

Early Stages of Forest Restoration after Windthrow in Ural (Russia): Observations and Mathematical Models

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ABSTRACT

This study presents data analysis and a model of early phases of forest regeneration after windthrow. Processes occurring in these phases are competition between young trees and herbaceous plants, development of young trees, and competition among different species of young trees. The model of early phases of forest regeneration after windthrow presented in the study is based on the authors' long-term observation data on forest regeneration collected in the area in the Middle Urals that had suffered heavy windthrow.

Keywords: boreal forest, interspecific competition, modeling, secondary succession, stand regeneration, storm disturbance, vegetation recovery

INTRODUCTION

Critical events in forest ecosystems, such as fires, insect outbreaks, and windthrows, cause the death of some if not all of the trees in a forest stand (Glenn-Lewin *et al.* 1992; Johnson and Miyanishi 2007; Perry *et al.* 2008). In the early phases of forest regeneration, young trees diversely and vigorously interact among each other and with herbaceous plants and are influenced by mature trees growing in the adjacent areas (via seeds) and weather factors (Pickett and White 1985; Glenn-Lewin *et al.* 1992; Chapin *et al.* 2002; Perry *et al.* 2008). In 15 to 20 years, the forest ecosystem 'cools down' and many of the interactions vanish or become insignificant (Pickett and White 1985; del Moral *et al.* 2007). However, it is the 'hot' stage of the tree growth that mainly determines whether the area will become a forest or a herb community and, if it is a forest, what species will dominate for a long time (Pickett and White 1985; Glenn-Lewin *et al.* 1992; Chapin *et al.* 2002; Perry *et al.* 2008). Thus, analysis and modeling of early phases of forest regeneration can be useful for both ecology and forest industry (del Moral *et al.* 2007).

The difference between windthrow and such critical impacts as fire or an insect outbreak that causes the death of the tree stand is the state of the area (soil, forest litter, microtopography, the presence of woody fragments) at the beginning of succession (Glenn-Lewin *et al.* 1992; Chapin *et al.* 2002). Fallen trees form lot of microtopographic constructions that differ in exposure, temperature, and humidity, creating heterogenic conditions for regeneration of plants that need different microenvironments to germinate and root (Clinton and Baker 2000; Peterson 2000; Harrington and Bluhm 2001).

The destruction of the tree stand by the wind affects the carbon balance of forest ecosystems (Chapin *et al.* 2002), increasing the pool of detritus and litter and decreasing the tree stand pool (Lugo 2000; McNulty 2002). The amounts of the litter and fragments of wood on the floor increase for a certain time following windthrow (Ostertag *et al.* 2003), causing a generally adverse effect on regeneration of woody plants (Chapin *et al.* 2002; Zhu *et al.* 2003). However, forest regeneration can only begin under particular conditions. For instance, for pine yearlings to survive, the lowest PAR irradiance must amount to 10% of direct sunlight and for 2-5-year-old pine trees – 15%. In thick grass stands or bushes, the irradiance at ground level can be below 4%, and, thus, regeneration occurs on grass-free mounds (Sannikov 1961; Sannikov and Sannikova 1985).

The nature and the intensity of these processes determine whether the area will be transformed for a long time into a meadow, in the course of herbaceous plant succession, when annual plants are replaced by perennial ones, or forest regeneration will occur (Glenn-Lewin *et al.* 1992; Smit and Olff 1998; Vandermeer *et al.* 2001; Chapin *et al.* 2002; del Moral *et al.* 2007; Perry *et al.* 2008). Due to these effects, the occurrence of early-successional species is less determined by specific environmental conditions than by the availability of habitable sites created by critical impacts. Thus, disturbances are necessary for the survival of these plant species (Sannikov and Goldammer 1996) and associated animals and birds (DeGraaf and Yamasaki 2003; Marshall 2009). During forest regeneration, pioneer species can be replaced by nonpioneer ones (Vandermeer *et al.* 2001), and this can ultimately change proportions of the species that have been previously present in the forest (Dyer and Baird 1997; Parker *et al.* 2001; Conner *et al.* 2005; del Moral *et al.* 2007). Non-native species, which may occur in the stand during succession, are then either replaced by native ones (Burley *et al.* 2008) or persist and dominate the native species (Laungani and Knops 2009), owing to, e.g., different age-related sensitivity of a tree to lighting conditions (Yamashita *et al.* 2000).

Many researchers use the classification proposed by Everham and Brokaw (1996) to differentiate four ways of plant regeneration in the areas damaged by catastrophic winds (Harrington and Bluhm 2001). These are resprouting or regrowth, recruitment of other tree species, the growth of lower stories released by the hurricane from top layer suppression, and repression of woody plants by herbs. Regeneration of the tree canopy due to recruitment of new trees occurs via germination

Table 1 Position and characterization of the 'Shaitanka' plot.

Parameter	Value
Geographical situation	59°25'55" N/ 60°01'30" E
Altitude	195-225 m
Mean annual temperature	+ 0.8 – 0.2°C
Mean annual precipitation	450-500 mm
Geology	Granite, porphyritic granite, gneiss
Soil type	Brown forest soil, < 60 cm thick soil layer
Mean tree height	17.7 m
Mean tree diameter	13.7 cm
Mean tree age, yr	Scotch pine, larch, birch - 65; aspen - 55; spruce, fir - 51
Major species of ground cover	<i>Calamagrostis arundinacea</i> , <i>Rubus idaeus</i> , <i>Rubus saxatilis</i> , <i>Cerastium pauciflorum</i> , <i>Aegopodium podagraria</i> , <i>Stellaria holostea</i> , <i>Galium boreale</i> , <i>Fragaria vesca</i> , <i>Aconitum excelsum</i> , <i>Carex rhizina</i> , <i>Rosa acicularis</i> , <i>Equisetum sylvaticum</i>

of the seeds brought from the parts of the forest unaffected by windthrow or the seed bank retained in the soil (Johnson and Miyanishi 2007; Burley *et al.* 2008). The distance to which woody plant seeds are transported can range between several dozen and several hundred meters (Shiyatov 1966; Sato and Hiura 1998; Johnson and Miyanishi 2007), but winged seeds of ash trees can be dispersed even 2-3 km (Bacles *et al.* 2006). Seed banks or seedling banks are another source of regeneration, as they actually remain intact in areas damaged by windthrow (Glenn-Lewin *et al.* 1992; Burley *et al.* 2008). Other scenarios of forest regeneration are also possible. For instance, regeneration of spruce stands damaged by windthrow in the Leningradskaya Oblast (the northern part of the Valdaisko-Onezhskaya ridge) occurred due to vigorous growth of the understory spruce trees (which was more vigorous in uneven-aged than even-aged forests) released by windthrow rather than through an 'outburst' of seed germination (Shorohova *et al.* 2008). Forest recovery in the Caribbean islands disturbed by a hurricane occurred via resprouting (Imbert and Portecop 2008), and regrowth was the main factor in forest regeneration in the south of the USA (Baldwin *et al.* 2001). Repression of forest regeneration is frequently observed in boreal forests of Siberia after such critical events as insect outbreaks. Sometimes no forest regeneration can occur for decades as growing herbaceous communities prevent the emergence of young trees (Kuzmichev *et al.* 2001).

Wind impacts and forest regeneration following windthrow were modeled in units and submodels of general simulations of forest growth (Bragg *et al.* 2004; Scheller and Mladenoff 2004; Schumacher *et al.* 2004; Purves *et al.* 2008) and in special simulations (Rammig *et al.* 2007) used, e.g., to predict recovery of subalpine forest in Switzerland damaged by Hurricane Vivian in 1990. These models consider not only regeneration and growth of trees, shrubs, and herbs and competition among all components of ecosystems but also such factors as alternation of years of good and poor seed yields, grazing by ungulates, artificial regeneration, and forest management practices (Weisberg *et al.* 2005).

Following the critical disturbance, the area may develop in either of the two ways: a new forest stand may emerge or the formerly forested area may be transformed into a herbaceous community for a long time (Pickett and White 1985; Glenn-Lewin *et al.* 1992; del Moral *et al.* 2007). To predict and control forest regeneration, one should know the conditions under which forest recovery occurs in a given area, the rate of this process, and whether the resulting forest stand will be of the same type as the stand that grew on this territory before the critical event (Chapin *et al.* 2002; del Moral *et al.* 2007). The type of the succession following critical events determines, to a large extent, the type of the management of succession dynamics. If forest regeneration is unlikely or/and the recovery rate is low, it is necessary to perform artificial forest regeneration, using certain technologies: cleaning up the area after a critical event, planting or cutting (del Moral *et al.* 2007; Johnson and Miyanishi 2007). On the other hand, artificial forest regeneration following hurricanes is very time- and money-consuming, and natural regeneration may be a better option (Stanturf *et al.* 2007). If harvested promptly, timber left after windthrow can be used commercially. Adverse effects of such timber harvesting after catastrophic events on the soil were not found to be significant or long-lasting (Schroeder 2007; Nelson *et al.* 2008; Peterson and Leach 2008).

The purpose of this study was to analyze and model early phases of forest regeneration following windthrow. The general model of early phases of forest regeneration after windthrow is based on the authors' long-term observation data on forest regeneration collected in the area in the Middle Urals that had suffered serious windthrow. The major ecological processes occurring after windthrow in boreal forests that should be modeled, are as follows:

- herbaceous plants grow and species that are native to the area compete with those brought there after the catastrophe;
- seeds of woody plants are transported into the area and germinate there;
- woody seedlings compete with herbs, which results in their growth or death; young trees emerge;
- young trees grow; different tree species compete; some of the trees die.

STUDY AREA AND MATERIAL

Field studies of forest regeneration processes following windthrow were performed in the 'Shaitanka' sample plot (quadrates 68 and 69 of the Shaitanskoye Forestry Section at the Novo-Lyalinskii Forestry Station of the Sverdlovskaya Oblast). A storm that occurred in this area on 30 June 1993 lasted about 15 min, with the maximal wind speed ≥ 30 m/s. The storm had felled all trees in the sample area (Lässig and Močálov 2000). The position and the characterization of the 'Shaitanka' sample plot before the storm are shown in **Table 1**. Tree and undergrowth inventory was performed annually (during 1994-99) and biennially (during 2000-06) in July-August. Three sample plots were used as study areas: Plot 1 – the area with unharvested windthrown timber and regeneration occurring naturally; Plot 2 – the area with regeneration occurring naturally, cleaned to remove most of the windthrown timber; Plot 3 – the area deep in the forest that withstood the storm. Woody plants growing in the sample plots were as follows: the aspen *Populus tremula*, the birch *Betula pendula* Roth., the linden *Tilia cordata* Mill., the bird cherry tree *Prunus padus* L., the rowan *Sorbus aucuparia* L., the willow *Salix alba* L., the spruce *Picea obovata* Ldb., the pine *Pinus sylvestris* L., the larch *Larix sibirica* Ldb., the fir *Abies sibirica* Ledeb, and the Siberian pine *Pinus sibiricus* Du Tour. Plot 1 and Plot 2 were divided into 11 layers, situated at different distances from the boundary of the remaining forest. The distance between neighboring layers was 25 m. In every layer, there were permanently marked inventory circles, each with radius 4 m (**Fig. 1**). Every young tree of height more than 0.2 m that grew within the inventory circles was examined to determine its species, origin (a seed or a sprout), the distance between the tree stem and the center of the inventory circle, the azimuth, the tree height or trunk diameter (for trees higher than 2 m). Tree inventory was performed in every inventory circle once a year (usually in August). Subsequent analysis involved such values as tree density N in the layer in the current year, the number of the trees that emerged, N_b , and died, N_d , within the layer over the time period between two inventories.

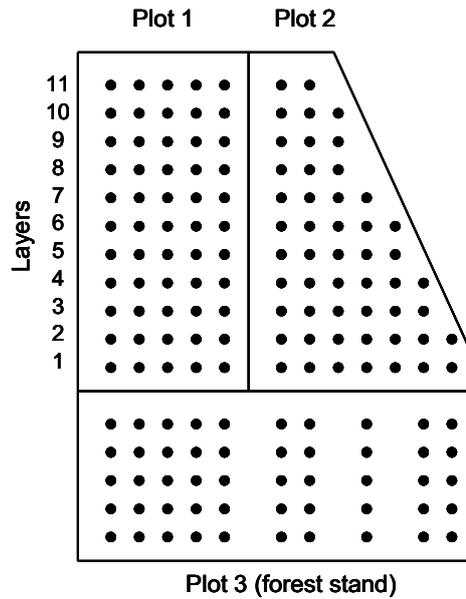


Fig. 1 Sample plots and layers of inventory circles in the study area. The stand in Plot 1 was left unharvested after windthrow, the stand in Plot 2 was logged after windthrow and the most wood removed, Plot 3 was undamaged.

RESULTS AND DISCUSSION

Based on field observations in the area damaged by windthrow conducted over 12 years (Plot 1 and Plot 3) and 7 years (Plot 2), we evaluated the rate of forest regeneration for these periods of time, including the emergence of new trees and their death. In the first year of monitoring, the understory density under the forest canopy (Plot 3) was one and a half to two orders of magnitude higher than the stand density on the windthrow damaged area (Fig. 2). By the end of the observation period, the understory density in the sample plot layers closest to the forest boundary had reached 15-20% of the understory density in the Plot 3. The density of the Siberian spruce – the major woody species in the control area – had not changed significantly over the observation period (Fig. 2), the increase in the density in the Plot 3 mainly occurring due to the growing number of codominant and minor tree species.

Forest regeneration in deforested areas is determined by such factors as the influx rate of seeds of various woody species from surrounding forest communities, germinating capacity of these seeds, which is related to the state of the soil and specific properties of the herbaceous plants, and death of a certain portion of the young woody plants. The regeneration rate, described by N_{fin} – tree density at the end of the observation period (Plot 1 – 2006; Plot 2 – 2002), was linearly dependent upon the distance of the inventory plot from the forest boundary for Plot 1, while for Plot 2 no such dependence was recorded (Fig. 3).

Final tree densities in Plots 1 and 2 were similar only in the layers closest to the forest boundary (Fig. 2). The layers with the same number were located at the same distance from the forest boundary in Plots 1 and 2 (Fig. 1); the compositions of herbaceous plants were similar too. The only difference was that Plot 2 was cleaned to remove windbroken trees while the forest in Plot 1 underwent natural regeneration. The rate of emergence of new woody plants in the area is determined by the rate of seed influx from the neighboring forest areas and the survival of the trees that grow from these seeds. The emergence of new trees with heights exceeding the critical height, $h_0 = 0.2$ m, is determined by the current tree density. As the tree density increases, the rate of emergence of new trees drops considerably (Fig. 4). This effect may be accounted for by heavier competition among trees in a denser forest stand.

The death rate of young trees was evaluated from the fraction of the trees that have died, $m = N_d/N$ since the previous inventory. Analysis of the tree death rate in all sample plots shows that it depend on the current tree density in the stand (Fig. 5). Few if any trees die until the critical level of tree density, $0.03 - 0.04$ trees·m⁻², is attained, no matter in what year of observation period this value is reached in each layer (Fig. 5). Once the critical level of the tree density has been reached, trees begin to die, the death rate increasing proportionally to the current tree density. The tree death rate is higher in uncleaned Plot 1 and reaches 0.3, whereas this value not exceeds 0.15 in Plot 2, from which broken trees are removed (Fig. 5).

Based on the analysis of the field data, we propose a simple model of forest regeneration. The model will consider regeneration from seeds, when new trees grow from the seeds brought into the area with the wind and by animals and birds. Let us write the following balance equation for density dynamics of young trees, N , that have reached the height 0.2 m:

$$\frac{dN}{dt} = [\text{numbers of new trees} - \text{number of dead trees}] = f(M, N, t) \cdot s(t) - g(N, t)N \quad (1)$$

where $s(t)$ is seed flux rate; M is mass of herbaceous plants in the area, considered as an external parameter as the herb growth rate is presumed to be significantly higher than the rate of emergence of trees, and the herbaceous mass reaches its maximum rather quickly (Pickett and White 1985); function $f(M, N, t)$ is the portion of young trees that have grown from seeds, which describes the effects of the herbs and the developed trees on the emergence of new trees; function $g(N, t)$ characterizes the portion of young trees of heights more than 0.2 m that have died during succession.

In the simplest case, $s(t) = s_0 = const$; $f(M, N, t) = f_0 = const$; $g(N) = g_0 = cons$, ($0 \leq f_0 \leq 1$; $0 \leq g_0 \leq 1$). Then, from (1) we obtain the Bertalanffy equation:

$$\frac{dN}{dt} = f_0 s_0 - g_0 N \quad (2)$$

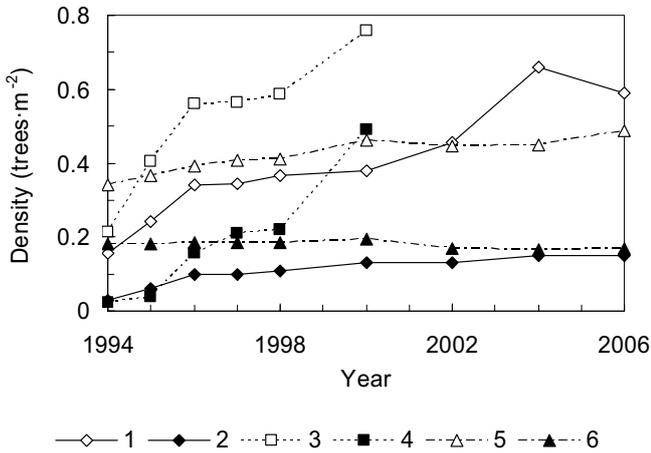


Fig. 2 The dynamics of forest regeneration rate in the study area. 1 – layer 1, Plot 1; 2 – layer 11, Plot 1; 3 – layer 1, Plot 2; 4 – layer 11, Plot 2; 5 – Plot 3, all species; 6 – Plot 3, the spruce *Picea odorata*.

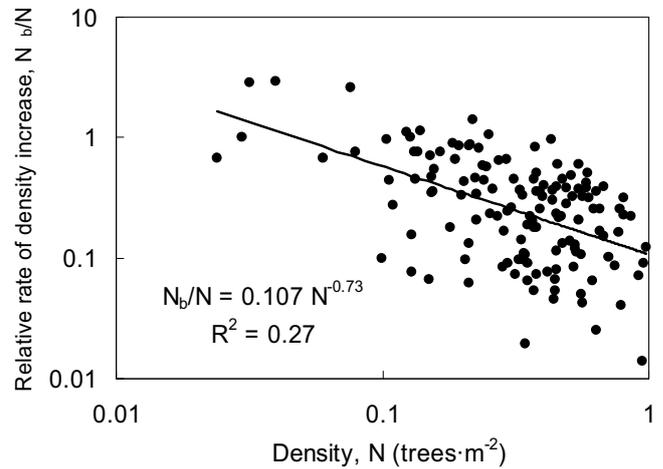


Fig. 4 Relationship between the relative rate of emergence of new trees and tree density for all layers and all years of study in Plots 1 and Plot 2.

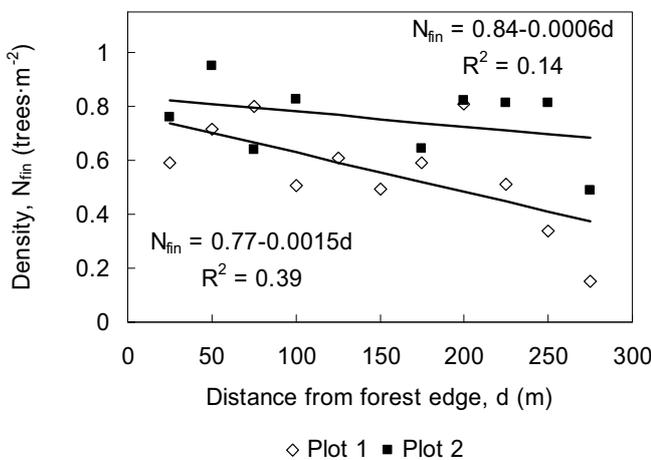


Fig. 3 Tree densities in different layers of sample plots at the end of the observation period.

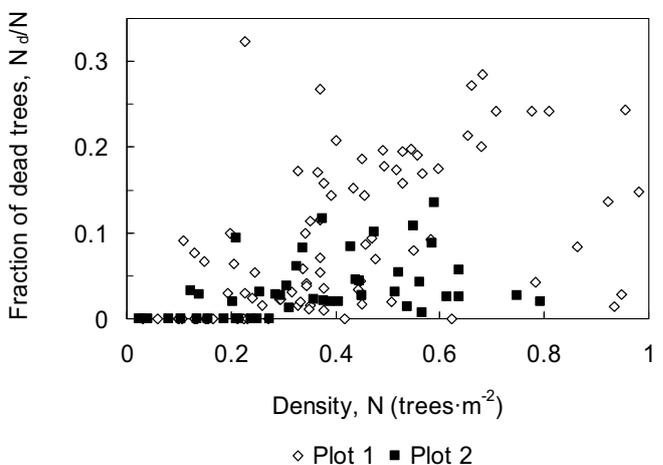


Fig. 5 Relationship between tree density and tree death rate. All layers in all observation years.

In model (2) there is one steady (when $dN/dt = 0$) stable state of the forest stand of density $N = f_0 \cdot s_0 / g_0$. Comparison of the simplest model (2) with the observation data for the Plot 3 shows that there is a qualitative agreement between observations in the forest that was not disturbed and the model (Fig. 6).

However, phase trajectories for tree densities in Plots 1 and 2 do not correspond with the equation 2. The phase portrait of the Bertalanffy equation (2) in the $\{N, dN/dt\}$ plane is a straight line $dN/dt = 0.099 - 0.209 \cdot N$ for the Plot 3 data, while the phase trajectories for the field data of Plots 1 and 2 have a maximum (Fig. 6). The model should also take into account the possible situation when there is no seed flux to the deforested area or it is insignificant. Probably this explains the decline of restoration's phase trajectories for trees growing on Plots 1 and 2 (Fig. 6).

In case then $s(t) \rightarrow 0$, the broken forest is replaced by herbaceous plant community with few trees rather than by a new forest.

To describe forest regeneration processes more correctly, the model (1) should be adjusted. In the general case, the model describing changes in tree density during succession without resprouting regeneration, with a constant seed influx, and with temporally stationary functions characterizing the emergence of new trees and the death of the currently existing ones can be written in the following form:

$$\frac{dN}{dt} = k(A - N) \cdot (N - N_r) \cdot s_0 - \frac{h_m N^q}{H + N^q} \cdot N \tag{3}$$

where k, A, N_r, h_m, H, q are constants.

For the case when the seed flux rate $s_0 \neq 0$, in (3) there are four steady density values ($dN/dt = 0$); two states with values N_1 and N_2 are stable, while states with values A and N_r are unstable (Fig. 7, curve 1). The state of the area in the vicinity of N_1 characterizes herbaceous community with few trees; unstable point N_r corresponds to the density at which woody plants 'break away' from the effect of herbaceous plants and competition with them, and forest regeneration begins; unstable point A characterizes the condition under which tree density reaches its maximum and mortality rate becomes high; point N_2 describes stable forest, in which decline processes are over. If the seed flux rate is high and $N_r \rightarrow 0$, equation (3) describes the situation when forest regeneration is the only option (Fig. 7, curve 2). If the seed flux rate $s = 0$ and in the initial state $N = 0$, i.e. all trees are dead after windthrow, equation (3) characterized by only one stable state $\{N = 0; dN/dt = 0\}$, i.e. no regeneration occurs after the critical event (Fig. 7, curve 3).

We can propose the following approximate ranges of values of parameters in the model (3) within which successful or unsuccessful forest regeneration scenarios will occur after windthrow:

1. Value s is large, value N_r is small, value A is large, $h_m \rightarrow 0$ and $H \gg N$. Then rapid forest regeneration is inevitable.

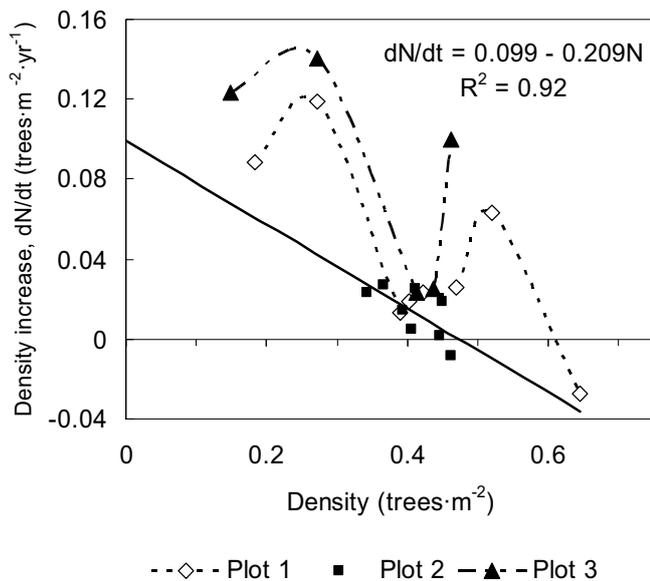


Fig. 6 Phase trajectories of the growth of young trees in the undamaged forest stand (Plot 3) and in the early phase of regeneration following windthrow (Plot 1 and Plot 2).

2. Value s is small, values N_r and A are small, parameter h_m is rather large, and $H \approx N$. In this case, forest regeneration occurs but at a low rate.

3. Value s is small or even equal to zero, N_r is rather high. Then, the area damaged by windthrow becomes occupied by herbaceous plant community, which persists indefinitely long.

CONCLUSION

The analysis of the data showed that in the territory of the Middle Urals, under steady-state conditions, when external effects are minimal, in undamaged mature forest stands there is a dynamic balance between growth and mortality of understory trees. The density of the trees of different species is maintained rather stable. The analysis of the data showed that under the studied conditions, forest regeneration following windthrow occurs rather slowly. Heavy external impacts (windthrow) that kill mature trees in the forest stand 'trigger' both the growth of herbaceous plants and forest regeneration processes. Under the conditions studied in this work, the competition between woody and herbaceous plants is rather quickly 'won' by young trees, but this 'victory' is not followed by rapid forest regeneration. Transformation of the herbaceous plant cover continues, but the effect of woody plants on the dynamics of the herbaceous species composition and the extent of their projective cover is reduced to the minimum.

Is there a relationship between the trends and dynamics in the early phases of forest regeneration and the specific type of the critical event (windthrow, cuttings, insect outbreaks, etc.)? Differences between regeneration rates in the area that was maintained in its natural state after windthrow and in the area from which storm-broken trees were removed suggest that the specific type of the critical event will, to a certain extent, determine the dynamics of subsequent forest regeneration. Later phases of forest regeneration are out of the scope of this study, but in boreal forests of the Urals and Siberia, in forest stands that are 20-25 years old and older, coniferous species usually get partly or completely replaced by hardwoods (the aspen, the birch). A deciduous or (sometimes) mixed forest is established, with hardwoods dominating. This succession phase lasts until deciduous trees reach the age of 80-100 years and die, and an even-aged coniferous forest stand forms under the canopy of the deciduous forest (Solomon 1992). Further succession dynamics of such stands involves asynchronous and prolonged death of coniferous trees and formation of uneven-aged climax coniferous forest (Shugart 1984).

It is certainly possible that in any of the abovementioned phases of succession such critical events as fire, insect outbreak or windthrow may occur, causing complete or partial death of the forest stand and making the forested area return to the initial phases of succession. The dynamics of succession following a new critical event must be different to a greater or lesser extent (Paine *et al.* 1998; Pascarella *et al.* 2004).

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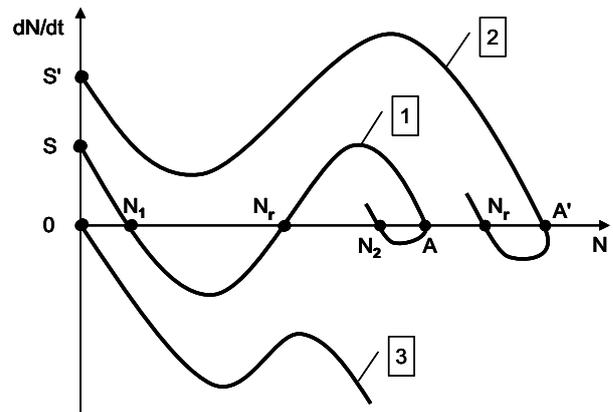


Fig. 7 Isoclines of the forest regeneration equation (3). Curve 1: the case with four steady density values, stable point N_1 corresponds to herbaceous community with few trees, in unstable point N_r herbaceous community is replaced by forest, in unstable point A the tree density reaches its maximum, point N_2 corresponds to stable forest. Curve 2: the case when a rate of emergence of new trees more than rate of their death and forest restoration is inevitably. Curve 3: The case when there are no trees nor seeds after a windthrow ($N = 0, s = 0$) and no forest regeneration.

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