Crossdating of disturbances by tree uprooting: Can treethrow microtopography persist for 6000 years?

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ABSTRACT

Establishing disturbance frequencies in different types of forest ecosystems is an area of considerable research. We use several overlapping dating methods – robust repeated tree–censuses, dendrochronology and radiometric techniques (radionuclides ^{14}C, ^{210}Pb, ^{137}Cs, ^{226}Ra) – to date 302 pit-mounds, formed by uprooting, in 3 different forest ecosystems. Our research goal was to better understand the disturbance frequencies in these ecosystems and establish the potential longevity of treethrow mounds. At the same time, we tested the applicability of multiple dating methods in different kinds of stands, including two sites in Central Europe and one in the Great Lakes region, USA.

We used tree-census data to establish the ages of the youngest (<37 yr) uprooting events, ^{210}Pb dating (including ^{137}Cs and ^{226}Ra) to date treethrow events younger than ca. 200 years, dendrochronological dating for sites less than ca. 400 years old, and radiocarbon dating for assumed older sites. In order to maximize the reliability of these age estimates, we compared the dates by evaluating different methods with maximal overlap – a method we call crossdating. Theoretically, our data provide (i) "minimum-limiting" ages of disturbance events, using dendrochronology, tree-censuses, ^{210}Pb- and/or ^{14}C-dating of samples from the organo-mineral sedimentation funnel within the treethrow pit, (ii) "real" ages of events, using dendrochronology, and/or (iii) "upper-real" or "maximum-limiting" ages of the events, using ^{14}C-dating on remnants of uprooted trunks and charcoal from buried A-horizons in mounds.

Responses in the radial growth of trees near by uprooting disturbances were usually detectable for 20 years, and were specific to each region and tree species. Repeated tree-censuses (13,795 trees from 72.84 ha) suggested that the ratio of bole breakages to uprootings was 2–3:1, and that the treethrow rotation period approximated 1250–1380 years for some sites in Central Europe. At our European, beech-dominated sites, the maximal longevity of the treethrow microtopography was ca. 220 years on the fine-textured Haplic Cambisols and exceeded 1700 years on sandy-loam Entic Podzols. Finally, on the sand-textured Albic Podzols of northern Michigan, even greater longevities were achieved, with one mound returning a ^{14}C age of 5260 ± 30 BP (median of calibration age 4077 BC) – by far the oldest feature reported in the literature. Sedimentation rates in treethrow pits, calculated using the ^{210}Pb technique, were 0.05–0.28 cm year^{-1} in the beech-dominated European forests, and 0.07–1.4 cm year^{-1} in the hardwoods of Michigan. Radiocarbon dating of fungal sclerotia in treethrow pits can also help inform the disturbance history.

1. Introduction

Determining the age of disturbance events is critical to understanding their role in the dynamics of natural ecosystems. Equally important is the assessment of exactly how long the effects of such disturbances are retained on the landscape. In disciplines such as pedoantracology (Robin et al., 2013) and dendrogeomorphology (Šilhán et al., 2012), the use of absolute dating techniques (radiometry, optically stimulated luminescence etc.) in landscape development and forest ecology studies is expanding rapidly. Moreover, many research questions regarding disturbance frequencies, soil development, and landscape stability await only an appropriate method of dating. Although it appears simple and straightforward – the age estimation of a sediment body or a rock or a soil

surface – there are a number of hidden assumptions built into each dating method and, therefore, into the interpretations of the dates. Therefore, we argue that a multiplicity of dating techniques, allowing for overlap and crossdating, is the most effective means by which forest disturbance events, and the microtopography that results from them, can be studied temporally (Dynesius and Jonsson, (1990)). Simply put, the accuracy and efficacy of dating techniques often restricts studies of disturbance history – in a broader sense historical contingency – in forest ecosystem dynamics (Phillips, 2004).

Tree uprooting dynamics affect all forests and impact a majority of forest ecosystem components, and at a number of spatial scales (Schaetzl et al., 1989; Ulanova, 2000). Unfortunately, our limited understanding of the frequencies and persistence of disturbance events in different ecosystems constrains further work on such related topics as soil formation (Šamonil et al., 2010a), soil biology (Nachtergale et al., 2002), plant ecology including bryology (den Ouden and Alaback, 1996; von Oheimb et al., 2007), forest ecology (Šebkova et al., 2012), lichenology (Lohmus et al., 2010) and geomorphology (Small, 1997). For the same reason, discussions about the validity of general ecological concepts in forest ecosystem dynamics is also limited because we lack a firm grasp on the temporal nature of the major disturbance events that impact the system, i.e., tree uprooting. For example, data from precisely-dated surfaces have recently revealed the limits of the traditional steady-state theory of soil formation, simply due to the biomechanical effects of trees (Phillips and Marion, 2006). As a result of these disturbances, divergent soil evolution has even been proposed for some regions, instead of the traditionally supposed convergent soil evolution (Phillips, 2006).

Because so little is known about the age, formation recurrence intervals, and potential longevity of pits and mounds formed by tree uprooting, our ability to determine how soil development rates are affected by these features is also limited. Studies of this topic are fragmental and represent isolated instances, making generalizations difficult. Soil development and ecosystem disturbance models must, as a result, operate using assumptions that are incompletely informed by data (Bormann et al., 1995; Kramer et al., 2004; Schaetzl, 1990; Skvorcova et al., 1983; Ulanova, 2000). Previous studies have been able to testify to the general importance of tree uprooting in soil formation, but have limited ability to inform the scientific community about rates or pathways of pedogenesis as affected by this type of pedogenic disturbance. At the same time, it is clear that a number of soil properties do not develop linearly (Bockheim, 1980; Schaetzl et al., 1994) and that assuming linear development can result in false conclusions. The impacts of polygenetic or even retrogressive soil development that occurs at sites disturbed by tree uprooting remains, therefore, largely unresolved (Šamonil et al., 2010a). For such research to be fully informed, we must date wide suites of soils and uprooting features with optimal accuracy, or (rather theoretically) perform long-term studies of processes at disturbed sites.

Although the adoption of individual techniques has general rules, the local particularities of forest ecosystems cannot be excluded (Phillips, 2004). Local processes and conditions contribute to the longevity of treethrow pit-mounds. However, little is known about the typical and maximal longevities of these features. A range of treethrow pit-mound longevity from 5 to 2420 years has been reported for different biomes worldwide (review by Šamonil et al., 2010a). Nonetheless, many areas remain unstudied and the effect of substrate and environment on pit-mound longevity is also poorly informed. Thus, we argue for the use of more and better dating techniques, and in different forest types, in order to enrich a pit-mound longevity database that can then properly inform other studies of disturbance cycles and soil formation. We also argue that the use of a single dating technique for all such instances cannot

provide adequate results, because no one technique has the accuracy to resolve the ages of pits and mounds over their maximum global age span (Dynesius and Jonsson, 1990; Zeide, 1981). Additionally, no one technique can be used for all pit-mound features, because the material needed for a given dating technique may not always be present, or the age of the feature may exceed the limit of the technique. And lastly, treethrow dynamics contain some particularities that affect the application of traditional dating techniques: (i) the erosive and sedimentation processes within pit-mounds with simultaneous soil-formation, (ii) mixing of material from original soil horizons with newly formed horizons, (iii) the considerable spatial isolation of processes, which frequently prevents the use of analogy with adjacent events, (iv) the fine spatial scale of treethrow pit-mounds, which limits the application of some methods, and (v) the limited validity of some general presumptions such as the steady-state model of soil formation.

In this study we applied tree-censuses, dendrochronology and radiometric techniques to date tree uprooting events in three different forested environments – two in Europe and one in North America. Our study applied multiple dating methods – a technique we call crossdating. We hope to add to the discussion about the longevity of treethrow features and the frequency of forest disturbance by uprooting, in regions with different types of soils and forest cover. As a result, we believe that our research will provide considerable additional data for subsequent studies of the effect of tree uprooting dynamics and its importance in soil formation and forest ecology.

2. Materials and methods

2.1. Study sites

We studied the ages of tree uprooting events at three localities of differing geology and soil parent materials, although all sites are well-drained (Fig. 1, Table 1). Haplic Cambisols have formed on flysch parent materials in the Razula reserve of the Czech Republic, Entic Podzols have developed on granite residuum in the Zofin reserve of the Czech Republic, and Albic Podzols occur in outwash parent materials at the Michigan sites (soil taxonomy according to Michéli et al., 2007). These soils form a gradient of soil formation and, as we later discovered, treethrow mound longevity. Significant differences in particle-size distribution also appeared among localities. While the fraction <0.01 mm reached nearly 50% in the B-horizon of Haplic Cambisols (Šamonil et al., 2010b), this fraction was practically absent in Albic Podzols; here, the fraction 0.1–2.0 mm predominated (ca 98% sand). At the Michigan sites, managed northern-hardwood forests are widespread. The central European sites are dominated by natural (spruce)-fir-beech forests (Table 1). The Zofin forest reserve has the longest history of continuous protection in the Czech Republic (since 1838) and, according
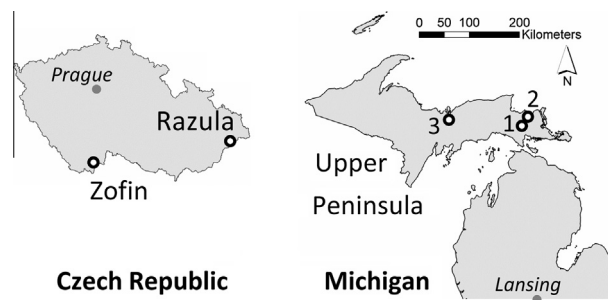

Fig. 1. Location of the Razula and Zofin study areas in the Czech Republic, and the research sites in Michigan, USA (see details in Sections 2. and Table 1). Locations of capitals are shown.

to our knowledge, is the fourth oldest, continuously protected reserve in Europe. This locality belongs to the International Long-Term Ecological Research network (CZ-LTER, www.lter.cz) and to the Smithsonian Institution Global Earth Observatory (SIGEO, www.sigeo.si.edu) as the first plot in continental Europe. The Razula forest reserve has been under protection since 1933.

2.2. Site selection criteria

Treethrow pit-mound pairs were selected for dating using a random stratified selection at the Razula site, from 1562 treethrow pit-mounds studied previously (Šamonil et al. 2008, 2009). In order to effectively utilize the dendroecological survey of Šamonil et al. (2009), a suppositional gradient of age (SGA) was constructed on the basis of directly measured characteristics (thickness of A-horizon on mound, steepness of mound etc.). Pit-mound features designated for dating were then chosen regularly along this gradient; this sampling scheme allowed us to obtain a representative selection of pit-mound pairs of various age, at the Razula site. We also dated additional pit-mounds using a mathematical model (Šamonil et al., 2009) and we calculated rotation period (how often an area equivalent to the entire study area is disturbed, see Pickett and White, 1985). Tree-census dating of tree uprooting events (see below) has been applied to this entire area since the 1970s, as at Zofin (see below).

At the Zofin site, treethrow pit-mounds were chosen for dating by using a random stratified selection method (Šamonil et al., 2011). We initially started with a set of 1733 treethrow pit-mounds, previously studied in detail (Šebkova et al., 2012), but because dendrochronology was one of our key approaches, we eliminated sites unsuitable for this technique, i.e., those strongly affected by the Kyrill windstorm on 18 January 2007 (Šebkova et al., 2012). Based on whole-area tree-census data, available since the 1970s, and indirect dating of all present pit-mounds (Šebkova et al., 2012) we also were able to calculate the rotation period in Zofin.

In Michigan, the set of treethrow features to date was selected subjectively across various northern hardwood stands (Fig. 1). Selected stands occurred on Haplic Podzols, on public land, and (as much as possible) with limited direct human historical management. Because radiocarbon dating was a key technique for this area, where we assumed that the microtopography is quite old, based on previous work (Schaetzl and Follmer, 1990), we only sampled sites that had a buried A-horizon in the mound (as per Schaetzl, 1986) or had retained the tree trunk from the uprooting event. Random selection of cases would not have been effective, therefore for this area. We excavated soil profiles in the frontal part of the treethrow mound (in the direction of treefall) at 70 treethrow pit-mounds. Where present, samples were removed for ^{14}C dating. This occurred where the mound retained remnants of the uprooted tree (raw or burnt wood) and/or a buried A-horizon with charcoal fragments (see Section 2.5.2.). Uprooted tree trunks with fresh pit-mounds often burn during or shortly after the uprooting event, resulting in burial of a charcoal-rich layer between the original undisturbed ground surface and the overturned root plate (Schaetzl, 1986; Schaetzl and Follmer, 1990). The clear connection between the uprooted tree or buried A-horizon with the dated pit-mound microtopography was determined by morphological study of the former and newly formed soil horizons. We found that the uprooting event lifted the substratum material behind trunk base (horizons Bw, Bs), and shifted the location of the original Bhs- and Bsm-horizons alongside of trunk base to a general vertical or overturned orientation. After viewing several examples of this phenomenon, it became apparent that similar processes of burial of the wood and charcoal from the uprooted tree were occurring during uprooting, and this "genetic" linkage

enabled us to select only wood that was associated with the uprooting even, for dating. In total, 14 treethrow pit-mounds were dated by radiocarbon, each differing in the acuteness of microtopography and the degree of podzolization on the mound, which were used a priori to assess the likely age of the features, in the field.

2.3. Dating by tree censuses

Repeated tree censuses have taken place at the Razula and Zofin sites since 1970s. Those within the 50 ha Zofin core zone exhibit no direct past management impacts (Šamonil et al., in press). The locations of all living trees with DBH ⩾ 10 cm were measured in 1975, 1997 and 2008 (Král et al., 2010a,b). For each tree, we determined the actual DBH as well as the health of each individual (living/dead/standing/lying/stump/treethrow pit-mound, etc.). At the same time, each tree was identified on the previous stem map. In 2008, we independently evaluated the effect of a storm on 18th January 2007, which significantly disturbed the tree layer (Šamonil et al., in press). By comparing individual stem maps we were able to determine if a tree had uprooted in 2008–2007, 2006–1997, 1996–1975 or before 1975; length of intervals between measurements delimit accuracy of dating. Identical surveys took place at Razula, across an area of 22.84 ha, in 1975, 1995 and 2009, except that all trees of DBH ⩾ 20 cm were measured until 1995; the threshold was reduced to a DBH of 10 cm in 2009 (see details in Král et al., 2010a). We lack similar data for the Michigan sites. Nonetheless, because forest stands in this region have been continuously affected by human management, and because of the expected great longevity of most treethrow features here, tree-census data would have been of limited use at these sites.

2.4. Dendrochronological dating

Dendrochronological dating was applied at all three localities. We studied the radial growth of trees that either (i) had rooted on a evaluated pit-mound feature, (ii) were newly grown in close vicinity to a pit-mound feature, or (iii) grew in the vicinity (within 9 m) of a pit-mound, but which clearly had been established before uprooting event. Ages of trees in categories (i) and (ii) defined the minimum-limiting age of treethrow events, whereas radial growth of trees in category (iii) revealed the direct influence of the tree uprooting event on the growth of nearby trees, and established the actual age of the uprooting event. We distinguished categories (ii) and (iii) on the basis of so called gap origin (Lorimer et al., 1988); if the initial growth of a tree had reached a calculated value, we supposed that the initial growth at the height of 1.3 m of this tree occurred in a gap (for details, see in Šamonil et al., in press). A treethrow event was considered to be successfully dated if the release event was cross validated in surrounding trees. The maximal error of this approach is 7 years (Šamonil et al., 2009). Partial results from the Razula and Zofin sites have been published by Šamonil et al. (2009) and Šebkova et al. (2012). In this paper, we present only aggregated releases that reached the 20% relevant boundary line (Black and Abrams, 2003) for successfully dated pit-mound features. We used the boundary line of Splechtna and Gratzer (2005) at Razula (see Šamonil et al., 2009), and the boundary line of Šamonil et al. (in press) at Zofin. We did not find any published boundary line for Acer saccharum and the number of data increments taken in Michigan did not reach the recommendation by Black et al. (2009) for the construction of a local boundary line. Because of this, release was determined according to Nowacki and Abrams (1997); identical releases were determined according to the competitive approach of Fraver and White (2005).

In the case of successfully crossdated treethrow features, we calculated the mean radial growth with a range ±20 years since

the disturbance event. The curves allow for a rough comparison of radial growth dynamics among the localities for these tree species, following fine-scale disturbance events such as the uprooting of a single tree. The 95% nonparametric bias-corrected and accelerated confidence intervals were constructed for mean values of core series sets where at least 7 trees occurred (Efron and Tibshirani, 1993).

2.5. Radiometric dating

2.5.1. ^{210}Pb dating

We also sampled 3 treethrow pits at Zofin and 1 in Michigan, all with an expected age of 100–300 years (based on dendrochronology and radiocarbon dating), using the ^{210}Pb method (Walker, 2005). Within treethrow pits, samples were taken from the upper organic (O) and upper mineral A horizon, down to the undisturbed mineral soil horizon, at 5 cm intervals, to a maximal sampling depth of 50–70 cm.

Samples were measured for ^{210}Pb by well-in-well geometry in a SILAR® low-background anticompton-anticoincidence device with a specially designed 40 × 40 mm Na(Tl) well-type LEADMETER® detector with a total efficiency of 46.2% (for 210Pb line of 47 keV) placed in a well-type guard NaI(Tl) detector 160 × 125 mm in 10 cm low-background lead shielding (Hamrová et al., 2010). A Canberra DSA 2000 multichannel analyzer controlled by GENIE 2000 software was used to determine the specific activities of isotopes (^{210}Pb, ^{226}Ra and ^{137}Cs). The measuring time for individual samples was 1 day, and 3 days for the background.

2.5.2. Radiocarbon dating

At the Michigan sites, after excavating 14 pit-mound pairs, including the undisturbed soil adjacent to them, we removed woody samples and charcoal from buried A-horizons, and if present, uprooted tree trunks. If the sample clearly originated from the uprooted trunk, we dated one sample per site, but for samples from buried A-horizons, we dated 2–3 samples per site. Distinguishing wood samples that may have originated from tree trunks vs those that are wood and charcoal on the forest floor, and later buried, can be challenging, particularly in older treethrow features. We relied on the observation that the decayed trunk leaves more cylindrical traces in soils, whereas the buried A-horizon materials leave more planar traces. Cylindrical traces were distinguished from planar traces by digging short transects orthogonal to direction of tree fall, as well as the direction of the main profile; the uprooted tree trunk was indicated by rather circular profile there. The majority of samples were taken in the field, although for a minority of samples we could isolate charcoal only after sieving in the laboratory. We were careful to remove possible contaminants (roots, fungal mycelia, molds, etc.) from datable wood and charcoal fragments. Tree species (as possible), degree of vitrification and the presence of bark were all determined later, under a microscope. We preferred to sample only the largest charcoal or woody fragments, with bark, as many of these were identifiable to species. We assumed that the samples from buried A-horizons provide maximum-limiting ages for the treethrow event, while samples originating from an uprooted trunk (in particular with the bark) more likely delimit the upper-real age of the event (Wang et al., 1996).

Based on the minimum-limiting age of trees growing on treethrow pit-mounds performed at the Zofin site, we determined that treethrow pit-mound pairs older than 350 years exist there. At the same time, clear remnants of uprooted tree trunks or buried A-horizons were absent in the older mounds, due to differential decay and fire frequency. For this reason, we had to search for other material suitable for dating the older events. To that end, we sampled the deepest and thus the oldest part of the "organo-mineral sedimentation funnel" within the 4 oldest treethrow pits at Zofin. After floating and passing of samples through sieves of 5.0, 2.0, 1.0, 0.5, and 0.25 mm openings, we selected the best samples for radiocarbon dating, by examination under the microscope (see below). We avoided dating amorphous organic materials due to the continuous inputs of fresh organic matter in soils, which makes the ^{14}C age of soil organic matter significantly younger than the true age of the soil, or in this case, the treethrow pit. Moreover, no extraction technique of a specific fraction of soil carbon has proven reliable for 14C dating, and results for a given procedure can vary among soils (see Dalsgaard and Odgaard, 2001; Schaetzl, 1992; Scharpenseel and Becker-Heidmann, 1992; Wang et al., 1996).

In addition to dating large, intact fragments of plant and animal bodies from the thick O and A horizons in the treethrow pits, we also dated spherical organic formations there, i.e., fungal sclerotia. We determined the taxonomic origin of these formations using DNA analyses (see Section 2.6.). We hypothetized that the growth and presence of sclerotia were connected with the decomposition of organic material during the gradual filling of a treethrow pit after a disturbance event. This presumption was validated by our observations of higher proportions of fungal sclerotia within pits, as compared to corresponding horizons in adjacent undisturbed soils, and by a decrease of sclerotia ages toward the surface, within pits. For full verification of this hypothesis, we dated (using ^{14}C) fungal sclerotia from the 50, 30, 15 and 5 cm depths within pits at Zofin, quantified their proportion in the 5.0–0.25 mm soil fraction (see van der Veen, 1984), and compared frequencies of sclerotia with those from adjacent undisturbed soils.

A total of 38 samples (Tables 2 and 3) were analyzed for radiocarbon dating at the Poznan Radiocarbon Laboratory (http://radiocarbon.pl) using accelerator mass spectrometry (AMS); the two largest samples were analyzed at the Nuclear Physics Institute of the ASCR using conventional, liquid scintillation counting (CT) techniques. Calibration of radiocarbon data to calendar years was computed using the OxCal program (Bronk Ramsey, 2001) and IntCal09 curve (Reimer et al., 2009). We calculated the median of the calibration probability distribution to assign a single, most likely, calendar date to each sample (Telford et al., 2004).

2.6. DNA analyses

Analysis of DNA from fungal sclerotia (approx. 0.05 g each) was performed to confirm its origin. DNA was extracted after surface sterilization with 3% hydrogen peroxide solution using the NucleoSpin® DNA Isolation Kit (Macherey-Nagel) according to the manufacturer's instructions using the SL1 solution and the SX Enhancer. The extracted DNA was cleaned using the Geneclean Turbo Kit (Biogenic). The DNA purity was checked on a Nanodrop and DNA concentration was quantified using the Quant-iT™ PicoGreen dsDNA Kit (Invitrogen).

For the identification of sclerotia, isolated DNA was analyzed by 454-pyrosequencing. A two-step PCR amplification using MID-containing composite primers was performed to obtain amplicon libraries following a previously described method (Baldrian et al., 2012) targeting the ITS1/2 regions of eukaryotic rDNA: ITS-1 (5′-TCCGTAGGTGAACCTGCGG-3′) and ITS4 (5′-TCCTCCGCTTATTGATATGC-3′) (White et al., 1990). PCR amplicons were quantified using the Quant-iT PicoGreen Kit (Invitrogen, USA). An equimolar mix of PCR products was prepared for each primer pair, and the pooled products were sequenced on a GS Junior sequencer (Roche). The pyrosequencing data were processed as described in Baldrian et al. (2012). After denoising and removal of the chimeric sequences, fungal sequences were shortened to 380 bases and clus-

tered at a 97% similarity level to obtain the Operational Taxonomical Units (OTUs). Consensus sequences were constructed for each cluster, and the closest hits were identified by performing a BLAST (blastn) search against the nucleotide database at NCBI (http://www.ncbi.nlm.nih.gov/blast).

3. Results and discussion

3.1. Tree census

Tree census data from Razula and Zofin have allowed for the detailed and thorough analysis of tree layer dynamics there, since the 1970s. In total, 2,526 living trees with DBH $\geqslant$ 20 cm were recorded at Razula (22.84 ha) in 1972. Fig. 2 shows the development of these 111 trees per hectare, up to 2009 at Razula. Over the past 37 years, 43 trees ha^{-1} had died (a total of 984 trees) and 219 trees ha^{-1} had been recruited. The decrease of the DBH threshold (Section 2.3.) resulted in an increment of another 215 trees ha^{-1} in 2009. Repeated tree censuses revealed the omnipresent decline of mature trees and the rapid recruitment and growth of juveniles at Razula. At both Razula and Zofin, many large trees of *Abies alba* had died and been replaced mainly by advanced regeneration of *Fagus sylvatica* (Šamonil et al., in press). However, natural regeneration was not as dynamic at Zofin, perhaps because of lesser human impacts in this forest reserve (Průša, 1985) and a lower air pollution load after the 2nd World War (www.emep.int). However, both factors most probably accelerated the dieback of *A. alba* in Central European fir-beech forests (Elling et al., 2009; Kozáková et al., 2011). Of an initial 225 trees ha^{-1}, an average of 138 living trees with DBH $\geqslant$ 10 cm had been recruited and 97 trees ha^{-1} had died at Zofin between 1975 and 2008.

Trees of DBH 55–75 cm predominated among dead trees at Razula. Within this category, broken trees prevailed, with a general proportion 2.8 times higher than trees that had been uprooted. At Zofin, trees with larger basal areas were also more often broken; the proportion of breakages was in total 2.0 times higher than uprootings. A higher proportion of uprootings here had occurred because of the Kyrill winter storm of 2007 (see Fink et al., 2009). Our results indicate a predominance of breakages over uprootings with a ratio of 2–3:1, which may be generally valid in natural (spruce)-fir-beech forests across Central Europe. This ratio increased with increasing DBH class. Contrary to those at Razula, mainly smaller trees with DBH $\leqslant$ 35 cm died at Zofin. The proportion of observed standing dead trees was marginal in both localities in the 2000s. Some dead trees decomposed entirely between measurements, rendering our assessment of the cause of death uncertain. The Kyrill storm on 18th of January 2007 contributed to this last category at Zofin. In the dense tangle of fallen trees we were sometimes not able to identify trees from previous tree censuses. Nonetheless, repeated tree-censuses represent a suitable and reliable dating method for younger disturbance events in forests in different environmental conditions.

Including the deaths of trees that had reached DHB values of 10 cm or larger after 1975, the tree uprooting dynamics at Zofin were 1.2 uprooting events ha^{-1} year^{-1}. Given that the average size of new uprooting features was 5.9 m^2 (only fresh pit-mounds without indications of uprooted trunk decay were used for calculation, Shapiro-Wilk's W test and Box-Cox transformation were applied), this represents a rotation period of approximately 1380 years. However, if we also take into account the post disturbance spread of mound materials by erosion onto adjacent, originally undisturbed sites, the rotation period for disturbance is reduced to approximately 870 years. The existence of exceptionally robust tree census data (Fig. 2) facilitated this calculation. Due to the considerable spatial variability of the tree layer in natural, beech-dominated forests, the use of traditional 1 ha plots is probably insufficient for the robust calculation of the role of tree uprooting in forest dynamics (Král et al., 2010a,b). At Razula, Šamonil et al. (2009) calculated, for a 10.8 ha area, a rotation period of 1250 years, suggesting that a rotation period of about 1200–1400 years in natural beech-dominated forests in Central Europe could have wide validity and application. Rotation period data expresses the aggregate importance of tree uprooting dynamics in a locality, but it does not address the spatial relations of this process, which must also be taken into account.

The probability of an individual tree being uprooted is spatially variable within a forest, commensurate with the local disturbance history (Šebkova et al., 2012; Janik et al., in press). *F. sylvatica* and *A. alba* regeneration occurs with higher probability on mounds in comparison to undisturbed sites or pits (Simon et al., 2011; Šebkova et al., 2012). At the same time, soils on mounds are generally loose and tree roots are therefore easily exposed as soils erode. This relationship is so predictable in some forests that it can be used for the indirect dating of treethrow microtopography (Zeide, 1981). The loose soil further weakens the stability of trees that have exposed roots, weakening their anchorage and altering the tree's natural center of gravity (Mayer, 1989). Both conditions render trees on mounds more susceptible to uprooting. As a result of these spatially non-random processes, we postulate that the pattern of disturbance by uprooting is complex but in some ways predictable, perhaps opening up an area of future research.

Complex disturbance pattern histories, together with different pit-mound sizes, allow for greater differences in maximal treethrow feature longevity (see below) and rotation periods between localities. Nonetheless, calculation of uprooting rotation periods assumes an approximately spatially balanced formation of uprooting events over time. However, indirect dating of treethrow pitmounds at our sites in Europe demonstrated the limits of this assumption because the process of uprooting seems to be rather
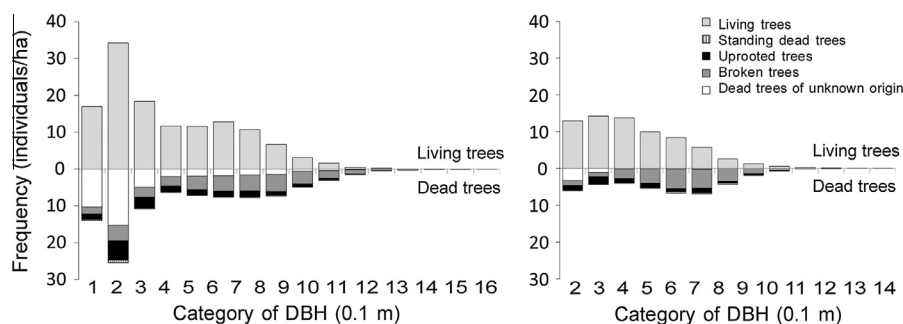

Fig. 2. Changes in the living tree layer in Razula (right) and Zofin (left) between the 1970s and 2000s. Only living trees in the 1970s were used in the analysis. We show the original category of DBH (see details in Section 2.3.).

episodic in time, even at coarse spatial scales (Šamonil et al., 2009; Šebková et al., 2012).

3.2. Dendrochronological dating

We applied dendrochronological methods to obtain minimum-limiting ages: up to 148 years for pit-mound sites in Michigan, up to 191 years at Razula and up to 392 years at Zofin. However, dendrochronology can also directly track disturbance events, as evidenced by the radial growth responses of surrounding trees to disturbances. Dynesius and Jonsson (1990) used, successfully, different dendrochronological techniques in dating treethrow events younger than 50 years in Scandinavian boreal forests. However, for older treethrow features, their success rate decreased to 25%. Šamonil et al. (2009) and Šebková et al. (2012) achieved higher success (60–70%) when dating events up to approximately 250 years of age, using similar techniques in (spruce)-fir–beech forests in the Czech Republic. The higher success in these studies was probably related to the finer criteria of dating, because we used the boundary line approach and a lower threshold value to determine release. Also the different forest type may have increased the success of this type of dating at this site. Both A. alba and F. sylvatica are highly shade-tolerant, and their response to disturbances could be more noticeable in Central Europe, as compared to Picea abies in boreal forests.

Release responses of trees to local-scale disturbance events were unique to each region, as well as tree species (Fig. 3). Except for A. alba, the responses of trees were visible for at least 20 years. A. alba responded faster and more intensively to disturbances, as compared to F. sylvatica at Razula but slowly than F. sylvatica at Zofin. More intensive radial growth of F. sylvatica after disturbance at Zofin, as compared to Razula could be connected with higher expected mean size of gaps after tree uprooting at Zofin. Growth reactions of P. abies were more variable. The responses of all A. saccharum trees within the small sample in Michigan were comparable to the average responses of trees in European forests.

We stress that we have only presented data for established releases that followed from tree uprooting events, crossdated in a core series of several trees, using standard dendrochronological techniques (Schweingruber et al., 1990). Studying tree responses to independently identified disturbance events (e.g. using tree censuses) revealed that some trees expressed low growth reactions; these disturbances would not have been detectable using dendrochronology alone. Šamonil et al. (2009) found that approximately 12% of trees responded to disturbance events by a growth change of ⩽ 10% of the boundary line in a natural fir-beech forest. However, Šamonil et al. (in press) concluded that releases within 20–50% of the boundary line were frequently false in the same forest type. These findings reveal the limits – and point out the possible errors – of dendrochronological techniques for dating fine level, localized disturbances in natural forests, at least for Central Eur-
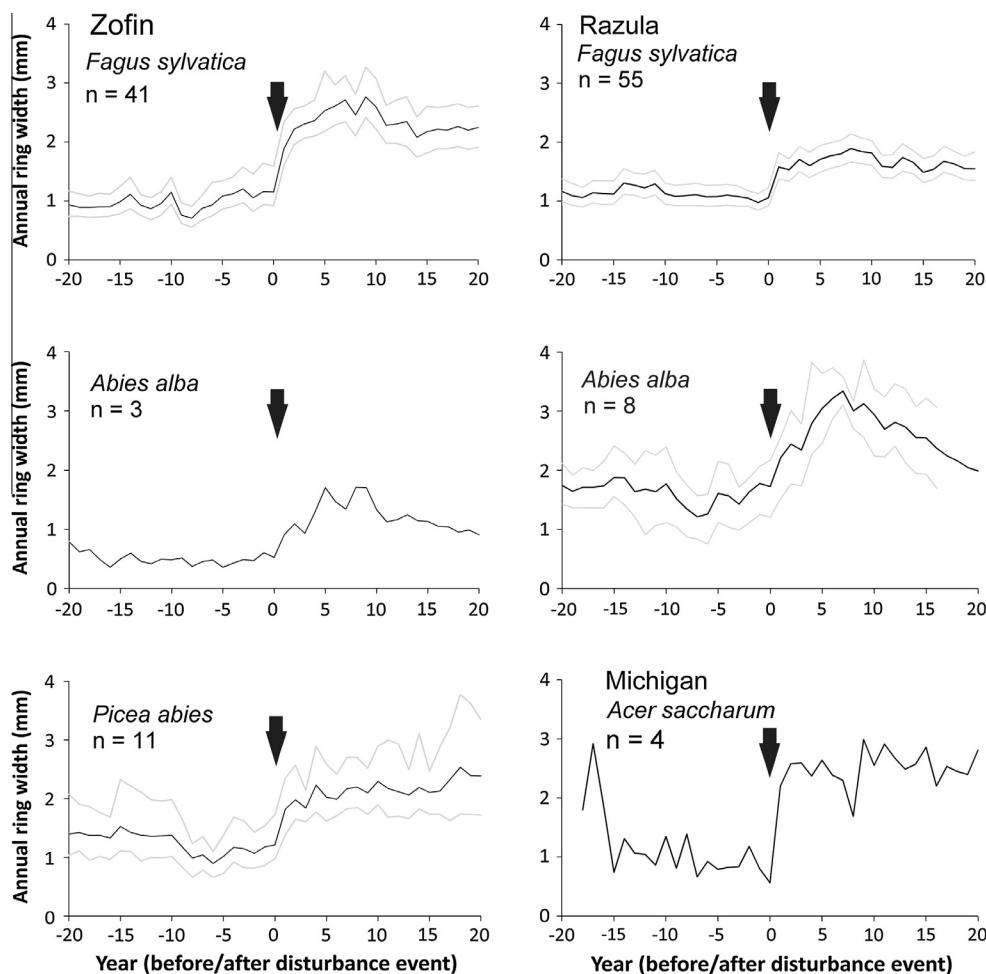

Fig. 3. Average response of trees to nearby, single tree, uprooting events according to locality and tree species. Arrows show disturbance events, thin lines show confidence intervals. Real ages of core series of trees responding to disturbance events were substituted for relative scale, where disturbance events represent zero years. The 95% nonparametric bias-corrected and accelerated confidence intervals were constructed for mean values of core series sets where at least 7 trees occurred (see details in Section 2.4.).

ope. Application of criteria to remove some of the false releases (e.g. weak growth responses of trees to climate changes) can, unfortunately at the same time eliminate some actual disturbance events from the data set. The proportion of these true responses is not known during individual disturbance dating or during studies of forest disturbance history (e.g. Panayotov et al., 2011).

Therefore, future research should examine responses of trees to known disturbance events empirically (see Stan and Daniels, 2010), and define dendrochronologically detectable threshold events, i.e., a "nugget of disturbance history" (Šamonil et al., in press). Dendrochronological studies of treethrow event ages could also be refined by comparing living core series with those taken from the trunks of recently uprooted trees (Lombardi et al., 2008). Furthermore, in regions where large stones are separated from the bedrock during tree uprooting, lichenometry could also be useful as a relative dating (supportive) method (Innes, 1985) for timeframes of a few hundred years (Brown, 2011). As far as we know, lichenometry has not been used for this application.

3.3. Radiometric dating

3.3.1. ^{210}Pb dating

One of the traditional techniques for detecting erosion rates and sedimentation velocities of soils is the use of "unsupported" ^{210}Pb dating (Walling et al., 2003), even though bioturbation can present a problem. According to our current knowledge, however, ^{210}Pb has not been previously applied to treethrow event dating. Organisms like earthworms or ants actively mix the soil to depths ranging from a few centimeters to a few meters and affect the vertical transport of radionuclides (Matisoff et al., 2011). Treethrow pit infilling is undoubtedly most rapid in the period immediately after uprooting. Later on, the infilling slows and presumably becomes more regular, making ^{210}Pb dating applicable for the topmost layers.

The exposure age of individual soil layers (consisting of mixed organic and mineral material), i.e., the length of time that they have existed in each treethrow pit, was calculated under the assumption of the "constant rate supply" model (Appleby and Oldfield, 1978). The specific activities of ^{210}Pb exponentially decreased from the topmost layers to background ("supported") activities at depths of 50–70 cm (Fig. 4). Relatively high activities of ^{226}Ra ("supported" fraction of ^{210}Pb: 0.12–0.23 Bq g^{-1}) in the lower mineral soil samples at Zofin proved to be problematic because of overlapped signal "unsupported" ^{210}Pb. High activities of ^{226}Ra were derived from high active Moldanubian granite bedrock (Verner et al., 2009). Hence just a few topmost samples with high "unsupported" ^{210}Pb ("atmogenic") were able to be dated.

^{210}Pb dating was successfully used for five horizons in the treethrow pit profile 111 (back to 1918 ± 11.5 years), four horizons in pit 160 (back to 1933 ± 4.5 years) and for two horizons in the treethrow pit 316 at Zofin (back to 1917 ± 29.3 years). Rates varied

between 0.15 and 0.28 cm year^{-1} in treethrow pits 111 and 160. The calculated sedimentation rates appeared to increased upwards in the profiles, almost certainly due to soil compaction in the lower layers. Theoretically, we would have expected decreasing rates of infilling over time, as the surfaces and root plate next to the pit gradually stabilized. The ^{210}Pb data had the opposite trend, clearly because of compaction in the pit, where soils have high organic matter contents and low bulk densities. Bioturbation is active in the upper profile, but it also decreases with depth, further explaining the compaction. Detailed clarification of the role of soil compaction during the sedimentation rate calculation requires additional research. A very low sedimentation rate 0.05 cm year^{-1} was calculated for the last treethrow pit 316 in Zofin.

^{137}Cs specific activities ("Chernobyl cesium") were relatively high in the topmost soil layers of all the European sites, illustrating that the Zofin site was quite highly contaminated by this anthropogenic radionuclide after the Chernobyl accident (Suchara et al., 2011). A maximum of 1.45 Bq g^{-1} was detected in treethrow pit-mound 111 at a depth of 5 cm, and the isotope remained detectable up to 55 cm depth (No. 160) because of downward transport, probably in percolating water (Matisoff et al., 2011).

In contrast, ^{137}Cs specific activities at the Michigan (pit-mound No. 6) were very different, radiometrically. The activities of the "supported" ^{210}Pb fraction were much smaller (0.007–0.024 Bq g^{-1} only) than at Zofin, probably as a result of the different mineral substrate (nearly pure quartz sand outwash) at the Michigan sites. Although absolute ^{210}Pb activities are also much lower in Michigan than at Zofin, ^{210}Pb dating was successfully applied to 11 samples, dating back to 1817 ± 98 years. We conclude that this dating technique is more applicable in areas with low acitivity of the "supported" ^{210}Pb fraction.

In Michigan, the calculated sedimentation rates (include effect of soil compaction, see above) increase from 0.07 cm year^{-1} at the bottom of the dated part of the profile to 0.68 cm year^{-1} in the upper part. Spikes of significantly higher deposition rates (1.40 and 0.95 cm year^{-1}) were observed in horizons at depths of 10 and 15 cm, possibly as a result of short-term events, such as storms or locally focused bioturbation (Matisoff et al., 2011), either of which may have led to an influx of fresh material to the pit. The ^{137}Cs specific activities are also relatively lower than in profiles at Zofin. As expected, in Michigan, there was no detectable anthropogenic contamination from "Chernobyl cesium". The first occurrence of elevated ^{137}Cs activity was measured at a depth of 40 cm, which according to ^{210}Pb dating theory (e.g. Walker, 2005) could be associated with the first test of nuclear weapons in the U.S. in 1945, or any time prior to the Nuclear Test Ban Treaty of 1963 (Delaet et al., 2005).

3.3.2. Radiocarbon dating

Oliver and Stephens (1977) used radiocarbon dating for a detailed analysis of the disturbance history of a small forest stand,
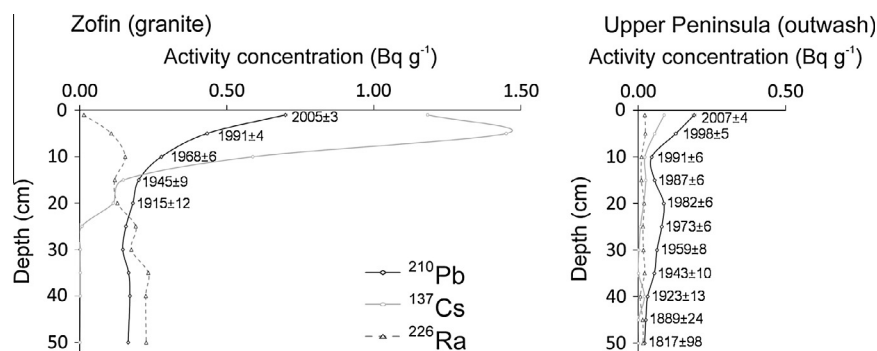

Fig. 4. Concentrations of selected radionuclides and calculated radiometric ages in selected treethrow pit soils, by depth and locality (see details in Section 2.5.1.).

but the application of these methods across larger areas has generally been limited, often due to its high cost and destructive nature. Disturbance by uprooting can be readily determined, by ascertaining the age of isolated uprooting events by dating uprooted tree trunks or organic materials from the buried A-horizon in or beneath older treethrow mounds (Embleton-Hamman, 2004; Gavin, 2003; Skvorcova et al., 1983). Note, however, that for events younger than about 100 years, ^{14}C dating is not considered sufficiently accurate (Walker, 2005). Currently, the oldest dated treethrow mound, with an uncalibrated ^{14}C age 2420 ± 70 years, was obtained on well-drained, sandy Podzols in the northern hardwood forests of northern Michigan (Schaetzl and Follmer, 1990). Before that, 2500–3000 year old micromorphological traces of pedoturbation were observed in soils in Canada after leveling of treethrow microtopography, due to erosion (Pawluk and Dudas, 1982). Like Schaetzl and Follmer (1990), we enjoined the synchronized action of two disturbance factors—wind and fire—in the radiocarbon dating of treethrow events in Michigan. In this environment, fire often follows shortly after a major uprooting event, burning the downed trunks and allowing the soil in the root plate to fall to the surface and rapidly form a mound. In so doing, charcoal fragments are often buried, and in these dry, sandy, acidic soils, they are excellently preserved (Schaetzl, 1986).

Our data from the Michigan sites revealed that the longevity of treethrow features can exceed 6000 years on sandy outwash (Fig. 5, Table 2), as demonstrated by the upper-real ages from remnants of uprooted trunks. The oldest treethrow feature dated returned a calibrated age of 4077 BC (^{14}C age 5260 ± 30 BP). To our knowledge, this finding is truly unique and represents the oldest known instance of treethrow pit-mound longevity. Many of the other sites here also returned ages that exceed the normally expected age range for treethrow pits and mounds (Table 2). For example, the oldest six pit-mounds are all greater than 4000 years in age.

The ^{14}C dating of uprooted trunk remnants, including charcoal, seems to be relatively reliable due to their known origin and clear linkage to disturbance event. We suggest that the deviation of these ^{14}C dates from the real age of the uprooting event is on the order of 10^2 years or less (Schaetzl, 1986). This deviation is caused by the potential time lag between the growth of dated tree ring and the sub-bark tree ring, i.e. the year of uprooting. In instances where we dated the sub-bark tree-ring, by obtaining a buried wood sample that retained its bark, the deviation between the real age of the disturbance and the ^{14}C age is nil. However, dating of buried trunk

fragments with their bark intact is not always possible; in warmer and wetter climate wood will decompose much more rapidly, negating the use of this method. Additionally, dating of charcoal is not always possible, due to the need for temporally connected wind and fire disturbances.

Radiocarbon dating of samples that originated from buried A-horizons has the small disadvantage because of the tenuous linkage between the death of the dated material (i.e., the initiation of the radiocarbon clock) and the actual age of the disturbance event. There also exists the possibility that the wood dated was not associated with the uprooting event, i.e., it was lying on the forest floor and buried by the root plate. We believe that by careful inspection of the soil morphology in the mound, this latter problem can be minimized. Despite our careful field work, we found wood of more than one tree species in a buried A-horizons, each with of different ^{14}C ages (e.g. No. 9 in Table 2). This was likely caused by the coupling of material from several different, pre-uprooting fire events (Gavin, 2003; Jull and Geertsema, 2006). In cases of different ^{14}C-ages, we assumed that the youngest sample represented the best maximum-limiting age of the treethrow disturbance event. Therefore, we argue that one possible solution to the potential problem of buried wood from pre-disturbance events is to date several samples, and compare the ages. Then, the youngest age can be used to best determine the maximum-limiting age of the treethrow event.

Applying this assumption at Zofin, radiocarbon dating of charcoal from pit was used to determine the maximum-limiting age of treethrow events (Table 3). However, by virtue of different natural processes in these forests and, as compared to the origin and location of charcoal in the mounds at the Michigan sites, the dates at Zofin may not be as closely connected with the real age of disturbance event. Dated charcoal fragments were probably much older than the disturbance event. Therefore, sensitivity of this dating seems to be low in correspond forest type and type of dated material. In case of treethrow pit No. 4 dating of above-ground plant parts and an insect wing revealed contamination, because ^{14}C ages on these features from the pit bottom were much younger than the reliable minimum-limiting age of trees growing on the dated treethrow (Table 3). Post-uprooting pedoturbation, of an unknown type, must have affected this treethrow feature to 60 cm depth.

Theoretically, fungal sclerotia from the organo-mineral sedimentation funnel within treethrow pits can be used to determine the minimum-limiting age of treethrow events in cases where more reliable materials, e.g., buried charcoal from trunks or plant
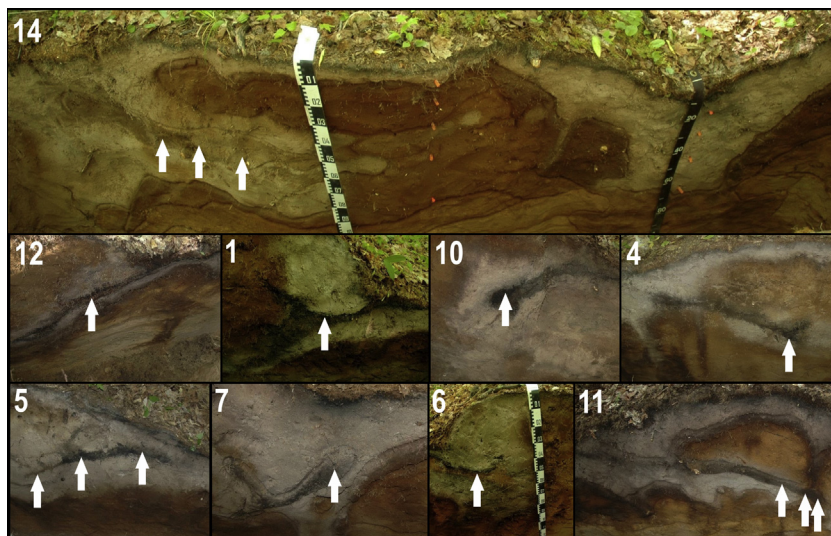

Fig. 5. Details of selected profiles through treethrows and positions of samples (arrows) dated using radiocarbon in Michigan (see details in Section 2.5.2.).

Table 1
Parameters of the site, environmental conditions, vegetation and character of data at individual localities.

Feature/locality	Razula	Zofin	Upper Peninsula
Parent material	Flysch	Granite	Outwash
Taxonomy	Haplic Cambisols	Entic Podzols	Albic Podzols
Location (Lat.-Long.) (°)	49.36N, 18.38E	48.67N, 14.70E	(1) 46.32 N, 85.06 W
			(2) 46.44 N, 84.82 W
			(3) 46.37 N, 86.70 W
Average soil reaction (pH_{H2O}) in B-horizon ± SD (n)	5.0 ± 0.2 (14)	4.5 ± 0.2 (13)	4.9 ± 0.2 (14)
Average soil reaction (pH_{KCl}) in B-horizon ± SD (n)	3.6 ± 0.1 (14)	4.1 ± 0.1 (13)	4.3 ± 0.3 (14)
Forest type	fir-beech forest	(spruce)-fir-beech forest	northern-hardwood
Main tree species	*Fagus sylvatica, Abies alba*	*Fagus sylvatica, Picea abies, Abies alba*	*Acer saccharum, A. pensylvanicum, A. rubrum, Quercus rubra, Tsuga canadensis, Pinus resinosa*
Range of altitudinal gradient (m a.s.l.)	600–812	730–837	215-270
Mean annual precipitation (mm)	1057	900	800
Mean average temperature (°C)	5.0–6.0	4.3	5.1
Treethrow pit-mounds studied in detail (#)	1562	1733	14
Area of repeated tree-census data (ha)	22.84	50.00	0
Treethrow pit-mounds directly dated/sites succesfully dated	51/37	237/178	14/14
Treethrow pit-mounds with dendrochronological data (no. of tree cores)	37 (213)	52 (537)	11 (20)
Treethrow pit-mounds with ^{210}Pb data (no. of samples)	0	3 (33)	1 (11)
Treethrow pit-mounds with ^{14}C data (no. of samples)	0	4 (15)	14 (27)
Indirectly dated treethrow pit-mounds (#)	1415	1289	0

seeds, are absent. After sampling, analysis of DNA from the sclerotia in the pits was first performed to confirm its fungal origin. Eukaryotic rRNA was amplified from all samples while bacterial 16S rRNA did not. Pyrosequencing revealed a mixture of fungal sequences in all samples, but more than 85% of the sequences in all samples belonged to the same OTU, which was identified as *Piloderma* sp. (sequence similarity > 98% with the JQ711958 sequence in GenBank). Although the frequency of fungal sclerotia rapidly decreased with depth in undisturbed soils, their frequency within the sedimentary funnel in the pits between 5 and 50 cm decreased only slightly. Whereas 411 and 380 fungal sclerotia $20 \, ml^{-1}$ of the 0.25–5.0 mm soil fraction occurred in treethrow pit No. 1 at 30 to 50 cm depths, only 52 and 17 fungal sclerotia $20 \, ml^{-1}$ occurred in the corresponding depth in the control (undisturbed) profile. Deep within the narrow funnel, in the mineral BC horizon, we found almost no fungal sclerotia. We suggest that the high densities of sclerotia were connected with the decomposition of fresh organic material during the gradual filling of the treethrow pit by litter, after the disturbance event, and its mixing with mineral material below. However, the low occurrence of sclerotia in mineral horizons, deep within treethrow pits, adds some uncertainty to the disturbance dating protocols; the presence of older sclerotia or older source of carbon within a fresh pit cannot be completely discounted. Dating more samples may partly resolve this uncertainty.

Because the pits infill slowly, the ^{14}C-age of sclerotia decreased nearer the surface in the dated profiles. Whereas sclerotia were 1010 ± 40 BP years old at a depth of 50 cm, they were only 395 ± 30 BP years old at a depth of 5 cm in treethrow pit No. 3 (Table 3). While less variation in ages were found from in deeper samples, the ages of two upper samples differed considerably. This difference probably resulted from slow infilling of the pit by organic materials, beginning immediately after the disturbance event, with a gradual decrease over time. Based on these data (Table 3), we suggest that the longevity of treethrow microtopography may reach 1700 years at Zofin.

3.4. Crossdating of treethrow events using multiple methods

Because all dating methods have their limitations, inherent assumptions, and potential for error, and because some methods return different estimates (minimum vs maximum vs real ages), we took the approach that multiple methods, with a maximum amount of time-scale overlap and mutual validation, was optimal for dating tree uprooting features. In this paper, we applied data on tree censuses, dendrochronology and radiometric approaches to the dating of uprooting events in three different forest environments (Fig. 6). In other situations, the application of other methods, not employed here, may have potential as well.

Because we wanted to gain independent information about treethrow event ages to inform research on rates of soil formation, we did not use weathering or pedologic data in a supportive dating role. Nonetheless, degree of soil development within treethrow mounds appears to be a reliable relative age predictor (Šamonil et al., 2010b; Schaetzl et al., 1990). For example, one of the older features in Michigan has a ^{14}C age 3600 ± 30 BP (No. 11), with a well-expressed E horizon within the mound. Conversely, mounds that were only a few hundred years old (Nos. 12, 2, 10) lack eluvial features in the mounds. Thus, our numerical dating information, when combined with soil development data, could help inform those studying the effects of microtopography on soil development, as well as the use of soil development as a relative age dating tool in general. Soil development within treethrow pits is even more complicated and hence, less useful as a dating tool, because it can be nonlinear or even retrograde (Šamonil et al., 2010a). The use of a Schmidt hammer (McCaroll, 1991) could possibly provide supportive information about the weathering of stones uncovered by tree uprooting.

The application of dendrochronological techniques proved to be very useful in this research (Fig. 6). Knowledge of the minimum age of treethrow, based on dendrochronology, allowed us to confidently determine the moment when surrounding trees responded to a disturbance event, and allowed for the elimination of partial, usually less noticeable, responses of individual trees to later stimulations of radial growth. Tree census data were able to precisely delimit the periods of disturbance events (from 2 to 22 years), where we most frequently found only one release in trees, all showing the exact time of disturbance. ^{210}Pb dating functioned similarly (including ^{226}Ra and ^{137}Cs). The activities of these radionuclides within samples taken from treethrow pits were in logical accordance with the activity of ^{14}C in uprooted trunks. Radiocarbon ages provided somewhat higher, maximum-limiting ages, or

Table 2
Radiocarbon ages of samples from treethrow pit-mounds in Michigan. Treethrow features are ordered according to age; upper-real or maximum-limiting ages nearby to real ages of disturbance event are accentuated. Dates in bold are the closest to the real age of tree-uprooting event.

Treethrow pit-mound pair	Type of buried material dated	Type of material	Depth (cm)	Age ^{14}C BP (year)	Calibrated date (95% probability, year)	Median (weighted) of calibration age (year AD/BC)
12	Tree trunk	Wood, deciduous tree, without bark	61	85 ± 30 BP	1688–1730 AD (25.6%), 1809–1927 AD (69.8%)	**1844 AD**
2	Tree trunk	Wood without bark, coniferous tree	47	90 ± 30 BP	1684–1733 AD (26.5%), 1807–1929 AD (68.9%)	**1842 AD**
10	Tree trunk	Wood without bark	24	0 ± 73 BP[a]	1680–1766 AD (28.0%), 1799–1939 AD (65.0%)	**1840 AD**
	Tree trunk	Burnt wood without bark, *Abies* sp.	30	140 ± 30 BP	1669–1781 AD (43.0%), 1798–1891 AD (36.8%), 1908–1945 AD (15.6%)	1809 AD
1	Tree trunk	Wood without bark	35	50 ± 73 BP[a]	1679–1767 AD (30.0%), 1798–1942 AD (61.0%)	**1832 AD**
6	Tree trunk	Wood without bark, deciduous tree	28	260 ± 30 BP	1520–1593 AD (27.8%), 1619–1670 AD (52.8%), 1780–1800 AD (12.6%), 1943–1954 AD (2.2%)	**1647 AD**
8	Tree trunk or A-horizon	Charcoal without bark, coniferous tree	23	930 ± 30 BP	1025–1169 AD (95.4%)	**1099 AD**
	Tree trunk or A-horizon	Charcoal of bark	35	5310 ± 40 BP	4258–4039 BC (93.4%), 4016–4000 BC (2.0%)	4139 BC
9	A-horizon	Charcoal, amorphous, without bark	40	1095 ± 35 BP	887–1017 AD (95.4%)	**948 AD**
	A-horizon	Charcoal without bark, coniferous tree	28	3875 ± 35 BP	2468–2278 BC (89.3%), 2251–2229 BC (4.3%), 2221–2210 BC (1.7%)	2365 BC
	A-horizon	Charcoal without bark, *Taxus* sp.	40	4170 ± 40 BP	2886–2831 BC (20.6), 2822–2630 BC (74.8%)	2761 BC
5	Tree trunk or A-horizon	Charcoal, amorphous, without bark	35	1755 ± 30 BP	176–190 AD (1.2%), 212–387 AD (94.2%)	**291 AD**
	Tree trunk or A-horizon	Charcoal, amorphous, without bark	55	6360 ± 50 BP	5470–5289 BC (85.1%), 5271–5225 BC (10.3%)	5349 BC
	Tree trunk or A-horizon	Charcoal of bark	20	6460 ± 40 BP	5485–5339 BC (95.4%)	5421 BC
11	Tree trunk	Charcoal without bark, *Populus* sp.	62	3600 ± 30 BP	2032–1887 BC (95.4%)	**1957 BC**
	Tree trunk	Charcoal, amorphous, without bark	45	3820 ± 30 BP	2454–2446 BC (0.6%), 2435–2420 BC (1.5%), 2405–2378 BC (3.8%), 2350–2194 BC (84.0%), 2177–2144 BC (5.5%)	2260 BC
4	Tree trunk	Charcoal of *Pinus* sp., without bark	60	3750 ± 30 BP	2282–2249 BC (8.2%), 2231–2116 BC (66.0%), 2100–2038 BC (21.2%)	**2163 BC**
14	Probably tree trunk	Charcoal without bark, coniferous tree	55	4480 ± 35 BP	3342–3086 BC (89.2%), 3062–3029 BC (6.2%)	**3217 BC**
	Probably tree trunk	Charcoal of bark	45	4660 ± 35 BP	3621–3610 BC (2.0%), 3521–3363 BC (93.4%)	3453 BC
	A-horizon	Charcoal of bark, amorphous	45	7210 ± 40 BP	6210–6136 BC (20.0%), 6121–6006 BC (75.4%)	6067 BC
13	Tree trunk	Charcoal of bark, coniferous tree	50	4550 ± 50 BP	3496–3461 BC (4.3%), 3376–3092 BC (91.1%)	**3225 BC**
7	Tree trunk	Charcoal without bark	37	4985 ± 35 BP	3936–3873 BC (14.6%), 3809–3691 BC (77.4%), 3686–3661 BC (3.4%)	**3759 BC**
3	Probably tree trunk	Charcoal, amorphous, without bark	30	5260 ± 30 BP	4229–4198 BC (13.5%), 4172–4089 BC (31.6%), 4084–3984 BC (50.4%)	**4077 BC**
	Probably tree trunk	Charcoal of *Pinus* sp., without bark	20	5265 ± 30 BP	4230–4197 BC (15.0%), 4174–3987 BC (80.4%)	4101 BC
	Probably tree trunk	Charcoal, amorphous, without bark	25	5340 ± 40 BP	4322–4292 BC (6.8%), 4266–4047 BC (88.6%)	4171 BC

[a] Conventional dating.

upper-real ages, for the disturbance events, as compared to minimum-limiting ages ascertained by the ^{210}Pb technique, tree censuses or dendrochronology. The parallel application of dendrochronology (minimum pit-mound age) and radiocarbon (maximum age) contributed to the detection of post-disturbance pedoturbation within Zofin treethrow pits No. 4 (see above, Table 3). Knowledge of minimum ages also allowed us to disqualify some false correspondences of ^{14}C activities with comparative data during radiocarbon calibration.

Despite our continued efforts at crossdating, the ages of some very old treethrow pit-mounds could only be established from one ^{14}C date, because of the lack of abundant datable material. Therefore, the reliability of crossdating decreased with increased age (particularly in the case of sclerotia, which we found in low numbers in B-horizons from soils outside of treethrow pits).

Nonetheless, we have no reason to doubt the ^{14}C ages on these older mounds, and they also provide perhaps our most important dates, as they speak to the overall longevity of these features on the forest landscape.

3.5. Implications of the age of treethrow microsites in forest ecology and management

Treethrow microsites increase biological and ecological diversity within the forest (den Ouden and Alaback, 1996; Nachtergale et al., 2002; Šamonil et al., 2008; von Oheimb et al., 2007) and impact the spatial variability of natural processes including soil formation (Šamonil et al., 2010a, 2011; Schaetzl, 1990). Ecologically, the conditions at treethrow microsites differ considerably from those at undisturbed sites. Treethrow mounds are generally drier

Table 3
Radiocarbon ages of samples from treethrow pit-mounds at Zofin. Treethrow features are ordered according to age; maximum-limiting age (charcoal) or minimum-limiting ages (other dated materials) nearby to real ages of disturbance event are accentuated. Dates in bold are the closest to the real age of tree-uprooting event.

| Treethrow pit-mound pair	Minimal age by dendrochronology (year)	Type of material	Depth (cm)	Age ^{14}C BP (year)	Calibrated date (95% probability, year)	Median (weighted) of calibration age (year AD/BC)
4	244	Burnt wood without bark	60	620 ± 30 BP	1292–1400 AD (95.4%)	**1350 AD**
		Wood without bark	60	60 ± 50 BP	1681–1763 AD (28.2%), 1801–1939 AD (67.2%)	1841 AD
		Leaf	60	105.26 ± 0.38 pMC	1951–1959 AD (95.4%)	–
		Wing of insect (Carabidae)	60	107.42 ± 1.86 pMC	1951–1960 AD (51.0%), 1991 AD–present (44.4%)	–
2	296	Fungal sclerotia	50	980 ± 40 BP	991–1157 AD (95.4%)	**1079 AD**
		Charcoal without bark	50	6160 ± 40 BP	5217–5000 BC (95.4%)	5118 BC
		Wood without bark	50	215 ± 35 BP	1639–1691 AD (32.4%), 1728–1811 AD (47.0%), 1922–1955 AD (16%)	1768 AD
3	370	Fungal sclerotia	5	395 ± 30 BP	1439–1523 AD (73.2%), 1573–1628 (22.2%)	1483 AD
		Fungal sclerotia	15	665 ± 30 BP	1276–1321 AD (49.9), 1350–1392 AD (45.5)	1318 AD
		Fungal sclerotia	30	960 ± 30 BP	1021–1155 AD (95.4%)	1095 AD
		Fungal sclerotia	50	1010 ± 40 BP	900–918 AD (2.7%), 966–1155 AD (92.7%)	**1021 AD**
		Charcoal without bark	80	5620 ± 70 BP	4616–4337 BC (95.0%)	4455 BC
1	392	Fungal sclerotia	5	805 ± 30 BP	1178–1274 AD (95.4%)	1235 AD
		Fungal sclerotia	15	1530 ± 25 BP	432–495 AD (32.0%), 504–600 AD (63.4%)	541 AD
		Fungal sclerotia	30	1720 ± 35 BP	242–405 AD (95.4%)	**322 AD**
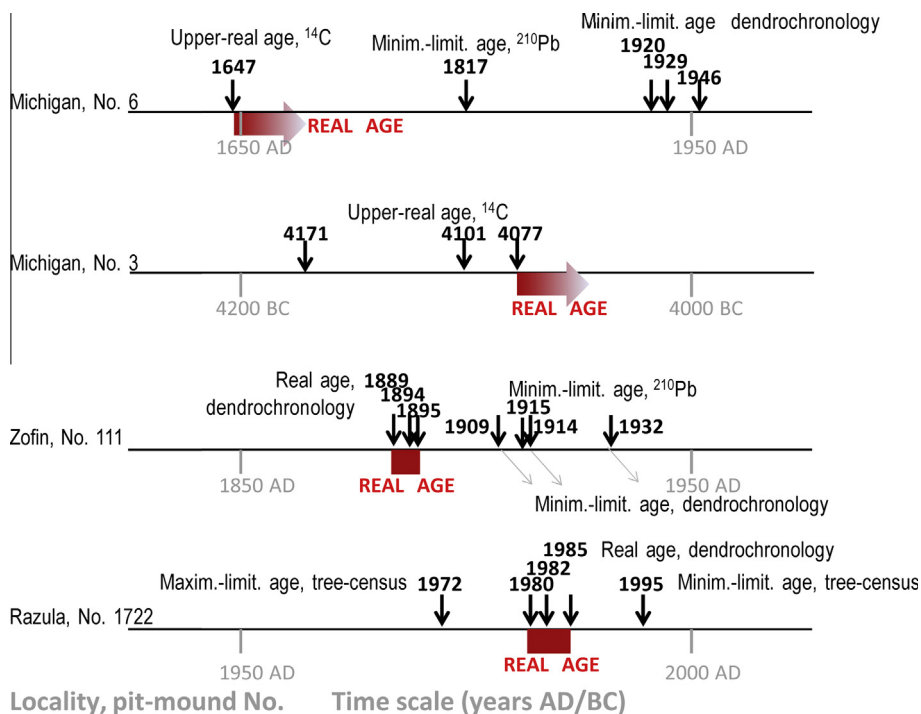
Fig. 6. Examples of crossdating of tree uprooting events using multiple methods. Interval of true age of disturbance event is demonstrated as well as different date points revealed by individual dating techniques (see details in Sections 2.3.–2.5.).

and warmer than their respective pits, while nearby currently undisturbed sites show close to average values (Clinton and Baker, 2000; Kabrick et al., 1997; Schaetzl et al., 1989). The ecological and erosive/sedimentation conditions of these microsites create their unique roles in forest ecology, and add complexity to forest management decisions. Ecological, erosive and sedimentation conditions are primarily determined by the convex or concave shape of microsites and remain generally valid until the total disintegration and leveling of the microtopography. Hence, the longevity of

treethrows is an important feature of the forest ecosystem (review by Šamonil et al., 2010a). To that end, our findings extend the possible maximal longevity of treethrows to more than 6000 years on the sandy sites of the northern Great lakes region, and to approximately 1700 years in European beech-dominated forests, dramatically changing our understanding of forest dynamics and illustrating that the individual microtopographic features formed by tree uprooting are, in places, semipermanent components of the forest floor. Because these features are, in some ecosystems,

more long-lasting that previously thought, their impact on soil genesis is more localized (for longer periods) and the disturbance cycles that formed them may locally occur less frequently than previously envisioned. During gradual disintegration of this micro-topography, the role of tree uprooting in forest dynamics slowly changes (e.g. Šebkova et al., 2012). These changes in the ecological role of treethrows in forest dynamics have not yet been properly studied.

Directly or indirectly dated, treethrow pits and mounds (Schaetzl and Follmer, 1990; Šebkova et al., 2012; Skvorcova et al., 1983) provide clear information about forest disturbances. These data can complement dendrochronological or repeated tree census studies that focus on disturbance history within the crown space of tree layer (e.g. Panayotov et al., 2011; Šebková et al., 2011). Detailed studies and archives of tree uprooting dynamics may reveal periods of repeated soil and forest disturbance or, on the contrary, long periods of relative quiescence and stability. In addition, direct human impacts can be found in forest dynamics data sets. The interactions between tree uprooting dynamics and individual components of forest ecosystems are interrupted by human intervention, even if their techniques are aimed at being natural, in managed forests. Intentional blocking of treethrow pit-mound formation in managed forests leads to the formation of incomplete relationships, and the resulting spatial patterns and dynamics of such forests are far from natural. In the future, the character of tree-soil interactions could be an important criterion in the assessment of historical human impacts and respective evaluations of the naturalness of forest ecosystems.

Acknowledgements

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