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Microtopography and ecology of pit-mound structures in second-growth versus old-growth forests

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ABSTRACT

Pit and mound microtopography is an important structural component of most forests, influencing soil processes and habitat diversity. These features have diminished greatly in northeastern U.S. forests since European settlement, as a result of the history of repeated logging, land-clearance followed by reforestation, and the smaller size of trees (and therefore windthrow features) comprising the prevailing second-growth forests. Despite the potential importance of this region-wide shift in forest microtopography on ecosystem structure and function, the differences in pit and mound size, distribution, and longevity between second-growth and old-growth forests are unexplored. Likewise, although many studies demonstrate that mounds and/or pits are hotspots for tree regeneration there is scant information about whether location on a mound or pit affects tree survival and growth beyond the seedling stage, or whether microtopographic regeneration patterns differ in old-growth and second-growth forests.

We compare a simulated hurricane experiment initiated in 1990 in second-growth forest (the pulldown) and an old-growth forest that was blown down by a hurricane in 1938 (Pisgah) to examine differences in pit-mound microtopography and ecology between second-growth and old-growth forest. At Pisgah, fewer, larger mounds comprised a similar areal coverage as at the pulldown. Repeated measurements of individual pit-mound structures in the pulldown revealed that pit infill proceeded more rapidly than mound erosion. Mound area increased but height decreased over time as soil from the mound tops eroded and spread around the mound base. Although 40% of mounds in the pulldown were > 1 m tall immediately after the manipulation (maximum of 2.9 m), after 25 years, maximum mound height was 0.9 m. In contrast, 11% of mounds at Pisgah remained > 1 m tall in 1989, 50 years after blowdown. At both sites, trees, especially *Betula* spp., were disproportionately found on mounds. Fewer trees than expected grew in pits at Pisgah. Tree mortality was somewhat higher on mounds and pits than on other substrates. As a mechanism to increase stand-level tree diversity, windthrow may be more critical in old-growth forests, in which niches for early-mid successional species are few, than in second-growth forest, in which early-mid successional species already comprise the majority of the trees. Pit-mound structures are a diminished component of second-growth forest, and silvicultural techniques designed to restore old-growth characteristics could include measures to preserve and enhance pit-mound features, and to cultivate large-diameter trees that will eventually create the large, long-lasting pit-mounds of the future.

1. Introduction

Trees build the basic structure of forested ecosystems. This is obvious for the canopy, with its variation in vertical stratification (Oliver, 1980; DeGraaf and Yamasaki, 2001) and horizontal spatial patterning (Franklin et al., 2002; Ishii et al., 2004). Trees also structure the forest floor in important ways. A subtle, but critical example is the pit-mound structures formed by the uprooting of trees. Pits and mounds are microtopographic features with a spatial extent that varies from a single treefall to dispersed large patches formed from multiple uproots across a landscape or even a large region that may persist for centuries following a tornado or hurricane (Foster et al., 1998). Longevity of pit-mound structures varies with climate, site, and soil conditions from less than a decade in some tropical regions (Putz, 1983) to centuries on sandy soils in cold temperate forest (Schaetzl and Follmer, 1990). In temperate forests, visible pit and mound topography may affect

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15–50% of the forest floor (Stephens, 1956; Lyford and MacLean, 1966; Sobhani et al., 2014). The forest process of uprooting and erosion mixes the soil and initiates new episodes of soil formation (Veneman et al., 1984; Lenart et al., 2010), alters ecosystem processes such as soil respiration (Miliken & Bowden, 1996; Kooch et al., 2015), and diversifies microhabitats for tree regeneration and ground-layer plants (Lyford and MacLean, 1966; Carlton and Bazzaz, 1998b; von Oheimb et al., 2007) as well as many other organisms.

Tree diameter is a strong predictor of pit-mound size (Sobhani et al., 2014) so as tree size increases through forest development, pit-mound size and longevity should correspondingly increase, analogous to the relationship between forest development stage, tree size, and canopy gap size (cf. Dahir and Lorimer, 1996). The history of land-use in much of the northeastern U.S. left a lasting imprint on the structure and function of the now re-forested landscape (Foster and Aber, 2004). Forest clearing in the 18th and 19th centuries followed by plowing or grazing eliminated mound and pit topography in areas converted to agriculture. Across the rest of the region the remaining forests were cut intensively and repeatedly, replacing the old-growth forests with smaller trees in second-growth stands that resulted in a progressive reduction in the frequency of production and size of mounds and pits. A major hurricane in 1938 initiated pits and mounds across the region, from southern Connecticut to northern Vermont, but with structures that may be much less robust in stature and longevity, and therefore quantitatively different in function with those from old-growth forests. The dramatic reduction in the size, abundance and landscape distribution of mounds and pits is a significant legacy of land use.

The implications of land use history and forest development on pit-mound size, distribution, and longevity are unexplored. Likewise, despite many studies demonstrating that mounds and/or pits are hotspots for tree regeneration (e.g., Hutnik, 1952; Lyford and MacLean, 1966; Peterson and Pickett, 1990), there is scant long-term data concerning the survival of trees established on mounds or pits (Carlton and Bazzaz, 1998a), or whether microtopographic patterns of regeneration differ in old-growth versus second-growth forest.

Here, we compare a designed and natural experiment to examine differences in pit-mound microtopography and ecology between second-growth and old-growth forest. Repeated pit-mound measurements and tree regeneration data are available from a simulated hurricane experiment (the "pulldown") initiated in 1990, and located in a second-growth forest in central New England (Cooper-Ellis et al., 1999; Barker Plotkin et al., 2013). The nearby 300+-year-old old-growth Harvard Pisgah Tract ("Pisgah") was blown down by the 1938 hurricane (Cline and Spurr, 1942) but left intact, and therefore retains impressive downed wood and pit-mound structures (Henry and Swan, 1974; Foster, 1988a; D'Amato et al., 2017). Fifty years after the hurricane, an intensive study and historical reconstruction of the site and its vegetation (Schoonmaker, 1992) included an inventory of mound sizes and tree regeneration on the mounds, pits, and other substrates. Through a comparative study of the designed pulldown experiment and the old-growth Pisgah stand, we test the following specific hypotheses:

(1) Within a site, the forest floor area covered by pit-mound structures produced by an uprooting event decreases over time, as mounds erode and pits fill.
(2) Following severe wind disturbance, old-growth forests, as represented by Pisgah, have fewer, taller, mounds than second-growth forests, as represented by the pulldown. This is primarily a function of the fewer, larger trees in old-growth versus second-growth forests.
(3) Tree diameter is a strong predictor of mound and pit area (cf. Sobhani et al., 2014), forming a relationship that does not vary by tree species. Alternately, varying root structures may lead to diameter-area relationships that vary by species. Robust prediction of mound-pit area for a wide range of forest sizes and types informs better prediction of the microtopographic consequences of uprooting events.
(4) Mounds persist longer than pits. We expect pits to fill with litter and soil from adjacent mounds, whereas mound erosion may be slowed by vegetation rooted on mounds.
(5) As found in earlier studies for tree seedlings (e.g. Carlton and Bazzaz, 1998a), we expect mounds to persist as favorable sites for trees as they develop from seedlings to small trees, especially for early-to-mid successional species. Conversely, we expect tree recruitment in pits to be low to absent.
(6) Trees on mounds continue to benefit from the elevated position and light levels experienced as seedlings, and are thus larger and grow more quickly than those on adjacent intact sites. However, because of continued mound erosion, these trees have a higher mortality rate than those on adjacent intact sites.

The two sites differ in dominant tree species before disturbance and today, and the measurements of each site were taken at different intervals following disturbance. However, the comparison provides the opportunity to bring together intensive measurements from a second-growth and an old-growth forest to yield insights into the dynamics and importance of pit-mound structures that would not be available if each site was presented alone. In particular, the comparison can generate an understanding of the structural differences of the forest floor between old-growth and second-growth forests that can inform silvicultural techniques designed to enhance late-successional characteristics (Franklin et al., 2002; Keeton, 2006; Bauhus et al., 2009) and allow scientists, landowners, and managers to anticipate some of the changes that current forests will undergo with ongoing development.

2. Materials and methods

2.1. The simulated hurricane experiment

The pulldown experiment is located on a gentle (5°) northwest slope at the Harvard Forest in central Massachusetts (42.49 °N, 72.20 °W, 300–315 m a.s.l.; Fig. 1a) on well-drained to moderately well-drained stony loams derived from glacial till overlying schist bedrock. The site was most likely a cleared pasture during the 1800s; the current *Quercus rubra-Acer rubrum* (red oak-red maple) forest developed following a clearcut in 1915. The study area is surrounded by similar forest. The climate is cool temperate (July mean 20° C, January mean −7 °C); 1100 mm average precipitation is distributed evenly throughout the year.

Details about the experiment can be found in Barker Plotkin et al. (2013). In brief, a 0.8 ha experimental site (50 × 160 m, the "pulldown") and 0.6 ha (50 × 120 m) control site were oriented approximately east to west and separated by a 30 m forest buffer. During peak hurricane season in early October 1990, 276 trees were toppled in a northwesterly direction of natural treefall (Boose et al., 2001), using a winch and steel cable attached ca. 6 m up the bole of each tree in an effort to simulate the damage to similar stands in the 1938 hurricane (Foster, 1988b). Force was applied by the winch only until the stem snapped or roots failed and the mass of the crown brought down the tree. Stems were not pulled beyond their initial point of repose. The winch was positioned off the study site so that all plant and soil disturbance resulted from uprooting or bole breakage, plus damage to 325 trees hit by the toppled trees (Cooper-Ellis et al., 1999). The manipulation effectively simulated the effects of a hurricane in terms of overstory damage, damage to intermediate and understory vegetation, and physical structure. Eighty percent of the canopy trees, and two-thirds of all trees > 5 cm diameter at breast height (dbh), were damaged directly or indirectly by the manipulation. Uprooting, which creates pit-mound structures, affected both trees pulled down and indirectly damaged trees, and was the most common form of damage (40% of the trees were uprooted; Cooper-Ellis et al., 1999; Fig. 1c).