The effects of windthrow on forests at different spatial scales: a review

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Abstract

This paper aims at reviewing the ecological effects of windthrow and the processes by which the structure and composition of the boreal forest are affected. The windthrow problem has been investigated at different levels: landscape; forest community; and fallen tree ecosystem. All original data are from the natural, protected, uneven-aged boreal spruce forests of the central Russian Plain. Mapping of vegetation was used to detect windthrow processes in primary forest communities. The scales of windthrow gaps in space and time determine the patch structure of the forest ecosystems. The main result of this phenomenon is the occurrence of gap-phase dynamics in forest communities. The development of gaps is very important for the survival of small- and broad-leaved trees in boreal coniferous forests.

In the case study of the scales of natural windthrow disturbances it was found that in uneven-aged spruce forests, 7–12% of the surface was covered by pit-and-mound topography. After widespread windthrow, this figure rised to 15–25%. In this context, a procedure for dating windthrow topography was developed, along with methods of diagnosing uprooting disturbances of the soil. Much attention was also paid to the structure and properties of soil where uprooting had occurred. It was found that the microsites which are found in pit-and-mound topography differ pedogenically. Furthermore, the nature and rate of recovery of the background soil profile after uprooting varied a lot, i.e. under the influence of shallow uprooting, the reconstruction of the background soil combination and processes was completed in 100–200 years. Where as in cases of major uprootings, it took more than a 200–300 year cycle.

The role of tree uprooting in maintaining stable tree and grass population structures in forest communities was found very important. The spatial distribution of trees was associated with pit-and-mound topography in all types of forests. Furthermore, spruce regenerated better on mounds and fallen trees than on undisturbed surfaces. Multi-aged tree regrowth was therefore being constantly formed in virgin forests. There was also increase in the community floristic richness due to the establishment of certain pioneer species from other communities in microsites disturbed by uprooting. The gene pool of a population was rejuvenated as the plants appeared in these microsites from seeds and spores, while propagation in undisturbed areas was predominantly vegetative. As a result, the structure of forest plant populations was found to be in a stable multi-aged state. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Norway spruce; Succession; Uprooting; Vegetation dynamics; Virgin forest; Windthrow

1. Introduction

Windthrow is a significant natural phenomenon in forests. Disturbance by wind varies spatially and temporally in forests, from large-scale catastrophic disturbances operating at the landscape level to small-scale perturbations operating at the scale of individual trees (Pickett and White, 1985; Kuuluvainen, 1994; Smirnova and Shaposhnikov, 1999). It is mainly trees and stands that are affected by windthrow. But windthrow can also change soil structure, influence tree

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Table 1
Three scales in the study of windthrow disturbance

Scale of disturbance	Phenomenon	Type of dynamics
Landscape	catastrophic windthrow	secondary succession
Forest community	single or multiple windthrow	gap-phase dynamics
Fallen tree ecosystem	pit-and-mound and log creation	micro-successions

recruitment and, although it has been much less studied than other impacts, windthrow can initiate ground layer successions (Bormann and Likens, 1979; Skvortsova et al., 1983; Falinski, 1986; Schaetzl et al., 1989a, b, 1990; Peterson and Pickett, 1990, 1991; Foster and Boose, 1992; Smirnova, 1994; Peterson and Carson, 1996).

This review emphasizes the different spatial levels of windthrow effects. We have adopted the multi-scale approach that is used in vegetation science (Allen and Hoekstra, 1990; Kotliar and Wiens, 1990; Maslov, 1990; Masing, 1994). This approach hinges on the thesis that vegetation is a multi-level phenomenon. The scale-related structural entities have been named territorial units. The boundaries of these units show different levels of distinctness along the spatial and temporal scales which have been used in their study. Usually, the territorial units are studied on global, regional, landscape (local), community (coenotic), population, pattern, and organism levels (Masing, 1994). The three main scales of windthrow disturbances that we have adopted are shown in Table 1.

This review identifies the different types of vegetation dynamics that are caused by different scales of windthrow disturbance. These ideas are illustrated by the case study examples of the south boreal spruce forests of the Central Forest Reserve (Russia). Investigations of catastrophic windthrow, and detailed studies of natural single and multiple tree windthrow, have been carried out there since 1976 (Skvortsova and Ulanova, 1977; Stroganova et al., 1979; Skvortsova et al., 1983; Ulanova, 1991; Pugachevsky, 1992; Vassenev and Targulyan, 1995; Smirnova and Shaposhnikov, 1999).

2. Material and methods

2.1. Study sites of the case studies

Our study was conducted in the natural, protected, uneven-aged virgin forests of Russia and Ukraine. The best-preserved primeval boreal spruce forests were selected for the study in the Central Forest Reserve (Tver' region, Russia), in the Costroma region, in the Middle Urals Mountains (Visim Nature Reserve), and in the mixed and beech forests of the Carpathian Mountains (Carpathian National Park). The nomenclature of forests types from the Carpathian Mountains follows the Braun-Blanquet approach (Matuszkiewicz, 1981); for other regions, it follows the North-European school (Frey, 1973).

The investigations were primarily carried out in the East-European taiga (southern taiga zone) in the Central Forest Reserve. This is located in the centre of the Russian Plain in the south-west part of the Valday Uplands at the watershed of the Volga and Western Dvina rivers. The area lies west of Rzhev between 56°26' and 39'N and 32°39' and 31°01'E at 300 m asl. The surficial geology is dominated by 10-m thick moraine deposits (Karpov, 1973). The spruce forests consist of Norway spruce *(Picea abies* (L.) Karst), with the species composition being dependent on the geomorphology. On flat areas the *Myrtillus* and *Oxalis-Myrtillus* types occur. These are replaced in wet places by *Hylocomium-Myrtillus* and *Sphagnum-Myrtillus* types. On the upper parts of relatively steep slopes, *Oxalis* type spruce forests grow on weak-soddy and pale-yellow podzolic soils with different humus richness (Stroganova et al., 1979). On the drier upper sections of these slopes, rather small areas of *Galeobdolon* type spruce forests are present. On the better-drained and more nutrient-rich ecosystems in the middle parts of slopes the spruce forests contain deciduous trees *(Tilia cordata* Mill., *Acer platanoides* L.) and nemoral species dominate the undergrowth, forming *Asperula* type forests. Soils there are soddy-brown podzolic and pale-yellow podzolic soils. On the lower parts of slopes directly adjoining riverbeds, the *Filipendula, Aconitum, Mercurialis* types of spruce forests are found.

2.2. *Methods*

Ten sample plots in different forest types (spruce, birch *(Betula pendula* Roth.), beech *(Fagus sylvatica* L.) forests) in four regions were studied. Most of the stands (8) were uneven-aged, as determined by ageing the trees. The plot sizes differed (from 0.2 to 0.7 ha), but were sufficiently large to provide a representative picture of the forest stand structure. There was no evidence of cutting or fires during the last 100–200 years.

Windthrow-affected areas were mapped at a scale of 1:100. All trees and shrubs were indicated on the map including the species, trunk diameter at breast height (DBH), age, and the patterns of windthrow. At mountain sites, we also identified streams, rock out-crops, and the direction and angle of slopes. All new and old uprootings were located on the map. Only specific pit-and-mound pairs and pits with more or less oblong or sickle shapes were mapped. Topographic depressions (pits) with a depth of >10 cm were included. The date of every uprooting and all mor-phological parameters of mounds and pits were deter-mined. We determined the area of pits and mounds by measuring the long and short axis of each and calcu-lating the area of an ellipse with those measures as axes.

At each plot, we made 100 releves with quadrats of 1×1 m^2 in undisturbed sites as well as in each pit and mound of uprootings. In other words, the selection of releves took into account the distribution of rather large patches inside community. We estimated cover (in %) for each tree, shrub, herb, and bryophyte species. The number and age of tree saplings and seedlings in quadrats were also determined.

3. Results and discussion

3.1. *Landscape level: catastrophic windthrow*

One of the most important disturbance agents for primeval boreal forests in nature reserves is cata-strophic windthrow (see Everham and Brokaw, 1996). In the Central Forest Reserve (Tver' region), hurricane winds with speeds of more than 20 m s^{-1} usually destroy all forests, regardless of type. Among the notable storms that have affected forests are those

Table 2
Distribution of stand areas according to windthrow damage degree Karpachevsky et al., 1999)[a]

Dominant tree species	Damage degree (% of total area)			
	High	Medium	Low	Absent
Populus tremula	41.3	24.4	8.8	25.5
Picea abies	42.2	23.1	7.0	*21.1*
Betula spp.	45.3	14.1	6.3	34.3
Alnus incana	42.7	10.3	5.8	41.2
Alnus glutinosa	32.2	2.4	0.5	64.9
Pinus sylvestris	8.1	1.0	0.1	90.8

[a] Damage degree: losses in growing stock high, 50%; medium, 31-50%; low, 10-30%; absent, 10%.

that occurred in 1969, 1987 and 1996. The most severe storm took place in 1987 when 10% of all forest areas were completely blown and 66% were partly affected Karpachevsky et al., 1999).

The most severe damage occurs in aspen (74.5%), spruce (73.2%) and birch (65.7%) forests (Table 2). Older forests have higher levels of damage than younger ones. Wind damage was prevalent in most productive forests, namely *Asperula* and *Galeobdolon* type spruce forests and well-drained forests such as *Oxalis* type spruce forest, and on wet soils along small rivers, the *Filipendula* type spruce forest (Table 3).

Catastrophic windthrow cause full destruction of tree canopy, significant soil perturbation and destroy regeneration. The understorey species also suffer greatly. There are major changes in environmental conditions (namely light availability and soil moist-ure) at the ground level and in the topmost soil

Table 3
Distribution of spruce forest types according to windthrow damage degree Karpachevsky et al., 1999)[a]

Spruce forest type	Damage degree (% of total area)			
	High	Medium	Low	Absent
Galeobdolon type	36.9	27.9	8.3	26.9
Asperula type	39.7	31.3	12.4	16.6
Oxalis type	48.8	26.1	7.8	17.3
Myrtillus type	43.2	22.3	4.5	30.0
Sphagnum-Myrtillus type	37.9	4.4	1.7	56.0
Sphagnum type	28.8	9.5	3.4	58.3
Filipendula type	46.7	21.9	6.8	24.6
Matteuccia type	7.5	48.9	0	43.6

[a] Damage degree: losses in growing stock high, 50%; medium, 31-50%; low, 10-30%; absent, 10%.

horizons. These changes tend to homogenise the originally heterogeneous site conditions in different forest types and lead to the development of very similar successional trends in the landscape (Karpachevsky et al., 1999). Successional pathways are largely determined by the survival patterns of the original stand, tree regeneration, and understorey. Sometimes, tree saplings may rapidly grow into canopy. Somesecondary succession pathways include recruitment of *Betula* species, *Populus tremula* L., *Tilia cordata* or *Picea abies.*

3.2. The forest community level: single and multiple windthrow

Windthrow has a strong ecological impact on forest communities (Stephens, 1956; Falinski, 1978, 1986; Skvortsova et al., 1983; Schaetzl et al., 1989a). The scales of windthrow gaps in space and time determine the patch structure of forest ecosystems. The main result of this phenomenon is the development of gap-phase dynamics in forest communities (Yamamoto, 1961; Veblen, 1992; Smirnova, 1994). The development of gaps is very important to the survival of small- and broad-leaved trees in boreal coniferous forests (Bobrov et al., 1999).

The gaps produced in forests vary greatly in size, but usually there is a preponderance of small gaps produced by the fall of one or a few trees. Regrowth occurs from three sources: (1) buried seeds, rhizomes, spores or other propagula; (2) plants established prior to gap formation; (3) lateral growth of branches from trees on the gap periphery (Collins et al., 1985).

An early response is the more rapid growth of the surrounding trees as they start to extend their branches into the sunlit space that has been created. There is something of a race to fill the gap, and if the gap is small the race will usually be won by the lateral growth of trees around the gap. There is no principal change in vegetation structure if the size of gap is not more that the height of the surrounding canopy trees (Smirnova, 1994; Smirnova and Shaposhnikov, 1999). Gap closure often takes place by the fast growth of saplings that were already present, but suppressed under the former canopy (Pugachevsky, 1992). They are released and grow up rapidly into the gap. For example, the growth rate of saplings of *Fagus sylvatica* in beech forests can be an order of magnitude

greater in gaps than beneath the intact canopy (Skvortsova et al., 1983).

If the size of a gap is more than the height of the surrounding canopy trees, the habitats change. First, light availability increases and the level of competition changes (Bormann and Likens, 1979; Collins et al., 1985). The mean size of gaps is 50×70 m and they occupy nearly 10% of the total area in the primeval spruce forests of the Central Forest Reserve (Georgievsky, 1992).

The first form of regrowth in large gaps is the release of dwarf saplings of the same (parent) trees; they are often found in groups. The second form is the invasion by new secondary species, such as *Betula* species, *Populus tremula, Tilia cordata* or *Sorbus aucuparia.* These species are usually replaced by spruce regrowth developing after the disturbance (Skvortsova et al., 1983; Bobrov et al., 1997). The mature phase is recognized as occurring 80–100 years after windthrow.

Most of the emphasis in the literature has been placed on gap size and its influence on the composition of the regenerating species (Leemans, 1991; Liu and Hytteborn, 1991; Peterson and Carson, 1996). This has led to questions about the roles of gaps in the regeneration process: Is gap creation necessary for seedling establishment and the formation of the sapling bank? Is a gap filled by trees from the existing sapling bank or from those newly established after gap creation? Woods (1984) and Uhl et al. (1988) have suggested that the only role of gaps is to release suppressed saplings, with the regeneration pattern being formed in advance of the disturbance. However, we consider that different situations exist for different regions and forest types.

3.3. The fallen-tree ecosystem: pit-and-mound topography and log creation

3.3.1. Area coverage of pit-and-mound topography
It is difficult to make a visual assessment of the area subjected to disturbances without mapping the extent of the windthrow. Our maps only showed pit and mounds that are clearly of windthrow origin. Only specific pit-and-mound pairs and pits with more-or-less oblong crescent shapes were mapped (Fig. 1). We estimated the area coverage of pit-and-mound pairs in different forest types to be between 7 and 25% of the
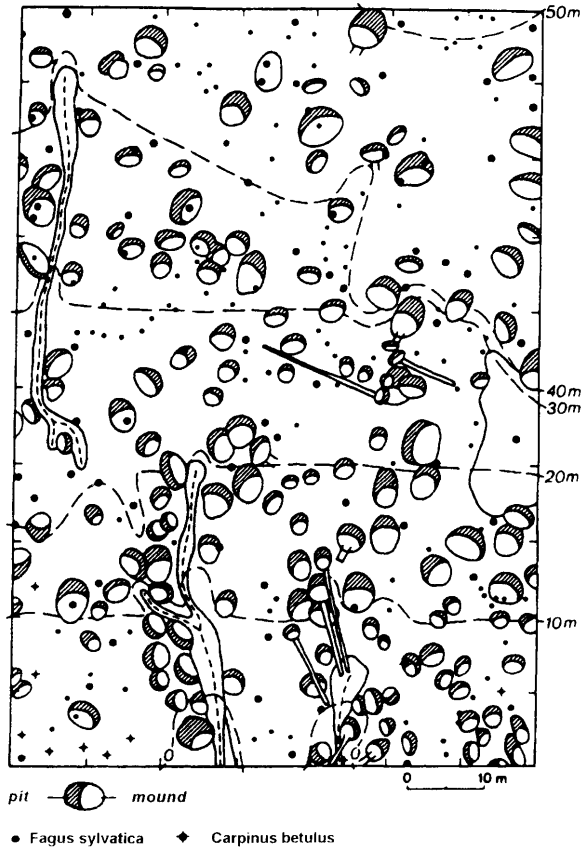
pit ─◖─ mound

● Fagus sylvatica   ◆ Carpinus betulus

Fig. 1. Patterns of windthrow in beech forest (Carpathian Mt.).

spread windthrow, uprootings affect between 15 and 25% of the total area. The greatest proportions of disturbance due to catastrophic windthrow are probably observed in even-aged spruce forests after the loss of secondary species (birches, aspens). In such forests, the surface coverage of pit-and-mound pairs may reach 40% of the land area. Although we did not find any such areas, published data indicate that pit-and-mound pair disturbances may occupy over 40% of the land area (Collins and Pickett, 1982; Lyford and MacLean, 1966).

In the Carpathian Mountains, pit-and-mound pairs in uneven-aged primary forests occupy from 11 to 15% of the total area. The surface coverage of windthrow-induced disturbances increases from the upper to the lower part of the forest belt. Pits and mounds caused by windthrow in beech forests occupy the largest areas (15%). As the slope increases the surface coverage of windthrow disturbances also increases. In the Ural Mountains, pit-and-mound pairs account for 8% of the ground area, possibly because the sample plot was located on a gentle slope.

3.3.2. Age dating of windthrow topography

Different authors have used a log decay scale with between five and nine divisions to determine gap age or the time since a windthrow event (Skvortsova et al., 1983; Hytteborn and Packham, 1987; Storozhenko, 1990; Liu and Hytteborn, 1991). The degree of decay of a log depends not only on the date of the windthrow, but also on log size and species, its position, i.e. whether it rests directly on the ground or on broken

total area (Table 4). Windthrow disturbances account for 7-12% of the total area in uneven-aged boreal spruce forests (Ulanova, 1991). In the case of a wide-

Table 4
Surface coverage of windthrows in different forest types

Forest type	Sample plot (ha)	Mounds (%)	Pits (%)	Pits+Mounds (%)
East-European taiga				
Asperula type spruce forest, CFR	0.64	4.7	7.5	12.2
Oxalis type spruce forest, CFR	0.48	3.5	3.3	6.8
Myrtillus type spruce forest, CFR	0.49	4.2	8.5	12.7
Oxalis type spruce forest, Kostroma region	0.20	3.7	2.7	6.4
Catastrophic windthrow in *Oxalis* type spruce forest, CFR	0.35	3.8	11.7	15.5
Oxalis type secondary spruce-birch forest, CFR	0.36	14.8	10.3	25.1
Mountain forests				
Oxalis type spruce forest, Urals Mt.	0.48	4.9	3.2	8.1
Plagiothecio-Piceetum tatricum, Carpathian Mt.	0.72	7.7	3.3	11.0
Abieti-Piceetum montanum, Carpathian Mt.	0.70	9.2	3.5	12.7
Dentario grandulosae Fagetum, Carpathian Mt.	0.70	9.1	5.8	14.9

Table 5
The windthrow decomposition degree scale

Years	Leaves, needles	Twigs	Branches	Roots	Trunk, log	Wood rot	Plants on trunk
1–10	±	+[a]	+	+	+	−	−
11–20	−[b]	−	+	+	+	+	+
21–50	−	−	−	+	+	++	++
60–90	−	−	−	−	+	++	++
100–200	−	−	−	−	−	−	−

[a] Present.
[b] Absent.

branches, and the status at the time of the windthrow event, i.e. dead or alive. Different parts of the same log can decompose at different rates. In this context, *Picea abies* logs were used to develop a log-decay scale and to estimate treefall age and a scale with five windthrow/log decay classes were used (Table 5). In our study, a chronological approach was adapted to study changes in the size and shape of pit-and-mound topographies, soil composition and vegetation structure in areas impacted by windthrow.

3.3.3. Different habitats of the fallen tree

Treefalls do not only create gaps in the canopy which locally improve the light conditions in the forest, they also create different microsites on the forest floor by disturbing the bottom layer and by adding woody debris to the ground (see Veblen, 1992). This process can promote the micro-environmental heterogeneity of the forest by creating pit-and-mound microrelief with exposed root mats, bare mineral soil, humus, and fallen logs (Stephens, 1956; Lyford and MacLean, 1966; Schaetzl et al., 1989b). A high diversity of microsites is created, each with specific nutrient pools, microclimates, and surface structures (Peterson and Campbell, 1993). This is important as recent investigations have emphasised the links between biodiversity and coarse woody debris in boreal forests, with different woody microhabitats supporting many species of bryophytes, lichens, fungi, insects, and birds (see Samuelsson et al., 1994).

3.3.4. Disturbance of soils

Much attention has been paid to the structure and properties of soil after uprooting (Schaetzl et al., 1989a, b, 1990; Peterson et al., 1990). The microsites found in pit-and-mound topography differ pedogeni-

cally. The nature and rate of recovery of the background soil profile after uprooting have been studied. In primeval forest ecosystems, podzolic texture-differentiated soils are regularly disrupted by uprooting. During the Holocene, every 'point' of the ecosystem has experienced the uprooted decomposed logs or pit stage between 10 and 20 times on average, the superposition of organo-mineral mounds on pits between three and five times, and the superposition of organic mounds on undisturbed soil between one and two times (Vassenev and Targulyan, 1995).

All uprooting elements are characterized by sharp changes in the soil profile (Skvortsova and Ulanova, 1977; Skvortsova et al., 1983). The upper horizons of the soil profile are lost in area of the pit. In the other uprooting elements, the profile is buried by organic-mineral or organic material (Fig. 2). Shortly after the windthrow event, the taxonomy of these soils differs markedly from the original ones; for example, the pits have bog and bog-podzolic soils. Decomposed logs and organic mounds disappear in 50–200 years, while the pits and organo-mineral mounds are preserved until the next windthrow event.

The gap in the tree canopy, exposure of the mineral substratum, buried soil, and formation of microtopography drastically changed the soil environmental regimes (Skvortsova et al., 1983). Temperature and soil moisture content, and the activities or a more diverse soil biota, all increase in the affected area. The soil conditions are characterised by reduction processes, the total amount of H^+ increases, and the nutrients usually become more concentrated.

Windthrow causes profound transformations of the soil material, resulting in increases in the total eluviation of the upper part of the profile and in the total thickness of eluvial horizons (Fig. 3)
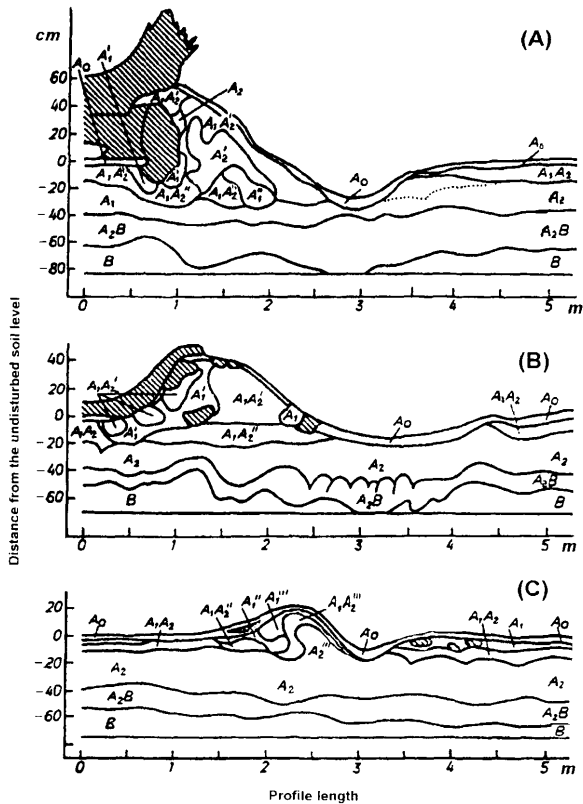
Fig. 2. Dynamic processes in soil profile after tree uprooting. Explanations: (A) 0–1 year; (B) 30–50 year; (C) more than 100 years.
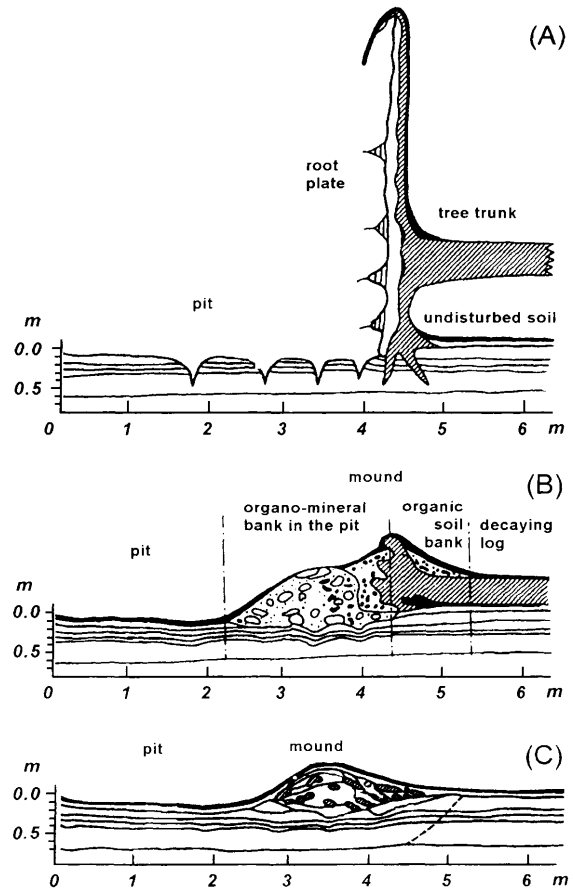

Fig. 3. Soil profiles in pit-mound complexes at 20–30 years (A), 50–60 years (B), 80–100 years (C) since windthrow (derno-podzolic soils, Central Forest Reserve). Explanations: A_0, litter; A,, humus accumulative horizon; A_2, eluvial podzolic horizon; B, illuvial horizon; A_1' mixed horizon; A_1' buried soil horizon; A_1''', new formed horizon; shaded parts, decaying wood.

(Vassenev and Targulyan, 1995). As a whole, the eluvial-illuvial profile differentiation is deepened and increased.

The disturbance caused by the windthrow, together with lateral processes and changes in the soil regime, intensify the main groups of soil-forming processes, including the metamorphic transformation of organic and mineral components, structural reorganization, change to grey or ashy colour, and segregation through eluviation/illuviation of various materials in solutions and suspensions (Vassenev and Targulyan, 1995).

All the elements of the pit-and-mound complex are characterized by soil profile successions, namely: (I) the genetic specificity of stages for every element; (II) the synchronization of stages for every element; (III) a similar direction of gradual successions from the

maximal contrast on initiation to the background patterns in the final stages; and (IV) the impossibility of returning to the original conditions in cases involving deep uprooting disturbances and the difficulty of returning to the approximate original conditions in cases following the creation of shallow pits.

When the uprooting is shallow, soil-forming processes become similar to those of undisturbed soils after 100–200 years. When major uprootings are involved, the reconstruction of the background soil combination and processes within the 200–300 years cycle is in principle impossible.

3.3.5. Tree recruitment

Micro-environmental heterogeneity consequently provides more opportunities for the regeneration of different tree species, especially for small-sized and light-demanding trees. Microsite creation may play an important role in the process of regeneration in boreal forests where the forest floor is usually covered by a thick carpet of moss (Bonan and Shugart, 1989; Korzukhin and Antonovski, 1992).

Seedling establishment can be affected by many factors, such as drought, diseases, herbivore attacks, etc. However, the importance of the substrate properties has been stressed by many authors in different forest studies (Skvortsova et al., 1983; Putz, 1983; Beatty, 1984; Hytteborn and Packham, 1987; Zasada et al., 1992). Seedlings and small saplings are concentrated on logs, in pits, or on boulders covered by a moss-litter carpet (Putz, 1983; Christy and Mack, 1984; Hytteborn and Packham, 1987; Peterson et al., 1990). Leemans (1991) has suggested that gaps are more often closed by newly established individuals after gap creation, rather than by the growth of previously suppressed trees. The seedling and sapling distribution patterns for *Picea abies* are different (Karpov et al., 1983; Pugachevsky, 1992). Seedling patterns are most likely influenced by seed dispersal and germination conditions, whereas sapling patterns are mainly affected by the differences in microsite quality. For instance, seedlings growing in pits (which are a good place for germination) are often killed by soil slides from the root plates during heavy rains, or suffer from flooding in the pits.

In our investigations, seedling and sapling survival of *Picea abies* were higher on decaying logs and mounds in three studied forest types (Fig. 4). They did not survive on undisturbed ground or near tree trunks. *Betula* seedlings and saplings were more common in pits and on root plates with bare soil (or humus), consistent with their light-demanding needs and small seeds. The *Salix caprea L.* saplings showed similar microsite preferences to *Betula* spp. The age population structure of *Picea abies* changed over time (Fig. 5), with spruce seedlings established on uprootings and decaying logs surviving and forming a new cohort in the population. Multi-aged regeneration was constantly occurring in the forests. Consequently, the creation of gaps and microsites by natural disturbances are two related major
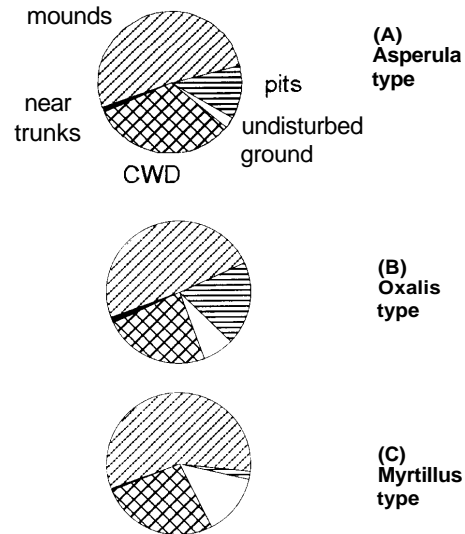

Fig. 4. Distribution of *Picea abies* seedlings and saplings on windthrow microtopography elements and on undisturbed ground in three types of spruce forests (Central Forest Reserve). Explanations: CWD, coarse woody debris. (A) *Asperula* type; (B) *Oxalis* type; (C) *Myrtillus* type.

environmental components determining the regeneration niche in forests.

3.3.6. Field-layer species diversity

Uneven-aged boreal spruce forests usually have a forest floor with a dense bryophyte carpet that largely prevents herb species establishment (Karpov, 1973). Windthrow disrupts the bryophyte carpet, causing mortality through both the relocation of the root system and the fallen log. As a result, a space that is initially free from potential competitors is created. Hence, competitive exclusion should be of minor importance in recently disturbed patches, thus favouring species coexistence (Grubb, 1977; Grime, 1979). At the same time, the micro-environmental heterogeneity of uprootings has a significant impact on the potential number of species that can establish, as many species have very specific habitat requirements.

The total field-layer species richness in all four of the spruce forest types was significantly greater due to species occurring in disturbed windthrown patches (Fig. 6). The proportion of such species varies from 17 to 23% of the total community species list. Patches of the forest floor where the underlying soil has been exposed by windthrow act as local centres of high
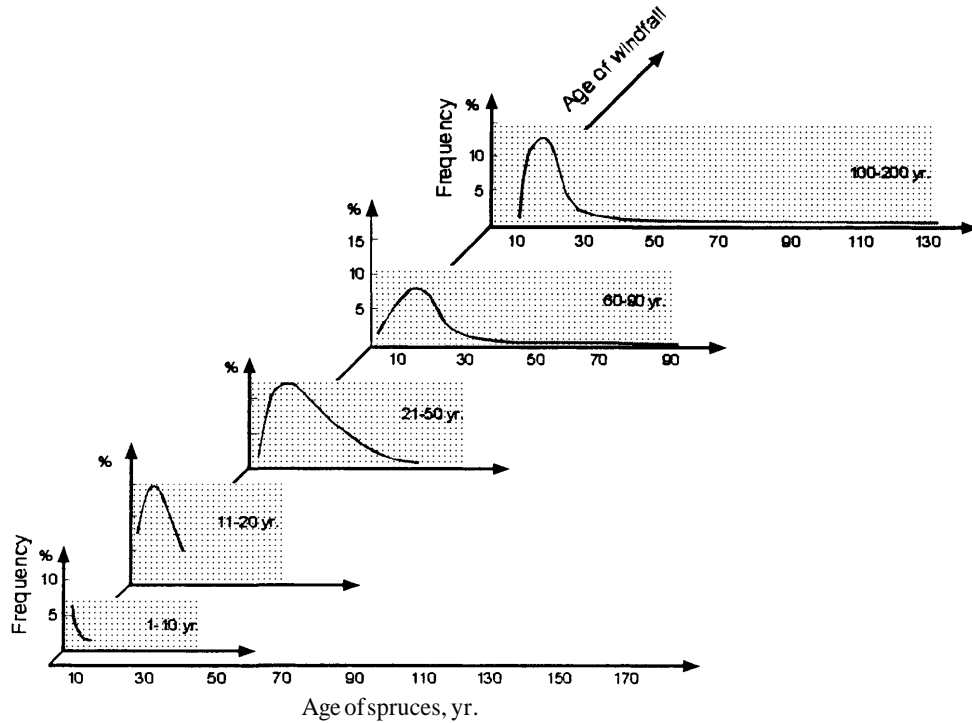
Fig. 5. Age structure of *Picea abies* on windthrow mounds *(Asperula* type spruce forest, Central Forest Reserve).

species diversity, not only for seed plants and ferns but also for bryophytes (Jonsson and Esseen, 1990) and the soil mesofauna (Bobrov et al., 1999). These species are generally shade-intolerant early successional species, such as *Rubus idaeus* L., *Juncus effusus* L., *Epilobium adenocaulon* Hausskn., and *Epilobium angustifolium* L. Most are able to germinate from

the forest soil seedbank (Skvortsova et al., 1983). The proportion of early colonizer species decreased with time following the disturbance (from 55% in 1-5 year to 10% in old uprootings) (Fig. 7).

Seed germination at disturbed sites also has very important genetic aspects for plant population rejuvenation, whereas plants at undisturbed sites mostly
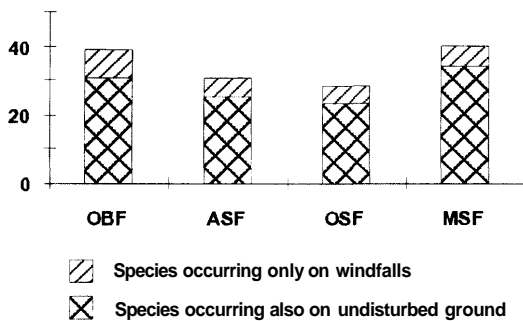

Fig. 6. Number of field-layer species in four different spruce forest types (Central Forest Reserve). Explanations: OBF, *Oxalis* type secondary spruce-birch forest, ASF, *Asperula* type, OSF, *Oxalis* type, MSF, *Myrtillus* type.
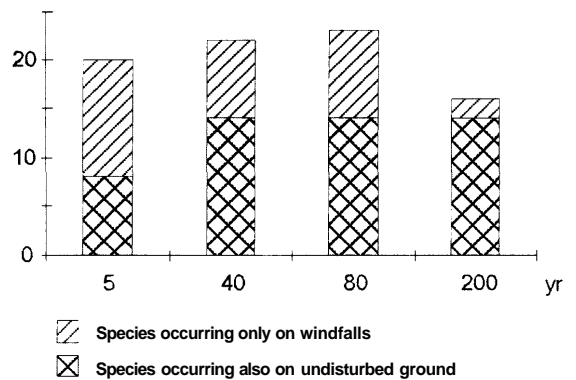

Fig. 7. Number of field-layer species in *Myrtillus* type spruce forest on windthrow of different age (Central Forest Reserve).
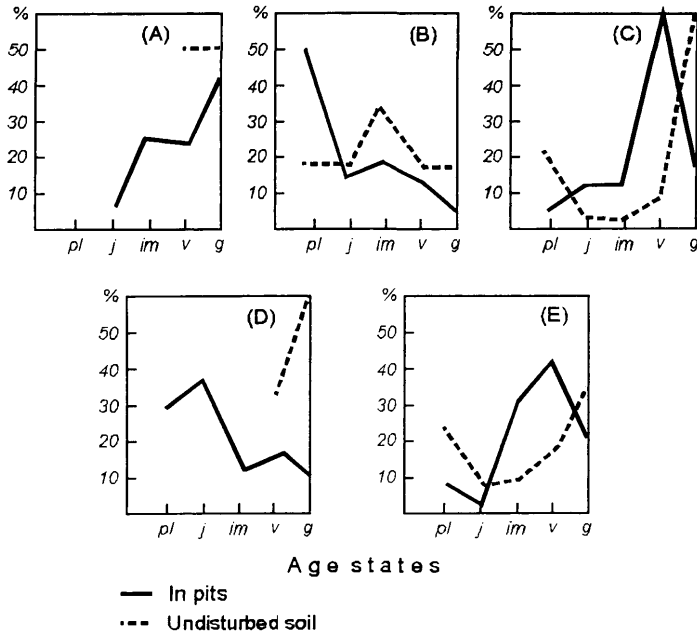
Fig. 8. Age-state diagrams for five species in windthrow pits and on undisturbed ground *(Myrtillus* type spruce forest, Moscow region). Explanations: (A) *Luzula multiflora;* (B) *Carex canescens;* (C) *Veronica officinalis;* (D) *Fragaria vesca;* (E) *Viola canina.* Age states: pl, seedlings; j, juvenile plants; im, immature; v, virginile; g, reproductive plants.

show vegetative propagation (Fig. 8). The whole population structure is consequently in a stable multi-aged state.

The process of vegetation development on pit-and-mound topography has been described as stages of vegetation micro-succession (Skvortsova et al., 1983). Each type of micro-succession is linked to the level of disturbance and the site nutrient regime. Vegetation on soddy-podzolic soils at nutrient-rich sites with good drainage could recover in pits after 10–20 years. For nutrient-poor soils with a differentiated profile and bad drainage, the floristic differences between pits and undisturbed areas disappear after ca. 80 years, while the species abundance differences disappear only after the pit fills in.

4. Conclusions

Windfall is a universal phenomenon, occurring in almost all kinds of boreal forests. This review emphasizes the different spatial levels of windthrow effects. The windthrow problem has been investigated at

different levels: landscape; forest community; and fallen tree ecosystem. The scales of windthrow gaps in space and time determine the patch structure of the forest ecosystems. The main result of this phenomenon is the occurrence of gap-phase dynamics in forest communities. The development of gaps is very important for the survival of small- and broad-leaved trees in boreal coniferous forests.

Disturbance through uprooting contributes significantly to the structural complexity of boreal forest ecosystems. Treefalls affect forest ecosystems in at least four ways (Jonsson, 1993): (I) it creates a light-gap in the tree canopy; (II) it increases nutrient availability in the forest floor; (III) it provides downed wood in the form of logs and branches; and (IV) uprooting creates pit-and-mound topography.

Much attention has been paid to the structure and properties of soil where uprooting had occurred. The microsites, which are found in pit-and-mound topography, differ pedogenically. The nature and rate of recovery of the background soil profile after uprooting have been studied. Under the influence of shallow

uprooting, the reconstruction of the background soil combination and processes is completed in 100–200 years, in cases of major uprootings, it takes more than a 200–300 year cycle.

The creation of gaps and microsites by windfall disturbances are two related major environmental components determining the regeneration niche for trees, shrubs, herbs, ferns and bryophytes in forests. Uprootings represent a patch dynamic system that maintains colonist species and high plant diversity in the forest floor. The spatial distribution of trees is associated with pit-and-mound topography in all types of forests. Spruce regenerates better on mounds and fallen trees than on undisturbed surfaces. Multi-aged tree regrowth is therefore being constantly formed in virgin forests. There is an increase in the community floristic richness due to the establishment of certain pioneer species from other communities in microsites disturbed by uprooting.

At last, windfall disturbances play an important role in increasing biodiversity in forest ecosystems. There are four different aspects in describing this phenomenon. First, increasing environmental above- and below-ground heterogeneity, i.e. the pit-and-mound microrelief increases the structural complexity of the forest floor (Jonsson, 1993). (I) It exposes a variety of substrates, such as humus, mineral soil, and roots and in some cases, rocks and stones. (II) It creates microtopographic variation in the forest floor, resulting in gradients of soil water content and small-scale temperature differences. (III) It damages, kills or dislocates the ground vegetation and creates space available for plant colonisation.

Second, in regard to, increasing species diversity, the number of species increases especially by shade-intolerant early successional species.

Third, in regard to, increasing of species population stability, the structure of species populations becomes more complete (from seedlings till senile individuals). As the result, the structure of forest plant populations is in a stable multi-aged state.

Finally, in regard to, increasing the degree of species genetic variation, the gene pool of a population is rejuvenated as the plants appear in these microsites from seeds and spores, while propagation in undisturbed areas is predominantly vegetative. Genetic variability of populations is generally considered important for population viability.

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