacLean, 1966) because of its potential influence on soil formation, sediment movement, drainage patterns, and forest ecology. Treethrow may disrupt soil development processes, thereby increasing mineral weathering processes and nutrient availability (Skvortsova and Ulanova, 1977; Collins and Pickett, 1982; Foster, 1988). It may be crucial in maintaining soil fertility in temperate coniferous forests, where natural podzolization can reduce soil fertility in as little as 300 years (Bormann et al., 1995). The uprooting of trees is the most obvious form of floralturbation (Schaetzl et al., 1989) and it is the greatest biotic influence on sediment movement (Mitchell, 1988). Uprooted trees bring buried material to the surface, including nutrients (Armson and Fessenden, 1973; Basevich, 1982), soil-organic carbon, and clasts (Schaetzl et al., 1990), exposing them to atmospheric and surficial processes. Moisture is lower and photosynthetically active radiation values are higher in mounds compared to pits (Clinton and Baker, 2000). In some cases, trees show a clear preference for pit microsites, as shown by a common primary species (*Cecropia peltata*) in Puerto Rico (Walker, 2000). In other cases, such as in a sugar maple-basswood forest in northeastern Wisconsin (Kabrick et al., 1997) and in mixed broadleaf and conifer forests in New Brunswick, Canada (Lyford and MacLean, 1966), trees were more likely to establish on mounds than in pits.

However, a connecting theory on the quantity of soil involved in the formation and decay of mound and pit formations has not emerged. Reports of mean area of mounds and pits have ranged from 1.5 m^2 for pits (Cremeans and Kalisz, 1988) to 16 m^2 for combined mound/pit complexes on Barro Colorado Island in Panama (Putz, 1983), with other estimates including 11.9 m^2 for "soil disturbance" from 22 freshly uprooted maple and beech trees in Michigan (Brewer and Merritt, 1978); 8.8 m^2 of "exposed soil and rock" per uprooted tree in the Luquillo Experimental Forest in Puerto Rico (Zimmerman et al., 1994); and 4.7 to 8 m^2, depending on treefall type, for mounds in central New York forests (Beatty and Stone, 1986). The use of different measuring techniques, variations in pit-and-mound ages, and confounding factors such as soil type, has impeded comparisons among sites. Researchers have selected a variety of factors to examine for influence on size, including mound shape (Beatty and Stone, 1986), restricting soil horizons (Mueller and Cline, 1959), landform position (Kabrick et al., 1997; Norman et al., 1995) and tree size, usually diameter (Mills, 1984; Putz, 1984; Mueller and Cline, 1959; Peterson, 2000) but also biomass (Clinton and Baker, 2000). Pit and mound dimensions have been reported by axes (Kabrick et al., 1997), and by volume (Mills, 1984; Shubayeva and Karpachevskiy, 1983; Norman et al., 1995), but most frequently by area (Putz, 1983; Zimmerman et al., 1994; Cremeans and Kalisz, 1988; Peterson, 2000). Also, pit and mound complexes of varying ages have been used to consider the endurance of pit-and-mound topography, but these means do not account for decay of these features on the landscape. Stephens (1956) estimated an average area of roughly 7.6 m^2 per pit-mound complex in a 0.4-hectare tract of Harvard Forest in Massachusetts that included some centuries-old complexes. Shubayera and Karpachevskiy (1983) measured a series of older mounds in Siberian forests and estimated that trees on their site turned over "as much as 5 m^3 of soil", based mostly on mounds they estimated had persisted for 80 to several hundred years, but they found no evidence of mounds younger than 20 years. Lyford and MacLean (1966) assessed the number of mostly older mounds and pits and the proportion of the landscape occupied by each in forest plots in New Brunswick, Canada, with their results indicating a mean mound size of 2.95 m^2 and a mean pit size of 0.85 m^2.

This study sought to find unifying or distinguishing relations by applying similar measuring and analytical techniques to three disparate sites, two in Colorado and one in Puerto Rico. The objective of the study was to consider potential influences on the sizes of mounds and pits at all three sites, to develop an understanding of the sequences of their decay at two sites with different environments, and to document their longevity on the landscape in one site. An intention was to obtain information contributing to the understanding of how the uprooting of trees affects sediment yield of a watershed. The analyses focus on the quantity of soil disturbed by tip-ups at the individual tree level for all three sites, and at the landscape level for two sites that involved catastrophic uprooting events in Colorado and Puerto Rico. In addition, the dynamics of short-term mound and pit decay were considered in a 2-year study to monitor a subsample of mound/pit complexes in Colorado and Puerto Rico. Century-scale decay estimates were developed for a Colorado site using tree-ring analysis to estimate mound/pit formation dates, and decadal-scale decay estimates were developed for Puerto Rico based upon the measurement of 20 mounds known to have fallen 9 years previously. In this study, "mound" refers to the disturbed soil, roots, and rocks that are uplifted by a fallen tree, and includes the freshly uprooted variety (sometimes known as earth balls, rootballs, or root plates) as well as older examples.

My role in this study was to conduct all the research and statistical analyses for these three sites, with guidance on field and laboratory methods provided by Dr. Waite R. Osterkamp at the Sangre de Cristo site, by Dr. Frederick N. Scatena in Puerto Rico, and by faculty and staff at the Laboratory of Tree-Ring Research (LTRR) in Tucscon, Arizona. Guidance on conducting the statistical analysis was provided by Dr. Robert Steidl of the University of Arizona, and LTRR faculty and staff. I wrote the original versions of the manuscripts, which have since benefited from editing and comments from Drs. Osterkamp and Scatena, as well as other committee members: Drs. Malcolm Hughes, Steve Leavitt, and Phillip Guertin.

Study sites

Three study sites were used for this research, two in montane and subalpine mixed conifer forests in Colorado, and one in the tropical moist evergreen broadleaf and associated forests of Puerto Rico. The uprooted trees measured in one of the Colorado sites, the Routt National Forest, and in Puerto Rico had been toppled during catastrophic windthrow events. The other Colorado site, in the Sangre de Cristo Mountains near Westcliffe, involved trees uprooted over several previous decades as dated by tree-ring analysis.

The Sangre de Cristo site was in about 30 ha of privately held land bordering the San Isabel National Forest. The elevation, about 2930 m, places the site in the distribution range for Douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), Ponderosa pine (*Pinus ponderosa*), Englemann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) (U.S. Department of Agriculture, 2001), although lodgepole pine (*Pinus contorta*) and white fir (*Abies concolor*) were more common than spruce and subalpine fir. Annual precipitation in Westcliffe averaged 397 mm, and ranged from 203 to 756 mm, for 1934 to 2002 (Wet Mountain Tribune, 1934-2002). The study site includes bedrock soils, glacial till, and organic-rich alluvium. Uprooted trees were surveyed along a 1-ha transect (500 m X 20 m), along a bedrock ridge, and in 500 m^2 plots designed to expand the sampling in till and initiate sampling in alluvium. Fifty pit-mound complexes containing trees that were successfully dated using tree-ring analysis were used for the study of mound/pit formation and decay. A subsample of 24 pit-mound complexes with trees that had died within 3 years of the survey was used retroactively to predict the initial size of older mounds and pits, and for comparisons with other freshly uprooted mounds and pits surveyed at other sites.

The Routt National Forest study site was among the more than 10,000 ha of Rocky Mountain forest between approximately 2250 and 3250 m in elevation that was damaged in the Routt-Divide blowdown on October 25, 1997 (Baker et al., 2002). The blowdown appears to have occurred when the jet stream dipped toward the surface as it crossed the Continental Divide, then accelerated and reversed direction when it became trapped under a strong upslope easterly cold front, thereby producing wind speeds in excess of 200 km hr^{-1} (USDA Forest Service, 1998). The study site was dominated almost exclusively by subalpine fir (*Abies lasiocarpa*) and Englemann spruce (*Picea englemannii*). Weighted mean annual precipitation is approximately 1000 to 1100 mm for the Elk River North Fork and Middle Fork watersheds, with most of it falling in the form of snow (USDA Forest Service, 1998). The soils at the site were coarse-textured and derived from glacial deposits, with sandy loams and loamy sands with rock fragments comprising the ridges and slopes, and reworked, poorly drained alluvium comprising the upland valleys (USDA Forest Service, 1998).

The Puerto Rico study plots were distributed around the island, which is at 18.5° North latitude in the Greater Antilles chain of the West Indies, in secondary and primary forests. Mean annual rainfall on the island ranges from slightly under 1000 mm to slightly over 4000 mm (The Climate Source, 2002), and study sites spanned the precipitation range. However, about 67% of plots were in the forest type Ewel and Whitmore (1974) classified as wet forest under the Holdridge (1967) system, with between 2000 mm and 4000 mm of annual rainfall. Surveying of uprooted trees within and outside of plots was done in the 3 months following the passage of Hurricane Georges, which on 21-22 September 1998 brought maximum sustained winds of 185 km hr^{-1} with gusts of up to 241 km hr^{-1} (Bennett and Mojica, 1998). Uprooted trees were in evergreen broadleaf forest of mixed species (including *Dacryodes excelsa, Cyrilla racemiflora, Sloanea berteriana, Inga vera, Swietiena* spp., and *Guarea* spp.), in stands of needleleaf trees (typically *Casuarina equisetifolia* or *Pinus caribaea*), and in palm forest dominated by *Prestoea montana*. Soil types were predominantly clay, but also included loam, sand, and various combinations of particle sizes and levels of soil organic matter.

Freshly uprooted mounds and pits were measured in the three study sites to answer the following questions: 1) Do initial sizes of mounds and pits vary by study site? 2) Are there factors influencing mound and pit size within each study site? 3) Can regression models be developed to predict the volume and area of mounds and pits at each site? 4) Can regression models be developed to predict the volume and area of mounds and pits when the freshly formed mound/pit complexes from the three sites are combined into one data set? The study additionally sought to answer the following questions regarding the decay rates of mounds and pits at sites in Puerto Rico and the Sangre de Cristo Mountains of Colorado: 1) Do decay rates differ between mounds and pits within a site? 2) Do decay rates of mounds and pits differ by site? 3) What do these decay rates imply about the longevity of mounds and pits on the landscape at these sites? 4) Can the study of mound and pit decay provide information on the potential for sediment yield as a result of tree uprooting?

PRESENT STUDY

The methods, results, and conclusions of this study are given in the appendices, three manuscripts written for publication in the Journal of Tropical Ecology (Appendix A), Catena (Appendix B), and Forest Ecology and Management (Appendix C). The following describes the method used to measure area and volume of mounds and pits, and summarizes the most important findings in these papers.

All three papers report soil disturbance at the individual tree level, with mound and pit area and volume measurements related to tree basal area (based on diameter at breast height) and other variables at the individual tree level. The papers report results for different sites, with supplementary information as relevant to that site. "Mound" refers to the disturbed soil, roots, and rocks that are uplifted by a fallen tree, and, in this study, includes the freshly uprooted variety (elsewhere termed earth balls, rootballs, or root plates) as well as older examples. Pits are the depressions, adjacent to mounds, that identify where the tree stood. Most mounds and pits were related to the most similar of four shapes (Fig. 1) for measuring and area calculation. The formulas below describe the area of: (1) an ellipse, (2) a half-ellipse, (3) a rectangle, and (4) a triangle.

$$\pi \ [\, 0.5\, (½\, d_1 + ½\, d_2)]^2 \qquad (1)$$

where d_1 = the length of the mound or pit, and d_2 = the width of the mound or pit.

$$½\, \pi\, [\, 0.5\, (r_1 + ½\, d_2)]^2 \qquad (2)$$

where r_1 = the length of the mound or pit, and d_2 = the width of the mound or pit.

$$d_1 * d_2 \qquad (3)$$

where d_1 = the length of the mound or pit, and d_2 = the width of the mound or pit.

$$\frac{1}{2} (d_1 * d_2) \qquad (4)$$

where d_1 = the length of the mound or pit, and d_2 = the width of the mound or pit.

The area was multiplied by average mound "thickness" or pit depth to compute volume. The thickness was ascertained at various points on the mound, with both sides considered as well as the top (when visible from either the ground or by standing on the fallen tree trunk) whenever possible. Pit depth was measured in several points of the pit, with the average calculated using measurements from the center and the edges, as well as points between for pits larger than about ½m^2.

Irregularly shaped mounds and pits were measured in three dimensions at 0.2-m intervals, and the averages of the appropriate axes were multiplied using formula (4) to estimate area, and then multiplying by average mound thickness or pit depth to obtain volume. This approach was limited to the Sangre de Cristo site, which contained many older mounds. At all sites, pits were measured only if they appeared capable of trapping sediment (i.e., had a detectable depth); otherwise, they were given an area and volume of zero for statistical analyses.

The first paper (Appendix A) reports findings from a study of uprooting in Puerto Rico in the aftermath of a hurricane. Uprooting frequency is considered, with soil disturbance, at the individual-tree and landscape levels. The second paper (Appendix B) reports results for a study of uprooting in the Sangre de Cristo Mountains of Colorado. Older mounds and pits, with ages estimated through the use of tree-ring analysis, are considered along with freshly formed complexes. The paper includes a section on the decay of mounds and pits based on a 2-year monitoring effort of a subsample of mounds and pits. The final paper (Appendix C) combines the data for freshly formed mound and pit complexes from the previous studies, as well as previously unreported results for data gathered at the Routt Divide blowdown in the Rocky Mountains of Colorado. Soil-disturbance patterns at the landscape level from Hurricane Georges and the Routt Divide blowdown are compared. In addition, results from a 2-year monitoring effort of a subsample of mounds and pits in Puerto Rico are compared to the results from the Sange de Cristo site, with exponential decay coefficients developed for short-term and longer-term mound erosion and pit infill.

APPENDIX A: Tree Uprooting and Soil Disturbance from Hurricane Georges in Puerto Rico

This study quantifies the volume and area of soil uplifted in 132 mounds formed by 152 trees in the months following the passage of Hurricane Georges over the Caribbean island of Puerto Rico, 21-22 September, 1998. Trees were tallied within and near 42 rectangular plots of 500 m^2 each in primary and secondary forests around the island. The depth, area, and volume of soil uplifted by windthrown trees were measured, with means of 0.33 m, 0.91 m^2, and 0.292 m^3, for uprooted trees in plots, relative to a mean tree diameter of 20.3 cm. In addition to considering the quantity of soil uplifted by individual trees and at the landscape level, this paper considers possible effects of site on the uprooting frequency by the hurricane.

Three questions guide these analyses: 1) How do internal variables (e.g., tree size, topography, soil type) and external variables (e.g., rainfall, position in relation to the hurricane) influence the uprooting rate of trees at the plot level? 2) How do internal and external variables influence the quantity of soil uplifted by windthrown trees?
3) Can useful models be constructed to predict the quantity of soil that is uplifted at tree and plot levels?

Variability in uprooting frequency was high among plots. For the 42 plots, the weighted mean proportion of uproots was 4.2% whereas the weighted mean proportion of snaps was 14.3%, and the mean proportion of downed trees (uproots plus snaps) was 20.5%. The combined distribution of uprooted and snapped trees is normally distributed, so it was unnecessary to use a weighted mean approach, described in detail in the paper; this is why the fractions do not equal unity. The proportion of uprooted trees had no correlation with the proportion of snapped trees. Needleleaf trees had a statistically borderline tendency to uproot more frequently than did broadleaf or palm trees. Considering all tree types, there was no statistically significant difference between the mean diameter of uprooted trees compared to the mean diameter of standing trees.

A logistic regression to determine if there were any variables that influenced whether a plot contained uprooted trees ($n = 25$) or not ($n = 17$) showed no statistically significant differences. A Poisson regression, which accounts for the lopsided distribution of the data given that 40% of the plots did not contain uprooted trees, showed that site variables influencing uprooting frequency among plots included soil type, proportion of needleleaf trees, ground slope, rainfall during the hurricane, exposure to the eye/eye wall of the hurricane, topography, and forest type.

When all 132 mound/pit complexes are included in the analyses of soil disturbance, tree basal area explained 61% of the variability of the mound volume and 53% of the variability in mound area. Loam-based mounds had the largest volume, followed by sand-based mounds, whereas clay-based mounds had the smallest volume when tree basal area was held constant using Multiple Linear Regression (MLR). Although neither tree type (needleleaf, broadleaf, or palm) nor topography (ridge, valley, or slope) had statistically significant effects on mound volume when considered independently with tree basal area, elements of each were influential when tested against a variety of potential influences. In the MLR model of mound volume with the best fit ($r^2 = 0.66$), mounds from needleleaf trees tended to be larger than those from broadleaf trees, those on ridges tended to be smaller than those on slopes, and those in loam tended to be larger than those in clay when other variables, including tree basal area, were constant.

When the 72 mound/pit complexes within the plots are considered in the analyses on soil disturbance, results of simple linear regression using tree basal area to predict mound area or volume are similar to those of regressions using all 132 mounds. A multiple linear regression model of variables (1) indicating whether a mound is based in loam and (2) tree basal area predicts about 60% of mound-volume variability. Mound thickness is more difficult to predict than mound volume or area, and tree basal area does not test as significant to thickness.

At the landscape level, simple linear regression models were developed for the 42 plots to predict the combined area of mounds in plots (m^2 ha^{-1}). The models explained 87% of the variation using the proportion of uprooted trees, 85% of the variation using the number of uprooted trees, and 84% of the variation using the proportion of stand basal area represented by uprooted trees as explanatory variables, after applying logit transformations to the explanatory variables. Similarly, simple linear regression models developed to predict the combined mound volume on the plots (m^3 ha^{-1}) explained 85% of the variation using the proportion of stand basal area represented by uprooted trees, 80% of the variation using the proportion of uprooted trees, and 79% of the variation using the number of uprooted trees per plot as explanatory variables, after applying logit transformations to the explanatory variables.

APPENDIX B: Mound and pit formation and decay in the Sangre de Cristo Mountains, Colorado

This study in the Sangre de Cristo Mountains of Colorado used an observational approach to compare mounds and pits created by uprooted trees within the past century. The study sought to consider the fate of the uplifted soil and rock fragments by observing changes in mound/pit complexes over short and long time frames. The approach was to monitor for 1 to 2 years to estimate interannual change in recently formed mounds and pits, and to use tree-ring crossdating to date mound/pit complexes of a variety of ages to estimate century-scale changes. Long-term rates were estimated by comparing trends in linear-regression models using 50 pit-mound complexes for which approximate formation dates were derived by applying dendrochronological techniques to uprooted trees at the mounds. Only pit-mound complexes that contained obvious remnants of uprooted trees were considered.

The effect of time on individual mounds and pits is more difficult to model than is the initial volume of either. MLR models using only mound/pit complexes within about 3 years of their formation predicted 74% and 73%, respectively, of the variability in mound and pit volumes, whereas the best models using mound/pit complexes of all ages predicted 63% and 54% of the variability in mound and pit volumes. Time and basal areas of tree trunks in the mound generally showed correlation with mound and pit volumes. Mounds on bedrock and till in this study tended to be comparable in size, but those formed in alluvium tended to be larger, when time and tree size were constant.

Variables other than time and tree size also correlated with mound and pit volumes. The effects of species varied, but conifers generally formed larger mounds than did aspen trees.

Mound volume tended to be larger than pit volume initially, with the mound:pit ratios gradually decreasing with time. Pits appear to persist on the landscape longer than do mounds, and the boles of fallen trees generally persist longer than both mounds and pits at the study site. Soil-based evidence of uprooting generally disappears within a century.

Short-term and decadal-scale exponential-decay coefficients for mounds and pits indicate that not all of the material eroded from a mound falls in the pit. Most of the soil from a subsample of monitored mounds appeared to move only short distances, slightly downslope but still near the treefall. The findings suggest that tree uprooting is important to *in-situ* soil processes, and perhaps ecological processes (not addressed by this study), but that it plays a small role in sediment export from the watershed.

APPENDIX C: A Comparative study of soil disturbance, uprooted trees, and mound and pit decay in Puerto Rico and Colorado

This paper integrates the results of the previous two papers with results from a third study site, the Routt Forest, in the Rocky Mountains of Colorado. Mounds and pits formed by uprooted trees at the three study sites were examined (1) to compare areas and volumes of mounds and pits relative to tree basal area, (2) to compare areas and volumes of mounds and pits formed during catastrophic events at the landscape scale, and (3) to characterize decay of mounds and pits after formation. The most important result in this paper, and of the entire study, was that there was no statistically significant difference among the three sites for area and volume of freshly formed mounds and pits, if tree basal area was included as a variable. Further, there was no difference in soil disturbance from catastrophic uprooting at the landscape level for the Puerto Rico and the Routt Forest sites.

This study showed that the influence of an uprooted tree's basal area on the area and volume of soil uplifted transcended other variables for these three disparate sites in Colorado and Puerto Rico. Tree basal area was a useful measurement of tree size because, unlike tree diameter, values can be summed when more than one tree forms one mound/pit complex. The formula for tree basal area is:

$$\pi r^2 \qquad (5)$$

where r = radius (m) at breast height (1.3 m).

Because a tree's basal area increases exponentially with the tree's radius, the relation between tree diameter and mound area or volume is exponential even though the relation between tree basal area and mound area or volume is linear. This means large trees generally uplift exponentially greater amount of soils than do small trees. The findings indicate that published mean mound sizes are relevant only to the sites in question, and only then if they are derived from trees of representative size on the landscape being considered.

For catastrophic uprooting, there was no statistically significant difference by site for stand-level projections of the amount of soil uplifted in either the Routt Forest of Colorado or the island of Puerto Rico. Simple linear regression models explained 85% and 87% of the areas and volumes, respectively, of soil uplifted at the landscape level by the proportion (%) of toppled trees in a plot. The relation using number and proportion of uproots, and proportion of basal area uprooted (all untransformed), to predict volume and area of soil uplifted per hectare are linear, indicating the proportion of soil disturbed for each unit of the explanatory variable is constant. This finding supports the extrapolation of mean mound area to the landscape, an approach that can be found in the literature, as long as the sampled data represent population variability.

The study found that mounds and pits decay in about 74 and 57% of the time, respectively, at the Puerto Rico site compared to the Sangre de Cristo site, based on their respective short-term exponential decay coefficients, *k*. Decay coefficients developed for the Sangre de Cristo site indicate that mounds and pits are reduced to 10% of their original volume within 30 and 78 years, respectively. Coefficients for mounds formed in 1989 at the Puerto Rico site suggest that a similar reduction in volume requires 17 years, whereas pits generally fill within a decade. Comparisons of short-term *k* with longer term *k* coefficients suggests that, of the material eroding from mounds, perhaps one-third re-enters the adjacent pit at the both the Sangre de Cristo and Puerto Rico sites.

Conclusions

This study showed that the influence of an uprooted tree's basal area on the area and volume of soil it uplifts transcended other variables for disparate sites in Colorado and Puerto Rico. This implies that an internal influence, tree size, is more important than external influences (e.g., wind speed) and other internal influences (e.g., soil type, species, topography). Because most of the variability in mound volume and area are explained using tree basal area, the formulas provided here (Appendix C, Table 3) may yield estimates for mound volume and area at other sites. The results would be a first approximation; as indicated in the studies at individual sites (Appendices A and B) and the combined data set (Appendix C), other variables—including soil type, tree type, and, in some cases, topography—exert secondary but detectable influences on mound size, particularly within a site. A tendency for mounds formed by needleleaf trees to be larger than mounds formed by broadleaf trees in Puerto Rico (Appendix A) is not detectable in the combined data set, which includes Puerto Rico, the Routt Forest and the Sangre de Cristo sites (Appendix C). Mounds formed in alluvium and other loamy soils tend to be larger than those formed in soils of predominantly clay or sand in the combined data set, whereas this tendency applies only to mound area in the Routt Forest data (Appendix C). In the combined data set, including a variable indicating whether a mound was formed in loam scarcely improves prediction of mound volume, although it does improve ability to predict mound area.

Just as the variables affecting the size of individual mounds appear to transcend site, the formulas developed to predict soil disturbance for catastrophic uprooting at the landscape scale—based on proportion of uprooted trees, number of uprooted trees, and proportion of basal area uprooted—also applied to both sites. Although mean stand basal area for the Puerto Rico and Routt Forest plots were statistically similar, the range of individual basal area stand values was 8.9 m^2 ha^{-1} to 70.3 m^2 ha^{-1}. Consequently, the regression equations developed in this study may be applicable to other forests. If so, the simple linear regression equations derived from this study may permit first-approximation estimates of soil disturbance at other sites. Using the proportion of uprooted trees to explain soil disturbance seems to be a more robust approach for such estimates than using the number of uprooted trees or the proportion of basal area uprooted. Including stand basal area as a variable in an MLR only marginally improved the predictive ability of equations, but may prove to be more useful with more research and data.

The simple linear regressions using individual tree basal area to predict mound area and volume are more robust than are the stand-level regressions because data points cover the assessed range. Therefore, researchers with tree-diameter information for individual uprooted trees could make more precise, and possibly more accurate, assessments using the regression equations developed for individual mounds and pits than by using the regression equations based on stand damage.

There are many advantages to having defined relations between tree basal area and the amount of soil uplifted, such as the ability to estimate the area of disturbed soil created from a specific disturbance event or from background uprooting for these sites and perhaps others. Similarly, it can be used to help quantify the rate of soil turnover for specific sites, if the uprooting rate is known as well as either proportion of uprooting or diameters of individually uprooted trees. In addition, the formulas can be used to estimate initial mound and pit volume of older mounds and pits for studies of decay. The latter was done in this study, as described above and in Appendices B and C.

The technique of estimating decay rate based on tree-ring dating of uprooted trees may be the most robust approach applied here. Although the technique requires an estimate of initial mound or pit size, the long time frames (up to about 84 years, in this study) seemed to reduce error. In contrast, using an estimated initial volume or area to assess decay in a shorter time frame, such as the 9 years since the passage of a previous hurricane in Puerto Rico, appeared less robust. Whereas longer-term decay rates for the Sangre de Cristo site were within about 10% under various approaches of estimating initial volume, decay rates for the Puerto Rico site fluctuated up to 50% depending on the approach used to estimate initial mound volume.

Estimating short-term decay rates using monitored trees theoretically could be more precise than estimating longer-term rates because the initial size of mounds and pits could be measured. The regression equations developed had more predictive power, as measured by the r^2 values, as shown in the Appendix B figures. However, using a short time frame, such as 2 years, limits the potential for accurate accounting of changes because the potential error is higher than expected changes. Measurements made with a meter stick or diameter tape are reliable to about 0.05 m. This accuracy means that the error (e.g., confidence intervals of 0.86 m^3 to 1.16 m^3 for a 1-m^3 mound) surpasses the expected change in mound volume of about 2% per year based on the material collected from the adjacent pit (e.g., confidence intervals of 0.97 to 0.99 m^3 yr^{-1} for a 1 m^3 mound). Thus, short-term decay estimates discussed here are based on the method of collecting material from the pits rather than visually measured changes. This technique, too, has error, mainly (1) the need to make assumptions about which materials fell from the mound, and (2) the need to estimate volume (cm^3) based on weight (g) using estimates for bulk density (g cm^{-3}).

As with any scientific endeavor, the completion of this project helps clarify what remains to be learned about this area of study. Ideas outlined below, organized by the following topics, are: (1) mound and pit formation at the tree level; (2) soil disturbance from uprooted trees at the landscape level; and (3) the decay of mounds and pits over time.

Of the three topics, this study addressed the first one most thoroughly. A supplement to these results for mound and pit formation at the tree level may be to expand the data set into additional environments to define the scope of applications. Ideally, the technique described here can be applied to randomly selected sites at the global level to test the regression formulas predicting mound area and volume. Of particular interest, given a larger data set, would be whether separate formulas should be developed for different soil types to make predictions more precise.

Another interesting research pursuit relating to the topic of individual mound and pit formation would be to consider the reason that mound and pit areas tend to be roughly identical for a given uproot complex, whereas mound volume tend to be greater than pit volume for a given complex. The tendency for mound volume to be greater than pit volume within the same complex has been found by others as well (Kabrick et al., 1997). This study found that the higher values for mound thickness compared to pit depth caused the discrepancy, but the mechanism behind the difference remains unexplained. Although neither measuring error nor mound expansion can be ruled out as reasons behind the difference, a more intriguing mechanism also could be considered: Could the soil now representing the pit be responding to the removal of the tree's weight and the direct exposure to the atmosphere by "decompressing", i.e., aerating and thus expanding with the increase in soil porosity? Although the soil in the mound could also be expected to expand slightly, the expansion would be minimal because the quantity of soil in the mound would be minimal compared to the quantity of soil underlying the pit. Using the biomass equation developed by Scatena et al. (1993) for all dicotyledonous trees in a Puerto Rican wet forest dominated by *Dacryodes excelsa*, an uprooted tree in Puerto Rico that was 30 cm in diameter and 20 m tall with a mound area of 0.77 m^2 would apply about 32 kiloPascals of pressure on the soil below (estimating a wet weight that is double the dry weight used for the biomass calculations, based on the branch wet:dry conversion rates used in this study, Appendix C). This exceeds the 20 kP of pressure that a tractor with 11 kW of power would place on the top 10 cm of soil with its front wheel (Horn and Lebert, 1994, citing Burger et al., 1988). Whether the removal of the tree's weight could explain the difference in mound thickness and pit depth is a question that would need to be explored further. If so, it implies an increased bulk density of soil below a tree that should be taken into consideration for calculations such as total soil carbon; it also could be considered as a contributing factor to the general observation that tree roots tend to be concentrated near the surface.

The second topic of interest, soil disturbance at the landscape level, could benefit from the inclusion of additional sites even more than the study of individual mound and pit formation. The proportion of uprooting in Puerto Rico plots did not exceed 30%, so extrapolations beyond that depend on results from the Routt Forest. The finding that the data points fall on the same line, with no statistical significance by site, is intriguing; still, it would be even more impressive if the finding held given the addition of more data points representing other sites, particularly with uprooting frequencies above 30%. Ideally, these would be randomly selected in a global context. A larger data set might allow the refinement of projections using soil type and perhaps stand basal area to improve predictions. The refinement of this data set probably should take precedence over the task of refining the data set of individual mounds and pits because of its greater applicability to previous research. Much effort has been applied to estimating uprooting frequency from specific catastrophic events. With refinement, the formulas predicting soil disturbance from the proportion of uprooted trees could be applied to the results of previous research. For example, regional research on uprooting from hurricanes could be used to estimate soil disturbance and regional soil turnover rate from hurricanes, as was done for Puerto Rico (Appendix A).

Of the three topics, the research on mound and pit decay is least complete. More so even than in the case of the other two topics, the data set would benefit from additional samples. Whereas 212 mound/pit complexes were analyzed for the tree-scale projections, and 52 plots were analyzed for the landscape-scale projections, only 15 mound/pit complexes were analyzed for short-term projections of mound and pit decay. The use of tree-ring dating to consider long-term decay of mounds and pits (with 50 mound/pit complexes used) is more thorough, and it is a technique that could be applied to other sites where wood from uprooted trees is datable and remains viable for decades or more. It would also be interesting to consider mound and pit decay in forests in which pit-mound topography is a prevalent feature. It seems likely that there is a characteristic pattern of decay and, at least in some forests, eventual stabilization of mounds and pits (with the older versions also known as hummocks and cradles). Perhaps the formulas developed to predict individual mound and pit sizes could be applied to forests with older mound-and-pit topography to help identify the point at which mounds and pits stablilize. Because in many cases, the formation can be related to a datable disturbance event (for example, see Stephens 1956), the projected fraction remaining of the mound/pit could be plotted by year with the hope of revealing an asymptote that indicates stabilization.

A relatively unexplored area of study related to the topic of decay is the fate of the soil that departs the mound. Movement of soil from a mound is difficult to monitor; although equipment to trap sediment could be installed, it would be difficult to determine whether trapped sediment came from the mound or from another upslope source. Further, knowing whether the trapped sediment would have settled into the local landscape or continued its movement to a river would be difficult to ascertain. Perhaps the approach adopted here, to pair tree-ring dating of older mound/pit complexes with estimates of initial volume of mounds and pits, is the most reliable means of considering the question of soil movement from mounds and into pits.

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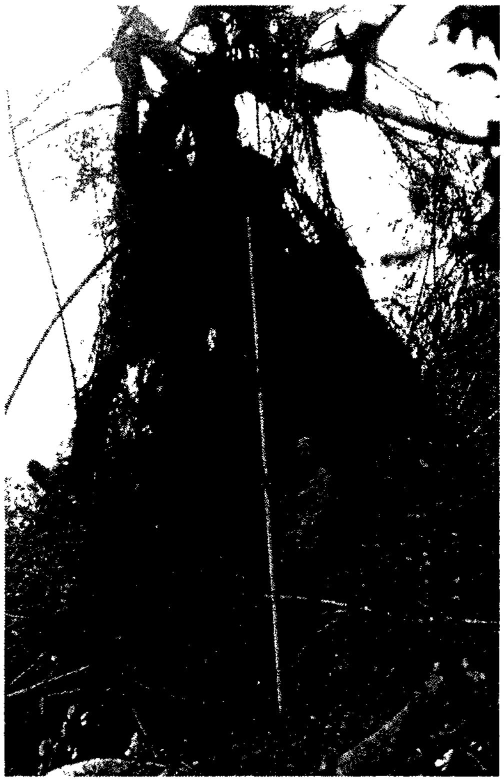
a)

b)



c)

d)

Figure 1. Images showing common shapes of mounds, which include (a) an ellipse (in the Sangre de Cristo Mountains), (b) a half-ellipse (background, in the Routt Forest of the Rocky Mountains), (c) a triangle (in Puerto Rico), and (d) an irregular rectangle (in the Sangre de Cristo Mountains).

APPENDIX A – TREE UPROOTING AND SOIL DISTURBANCE FROM HURRICANE GEORGES IN PUERTO RICO

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ABSTRACT

Trees uprooted and snapped by Hurricane Georges on 21-22 September 1998 were tallied in 42 rectangular plots of 500 m^2 each in primary and secondary forests around the island of Puerto Rico. The depth, area, and volume of soil uplifted by windthrown trees were measured, with means of 0.33 m, 0.91 m^2, and 0.292 m^3, given our mean diameter of 20.3 cm for uprooted trees in plots. Tree size, represented here by tree basal area, is crucial when assessing soil disturbance, as the area and volume of uplifted soil increase exponentially as a tree grows larger. Factors affecting uprooting frequency include stand basal area, soil type, the proportion of needleleaf trees in a plot, and topography. The proportion of uprooted trees, the number of uprooted trees, or the proportion of basal area uprooted can explain 84% or more of the variation in hurricane-created mound area ha^{-1} using simple linear regression models, whereas the same explanatory variables, respectively, explain 80%, 79%, and 87% of the variation in mound volume ha^{-1}. Results indicate that soil-turnover period from tree uprooting during hurricanes in Puerto Rico is between 1,600 y and 4,500 y.

KEY WORDS: disturbance, hurricane, LEF, mound and pit, Puerto Rico, soil, treefall, tropics, windthrow, uprooting.

INTRODUCTION

The uprooting of trees is a surficial disturbance that reallocates soil, biomass, carbon, and nutrients in forested watersheds. Uprooting is the most pervasive form of soil bioturbation (Mitchell 1988). Although many studies agree that the process has an important influence on soil-nutrient cycling (Armson and Fessenden 1973, Basevich 1982), soil morphology (Lorio and Hodges 1971, Burns 1984), and forest ecology (Skvortsova and Ulanova 1977, Collins and Pickett 1982, Foster 1988), only a few studies have assessed the quantity of soil uplifted by uprooting in tropical forests (Putz 1983, Zimmerman et al. 1994, Larsen 1997).

This study quantifies the volume and area of soil uplifted by 152 trees in the months following the passage of Hurricane Georges over the Caribbean island of Puerto Rico, 21-22 September 1998. Three questions guide these analyses: 1) How do internal variables (e.g., tree size, topography, soil type) and external variables (e.g., rainfall, position in relation to the hurricane) influence the uprooting rate of trees at the plot level? 2) How do internal and external variables influence the quantity of soil uplifted by windthrown trees? 3) Can useful models be constructed to predict the quantity of soil that will be uplifted at the tree level and plot level?

METHODS

Study area

Puerto Rico is a tropical island in the Greater Antilles chain of the West Indies, centered on approximately 18.5° North and 67° West. Almost all of the island's 890,000 ha could support forests. Given temperature and precipitation patterns, Ewel and Whitmore (1973) used the Holdridge (1967) system to estimate that approximately 60% of island area would support moist forests (between 1000 mm and 2000 mm annual rainfall), 25% would support wet forests (between 2000 mm and 4000 mm annual rainfall), and 14% would support dry forests (< 1000 mm annual rainfall). Extensive clearing for agriculture reduced the island's forest cover to a low of about 12% in the late 1940s (Koenig 1953). Since then, forest cover has increased to about 32% of island area (Franco et al. 1997).

Forests throughout Puerto Rico comprise the study area for this paper (Fig. 1), including the Bisley and El Verde sections of the protected Luquillo Experimental Forest (LEF), state forests in the island's interior, and forest stands and plantations on private and municipal land. About 65% of the plots are in what the Holdridge (1967) system classifies as subtropical wet forest (Ewel and Whitmore 1973) and 64% contain predominantly broadleaf trees (Table 1). The eye of the hurricane passed over about 40% of the plots, generally bringing higher rainfall (Fig. 1) along with the typically stronger winds of the eye wall. The hurricane brought maximum sustained winds of 185 km h^{-1} with gusts up to 241 km h^{-1} (Bennett and Mojica 1998).

Data collection and analysis

From 23 September through December 1998, measurements were taken on the volume of soil disturbed by 152 freshly uprooted trees in 132 mounds in and near plots. Forty-two plots were established in the Caribbean National Forest's Luquillo Experimental Forest (LEF), state forests in the island's interior, and forest stands and plantations on private and municipal land. Data from 18 plots in private and state forests were collected during a 2-week trip across the island that began Oct. 18. Other data-collection efforts began within days of the hurricane and continued through Dec. 20, with day trips arranged to include a variety of secondary forests as well as the four major LEF forest types – tabonuco (subtropical wet forest dominated by *Dacryodes excelsa*), palm (lower montane wet forest dominated by *Prestoea montana*), Palo colorado (lower montane wet forest dominated by *Cyrilla racemiflora*), and dwarf (lower montane rain forest dominated by *Tabebuia rigida* and *Ocotea spathulata*) (forest types from Ewel and Whitmore, 1973; dominant species from Brown et al., 1983).

Forest stands were selected based on a mapped location (for example, state forests) or when viewed from the road during field excursions designed to expand study relevance to the island as a whole rather than a particular forest type. Random sampling of plots was not attempted because the intention was to sample a variety of forest types across the island, where urbanization dominates the landscape (Franco et al. 1997). To prevent bias within a forested stand, the plots were initiated 25 paces from the entry point or from the previous plot in a predetermined direction. Forty percent of the plots did not include uprooted trees, two plots included landslides, and one plot showed evidence of a recent surface fire. The approach sampled a wide variety of forest types, but the proportions are not necessarily representative of forest-type distribution on the island.

Plots were 500 m^2, with dimensions of either 20 X 25m or 10 X 50 m. Stand basal area was assessed with a relascope (Bitterlich's Spiegel Relaskop), with diameter measurements of standing trees taken as well on a subset of seven plots. This subset was used to correct the relascope-generated basal area for each plot based on a correlation between the relascope measurements and actual measurements. A hand-held clinometer was used to measure hillslope gradient at the plot scale. Aspect was taken using a Brunton compass. Topographic categories were assigned as follows: ridges are local divides that receive no upland runoff; slopes are areas that receive and transmit runoff; and valleys are low-gradient areas that receive concentrated runoff. Elevation values for sites were approximated to within 50 m (± 50 m) using topographic maps (U.S. Geological Survey 1951, National Geographic 1996) in conjunction with a road map. Forest types were assigned based on the Life Zone map in Ewel and Whitmore (1973). A map by the U.S. Global Change Research Program National Assessment Synthesis Team (2000) was used to derive precipitation during the event (using midpoint values for rainfall categories) and to determine whether the hurricane eye went over the plot.

Each tree in a plot > 10cm in diameter was noted as standing live, standing dead, snapped, or uprooted, and classified as a needleleaf (typically *Pinus caribaea* or

Casuarina equisetifolia), palm (*Prestoea montana*), or broadleaf tree. (Hundreds of broadleaf species thrive in Puerto Rico, including *Cecropia schreberiana, Cyrilla racemiflora, Dacryodes excelsa, Sloanea berteriana,Guarea* sp., *Manilkara bidentata, Swietiena* sp., and *Inga vera.*) Standing and snapped trees were included if they were >10cm in diameter, and uprooted trees of any size were included if they disturbed soil and if at least 50% of their pits fell within plot boundaries. Uprooted trees in the vicinity of the plots or along the path or road also were measured for the expanded data set. Tree diameter at breast height (1.3 m), bole length, slope of the fallen bole, ground slope, and treefall direction were measured at each fallen tree. Tree basal area, derived from diameter at breast height [π ($\frac{1}{2}$d)^2), was used to represent tree size because values can be summed when more than one tree forms a mound/pit complex. For area assessments, mounds and pits were related to the most similar shape (ellipse, half-ellipse, triangle, or rectangle) for measuring and calculation purposes. The area value was multiplied by approximate mound "thickness" or pit depth to compute volume. "Mound" here refers to the disturbed soil, roots, and rocks that are uplifted by a fallen tree. Pits are the depressions adjacent to mounds. In this study, pits were measured only if they appeared capable of trapping sediment; otherwise, they were given a value of zero. The proportions of roots and of clasts in the mound were estimated visually. Dominant particle size (clay, loam, sand) and apparent organic matter content (low, medium, high) were estimated based on visual and tactile impressions. Approximate age of the trees was based on the average annual diameter increase of 0.395 cm based on measured growth of 18 species of Puerto Rican trees (Crow and Weaver 1977).

Statistical analyses

Analyses were conducted on three interrelated data sets: 1) a set of 42 plots, from which uprooting frequency and soil disturbance were estimated; 2) a set of 72 mounds containing 79 trees from the plots, from which means for individual uprooted trees were estimated and linear regressions predicting soil disturbance for individual mounds were developed; and 3) an expanded set including the 72 plot-based mounds and an additional 60 mounds containing 73 trees, from which linear regressions predicting soil disturbance for individual mounds were refined.

Data were analyzed using the JMP computer software developed by the SAS Institute Inc. (Sall and Lehman 1996). An alpha level of 0.05 was set to test statistical significance of results. Linear regression models employed the method of least squares. Parameter estimates follow the form of $y = a + bx_1 + bx_2$, where a = the intercept, and b = the slope of the parameter (Ramsey and Schafer 1997). Data were transformed as necessary to meet assumptions of parametric tests, i.e., Gaussian (normal) distribution. In some cases where an abundance of zero values for data points made a normal distribution impossible even with a transformation, the zero values were excluded during the analysis and weighted in later. For example, only 25 of the plots contained uprooted trees, so a preliminary mean of uprooting proportion was derived from the 25 plots with uprooted trees, which yielded normal curves (Shapiro-Wilk W test). The results were multipled by 25 and divided by 42 to account for the 17 plots without uprooted trees. The same approach was used to test mean pit volume, area, and depth, although the latter could not be transformed into a normal curve even with zero values excluded.

When employing a log or related logit transformation, an "x + 1" approach was used if necessary. The typical logit approach [ln (fraction of uprooted trees / 1 – fraction of uprooted trees)] (Ramsey and Schafer 1997) was used when excluding plots with zero uprooted trees. When plots with no uprooted trees were included, the formula was adapted to {ln [(percentage of uprooted trees + 1) / (100 – percentage of uprooted trees)+1]}. A correction factor was developed for the relascope readings using a correlation developed from the subset of seven comparison plots in which each standing tree was measured [(Actual basal area (m^2 ha^{-1}) = 6.528 + 0.619 (relascope value, m^2 ha^{-1}), $r^2 = 0.770$].

Uprooting frequency. To estimate the mean proportion of uprooted trees on plots, a logit transformation was applied to the 25 plots with uproots so they would conform to a Gaussian curve; the backtransformed value was weighted to include the 17 plots without uproots. The variables tested for influence on uprooting frequency at the plot level were: total number of trees; stand basal area (m^2 ha^{-1}); proportion of needleleaf trees; proportion of palm trees in plot; topography (slopes, ridges, and valleys); slope of the plot-scale landscape (°); predominant soil type (clay, loam, or sand); elevation (m); forest type (dry, moist, wet, and rain forests); whether the hurricane eye went over the plot; and rainfall during the hurricane. For the Poisson regression analysis, the response was a fraction with numerical values for the numerator, the number of uproots, and for the denominator, the number of trees on each plot. A logistic regression was used to check for differences among the 25 plots with uprooted trees and the 17 plots without uproots. The number of uproots of a given tree type was divided by the total number of the same tree type for each plot to compare uprooting frequency among the three tree types (needleleaf, palm, broadleaf evergreen). Only eight plots contained needleleaf trees, whereas 22 contained palms and 40 contained broadleaf trees.

Soil disturbance. At the tree level, statistical analyses considered n to be mounds because two or more trees sometimes fell together, yielding one mound. Tree diameters were converted into tree basal area for the same reason. The height of the tallest tree was used for height analyses. Pit boundaries often were difficult to detect, either because they quickly blended into steep slopes, were covered by leaf litter, or faded into ephemeral streams. In this study, therefore, the mound is viewed as the more accurate measure of the soil displaced from the pit, given that mound soil bulk density was identical to the bulk density of nearby soil (unpublished data for a subset of 10 trees, this study). The variables tested for influence on mound size were: topography; tree type; treefall direction (downslope vs. upslope); aspect (0-360°); tree slope (0-90°); local ground slope (0-90°); forest basal area (m^2 ha^{-1}); tree basal area of the uprooted tree(s) (cm^3); number of trees in the mound; height of the tallest tree (m); soil type; soil organic matter (low, medium, or high); fraction of clasts; fraction of roots; and number of days between the hurricane's passage and measurements. Mound and pit analyses were done separately, except in one case: To make the results comparable to a study by Putz (1983) reporting mound/pit area, mound areas were doubled to approximate mound/pit area (for results reported in Fig. 4 and Table 6). This approach was taken because pits in this study were measured only if they were deemed capable of trapping sediment.

At the plot level, results were used to model the area and volume of soil uplifted (i.e., combined mound area and volume) using 1) number of uproots; 2) proportion of uproots; and 3) proportion of the stand basal area uprooted. Linear regressions used the number of uproots, the logit of the proportion of uproots, and the logit of the proportion of the basal area uprooted. Plots without uproots (i.e., zero values) were included in all regressions. The mean area of soil uplifted per plot was estimated by taking the natural-log transformation of the per-ha extrapolation only for those plots with uproots ($n = 25$) and then weighting the resulting mean to include all 42 plots. The resulting estimate for mound area is paired with the hurricane return rate to consider the role of hurricane-uprooted trees on soil turnover rate and period in Puerto Rico.

RESULTS

Uprooting frequency

Needleleaf trees tended to uproot more frequently than broadleaf and palm trees, although none of the distributions were Gaussian. The proportion of needleleaf trees uprooting was about four times higher than the proportion of broadleaf trees uprooting and about 15 times higher than the proportion of palms uprooting when all eight plots with needleleaf trees were included ($p < 0.05$, Tukey-Kramer HSD comparisons for all pairs). This proportion was twice as high as that of broadleaf trees and about nine times higher than that of palms after excluding two plots with only two needleleaf trees each, although the difference between needleleaf and broadleaf was not considered significant at the 0.05 level (Tukey-Kramer HSD comparisons for all pairs). Considering all tree types, there was no statistically significant difference between the mean diameter of uprooted trees compared to the mean diameter of standing trees. Among plots, variability in damage was high (Table 3). For all 42 plots, the mean proportion of uproots was 4.2% whereas the mean proportion of snaps was 14.3%, and the mean proportion of downed trees (uproots plus snaps) was 20.5% (Table 3). The proportion of uprooted trees had no correlation with the proportion of snapped trees ($r^2 = 0.009$, $n = 42$), even when only the plots with uproots were used ($r^2 = 0.003$, $n = 25$) or when log-transformed ($r^2 = 0.036$ when $n = 42$, 0.0001 when $n = 25$). Rainfall during the hurricane was positively correlated with the passage of the hurricane eye ($r^2 = 0.91$), so these two variables cannot be considered independent of one another. A logistic regression to determine if there were variables that influenced whether a plot contained uprooted trees ($n = 25$) or not ($n = 17$) found no statistically significant differences.

A Poisson regression, which accounts for the skewed distribution of the data, found that many of the site variables influenced uprooting frequency among the 42 plots. Plots exposed to the hurricane eye—and therefore to the eye wall, which often contains the strongest winds and most intense precipitation of a hurricane (Aguado and Burt 1999)—had a higher uprooting frequency than those not exposed to the eye ($p < 0.0001$). The proportion of needleleaf trees on the plots had a positive influence on uprooting frequency ($p < 0.0001$, range of 0 to 100% needleleaf trees per plot), whereas the proportion of palms had no influence ($p = 0.8480$, range 0 to 72% palm trees per plot). Ground slope (in degrees) had a positive influence ($p = 0.0390$), as did elevation ($p < 0.0001$) and rainfall during the storm ($p < 0.0001$). The stand basal area exerted a negative influence ($p = 0.0387$), i.e., uprooting frequency decreased as basal area increased. Uprooting rates were highest on ridges ($p < 0.0001$) and were higher on slopes ($p = 0.0014$) than in valleys. When forest type was tested (using the four types identified in Table 1), uprooting frequency was higher in moist forests ($p < 0.0001$) and lower in rain forests ($p < 0.0001$) than in wet forests. When soil type was tested, uprooting frequency was lowest in loamy soils ($p < 0.0001$), and lower in clay soils ($p = 0.0014$) than in sandy soils.

Soil disturbance

All uprooted trees. Tree basal area explained 61% of the variability of the mound volume (F-test, $p < 0.0001$) and 53% of the variability in mound area (F-test, $p < 0.0001$) when all 152 uprooted trees are included in the analysis (Figs. 2a and c, Table 4). Several variables were considered statistically significant in multiple linear regression models, but no combination in a variety of models tested explained more than 66% of the variability in mound volume. Loam-based mounds had the largest volume ($p = 0.0030$), followed by sand-based mounds ($p = 0.0414$), whereas clay-based mounds had the smallest volume when tree basal area was constant using MLR. Although neither tree type nor topography had a statistically significant effect on mound volume when considered independently with tree basal area, elements of each were influential when tested against a variety of potential influences. In the MLR model of mound volume with the best fit ($r^2 = 0.656$), mounds from needleleaf trees tend to be larger than those from broadleaf trees ($p = 0.0010$), those on ridges tend to be smaller than those on slopes ($p = 0.0264$), and those in loam tend to be larger than those in clay ($p = 0.0061$) when these variables are considered together with tree basal area ($p < 0.0001$).

Uprooted trees in plots. The mean pit volume was about 66% the size of the mean mound volume of 0.292 m^3 when pits with zero values were excluded, and about 40% the mean mound volume when zero values were included (Table 2). The number of days after the hurricane had no effect on pit depth ($p = 0.2278$) or pit volume ($p = 0.3209$) when considered with tree basal area in a multiple linear regression. Generally, the soil contained few rocks, with clasts visible in about 26% of mounds. Mounds averaged about 30% roots. Slightly more than 75% of trees fell downslope, typically tree falling almost directly downslope (Table 2). Twice as many uprooted trees (i.e., about 50% vs. 25%) fell generally northwest (230° to 360°) whereas half as many (i.e., 13% vs. 25%) fell in the general easterly direction of the hurricane's forward movement (45° to 135°) than would be expected by chance.

The regression equation predicting mound volume based on tree basal area for the full data set of newly formed mounds (n = 132 mounds) is contained within the intervals for the plots-only data set (n = 72) (Figs. 2b and d, Table 4). Similarly, the regression equation predicting mound area based on tree basal area for the full data set of newly formed mounds (n = 131) is contained within the larger 95% confidence intervals for the plots-only data set (n = 71). The regression coefficient (r^2) is lower for the regression model using only plots-based mounds, probably because of the smaller sample size (Table 4). MLR was used to determine whether other parameters influenced mound volume when tree size (tree basal area) was constant. Considering soil type, tree type, and topography, the only parameter deemed influential was loamy soil (p = 0.0020), which had a positive influence on mound volume. A multiple linear regression model that includes a parameter indicating whether a mound is based in loam along with tree basal area can predict about 60% of mound volume variability (adjusted r^2 = 0.595), the best fit for a MLR model using plot-based trees to predict mound volume in which all parameters are deemed significant.

When testing mound area against tree basal area, the MLR model with the best fit of significant variables (adjusted r^2 = 0.591) includes parameters taking into account the tendency for mounds of palm trees to be smaller than for other types of trees (p = 0.0042), and for mounds in the eye of the hurricane to be smaller than those outside of the eye ($p < 0.0001$) along with tree basal area ($p < 0.0001$). The more complex model is an appreciable improvement over the simpler model using tree basal area (Table 4).

Mound thickness is more difficult to predict than mound volume or area, and tree basal area does not test as significant. The best model using significant parameters predicts about 39% of the variability in mound depth (adjusted $r^2 = 0.391$), taking into account a tendency for mounds on slopes to be thicker than those in valleys ($p = 0.0012$) and on ridges ($p = 0.0004$), those in the eye of the hurricane to be thicker than those outside of the eye ($p = 0.0023$), and an increase in thickness with the height of the tallest tree in the mound ($p < 0.0001$).

To predict the combined area of mounds in plots (m^2 ha^{-1}), simple linear regression models can explain 87% of the variation using the proportion of uprooted trees, 85% of the variation using the number of uprooted trees, and 84% of the variation using the proportion of stand basal area represented by uprooted trees as explanatory variables, respectively (Table 5). Similarly, to predict the combined mound volume on the plots (m^3 ha^{-1}), simple linear regression models can explain 85% of the variation using the proportion of stand basal area represented by uprooted trees, 80% of the variation using the proportion of uprooted trees, and 79% of the variation using the number of uprooted trees per plot as explanatory variables, respectively (Table 5).

Soil turnover

To estimate soil turnover from Hurricane Georges, the mean area of soil uplifted from this study, 37.1 m^2 ha^{-1} (Table 3), was paired with the islandwide hurricane return rate of once per decade based on the period 1851-1996 (Elsner and Kara 1999), yielding an annual soil turnover rate of 3.71 m^2 ha^{-1} y^{-1}, (95% confidence intervals of 6.18 to 2.21 m^2 ha^{-1} y^{-1}). This represents a soil turnover period of 2,695 y (95% confidence interval of 1,618 to 4,525 y).

DISCUSSION

Uprooting frequency

Uprooting frequency was highly variable among the plots and was related to many variables. Given the variety of influences, it is difficult to draw strong conclusions about any one parameter or set of parameters. Using small plots (500 m^2) increased homogeneity within plots (*sensu* Pickett and White 1985), but it also increased the number of plots without uproots. Having a high proportion (40%) of plots with no uproots complicated statistical analyses. It also exaggerated variability in uprooting damage when expressed in hectares. Although few hectares of forest escaped uprooting entirely (personal observation), it is estimated that 40% of total forested area, generally at scales smaller than a hectare, had no uprooting damage. Variability is the norm in treefall damage once wind velocity crosses a threshold of 120 km h^{-1} (Scatena et al. 1991, Francis and Gillespie 1993), as occurred during Hurricane Georges (Bennett and Mojica 1999). Given the lack of correlation between frequency of uprooting and stem breakage, this study can join the 16 papers on wind damage to forests reviewed by Everham and Brokaw (1996) that found no evidence for increased homogeneity of damage with increasing wind velocity.

The uprooting rate was greater in plots exposed to the hurricane eye than in plots out of the storm center. However, rainfall also had a positive influence on uprooting rate, and the high correlation between rainfall and the hurricane eye makes it difficult to pinpoint which effect is at work. Whereas wind velocity should be more important in whether a tree falls, whether the tree uproots or snaps theoretically could depend on the level of soil saturation at the time of the event and other site factors (Scatena and Lugo 1995, Everham and Brokaw 1996).

The finding, supported by the literature, that needleleaf trees are more susceptible to uprooting than are broadleaf trees is tentative because of small sample size (n = six plots with more than two needleleaf trees) and the potential influence of other factors. Needleleaf trees uproot more easily than palms, possibly because palms have a well-documented tendency to shed fronds early in a hurricane in exchange for low uprooting rates of <1% (Frangi and Lugo 1991), 1.5% (Zimmerman et al. 1994) and 1.5% (this study). Pines were more susceptible to uprooting than were nearby hardwoods during hurricanes in Nicaragua (Boucher et al. 1990), in states bordering the Gulf of Mexico (Touliatos and Roth 1971), and in Jamaica (Sugden 1992), although slash pine (*Pinus elliottii)* was one of the most resistant species in the Everglades (Craighead and Gilbert 1962). Some of the needleleaf trees in this study are *Casuarina equisetifolia*; the species is a legume with segmented but otherwise conifer-like leaves at the macroscopic level, although its wood is much denser (0.80 g cm^{-3} to 0.97 g cm^{-3}, Kondas 1983) than the typical "softwood" pine (0.29 g cm^{-3} to 0.60 g cm^{-3}, Thomas 1991). Three *Casuarina*-

dominated plots between the coast and the San Juan airport sustained roughly twice the typical uprooting rate, although damage could have been related to the exposure of the stand as well. Francis (2000) found 8% of *Casuarina* and 12% of pines ($n = 50$ in both cases) were uprooted or snapped in urban areas of Puerto Rico during Hurricane Georges, rates much lower than the combined damage in this study of 55% for needleleaf trees ($n = 181$ trees in 6 plots), including trees that snapped at 12 m and below. If *Casuarina* and other needleleaf trees share a propensity for damage during storms, it might be related to a tendency to retain half or more of their leaves in high winds (personal observation) or perhaps to root morphology. Conifers generally have fewer but larger roots than do broadleaf trees, which is a less stable condition (Kozlowski 1971) that concentrates fewer roots downslope (Steinbrenner and Gessel 1956). Also, *Casuarina* stands in this study tended to occur on sandy soils, which had the highest uprooting frequency of the three soil types.

This study found ridges had the highest uprooting rates, followed by slopes and valleys. The susceptibility of ridges compared to valleys was reversed in a study of tree damage during Hurricane Hugo reported in Scatena and Lugo (1995) and Basnet et al. (1992), but both studies included snapped trees as well as uproots and were confined to the tabonuco forest. The dominant species, tabonuco (*Dacroydes excelsa*), prefers ridges (Scatena and Lugo 1995), and is largely resistant to uprooting due to widespread root-grafting among individuals (Basnet et al. 1993). Other factors in this study also influenced the finding that ridges were most susceptible to damage, including effects from tree type, tree size, species diversity, previous disturbance, forest type, and individual species. Other studies found topography has an inconsistent influence on treefall damage (Everham and Brokaw 1996), and tends to operate at spatial scales larger than the plot sizes considered here (Boose and Fluet 1994, Everham and Brokaw 1996, Walker 1991).

Soil disturbance

The generally higher means for mound dimensions than pit dimensions (Table 2) appear to be related to differences in thickness vs. depth. Mean areas for mounds and pits, 0.91 and 0.86 m^2, respectively, are statistically identical. However, the 95% confidence intervals for area, volume, and depth overlap only when pits with zero values are excluded from the analysis. About 65% of pits were given values of zero because depth was not detectable. Although untested, soil beneath windthrown trees theoretically may have decompressed slightly in response to the removal of the weight of the tree.

The mean mound thickness in this study of 0.33 m (95% confidence interval of 0.28 to 0.38m) approximates root distribution in Puerto Rican soils (Brown et al. 1983), in which rooting depth is concentrated in the upper 0.24 to 0.40 m of soil. Simon et al. (1990) suggested high root density contributed to their finding high shear strength in the upper 0.25 m of LEF soils, and that the decline in root density contributed to a minimum shear strength at 0.50 m below the surface. The authors also found the mean depth of landslides they measured to be 0.50 m. The drop in shear strength, if it occurs in other Puerto Rican soils, probably contributes to the finding of this study that mean depth of soil uplifted is less than 0.50 m.

More so than pit depth/mound thickness, the area and volume of the mound increases with tree basal area (Fig. 3). Thus, a tree's potential contribution to soil disturbance increases with its age. Using the regression equation for mound volume (Fig. 2a) and estimating age by tree diameter using annual-growth increments reported in Crow and Weaver (1977), a 100-year-old tree would lift an average of 84 times more soil than would a 10-year-old tree. This is a rough estimate because growth rates for individuals depend on genetic differences among and within species, tree age, and access to environmental resources such as insolation, precipitation, and soil nutrients. Tree-ring analysis, so precise in aging trees of many temperate species, remains challenging in the tropics; tropical trees often have indistinct or non-annual growth rings, making them difficult and sometimes impossible to date accurately (Boone and Chudnoff 1972, Jacoby 1989, and Roig 2000). Yet the finding that soil disturbance increases in a non-linear way with tree size/age is robust. The tendency for larger trees to uplift exponentially more soil applies to stand level as well, as the discussion below on mound area illustrates.

The quantity of soil disturbed by an individual tree is highly correlated to tree basal area (or other variables related to tree size) to a degree that renders other factors unimportant by comparison. Because of this, the regression equation from the set of 152 uprooted trees can be used for most purposes rather than the plots-only data set; its 95%

confidence interval is within the intervals for the smaller data set (Table 4), indicating that the larger data set supports a more precise version of the same interpretation. Additionally, the dependence of mound size on tree size makes comparisons to other published reports of soil disturbance irrelevant unless values are related to tree size. In this study, mound area averaged about 0.9 m^2, so the combined mound/pit complex averaged about 1.8 m^2. This compares to a mean "root mass" area of 3.2 m^2 for 20 trees uprooted by Hurricane Hugo along a trail in the Bisley section of Puerto Rico's Luquillo Experimental Forest (LEF) (A. Daniel, U.S. Forest Service written communication, 1989); an average of 8.8 m^2 of "exposed soil and rock from uprooted trees" per tree uprooted by Hurricane Hugo in Puerto Rico's El Verde section of the LEF (Zimmerman et al. 1994); and about 16 m^2 of mound/pit area created by the "average uprooted tree" in the old forest on Barro Colorado Island (BCI) in Panama (Putz 1983, $n = 94$).

Most of the differences between mean mound/pit areas disappear when tree size is considered by using the diameter of the largest tree in a mound to predict mound/pit area (Fig. 4, Table 6). When the areas for all the freshly uprooted trees in this study are plotted with the estimated coordinates for the 88 recognizable points for the BCI trees [as extracted from Figure 1b in Putz (1983)], there is no difference between the resulting regression equation and the regression equation reported by Putz (1983) for BCI trees alone (Table 6). Including the 20 trees uprooted and measured after Hurricane Hugo in Puerto Rico (with measured mound area doubled to represent mound/pit area) similarly confirms the stability of the equation (Table 6), although the Hugo mounds tend to be slightly larger for a given tree size than are those measured after Georges and in BCI (p = 0.0002 in a multiple linear regression that included the data source as a predictor along with tree diameter). The Hugo mounds were visually selected within one forest type (subtropical wet forest), and one soil type (loamy clay), and it is likely that measuring technique differed as well, so variation may indicate mounds from Hurricane Hugo were larger than those from Hurricane Georges. Measuring technique may have influenced the results from Hurricane Hugo reported in Zimmerman et al. (1994) as well, but it seems likely that tree size is the main factor contributing to the greater mean mound/pit area found in their study compared to this one. Although neither individual diameters nor mean diameter of trees uprooted in LEF's El Verde are given by Zimmerman et al. (1994), the authors noted that intermediate or large trees were more likely to be windthrown than small trees in six of 25 species assessed.

Given the importance of tree size to soil disturbance, it is surprising that mean tree basal area, stand basal area, and the number of trees in a stand have no statistically significant influence in MLR models developed from this study using the proportion of uprooted trees in a plot to predict soil area or volume disturbed. This suggests that closed-canopy Puerto Rican forests, or at least the ones in which plots were established for this study, are structurally similar enough to yield consistent results for soil disturbance. The uprooted trees on our plots were generally small in diameter, probably for two reasons: 1) many of the plots were in secondary forest, which in Puerto Rico means regrowth since the mid-1900s; and 2) many of the larger trees had fallen during Hurricane Hugo nine years previously. With respect to the first point, basal area of forest stands outside the LEF's protected boundaries tend to be much lower than the range of 35 to 85 m^2 ha^{-1} reported by Brown et al. (1983) for the LEF. A 1990 survey of timber stands of the island found the mean basal area of moist and wet forest stands were 9 and 13 m^2 ha^{-1}, respectively (Franco et al. 1997). The forest stands in this study had a mean basal area of 24.5 m^2 ha^{-1} for all plots, with 60% of them outside the LEF. With respect to the second point, in 1989 the LEF was hit directly by Hurricane Hugo, which likely thinned out many of the medium and/or large trees assumed vulnerable to uprooting (Basnet et al. 1992, Imbert et al. 1996, Everham and Brokaw 1996, Zimmerman et al. 1994). Before Hugo, 33 years had passed since a hurricane of this magnitude struck the island directly, and 57 years since a hurricane of this magnitude had passed directly over the Luquillo Experimental Forest (Scatena and Larsen 1991).

Soil turnover

Soil-turnover period, the mean residence time for the top layer of soil to be unperturbed by uprooting, is estimated from tree uprooting frequency by background gap, hurricanes, and landslides. In a study of two Bisley large plots within the LEF during the 2 years before Hurricane Hugo, the mean diameter of 21 gap-forming trees was 46.8 cm, which was among the largest 5% of standing trees (Scatena and Lugo 1995). Coupling that value with the equation in Table 4 (when n = 132) to estimate mean mound area, the soil-turnover period from background uprooting is about 7,700 years (mean of 7,692 y, 95% confidence interval, 1,495 to 41,150 y). If the estimate reported in Larsen (1997) that historic landslide formation in the Canóvanas, Icacos, and Mameyes watersheds disturbed between 0.5% to 2% of each basin per century applies generally to Puerto Rico, the soil-turnover period from landslides is between 5,000 and 20,000 y. Similarly, Guariguata (1990) reported that between 0.08% and 0.3% of slopes in the LEF were disturbed by landslides per century, which results in a soil-turnover period of 3,300 y to 125,000 y for LEF slopes. Comparing the results for background uprooting and soil disturbance by landslides to the soil-turnover period of about 2,700 y from this study, soil turnover in Puerto Rico is dominated by trees uprooted during hurricanes. Only on slopes greater than 30° are landslides be potentially more important (Simon et al. 1990). Valleys may be locally inundated by landslide debris, but only hurricanes and background uprooting overturn soil in valleys and on ridges. In addition, evidence indicates the majority of landslides in Puerto Rico occurs during hurricanes (Larsen 1997). The importance of hurricane-caused vs. background uprooting may fluctuate from decade to decade, depending on hurricane return rate and the size of the trees available for uprooting, but overall hurricanes appear to be the driving force on soil turnover in Puerto Rico.

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Table 1. Description of some characteristic features of the 42 plots assessed in Puerto Rico.

Parameters	**Categories and number of plots in each category**				
Location in relation to hurricane eye	Within eye 17	Outside eye 26			
Predominant grain size of soil	Clay 31	Loam 4	Sand 8		
Dominant tree type	Needleleaf >75%, n = 5 (>3% but <25%, n = 4)	Palm >40%, n = 10 (>3% but <40%, n = 13)	Broadleaf >60%, n = 27		
Topographic setting	Slope 24	Valley 12	Ridge 7		
Forest Type	Dry 4	Moist 7	Wet 28	Rain 4	
Aspect	North (316-45°) 9	East (46-135°) 9	South (136-225°) 13	West (226-315°) 11	
Elevation (m)	0-200 11	201-400 10	401-600 5	601-800 12	>800 4
Rainfall during hurricane (mm)	<130 11	~130-250 10	~251-380 5	~381-510 12	>510 4

Table 2. Results from individual uprooted trees measured in the 42 plots.

Category	Mean	95% Confidence Interval	Median	Range	Transformation formula used (NT means Not Transformed)	*n*
Treefall direction (< 90 ° = downslope)	42.7	33.6 to 53.9	52.5	0 to 170.0	Ln(degree of treefall direction – degree of slope +8) *	72
Slope of uproot (°)	+1.5	-2.8 to +5.8	0	-35 to +57	NT *	72
Slope of ground (°)	-20.1	-16.9 to –23.3	-20.0	-63 to 0	NT *	72
Tree basal area(of trees(s) in mound at breast ht, m^2)	0.037	0.029 to 0.047	0.038	0.002 to 0.349	Ln (Tree basal areaof tree(s) in mound, cm^2)	72
Diameter at breast height of uprooted trees (cm)	20.3	18.0 to 22.9	20.4	5.1 to 65.5	Ln(tree diameter at breast height, cm)	79
Height of uprooted trees (m)	11.3	9.9 to 12.8	12.0	2.5 to 27.0	Ln(Height of tallest tree in mound)	72
Mound thickness (m)	0.33	0.28 to 0.38	0.35	0.05 to 1.10	Ln(Mound thickness, m)	72
Mound area (m^2)	0.91	0.68 to 1.20	0.84	0.05 to 15.90	Ln(SB area, m^2)	72
Mound volume (m^3)	0.292	0.202 to 0.422	0.340	0.002 to 4.502	Ln(SB vol, cm^3)	72
Soil alone in typical mound (m^3)	0.193	0.134 to 0.279	0.248	0.002 to 3.598	Ln(Soil only in SB, cm^3)	72
Proportion of soil in mound (%)	66.9	62.7 to 71.2	70.0	0 to 100	Soil fraction *	72
Proportion of roots in mound (%)	29.0	25.4 to 32.6	30.0	0 to 100	Root fraction *	
Proportion of clasts in mound (%)	4.6	2.4 to 6.9	0	0 to 50	Ln(Fraction of clasts +1) *	72
Pit depth (m) Top: without zeros (After averaging in zeros)	0.29 (0.18)	0.24 to 0.34 (0.15 to 0.21)	0.25	0.05 to 0.90	Pit depth * ‡	45 72
Pit area (m^2) Top: Without zeros (After averaging in zeros)	0.86 (0.54)	0.63 to 1.19 (0.39 to 0.75)	0.98	0.071 to 8.254	Ln(Pit area, m2) ‡	45 72
Pit volume (m^3) Top: without zeros (After averaging in zeros)	0.200 (0.122)	0.134 to 0.298 (0.082 to 0.182)	0.251	0.008 to 2.513	Ln(Pit volume, m3) ‡	45 72

* Data were not normally distributed ($p < 0.05$) as tested by a Shapiro-Wilk W test.

‡ Plots with zero values were initially excluded and weighted in later, as described in Methods.

Table 3. Results for variables involving continuous measurements in the 42 plots. NT = Not transformed.

Category	Mean	95% C.I.	Median	Range	Transformation, if used	*n*
Basal area of site (m^2/ha)	24.5	22.3 to 26.7	23.9	11.8 to 42.4	NT (Relaskope values corrected for bias as described in text.)	42
Number of total trees per plot (and per ha)	41.1 (822)	34.9 to 47.4 (698 to 948)	39.0 (780)	7 to 94 (140 to 1880)	NT	42
Tree basal areaof individual trees on plots (m^2)	0.030 (0.043)	0.024 to 0.038 (0.031 to 0.055)	0.0306 (0.033)	 (0.013 to 0.256)	NT § (*)	42 (42)
Mean diameter (cm) of standing trees per plot	19.5 (23.4)	 (19.8 to 26.5)	19.7 (20.5)	 (13.1 to 57.1)	Conversion from mean tree basal area	42
Slope of ground (°) (All sites)	-17.2	-21.3 to –13.0	-17.5	-45 to 0	NT *	42
Angle of hillslopes (°) (Slopes only)	-26.8	- 23.1 to –30.5	-26	-10 to – 45	NT	24
Elevation (m)	460	364 to 555	450	10 to 1000	NT *	42
Precipitation during Georges (mm)	280	230 to 320	200	130 to 560	NT *	42
Uproots per ha (#)	 35.8	 26.3 to 46.8	60	20 to 200	Square root of number of uproots ‡	25‡ 42
Proportion of uproots (%)	 4.16	 3.13 to 6.90	7.05	1.5 to 29.41	Ln[%uproots/(100-%uproots)] ‡	25‡ 42
Proportion of snaps (%)	 14.29	 9.15 to 21.51	16.21	1.33 to 91.67	Ln[%snaps/(100-%snaps)] ‡	25‡ 42
Proportion felled (%) (uproots + snaps)	 20.52	 13.89 to 29.05	20.59	1.33 to 91.67	Ln[(%uproots+ snaps) / (100-%uproots+ snaps)] ‡	25‡ 42
Area of earth uplifted per site (m^2/ha)	 37.1	 22.1 to 61.8	73.3	1.4 to 344.9	Ln(Mound area + 1, m2) ‡	25‡ 42
Volume of earth uplifted per site (m^3/ha)	 13.3	 7.2 to 24.1	26.0	0.28 to 139.0	Ln(Mound volume +1, m3) ‡	25‡ 42

§ Values using two preceding rows given (mean basal area ha-1 / mean # total trees ha-1) because distribution of mean tree basal area per plot remained non-Gaussian even after log transformation. However, mean tree basal areaper plot values are given in parentheses to provide comparison and actual range.

* Data were not normally distributed ($p < 0.05$) as tested by a Shapiro-Wilk W test.

‡ Plots with zero values were initially excluded and weighted in later, as described in Methods.

Table 4. Simple linear regression coefficients predicting volume and area of individual mounds from uprooted trees. All intercepts and slopes in the table are significantly different from zero ($p < 0.0001$). r^2 = coefficient of determination.

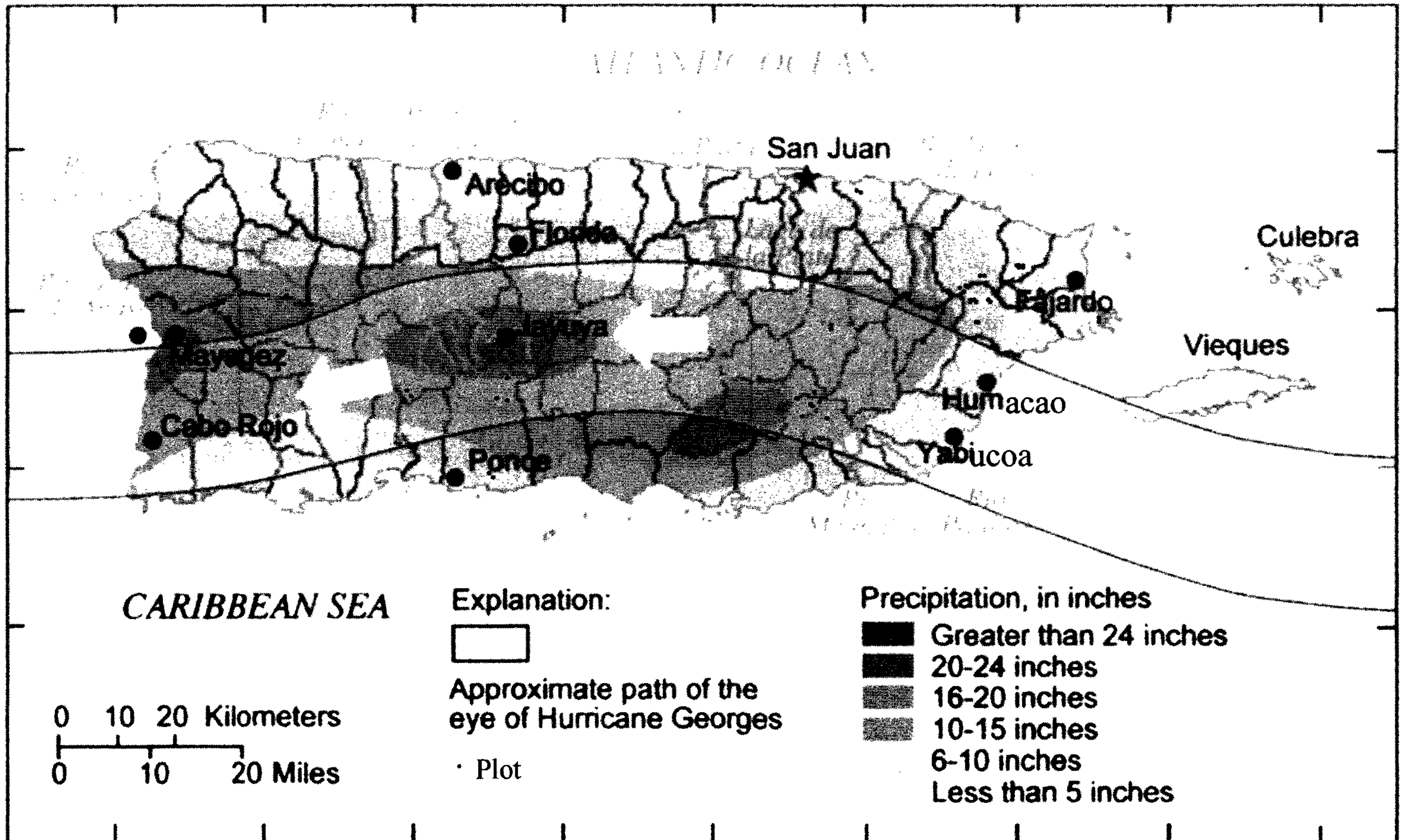
Response (y)	*Intercept*	**95% confidence interval for intercept**	**Slope**	**Predictor (x)**	**95% confidence interval for slope**	r^2	**n**
Ln(Mound volume, cm^3)	6.56	5.65 to 7.48	1.036	Ln(Trunk area, cm^2)	0.89 to 1.18	0.61	132
Ln(Mound volume, cm^3)	6.28	4.85 to 7.70	1.068	Ln(Trunk area, cm^2)	0.83 to 1.31	0.53	72
Ln(Mound area, cm^2)	4.86	4.10 to 5.63	0.744	Ln(Trunk area, cm^2)	0.63 to 0.86	0.53	131
Ln(Mound area, cm^2)	4.80	3.61 to 5.99	0.728	Ln(Trunk area, cm^2)	0.53 to 0.93	0.44	71

Table 5. Simple linear regression coefficients predicting soil disturbance at the plot level. All logit formulas are for cases where plots without uproots are included, as described in the methods section. All intercepts and slopes in the table are significantly different from zero ($p < 0.0001$). r^2 = coefficient of determination.

Response variable (y)	**Intercept**	**95% confidence interval for intercept**	**Slope**	**Explanatory variable (x)**	**95% confidence interval for slope**	**r^2**
Ln[(Mound vol in m^3 ha^{-1} +1) *1 000 000]	13.919	13.513 to 14.324	0.3834	SqRt(#uproots ha^{-1})	0.3194 to 0.4475	0.79
Ln[(Mound area in m^2 ha^{-1} +1) *10 000]	9.475	9.069 to 9.881	0.4772	SqRt(#uproots ha^{-1})	0.1431 to 0.5413	0.85
Ln[(Mound vol in m^3 ha^{-1} +1) *1 000 000]	20.384	19.596 to 21.170	1.4147	Logit(%uprooted trees)	1.1914 to 1.6380	0.80
Ln[(Mound area in m^2 ha^{-1} +1) *10 000]	17.534	16.778 to 18.289	1.7645	Logit(%uprooted trees)	1.5500 to 1.9790	0.84
Ln[(Mound vol in m^3 ha^{-1} +1)*1 000 000]	19.457	18.903 to 20.010	1.1997	Logit(% Stand Basal Area uprooted)	1.0394 to 1.3600	0.85
Ln[(Mound area in m^2 ha^{-1} +1) *10 000]	16.156	15.468 to 16.843	1.4256	Logit(% Stand Basal Area uprooted)	1.2265 to 1.6247	0.84

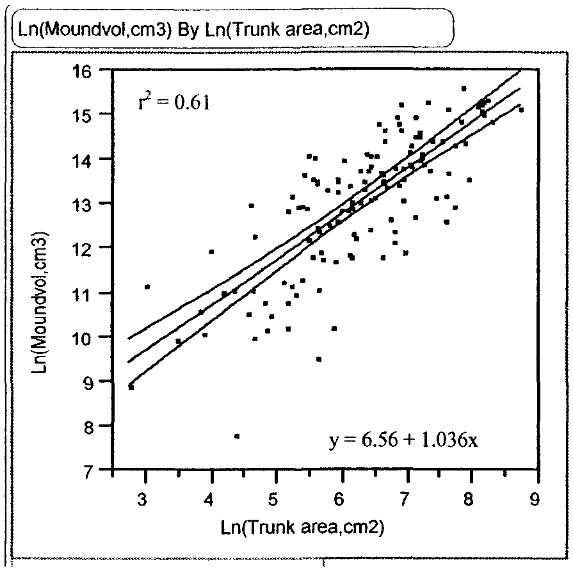
Table 6. Simple linear regression equations from other tropical studies using tree diameter to predict the area of soil disturbed by uprooted trees are compared to results from this study.

Response (y)	**Intercept**	**95% confidence interval for intercept**	**Slope**	**Explanatory variable (x)**	**95% confidence interval for slope**	**r^2**	**n**
Log_{10} (Mound/pit area, m^2), BCI trees alone (Putz 1983)	1.35	Not given	1.51	Log_{10} (diameter largest tree, m)	Not given	0.68 (S.E. = 0.11)	94
Log_{10} (Mound/pit area, m^2), BCI trees, along with PR mounds, doubled to approximate mound/pit area.	1.34	1.25 to 1.43	1.49	Log_{10} (diameter largest tree, m)	1.33 to 1.65	0.61	211
Log_{10} (Mound/pit area, m^2), BCI trees, PR mounds and Hugo mounds, with mound area doubled to approximate mound/pit area for the latter two.	1.36	1.27 to 1.45	1.49	Log_{10} (diameter largest tree, m)	1.33 to 1.65	0.60	231

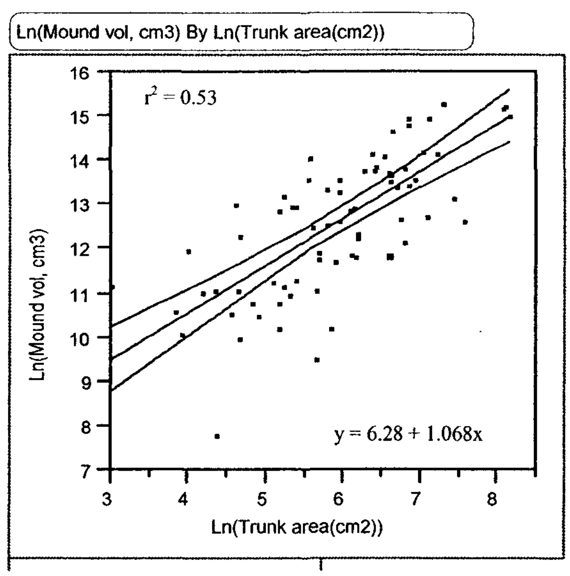


Adapted from a map prepared by the National Assessment Synthesis Team, U.S. Global Change Research Program, 2000

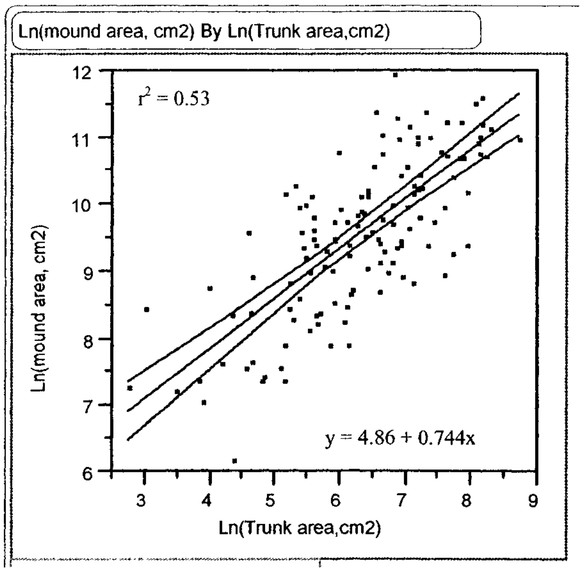
Figure 1. The map shows the path of Hurricane Georges across Puerto Rico, with red points indicating the approximate locations of the 42 plots assessed in this study.


Ln(Moundvol,cm3) By Ln(Trunk area,cm2)
r² = 0.61
y = 6.56 + 1.036x
Ln(Moundvol,cm3)
Ln(Trunk area,cm2)

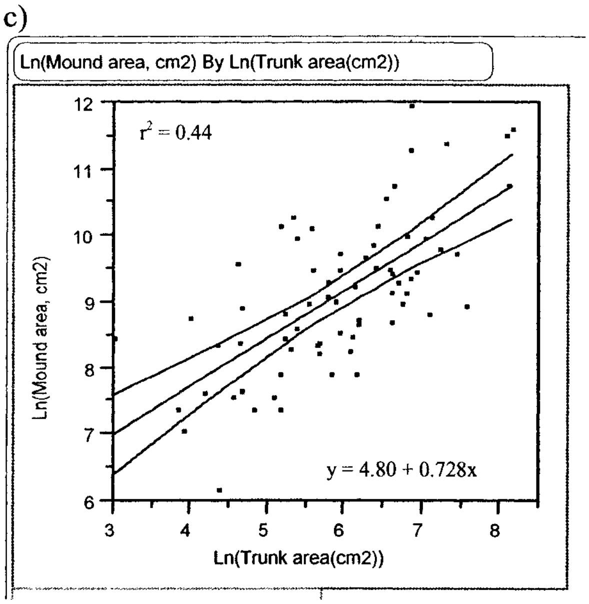
a)


Ln(Mound vol, cm3) By Ln(Trunk area(cm2))
r² = 0.53
y = 6.28 + 1.068x
Ln(Mound vol, cm3)
Ln(Trunk area(cm2))

b)



c)



d)

Figure 2. Graphs show the results of simple linear regression models using tree basal area to predict (a) mound volume of 132 freshly uprooted mounds measured in Puerto Rico, (b) mound volume of a plot-based subsample of 72 mounds, (c) mound area of 132 freshly uprooted mounds, and (d) mound area of a plot-based subsample of 72 mounds. Details on equations are given in Table 4.

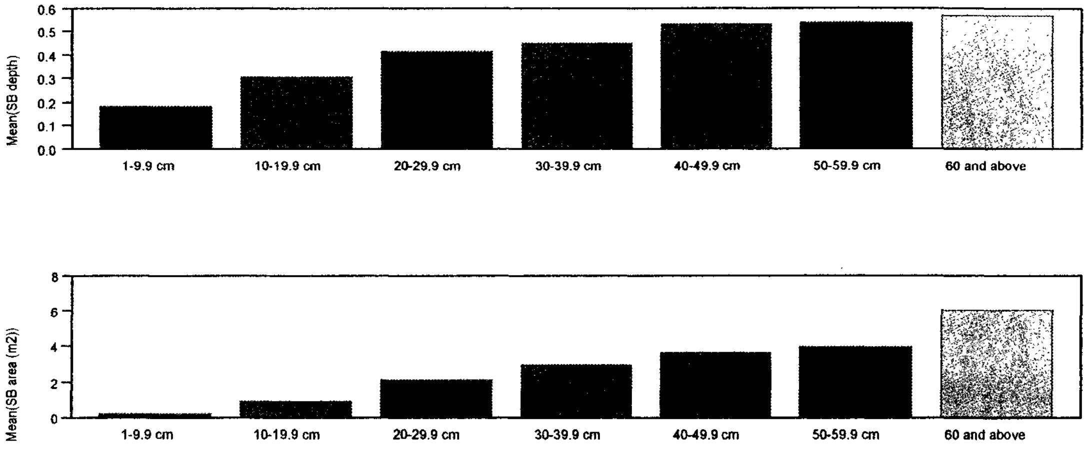


Figure 3. Mean mound thickness (comparable to pit depth), top, is less consistently affected by tree size than mound volume, below. The results here are from the expanded data set of 132 freshly uprooted mounds measured in Puerto Rico.

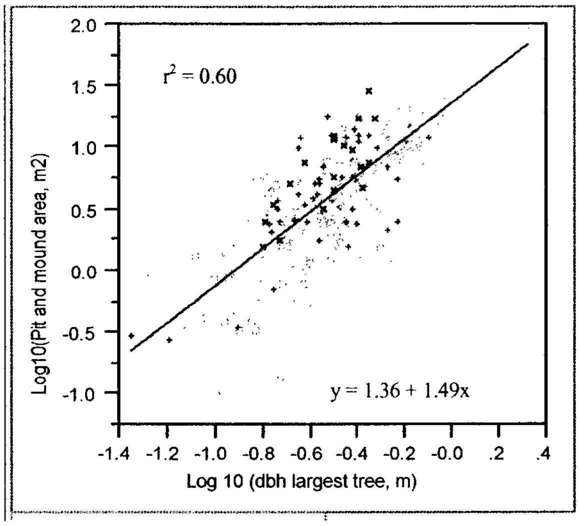


Figure 4. A simple linear regression using tree diameter to predict combined mound/pit area for individual uproots. Squares represent plot samples and crosses represent non-plot samples from this study, Xs represent sample points from the 1989 Hugo study, and triangles represent sample points extracted from Putz (1983).

APPENDIX B -- MOUND AND PIT FORMATION AND DECAY IN THE SANGRE DE CRISTO MOUNTAINS, COLORADO

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Abstract

A complex of soil, rocks, and roots is lifted to the surface when a tree falls by uprooting. Models to relate the dimensions of mounds and adjacent pits to the sizes of uprooted trees were developed for a site in the Sangre de Cristo Mountains, Colorado. The study was designed to identify the fate of components of the uplifted soil by monitoring changes in mound and pit characteristics during periods of up to 2 years; tree-ring crossdating of toppled trees was used to date mound/pit complexes of various ages to estimate century scale change. Using a decay-rate approach for mounds and pits, results indicated that roughly two-thirds of the sediment eroded from mounds typically returns to pits, the remainder moving downslope.

Keywords: Mound, pit, uprooting, soil disturbance, coniferous forest, Sangre de Cristo Mountains, Colorado.

1. Introduction

The uprooting of trees is the most obvious form of floralturbation (Schaetlz et al., 1989), and is the greatest biotic influence on sediment movement (Mitchell, 1988). Uprooted trees bring buried material to the surface, including nutrients (Armson and Fessenden, 1973; Basevich, 1982), soil-organic carbon, and lithic clasts, exposing them to atmospheric and surficial processes. Few studies have examined in detail the quantity of soil material unearthed by freshly uprooted trees or the decay sequences of mound/pit complexes, despite its importance to soil and ecological processes. This study, in a montane forest in the Sangre de Cristo Mountains of Colorado, USA, provided an opportunity to measure and model mound-and-pit formation at the individual tree level, and to consider short-term and long-term decay rates of mounds and pits. Short-term rates were estimated by monitoring pit deposits of eight trees during 1- and 2-year periods. Long-term rates were estimated by comparing trends in linear-regression models using 50 mound/pit complexes that were dated using dendrochronological techniques.

Because this study focuses primarily on mounds, and secondarily on pits, the nomenclature “mound and pit” is used rather than the more conventional “pit and mound.” Here, “mound” refers to the disturbed soil, roots, and rocks that are uplifted by a fallen tree, and includes the freshly uprooted variety (sometimes known as earth balls, rootballs, or root plates) as well as older examples. “Pit” refers to the adjacent depression left by the uprooted tree. Only mound/pit complexes that contained obvious remnants of uprooted trees were considered in this study.

The objective of the study was to consider potential influences on the sizes of mounds and pits, to document their longevity on the landscape in a montane environment of Colorado, and to develop an understanding of the sequences of their decay. An intention was to obtain information contributing to the understanding of how the uprooting of trees affects sediment yield of a watershed.

2. The study area

The study site, in the Sangre de Cristo Mountains of southern Colorado, is in a subalpine forest at about 2930 m a.s.l. The study area is within 30 ha of privately held land bordering the San Isabel National Forest, about 15 km south of Westcliffe, Colorado (Fig. 1). Dominant species at the site include Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), and white fir (*Abies concolor*), whereas limber pine (*Pinus flexilis*), Colorado blue spruce (*Picea parryana*), and subalpine fir (*Abies lasiocarpa*) occur less frequently. The climate is cool, with mean monthly temperatures in Westcliffe (elevation 2405 m) ranging from -5.3° C in January to 17.3° C in July (National Climatic Data Center, 1961-1990). Annual precipitation in Westcliffe averaged 400 mm, and ranged from 200 mm to 750 mm, for 1934 through 2002 (Wet Mountain Tribune, 1934-2002). Although snow pack may have a more important role at the higher altitude of this research site, in Westcliffe two-thirds of precipitation occurs in the relatively warm months of April through September (National Climatic Data Center, 1961-1990). At the site, it is not unusual to see hail in July (personal observation).

The landscape includes upland valleys that trap fine-grained, organic-rich alluvium, slopes and ridges of bedrock veneered by thin soils weathered from sandstone and conglomerate of the Sangre de Cristo Formation, and slopes of glacial till (boulders and cobbles with interstitial gravel and fines). "Till" in this paper will always be used in a glacial context. The path of glacial movement through the research site during the Wisconsin Glacial Stage (Peterson, 1971) determined the present position of Middle Colony Creek, as shown by deposits of till adjacent to and underlying the stream bed. Some of the bedrock area has a surface layer of sandy colluvium, typically less than 1 m thick.

Soils on bedrock and glacial till at the research site were identified as part of the Sangre de Cristo Soil and Ecological Unit Survey for Middle Colony Creek, San Isabel National Forest (USDA Forest Service, 2002). The bedrock area mostly has Ula soils, which are well-drained, fine-grained loams that form in residuum and colluvium derived from sandstone, and Bowen soils, dark reddish-brown gravelly sandy clay loams formed in residuum derived from sandstone, with included area comprising the remainder of the map unit. Effective rooting depth is 1m or slightly more.

Soils in till are largely loamy skeletal Typic Cryoboralfs from the Leadville Family that, in the Middle Colony Creek Basin, form in glacial deposits derived from sandstone and conglomerate beds of the Sangre de Cristo Formation. Leadville soils tend to be deep and well-drained, with a 1 to 3% surface cover of stones. Effective rooting depth is about 1.5 m. Both soil types, which also predominate in the San Isabel National Forest mapping unit directly west of the research area, are associated with Douglas-fir, white fir, ponderosa pine, and, to a lesser degree, aspen. Aspen is generally most prevalent at moist sites on alluvium deposited by overland flow and ephemeral streams.

Previous land use at the site has included logging, although there is no evidence for clear-cutting. About three-fourths of trees sampled in a 1986 study had established prior to the last logging episode of the 1930s (McConnell, 1988). Selective logging and the subsequent creation of forest gaps, as reported by McConnell (1988), affected tree density and species composition in ten 0.01-ha plots of the logged forest of the research site. The plots had a higher density of trees and a greater abundance of aspen and white fir than did eight 0.01-ha plots in a nearby undisturbed stand of trees in the San Isabel National Forest.

3. Methods

3.1. Field methods

Mound/pit complexes were measured in the three types of substrates within the study area; 70% of the complexes were in areas of bedrock, 18% were in till, and 12% were in alluvium. The latter were in upland valleys of convergent flow, those in till were in gently sloping areas bordering Middle Colony Creek, and those in bedrock areas were on interfluves and adjacent ephemeral-runoff conduits. About 86% of the mound/pit complexes studied either were in a 1-ha transect (500 x 20 m) that was established in 1998, or in one of five 50 x 10-m quadrats established in 1999 to provide greater sampling coverage of till and to include mounds formed in alluvium. The remaining 14% were from a bedrock ridge containing numerous freshly uprooted trees.

Most mound/pit complexes were related to the most similar shape (ellipse, half-ellipse, triangle, rectangle) or occasionally the combination of two shapes, for which the appropriate dimensions were measured and an approximate area computed. The resulting value for area was multiplied by the average "thickness" of the mound or the depth of the pit to obtain volume estimates. If the mound or pit shape was irregular, measurements were taken at 0.2-m intervals for width, length, and depth of pits, and width, length, and height of mounds, and the averages of the axes were multiplied to obtain estimates of volume. Other information assessed during the survey of each mound/pit complex included species and diameter of the uprooted tree, bole length, decay class of the bole (Table 1), treefall direction, tree slope, ground slope, general hillside aspect, and substrate type. Species were identified at the site or by microscope based on the anatomy of a wood sample. Ponderosa and lodgepole pines cannot be distinguished by their wood anatomy alone (Schweingruber, 1993), but it was possible to distinguish them based upon their bark and distribution. Spruce and fir wood anatomy also appear similar under a microscope. Consequently, all spruce and fir trees were identified as white fir, except for one spruce that had been identified as such in the field. The decision to identify ambiguous "spruce-fir" trees as white fir was based on an abundance of fir trees relative to spruce. For example, McConnell (1988) surveyed 56 white firs and 3 spruces in a 0.1-ha plot near this site.

3.2 Dendrochronological methods

This paper reports results for only those mound/pit complexes containing trees for which reliable death dates could be determined using crossdating and related techniques of dendrochronology. Cores, wedges, and/or cross-sections were sampled from trees, surfaced with a series of progressively finer sandpaper grades ending in either 600-grit or 15-micron. Aspen samples were finished with a 15-micron abrasive, which was used also for apparent suppression periods in many conifer samples. Ring widths were measured to an accuracy of 0.01 mm with a Henson incremental measuring machine connected to the TRIMS computer program. Samples were dated, through visual crossdating and by using the computer program COFECHA (Holmes, 1983), by comparing the ring-width series to a chronology developed from 12 living Douglas fir trees from the site. COFECHA identifies the best correlations to the live-tree master chronology for 50-year segments along the ring-width series produced for each uprooted tree. These correlations were compared to visual inspections of the plotted tree-ring series to ensure that the projected death dates lined up narrow rings in the expected pattern. At this site, almost all trees (of the live and dead ones sampled) contained narrow rings in 1893, 1902, and 1934, relative to neighboring rings. Five of seven uprooted aspen trees in the study were alternatively dated by ring-counting forward from "marker years" that had been previously identified in the absolutely dated cores from living trees. At this site, these markers consisted of lighter-colored rings in 1873, 1879/1880, and 1945. The bleaching results from defoliation (Hogg, 2002a), typically from pest infestation or possibly drought (Hogg, 2002b). Verification using two uprooted aspen that retained green leaves indicated this method could be reliable only to about 2 rings years per century. The accuracy of death dates for other species varies from 0 years for undecayed samples with excellent correlation with the living chronology (up to $r^2 = 0.76$), to an estimated 20 years for samples with decayed outer rings or extreme growth suppression at the end of the tree-ring series (Appendix D, Table 3). This rough estimate for decayed outer rings is based on the finding by Mast and Veblen (1994) that the maximum number of rings eroded from samples without bark, compared to samples with bark from the same tree, was 2 to 9 years for spruce and 2 to 8 years for fir. In this study, 86% of the dated trees contained bark or bark remnants. Error resulting from growth suppression is more difficult to estimate; one Douglas-fir at the site apparently stopped producing detectable annual rings mid-stem about 14 years before it fell over, yet it retained green leaves when initially surveyed. In all cases except where uprooted trees remained alive at the time of survey, it is possible that death of the tree preceded its uprooting, and thus mound formation, by one or more years. Also, it is feasible that a few uprooted trees maintained enough viable roots to sustain themselves for a year or more after mound formation. There was no evidence of resprouting among any of the downed trees.

3.3 Soil bulk-density methods

Soil bulk density for the site was estimated based on three 0.5-m profiles, two in bedrock soils and one in till. For each profile, soil samples at three levels were collected from a dug pit: 0 to 0.1 m, 0.1 to 0.3 m, and 0.3 to 0.5 m. An attempt was made to remove soil without clasts in the form of a rectangular solid, after which water was poured from a calibrated beaker into a plastic bag fitted into the rectangular void (using a board for the fourth side) to approximate the volume of the harvested soil. The samples were dried at 65° C to a constant weight. The nine values were averaged to estimate a mean bulk density (1.04 g cm^{-3}), which was used to convert soil weights into volumes (section 3.4).

To compare bulk densities of the upper soil layers with those of earlier pits, a paired-sample test was conducted. Three cores were taken from the top 0.1 m of 10 older pits that were identified from root remnants and sometimes by a decaying bole. Another three cores were taken from the top 0.1 m of an apparently undisturbed patch of soil within 1 m of the pit. Following drying and weighing, bulk densities of the two suites of samples were computed and compared in a paired *t*-test.

3.4 Monitoring methods

A subset of mound/pit complexes, eight of which were successfully dated, was monitored for inter-annual change. Pits, the bottoms of which had been lined with cement, plastic, or newspaper to identify material re-entering the pit, and mounds were re-measured either one or two years following the initial survey. Deposited material was air-dried and weighed after being divided into soil, wood/branches, leaf litter, and rocks. Subsamples of soil, wood, and litter were oven-dried at 65° C to constant weight to provide conversion factors for air-dried samples. Sample weights were converted to volume using techniques relevant to the material. Soil dry weight was converted to volume using a bulk density of 1.04 g cm^{-3} (using methods described in section 3.3), so volumes are based on the undisturbed bulk density of soil. Wood/branch dry weight was converted to volume using the average specific gravity, 0.48 g cm^{-3}, of three conifer species (*Pseudotsuga menzisii, Pinus ponderosa*, and *Pinus contorta*) reported by Schweingruber (1993). A conversion factor of 0.18 g cm^{-3} was developed for leaf litter by cutting a subsample of needles into roughly 1-cm pieces and packing them tightly into a container of known volume for weighing. Large rocks that fell into monitored sections of the pit were measured in three dimensions to compute an estimate of clast volume. Small rocks that were collected with the soil and later sorted out were weighed, and their volume was estimated using a standard rock density of 2.65 g cm^{-3}.

A conversion factor, the reciprocal of the fraction of a pit that was covered by cement, plastic, or paper, was applied to the material collected from the pit to estimate the amount of refilling. Change in mound volume was estimated by subtracting from the initial mound volume the product of the pit conversion factor and the sum of the annual values for deposits of soil, wood and rocks, using the assumption that the material fell from the mound into the pit. Change in pit volume was estimated by subtracting from the initial volume the product of the pit conversion factor and the sum of the annual values for eroded soil, wood, clasts, and litter.

3.5 Statistical methods

Data were analyzed using the JMP computer software developed by the SAS Institute Inc. (Sall and Lehman, 1996). An alpha level of 0.05 was set to test statistical significance of results. With log-transformations, an "x + 1" approach was used if necessary, except when determining long-term decay coefficients for mounds and pits. Tree diameter was converted to tree basal area by computing for the area of a circle [$\pi(½d^2)$, where d = diameter in m]. When multiple trees formed one mound, values for tree basal areawere summed, and the species of the largest tree was used. Multiple Linear Regression (MLR) models employing the method of least squares were used to test the influence of a variety of parameters on mound and pit sizes. Coefficients are given in tables to include 95% confidence intervals and cumulative r^2. The results take the form of: Response variable = Intercept + Slope (Parameter_1) + Slope (Parameter_2) … + Slope (Parameter_n). Using Table 2 as an example, the equation would look like: Ln(Mound volume, m^3) = 0.94 + 0.899Ln (Tree basal area, m^2) + 1.636 if in till + 1.703 if in alluvium + 1.194 if on a ridge.

Parameters used in the initial step of stepwise approaches to consider influences on mound and pit volumes included tree height (bole length, m), tree basal areas of a mound (transformed using the common log), the number of trunks in a mound, ground slope (degrees), tree species (Douglas-fir, ponderosa pine, white fir, lodgepole pine, or aspen), years since the death of the most recently deceased tree in a mound (transformed using the common log), topography (ridge or valley, with slope as the reference level), substrate type (till or alluvium, with bedrock as the reference level). The reference level is an arbitrary designation in a statistical model; it is the subcategory to which other subcategories in a category are being compared (Ramsey and Schafer, 1997, pp. 237). For example, when one indicator variable identifies ridges, and a second identifies valleys, those that are not specifically identified with topographic indicator variables are slopes, making slope the reference level. Parameters were included in a standard least squares model if they were statistically significant at the set alpha level. In addition to stepwise testing, parameters were tested individually in MLRs, along with tree basal area and presumed mound/pit age, for influence on mound volume. Tree basal area, representing tree size, was crucial to considering mound size in related research (Appendix A).

Negative exponential decay models were developed to consider decay rates of mounds and pits (i.e., decay of mound, infill of pit). The model of decay used is based on one described in Olson (1963), where the fraction remaining, X, of the initial volume, X_0, can be expressed as:

$$\text{natural log} (X / X_0) = - k t \qquad (1)$$

The values of *k* are the slopes from the simple linear-regression equations using time (years, untransformed) to predict the fraction of remaining mound or pit volume {Ln[(Remaining volume at *t*)/(Initial volume at t_0)]} (Olson, 1963). This decay model was selected to facilitate comparisons because there are published *k* values for wood decomposition (Fahey, 1983; Harmon et al., 1995). The higher the value of *k*, a dimensionless exponential decay coefficient, the more rapidly a feature is likely to decay.

To calculate short-term *k* values, data from the eight monitored mound/pit complexes were analyzed. The material falling into pits was used to estimate change in the volumes of mounds and pits (section 3.4), with the period between the lining of a pit and and the extraction of material from it representing time (0.88 to 1.94 yr). To calculate long-term *k* values, the data set of 50 mound/pit complexes was used, with time represented by the number of years since presumed mound formation (i.e., the death of the most recently deceased tree). To estimate volume changes, sequential steps were taken (separately for mounds and pits):

1) Mounds or pits older than 3 years were excluded from the data set.
2) A stepwise approach was used to develop an MLR model to predict mound (n = 23) or pit (n = 24) volume (Tables 2, 3).

3) The model was used to predict the natural logs of mound or pit volumes as if they were fresh. The antilog of the predicted value was considered a best estimate of the initial mound or pit volume.
4) The "actual" measured volume of a mound or pit was divided by the predicted "initial" volume of the mound or pit to yield a value for the "fraction remaining" of mound or pit volume. Mounds or pits for which the measured volume exceeded the predicted volume were given a value of 1 for "fraction remaining," while those with no remaining volume were given a value of 0.0001.
5) A simple linear-regression model was created using "time" (years since presumed mound/pit formation) as the explanatory variable and the natural log of the "fraction remaining" as the response variable.
6) The slope of the line was interpreted as representing the exponential decay coefficient, k (Olson, 1963), at the century scale.

4. Results and discussion

4.1 Modeling mound and pit size

Tree basal area and time were, as expected, influential in predicting mound and pit dimensions. These two variables were most predictive of mound area ($r^2 = 0.48$) and pit area ($r^2 = 0.45$) and less predictive of mound and pit volumes, mound thickness, and pit depth in Multiple Linear Regression (MLR) models (Table 4). In one analysis, time had no statistically significant ability to predict pit volume at the assigned alpha level when tested with trunk area, given the restriction of using only mound/pit complexes for which reliable dates of tree death could be determined (Table 4). It is assumed, however, that time would have tested as significant in all cases if more mound/pit complexes with trees in decay classes 3, 4, or 5 had been dated (Table 1).

A negative correlation occurred between time (years since death) and tree basal area. The correlation coefficient was low ($r^2 = 0.103$) but significant ($p = 0.02$). It is possible that the trend indicates decay of outer wood for trees on older mounds (which would yield erroneously old ages of the mound/pit complexes), but this possibility seems unlikely because most of the dated trees contained remnants of bark. More likely, the negative correlation coefficients are a result of small sample size ($n = 13$ for mounds dated older than 20 years).

When predicting mound volume, mounds in alluvium tended to be larger than those in bedrock or till, both when substrate was tested independently with tree basal area and time ($p = 0.0033$) and when tested in a stepwise approach (Table 5). Species, topography, and tree slope had no demonstrable effect on predicted mound volume when tested independently with tree basal area and years since tree death. Ground slope had a borderline effect in increasing predicted mound size when tested with tree basal area and years since death ($p = 0.0600$). Tree height proved influential in a stepwise approach to modeling mound volume (Table 5). The influence of tree basal area on predicted mound volume was negligible when the parameters in Table 5, such as time, were included. Mounds formed when the dominant tree was aspen, the only broadleaf species in the study, tended to be smaller than mounds formed by conifers when modeled with other parameters using the stepwise approach (Table 5).

When the eight mounds formed in alluvium are excluded from the data set, the resulting stepwise model to predict mound volume (Table 6) includes only one term in common with the MLR model for the full data set: time. Without the influence of the large mounds in alluvium masking other factors, the positive correlation between tree basal area and mound volume became significant, as expected. Positions on ridges, and complexes related to ponderosa pine trees also had a positive influence on predicted mound size. The influence of a ridge position, however, should be viewed with caution because it involved selected mounds as opposed to mounds that were in plots. In addition, four of the seven mound/pit complexes designated as Ponderosa-formed contained other trees as well.

A different set of variables influenced the prediction of pit volume in a stepwise approach to an MLR model (Table 7), with the similarities being that tree height proved influential in a stepwise approach to modeling pit volume as well (Table 7) and pit volume was positively correlated with alluvium. Aspen had no detectable influence on predicted pit volume, whereas pits formed by lodgepole pines tended to be larger than those formed by other species. Time had no statistically significant influence on pit volume, as with the MLR model for pit volume described in Table 4. As was the case with mound volume, excluding mound/pit complexes based in alluvium changed the model for pit volume (Table 8). Given this exclusion, the best-fitting MLR could predict about 55% of the variation in pit volume using tree height, the number of tree trunks in the mound, topography, and an indicator identifying when the dominant tree was aspen (stepwise approach, MLR). Both ridges and valleys exerted a positive influence on pit volume, and the aspen indicator was negatively correlated with pit volume, as it was in the full model predicting mound volume (Table 5).

In the MLR full model and the models using tree basal area and time to predict mound volume, the volumes of the five largest mounds are above the 95% confidence interval of the regression line fit. All were surveyed within three years of tree death and presumed mound formation, and four of the five mounds contained more than one tree, with two containing four trees, and the fifth was created in alluvium by a 73-cm diameter, 28-m tall lodgepole pine. That data from these mounds conform less well to the linear regression model indicates that summing tree basal areas does not fully account for the influence of toppled clusters of trees. It could also mean that tree size may affect mound size more than is suggested by the MLR equation of this data set, in which the mean diameter of the largest tree per mound is 33.6 cm (95% confidence interval, 29.8 to 37.4 cm). When tree height and number of tree trunks per mound are included with tree basal area and years since death in a MLR model predicting mound volume, both have a statistically significant positive influence on mound volume ($p = 0.0215$ and 0.0335, respectively).

4.2. Modeling mound and pit decay

The short-term exponential decay coefficient, *k*, was 0.031 for mounds and 0.068 for pits (Fig. 2), which was computed using the approach described in section 3.5. This is *k* in Eq. (1), which can be rewritten as:

$$X / X_0 = e^{-kt} \qquad (2)$$

in which X is the remaining mound or pit volume, X_0 is the initial mound or pit volume, and *t* is years. In both cases, the probability is high that the intercept was zero ($p = 0.4113$ for pits, $p = 0.2986$ for mounds), whereas the decay rates for mound and pit volumes were significantly different from zero ($p = 0.0126$ for pits, $p = 0.0222$ for mounds).

Using the full data set to estimate century-scale decay rates resulted in *k* values of 0.078 for mounds (Fig. 2c) and of 0.029 for pits (Fig. 2d). Both slopes were significantly different from zero ($p < 0.0001$ for mounds, $p = 0.04$ for pits) and both intercepts were also significant ($p = 0.03$ for mounds, $p = 0.02$ for pits). The long-term decay coefficients indicate that mounds are reduced to 50% of their initial volume in about 9 years and to 10% of their initial volume in about 30 years, whereas the corresponding reductions for pits are 50% in about 24 years and 10% in about 78 years.

Detecting change in mound size from one year to the next using only field measurements of area and volume was not possible given the methods and time scale used in this study. Measurements made with a meter stick or diameter tape are reliable only to about 0.05 m in any dimension. This level of accuracy means that the error of the measuring technique (e.g., confidence intervals of 0.86 m^3 to 1.16 m^3 for a 1-m^3 mound) surpasses the expected change in mound volume of about 2% per year based on the material collected from adjacent pit (e.g., confidence intervals of 0.97 to 0.99 m^3 yr^{-1} for a 1-m^3 mound). Because of this, all short-term decay estimates are based only on the material collection method.

Before interpreting the different decay coefficients, effects related to measuring technique must be considered. First, short-term rates might be close to initial decay rates in some cases because six of the eight monitored complexes were dated at 3 yrs when monitoring began (Fig. 3). Second, a higher short-term rate for pit decay than mound decay was guaranteed, all else being equal, by the method, which involved using only a portion of the pit material to model mound decay but using all the pit material to model pit decay. Finally, the short-term pit decay rates might be overestimated by the pit conversion factor. To be consistent, the quantity of material collected was multiplied by the reciprocal of the proportion of the pit monitored (the pit conversion factor). Those sites most likely to trap sediment, however, were also the sites most likely to be selected for monitoring. Perhaps as a consequence of this approach, the mound/pit complexes with the highest conversion factors tend to show the greatest rates of change (Table 9). This potential overestimation is probably not a problem for mounds because the short-term decay rate does not include material that migrated from the mound to elsewhere on the landscape, i.e., outside of the pit.

The short -term decay coefficient for mounds is lower than the long-term coefficient, whereas the reverse is true for pits. Also, the short-term coefficient, k, for mounds is less than half that of pits, whereas the long-term rate is more than double that of pits. However, it seems likely that the pattern shown by the pits, of rapid short-term decay followed by slower long-term decay, probably is real—but for mounds as well as pits. In other words, the differences provide evidence that not all of the material eroding from the mound falls into the adjacent pit.

A pattern of more rapid short-term decay than long-term decay for the studied mounds and pits is evident when volume of mounds and pits are considered by age (Fig. 3). Leaf litter also tends to decompose most rapidly immediately after deposition, suggesting that leaching of organic litter is most intense initially (e.g., Harmon et al., 1990). Mounds too may erode most rapidly immediately after formation but stabilize as gravity helps to settle loose soil and rock fragments. A similar pattern is anticipated for pits, with mound material comprising most of the initial infill and leaf litter supplying increasing proportions of the infill with time. Evidence for this conjecture is that leaf litter and other low-density material appear to be most abundant at the surface layer of partially filled pits. In this study, root remnants were used to identify old pits at which bulk density of the near-surface layer could be compared to apparently undisturbed soil. The difference in bulk density of 0.15 g cm^{-3} for the top 0.1 m of former pits was significantly lower (about 77%) than that of soil sampled within 1 m of pit boundaries ($p = 0.006$, one-sided paired t-test). In two studies that involved dissecting and mapping soil-profile sections of old mound/pit complexes, researchers found organic O and A soil layers in the pits on top of the E layer, whereas mounds contained much thinner O and A layers atop a thick, complex B horizon (Schaetzl and Follmer, 1990; Veneman et al., 1984).

Applying the long-term trend of more rapid decay of mounds than of pits to short-term mound and pit decay suggests that only part of the material eroding from the mound reaches the adjacent pit. Disturbed sediment was detected directly downslope at five of the eight monitored mound/pit complexes (Table 9). The measured volume of these deposits in all cases was equal to or greater than the annualized quantity of mound material deposited in the adjacent pit. At the oldest mound/pit complex (10 years at the start of monitoring), the downslope deposit was about 20 times greater than the estimated annual volume of material in the adjacent pit. In addition, five erosion pins in the alluvium-based pit documented an average loss of 4.2 cm yr^{-1} (S.E. of 0.50) and three pins immediately downslope of the pit registered mean deposition of 0.8 cm yr^{-1} (S.E. of 0.47). The movement of sediment was caused largely by ground-water seepage into and from the pit, but the example demonstrates that soil eroded from mound/pit complexes may be deposited within a short distance.

Other evidence that not all mound material refills the pit is found in a series of simple regression analyses (Table 10) for volume data from dated mound/pit complexes. The ratio of the volume of pit sediment to mound volume is small initially, after formation of the mound/pit complexes. The ratio reaches 1.0 for complexes older than 15 years and increases much more for complexes older than about 20 years, the result of mounds being removed by erosion. It should be noted that a mound was considered to be without volume if soil was no longer attached to roots, even if roots remained, whereas roots had contributed to mound volume when still integrated with soil. However, pits seem unlikely to receive additional mound material once only decay-resistant roots remain. Other studies also have found that mounds tend to erode more rapidly than pits fill (Lyford and MacLean, 1966; Cremeans and Kalisz, 1988; Schaetzl and Follmer, 1990).

Although direct measurements of the quantity of material eroded from the mound are not available, comparisons of *k* values for erosion of mounds and filling of pits may permit estimates of the proportion of material that erodes from the mound without falling into the pit. Considering that the long-term rate for filling of pits is about 37% of that for mound erosion, it is inferred that roughly two-thirds of the eroded mound sediment does not re-enter the pit. This is more than the 50% assumed by Denny and Goodlet, 1956, and Mills, 1984 for their estimations of sediment movement from mound/pit formation.

At the relatively dry and temperate study site near Westcliffe, rates of mound erosion and pit filling appear to be greater than rates of wood and root decay. The observation that exposed roots are often the only evidence of an old mound/pit complex is consistent with comparison of *k* for mounds and pits with those for wood at another high-altitude temperate site. Fahey (1983) reported *k* decay coefficients for lodgepole pine in

Wyoming ranging from 0.012 to 0.020, much lower than the long-term decay coefficients for mounds and pits determined in this study. Similarly, tree-ring-dated logs of lodgepole pine and Englemann spruce were found to persist for at least 150 years in a subalpine forest of Colorado (Brown et al., 1998). The authors also note that they selected logs with "intact root masses and tip-up pits at the base," indicating they similarly observed that logs and pits persisted longer than mounds at their central Rocky Mountain site.

The finding here that mound/pit complexes are reduced to about 5% of their original size within a century (using the long-term *k* value for pits) contrasts with findings by other researchers that mound/pit complexes in North American forests persist for hundreds (Stephens, 1956; Lyford and MacLean, 1966; Beke and McKeague, 1984) or thousands of years (Schaetzl and Follmer, 1990). Cremeans and Kalisz (1988), however, found evidence for rapid decay of mound/pit complexes on the Cumberland Plateau of Kentucky in that mound-and-pit topography covered less than 3% of the surface. The results of our study suggest that roughly two-thirds of the soil eroded from the mound moves downslope. It also appears that these soil deposits often remain detectable on the landscape, at least in the short term. Given the generalization that about 10% of soil loss contributes to sediment yield (Meade and Parker, 1985; Meade et al., 1990), it seems unlikely that soil disturbance from uprooted trees has a measurable effect on sediment yield except perhaps shortly after a catastrophic uprooting event or when uprooting occurs along a riparian zone.

5. Summary

This study of mound/pit complexes in the Sangre de Cristo Mountains of Colorado used an observational approach to compare mounds and pits created by uprooted trees within the past century. The study sought to consider the fate of the uplifted soil and rock fragments by observing changes in mound/pit complexes over short and long time frames. The approach was to monitor for 1 to 2 years to estimate interannual change in recently formed mounds and pits, and to use tree-ring crossdating to date mound/pit complexes of a variety of ages and to estimate century-scale changes.

The effect of time on individual mounds and pits is more difficult to model than the initial volume of either. MLR models using only mound/pit complexes within about 3 years of their formation could predict 74% and 73%, respectively, of the variability in mound and pit volumes (Tables 2, 3), whereas the best models using mound/pit complexes of all ages predicted 63% and 54% of the variability in mound and pit and volumes (Tables 5, 6). Time and basal areas of tree trunks in the mound generally showed correlation with mound and pit volumes. Mounds on bedrock and till in this study tended to be comparable in size, but those formed in alluvium tended to be larger, when time and tree size were held constant. Variables other than time and tree size also correlated with mound and pit volumes. The effects of species varied, but conifers generally formed larger mounds than did aspen trees.

Pit volume tended to be smaller than mound volume initially, and the pit:mound ratio gradually decreased with time. Pits appear to persist on the landscape longer than do mounds, and the boles of fallen trees generally persist linger than both mounds and pits at the study site. Soil-based evidence of uprooting generally disappears within a century, leaving root remnants, possibly a decaying bole, and perhaps a circle of rocks as indicators of uprooting events. Short-term and long-term decay rates of mounds and pits developed for this study indicate that not all of the material eroded from a mound falls in the pit. Perhaps two-thirds of mound material moves downslope, but probably short distances, to sites still near the treefall. The findings suggest that tree uprooting is important to *in-situ* soil processes, and perhaps ecological processes (not addressed by this study), but that it plays a small role in sediment export from the watershed.

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Table 1. Five decay classes, modified from systems developed by Arthur and Fahey (1990) and Brown et al. (1998), were developed for this study. The tree with the most recent death per mound was used. Each tree was placed in one of the categories described below.

Decay class	**Description of Decay Class**	**No. trees in decay class**	**Mean no. years since death (S.E.)**
1	Leaves, either brown or green, remain on attached limbs	21	2.5 (1.8)
2	Most or all needles gone, small branches remain, 75-100% of bark remains, bole solid	15	12.7 (2.2)
3	Small branches gone, 50-75% of bark present, decay may be evident in bole	10	26.8 (2.7)
4	<50% bark present, bole decay evident, settling of stem and may grade to duff further down stem	4	75.3 (4.2)
5	All organic matter of tree, with possible exception of roots, grades into soil, but "imprint" of former tree still recognizable	0	---

Table 2. Multiple linear regression coefficients developed to predict Ln(Mound volume, m^3) using 23 mound/pit complexes dated at three years old or less. The adjusted r^2 (coefficient of determination) is 0.747 for the model. “Indicator” values mean the coefficient is used only if the parameter applies to the mound in question.

Term	**Coefficient**	**95% confidence interval for value**	***p***
Intercept	0.940	-0.135 to 2.016	0.08
Ln(Tree basal area, m^2)	0.899	0.492 to 1.306	0.0002
Till indicator	1.636	0.707 to 2.565	0.002
Alluvium indicator	1.703	0.893 to 2.513	0.0003
Ridge indicator	1.194	0.362 to 2.027	0.008

Table 3. Multiple linear regression coefficients predicting Ln(Pit volume, m^3) for 23 pits dated at three years old or less at the Sangre de Cristo site. The adjusted r^2 (coefficient of determination) for the full model is 0.801. "Indicator" values mean the coefficient is used only if the parameter applies to the pit in question.

Term	**Coefficient**	**95% confidence interval for value**	***p***
Intercept	0.302	-0.716 to 1.321	0.5
Ln(Tree basal area, m^2)	0.908	0.532 to 1.283	<0.001
#trunks/mound	0.405	0.095 to 0.715	0.01
Alluvium indicator	1.566	0.830 to 2.301	0.003
Broadleaf indicator	-0.707	-1.396 to -0.018	0.05
Ridge indicator	0.816	0.090 to 1.542	0.03

Table 4. Multiple linear regression coefficients predicting mound volume and pit volume for 50 pit-mound complexes measured at the Sangre de Cristo research site. In all cases, the *p* that the intercept is equal to zero is < 0.0001. r^2 = coefficient of determination.

Response (y)	**Intercept**	**95% confidence interval, intercept**	**Slope for Parameter$_1$, Log$_{10}$(Trunk area)**	**95% confidence interval, intercept**	***p* that slope is equal to zero**	**Slope for Parameter$_2$, Log$_{10}$(Number of years since tree death)**	**95% confidence interval, intercept**	***p* that slope is equal to zero**	**Adjusted r^2**
Log$_{10}$(Mound vol +1, m^3)	0.619	0.455 to 0.783	0.292	0.137 to 0.448	0.0005	-0.155	-0.240 to –0.070	0.0006	0.461
Log$_{10}$(Pit vol +1, m^3)	0.515	0.368 to 0.662	0.298	0.155 to 0.441	0.0001	-0.065	-0.141 to 0.011	0.0932	0.376
Log$_{10}$(Mound area +1, m^2)	0.878	0.660 to 1.095	0.352	0.146 to 0.558	0.0013	-0.245	-0.357 to –0.133	<0.0001	0.484
Log$_{10}$(Pit area +1, m^2)	1.005	0.771 to 1.240	0.528	0.300 to 0.756	<0.0001	-0.131	-0.253 to 0.009	0.0353	0.446
Mound thickness, m	0.571	0.406 to 0.736	0.143	-0.014 to 0.299	0.0721	-0.147	-0.232 to –0.063	0.0011	0.305
Pit depth, m	0.391	0.287 to 0.495	0.096	-0.007 to 0.198	0.0663	-0.063	-0.116 to –0.010	0.0210	0.221

Table 5. Multiple linear regression coefficients predicting Log_{10}(Mound volume +1, m^3) for 50 mounds measured at the Sangre de Cristo research site. Cumulative r^2 is shown in the last column. The adjusted r^2 for the full model, which corrects overestimates of predictive power that occur with each variable added, is 0.650.

Term	**Value**	**95% confidence interval for value**	**p that value is equal to zero**	**cumulative r^2**
Intercept	0.018	-0.150 to 0.186	0.8324	
Tree height (m)	0.019	0.010 to 0.028	< 0.0001	0.394
Log_{10}(Years since tree death)	-0.161	-0.232 to –0.091	< 0.0001	0.515
Alluvium indicator	0.224	0.123 to 0.32600	< 0.0001	0.622
Aspen indicator	-0.161	-0.276 to –0.046	0.0071	0.679

Table 6. Multiple linear regression coefficients predicting Log_{10}(Pit volume +1, m^3) for 49 pits measured at the Sangre de Cristo research site. Cumulative r^2 is shown in the last column. The adjusted r^2 for the full model, which corrects overestimates of predictive power that occur with each variable added, is 0.547.

Role of parameter	**Value**	**95% confidence interval for value**	**p that value is equal to zero**	**cumulative r^2**
Intercept	-0.224	-0.338 to 0.111	0.0002	
Tree height (m)	0.022	0.015 to 0.030	< 0.0001	0.403
Alluvium indicator	0.164	0.073 to 0.256	0.0008	0.532
Lodgepole indicator	0.136	0.008 to 0.265	0.0374	0.575

Table 7. Multiple linear regression coefficients predicting Log_{10}(Mound volume +1, m^3) for 42 mounds measured in bedrock and till at the Sangre de Cristo research site. Mounds in alluvium are excluded. Cumulative r^2 is shown in the last column. The adjusted r^2 for the full model, which corrects overestimates of predictive power that occur with each variable added, is 0.543.

Term	**Value**	**95% confidence interval for value**	**p that value is equal to zero**	**cumulative r^2**
Intercept	0.359	0.221 to 0.497	<0.0001	
Log_{10}(Years since tree death)	-0.096	-0.156 to -0.033	0.0041	0.260
Log_{10}(Trunk area, m^2)	0.171	0.053 to 0.288	0.0056	0.398
Ponderosa indicator	0.143	0.052 to 0.233	0.0029	0.481
Ridge indicator	0.162	0.055 to 0.267	0.0041	0.589

Table 8. Multiple linear regression coefficients predicting Log_{10}(Pit volume +1, m^3) for 42 pits measured in bedrock and till at the Sangre de Cristo research site. Pits in alluvium are excluded. Cumulative r^2 is shown in the last column. The adjusted r^2 for the full model, which corrects overestimates of predictive power that occur with each variable added, is 0.544.

Role of parameter	**Value**	**95% confidence interval for value**	**p that value is equal to zero**	**cumulative r^2**
Intercept	-0.166	-0.256 to –0.077	0.0006	
Tree height (m)	0.013	0.008 to 0.019	<0.0001	0.318
Aspen indicator	-0.166	-0.250 to –0.080	0.0004	0.436
No. trunks in mound	0.051	0.010 to 0.092	0.0159	0.502
Valley indicator	0.069	0.013 to 0.125	0.0174	0.545
Ridge indicator	0.086	0.007 to 0.165	0.0159	0.601

Table 9. Information on short-term mound and pit decomposition rates from monitored complexes is given below. All monitored complexes were dated to 1996 except for U12 (1988) and 0-11 (1994). In the first column, B refers to bedrock, and T to till.

Mound# (Substrate)	**Age (years)**	**% of pit monitored**	**Mound volume, initial (m3)**	**Change in mound volume (% yr-1)**	**Pit volume, initial (m3)**	**Change in pit volume (% yr-1)**	**Soil deposited downslope (m3)**	**Ratio of Soil deposited: Mound material collected (yr-1)**
U3 (B)	1.94	12.0	1.00	-4.7	0.69	-7.3	0.048	1.03
U6 (B)	1.92	17.6	0.52	-2.5	0.23	-9.3	0.038	2.95
U12 (T)	1.94	23.3	0.27	-1.9	0.19	-3.1	0.099	19.45
U26 (T)	1.94	8.1	1.30	-2.8	0.72	-7.3	0.368	10.09
U22 (B)	0.92	13.1	0.89	-3.6	0.91	-6.2	0.078	2.44
0-6 (B)	0.89	33.9	2.22	-1.1	0.96	-5.4	--	--
0-11 (B)	0.88	63.5	0.41	-0.6	0.20	-3.4	--	--
0-13 (B)	0.88	25.8	0.51	-0.9	0.22	-3.6	--	--

Table 10. Values for the slope of simple linear regressions correlating pit volume and mound volume. The slope is themean proportion of pit volume as it relates to mound volume. Differences relate to the pit-mound complexes that were tested, described in the first column. In all cases, the intercepts were considered indistinguishable from zero ($p > 0.05$) and so are not reported here. The r^2 value refers to the coefficient of determination.

Pit-mound complexes included in regression correlation	**Slope (i.e., ratio of pit/mound volumes)**	**95% confidence intervals for slope**	**p**	**n**	**r^2**
Monitored complexes	0.444	0.156 to 0.732	0.0092	8	0.704
All complexes dated to 3 years or less (except large lodgepole in alluvium, W13-U1)	0.343	0.168 to 0.217	0.0006	22	0.455
All complexes dated to > 3 years old	0.601	0.052 to 1.151	0.0333	26	0.175
All complexes dated at 15 years old or more	1.000	0.018 to 1.983	0.0464	19	0.213
All complexes dated at 20 years or more	3.280	1.620 to 4.941	0.0012	13	0.632

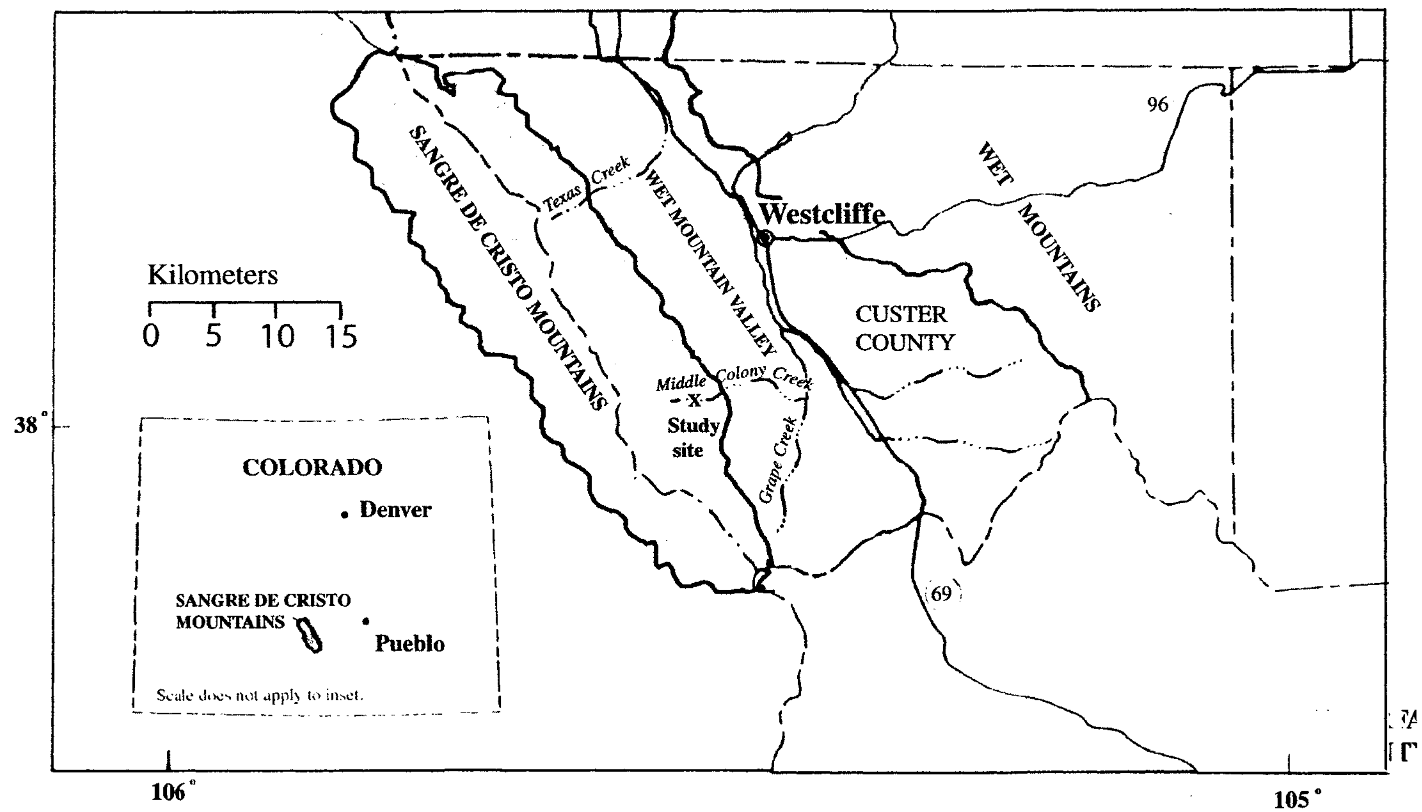
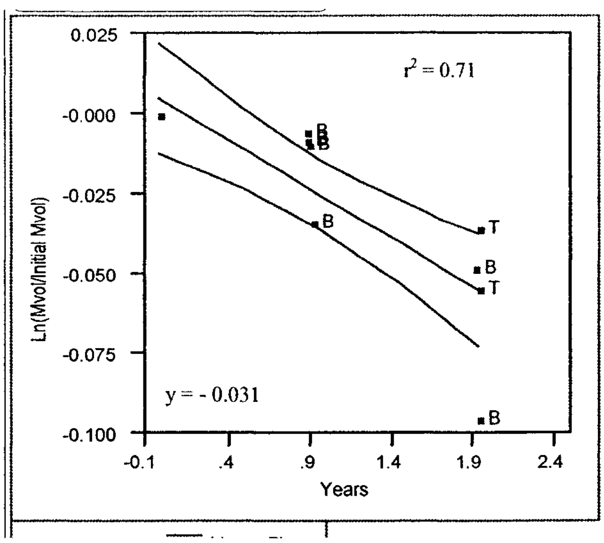
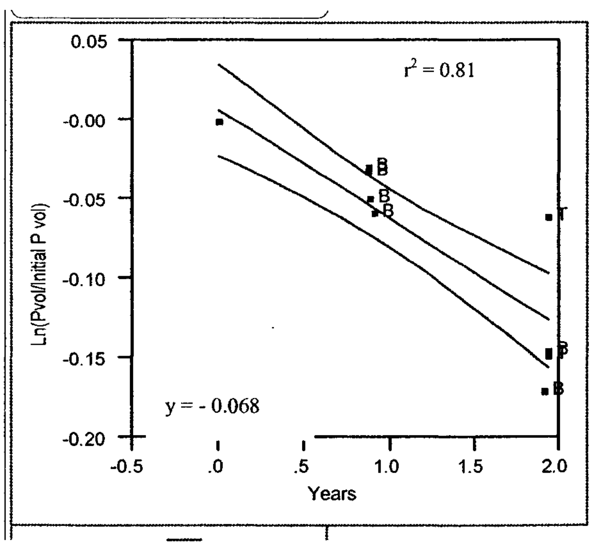


Figure 1. Map showing location of the study site in the Sangre de Cristo Mountains, south of Westcliffe, Colorado.



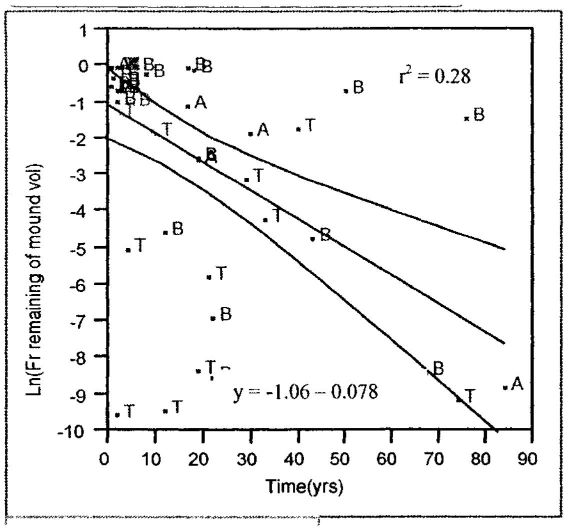
r² = 0.71
y = - 0.031
Ln(Mvol/Initial Mvol)
Years

a)

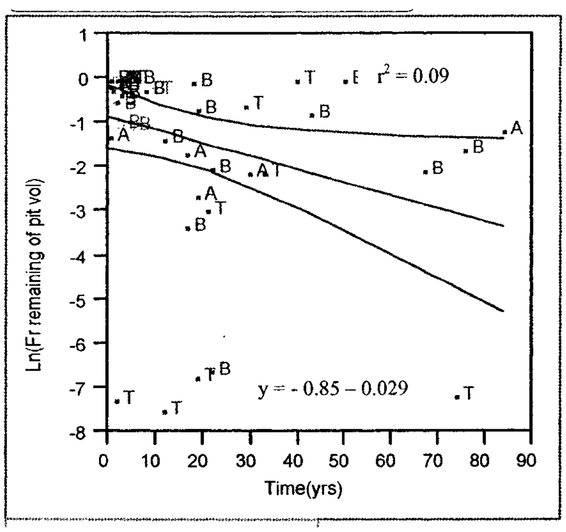


r² = 0.81
y = - 0.068
Ln(Pvol/Initial P vol)
Years

b)

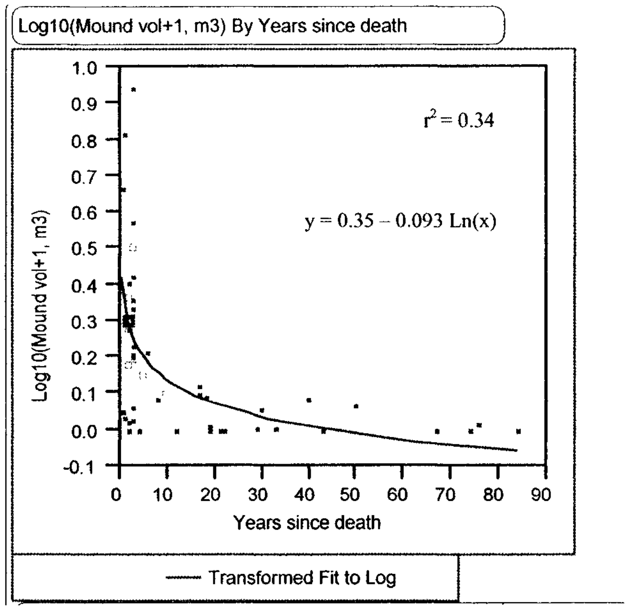


c)

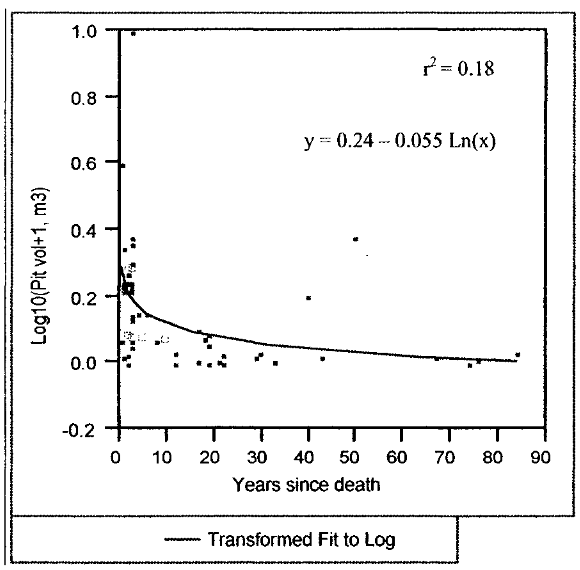


d)

Figure 2. Graphs showing *k* values (decay rates) for (a) short-term decay of mounds, (b) short-term filling of pits, (c) long-term decay of mounds, and (d) long-term filling of pits. The *k* values are the slopes of the respective lines. Data points are for bedrock (B), till (T), and alluvium (A).



a)



b)

Figure 3. Graphs relating the volumes of (a) mounds or (b) pits to the number of years since death of the uprooted tree(s) that formed the pits and mounds. Both variables are log-transformed. Open-squares indicate that the measured mound/pit complex was also monitored.

APPENDIX C – A COMPARATIVE STUDY OF SOIL DISTURBANCE AND FROM UPROOTED TREES AND MOUND AND PIT DECAY IN PUERTO RICO AND COLORADO.

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Abstract

The toppling of trees forms mounds of disturbed sediment and pits from which the mound removes sediment, rocks, and organic matter. Sites of uprooted trees in Puerto Rico and Colorado were examined (1) to compare areas and volumes of mounds and pits relative to tree size, (2) to compare areas and volumes of mounds and pits formed during catastrophic events at the landscape scale, and (3) to consider decay of mounds and pits after formation. For a given basal area, the analyses found no difference among sites in area and volume of freshly formed individual mounds and pits. For landscape-level catastrophic uprooting, the percent of toppled trees in a plot can explain 85% and 87% of the areas and volumes, respectively, of the quantity of soil uplifted. Exponential decay coefficients developed by monitoring mound/pit complexes indicate that mounds and pits at the humid tropical site in Puerto Rico decay in about 74% and 57% of the time, respectively, of mounds and pits at a temperate Colorado site. Decay coefficients developed for the Colorado site indicate that mounds and pits are reduced to 10% of their original volume within 30 and 78 years, respectively. Coefficients for Puerto Rico suggest that a similar reduction in volume requires 17 years, whereas pits generally fill within a decade.

1. Introduction

The study of mound-and-pit microtopography has interested scientists for at least 65 years (Lutz, 1940) because of its potential influence on soil formation, drainage patterns, and forest ecology. Treethrow may disrupt soil development, thereby increasing weathering processes and nutrient availability (Skvortsova and Ulanova, 1977; Collins and Pickett, 1982; Foster, 1988). It may be crucial to soil fertility, especially in temperate coniferous forests, where natural podzolization can reduce soil fertility in as little as 300 years (Bormann et al., 1995). Moisture is lower and photosynthetically active radiation values are higher in mounds compared to pits (Clinton and Baker, 2000). Some trees, such as *Cecropia peltata* in Puerto Rico, prefer to establish in pits (Walker, 2000). Mound microsites are preferred by other trees, such as red pines (*Pinus resinosa*) in New Brunswich, Canada (Lyford and MacLean, 1966), and sugar maple (*Acer saccharum*) and basswood (*Tilia americana*) in northeastern Wisconsin (Kabrick et al., 1997).

Despite the geomorphic, biological, and ecological importance of the uprooting process, empirical relations between the quantity of soil involved in mound-and-pit formation and decay that encompass more than one site have not emerged. The use of different measuring techniques, variations in mound/pit ages, and confounding factors such as soil type have impeded comparisons among sites. Researchers have examined a variety of factors for influence on mound or pit size, including mound shape (Beatty and Stone, 1986), restricting soil horizons (Mueller and Cline, 1959), landform position (Kabrick et al., 1997; Norman et al., 1995) and tree size, usually diameter (Mills, 1984; Putz, 1984;

Mueller and Cline, 1959; Peterson, 2000) but also biomass (Clinton and Baker, 2000). Mound and pit dimensions have been reported by length of axes (Kabrick et al., 1997) and by volume (Mills, 1984; Shubayeva and Karpachevskiy, 1983; Norman et al., 1995), but most frequently by area (Putz, 1983; Zimmerman et al., 1994; Cremeans and Kalisz, 1988; Peterson, 2000).

Mean mound and pit areas varied by site, ranging from 1.5 m^2 for pits of the Cumberland Plateau in in Kentucky, USA (Cremeans and Kalisz, 1988) to 16 m^2 for combined mound/pit complexes on Barro Colorado Island in Panama (Putz, 1983). Other estimates included: 11.9 m^2 for "soil disturbance" from 22 freshly uprooted maple and beech trees in Michigan (Brewer and Merritt, 1978); 8.8 $m^2$of "exposed soil and rock" per uprooted tree in the Luquillo Experimental Forest in Puerto Rico (Zimmerman et al., 1994); and 4.7 m^2 to 8 m^2, depending on mound type, for mounds in central New York forests (Beatty and Stone, 1986). Stephens (1956) estimated a mean area of about 7.6 m^2 per mound/pit complex in a 0.4-hectare (1 acre) tract of Harvard Forest in Massachusetts that included centuries-old complexes. Based on mounds estimated to be mostly 80 to several hundred years in age, Shubayera and Karpachevskiy (1983) concluded that uprooted trees in Siberia disturbed "as much as 5 m^3 of soil"; they found no evidence of mounds younger than 20 years. Lyford and MacLean (1966) assessed the number of mostly old mounds and pits and the proportion of the landscape occupied by each in forests of New Brunswick, Canada; results indicated mean mound and pit areas of 2.95 m^2 and 0.85 m^2, respectively.

The present study sought to find unifying or distinguishing relations between site variables and mound and pit size by applying consistent measuring and analytical techniques to disparate sites in two different mountain ranges in Colorado and across the island of Puerto Rico. The analyses focus on the quantity of soil disturbed by tip-ups at the individual tree level for all sites, and at the landscape level for two sites of catastrophic uprooting in Colorado and Puerto Rico. In addition, the dynamics of short-term mound and pit decay were considered in a 2-year study to monitor a subsample of mound/pit complexes in Colorado and Puerto Rico. Decadal-scale decay estimates were developed for a Colorado site using tree-ring analysis to estimate mound/pit formation dates, and annual-scale decay estimates were developed for Puerto Rico based upon the remeasurement of mounds known to have fallen in 1989.

2. Methods

2.1 Study sites and sampling technique

Two of the three study sites were in temperate mixed-conifer forest in Colorado, and the other was in tropical moist forest, with predominantly broadleaf trees, of Puerto Rico. The uprooted trees measured in Colorado's Routt National Forest and in Puerto Rico had been toppled during catastrophic windthrow events. The trees at the Colorado site in the Sangre de Cristo Mountains uprooted over several previous decades as dated by tree-ring analysis.

The Sangre de Cristo site was in about 30 ha of private land bordering the San Isabel National Forest. The elevation, about 2930 m, places the site in the distribution range for Douglas fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), Ponderosa pine (*Pinus ponderosa*), Englemann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) (U.S. Department of Agriculture, 2001), although lodgepole pine (*Pinus contorta*) and white fir (*Abies concolor*) were more common than spruce and subalpine fir. Annual precipitation in nearby Westcliffe averaged about 400 mm, and ranged from about 200 to 750 mm (Wet Mountain Tribune, 1934-2002). The study site has soils formed on bedrock and (glacial) till and organic-rich alluvium. Uprooted trees were surveyed along a bedrock ridge, in a 500 X 20-m transect that was established in 1998, and in five 50 x 10-m plots established in 1999 to increase sampling coverage of till and to include mounds formed in alluvium. Fifty mound/pit complexes containing uprooted trees successfully dated by tree-ring methods were studied for mound/pit formation and long-term decay. A subsample of eight mound/pit complexes was monitored to estimate short-term decay. A subsample of 24 mound/pit complexes with trees that had died within 3 years of the survey was used for comparisons of freshly uprooted mounds and pits. (For details of the study design, see Appendix B.)

The Routt National Forest site, in the Rocky Mountains, was part of 10,000 ha damaged in the Routt-Divide blowdown on 25 October 1997 at elevations between 2250 m and 3250 m (Baker et al., 2002). The blowdown appears to have occurred when the jet stream dipped toward the surface as it crossed the Continental Divide, then accelerated and reversed direction when trapped under a strong upslope easterly cold front (USDA Forest Service, 1998). Estimated wind speeds slightly in excess of 200 km hr^{-1} toppled up to 90% of trees in some areas (USDA Forest Service, 1998). The study site was west of the Mount Zirkel Wilderness Area and, like much of the blowdown forest, was dominated by subalpine fir (*Abies lasiocarpa*) and Englemann spruce (*Picea englemannii*). Weighted mean annual precipitation for the watershed is approximately 1000 mm, most falling as snow (USDA Forest Service, 1998). On the research site, soils on ridges and slopes are coarse-textured sandy loams and loamy sands with rock fragments derived from glacial deposits, whereas those in upland valleys are reworked, poorly drained alluvium (USDA Forest Service, 1998).

In Puerto Rico, a tropical Caribbean island at about 18.5° North and 67° West in the West Indies, study plots were distributed in secondary and primary forests. Mean annual rainfall on the island ranges from slightly under 1000 mm to slightly over 4000 mm (The Climate Source, 2002), and study sites spanned the precipitation range. However, about 67% of plots were in the forest type Ewel and Whitmore (1974) classified as wet forest under the Holdridge (1967) system, with between 2000 mm and 4000 mm annual rainfall. Surveying of uprooted trees within and outside of plots was done in the 3 months following Hurricane Georges, which on 21-22 September 1998 brought maximum sustained winds of 185 km hr^{-1} with gusts of up to 241 km hr^{-1} (Bennett and Mojica, 1998). Uprooted trees were in evergreen broadleaf forest of mixed species (including *Dacryodes excelsa, Cyrilla racemiflora, Sloanea berteriana, Inga vera, Swietiena* spp., and *Guarea* spp.), in stands of needleleaf trees (typically *Casuarina equisetifolia* or *Pinus caribaea*), and in palm forest dominated by *Prestoea montana*. Soils are predominantly clay, but include loams and sand, and varying levels of soil organic matter.

2.2 Comparison by individual mound/pit complexes

At the Sangre de Cristo, Routt Forest, and Puerto Rico sites, all mounds and pits were measured by the senior author. Most mounds and pits were related to the most similar shape (ellipse, half-ellipse, triangle, or rectangle) for measuring and area calculation purposes. The area was multiplied by average mound "thickness" or pit depth to compute volume. Irregularly shaped mounds and pits were measured in three dimensions at 0.2-m intervals, and the averages of the appropriate axes were multiplied to estimate area or volume. "Mound" refers to the disturbed soil, roots, and rocks that are uplifted by a fallen tree, and, in this study, includes the freshly uprooted variety (elsewhere termed earth balls, rootballs, or root plates) as well as older examples. Pits are the depressions, adjacent to mounds, that mark the place where the tree once stood. In this study, they were measured only if they appeared capable of trapping sediment (i.e., had a detectable depth); otherwise, they were given an area and volume of zero for statistical analyses. Other information collected at each pit/mound complex included species and diameter at breast height (dbh, 1.3 m) of the uprooted tree, bole length, treefall direction, tree slope, ground slope, and general hillside aspect. Tree basal areas, derived from dbh

(π ($\frac{1}{2}$ dbh)^2), were used to represent tree size because they could be summed when more than one tree formed a mound/pit complex.

To expand the data set, 88 recognizable points of 92 values were extracted from a simple linear regression model using tree diameter to predict mound/pit area of freshly uprooted trees in Barro Colorado Island, Panama (Putz 1983, Figure 1b). Tree diameter was converted to tree basal area and mound/pit area was halved to approximate mound area and facilitate comparisons with data from this study. Because Putz (1983) used an ellipse to approximate combined mound/pit area, the halved results should be comparable to a half-ellipse, one of four shapes used to determine mound area in this study. An additional 106 data points were extracted from a simple linear regression model using tree diameter to predict pit area of recently uprooted trees from two separate windthrow events in Pennsylvania (Peterson, 2000, Figure 4). Peterson (2000) used an ellipse shape to approximate pit areas resulting from two tornadoes: the Kane tornado, which reached estimated wind speeds of 333-419 km/h on 31 May 1985; and a smaller tornado on 28 August 1994, with estimated wind speeds of 117-181 km/hr. The tornadoes struck adjacent but non-overlapping regions of the Tionesta Scenic and Research Natural Areas, which is comprised of hardwood forests dominated by beech (*Fagus grandifolia*), hemlock (*Tsuga Canadensis*) (Peterson, 2000).

2.3 Comparison by plots

Standing trees >10 cm at breast height were counted in plots of 500 m^2. Uprooted trees >8 cm at breast height were included in the plot tally of uprooted trees, and soil area and volume disturbed by toppled trees of any size were included in the tally of soil disturbed. In the Routt Forest, standing and fallen trees in each plot were measured about 10½ months after the uprooting event, and the results were converted to initial stand basal area (m^2 ha^{-1}). A 250 X 20-m transect was established that traversed a slope with a surface comprised of sandy loam/loamy sand containing many cobbles, and an upland valley of organic-rich alluvial fines. The transect was divided into 10 plots of 500 m^2 each. Although the plots are not independent of one another (Ramsey and Schafer, 1997), this should pose less of a problem when assessing internal influences, such as the effects of stand characteristics on soil disturbance, than when assessing external influences, such as uprooting frequency for the blowdown site. The latter was not attempted in this study.

In Puerto Rico, a relascope was used to approximate stand basal area in 40 of the 500 m^2 plots, with individual measurements of trees used for two old-growth plots containing a few large trees. Selections of plots were based on mapped location (for example, state forests) or study relevance as observed during field visits. To prevent bias, the plots were initiated 25 paces from the entry point or the previous plot in a predetermined direction. Forty-two plots were established, distributed among the Caribbean National Forest's

Luquillo Experimental Forest (LEF), state forests in the island's interior, and forest stands and plantations on private and municipal land.

For statistical analyses at the landscape level, the areas and volumes of individual mounds and pits within each plot were summed, and these values were extrapolated to a hectare scale. The "number of uprooted trees" in plots were similarly extrapolated. The "proportion of uprooted trees" represents the percentage of trees that uprooted in a plot, and the "proportion of basal area uprooted" represents the percentage of basal area of uprooted trees relative to the initial value for stand basal area. The initial value included all downed trees; the basal areas of uprooted and snapped trees were added to values for standing basal area, which were derived from either the measured dbh of standing trees or from estimates for stand basal area based on relascope readings.

2.4 Comparison of mound and pit decay rates

A subset of mound/pit complexes was monitored for short-term changes at the Sangre de Cristo site of Colorado and in Puerto Rico's Luquillo Experimental Forest. In Colorado, pits of six mound/pit complexes were partially lined (with concrete, plastic, or newspaper) within 3 years of presumed formation, and two pits were lined within 5 and 10 years of presumed formation, respectively, based on tree-ring dating. Half were assessed for one year and the other half for 2 years of material deposition. In Puerto Rico, nine pits were plastic-lined within 3 weeks of formation, and pit fill was collected 2 months later. Seven linings remained viable to permit a 2-year collection.

Pit deposits from the Sangre de Cristo site were air-dried and weighed after being divided into soil, wood/roots, leaf litter, and rocks. Pit deposits from the Puerto Rico site were separated into the same categories and weighed in the field; subsamples of soil, wood, and litter were oven-dried to constant weight at 65° C to provide conversion factors of wet or air-dried to dry weights. Soil volumes were based on mean bulk density of undisturbed local soil. Soil weights of the Sangre de Cristo samples were converted to volume using a mean bulk density of 1.04 g cm^{-3} that was based on three 50-cm profiles, two in bedrock and one in till. Soil weights of Puerto Rico samples were converted to volume using a mean bulk density of 0.89 g cm^{-3} for the upper 60 cm in the same forest, the Bisley section of the Luquillo Experimental Forest, as determined by Silver et al. (1994).

Wood/root weight of Sangre de Cristo samples were converted to volume using a mean wood density of 0.48 g cm^{-3}, the average density of three dominant conifers at the site, *Pseudotsuga menzisii, Pinus ponderosa*, and *Pinus contorta* (Schweingruber, 1993). Wood/root weights for Puerto Rico samples were converted to volumes using a mean wood density of 0.56 g cm^{-3}, derived from densities reported by Reyes et al. (1992) for dominant hardwoods *Dacryodes excelsa, Sloanea berteriana, Guarea* spp., and *Ocotea leucoxylon* (Scatena and Lugo, 1995), and *Tectonis grandis*, which was locally dominant at the site of five of the seven monitored complexes.

Leaf-litter weights of the Sangre de Cristo samples were converted to volumes using a density of 0.18 g cm^{-3}, developed by cutting a subsample of dried needles into roughly 1-cm pieces and packing them into a container of known volume for weighing. Leaf-litter weights of the Puerto Rico samples were converted using the Puerto Rico: Sangre de Cristo ratio of wood density values (0.56/0.48) to yield a conversion factor of 0.21 g cm^{-3}. At the Sangre de Cristo site, large rocks that fell into monitored pits were measured in three dimensions to estimate volume. Small rocks were weighed, and volumes were estimated using a standard rock density of 2.65 g cm^{-3}. In Puerto Rico, rocks rarely fell into the pits, but the few that did were weighed and converted to volume using 2.65 g cm^{-3}.

For both sites, a conversion factor—the reciprocal of the fraction of the pit that was lined—was applied to the sample to estimate values for deposition for the entire pit (Table 1). Mound-volume changes were estimated by subtracting from the initial mound volume the deposition volumes for soil, wood, and rocks, assuming that the material fell from the mound into the pit. Pit-volume changes were estimated by subtracting from the initial pit volume the deposition volumes for litter, soil, wood, and rocks.

An exponential decay coefficient, *k*, was calculated based on the volume changes (Olson 1963). When the explanatory variable (x) is time and the response variable (y) is the natural log of the fraction remaining (i.e., the remaining volume divided by the initial volume) in a simple linear regression, the negative slope of the line will be *k*, the exponential decay coefficient:

$$\text{natural log} (X / X_0) = -kt \tag{1}$$

or:

$$X / X_0 = e^{-kt} \tag{2}$$

in which X is the remaining volume at time t, and X_0 is the initial volume at t_0. Short-term *k* coefficients were calculated for the Sangre de Cristo and Puerto Rico sites using samples collected after 2 years and one other, shorter, time period (Table 1).

To calculate longer-term *k* coefficients for the Sangre de Cristo site, uprooted trees were dated using dendrochronological methods. After determining that there were no volume differences related to the passage of time among pits and mounds formed within 3 years of the survey, regression formulas were developed for a subset of complexes (Table 2). Instead of using an "x + 1" approach, which resulted in negative values following backtransformations, mounds or pits with zero values were given a value of 0.0001. The formulas thus developed were used to predict the initial volumes of mounds and pits. Mounds and pits in which the initial volume exceeded the predicted volume were given a value of 1 for "fraction remaining". Using time since tree death as the explanatory variable, and the natural log of the fraction of volume remaining as the response variable (Equation 1), the resulting *k* is a decadal-scale assessment of mound and pit decay.

Owing to difficulties in identifying annual rings of tropical trees (Boone and Chudnoff, 1972; Jacoby, 1989; Roig, 2000), a different approach was used for 20 Puerto Rico mounds formed in 1989. The 20 mounds were measured by U.S. Forest Service volunteers about 2 months after a 1989 hurricane. The trees were unlabeled and specific mounds could not be identified, but their locations along a research trail and similar states of decay made them identifiable as a group. Twenty mounds along the research trail were remeasured in 1998 as part of this study. An annual-scale *k* coefficient was estimated from the slope when the explanatory variable was time since mound formation and the response variable was the natural log of the fraction of mound remaining (Equation 1). The fraction of mound remaining was based on either (1) volume or (2) area, using two different sets of assumptions for initial values:

(1) Initial mound volume was approximated by multiple linear regression of data from 132 mounds formed during Hurricane Georges in 1998 (Table 2). Mounds for which the initial volume exceeded the predicted volume were given a value of 1 for "fraction remaining".

2) Initial mound area was approximated by simple linear regression of data from measurements of 1989 by A. Daniel and others (U.S. Forest Service, written communication, 1989) (Ln[mound area, m^2] = - 4.678 + 0.890Ln[tree basal area, cm^2], $r^2 = 0.64$). Mound area was used because statistical analyses indicated area measurements more closely approximated values for trees of comparable size uprooted during Georges than did volume measurements. (The area and volume measurements appear to have included all roots rather than just soil-covered roots, as

in this study.) The measured areas of 1998 were used as the numerator for the fraction of mound area remaining.

3. Results

3.1 Comparison by individual mound/pit complexes

Individual mound size did not differ among the three sites for volume, area, or thickness, as long as tree basal area was considered in multiple linear regression (MLR). Consequently, simple linear regression models partly explain volume and area of mounds from all three sites, with the data combined (Fig. 1). Tree basal area was related to pit depth ($p < 0.0001$), but could not be used to predict it ($r^2 = 0.032$). For the combined data, volume and area did not vary among sites for pits that could trap sediment (i.e., when pits with zero values were excluded) for a given tree basal area. However, when pits with zero values were included, those in the Routt Forest tended to be larger than those in Puerto Rico for a given tree basal area ($p = 0.002$). This indicates that more pits in Puerto Rico blended into slopes, bordered ephemeral streams, or were obscured by leaf litter. Otherwise pit volume and area were comparable at all sites for a given tree basal area.

When mound-area values extrapolated from Putz (1983) for uprooted trees in Barro Colorado Island, Panama, were added to the combined data set as described in section 2.2, site was not significant in MLR. There is inconclusive evidence, however, that the mounds of the Sangre de Cristo site were slightly smaller than those at other sites ($p = 0.07$) (Table 3). When pit-area values extracted from Peterson (2000) were included in the data set, they were significantly different ($p < 0.0001$, multiple linear regression analysis) than those found in this study and the halved values of mound/pit areas reported by Putz (1983). The pit areas from Peterson (2000) averaged about 22% larger (95% confidence interval of 11% to 34%) than predicted by the regression formula developed in this study (Table 3, last row).

For the three sites in this study, mound area was statistically identical to pit area for a given complex, when pits with zero values were excluded (pit-to-mound ratio of 1.003, 95% confidence interval of 0.934 to 1.073, intercept not significant). However, pit volumes were about 61% of mound volumes when zero values were excluded (95% confidence interval of 55% to 68%, intercept not significant) and were about 52% of mound volumes when zero values were included (95% confidence intervals of 45% to 59%, intercept not significant). This is because pit depth averages about 53% of the corresponding mound thickness when zero values are excluded, and 36% of mound thickness when zero values are included, although intercepts test as significant in both cases (95% confidence intervals of slopes, 43% to 63%, and 25% to 47%, and of intercepts, 0.021 to 0.110, and 0.020 to 0.119, respectively).

3.2 Comparison by plots

Because mounds and pits formed by the Routt Divide blowdown and Hurricane Georges were measured at the plot scale soon after the events, data from both sites were combined for comparison. Although the Puerto Rico plots contained a smaller proportion of uprooted trees than did the Routt Forest plots (0 to 29%, and 0% to 72%, respectively), the combined data set can be used to predict the volume and area of soil uplifted per hectare by proportion of uprooted trees (Fig. 2). When the explanatory variables were the number of uproots, or the proportion of basal area uprooted, the Puerto Rico data were less integrated (Table 4a). However, there was no significant difference by site when site was included as a variable in an MLR model testing the influence of proportion of uproots, number of uproots, and basal area of uprooted trees, respectively, on the extrapolated area and volume of soil uplifted per hectare. Excluding one of the Routt Forest data points that residual error indicated was forcing some regressions (for examples, see Fig. 3) generally improved agreement between the sites in equations predicting volume of soil disturbed per hectare. After excluding this point, 95% confidence intervals for all three explanatory variables (proportion of uproots, number of uproots, and basal area of uprooted trees, respectively) overlapped in all cases (Table 4b).

Overall, the best relation involves the use of proportion of uprooted trees to explain the volume of soil uplifted (Table 4). In most other cases, the higher proportion and number of uprooted trees in some Routt Forest plots seem to drive the relation (Table 4a and 4b, Fig. 3), with the leverage from the these points possibly creating more agreement among data than would otherwise occur (Ramsey and Schafer, 1997). Because of the relatively sparse data for higher values of the explanatory variables, the equations for stand-level disturbance (Tables 4a and 4b) may be less robust than are the equations predicting soil disturbance at the individual tree level (Table 3). The pattern of residual error indicates the Puerto Rico data generally conform better to the regression fit when the Routt Forest plot with the most damage is excluded from the analysis (Fig. 3).

When ground slope, proportion of needleleaf trees, and stand basal area were tested along with the expected influences (e.g., proportion of uproots, number of uproots, proportion of basal area uprooted) in multiple linear regressions, stand basal area was statistically significant if (1) the proportion of trees uprooted was used to predict volume of uplifted soil ($p = 0.02$, adjusted $r^2 = 0.88$); (2) the proportion of basal area uprooted was used to predict volume of uplifted soil ($p = 0.003$, adjusted $r^2 = 0.88$); and (3) the proportion of basal area uprooted was used to predict area of uplifted soil ($p = 0.03$, adjusted $r^2 = 0.83$). Despite the significance of stand basal area, its inclusion in the model hardly improved predictions of variation in uplifted soil volume; for example, the r^2 value rose from 0.87 to 0.88 when modeled with the proportion of uprooted trees. There was no significant difference between initial mean stand basal area in the Routt Forest compared to that of the Puerto Rican forests (36.3 m^2 ha^{-1} compared to 30.5 m^2 ha^{-1}, 95% confidence intervals of 28.5 to 44.0 m^2 ha^{-1} and 26.9 to 34.2 m^2 ha^{-1}, respectively, $p = 0.17$). The mean stand basal area for the combined data was 31.6 m^2 ha^{-1}, with individual stand values ranging from 8.9 m^2 ha^{-1} to 70.3 m^2 ha^{-1}.

3.3 Comparison of mound and pit decay rates

In Puerto Rico, the short-term exponential decay coefficient, *k*, was not significantly different after 2 months compared to 2 years for mounds or pits (Table 5). In Colorado, short-term *k* coefficients for mounds after one year were about half the values after 2 years, whereas short-term *k* coefficients for pits after one year were about 70% of the value after 2 years. Pit-infill rate based on erosion pins in Puerto Rico is similar to values for pit infill based on recovery of material at the same site (Table 1), indicating that sampling technique was effective. Based on the 2-year *k* coefficients, mounds and pits at the Puerto Rico site decay in about 74% and 57% of the time, respectively, as mounds and pits at the Sangre de Cristo site (Table 1). Most monitored mounds in Puerto Rico were larger than those in Colorado (Table 1). This difference in initial volume may have reduced the relative differences in *k* coefficients for mounds; the mean volume of soil, wood, and rocks collected from pits after two years was about four times higher in Puerto Rico than in Colorado, at 0.074 m^3 (S.E. of 0.016) and 0.019 m^3 (S.E. of 0.007), respectively, yet the difference in volume changes was less than two times higher (reciprocal of 0.74 is 1.35).

Decadal-scale estimates of *k* for the Sangre de Cristo site, based on tree-ring dating (Table 5), indicate mounds decrease in volume by 50% within about 9 years, by 90% within 30 years, and by 99% within 60 years. The corresponding times for pits are 24 years (50%), 78 years (90%), and 150 years (99%). A decadal-scale *k* is unavailable for mounds and pits of Puerto Rico, but based on the annual-scale *k* for mounds (Table 5), mounds may disappear within 33 years (99%). The average of the two annual-scale coefficients, 0.138 (Table 5), indicates that mounds decayed to 25% of their original size (volume or area) in a little over 10 years. At this rate, fresh mounds at the Puerto Rico site decrease in size by 50% in about 5 years, and by 90% in about 17 years. Although the annual-scale *k* coefficient might be inappropriate for extrapolation to longer time periods, the results imply that the mounds of Puerto Rico decay roughly 50% faster than mounds at the Sangre de Cristo site. Pits were not measured in the 1989 survey, but in 1998 only six pits could be distinguished at the 20 mound/pit complexes, indicating that pits were filling faster than mounds were eroding.

Comparing long-term decay rates with short-term rates (Table 5) suggests how much mound material falls beyond the pit at the Sangre de Cristo and Puerto Rico sites. At the Sangre de Cristo site, than the 2-year rate is about 38% of the decadal-scale rate, whereas in Puerto Rico, the 2-year rate is about 30% of the average of the two annual-scale rates. This might indicate that, at both sites, about two-thirds of the mound material does not re-enter the pit. For both estimates, a constant decay rate is assumed; if initial decay rates are higher than long-term rates, the proportion of eroding mound material falling beyond the pit would be greater.

4. Discussion

4.1 Comparison of individual mound/pit complexes

No significant difference in size was found for mounds in tropical humid Puerto Rico compared to mounds in cool temperate Colorado. Thus, it is possible that the formulas derived here between tree basal area and mound volume and area apply to a wide variety of forests. Results strongly indicate that tree size—as measured by basal area—has a sufficient effect on mound and pit size that it predominates over other variables. Owing to the influence of tree size, published mound and pit measurements reported have little value unless paired with tree diameters or basal areas. Providing a mean diameter for uprooted trees may not necessarily suffice because the exponential relation between diameter and area or volume of soil uplifted suggests that several large trees could exert an influence not reflected by the mean.

This evaluation did not test for differences among soils, in part because different nomenclature was used for the temperate vs. tropical sites (i.e., tropical soils were described by predominant particle size whereas temperate soils were described by substrate). There was, however, a statistically significant tendency for mounds formed in loamy soils and alluvium to be larger than mounds formed in other soil types or substrate at a given site (Appendices A and B). There was evidence also that mounds formed by toppling of needleleaf trees were larger than mounds formed by palms and perhaps broadleaf trees in Puerto Rico (Appendix A). Limited data from the broadleaf trees at the Sangre de Cristo site suggest that mounds formed by conifers tend to be larger than mounds formed by aspen, the only broadleaf sampled, at the Sangre de Cristo site. Confounding this relation is the regeneration style of aspen; most aspen trees are clones, with individual trees sharing a common root system (Arno and Hammerly, 1977).

Overall, results of this study suggest that variability of mound volume and area within sites is greater than variability among sites. For this reason, and because this study was designed to accommodate natural variability, the similarities among sites seemed to transcend the differences. Furthermore, it appears that mound/pit complexes measured by Putz (1983) on Barro Colorado Island, Panama, conform to the regression line developed for the data in this study (Fig. 1c).

In contrast, although results indicate mound and pit areas to be comparable, the pit areas from Peterson (2000) tended to average about 22% larger than predicted by formulas developed in this study. This result suggests caution may be in order when extrapolating relations either 1) from mounds to pits, or 2) from these sites to other sites. Applying an ellipse formula, as did Peterson (2000) for pit area calculations, to the axes for the mounds in the Puerto Rico data set ($n = 132$) indicates there was no statistically significant difference related to the area calculation used ($p = 0.62$, test of means). However, mounds based in loams were predicted to be, on average, 41% larger in area than mounds based in clay in the Puerto Rico data set. The pits measured by Peterson (2000) were formed in podzols; the high organic content typical of podzols might make them comparable to loams regarding mound and pit formation. Alternatively, tree species or other site variables could be factors. Peterson (2000) considered and rejected the hypothesis that differences in wind speed create differences in pit area; pits created by the two tornadoes, one with a wind speed double or more the other, were comparable in area for a given tree diameter based on his analysis and the re-analysis of his extracted data here.

4.2 Comparison by plots

The soil volume and area uplifted by tip-ups in Puerto Rico and the Routt Forest fit the same regression lines for the number of uprooted trees, the proportion of uprooted trees, and the proportion of basal area uprooted. This similarity in the amount of soil uplifted among sites occurs at the landscape scale despite differences in climate, dominant tree type, soil type, and the presence vs. absence of till. Forest structure at the two sites appears different, with trees of Puerto Rico growing in closed canopies whereas the trees of the Routt Forest tend to grow in clumps within openings in the canopy. Conversely, initial mean basal area was higher in the Routt Forest than in Puerto Rico, but no significant difference was shown. Although tropical moist forests tend to have higher net ecosystem productivity than do temperate alpine forests (Holdridge, 1967), many of the Puerto Rico stands surveyed in this study represented secondary growth since the 1950s (Franco et al., 1997), and all are subject to damage by hurricanes with recurrence intervals of 10 to 60 years (Elsner and Kara, 1999; Scatena and Larsen, 1991). The Routt Forest probably experienced fewer high-intensity windstorms in recent decades than did Puerto Rico, thereby resulting in stand basal areas comparable to those of Puerto Rico before the 1997 blowdown. The USDA Forest Service (1998) estimated the last stand-level disturbance at the blowdown site had occurred 300 to 350 years ago given the absence of trees older than 300 years; Englemann spruce can live about 600 years, and subalpine fir can survive about 400 years (Rebertus et al., 1992). Consequently, the forest structure at these two sites might be more similar than would be expected given their differences in climate, elevation, and dominant tree type.

Stand basal area, when included with other explanatory variables in MLRs, did little to improve predictions of soil disturbance for these sites. However, it seems likely that stand basal area will prove important given more data, but comparable studies presently area not available. With more data, a multiple linear regression that includes stand basal area may be more applicable to other forests than a simple linear regression using merely the proportion of basal area uprooted or the proportion of uprooted trees to predict soil disturbance.

4.3 Comparison of mound and pit decay rates

The results from this study indicate that mounds and pits remain on the Colorado landscape roughly twice as long as they do on the Puerto Rico landscape (Table 5). Even in Colorado, however, mounds and pits are projected to disappear within about 60 and 150 years, respectively. These times are shorter than the hundreds of years reported in other studies, particularly for United States forests on the eastern third of the continent (Stephens, 1956; Kabrick et al., 1997; Habecker et al., 1990) and in Siberian (Shubayera and Karpachevskiy, 1983) and Canadian (Lyford and MacLean, 1966) forests dominated by till. Further, Schaetzl and Follmer (1990) used radiocarbon dating of buried wood and charcoal in their study of treethrow mounds in Michigan and Wisconsin to estimate that some formations had persisted for thousands of years. Our study did not consider microtopography to be remnant mounds and pits unless a tree bole in some state of decay could be observed. Nevertheless, there was little evidence for ancient mound/pit topography in Colorado; generally the surface seemed level around decaying roots, crumbling boles, or the occasional circle of rocks suggestive of an ancient treethrow.

The observation that roots and often boles persist on the landscape longer than mounds and pits is consistent with comparisons of *k* coefficients reported by Fahey (1983) for wood decomposition. Values ranged from 0.012 to 0.020 for lodgepole pine at a Wyoming site, indicating wood in such an environment can persist on the landscape potentially three times longer than mounds. Values for *k* coefficients for large logs in nine temperate coniferous forests averaged 0.023 and ranged from 0.006 for Douglas-fir to 0.050 for mixed conifers (Chambers et al., 2000), again indicating decay rates that were mostly lower than that of mounds and pits.

In Puerto Rico, most evidence of past uproots seemed related to the passage of Hurricane Hugo 9 years earlier. Some of the Hugo mounds appeared to be stabilizing as hummocks, but the landscape did not appear cratered to the extent reported for other forests, such as Lyford and MacLean's (1966) estimate that mound/pit microtopography covered 48% of the forest floor in New Brunswick, Canada. Mound/pit microtopography in some forest stands in Puerto Rico might be closer to Stephen's (1956) report of 14% coverage in Harvard Forest than to reports of about 1% coverage in Panama (Putz, 1983). Wood decay tends to be much faster in moist tropical environments than in semi-arid temperate areas. Chambers et al. (2000) reported k coefficients for boles of large Amazonian trees of 0.167, in the same range as annual-scale k coefficients for Puerto Rico mounds, although decay-rate constants varied by 1.5 orders of magnitude and were negatively related to bole diameter. Harmon et al. (1995) reported a wide range of decay rates from their study in Quintana Roo, Mexico, with k coefficients for 30-cm bole segments ranging from 0.008 for *Manilkara zapota* to 0.615 for *Bursera simaruba*. Both genera exist in Puerto Rico. These comparisons indicate that tree species may determine whether mounds outlast boles in Puerto Rico. Large trees tend to decompose more slowly than small ones, but they will also form larger mounds. Lyford and MacLean (1966) found larger mounds tend to endure longer on the landscape.

Putz (1983) observed that few old mound and pit complexes persisted in Barro Colorado Island, Panama, with those remaining identifiable only by fallen boles and their roots. Rainfall on Barro Colorado Island, 2600 mm yr-1 (Dietrich et al., 1996), is comparable to annual rainfall in Puerto Rico, with the exception that Barro Colorado Island precipitation is more seasonally concentrated. The Sange de Cristo site's mean annual precipitation of about 400 mm is much lower than either tropical site, but perhaps the thawing and freezing cycles combined with steep slopes make the site susceptible to erosion.

Cremeans and Kalisz (1988) found evidence of mound/pit topography on only 0.4% of ridges and 2.4% of coves in Kentucky. Similarly, Mitchell (1988) found mound/pit microtopography was not a strong feature in an Australian forest dominated by eucalyptus (*Eucalyptus mannifera*). Perhaps mound/pit microtopography forms best under conditions of gentle slopes, as in the eastern U.S. forests; at the sites in Colorado and Puerto Rico, steep slopes and roughly level valleys dominate the landscape.

Putz (1983) used erosion pins in 32 pits in Panama to estimate a mean pit infill rate of 8.1 cm yr^{-1}, from which he projected pits would last up to 10 years. The mean deposition rates using erosion pins in Puerto Rican pits of 1.68 cm yr^{-1} (initial) and 1.28 cm yr^{-1} (minimum annual average for 2 years of deposition) is consistent with a 10-year longevity of pits based on material infill rates (Table 1). This rate seems reasonable for pits, given that six of 20 trees uprooted by Hurricane Hugo had pits 9 years after the event. Mounds were projected to endure on the landscape for up to 30 years based on the annual-scale k coefficient. All 20 mounds remained recognizable 9 years later, and nine of the 20 remained larger than the mean for a freshly formed mound by a similar-sized tree uprooted during Georges, given the regression formula developed based on the broader sampling of trees (Table 2).

5. Conclusions

This study related basal area of trees to geometries of mound and pit complexes and showed that the influence of an uprooted tree's basal area on the area and volume of soil it uplifted transcended other variables at three disparate sites in Colorado and Puerto Rico, as well as at a fourth site in Panama (Putz 1983). Pit areas measured by Peterson (2000) in Pennsylvania, however, were about one-quarter larger than the mean mound area predicted by the equation developed from the combined data set. This suggests that individual site variables, particularly soil type, can exert a potentially measurable influence.

Tree basal area is a useful measurement of tree size because, unlike with tree diameter, values can be summed when more than one tree forms one mound/pit complex. In this study, tree basal area is assumed to be a proxy for stem biomass; tree basal area (πr^2) is derived from diameter and is directly proportional to tree diameter raised to the second power (Tree basal area (m^2) = 1.27 D^2 (m^2), $r^2 = 1.00$, n = 169). Tree diameter squared (D^2) is often used to estimate stem biomass (e.g., Scatena et al., 1993), which is relevant because globally, root biomass is proportional to stem biomass across wide ranges of plant species and sizes (Enquist and Niklas, 2002). In this context, the results of this study—of similar-sized trees at a variety of sites uplifting similar quantities of soil—imply that stem: root biomass is the main influence of mound and pit size, and that soil type and perhaps tree species have secondary effects. Specifically, the fall of the stem exerts a force on the perpendicular root system; because root system mass is proportional to stem mass, the force unearths a predictable part of the root system, and soil and rocks clinging to the roots. The amount of root system unearthed appears more related to stem size than to the pressure exerted on the stem, given Peterson's (2000) finding of no difference in pit areas for similar-sized trees uprooted by two tornadoes with vastly differing wind speed.

Because the relation between tree basal area and stem size is a power function, differences in the amount of soil uplifted based on tree diameter are exponential despite the linear relation between tree basal area and mound area or volume. This indicates that a large-diameter tree generally uplifts an exponentially greater amount of soil than does a small tree. The findings also indicate that published mean mound sizes pertain only to the study sites, and to trees of representative size at those sites.

Stand-level projections of the amount of soil uplifted adequately described conditions in the Routt Forest of Colorado and in Puerto Rico for sites of catastrophic uprooting events. The relations between proportion of uproots and proportion of basal area uprooted to predict volume and area of soil uplifted are linear, indicating that the proportion of soil disturbed for each unit of the explanatory variable is constant. This supports the validity of extrapolating mean mound area to the landscape (Mills, 1984; Brewer and Merritt, 1978) if the data are representative of population variability.

In this study, mean stand basal area for the Routt Forest and Puerto Rico sites were not statistically different, and given the wide range of individual basal area stand values (8.9 m^2 ha^{-1} to 70.3 m^2 ha^{-1}), the equations derived may be applicable to other forests as well. Using the proportion of uprooted trees to explain soil disturbance seems to be a more robust approach than using the number of uprooted trees or the proportion of basal area uprooted. Including stand basal area as a variable in a MLR only marginally improved the predictive ability of equations, but may be more useful if the data set encompasses other forest types.

Using the material falling into a lined pit to estimate short-term exponential decay coefficients, *k*, an approach comparable to using erosion pins to estimate pit infill rate, indicates mounds and pits decay about twice as rapidly at the Puerto Rico site as the Sangre de Cristo site. A comparison of short-term values with longer term *k* suggests that, of the material eroding from mounds, about one third re-enters the adjacent pits at both sites. The values indicate that mounds and pits at both sites decay more rapidly than in other forests, where mound/pit topography apparently has persisted for hundreds (Stephens, 1956; Kabrick et al., 1997; Habecker et al. 1990) or thousands of years (Schaetzl and Follmer, 1990). These features appear to decay to about 10% of their former volume within about 80 years in Colorado and less than 20 years in Puerto Rico.

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Table 1. Results of the pit material collection technique, given below, were used to calculate short-term exponential decay coefficient (*k*) for mounds and pits. All Colorado monitored complexes were dated to 1996 except for U12 (1988) and 0-11 (1994).

Site (Pit-mound complex #)	**Time (yrs)**	**% of pit monitored**	**Mound volume (m3), initial**	**Change in mound volume (% yr-1)**	**Pit volume (m3), initial**	**Change in pit volume (% yr-1)**
CO (U22)	0.92	13.1	0.89	-3.9	0.9	-6.2
CO (0-6)	0.89	33.9	2.22	-1.2	1.0	-5.4
CO (0-11)	0.88	63.5	0.41	-0.7	0.2	-3.4
CO (0-13)	0.88	25.8	0.51	-1.07	0.2	-3.6
CO mean, ~one yr (S.E.)	**0.89 (0.01)**	**34.0 (10.6)**	**1.01 (0.42)**	**1.72 (0.736)**	**0.6 (0.2)**	**-4.64 (0.69)**
CO (U3)	1.94	12.0	1.00	-3.5	0.69	-7.3
CO (U6)	1.92	17.6	0.52	-2.0	0.23	-9.3
CO (U12)	1.94	23.3	0.27	-2.0	0.19	-3.3
CO (U26)	1.94	8.1	1.30	-2.1	0.72	-7.3
CO mean, ~two yrs (S.E.)	**1.935 (0.01)**	**15.3 (3.3)**	**0.77 (0.233)**	**-2.39 (0.3738)**	**0.46 (0.143)**	**-6.80 (1.25)**

Table 1, continued.

Site (Pit-mound complex #)	Time (yrs)	% of pit monitored	Mound volume (m3), initial	Change in mound volume (% yr-1)	Pit volume (m3), initial	Change in pit volume (% yr-1)	Annualized soil erosion/ deposition, erosion pins (no. of pins)	Change in pit depth, erosion pins (% yr-1)
PR (C2)	0.23	53.4	1.30	-6.2	0.73	-11.0	+4.04 (4)	-23.8
PR (C3)	0.23	59.0	1.29	-4.6	0.63	-9.3	+1.44 (4)	-11.0
PR (C4)	0.23	100	1.72	0	0.52	0	--	--
PR (C6)	0.22	100	1.20	-1.6	0.68	-2.8	-2.95 (4)	+21.1
PR (C7)	0.19	44.7	2.53	-7.6	1.57	-12.3	+4.74 (4)	-22.6
PR (C8)	0.19	100	2.48	-4.2	0.52	-19.9	+1.42 (3)	-15.8
PR (C9)	0.19	100	2.35	-13.1	0.86	-35.9	+1.42 (3)	-10.9
PR mean, ~two mos (S.E.)	**0.21 (0.01)**	**79.5 (9.8)**	**1.84 (0.23)**	**-5.32 (1.63)**	**0.79 (0.14)**	**-13.03 (4.53)**	**+1.68 (1.10)**	**-10.4 (8.21)**
PR (C2)	2.01	53.4	1.282	-5.3	0.712	-9.8	+1.89 * (3)	-11.7
PR (C3)	2.01	59.0	1.277	-6.0	0.617	-12.5	+1.19 (2)	-9.4
PR (C4)	2.03	100	1.72	-1.3	0.520	-4.5	--	--
PR (C6)	2.03	100	1.196	-2.1	0.676	-3.8	+0.35 (4)	-2..35
PR (C7)	2.03	44.7	2.493	-4.1	1.533	-6.9	+0.84 (3)	-4.17
PR (C8)	2.01	100	2.460	-3.5	0.500	-17.6	+0.65 (3)	-7.43
PR (C9)	2.02	100	2.291	-6.2	0.801	-17.7	+2.77* (4)	-21.8
PR mean, ~ two yrs (S.E.)	**2.02 (0.01)**	**79.5 (9.8)**	**1.82 (0.22)**	**-4.05 (0.71)**	**0.766 (0.134)**	**-10.37 (2.18)**	**+1.28 (0.37)**	**-9.49 (2.83)**

* All erosion pins were buried, so this represents a minimum estimate.

Table 2. Multiple linear regression coefficients developed to predict initial volumes in studies of longer term mound and pit decay. For the Sangre de Cristo study, 23 mound/pit complexes dated at three years old or less were used to develop regression formulas, with adjusted r^2 (coefficient of determination) values of 0.747 for the mound model, and 0.801 for the pit model. For the Puerto Rico study, 132 mounds formed by Hurricane Georges were used to develop regression formulas, with adjusted r^2 value of 0.649.

Term	**Coefficient**	**95% confidence interval for value**	*p*
Variables to predict Ln(Mound volume, m^3), Sangre de Cristo site			
Intercept	0.940	-0.135 to 2.016	0.08
Ln(Tree basal area, m^2)	0.899	0.492 to 1.306	0.0002
Till indicator	1.636	0.707 to 2.565	0.002
Alluvium indicator	1.703	0.893 to 2.513	0.0003
Ridge indicator	1.194	0.362 to 2.027	0.008
Variables to predict Ln(Pit volume, m^3), Sangre de Cristo site			
Intercept	0.302	-0.716 to 1.321	0.5
Ln(Tree basal area, m^2)	0.908	0.532 to 1.283	<0.001
#trunks/mound	0.405	0.095 to 0.715	0.01
Alluvium indicator	1.566	0.830 to 2.301	0.003
Broadleaf indicator	-0.707	-1.396 to -0.018	0.05
Ridge indicator	0.816	0.090 to 1.542	0.03
Variables to predict Ln(Mound volume, m^3), Puerto Rico site			
Intercept	5.984	5.043 to 6.925	<0.0001
Slope indicator*	0.314	-0.040 to 0.668	0.08
Needleleaf indicator	0.735	0.278 to 1.191	0.002
Ln(Tree basal area, cm^2)	1.058	0.921 to 1.196	<0.0001
Loam indicator	0.559	0.178 to 0.941	0.004

* The original formula found mounds formed on ridges were smaller than those on slopes, with a $p < 0.05$; as these mounds were formed on a slope rather than a ridge, a "slope" parameter was included here despite a $p > 0.05$. None of the trees in this sample were needleleaf, and all were in loamy soil.

Table 3. Simple linear regression coefficients predicting quantity of soil in individual mounds from uprooted trees from four different data sets, reported individually and when combined as one group of points. This study included sites in Puerto Rico and Colorado, in the Routt Forest (Rocky Mountains) and the Sangre de Cristo Mountains. In addition, data points were extracted from Putz (1983) and used for further comparison. All intercepts and slopes in the table are significantly different from zero (with $p < 0.01$). r^2 = coefficient of determination. The resulting equation from this data, using the second row as an example, would look like: Ln(Mound volume, m^3) = 2.262 + 1.029Ln(Tree basal area, m^2). C.I. is confidence interval.

Data set	Response (y)	Intercept	95% C.I.	Slope	Predictor (x)	95% C.I.	r^2	n
Puerto Rico (PR)	Ln(Mound volume, m^3)	2.262	1.797 to 2.728	1.029	Ln(Tree basal area, m^2)	0.882 to 1.175	0.605	128
Routt Forest (RF)	Ln(Mound volume, m^3)	2.687	2.211 to 3.162	1.230	Ln(Tree basal; area, m^2)	1.045 to 1.416	0.749	61
Sangre de Cristos (SC)	Ln(Mound volume, m^3)	2.340	1.011 to 3.670	1.172	Ln(Tree basal area, m^2)	0.608 to 1.736	0.471	23
Combined , this study (PR, RF, SC)	**Ln(Mound vol, m^2)**	**2.308**	**1.985 to 2.632**	**1.061**	**Ln(Tree basal area, m^2)**	**0.951 to 1.172**	**0.631**	**212**
Puerto Rico (PR)	Ln(Mound area, m^2)	2.479	2..087 to 2.871	0.737	Ln(Tree basal area, m^2)	0.613 to 0.861	0.526	127
Routt Forest (RF)	Ln(Mound area, m^2)	3.553	3.110 to 3.997	1.166	Ln(Tree basal area, m^2)	0.993 to 1.340	0.755	61
Sangre de Cristos (SC)	Ln(Mound area, m^2)	2.653	1.479 to3.828	0.925	Ln(Tree basal area, m^2)	0.427 to 1.424	0.415	23
Barro Colorado Island (BCI)	Ln(Mound area, m^2)	2.616	2.381 to 2.850	0.747	Ln(Tree basal area, m^2)	0.634 to 0.860	0.668	88
Combined (PR, SC, RF and BCI)	**Ln(Mound area, m^2)**	**2.695**	**2.500 to 2.5889**	**0.815**	**Ln(Trunk area, m^2)**	**0.743 to 0.887**	**0.626**	**299**

Table 4a. Simple linear regression coefficients predicting the quantity of soil uplifted based on three different explanatory variables. The intercepts were not significant so they are not shown. The slopes are all significantly different from zero ($p = 0.0001$ or less). The resulting equation from this data, using the third row as an example, would look like: Volume of soil disturbed ($m^3 ha^{-1}$) = 5.797(Uprooted trees, % of all trees and stems).

Predictions for volume of soil uplifted					
Data set	**Response variable**	**Slope**	**Explanatory variable**	**95% C.I.**	**r^2**
Combined	Volume of soil uplifted ($m^3 ha^{-1}$)	5.797	% uprooted trees	5.156 to 6.437	0.869
Colorado	Volume of soil uplifted ($m^3 ha^{-1}$)	5.963	% uprooted trees	3.923 to 8.003	0.850
Puerto Rico	Volume of soil uplifted ($m^3 ha^{-1}$)	4.792	% uprooted trees	3.553 to 6.032	0.604
Combined	Volume of soil uplifted ($m^3 ha^{-1}$)	0.839	#uprooted trees ha^{-1}	0.765 to 0.912	0.913
Colorado	Volume of soil uplifted ($m^3 ha^{-1}$)	0.882	#uprooted trees ha^{-1}	0.727 to 1.037	0.956
Puerto Rico	Volume of soil uplifted ($m^3 ha^{-1}$)	0.621	#uprooted trees ha^{-1}	0.441 to 0.802	0.548
Combined	Volume of soil uplifted ($m^3 ha^{-1}$)	4.495	% Basal area uprooted	3.950 to 5.040	0.846
Colorado	Volume of soil uplifted ($m^3 ha^{-1}$)	5.164	% Basal area uprooted	3.484 to 6.844	0.863
Puerto Rico	Volume of soil uplifted ($m^3 ha^{-1}$)	2.816	% Basal area uprooted	2.124 to 3.508	0.629
Predictions for area of soil uplifted					
Data set	**Response variable**	**Slope**	**Explanatory variable**	**95% C.I.**	**r^2**
Combined	Area of soil uplifted ($m^2 ha^{-1}$)	15.166	% uprooted trees	13.382 to16.951	0.854
Colorado	Area of soil uplifted ($m^2 ha^{-1}$)	15.751	% uprooted trees	10.594 to 20.908	0.861
Puerto Rico	Area of soil uplifted ($m^2 ha^{-1}$)	9.040	% uprooted trees	5.580 to 12.500	0.411
Combined	Area of soil uplifted ($m^2 ha^{-1}$)	2.206	#uprooted trees ha^{-1}	2.005 to 2.408	0.907
Colorado	Area of soil uplifted ($m^2 ha^{-1}$)	2.309	#uprooted trees ha^{-1}	1.879 to 2.738	0.951
Puerto Rico	Area of soil uplifted ($m^2 ha^{-1}$)	1.343	#uprooted trees ha^{-1}	0.904 to 1.782	0.489
Combined	Area of soil uplifted ($m^2 ha^{-1}$)	11.596	% Basal area uprooted	9.992 to 13.200	0.861
Colorado	Area of soil uplifted ($m^2 ha^{-1}$)	13.545	% Basal area uprooted	9.114 to 17.976	0.861
Puerto Rico	Area of soil uplifted ($m^2 ha^{-1}$)	5.400	% Basal area uprooted	3.459 to 7.340	0.442

Table 4b. Simple linear regression coefficients predicting the quantity of soil uplifted given the exclusion of one Routt Forest plot that appeared to be forcing the lines upward. Intercepts were not significant so they are not shown. The slopes are all significantly different from zero ($p = 0.0001$ or less).

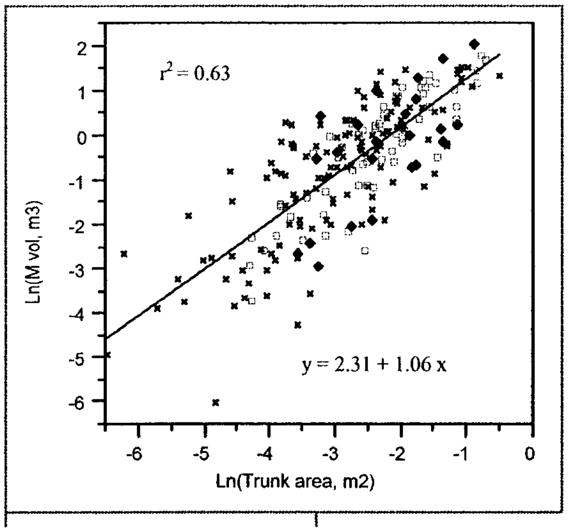
Predictions for volume of soil disturbed					
Data set	**Response variable**	**Slope**	**Parameter**	**95% C.I.**	**r^2**
Combined	Volume of soil uplifted (m^3 ha^{-1})	4.833	% uprooted trees	4.335 to 5.331	0.886
Colorado	Volume of soil uplifted (m^3 ha^{-1})	4.707	% uprooted trees	3.782 to 5.633	0.954
Puerto Rico	Volume of soil uplifted (m^3 ha^{-1})	4.792	% uprooted trees	3.553 to 6.032	0.604
Combined	Volume of soil uplifted (m^3 ha^{-1})	0.731	#uprooted trees ha^{-1}	0.655 to 0.806	0.886
Colorado	Volume of soil uplifted (m^3 ha^{-1})	0.742	#uprooted trees ha^{-1}	0.688 to 0.796	0.993
Puerto Rico	Volume of soil uplifted (m^3 ha^{-1})	0.621	#uprooted trees ha^{-1}	0.441 to 0.802	0.548
Combined	Volume of soil uplifted (m^3 ha^{-1})	3.716	% Basal area uprooted	3.277 to 4.155	0.855
Colorado	Volume of soil uplifted (m^3 ha^{-1})	4.087	% Basal area uprooted	3.003 to 5.172	0.919
Puerto Rico	Volume of soil uplifted (m^3 ha^{-1})	2.816	% Basal area uprooted	2.124 to 3.508	0.629
Predictions for area of soil disturbed					
Data set	**Response variable**	**Slope**	**Parameter**	**95% C.I.**	**r^2**
Combined	Area of soil uplifted (m^2 ha^{-1})	12.827	% uprooted trees	11.246 to 14.409	0.844
Colorado	Area of soil uplifted (m^2 ha^{-1})	12.907	% uprooted trees	9.366 to 16.448	0.914
Puerto Rico	Area of soil uplifted (m^2 ha^{-1})	9.040	% uprooted trees	5.580 to 12.500	0.411
Combined	Area of soil uplifted (m^2 ha^{-1})	1.965	#uprooted trees ha^{-1}	1.743 to 2.186	0.866
Colorado	Area of soil uplifted (m^2 ha^{-1})	2.030	#uprooted trees ha^{-1}	1.604 to 2.457	0.948
Puerto Rico	Area of soil uplifted (m^2 ha^{-1})	1.343	#uprooted trees ha^{-1}	0.904 to 0.796	0.489
Combined	Area of soil uplifted (m^2 ha^{-1})	9.646	% Basal area uprooted	8.175 to 11.118	0.780
Colorado	Area of soil uplifted (m^2 ha^{-1})	11.135	% Basal area uprooted	7.273 to 14.996	0.869
Puerto Rico	Area of soil uplifted (m^2 ha^{-1})	5.400	% Basal area uprooted	3.459 to 7.340	0.442

Table 5. Values for *k*, an exponential decay coefficient, are summarized below. This negative decay constant fits into formulas 1 and 2 described in the Methods sections and Olson (1963).

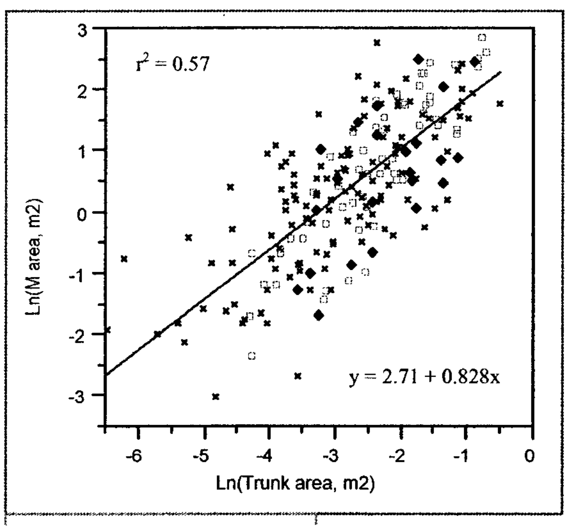
Site	**Feature**	**Short-term *k** (using Ln(1) at t_0)**	**Two-year *k* (using Ln(1) at t_0)**	***k* when both intervals included**	**Annual *k*, approach 1[§]**	**Annual *k*, approach 2[§]**	**Decadal-scale k**
Colorado	**Mounds**	0.016	0.030	0.031			0.078
Puerto Rico	**Mounds**	0.047	0.042	0.042	0.115	0.160	
Colorado	**Pits**	0.048	0.068	0.068			0.029
Puerto Rico	**Pits**	0.110	0.116	0.120			

* This value is for approximately one-year in Colorado, and for approximately two months in Puerto Rico.

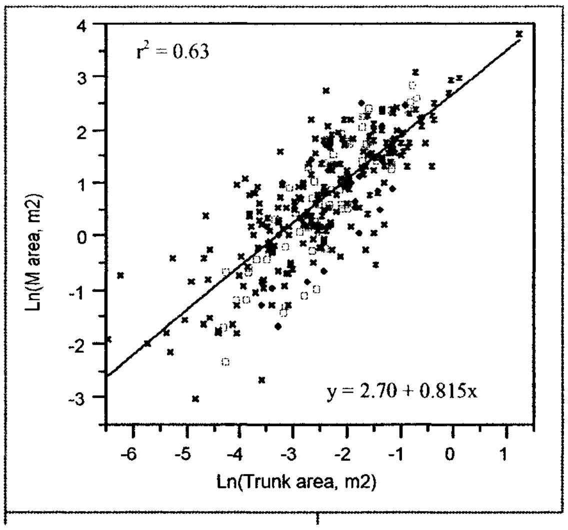
§ Based on description in Methods section.


r² = 0.63
y = 2.31 + 1.06 x
Ln(M vol, m3)
Ln(Trunk area, m2)

a)

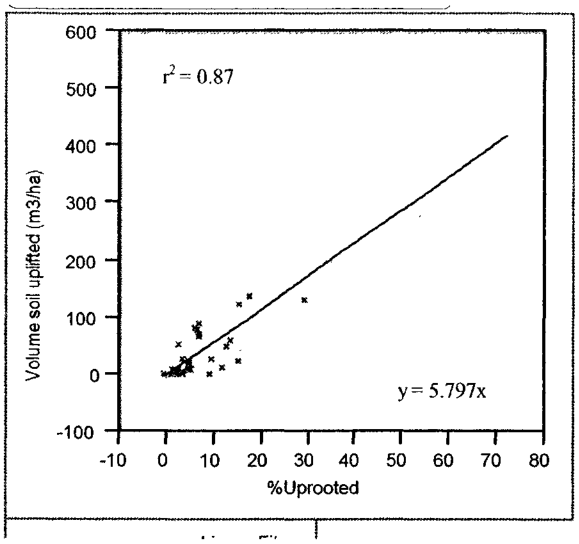

r² = 0.57
y = 2.71 + 0.828x
Ln(M area, m2)
Ln(Trunk area, m2)

b)

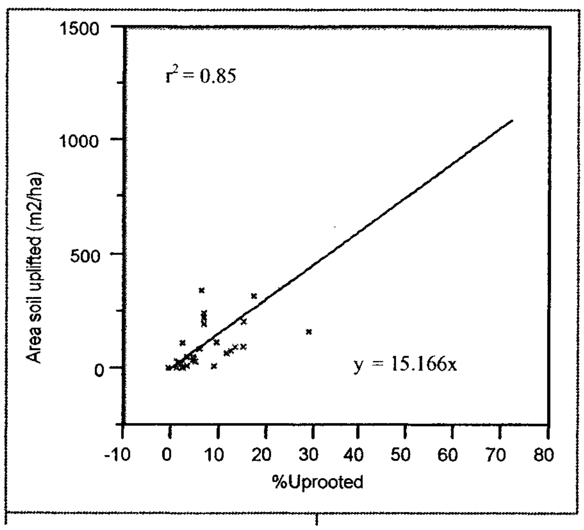


c)

Figure 1. Graphs showing simple linear regressions using tree basal area to predict mound (a) volume and (b and c) area using data from (a and b) the three sites in this study, and (c) our study sites along with data from Barro Colorado Island, Panama, as reported by Putz (1983). See table 3 for details on the regression equations and r^2 values.

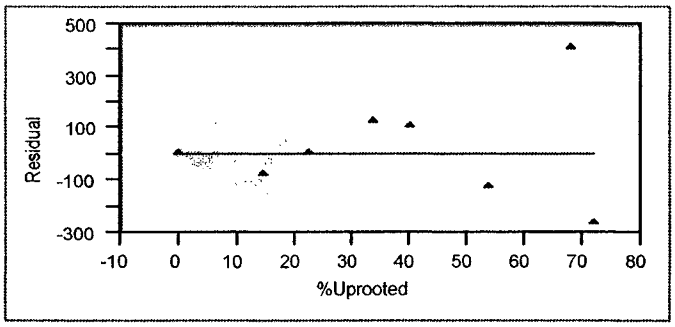


a)



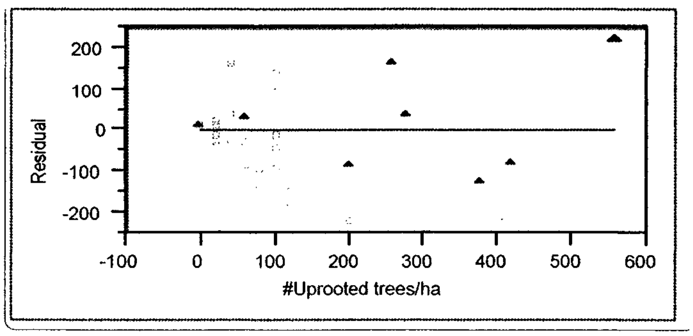
b)

Figure 2. Graphs of simple linear regressions using the proportion of uprooted trees on plots in Puerto Rico (X's) and the Routt Forest (open squares) to predict (a) the volume of soil uplifted and (b) the area of soil uplifted, per hectare. See table 4 for details on the equations and r^2 values.



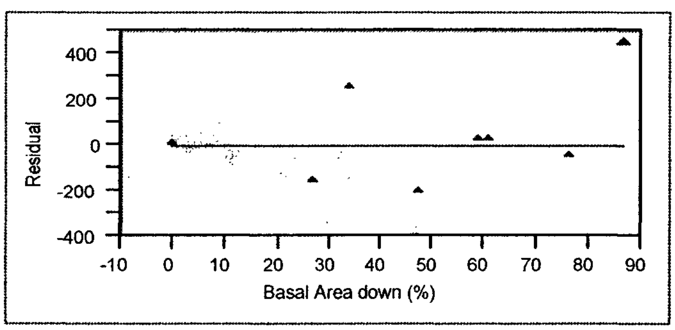
Residual
500
300
100
-100
-300
-10
0
10
20
30
40
50
60
70
80
%Uprooted

a)



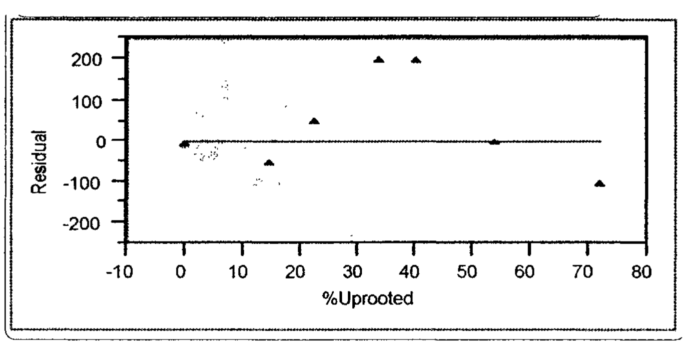
Residual
200
100
0
-100
-200
-100
0
100
200
300
400
500
600
#Uprooted trees/ha

b)



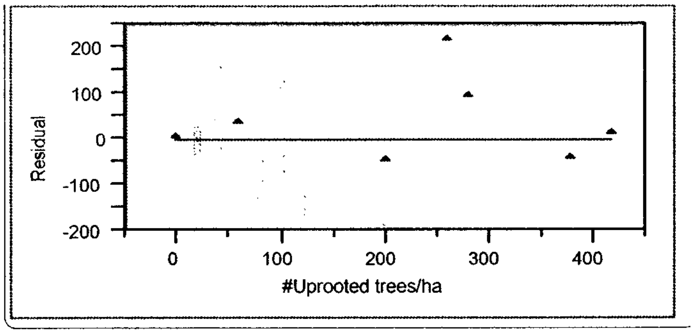
Residual
400
200
0
-200
-400
-10
0
10
20
30
40
50
60
70
80
90
Basal Area down (%)

c)

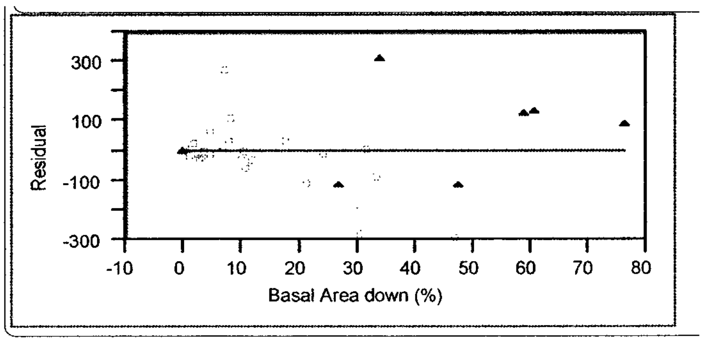


Residual
200
100
0
-100
-200
-10
0
10
20
30
40
50
60
70
80
%Uprooted

d)



e)



f)

Figure 3. Graphs showing residual error for simple linear regressions to predict the area of soil uplifted for plots in Puerto Rico (open squares) and the Routt Forest, Colorado (triangles). The first three graphs show residual error for all 52 plots when the explanatory variables are (a) the proportion of uprooted trees, (b) the number of uproots, and (c) the proportion of stand basal area uprooted. The last three graphs show residual error for the same plots and same explanatory variables, respectively, after excluding one heavily damaged plot in the Routt Forest. See tables 4a and 4b for details on the equations.

APPENDIX D – SUPPLEMENTARY TABLES

Table 1. Some attributes of the 42 plots in Puerto Rico assessed for uprooting frequency and soil disturbance following Hurricane Georges. N = needleleaf trees, P = palm trees, B.A. = basal area, M = mound, Elev = elevation.

Plot #	Municipality	Forest type	%N	%P	Stand B.A. (m^2/ha)	#Trees	#Snaps	#Uproots	M volume (m^3/plot)	Soil	Topography	Elev (m)	Aspect (°)
1	Patillas	Wet	0	0	40	22	4	0	0	Clay	Slope	700	0
2	Naguabo	Wet	0	17.9	18	39	5	2	1.05	Sand	Slope	550	170
3	Patillas	Wet	0	3	20	33	9	4	0.588	Clay	Ridge	700	240
4	Patillas	Wet	0	19.1	27	47	10	6	2.515	Clay	Slope	600	270
5	Cayey	Wet	0	0	9	26	1	1	0.32	Clay	Valley	400	300
6	Ponce	Moist	0	0	22	17	11	0	0	Clay	Slope	300	250
7	Ponce	Moist	0	0	13.7	17	7	5	6.531	Clay	Slope	300	250
8	Adjuntas	Wet	0	38.2	20	34	7	0	0	Clay	Slope	1000	90
9	Adjuntas	Wet	0	56.9	48.8	72	4	2	2.641	Clay	Slope	1000	110
10	Adjuntas	Wet	100	0	58	64	1	10	6.147	Clay	Ridge	500	230
11	Maricao	Wet	24.1	13.8	28.5	29	2	4	2.953	Clay	Ridge	800	180
12	Maricao	Wet	0	4.9	31.5	41	7	2	1.155	Clay	Ridge	800	230
13	Patillas	Wet	91	0	43	67	18	1	0.014	Clay	Ridge	700	120
14	Patillas	Wet	0	10	19	40	2	0	0	Clay	Valley	300	180
15	Patillas	Wet	0	60	22.8	50	4	5	1.345	Clay	Ridge	500	320
16	Caguas	Moist	0	0	20	28	21	1	0.126	Clay	Valley	200	220
17	Caguas	Moist	0	0	23	34	23	1	0.0284	Clay	Valley	200	200
18	San Juan	Moist	75	0	12	28	17	5	6.948	Sand	Valley	10	160

Table 1, continued.

Plot #	Municipality	Forest type	%N	%P	Stand B.A. (m^2/ha)	#Trees	#Snaps	#Uproots	M volume (m^3/plot)	Soil	Topography	Elev (m)	Aspect (°)
19	San Juan	Moist	91.7	0	10	12	11	0	0	Sand	Valley	10	140
20	San Juan	Moist	89.5	0	8.5	19	13	1	0.434	Sand	Valley	10	120
21	Luquillo	Wet	0	42.9	28	42	2	0	0	Clay	Slope	350	270
22	Luquillo	Wet	0	38.6	36	57	0	0	0	Clay	Slope	350	270
23	Luquillo	Wet	0	16.7	44	48	1	0	0	Clay	Slope	350	280
24	Luquillo	Wet	0	23.1	28	39	5	7	1.104	Clay	Slope	250	90
25	Luquillo	Wet	0	52.4	43	42	6	4	0.137	Clay	Slope	250	90
26	Luquillo	Rain	0	0	30	94	0	0	0	Clay	Slope	1000	100
27	Luquillo	Rain	0	0	24	50	0	0	0	Clay	Ridge	1000	30
28	Rio Grande	Wet	0	71.4	27	28	5	2	4.44	Clay	Slope	200	300
29	Rio Grande	Wet	0	65.4	33	26	4	0	0	Clay	Slope	200	340
30	Rio Grande	Wet	0	30.6	35	48	3	3	4.125	Clay	Slope	250	40
31	Luquillo	Wet	0	49.3	34	71	0	5	3.989	Clay	Slope	650	160
32	Luquillo	Wet	0	34.3	32	70	5	5	3.545	Loam	Slope	650	190
33	Luquillo	Wet	0	0	39	75	1	0	0	Loam	Slope	750	170
34	Luquillo	Wet	0	47.3	36	74	0	0	0	Loam	Slope	750	0
35	Luquillo	Wet	0	0	37	55	2	3	0.481	Loam	Slope	750	30
36	Luquillo	Rain	3.57	42.9	25	28	6	1	1.3	Sand	Slope	650	20
37	Luquillo	Rain	0	43.4	30	53	4	2	0.238	Sand	Slope	650	30
38	Fajardo	Dry	0	0	18	26	5	0	0	Clay	Valley	40	90
39	Fajardo	Dry	5.88	0	18	34	6	0	0	Clay	Valley	40	90
40	Ponce	Dry	0	0	36	14	5	0	0	Clay	Valley	25	180
41	Ponce	Dry	0	0	36	7	0	0	0	Clay	Valley	25	180
42	Naguabo	Wet	7.14	25	22	28	4	2	3.384	Sand	Slope	550	170

Table 2. Details on how the trees in the 50 mounds used in the paper written for Catena were dated. More information on the dendrochonological methods employed can be found in the section 3.2 of Appendix B.

JMP#	Tree#	1^{st}– last rings		Cofecha r^2	#Segments correlating	Notes
1	U1	1874	1996	0.58	4 of 4	
2	U2	1805	1986	0.47	6 of 6	
3	U3	1814	1982	0.55	6 of 6	Two to three tiny rings evident at end, along with resin ducts, which in DF mean stress or trauma. Tree had some green leaves so dated at 1996.
4	U4	1810	1948	0.47	3 of 5	Last 3 segments fit.
	U4-in pit	1954	1999			Live aspen growing in pit of U4, cored in 1999.
5	U6	1780	1975	0.56	7 of 7	But U1, underneath it, dated to 1996 so 1996 used.
6	U10	1871	1996	0.41	4 of 4	U8-U11 fell together in one pit-mound complex; U10 dated.
7	U12	1903	1988	0.34	2 of 2	
8	U13	1869	1958	0.46	2 of 3	Last two segments fit 1958 death. Marker years fit, but first 25 years more erratic than chronology.
9	U17	1877	1969	0.64	3 of 3	
10	U18	1843	1996	Defoliation rings		Aspen, dated by ring-counting forward from defoliation rings at 1873 and 1880.
11	U19	1890	1979	0.63	3 of 3	
12	U22	1849	1996	0.65	5 of 5	
13	U23	1833	1976	0.51	4 of 5	Last 4 segments correlate to 1976 death, skelplot fits throughout.
14	U24	1837	1976	0.36	5 of 5	
15	U25	1810	1979	0.54	6 of 6	
16	U26	1806	1996	0.48	7 of 7	

Table 2, continued

JMP#	**Tree#**	**1st– last rings**		**Cofecha r^2**	**#Segments correlating**	**Notes**
17	U28	1818	1980	0.49	4 of 6	Skelplot lines up throughout.
18	U30	1863	1955	0.54	3 of 3	
19	U33	1824	1931	0.64	3 of 3	
20	U41	1818	1922	0.46	3 of 3	
21	U43	1860	1977	0.42	4 of 4	
22	U45	1734	1924	0.39	3 of 6	Last 3 segments correlate, skelplot fits throughout match. Chronology only goes back to 1773.
23	U47	1889	1965	0.56	2 of 2	
24	U48	1809	1986	0.37	3 of 6	Last 3 segments conform to 1986 death. Local suppression 1855-1890, perhaps due to canopy position, may be throwing off earlier correlation.
25	U51	1876	1981	0.53	3 of 3	
26	W11-U2	1877	1996	0.32	3 of 4	Correlation drops after 1976. Death date probably 1997.
27	W11-U6	1914	1998	Defoliation ring		Aspen, dated by ring-counting forward from light ring at 1945.
28	W13-U1	1860	1996	0.39	5 of 5	
29	W13-U2	1877	1980	0.53	3 of 3	
30	W13-U3	1890	1969	0.38	2 of 2	
31	W13-U4	1895	1996	~0.30	2 of 3	Last 2 segments correlate well.
32	W13-U5	1855	1996	0.31	3 of 5	1st, 2nd, 5th segments correlate. In middle narrow rings mostly match but magnitude off.
33	W14-U1	1893	1992	0.30	3 of 3	
34	W14-U2	1861	1999	Defoliation rings		Aspen, dated counting forward from lighter-colored defoliation rings; Also, tree has green leaves.
w/u2	W14-U3	1879	1999	0.37	2of 4	1st and last segments correlate; Also, tree had green leaves, and fell with W14-U2.

Table 2, continued.

JMP#	Tree#	1st– last rings		Cofecha r^2	#Segments correlating	Notes
35	W14-U4	1868	1983	0.41	3 of 4	
w/u4	W14-U5					
w/u4	W14-U6					
36	W14-U8	1890	1999	Defoliation ring		Aspen, dated by ring-counting forward from light ring at 1945.
37	W14-U9	1846	1916	0.4	2 of 2	
38	W14-U10	1862	1997	Defoliation rings		Aspen, dated by ring-counting forward from pest rings at 1873, 1880 and 1945.
39	W15-U3		2000	Defoliation rings		Also, green leaves on 2 aspen and 1 LP in mound (w/ U4 and U5).
w/u3	W15-U4	1867	1999	0.37		2 of 4 Last 2 segments correlate well.
w/u3	W15-U5	1832	2000	Defoliation rings		Aspen, dated by ring-counting forward from light ring at 1879.
40	W15-U6	1890	1997	0.36	3 of 3	
41	W17-U1	1895	1996	0.37	2 of 3	Date of 1997 (W17-U2) used because most recent death in mound.
w/u1	W17-U2	1891	1997	0.73	3 of 3	
42	W17-U3	1907	1996	0.76	3 of 3	
43	99-U1	1999				Fell between survey in summer 1998 and summer 1999.
44	0-6	1860	1996	0.58	5 of 5	
45	0-7	1815	1996	0.5	6 of 6	
46	0-8	1883	1996	0.45	3 of 4	
47	0-9	1895	1996	0.58	3 of 3	
48	0-11	1862	1994	0.45	3 of 4	1st, 2nd and last segments correlate well.
49	0-12	1824	1993	0.42	5 of 6	First 4 and last segments correlate well.
50	0-13	1810	1996	0.58	7 of 7	