VEGETATION DIVERSITY ON THE MICROSITES CAUSED BY TREE UPROOTING DURING A CATASTROPHIC WINDTHROW IN TEMPERATE BROADLEAVED FORESTS

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РАЗНООБРАЗИЕ РАСТИТЕЛЬНОСТИ НА ЭЛЕМЕНТАХ ВЕТРОВАЛЬНО-ПОЧВЕННЫХ КОМПЛЕКСОВ НА УЧАСТКАХ КАТАСТРОФИЧЕСКОГО ВЕТРОВАЛА В ШИРОКОЛИСТВЕННЫХ ЛЕСАХ

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Abstract. We analyzed the diversity of vascular plant species growing on microsites formed after tree falls with uprooting as a result of catastrophic windthrow that occurred in the temperate broadleaved forests of the Kaluzhskie Zaseki Reserve in 2006. Size characteristics of pits and mounds formed by uprooting of 110 individuals of 9 tree species were measured. Vegetation on microsites formed by 45 fallen trees of 8 species was described. We distinguished the following microsites: 1) top of the mound; 2) back side of the mound; 3) front side of the mound (from the trunk side); 4) pit over the mound; 5) pit in front of the mound in the case of rotational treefalls; 6) part of the trunk close to the roots (deadwood). Vegetation on 45 plots of 1x1 m in size and located close to but not affected by tree uprooting (reference plots, or reference communities) was also described. The results of the indirect ordination analysis revealed that the ecological and phytocoenotic differences between the plant associations of *Quercus* – *Tilietum cordatae* and *Aceri campestre* – *Tilietum cordatae* persisted in the areas of catastrophic windthrow both on the plots of reference communities and in vegetation overgrowing pits and mounds. Ordination showed differences between the vegetation in the microsites formed by tree uprooting in a series of mound – deadwood – pit – reference community. On 251 plots, 78 vascular plant species were totally registered, among them 26 species were not found in the reference plots but occurred in the pit-and-mound microsites; 6 species were not found before the windthrow study in the descriptions of broadleaved and aspen forests of the Reserve, and 8 species were found in the descriptions of those forests no more than three times. New species are mostly species from the boreal (*Phegopteris connectilis*, *Sambucus racemosa*), nitrophilous (*Rubus*

caesius), water-marsh (*Epilobium hirsutum*, *Epilobium palustre*), meadow-edge (*Bromopsis inermis*, *Hypericum hirsutum*, *Conyza canadensis*, *Vicia cracca*), and piny (*Calamagrostis epigeios*) ecological-coenotic groups. In general, the increase in plant diversity in the area of catastrophic windthrow is caused by the massive emergence of new microsites (pits, mounds and deadwood) and the subsequent appearance of species with different ecological and coenotic traits.

Keywords: windthrow, Kaluzhskie Zaseki Reserve, pit-and-mound topography, plant species diversity, DCA, ecological-coenotic groups.

For citation: Khanina L.G., Bobrovsky M.V., Zhmaylov I.V. Vegetation diversity on the microsites caused by tree uprooting during a catastrophic windthrow in temperate broadleaved forests. Russian Journal of Ecosystem Ecology. 2019;4(3). Available from: <https://doi.org/10.21685/2500-0578-2019-3-1>

Аннотация. Проанализировано разнообразие видов сосудистых растений, произрастающих на элементах ветровально-почвенных комплексов (ВПК) и образованных при падении деревьев в результате катастрофического ветровала 2006 г. в широколиственных лесах на территории заповедника «Калужские засеки». Получены размерные характеристики элементов ВПК для 110 вывалов 9 видов деревьев. Описана растительность 45 вывалов 8 видов деревьев на следующих элементах ВПК: вершина бугра, задняя и передняя стенки бугра, западина, передний клин (для провернутых вывалов) и прикомлевая часть ствола упавших деревьев (валеж). Растительность описана также на 45 площадках 1×1 м, расположенных рядом с ВПК, но не нарушенных ветровалом (фон или фоновые сообщества). Результаты непрямого ординационного анализа выявили, что экологические и ценотические различия между ассоциациями *Quercus-Tilietum cordatae* и *Aceri campestris-Tilietum cordatae* сохраняются на участках массового ветровала как во фрагментах фоновых сообществ, так и в растительности на зарастающих вывалах деревьев. Одинация выявила различия растительности на микросайтах, формирующихся при вывале деревьев, в ряду бугор – валеж – западина – фон. Всего на 251 площадке зарегистрировано 78 видов сосудистых растений, из которых 26 видов не встречались вне микросайтов вывалов, а присутствовали только на элементах ВПК; 6 видов не были встречены до исследования ветровала в описаниях широколиственных лесов и осинников заповедника и 8 видов были встречены там не более трех раз. В основном виды, присутствующие только на элементах ВПК, относятся к бореальной (*Phegopteris connectilis*, *Sambucus racemosa*), нитрофильной (*Rubus caesius*), водно-болотной (*Epilobium hirsutum*, *Epilobium palustre*), лугово-опушечной (*Bromopsis inermis*, *Hypericum hirsutum*, *Conyza canadensis*, *Vicia cracca*) и боровой (*Calamagrostis epigeios*) эколого-ценотическим группам. В целом увеличение разнообразия растений при катастрофическом ветровале связано с массовым появлением новых микросайтов (элементов ВПК) и с увеличением участия на них видов разной экологической и ценотической приуроченности.

Ключевые слова: ветровал, заповедник «Калужские засеки», ветровально-почвенный комплекс, видовое разнообразие растительности, DCA, эколого-ценотические группы.

Introduction

Along with fires and mass outbreaks of insect pests, catastrophic windthrows are one of the major disturbances of forest ecosystems, and require study, analysis and assessment of their causes and consequences. Studying these disturbances is particularly relevant today, in the context of global changes of climate and natural resource management; such studies could be useful for forecasting the state of ecosystems and promoting sustainable ecosystem management [1–4]. There are a lot of papers on the mechanisms of windthrows [5–8], the influence of catastrophic windthrows, pit-and-mound topography and deadwood on soil properties, biogeochemical cycles in ecosystems and carbon sequestration [9–21].

Traditionally, when studying windthrows, much attention is paid to their impact on forest vegetation changes. Assessing the influence of

single and massive windthrows on the renewal of woody species is one of the focuses of the research [22–27]. The majority of studies are performed in boreal [28–30] and, less frequently, mixed hemiboreal [25, 26] forests. The studies performed in nemoral forests mainly focus on the changes in mono- and oligodominant forests with beech (*Fagus sylvatica*) predominance [31, 32], and most often these are mountain forests. Studies of the effect of windthrows and gap mosaic on the ground layer of vegetation are quite uncommon [33–40]; they rarely consider the microsite structure associated with the pit-and-mound topography [34, 36, 37, 40]; although studies on different species overgrowing deadwood are more frequent [41–43].

The aim of our research was to study the processes of overgrowing and to assess the diversity of vascular plants in pits and mounds formed after treefalls with uprooting in the areas of catastrophic windthrows in broadleaved forests. The research was carried out in the Kaluzhskie

Zaseki Reserve, which is located in the subzone of broadleaved forests and which suffered from a massive windthrow in 2006.

Materials and methods

The study area. The Kaluzhskie Zaseki State Nature Reserve is located in the eastern European part of the broadleaved forest zone [44] in the south-east of the Kaluga Oblast where it borders with the Orel Oblast and the Tula Oblast; the geographical coordinates of the Reserve range from 53.5 to 53.9 ° N and from 35.6 to 35.9 ° E (Fig. 1). The Reserve was established in 1992 to protect the old-growth multi-species broadleaved forests growing on the site of the former Zaokskaya Abatis belt, which was the line of

defence of the Muscovite state in the 16–18th centuries [45–47]. The stands of broadleaved forests are dominated by the common oak (*Quercus robur*), which is more than 300 years old in some patches. The maximum age of trees of other broadleaved species (common ash, *Fraxinus excelsior*; small-leaved lime, *Tilia cordata*; wych elm, *Ulmus glabra*; Norway maple, *Acer platanoides*, and field maple, *A. campestre*) varies from 150 to 170 years. Along with the broadleaved forests, there are forests dominated by aspen (*Populus tremula*), warty birch and downy birch (*Betula pendula* and *B. pubescens*), Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and black alder (*Alnus glutinosa*); small areas are occupied by meadows [48].

Fig. 1. Location of the Kaluzhskie Zaseki State Nature Reserve.
On the left side of the scheme you can see: 1 – boreal; 2 – hemiboreal; 3 – nemoral forest zones

The Reserve is located on the Russian platform, in the northwestern part of the Central Russian Upland, in the watershed of the Oka and Vytebet rivers (a tributary of the Zhizdra River). The prevailing elevation varies from 150 to 250 m above the sea level, the highest point is 275 m asl. The erosive hilly terrain is formed by a gently sloping cover of glacial moraine and is densely dissected by ravines, gullies and rivers. The average annual temperature is 4.4 °C. The average annual precipitation is 700 mm [49].

A massive windthrow occurred in the Southern section of the Reserve (mainly within the Yagodnenskoye Forest District) in August 2006 due to a hurricane wind accompanied by a heavy

thunderstorm, sometimes with hail. According to satellite images and ground mapping the total area of the damaged forests is 285 ha: there are 291 damaged patches with the areas ranging from 0.04 to 51 ha (Figs. 2 and 3); middle-aged and mature aspen and birch forests were the most severely broken, while old-aged oak forests were the least affected [50]. During the windthrow, some of the trees fell with uprooting that formed pit-and-mound topography (Fig. 4), and some of the trees were broken off. The analysis of the number of damaged trees on five sample plots established in 2010 showed that the number of broken trees and those fallen with uprooting was approximately the same; at that, the area occupied by lying tree trunks

was vaster than the area occupied by pit-and-mound topography: the proportion of the former ranged from 17 to 32 % and the latter from 6 to 25 % of the plot

area [50]. The average stock of deadwood varied from 198 to 463 m³/ha.

Fig. 2. Patches of the 2006 massive windthrow (the black icons) within the Southern section of the Kaluzhskie Zaseki Reserve. Circles 1–3 are the Areas where pit-and-mound topography was studied

The pit-and-mound topography was studied in three local areas (Fig. 2). Area 1 is located near Yagodnoye village; before the windthrow there was an aspen-broadleaved forest with the predominance of *Populus tremula*, *Tilia cordata*, *Quercus robur* with the presence of *Picea abies* (sample plots 1 and 3 in [50]). Soddy podbours and soddy-podzolic soils on the fluvioglacial sands dominate. Area 2 is located near Nogaya village; before the windthrow it was occupied by a broadleaved forest with the predominance of *Fraxinus excelsior* and *Populus tremula* with the presence of *Tilia cordata*, *Acer platanoides*, *Quercus robur*, *Betula* spp. (sample plots 4 and 5 in [50]). Soddy-podzolic and grey soils including gleyic soils on the loams prevail. Area 3 is located in the south-east of the Southern section of the Reserve; before the windthrow it was a broadleaved forest with *Populus tremula* and *Betula* spp. The prevailing soils are soddy podbours located on two-term deposits (thin fluvioglacial sands on morainic loams). Overall, the vegetation of Area 1 can be attributed to the *Quercus-Tilietum cordatae* association, Laivinsh

1986 ex Laivinsh in Solomesč et al. 1993. Diagnostic species of this association belonging to the nemoral ecological-coenotic group (ECG) show high constancy, at the same time boreal species (*Gymnocarpium dryopteris*, *Luzula pilosa*, *Maianthemum bifolium*, *Phegopteris connectilis*, etc.) can also be found here. Vegetation of Area 2 can be attributed to the *Aceri campestris* – *Tilietum cordatae* ass. nov. hoc loco [51], it shows high constancy of *Acer campestre*, *Euonymus europaea*, and *Allium ursinum*. *Aceri campestris* – *Tilietum* association is usually found on wetter and richer soils [51]. The vegetation of Area 3 falls in between these two associations.

Sampling design. To assess the vegetation diversity of pits and mounds formed after treefalls with uprooting in the patches of the catastrophic windthrow, in 2010 (4 years after the windthrow) we investigated the vegetation of the following microsites (Fig. 5): 1) top of the mound; 2) back (relatively to the position of the trunk) side of the mound; 3) front side of the mound; 4) pit over the mound (i.e. pit in the usual sense of the term); 5) pit in front of the mound (only in the case of

Fig. 3. Massive windthrow in the Kaluzhskie Zaseki Reserve. Photo by M. V. Bobrovsky

Fig. 4. Pit-and-mound microsites on the patches affected by the 2006 massive windthrow in the Kaluzhskie Zaseki Reserve. Photo by M. V. Bobrovsky

Fig. 5. Investigated pit-and-mound microsites for non-rotational (I) and rotational (II) treefalls:
1 – top of the mound; 2 – back side of the mound; 3 – front side of the mound; 4 – pit over the mound;
5 – pit in front of the mound; 6 – deadwood

rotational treefalls [19]); 6) deadwood, the part of the trunk close to the roots of a fallen tree (vegetation was listed on a plot of 1 m²).

We measured diameter at 1.3 m from the root collar (DBH) and size of the pits and mounds of 110 trees fallen with uprooting. For each microsite, mentioned above and formed by 45 fallen trees, vascular plant species were listed and their percentage cover was visually estimated for two vegetation layers: layer *C* with the height of herbaceous plants and layer *B* consisting of higher trees and shrubs. Next to each described fallen tree we also listed vascular plant species at a reference plot of 1×1 m, which was not affected by treefalls. Sometimes there was no vegetation on the deadwood, the back/front side of the mound or in the pit in front of the mound. The area occupied by bare soil, leave or woody litter and green mosses was also estimated (in percent) on each microsite. Totally, 251 vegetation plots were sampled: 206 pit-and-mound microsites and 45 reference plots.

Field data analysis. In order to analyze variations in the vegetation, indirect ordination analysis of vegetation plots was conducted on the numeric scores of species abundance using the Detrended Correspondence Analysis (DCA) method [53] performed by the PC-ORD 6.21 program [52]. The numeric scores of abundance were obtained from the percentage cover of the species according to the following rules: cover less than 1 % – 0.5; cover 1 to 10 % – 1; 10 to 25 % – 2; 25 to 50 % – 3; 50 to 75 % – 4, above 75 % – 5. The ordination effectiveness was evaluated by the after-the-fact coefficient of determination between relative Euclidean distance in the unreduced species space and Euclidean distance in the ordination space [52]. To assess the significance of ordination axes, we performed a randomization test

(Monte-Carlo procedure). It should be noted that according to the PcOrd program authors [52], only the significance of the first axis of DCA may be assessed correctly enough.

To interpret the ordination axes, correlation vectors with the environmental characteristics of the plots and with the number of species of different ecological-coenotic groups were built. Landolt's indicator species values [54] weighted by species abundance and averaged for plots were used as their environmental characteristics. The EcoScale program [55] was used to calculate these weighted averages. Ecological-coenotic groups (ECGs) were understood as described by O. V. Smirnova and L. B. Zaugolnova [56, 57] and further specified by V. E. Smirnov et al. [58, 59]. The following six ECGs were used in this work: boreal (Br), nemoral (Nm), nitrophilous (Nt), piny (Pn), meadow-edge (Md), and water-marsh (Wt). The ecological characteristics of the plots and the number of species of different ECGs were also used to assess the environmental conditions and structural diversity of vegetation on the microsites, respectively.

Dominant, constant and indicator species were identified to characterize the vegetation of the microsites and reference plots. The indicator species were determined by the IndVal method [60], which takes into account the occurrence and average abundance of species in the plots of each group, as well as the average abundance of species in all groups of plots. The statistical significance of the obtained indicator values (*IV*) was checked by the Monte-Carlo procedure; the species with the probability of incorrect rejection of the null hypothesis (*p*) not more than 0.05 were seen as indicators for a microsite.

Alpha-, beta-, and gamma-diversity [61] of vascular plants in the microsites were also calculated. Compositional diversity was calculated as the average number of species per plot (species density) and the total number of species in all plots of the corresponding microsite or in the reference community (species richness). The differential diversity was estimated using the Whittaker index and calculated according to the formula

$$\beta_w = \frac{\gamma}{\bar{\alpha}} - 1, \text{ where } \gamma \text{ stands for species richness; } \bar{\alpha} - \text{for species density.}$$

To analyze the contribution of microsites to the total plant diversity of the broadleaved forests of the Reserve we compared the list of species of the microsites with the species list of reference plots and the species lists of broadleaved, nemoral aspen and nemoral birch forests taken from the general database of the geobotanical relevés of the Reserve [62].

Results and discussion

Dimensions of pit-and-mound microsites. Mounds and pits of 9 tree species were measured (Table 1). As in the earlier study performed by M. V. Bobrovsky [63] on the same windthrow sites in 2007 and 2009, it turned out that the *Picea abies* treefalls are the largest in size. Among deciduous trees, in our research, *Ulmus glabra*, *Betula* spp., and *Quercus robur* on average formed the highest mounds when fell with uprooting; *Acer*

platanoides, *Ulmus glabra*, and *Betula* spp. formed the longest pits. It should be noted that in general the dimensions of mounds and pits differed from the values obtained earlier for the same microsites: immediately after the windthrow the mounds were higher and the pits longer; this decrease in the size is an obvious process occurring over time due to the crumbling of the soil clods. On average, bare soil occupied the largest areas on the mounds (Fig. 6); leaf litter prevailed in the pits and in the reference plots; proportion of green mosses was highest on the deadwood and on tops of the mounds.

Vegetation description. The highest number of vegetation plots was sampled at *Fraxinus excelsior* treefalls (vegetation on ten fallen trees was described), followed in descending order by the treefalls of *Populus tremula* (8), *Tilia cordata* and *Ulmus glabra* (7 each), *Betula* spp. and *Quercus robur* (4 each), *Acer platanoides* (3), and *Picea abies* (2). The results of indirect ordination analysis of vegetation plots revealed no significant difference between the vegetation growing on the microsites formed by trees of different species. However, the results showed the presence of two main gradients along which the vegetation varies (Fig. 7). The cumulative coefficient of determination for the first three axes is rather high (52.4 %); the first and second axes are significant ($p_1 = 0.054$, $p_2 = 0.015$), that generally indicates a rather high quality of the ordination [52].

Table 1

Size of the microsites of 110 fallen trees of different species measured in 2010 at the windthrow of 2006 (the Southern section of the Kaluzhskie Zaseki Reserve), cm

	Mound height		Mound width		Mound thick		Pit length		DBH*		n**
	Mean value	Error	Mean value	Error	Mean value	Error	Mean value	Error	Mean value	Error	
<i>Acer campestre</i>	35.0	5.0	70.0	20.0	25.0	5.0	40.0	0.0	10.5	3.5	2/2
<i>Acer platanoides</i>	105.0	6.5	267.5	13.1	62.5	2.5	137.5	8.5	25.0	2.9	5/4
<i>Betula</i> spp.	121.1	12.7	258.9	23.6	67.2	7.4	131.1	18.1	29.3	1.8	12/9
<i>Fraxinus excelsior</i>	95.3	9.2	223.7	18.8	63.4	4.3	100.3	12.3	24.3	1.1	19/19
<i>Picea abies</i>	240.0	28.3	615.0	49.5	65.0	35.4	235.0	63.6	43.3	12.1	3/2
<i>Populus tremula</i>	102.2	7.9	215.0	11.4	75.0	4.7	87.8	9.7	32.4	1.2	20/18
<i>Quercus robur</i>	120.0	17.6	274.0	41.2	72.0	4.9	118.0	15.0	40.9	6.2	7/5
<i>Tilia cordata</i>	78.9	6.3	196.7	11.1	62.8	3.2	72.3	8.4	21.7	1.1	33/32
<i>Ulmus glabra</i>	132.5	14.6	330.0	33.2	58.8	3.5	135.0	7.1	30.7	2.2	9/8

Note: * diameter at 1.3 m height; ** sample size for DBH / other variables.

Variation of the vegetation along the first axis is defined by ecotopic and floral factors: Areas 1 and 2 are distinguished quite well along this axis, whereas Area 3 lies in between (Fig. 7a). Thus, the vegetation on the soddy podbours / soddy-podzolic soils on fluvioglacial sands (*Quercus* – *Tilietum cordatae* ass.) and the vegetation on soddy-

podzolic and grey soils on the loams (*Aceri campestre* – *Tilietum cordatae* ass.) is differentiated well along the first axis; the vegetation on the soddy podbours on two-term deposits lies between these associations in the ordination diagram.

Fig. 6. The mean proportion of areas of various substrates and green mosses on the pit-and-mound microsites and the reference plots in the studied windthrow areas

Fig. 7. Ordination of vegetation plots by DCA: *a* – studied Areas 1–3 in accordance with Fig. 2; *b* – microsites: the "mound" consists of the top of the mound and the front/back sides of the mound; "the pit" includes the pits over and in front of the mound; "deadwood" and "reference plot" – see the text. Vectors: SpC – the number of species in the layer C; Br, Nm – the number of species of the boreal, nitrophilous, and nemoral ecological-coenotic groups; W, N, F, D – ecological characteristics of plots calculated by the Landolt's tables: soil moisture variability, fertility, moisture, and aeration

Among the analyzed environmental characteristics, soil moisture F, variability of moisture W, and soil fertility N correlate most with the first axis: $r = 0.69$, 0.61 , and 0.48 , respectively. Their vectors are directed towards the wetter and richer in soil biotopes of *Aceri campestris* – *Tilietum cordatae* ass. located on the loams and with a large number of nitrophilous species (Nt, $r = 0.65$). The aeration vector D associated with the granulometric composition of the soil (the higher the value is, the larger fractions there are in the soil) is directed towards Area 1, located on fluvioglacial sands ($r = -0.60$).

On the second axis of the ordination diagram (Fig. 7b), the vegetation varies along the microsites on the plots of massive windthrows: from the vegetation on the mounds (consisting of the top of the mound and the front/back sides of the mound) through the vegetation of the pits (pits over and in front of the mound) to the vegetation of the reference plots; the vegetation on the trunks of the

fallen trees occupies an intermediate position in the diagram between the vegetation of the mound and that of the pit. Among the analyzed characteristics, the number of boreal and nemoral species ($r = 0.52$ and -0.60 , respectively) shows the largest correlations with the second axis which means that there is a relatively larger number of boreal species in microsites of the mound and a relatively larger number of nemoral species in the reference plot and in the pits. Both the vectors of the species number in the layer C and of the nemoral species are directed towards the pits and the reference plots (SpC, $r = -0.53$), where the most species of vascular plants occurred (Fig. 8; Table 2). No strong correlations between the ecological characteristics of the plots and the second axis are observed, that means that there are no important differences between the ecological characteristics of the studied microsites according to the Landolt's tables [54].

Fig. 8. Box plots of the number of vascular plant species per plot occurred in the microsites: 1 mound, 2 front and 3 back sides of the mound, 4 pit over the mound, 5 pit in front of the mound, 6 deadwood, 7 reference plot of 1×1 m. The midline is the median, the box sides represent the first and third quartiles; the length of the vertical segments is determined by the distance from the box side to the smallest/largest value that falls within one-and-a-half interquartile range from the lower/upper side of the box; single points are outliers

In general, indirect ordination revealed differences in the vegetation of three investigated areas (along the first axis) as well as differences between microsites and the reference communities (along the second ordination axis). The analysis of dominant, constant and indicator species of the investigated microsites and reference plots made it possible to specify the observed difference.

Dominant species, or the species covering over 50 % of an analyzed area, differed for the

microsites and reference plots. Mounds and pits were dominated by tall herbaceous species growing on rich soils, i.e. *Rubus idaeus*, *Urtica dioica*, *Impatiens noli-tangere*; undergrowth of *Padus avium* also occurred there with high coverage. Besides, *Tilia cordata* individuals of seed origin covered from 30 to 60 % of some pits, whereas it was never seen in the forest not affected by windthrow (only lime individuals of vegetative origin occurred there). Reference plots (over 75 %

of the coverage) were dominated by the typical nemoral species *Aegopodium podagraria*, *Carex pilosa*, and *Mercurialis perennis*; the nitrophilous species *Urtica dioica* with high cover (50 and 80 %)

was found in two plots. The deadwood was dominated (with 40 % of the coverage) by the nemoral herbs *Galeobdolon luteum* and *Glechoma hirsuta*.

Table 2

Species diversity of vascular plants on the pit-and-mound microsites and in the reference plots in the 2006 windthrow in the Kaluzhskie Zaseki Reserve

	Mean number of species	Standard error of the mean	Total number of species	Whittaker index	Number of the plots
Mound, top	4.6	0.31	43	8.3	45
Front side of the mound	4.2	0.29	38	8.0	44
Back side of the mound	3.5	0.33	28	7.0	37
Pit over the mound	8.6	0.49	59	5.9	45
Pit in front of the mound	5.1	0.36	26	4.1	23
Deadwood	2.7	0.43	10	2.8	12
Reference plots	10.0	0.32	52	4.2	45

Constant species of microsites, as well as dominant ones, mostly overlapped but they differed from constant species of reference plots, although two nemoral species, *Glechoma hirsuta* and *Galeobdolon luteum*, were found in more than 50 % of plots on almost every microsite and in reference plots as well. On the treefall mounds, their tops, front and back sides and in pits, *Rubus idaeus* occurred in 50 % of cases (Fig. 9a). The nitrophilous herb *Impatiens noli-tangere* occurred

on the mounds rarer than *Rubus idaeus* but it was found in 75 % and 50 % of the pits located in front of the mounds and on deadwood, respectively (Fig. 9b). *Aegopodium podagrarium* and *Urtica dioica* occurred on 58 % of the pits located in front of the mounds. The typical nemoral species *Pulmonaria obscura*, *Asarum europaeum* and *Mercurialis perennis* occurred on over 50 % of the reference plots.

Fig. 9. The position of *Rubus idaeus* (a) and *Impatiens noli-tangere* (b) in the ordination diagram. Microsites: 1 – mound; 2 – pit; 3 – deadwood; 4 – reference plots

The composition and abundance of plant species on different microsites overlapped to a large extent, therefore there were only a few indicator species of microsites, and they had relatively low indicator values. For the mounds it was nemoral sedge *Carex digitata*; for pits *Tilia cordata*, and for pits in front of the mounds *Impatiens noli-tangere*. In the reference communities, the highest indicator values were shown by *Pulmonaria obscura* and *Aegopodium*

podagrarium. When joining the elements of pit-and-mound topography into larger units, as mound (together with the mound top, front, and back sides), pit (with the pits over and in front of the mound) and deadwood, *Rubus idaeus* was found to be the indicator species for the mound ($IV = 27.6$ %), and *Urtica dioica* for the pit (22.9 %), whereas *Pulmonaria obscura* and *Aegopodium podagrarium* remained the most vivid indicators of the reference communities ($IV = 60.3$ and 60.0 %, respectively).

Thus, although the pit-and-mound microsites differed slightly from the reference plots in ecological characteristics, they showed a relative increase in the number and abundance of tall herbaceous species of the boreal and nitrophilous ecological-coenotic groups demanding rich soil. It can be assumed that this is due to an increase in available nitrogen in the pit-and-mound microsites and an increase in the illumination in general in the areas of massive windthrow due to simultaneous fall of many tree individuals.

Vegetation diversity assessment. A total of 78 species of vascular plants were listed at 251 vegetation plots: 12 tree, 4 shrub, and 62 herbaceous species. At that, 26 species occurred only in the pit-and-mound microsites and were not found in the reference plots; these species are as following: 3 tree species (*Salix caprea*, *Pinus sylvestris*, and *Betula pendula*), 2 shrub species (*Euonymus verrucosa* and *Sambucus racemosa*), and 20 herbaceous species. Six vascular plant species were not listed before the windthrow study in the relevés of broadleaved, nemoral aspen, and nemoral birch forests of the Reserve. Those are the meadow species *Erigeron (Coniza) canadensis* and *Hypericum hirsutum* which are rarely found in the Reserve in general; *Trifolium pratense* which is common for the meadows; nitrophilous semishrub *Rubus caesius*, which rarely occurred in the Reserve; and two water-marsh species: the fairly common *Epilobium palustre* and the rare species *E. hirsutum*, which was firstly found in 2010 on the windthrow and in the floodplain of the Moshok River (as N. M. Reshetnikova observes, *Epilobium hirsutum* has been spreading quite successfully throughout the Reserve since 2014). Eight plant species found on the pit-and-mound microsites have been listed in geobotanical relevés of broadleaved and aspen forests of the Reserve less than three times [62], i.e. the boreal shrub *Sambucus racemosa*, the boreal fern *Phegopteris connectilis*, the meadow-edge species *Impatiens parviflora*, *Bromopsis inermis*, *Leontodon autumnalis*, *Vicia cracca* and *Cirsium arvense*, as well as the piny grass *Calamagrostis epigeios* and the nemoral herb *Chelidonium majus*. Thirteen species of plants were found only in one microsite. Tree individuals of seed origin for many tree species, such as *Tilia cordata*, *Ulmus glabra*, *Fraxinus excelsior*, *Acer platanoides*, *Padus avium*, *Salix caprea*, *Betula* spp., and *Populus tremula*, were often found on the pit-and-mound

microsites. Highest compositional diversity was observed in pits located over the mounds and in reference plots (see Fig. 8, 9; Table 2). The mean number of species per plot was higher in reference plots, whereas the total species richness was higher in pits. The compositional diversity of vegetation on other microsites decreased as follows: top of the mound – front side – back side – pit in front of the mound – deadwood. Beta diversity was highest on the mound microsites; it was lower in the pits and reference plots. The structural diversity of vegetation was also higher on the mounds and in the pits due to the boreal, nitrophilous, water-marsh and meadow-edge species (Fig. 10). The contribution of species of these groups into diversity is more evident in the ecological-coenotic spectra of the total species lists than in the spectra of their mean number. In general, ecological-coenotic structure of vegetation in the reference plots was similar to the structure of broadleaved and aspen forests in the Reserve [48] where the proportion of nemoral species is 80–90 %. In the pit-and-mound microsites, proportion of nemoral species is lower (from 50 to 71 %); the number and proportion of boreal species are highest in all mound microsites and in the pits located over the mounds.

When assessing the total plant species diversity, it should also be noted that high cover of green mosses was observed on the mounds and on the deadwood (see Fig. 6). On average, mosses occupied 15 % of the mound back side area, 46 % of the mound front side area and 55 % of the tops of the mounds. The mean cover of green mosses in the lying trunks close to the roots was 62 %, whereas the cover of green mosses in reference plots was 1–2 %. This means that the windthrow significantly increased the participation of mosses in the ground layer of the studied broadleaved forest communities.

Thus, the analysis of vegetation listed 4 years after the windthrow on 45 treefalls and on 45 reference plots of 1×1 m showed the increased diversity of vascular plants due to the emergence of new microsites. Our observations showed, as compared to single treefalls in the broadleaved forest, a massive windthrow causes the greater percentage of trees to fall with uprooting creating large pits and mounds. As a result, new microsites are forming and species with various ecological-coenotic traits can settle and grow there.

Fig. 10. Ecological-coenotic structure of the average and total number of species of vascular plants on the pit-and-mound microsites: 1, 2 and 3 top, front and back sides of the mound; 4 and 5 pits over and in front of the mound, 6 deadwood, 7 reference plot of 1×1 m. Nm nemoral, Br boreal, Pn piny, Nt nitrophilous, Wt water-marsh, and Md meadow-edge ecological-coenotic species

Changes in vegetation due to the presence of mounds and pits caused by treefalls with uprooting are still rarely a focus of research. Our results showing an increase in the structural and species diversity of vegetation caused by the emergence of new microsites are generally consistent with the results obtained earlier for beech forests of northern Germany [34], coniferous forests dominated by *Tsuga canadensis* and *Pinus strobus* in the United States [40] and dark coniferous taiga of the Pechora-Ilych Reserve [36, 37, 64].

Conclusion

Our research has shown that pit-and-mound microsites formed during massive windthrows contribute to increased diversity of ecological-coenotic structure of vegetation of broadleaved forests, promote the emergence of species of boreal, nitrophilous, water-marsh, meadow-edge and piny ecological-coenotic groups of vegetation. The presence of bare substrate on the microsites contributes to the appearance of tree individuals of seed origin for many tree species. The participation of mosses in the ground cover increases significantly. Due to the unique character of

polydominant broadleaved forests of the Kaluzhskie Zaseki Reserve it is possible to obtain fundamentally new data on the course of autogenic succession after catastrophic windthrows in the broadleaved forest region. These data and knowledge are important and can help us address the fundamental problems of biodiversity conservation and maintenance of ecosystem sustainability.

Acknowledgements

The authors express their gratitude to Miroslav Stamenov, Elizaveta Ivanishcheva and Anastasia Mikhaleva for their assistance in collecting field data. Analysis of the field data and the article preparation were carried out within the framework of state assignments of the Institute of Mathematical Problems of Biology of the Russian Academy of Sciences – a branch of M. V. Keldysh Institute of Applied Mathematics of the Russian Academy of Sciences, and the Institute of Physico-Chemical and Biological Problems in Soil Science of the Russian Academy of Sciences (0120-2019-0005, reg. No. AAA A-A18-118013190176-2).

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