Development of two boreal forests after large-scale windthrow in the Central Urals

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Abstract

The processes of natural regeneration after windthrow were investigated in two permanent study areas located in the southern and middle taiga of the Central Urals. The forest types were dominated by *Pinus silvestris* and *Larix sibirica* in the north (Pinetum vacciniosum) and by *Abies sibirica* and *Picea obovata* in the south (Piceetum oxalidosum).The number of trees in the two study areas sharply increased over the seven years following the windthrow, mainly due to an increase in the number of broadleaved trees, with *Betula pendula* and *Populus tremula* predominating. Regeneration was most abundant on sites where the windfall debris was cleared, and was least on those that remained uncleared. The regeneration established after the windthrow was dominated by broadleaved species, while advance regeneration before the storm was dominated by conifers. Advance regeneration of conifers mostly survived in areas where the windfall debris was not cleared, but the rate of coniferous regeneration was higher in the cleared part of the windfall. The reasons for the sudden increase in regeneration by broadleaved species, as well as the difficulties associated with coniferous regeneration, are analysed. The type of silvicultural management greatly affects the number of young trees that survive following windthrow. The preliminary conclusions are that natural processes should be integrated more often into the management of forests in the Urals as well as in other mountainous regions.

Keywords: windthrow, regeneration, forest development, natural forest, boreal forest, Ural mountains, Russia

1 Introduction

Wind activity is not exclusive to the Central Urals, but in comparison to the more mountainous northern and southern parts of the Urals, the frequency of windthrow events is higher (TURKOV 1979). Strong winds occur when atmospheric fronts pass over the mountain range. Air masses break through the lower terrain of the Central Urals and the Čusovaja River valley, which form a broad saddle within the Urals. Winds here can achieve very high speeds. However, large-scale wind storms occur in the Central Urals comparatively rarely – once every 50 to 75 years. Small-scale windthrow occurs at the scale of forest enterprises about once every 9 years on average (LÄSSIG and MOČALOV 2000), and scattered windthrow occurs practically every year. According to TURKOV (1979), severe windthrow events occurred in the Urals in 1799, 1859, 1879 and 1892.

During the 20th century, the scale and frequency of windthrow events in this region seem to have increased. Since about 1965, several large forests in the Perm and Sverdlovsk region have been totally devastated or badly damaged. According to the forest administration in the Sverdlovsk region, windthrow is one of the main causes of forest damage. Since 1965, stands in 46 out of 51 forest enterprises have suffered from windthrow (MOČALOV and LÄSSIG 1998). In 1995, windthrow occurred as a result of strong winds combined with wet snow, heavily damaging more than 350 000 ha of forest (SMOLONOGOV 2000).

Over the last twenty years, a number of studies have been made of windthrow and its consequences in Europe (FISCHER 1992; FISCHER 1998; LÄSSIG 2000; LÄSSIG and MOČALOV 2000; SCHMIDT-SCHÜTZ and HUSS 1998; SCHÖNENBERGER *et al.* 1992; SKVORZOVA *et al.* 1983; ULANOVA 2000). Most windthrow has complex and long-lasting effects because, on a large scale, it causes disturbances throughout the whole forest ecosystem and recovery can take decades.

Since 1994, USFEU scientists have been investigating the consequences of windthrow in the Central Urals. They are looking at trends in regeneration processes after windthrow, focusing on biodiversity in the windthrow areas and in adjacent stands, and on searching for effective methods of regeneration, comparing regeneration processes with and without human intervention. These investigations have the following features:

– They are being performed in permanent study areas (PSA) of more than 10 ha each. The PSAs are located in vast windthrown boreal forests, embracing different types of forest vegetation of the southern and middle taiga.
– They are located in forests that have been developing naturally for a long time, i.e. without or with minimal silvicultural measures, in contrast to the forests of Central Europe, which have mostly been managed for decades.
– They are designed to analyse how the regeneration process starts after windthrow damage.
– Their findings are not only of scientific, but also of practical significance; in particular, they will reveal measures for better regeneration in different forest types after windthrow.
– They are being carried out jointly by the USFEU (Yekaterinburg) and WSL (Birmensdorf).

This article presents the main findings of a seven-year investigation (from 1994/95 to 2001) into regeneration after windthrow on two PSAs in the Sverdlovsk region.

2 Study sites and methods

The investigations were undertaken on PSAs located on plots Nos. 68–69, forest division Šajtanka, Novo-Lialinsky forest district (subzone middle taiga) and on plot No. 105, Atig forest division, Nižnij Sergi forest district (subzone southern taiga) in the Sverdlovsk region. At Šajtanka, the windthrow took place in June 1993 and at Nižnij Sergi, the wind event occurred in July 1994. Table 1 presents the main characteristics of the study areas.

The Urals case study, like that in the Swiss Alps (SCHÖNENBERGER *et al.* 1992), is relying on long-term observation of forest regeneration after large-scale windthrow in variants with different treatments but without any replication of the variants:

Variant 1 – woody debris uncleared;
Variant 2 – woody debris cleared, with natural regeneration;
Variant 3 – woody debris cleared, with planting;
Variant 4 – intact forest adjacent to the windthrow area.

A 25 m grid of permanent circular sampling plots with a radius of 4 m (50.27 m^2) was established to estimate the natural regeneration. All trees 20 cm or higher were examined annually to obtain the following data: distance from the centre of the plot, azimuth (by means of a surveying compass), height, propagation (seed, vegetative or planted) and condition (healthy, moderate or dead). This method is widely used in Switzerland and other European countries (SCHÖNEN-

BERGER *et al.* 1992; LÄSSIG *et al.* 1995; SCHMIDT-SCHÜTZ and HUSS 1998). It allows sampling of a much higher percentage of the study area than with the methods commonly applied in Russia (POBEDINSKY 1966; GOSKOMLES SSSR 1984; Federal'naja sluzhba lesnogo chozyaistva Rossii 1997). The site of each tree can be described exactly, thereby contributing to a better understanding of the long-term growth dynamics of the trees.

The total number of sample plots in all the variants of the study on PSA Šajtanka was 236 (1.186 ha) and on PSA Nižnij Sergi 134 (0.674 ha). Natural regeneration per 1 ha was calculated with the formula: 10 000 N/50.27 X, where N = the number of plants on the PSA, X = the number of sample plots in each variant. The relative abundance of young growth was defined as the ratio of the number of sample plots with regeneration to the total number of sample plots in each variant, expressed as a percentage.

Table 1. Description of the study areas at Šajtanka and Nižnij Sergi in the Urals (* according to GPS – data of Moiseev, unpublished. P *Pinus silvestris;* L *Larix sibirica;* B *Betula pendula;* A *Populus tremula;* S *Picea obovata;* F *Abies sibirica;* W *Salix* spp.).

	Šajtanka	Nižnij Sergi
Location *	59°25'55''N/ 60°01'30''E	56°34'21''N/ 59°29'21''E
Area (ha)	20 (out of 317.2)	12 (out of 146.54)
Elevation (m a.s.l.) *	195–225	450–470
Mean annual temperature (°C)	+0.2 – +0.8	0.0 – +0.5
Mean annual precipitation (mm)	400–500	500–600
Geology	Granite, Granoporfyr	Quarzite, Sandstone
Soil type	podsolic brown earth <60 cm	podsolic brown earth <60 cm
Forest community	Pinetum vacciniosum	Piceetum oxalidosum
Tree species composition (%): stand	30 P 20 L 40 B 10 A + S, F	40 F 40 S 20 B + P, W
windthrow	10 P 20 L 60 B 10 A + S, F	10 F 50 S 30 B10 + P
Mean stand height (m)	17.7	19.6
Mean stand diameter (cm)	13.7	26.3
Mean age of tree species (years)	P,L,B – 65; A – 55; S,F – 51	F,S – 90; P – 80

3 Results

At the two study areas, the regeneration data obtained under the canopy of the adjacent stands (variant 4) showed that before windthrow, the number of young conifers was almost the same on the different variants. The disastrous effect of wind is evident if the regeneration data one year after windthrow from variant 4 are compared with those from the uncleared area (variant 1). The other variants of the study showed less significant results in this respect, as the amount of regeneration was reduced by the clearing of woody debris and the cultivation of soil before planting. Figures 1 and 2 show that a much larger proportion of the young growth present before the storm was destroyed at Šajtanka than at Nižnij Sergi, and that most coniferous saplings were destroyed.

Thus, one year after windthrow, all the variants in the windthrow area at Šajtanka had only 7.5–17.3% of the numbers of conifers found in the adjacent stand, whereas at Nižnij Sergi there were 28.1–84.1%.

Analysis of the height distribution of the regeneration (small: up to 50 cm, medium: 51–150 cm, and tall: more than 150 cm) and of the age distribution showed that the majority

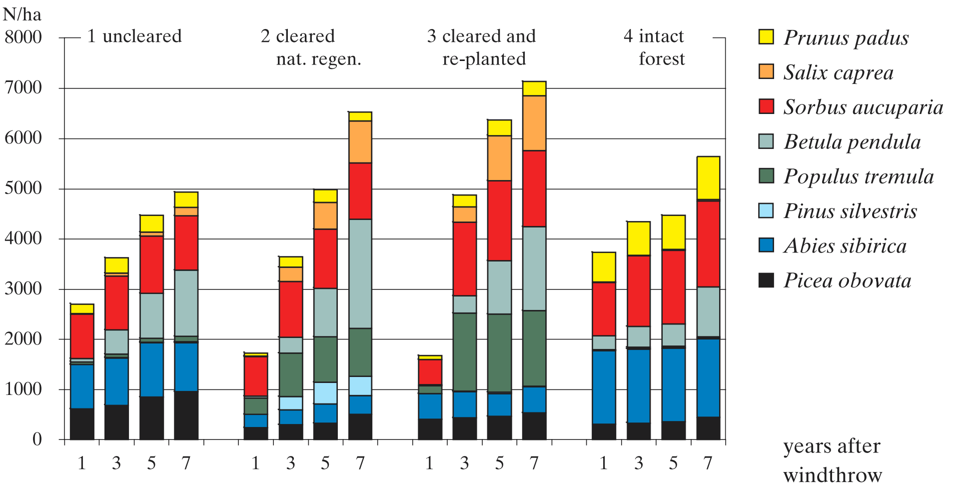

Fig. 1. Abundance of tree species in the natural regeneration (h >20 cm) on the study area Nižnij Sergi (Central Ural).

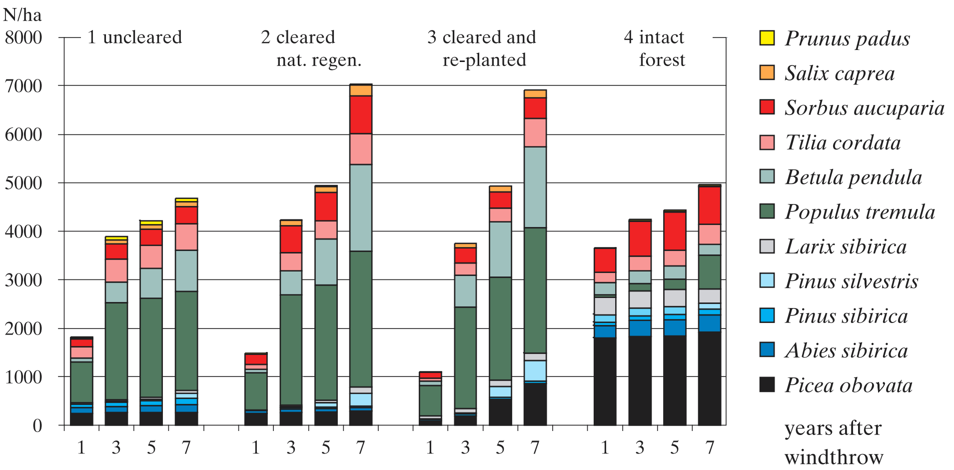

Fig. 2. Abundance of tree species in the natural regeneration (h >20 cm) on the study area Šajtanka (Central Ural).

of the coniferous young growth was present prior to the windthrow. At Nižnij Sergi, more young conifers remained undamaged than at Šajtanka. On both PSAs the largest number of undamaged conifers was found in the uncleared variant.

At Šajtanka the regeneration of five coniferous and six broadleaved species was recorded (Table 2) and the corresponding figures for Nižnij Sergi were three coniferous and five broadleaved species (Table 3). At Šajtanka, one year after windthrow, broadleaved saplings were already much more numerous than coniferous saplings, while under the canopy of the intact forest the situation was reversed. Assuming that the damage to coniferous and broadleaved regeneration from windthrow was approximately equal, it seems that broadleaves were able to re-establish extremely rapidly despite the changes in site conditions. At Nižnij Sergi, one year after windthrow, more broadleaved than coniferous young growth was also found in the cleared variant. Three years later, many broadleaves were also evident in the other variants.

Over the seven years of observation, the total number of trees increased 2.6–6.3 times in the different variants at Šajtanka, and 1.8–4.8 times at Nižnij Sergi. Despite the differences between the two PSAs in the amount of advance regeneration and the site conditions at the outset, after seven years the total number of trees at both sites was roughly the same. The number of individuals on both PSAs and in the different variants increased at different rates; yet in all cases the newly established trees were mainly broadleaves. The number of broadleaves increased most in the variants with clearing: while the factor in the (uncleared) variant 1 at Šajtanka was only 2.9, it was 5.3 in variant 2 and 6.0 in variant 3. At Nižnij Sergi it was 2.5 in variant 1, 4.3 in variant 2, and 7.9 in variant 3.

The proportion of conifers also increased, though slowly, especially on mineral soils in the cleared variants. This is most evident in variant 3, due to planting. At Šajtanka, conifers increased in number by a factor of 1.5 in variant 1, 2.5 in variant 2, and 7.5 in variant 3. At Nižnij Sergi they increased by 1.3 in variant 1, 2.5 in variant 2, and 2.2 in variant 3.

Although at Šajtanka the absolute number of young conifers after seven years was only about half that at Nižnij Sergi, the rates of growth on the two PSAs were almost identical (the data are not presented here). The number of trees also increased under the intact forest cover (variant 4) and, as on the windthrow area, the increase was more significant among broadleaves.

The proportion of the various tree species in regeneration differed and also changed over time. At Šajtanka (Table 2), *Picea obovata* predominated among the conifers in all variants. At the same time, even though the proportion of *Pinus silvestris* in the parent stand was comparatively small, its numbers gradually began to increase in the windthrow area. Among the broadleaves at the windthrow *Populus tremula* predominated, though its regeneration under the intact forest (variant 4) was poor. *Populus tremula* predominated in the first three years after windthrow, but its proportion then continuously decreased while *Betula pendula* young growth started to increase rapidly in all variants. There was a significant proportion of underwood species such as *Tilia cordata* and *Sorbus aucuparia* in the regeneration.

At Nižnij Sergi (Table 3), *Abies sibirica* and *Picea obovata* were the predominant conifers. Among the broadleaves at Nižnij Sergi, *Betula pendula*, which continued to increase proportionally, and *Sorbus aucuparia* predominated. The numbers of young *Populus tremula* and *Salix caprea* increased here in the cleared variants, while under the intact forest and in the uncleared variant these species occurred seldomly. The underwood species *Sorbus aucuparia*, *Salix caprea* and *Prunus padus* were also quite frequent here.

The height distribution of the saplings varied between the variants. In all the variants in both PSAs, the medium and tall classes of re-growth (more than 70%) were predominant. At the same time, the proportion of small re-growth (up to 50 cm in height) in the cleared variants was more than twice that in the uncleared areas. In general, the broadleaves were much taller than the conifers. This was related to their higher growth rates and, partly, to the older age of the trees (establishment from suckers immediately following the windthrow).

In all the variants of the study, the regeneration was very healthy. The proportion of trees in moderate condition did not exceed 10%. The type of damage differed between conifers and broadleaves. While conifers suffered mainly from mechanical damage and frost, broadleaves were damaged primarily by rodents, hares, moose, and insects.

Table 2. Tree species composition of natural regeneration one, three, five, and seven years after windthrow on the four different variants at Šajtanka (%).

Variant	Tree species	Years after windthrow 1	3	5	7
1 uncleared	*Picea obovata*	13.7	6.9	6.4	5.7
	Abies sibirica	6.2	3.1	3.2	3.6
	Pinus sibirica	4.1	2.4	2.4	2.7
	Pinus silvestris	0.4	0.5	0.8	2.2
	Larix sibirica	1.3	0.7	1.0	1.3
	Conifers (all)	**25.6**	**13.6**	**13.9**	**15.4**
	Populus tremula	46.4	51.5	48.3	43.8
	Betula pendula	4.3	10.9	14.7	18.2
	Tilia cordata	12.6	12.0	11.4	11.5
	Sorbus aucuparia	8.8	8.2	7.9	7.7
	Salix caprea	1.1	2.0	2.0	2.1
	Prunus padus	1.3	1.8	1.8	1.4
	Broadleaves (all)	**74.4**	**86.4**	**86.1**	**84.6**
2 cleared / nat. regen.	*Picea obovata*	16.5	6.4	5.6	4.2
	Abies sibirica	3.9	1.7	1.5	1.0
	Pinus sibirica	0.7	0.7	0.6	0.4
	Pinus silvestris	0.2	0.4	1.8	3.7
	Larix sibirica	0.2	0.8	1.1	1.8
	Conifers (all)	**21.6**	**10.0**	**10.6**	**11.2**
	Populus tremula	51.5	53.6	48.0	39.8
	Betula pendula	4.4	11.6	19.1	25.4
	Tilia cordata	7.0	8.9	7.7	9.0
	Sorbus aucuparia	14.1	13.2	11.9	11.1
	Salix caprea	1.2	2.5	2.5	3.1
	Prunus padus	0.2	0.3	0.3	0.3
	Broadleaves (all)	**78.4**	**90.0**	**89.4**	**88.8**
3 cleared / planted	*Picea obovata*	8.5	2.7	2.0	1.7
	Abies sibirica				
	Pinus sibirica	2.6	1.0	1.0	0.8
	Pinus silvestris	1.3	0.6	4.3	5.7
	Larix sibirica	5.6	2.5	2.9	2.5
	Conifers (all)	**18.0**	**6.8**	**10.2**	**10.7**
	Populus tremula	56.5	57.2	47.7	42.6
	Betula pendula	8.2	17.9	25.5	27.5
	Tilia cordata	5.2	7.0	6.4	9.6
	Sorbus aucuparia	11.1	8.6	7.6	6.9
	Salix caprea	1.0	2.5	2.6	2.7
	Prunus padus				
	Broadleaves (all)	**82.0**	**93.2**	**89.8**	**89.3**
4 intact forest	*Picea obovata*	49.2	43.3	41.4	38.8
	Abies sibirica	6.8	7.7	7.5	7.0
	Pinus sibirica	2.0	2.2	2.5	2.5
	Pinus silvestris	4.3	3.7	3.7	2.4
	Larix sibirica	9.7	8.4	8.0	5.8
	Conifers (all)	**71.9**	**65.3**	**63.1**	**56.5**
	Populus tremula	1.4	3.6	4.8	14.2
	Betula pendula	6.9	6.2	6.1	4.4
	Tilia cordata	6.0	7.2	7.3	8.3
	Sorbus aucuparia	13.3	16.9	17.8	15.7
	Salix caprea	0.1	0.1	0.2	0.1
	Prunus padus	0.4	0.7	0.8	0.7
	Broadleaves (all)	**28.1**	**34.7**	**36.9**	**43.5**

Table 3. Tree species composition of natural regeneration one, three, five, and seven years after windthrow on the four different variants at Nižnij Sergi (%).

		Years after windthrow			
Variant	Tree species	1	3	5	7
1 uncleared	*Picea obovata*	22.6	18.9	19.0	19.4
	Abies sibirica	32.7	26.1	24.4	19.9
	Pinus silvestris	0.2	0.2	0.2	0.3
	Conifers (all)	**55.5**	**45.2**	**43.6**	**39.6**
	Populus tremula	1.9	1.9	1.6	2.1
	Betula pendula	2.3	13.4	20.1	26.7
	Sorbus aucuparia	32.7	29.4	25.5	22.1
	Salix caprea	0.4	1.7	1.8	3.4
	Prunus padus	7.2	8.4	7.4	6.1
	Broadleaves (all)	**44.5**	**54.8**	**56.4**	**60.4**
2 cleared / nat. regen.	*Picea obovata*	14.0	8.1	6.7	7.7
	Abies sibirica	14.9	8.3	7.7	5.7
	Pinus silvestris		7.3	8.6	6.0
	Conifers (all)	**28.9**	**23.7**	**23.0**	**19.4**
	Populus tremula	19.2	23.6	18.2	14.7
	Betula pendula	2.2	8.7	19.5	33.3
	Sorbus aucuparia	45.5	30.5	23.7	17.1
	Salix caprea	0.4	7.9	10.6	12.9
	Prunus padus	3.8	5.6	5.0	2.6
	Broadleaves (all)	**71.1**	**76.3**	**77.0**	**80.6**
3 cleared / planted	*Picea obovata*	24.2	9.0	7.4	7.5
	Abies sibirica	30.3	10.8	7.1	7.3
	Pinus silvestris		0.1	0.4	0.1
	Conifers (all)	**54.5**	**19.9**	**14.9**	**14.9**
	Populus tremula	10.0	31.8	24.4	21.1
	Betula pendula	0.9	7.0	16.6	23.5
	Sorbus aucuparia	29.9	30.2	25.1	21.2
	Salix caprea		6.2	14.1	15.4
	Prunus padus	4.7	4.9	4.9	3.9
	Broadleaves (all)	**45.5**	**80.1**	**85.1**	**85.1**
4 intact forest	*Picea obovata*	8.4	7.7	8.1	7.9
	Abies sibirica	39.2	33.9	32.6	27.9
	Pinus silvestris	0.2	0.2	0.3	0.2
	Conifers (all)	**47.8**	**41.8**	**41.0**	**36.0**
	Populus tremula	0.2	0.6	0.6	0.3
	Betula pendula	7.2	9.5	10.0	17.6
	Sorbus aucuparia	28.7	32.4	32.7	30.4
	Salix caprea	0.1	0.4	0.4	0.6
	Prunus padus	16.0	15.3	15.3	15.1
	Broadleaves (all)	**52.2**	**58.2**	**59.0**	**64.0**

One major indicator characterising the distribution of young growth over an area is the percentage of sample plots with a particular species in the total number of sample plots. This percentage significantly increased shortly after the windthrow for all predominant species in both PSAs (Table 4). Seven years later the distribution had become fairly even, especially in the cleared variants. The spatial distribution of broadleaves was more uniform than that of conifers. The abundance of the latter was highest in the uncleared variant.

The type and intensity of management of windthrow areas significantly influenced the regeneration process. The cleared variants were characterised by (1) the largest quantity of regeneration, (2) the greatest difference in numbers between broadleaves and conifers (2.9–7.9 times more broadleaves), and (3) the greatest increase in the number of conifers.

In variant 3, one year after windthrow, both PSAs were partially planted with 3-year-old seedlings of *Picea obovata* and *Pinus silvestris* with a density of 2500 to 3300 plants/ha. Taking into consideration a possible bias in the calculation method (only trees over 20 cm of height were measured), the proportions of planted trees in the total regeneration seven years after the storm were 12.1% at Šajtanka and 12.6% at Nižnij Sergi, and the proportions of planted conifers were 56.3% and 49.0%, respectively. Thus, planting contributed to the regeneration. However, given the continuing increase in the number of broadleaves, the effect of planting so far has been to prevent a further shift of the species composition towards broadleaves.

Table 4. Proportion of tree species on sample plots one and seven years after windthrow on the four different variants at Šajtanka and Nižnij Sergi (%).

				Šajtanka				
Variant	1 uncleared		2 cleared / nat. regen.		3 cleared/planted		4 intact forest	
Years after windthrow	1	7	1	7	1	7	1	7
Picea obovata	60.8	60.8	36.4	47.3	21.8	76.4	97.3	97.3
Abies sibirica	35.3	47.1	10.9	12.7			48.0	52.0
Pinus sibirica	29.4	33.3	3.6	9.1	9.1	20.0	24.0	36.0
Pinus silvestris	3.9	23.5	1.8	49.1	5.5	56.4	41.3	30.7
Larix sibirica	7.8	17.6	1.8	38.2	18.2	36.4	56.0	53.3
Conifers (all)	**78.4**	**86.3**	**40.0**	**83.6**	**36.4**	**89.1**	**100.0**	**100.0**
Populus tremula	58.8	72.5	54.5	89.1	58.2	89.1	18.7	68.0
Betula pendula	35.3	78.4	18.2	94.5	29.1	92.7	60.0	57.3
Tilia cordata	49.0	70.6	25.5	52.7	12.7	41.8	36.0	48.0
Sorbus aucuparia	47.1	64.7	47.3	81.8	36.4	67.3	68.0	88.0
Salix caprea	7.8	27.5	9.1	50.9	5.5	38.2	2.7	2.7
Prunus padus	7.8	19.6	1.8	7.3			5.3	12.0
Broadleaves (all)	**86.3**	**100.0**	**76.4**	**98.2**	**70.9**	**96.4**	**90.7**	**100.0**
Total	**94.1**	**100.0**	**76.4**	**98.2**	**72.7**	**100.0**	**100.0**	**100.0**
Planting					**0.0**	**56.4**		
				Nižnij Sergi				
Picea obovata	73.7	78.9	48.1	66.7	64.0	96.0	56.8	68.2
Abies sibirica	86.8	84.2	63.0	77.8	60.0	60.0	86.4	88.6
Pinus silvestris	2.6	5.3		22.2		4.0	2.3	4.5
Conifers (all)	**92.1**	**92.1**	**70.4**	**96.3**	**72.0**	**100.0**	**90.9**	**93.2**
Populus tremula	2.6	7.9	25.9	51.9	24.0	44.0	2.3	6.8
Betula pendula	23.7	78.9	11.1	81.5	8.0	84.0	27.3	50.0
Sorbus aucuparia	73.7	63.2	66.7	74.1	52.0	72.0	88.6	88.6
Salix caprea	5.3	31.6	3.7	55.6		76.0	2.3	13.6
Prunus padus	23.7	31.6	11.1	22.2	8.0	28.0	38.6	43.2
Broadleaves (all)	**86.8**	**94.7**	**77.8**	**96.3**	**60.0**	**100.0**	**95.5**	**93.2**
Total	**97.4**	**97.4**	**92.6**	**100.0**	**80.0**	**100.0**	**95.5**	**95.5**
Planting					**8.0**	**44.0**		

4 Discussion

The findings from this study are consistent with those of LÄSSIG *et al.* (1995) and SCHMIDT-SCHÜTZ and HUSS (1998). They also support previous findings that both the total number of young trees and the species diversity in windthrow areas in the Central Urals are greater than in the Swiss Alps (LÄSSIG and MOČALOV 2000). This corroborates the premise that regeneration processes are more dynamic in the naturally developed taiga forests of Russia than in the managed forests of Central Europe (SYRJÄNEN *et al.* 1994).

Establishment of regeneration

Broadleaves react to the abrupt changes in ecological conditions caused by windthrow with a "regeneration outbreak" (GROMTSEV 2002), as observed in the initial stage of this study. This is quite natural (FISCHER 1992; SCHMIDT-SCHÜTZ and HUSS 1998) and can be explained by a range of advantages that broadleaves have over conifers under these conditions. One of the main reasons for the big increase in broadleaved species that occurred at both sites after windthrow is the high capacity for vegetative reproduction of broadleaved trees. This is particularly true under the conditions that are created by windthrow, and any subsequent harvesting and clearing of windfall debris. This is substantiated by the findings from the two study areas: broadleaved regeneration by suckers prevailed over seeding, especially in the cleared variants.

Betula pendula, *Tilia cordata* and some other species can also propagate by suckers. *Populus tremula* is very abundant as root suckers, and its young trees can produce shoot offsets. KONOVALOV *et al.* (1981) found that the root system of one *Populus tremula* tree spread over 0.1 ha. This explains why, after the felling of a one hectare stand of conifers containing only ten *Populus tremula* trees, the whole clearing can become covered with *Populus tremula* shoots. This may explain why *Populus tremula* was so dominant at Šajtanka, where its proportion in the parent stand was 10 percent. *Populus tremula* root systems can persist for two or three years, even when the trunk itself is dead (Ulanova, unpublished). Consequently, even though there may be only a few *Populus tremula* trees scattered in the original forest stand, as observed at Nižnij Sergi, after windthrow or clear cutting the area can become intensively re-colonised by *Populus tremula* root suckers.

Boreal forests arising from vegetative propagation have a shorter life-span than those which are self-seeded (LUGANSKY *et al.* 1996). Stands arising from shoot and root offsets are often subject to rot, which shortens their lives. During the first years after windthrow, forests originating vegetatively grow much faster than self-seeded ones, but their rapid growth is often accompanied by the emergence of rot, spreading from old stumps and root systems. This is particularly characteristic of *Populus tremula*, with almost all trees of only 12–15 years of age in the Urals affected by trunk rot (LUGANSKY *et al.* 1996).

The almost annual and exceptionally abundant seed production of pioneer broadleaves (ROHMEDER 1972) and the long dispersal distances of the seeds also contribute to their rapid colonisation of windthrows and other open areas. Up to 900 million seeds per hectare have been observed in Central Europe (cited in ROHMEDER 1972). In the Urals, even in low-yield years, two to three million *Betula pendula* seeds per hectare are deposited (KONOVALOV *et al.* 1981). The seeds of *Betula pendula* are very light; they are blown around very easily and are disseminated up to 1.6 kilometres (SCHMIDT 1918). *Populus tremula* also bear seeds abundantly each year, though self-seeded regeneration is weak as the seedbed conditions required for germination consist of a moderately moist mineral soil without herb and moss cover or litter. Consequently, regeneration by *Populus tremula* seeds is insignificant in open areas in the relatively dry region of the Urals. It regenerates mainly through suckers, which grow very quickly even in the first year (KONOVALOV *et al.* 1981).

Factors affecting regeneration

After windthrow, the young conifers have to adapt to the sudden change from the shelter of the forest canopy to open conditions. The scattered light and high relative air humidity under the canopy are no longer present. The open microclimate (which leads, for example, to frost) is unfavourable for young *Picea obovata* (LUGANSKY *et al.* 1996). In open territory the amplitude of the temperature fluctuation is greater than under the forest canopy, and *Picea obovata* and *Abies sibirica*, in contrast to *Betula pendula* and *Populus tremula*, are very sensitive to late spring and early autumn frosts (LUGANSKY *et al.* 1996). Frosts also impede *Picea obovata* regeneration by seed. In addition, *Picea obovata* only produce seeds abundantly on average every three to four years (KONOVALOV *et al.* 1981).

Coniferous regeneration in windthrow areas is also hampered by competition from herbs, most of which grow faster than conifers. The herb layer not only prevents seed germination in spring but it also hampers shoot growth in autumn as its debris and the large leaves of *Populus tremula* press down on the shoots and may kill them (KONOVALOV *et al.* 1981). The conditions for the regeneration of *Betula pendula* and *Populus tremula* are much better as the trunks and stumps that are left produce fast-growing suckers and the existing regeneration as well as the many seedlings which germinate annually on the bare soil produce longer shoots during their first few years than the herb layer. These young trees are thus easily able to compete with the herb cover (KONOVALOV *et al.* 1981).

Successful regeneration of conifers greatly depends upon favourable conditions for germination and the success of self-seeding, since most propagate exclusively by seed and bear much fewer seeds than broadleaves (KONOVALOV *et al.* 1981). Such conditions include the quality and quantity of woody debris, the amount and structure of litter and surface humus, the state and competitive ability of undergrowth and ground cover, light, temperature, moisture and aeration, and the biological and ecological requirements of the species and their interactions.

One very significant prerequisite for the self-seeding of trees is a suitable substrate. *Pinus silvestris* and *Larix sibirica* seeds seldom germinate on litter (KONOVALOV *et al.* 1981) but need bare soil. In gaps in the cover the seeds fall directly on the ground. Later, regeneration only continues when the litter becomes mixed with the humus and soil. The denser the litter and the thicker the soil cover, the worse the conditions for the emergence of *Pinus silvestris* and *Larix sibirica* seedlings (KONOVALOV *et al.* 1981). Therefore, surface scarring from windthrow may actually benefit seeding. On the other hand, uncleared debris decreases evaporation from the soil surface while promoting the accumulation of organic material and growth of the vegetation cover. This may have been important at Šajtanka, which has a rather dry climate. There, windfall clearing appeared to greatly intensify evaporation and the drying of the soil surface.

The regeneration process of conifers immediately after windthrow is slow. It becomes more rapid when a mossy cover appears under the canopy of young *Populus tremula* trees (KONOVALOV *et al.* 1981). Consequently, for further *Picea obovata* regeneration in young *Populus tremula* forests, not only is the absence of frost important, but also the presence of a suitable substrate for germination. *Picea obovata* seeds sprout perfectly in loose damp litter which does not prevent the rootlets penetrating the soil substrate, but may fail to sprout if the litter becomes too dry (KONOVALOV *et al.* 1981)

Soil conditions at both Šajtanka and Nižnij Sergi are unfavourable for conifer self-seeding (Nechaeva, unpublished). In both PSAs, the soil cover was characterised by coarse humus brown forest soils, which have a heavy fine earth where sandy loam and light clay dominate.

At Šajtanka, the litter was coarse and shallow with few nutrients. Lack of moisture impedes decomposition, so that the litter accumulates and dry raw-humus is formed. The greatest increase in regeneration took place on deeper soils (up to 24.6 cm) in variant 2, but the increase was less on the shallower soils in variant 1. The soils in variant 2 were more acidic and had the lowest contents of mobile nutrients, but the fine soil layers were thicker and the litter was the least dense. The numbers of conifers increased in variant 3, which can be explained not only by the planting but also by the high moisture content and nutrient supply in the soil.

At Nižnij Sergi, there was a rather thick raw-humus layer. Coarse humus is formed as a result of soil dampness and poor aeration, which leads to rotting processes and retards litter decomposition, as well as producing a low pH-value and restricting decomposition activities by microorganisms. Increases in the extent of regeneration took place unevenly in the different variants and was distinctly correlated to the soil dampness and ground-water level (Nechaeva, unpublished). In variant 2, the rate of coniferous regeneration increase was highest where the soil was best drained (ground water level at 0.8 m) but this site had the lowest levels of mobile nutrients. As a result of stagnant or non-stagnant short-term water logging, the formation of raw-humus layers on gley soils in variants 1 and 3, and a ground water level very near the surface (0.2–0.3 m), anaerobic conditions occurred. This in turn impeded the rate of regeneration increase because the seeds became waterlogged, particularly in spring and autumn.

Development of regeneration

A herb cover usually hinders self-seeding by conifers, but once seeds have germinated it can also favour seedlings. In particular it protects species like *Picea obovata* and *Abies sibirica* which are shade-tolerant and sensitive to frost (Lugansky *et al.* 1996). The rapidly spreading *Calamagrostis* spp. and *Carex* spp. occurred in the windthrow areas (Nechaeva, unpublished). Their roots easily penetrated the coarse humus layer, invading the bare ground. As a result, there was a rapid increase in rhizome area coverage and thickness, which at Šajtanka totalled 10–15 cm in seven years. Dryness of the upper soil layer, intensified by the spreading of *Calamagrostis* spp., was the main factor hindering *Populus tremula* germination (Nechaeva, unpublished). Other factors unfavourable for *Populus tremula* germination are excessive insolation, sandblasting of seedlings on bare areas (Sannikov 1976), and litter fall from *Populus tremula* trees.

Different types of litter have different biochemical effects. *Populus tremula* leaves, *Picea obovata* needles, *Calamagrostis arundinacea* and *Vaccinium vitis-idaea* leaves and root systems impede the sprouting and growth of *Pinus silvestris* shoots up to an age of two years. The influence of species such as *Betula pendula*, *Vaccinium myrtillus* and *Pteridium aquilinum* can also be positive as the seedlings take advantage of shading (Lugansky *et al.* 1996). During their first few years, *Betula pendula* and *Populus tremula* grow faster than *Pinus silvestris*. They have a strong mechanical influence on the crowns of any adjacent *Pinus silvestris* trees close-by as they whip the pine shoot tips, leading to decreased apical growth and resulting in sparse and multiple crowns.

Strongly developed undergrowth, consisting of, for example, *Tilia cordata, Sorbus aucuparia, Prunus padus,* and *Salix* ssp., could also hinder the growth of young conifers. *Tilia cordata* leaf fall, for instance, prevents *Picea obovata* seeds germinating and hinders seedling growth (Konovalov *et al.* 1981). However, undergrowth can protect young conifers against the effects of low temperatures and direct sun.

The composition and distribution of the undergrowth depend on the general relief of the terrain and the micro-relief of the windthrow area. At Nižnij Sergi, where the soils were wetter, small mounds were the most favourable sites for the success of *Picea obovata* and *Abies sibirica* establishment. Shallow roots here were less desiccated. Pits, in contrast, were unfavourable as the soil was much denser, its aeration was poor and stagnant wetting was frequent. As a result the young growth suffered from frost. At Šajtanka, in contrast, only the pits were waterlogged.

In both windthrow areas there were typical micro-habitats such as skid trails, troughs, mounds, rocky outcrops, forest roads and debris. Debris comprised fallen trees and felling waste and was present in considerable quantities on the cleared plots. It is obvious that in such habitats the micro-conditions were unsuitable for self-seeding development, as the upper soil layer often became too dry (however, some site data remain unanalysed).

Severe wind, resulting in windthrow or windbreak, is an exogenous factor affecting species composition. When deciding on further plantation development, especially the development of conifers in windthrow areas, the rich findings from studies in clear-cuts should be consulted. The site conditions and the forest development in clear-cuts are rather similar to those in cleared windthrow areas, even though the species number of herbs and dwarf shrubs is much higher in clear-cuts (Ulanova, unpublished).

Changes in tree species

Numerous studies have shown that in cleared areas throughout almost all the forest and forest-steppe zones in the Ural region, commercially valuable conifers are replaced by broadleaves, mainly *Betula pendula* and *Populus tremula* (Skvorzova 1983; Smolonogov 2000; Turkov 1979). *Betula pendula* already makes up about 35% of Ural forest trees and *Populus tremula* approximately 5% (Lugansky *et al.* 1996). In the Pre-Ural, for instance, regeneration in partially harvested coniferous forests takes place without changes in species composition in only 20–25% of the forests, while on clear-cuts up to 95% of the area is quickly covered by broadleaves (Lugansky *et al.* 1996). Unless special steps are taken, e.g. seed conservation, scarification for coniferous self-seeding, or composition regulation by improvement felling) coniferous regeneration takes place on only 6.9% of the total forest area in the Urals (Černov 2001).

The succession process back to a conifer-dominated forest is long and complex. Re-establishment of conifers may easily take 100 years or more, even though this is a “short-term” process for boreal forests (Konovalov *et al.* 1981). During the phase of dominance by broadleaved species, coniferous growth begins to develop under the canopy (Fischer 1992). The canopy of *Betula pendula* improves the micro-climatic conditions and weakens competition from the herb and dwarf shrub cover, both of which favour *Picea obovata* re-growth. Further, *Picea obovata* benefits from the protection of the nutrient cycle in the soil provided by *Betula pendula* leaves. On certain sites *Populus tremula* also promotes coniferous re-growth: According to Mikhailov (1987), for the first 10–12 years *Populus tremula* formed a pioneer forest where *Picea obovata* regeneration was absent or, at least, rather limited, occurring only in gaps. When the *Populus* trees were 12–25 years old, *Picea* young growth emerged under their canopy. At 25–50 years, *Populus* started to compete strongly with *Picea* and could even suppress it. At 50–60 years *Populus* began to decline and conditions for the further development of *Picea* clusters became favourable.

Disturbances due to wind play a major role in restoring the diversity of the local terrain, the species composition and the stand structure of boreal forests (Karpačevskij *et al.* 1978; Timofeev 1957; Skvorzova *et al.* 1983). In the long-term, every spot of a phytocoenosis undergoes a radical change in the soil and vegetation due to such disturbances (Gromtsev 2002). After windthrow the diversity of sites and structures greatly influences the distribution and germination success of seeds, as well as the growth of young trees (Fischer 1992; Lässig *et al.* 1995; Turkov 1979; Ulanova 2000). Windthrow, therefore, is one of the driving forces behind the spontaneous dynamics in gap-mosaic regimes, which is most characteristic of close-to-nature, *Picea obovata* dominated forests (Gromtsev 2002; Skvorzova *et al.* 1983).

Pinus silvestris forests in the Urals are less subject to species change than *Picea obovata* forests. Where *Pinus silvestris* forests occur in a comparatively dry climate, *Pinus silvestris* may be replaced by *Betula pendula* rather than by *Populus tremula*. Under a canopy of *Populus tremula*, *Pinus silvestris* regeneration is much more difficult than *Picea obovata* regeneration because *Pinus silvestris* is a light-demanding tree species (LUGANSKY *et al.* 1996).

At Šajtanka, *Pinus silvestris* replacement by *Picea obovata* is widespread both under the canopies of planted stands and in clearings, and occurs mainly on damp and rich loamy soils. Once established under a canopy of *Pinus silvestris* trees, *Picea obovata* forms a dense layer of acidic litter, strengthening its position and weakening that of *Pinus silvestris* (LUGANSKY *et al.* 1996). In the Urals, *Pinus silvestris* domination is enhanced by the regular occurrence of forest fires and by its greater (than *Picea obovata*) capacity to regenerate in clearings and burnt forests as a result of it being less sensitive to temperature fluctuations (LUGANSKY *et al.* 1996). Nevertheless, *Picea obovata* can prosper under the *Pinus silvestris* canopy, where it is protected from frost, and it becomes deep-rooted (KONOVALOV *et al.* 1981; LUGANSKY *et al.* 1996).

The relations of *Abies sibirica* to *Populus tremula* and *Betula pendula* are very similar. In the Urals, *Abies sibirica* rarely forms pure stands. It usually grows together with *Picea obovata*, in different relative proportions at different stages (KONOVALOV *et al.* 1981). *Abies sibirica* has a shorter life span than *Picea obovata* because of its susceptibility to trunk rot which eliminates it from *Populus tremula* stands (KONOVALOV *et al.* 1981). Therefore, together with *Populus tremula*, it is expected to become rarer in older stands. Consequently, *Picea obovata* is likely to become the dominant tree species in the final stage of stand development. In younger stands such as those at Nižnij Sergi, *Abies sibirica* was often more frequent than *Picea obovata*. This is probably due not only to its having a greater proportion of regeneration surviving the windthrow, but also to its shade tolerance, which is even higher than that of *Picea obovata.* Another factor is its ability to reproduce vegetatively.

In the Central Urals, *Pinus sibirica* and *Larix sibirica* also seldom form pure stands. *Pinus sibirica* occurs more often in *Picea obovata* than in *Abies sibirica* forests. Its regeneration in clearings is difficult, as its heavy seeds are rarely dispersed by wind; the normal mode of dispersion is by birds and small mammals (KONOVALOV *et al.* 1981). At Šajtanka, young *Pinus sibirica* were rather numerous as many survived the windthrow. Nižnij Sergi is outside the natural range of *Pinus sibirica*. *Larix sibirica* is usually found in *Pinus silvestris* stands, and it may dominate in the tree species composition in the Northern and Southern Urals.

5 Conclusions

Close-to-nature forests such as those in Šajtanka and Nižnij Sergi are very rich in tree species. Before the storm there was a high density of saplings available for regeneration. Windthrow partly destroyed these in some areas, as did harvesting and clearing operations. Foresters should consider that after windthrow, forest management practices will eventually change both the tree species composition and its spatial distribution. Both will be of importance for the future development and utilisation of the stand.

Practically everywhere in the Urals there are short-term (up to 100 years) and long-term (more than 100 years) changes in the species composition in clear-cuts. In windthrow areas with a high regeneration density, however, the period of domination by broadleaved species extends for 40–50 years (SMOLOGONOV 2000). Most recent studies confirm the hypothesis that advance regeneration in the Central Ural plays a decisive role in the re-establishment of coniferous stands in clearings. In certain cases coniferous regeneration cannot succeed without the help of silvicultural treatments that promote it (SANNIKOV 2001; TOROPOV 2001).

At this stage of investigation it may be too early to draw final conclusions about the effectiveness and advantages of any particular type of management of the windthrow areas. Summarising over the two study areas, although there was less regeneration in the uncleared variant, it seemed to have some advantages over the cleared variant: the greatest density of young conifers that had survived the windthrow occurred amongst the fallen timber and the young trees were more evenly distributed. The highest proportion of conifers to broadleaves in the re-growth also occurred in uncleared areas, and there was a higher proportion of self-seeding than of vegetative propagation; after seven years, the largest proportion of medium and tall re-growth also occurred in uncleared plots. These results are important for the long-term utilisation strategy of the forest in the Urals because conifers are the only late successional species in the Central Urals, and they are much more valuable to Russian foresters than early successional species such as *Betula pendula* and *Populus tremula*.

The results from studies undertaken in forests which have developed naturally after harvesting some decades ago are not only useful to forest managers in the Urals but also to those in other mountainous regions. The Ural forests are much denser and have a greater species diversity than the intensively managed coniferous forests of the European Alps. It would therefore seem worthwhile to think about integrating natural processes into the management of Central European forests more often. This would help to reduce the costs of clearing and re-planting, which are both very time-consuming and labour intensive, especially in remote areas. Moreover a close-to-natural management based on the abundant natural regeneration would help preserve the diversity of the forests.

In addition, forests such as those in this study offer opportunities for the scientific study of long-term natural processes in stands that have been undisturbed for several decades. There are very few near-natural forests left in Central Europe and almost no virgin forests. Most of the forests in the Alps, for instance, have been intensively managed for centuries and many have become homogeneous in structure, poor in biodiversity and sluggish in regeneration. These forests are unsuitable as study sites for investigations into whether close-to-nature forests are more resistant and resilient to storm damage. The comparatively untouched forests of the Urals, however, could serve as useful references for mountain forests in Central Europe, providing us with a deeper knowledge of natural regeneration processes and a valuable aid in developing silvicultural ideas.

Acknowledgements

This project was made possible thanks to the ongoing support within the partnership of the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) and the Ural State Forest Engineering University (USFEU). The research for part of the work presented here was carried out within two Institutional Partnership Projects as part of two federal programmes dealing with "Scientific Co-operation between Eastern Europe and Switzerland", financed by the Swiss Federal Department of Foreign Affairs and managed by the Swiss National Science Foundation (7IP 050152 between 1997 and 1998, 7IP 062658 between 2000 and 2003). The authors would also like to express their thanks to all those forestry students of the Ural State Forest Engineering University who did most of the measurements in the field and helped to store the data electronically, in particular to the post-graduate students K. Zotov and D. Gribaschov. We are also grateful to Mrs. Margaret J. Sieber and Silvia Dingwall for constructive help in translating the manuscript, and to Peter Brang, John Innes, Walter Schönenberger and two unknown scientists for their careful review of an earlier draft.

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Accepted 16.10.02