

Climatic control of stand thinning in unmanaged spruce forests of the southern taiga in European Russia

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ABSTRACT

The demography of *Picea abies* trees was studied over a period of about 30 yr on permanent plots in six forest types of an unmanaged forest located in a forest reserve of the Southern Taiga, NW of Moscow. This study encompassed a broad range of conditions that are typical for old growth spruce forests in the boreal region, including sites with a high water table and well drained sites, podzolic soils, acidic soils and organic soils. At all sites stand density, tree height, breast height diameter and age has been periodically recorded since 1968. Tree density ranged between 178 and 1035 trees ha⁻¹ for spruce and between 232 and 1168 trees ha⁻¹ for the whole stand, including mainly *Betula* and *Populus*. Biomass ranged between 5.4 and 170 t_{dw} ha⁻¹ for spruce and between 33 to 198 t_{dw} ha⁻¹ for the whole stand. Averaged over a long period of time, biomass did not change with stand density according to the self-thinning rule. In fact, on most sites biomass remained almost constant in the long term, while stand density decreased. The study demonstrates that the loss of living trees was not regulated by competitive interactions between trees, but by disturbances caused by climatic events. Dry years caused losses of minor and younger trees without affecting biomass. In contrast, periodic storms resulted in a loss of biomass without affecting density, except for extreme events, where the whole stand may fall. Dry years followed by wet years enhance the effect on stand density. Since mainly younger trees were lost, the apparent average age of the stand increased more than real time (20% for *Picea*). Average mortality was $2.8 \pm 0.5\%$ yr⁻¹ for spruce. Thus, the forest is turned over once every 160–180 yr by disturbances. The demography of dead trees shows that the rate of decay depends on the way the tree died. Storm causes uprooting and stem breakage, where living trees fall to the forest floor and decay with a mean residence time ($t_{1/2}$) of about 16 yr (decomposition rate constant $k_d = 0.042$ yr⁻¹). This contrasts with trees that die by drought or insect damage, and which remain as standing dead trees with a mean residence time of 3–13 yr until they are brought to ground, mainly by wind. These standing dead trees require an additional mean residence time of about 22 yr for decay on the ground ($k_d = 0.031$). In conclusion, we demonstrate that, rather than competitive interactions, it is climate extremes, namely drought, rapid changes of dry years followed by wet years, and storm that determine stand structure, biomass and density, which then affect the net exchange with the atmosphere. The climatic effects are difficult to predict, because the sensitivity of a stand to climate

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[†]In memory of Dr. Vladimir I. Abrazko. He maintained the experimental plots for decades and died in 2000.

extremes depends on the past history. This may range from no effect, if the stand was recovering from an earlier drought and exhibited a relatively low density, to a total collapse of canopies, if drought reduces stand density to an extent that other climatic extremes (especially wind) may cause further damage.

1. Introduction

In the carbon cycle of natural forest ecosystems, the processes that lead to “removal” of living biomass by mortality is poorly understood. It is generally thought that in forests which are undisturbed by logging, tree mortality is based mainly on competitive interactions which are related to stand density (Westoby, 1984). This contrasts managed forests, where tree height and not density was found to be a predictor for biomass (Eichhorn, 1904). However, tree mortality is also related to external parameters, such as insect attack, wind-throw, or fire (e.g. Lee, 1971; Weber et al., 1986; Wirth et al., 1999). Thus, mortality in pristine forest may depend on a whole range of biological and abiotic parameters. In the following we will investigate the relations between competitive interactions (self-thinning) and climatic disturbances on tree mortality, and we follow the fate of these trees in the decomposition process.

The self-thinning rule describes the relation between biomass and plant density. For given light conditions, even-aged stands with closed canopies will increase biomass at the expense of tree density. Some individuals die so that others can get bigger. Originally, Yoda et al. (1963) described the change of biomass of plant individuals as related to density as an exponential decay curve with slope $-3/2$. This rule was extended by Westoby (1984) in order to describe the biomass changes of whole stands as related to density on an area basis. Multiplying Yoda's equation by the number of individuals per area, the exponential decay curve obtains a slope of -0.5 . The earlier observation by Eichhorn (1904), who found for managed forests that stand biomass was related to tree height, and not to density, emerges as special case of the more general self-thinning rule when disturbances such as harvest interfere with the natural thinning process. In the following we will study the self-thinning process on a plot basis as described by Westoby (1984) because this model has a structural, geometric basis (Osawa, 1993). Also, in forestry it turns out that the observation by Eichhorn (1904) holds only under certain conditions; a range of slopes emerge for the Eichhorn

“rule” depending on site conditions and management (Assmann, 1961; Mitscherlich, 1978).

In the following we will investigate the processes that lead to tree death in a natural unmanaged forest. Even if competition for light is the dominant factor causing differences in the development of individual trees, light suppression by itself very rarely causes trees to die. In most cases, even in unmanaged, self-thinning stands, other factors, such as climatic extremes or insects, will eventually bring an individual tree to fall, which then results in more space for the remaining population, or for sub-canopy trees to reach the main canopy. The processes that lead to death of mature trees under unmanaged conditions are generally not being observed. In fact, dead trees and coarse woody debris on the forest floor were often not even recorded, or mortality was often averaged across all tree species (e.g. Alexeyev and Birdsey, 1994; Isaev et al., 1993; Isaev and Korovin, 1997). There are only few studies on the fate of dead trees during decomposition (Storojenko, 1990; Storojenko et al., 1992; Harmon et al., 1995; 2000; Chambers et al., 2000; Wirth et al., 2002).

Using the self-thinning model to estimate tree mortality in inventory studies has problems even in even-aged natural forests. Schulze et al. (1995) showed for *Larix gmelinii* stands of Yakutia that biomass remained constant at decreasing stand density due to fire and nutrient limitations. Tree death by repeated ground fires and slow recovery due to low nutrient supply changed the self-thinning trajectories to even become temporarily positive in *Pinus sylvestris* stands of central Siberia (Wirth et al., 2002). Compared to even-aged stands that regenerate after fire, the interactions between competition and habitat conditions are more complicated under conditions of higher rainfall, where even-aged natural forests may establish after insect outbreak, or wind-throw, and where the bimodality of plant size in cohorts has been related to competition (Franc, 2001).

In the present study, carried out in a forest reserve, we will investigate factors that lead to tree mortality and thinning in unmanaged stands of *Picea abies*. We will also investigate the fate of dead trees in this

population. The study is based on long-term observations of stand density, growth and death of all individual trees and the fate of standing dead trees in relation to climatic extremes on permanent plots since 1968 (Karpov, 1973; 1983; Pugachevski, 1992). It will be shown that a series of events, such as drought and water-logging or strong winds, cause tree death, which may or may not be compensated by the remaining stand in a way that follows the self-thinning rule. Competition may have the role of pre-selecting the individuals that are sensitive to disturbance. We demonstrate that external events and not competitive interaction are the main driving forces for thinning and that the decomposition of coarse woody debris depends on additional delays such as the stability of standing dead trees, which in turn depends on climatic events. Thus a new role of climatic extremes emerges in regulating vegetation structure in boreal forest.

2. The study region

The observations were carried out in the Central Forest Biospheric State Reserve (56°N and 33°E), which is located in the Nelidovski administrative region about 350 km NW of Moscow. The region has

been described in detail by Schulze et al. (2002, this issue, see references to Russian literature there).

Climatically, the region is located in a transition zone between European oceanic and continental climate, with intensive atmospheric circulation and a strong seasonal cycle (Alisov, 1965; Myachkova, 1983). The western transport of air masses and cyclones dominate the atmospheric circulation throughout the year. In winter, about 10 cyclones per month pass from NW to SE, and polar air masses may reach the region with anticyclones passing from NE to SW. In summer, 4–5 cyclones per month carry North Atlantic moist air masses as well as dry Arctic air to the study region.

Vyshnii Volochek, the oldest weather station in the region (1891–1996) located about 100 km north of the study site, shows climatic conditions very similar to those at Fyedorovskoe, the weather station at the central forest reserve (CFR). We thus use the Vyshnii Volochek data to describe the long-term trend (Fig. 1). There is a slight increase of annual average temperatures over the last 100 yr ($0.005\text{ }^{\circ}\text{C yr}^{-1}$) which results mainly from an increase in winter rather than summer temperatures (Table 1). Temperature sums average $2091 \pm 64\text{ }^{\circ}\text{C}$ for the period above $10\text{ }^{\circ}\text{C}$ average daily temperature. Precipitation may be as low as 400 mm in dry years (1963) and exceed 800 mm in

Table 1. *Climatic conditions at Vyshnii Volochek and at Fyedorovskoe*

	Vyshnii Volochek 56°00'N, 34°40'E		Fyedorovskoe 56°27'N, 32°57'E
Period	1898–1995	1970–1995	1970–1995
Temperature, °C			
Absolute max	22.0 (1938)	20.8 (1972)	19.6 (1972)
Average max	17.2 ± 1.6	16.6 ± 1.5	16.0 ± 1.5
Annual mean	3.7 ± 0.9	3.8 ± 1.0	3.9 ± 1.1
Absolute min	−25.2 (1940)	−20.6 (1987)	−18.9 (1987)
Average min	$−9.6 \pm 4.1$	$−8.5 \pm 4.4$	$−8.5 \pm 4.2$
Precipitation, mm			
Absolute max	850 (1953)	787 (1977)	954 (1990,1998)
Annual mean	629 ± 101	621 ± 93	711 ± 121
Absolute min	391 (1963)	$404 \pm (1972)$	538 (1972)
For $T > 5\text{ }^{\circ}\text{C}$	374 ± 97	386 ± 94	434 ± 96
For $T > 10\text{ }^{\circ}\text{C}$	304 ± 84	309 ± 82	322 ± 86
For May–Sept.	349 ± 87	359 ± 85	397 ± 98
May–Sept. max	493 (1991)	493 (1991)	603 (1998)
May–Sept. min	101 (1939)	203 (1992)	178 (1997)
Growing season			
Days $> 5\text{ }^{\circ}\text{C}$	170	172	172
Days $> 10\text{ }^{\circ}\text{C}$	127	129	124

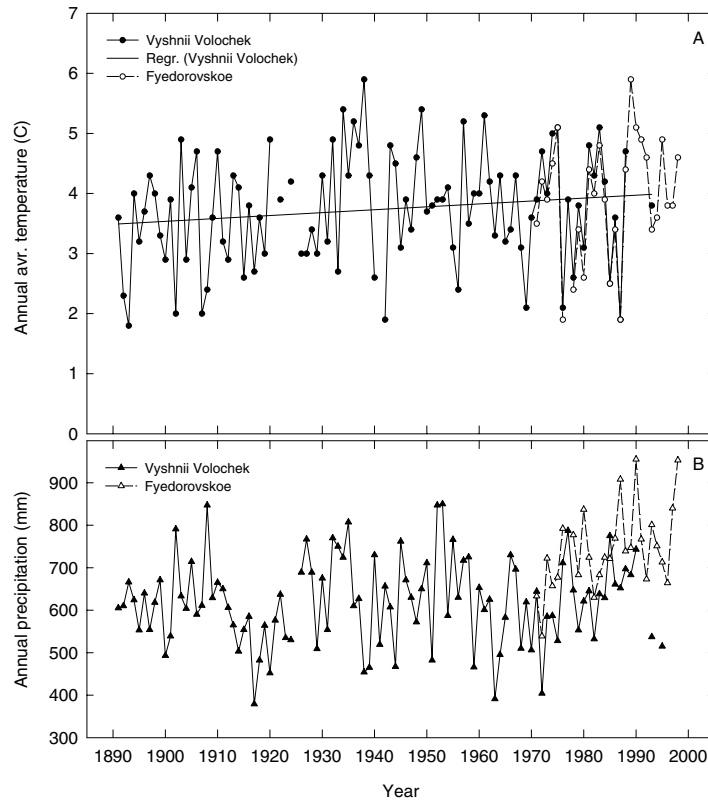


Fig. 1. 100-yr record of annual average temperature and precipitation at the Vyshnii Volochek weather station and (since 1968) at Fyedorovskoe in the Central Forest reserve.

wet years (1953), with mainly high summer rainfall in wet years. There is no obvious trend in precipitation. The variation of precipitation is greatest in summer, while the variation of temperature is greatest in winter. There is no correlation between annual or summer precipitation and temperature. Summer precipitation (days $> 10^{\circ}\text{C}$) is about half of total precipitation. The growing season ($T > 5^{\circ}\text{C}$) lasts on average 172 days. Snow of up to 60 cm depth covers the ground for 131–135 days.

At Fyedorovskoe mean wind speed was 3.2 m s^{-1} (1995–1999) with SW to SE being the main wind direction for 58% of the time. High wind speeds (4.55 m s^{-1}) come from WSW. Violent storms ($\sim 27\text{ m s}^{-1}$) occur approximately once a decade during the warm season, and these storms uproot or break trees along local wind trajectories. The last major wind-throws occurred in 1987 and 1996, but minor storms may uproot trees locally.

There are not only large inter-annual variations of summer temperatures and precipitation but also indications for climatic cycles. These become apparent from the standard residuals, which describe the relative deviation of single observations from the long-term trend (Fig. 2). The standard residuals allow a separation of climatic extremes from random variation. There is a long-term precipitation cycle lasting 4–8 yr with summer rain below or above average, and this cycle is opposite to a trend in temperature. Extremely wet years were 1980, 1987 and 1990, when low summer temperatures coincided with high rainfall. There were some extreme dry years, namely 1972, 1975, 1992 and 1995, when standard residuals of summer precipitation were low but standard residuals of temperature were high.

A positive water balance (precipitation exceeding evaporation) combined with poor drainage promotes bog formation. A water level of $> 0.40\text{ m}$ depth is

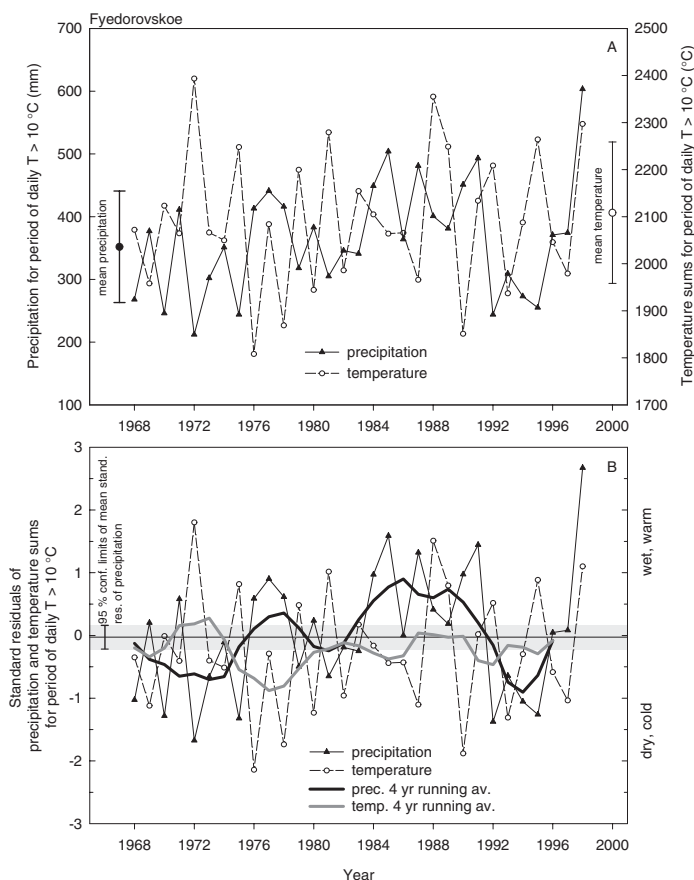


Fig. 2. (A) Long-term record of summer precipitation and temperature sums for daily average temperatures $>10^{\circ}\text{C}$. (B) Standard residuals of summer precipitation and temperature sums for daily average temperature $>10^{\circ}\text{C}$ at the Fyedorovskoye weather station.

characteristic for spruce forest on sedge bogs (dominated by *Eriophorum*) and on *Sphagnum* peat, but the water table may rise from -1 to 0.20 m even on drained sites which are characterized by *Dryopteris*, *Oxalis* and *Tilia* (Fig. 3A). A climatic cycle becomes more obvious from soil water observations. The standard residuals of the water table (Fig. 3B) show a 15 yr cycle with very high groundwater levels (1976–1991), preceded and followed by years with low groundwater levels (for detail see Vygodskaya et al., 2002). High groundwater levels were mostly associated with cold summers (1976, 1979, 1980, 1982–1984, 1986–1987, 1990) and less often with warm summers (1981, 1988–1989). In cold and wet summers, soil water content in the main root horizon (0–0.2 m deep) was 75–86%

of the soil water content at field capacity. This contrasts wet and warm summers when relative soil water content reached only 55–65%. Water content at field capacity varies between 185 mm on sites characterized by *Eriophorum* and 119 mm on sites characterized by *Oxalis* (V. Abrajko, unpublished data). The climatic extremes are listed in Table 2, where the changes between dry and wet years and storm events have special ecological significance.

Besides variations in the yearly averages, there is a high seasonal dynamic in the soil water status, which is important for tree growth and death (Fig. 4). Under average conditions soils are wet and waterlogged in spring, but with the onset of transpiration the water table is lowered to reach about -0.40 m under

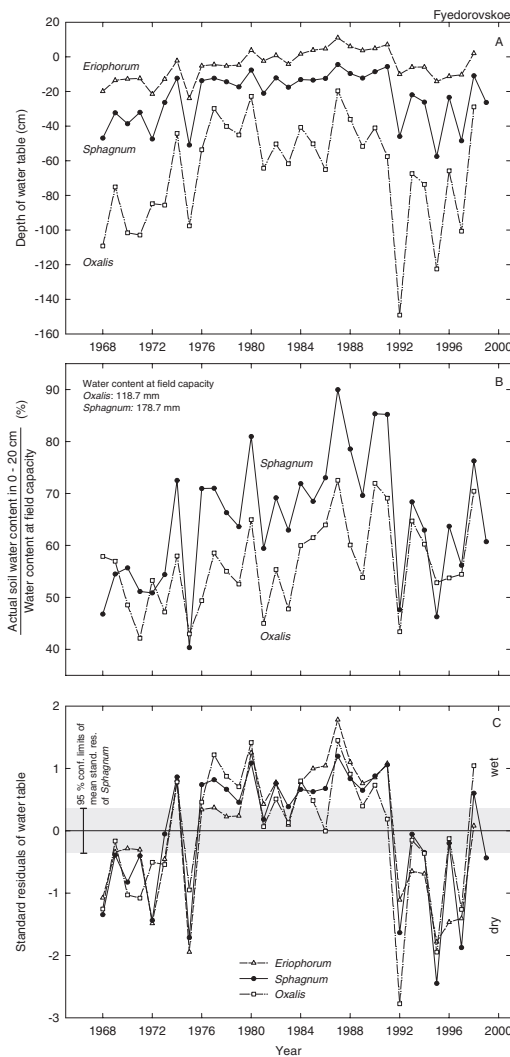


Fig. 3. (A) Seasonal trend of the depth of the water table and soil water content (expressed as ratio of actual soil water content/water content at field capacity for 0–0.2 m soil depth). (B) Standard residuals of water table changes for the period between 1968 and 1999 for the *Eriophorum*, *Oxalis* and *Sphagnum* sites.

Sphagnum and -0.80 m on well drained sites by the end of the growing season. However, these average conditions are significantly changed, e.g. in wet years (such as 1987) when soils were waterlogged all year long except for July. In 1990 soils were waterlogged in August. In contrast, during the warm and dry years of 1972 and 1992 water table decreased to -1.20 m

Table 2. Years of climatic extremes during the study period 1972–2000

Year	Water status	Wind	Rainfall	
			Total	Summer
1972	Dry		539	277
1975	Dry		677	293
1976	Wet		729	377
1980	Wet		837	511
1987	Wet	Storm	908	682
1990	Wet		955	510
1992	Dry		673	227
1995	Dry		713	328
1996		Storm	664	371

in summer, and plant available water was depleted to that depth.

3. The study sites

Picea abies (L.) Karst. mixed with a hybrid *Picea fennica* (*P. abies* \times *P. obovata*) (Minyaev and Konechnaya, 1976) cover 37% of the reserve area. Additional 11% of total area are mixes spruce forests with broad leaved trees. *Pinus sylvestris* forest covers about 8%, bogs and grasslands 19%, and small-leaved deciduous trees 33% of the Central Forest Reserve (24 645 ha). *Betula* and *Populus* are also early successional species after wind-throw of the conifers as well as after logging or fire. The large area covered by *Betula* and *Populus* indicates the significance of disturbances in this region. In fact, aerial photographs indicate that 50% of the whole territory is affected mainly by wind-throws and in part by logging.

In the following, we will refer to spruce communities by their main associated species, for example the *Picea* community on *Sphagnum* peat will be referred to as “*Sphagnum*-site,” as seen in Fig. 3 showing the water table data.

The first part of this study focuses on six permanent sample plots to demonstrate the dynamics of tree density and wood biomass from 1972 until 1988. The second part of this study focuses on only four study sites, namely the *Tilia*-, the *Oxalis*-, the *Sphagnum*- and the *Eriophorum*- community, where the dynamics of dead trees was investigated at greater detail.

The plots cover the diversity of habitats with *Picea abies* as dominant species. According to the

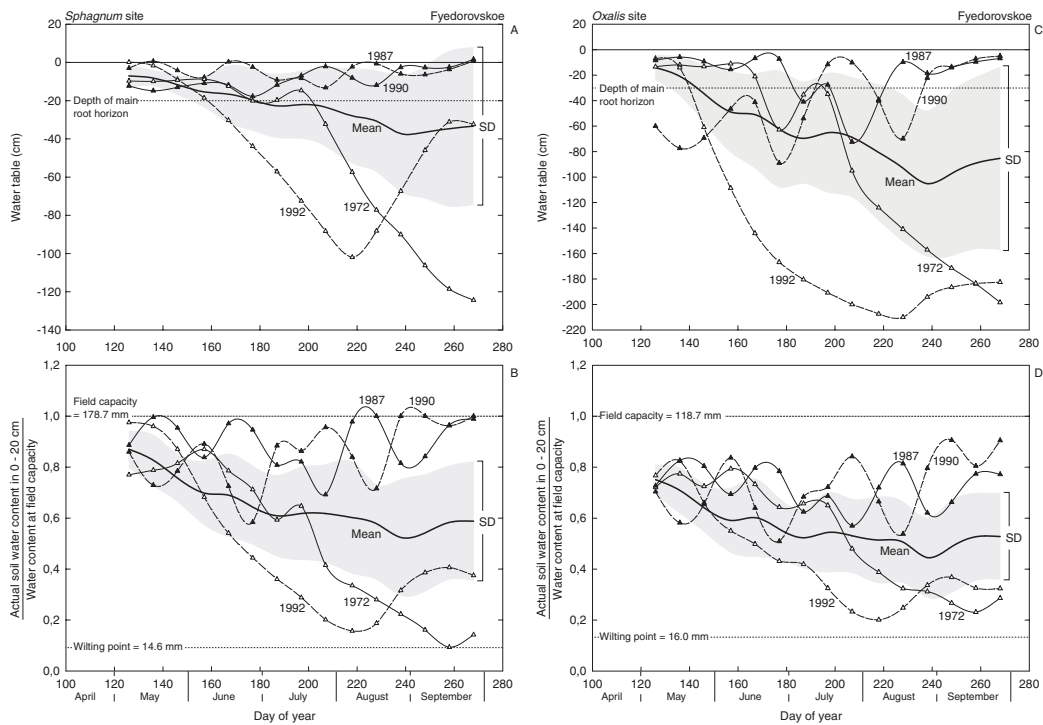


Fig. 4. Seasonal changes of the water table (A and C) and seasonal changes of soil water storage in 0–20 cm soil depth (B and D) for the *Sphagnum* and *Oxalis* sites. The figures show for the water table the depth of the main root horizon, and for soil water storage the field capacity as well as the wilting point, and the seasonal change as average and standard deviation for the period between 1968 and 1990. In addition two very wet years (1987 and 1990) and two dry years (1972 and 1992) are shown. The hatched area indicates times when the wet or dry years exceed the boundaries of the standard deviation of average conditions.

Russian phytosociological classification (Sukachev, 1931) these habitats include:

A *Tilia* site representing a “Piceetum tilioso-asperulosum” on well drained, loamy podzolic soil (Fahlerde, Eutric podzoluvisol) with 65–70% ground cover of rich herbaceous vegetation including *Asperula odorata*, and a moss layer (15–20% cover). This forest type represents 12% of the area covered by spruce in the Central Forest Reserve.

The *Dryopteris* site representing a “Piceetum oxalidoso-dryopteritosum” on well drained weak humus podzols with signs of surface gley with *Dryopteris dilatata* and *Oxalis acetosella* covering 60–70% of the forest floor. 15–20% of the forest floor is covered by mosses. This forest type represents 6% of the spruce area of the Central Forest Reserve.

The *Oxalis* site representing a “Piceetum myrtilloso oxalidosum” on drained podzolic gleyic soil

(gleyic podzololavisol) with mainly *Oxalis acetosella* and *Vaccinium myrtillus* covering 45% of the forest floor (35–40% moss cover). There are several *Oxalis*-associations which cover together about 30% of the spruce area.

The *Vaccinium* site represents a “Piceetum myrtillosum” growing on less drained peaty podzolic gley (gleyic podzololavisol) with *Vaccinium myrtillus* and *V. vitis idaea* covering 80–100% of the forest floor. This forest type represents 18% of the spruce area.

The *Sphagnum* site represents a “Piceetum sphagnoso myrtillosum” on peaty podzolic gley (Gleysol) with *Vaccinium myrtillus* and *V. vitis idaea* covering 30% and *Sphagnum girgensohnii* covering 94% of the forest floor. This forest type represents about 7% of the total spruce area. This forest type contains the intensive study site with flux measurements.

The *Eriophorum* site represents a “Piceetum eriophoroso-myrtilloso-sphagnetosum” on bogged peat gley (Gleysol) with *Eriophorum vaginatum* and other sedges covering 35% and *Sphagnum* mosses 70% of the forest floor. This forest type represents about 1% of the total spruce area.

The selected six forest types represent about 70% of the forest cover by *Picea* (Karpov and Shaposnikov, 1983).

4. Methods

Breast height diameter (Dbh = $D_{1.3}$) and height (H) of all canopy trees (with $D_{1.3} > 6$ cm, $H > 8$ m, of all trees (*Picea* plus associated other species) of the six observation plots were measured every 2–4 yr between 1972 and 1988 (Pugachevskii, 1992) as a basis for calculating wood (stem + bark) volume according to biomass tables. The study excludes seedlings and possible regeneration being smaller than above dimensions. Wood volume was converted to dry weight using an average wood density of 450 kg m^{-3} for the *Eriophorum* spruce forest (site with slowest growth), 410 kg m^{-3} for the *Sphagnum* stand, and 380 kg m^{-3} for other forest types (Karpov, 1973; 1983). Wood density of *Betula* was 488 kg m^{-3} for the *Eriophorum* site, 485 kg m^{-3} for the *Sphagnum* site and 465 kg m^{-3} for all other sites. Following Trendlenburg and Mayer-Wegelin (1955) wood density of *Populus* was set as 371 kg m^{-3} . Leaf area index (LAI), was measured from harvested trees (Alexeyev, 1975).

At four sites the regular inventories included a documentation of living spruce trees, fallen living trees, standing dry trees and fallen trees (original data filed at the Central Forest Reserve). This information is available for the *Sphagnum* site from 1972 to 2000, and for the *Oxalis* site from 1968 to 1990. The inventories at the *Eriophorum* and *Tilia* site started 1972 and terminated between 1988 and 1992. The available data were used to track mortality dynamics of individual trees that were alive before 1972 and quantify the period between tree death and falling and determine decomposition on the ground.

5. Results

5.1. Inventory data

The long-term observation plots at all sites were established in stands older than 100 yr (Table 3). In

all sites *Picea* was the dominant but not the only species. Associated tree species were mainly *Betula pendula*, *Betula pubescens*, *Populus tremula* and *Pinus sylvestris*. The contribution of these associated species to total stand biomass change over time, and may even become significant as the stands age or degrade.

Breast height diameter increased with site quality, (Bonitet = Site index: V being low, I being high). Some of the associated species, especially *Populus*, were represented by a small number of individuals, but these may reach very large dimensions (74 cm Dbh at the *Oxalis* site). Average tree height increased for *Picea* from about 13 m at the *Eriophorum* site to 29 m at the *Tilia* site. *Populus* may become 8 m taller than *Picea*, and also *Betula* may exceed the height of *Picea* on rich soils. Stem biomass (derived from mass-tables) increased with site quality, while whole number of trees decreased from more than 1200 at the *Eriophorum* site to less than 300 individuals ha^{-1} in the *Tilia* community. LAI ranged between 8 and 9 in the *Oxalis* and the *Sphagnum* community.

5.2. Dynamics of living spruce canopy trees and wood biomass

Comparing inventories over a period of 16 yr indicates the long-term stand dynamics (Table 4). In all stands the loss of individuals of the spruce population was quite similar to the loss of individuals of all tree species in that stand, which justifies our focusing analysis on *Picea*. All stands decreased tree density with increasing stand age, with an average rate of $2.8 \pm 0.5\% \text{ yr}^{-1}$ of the spruce population and of $2.7 \pm 0.4\% \text{ yr}^{-1}$ of the whole stand. Only the *Eriophorum* site showed a larger loss of individuals for reasons to be discussed below. In absolute terms, during 1972–1988 about 16–20 trees ha^{-1} were dying each year, with a lower rate at the *Tilia* site and a higher rate at the *Eriophorum* site. Extrapolating the density/age relation of Table 2, the general trend suggests, that the dominating tree canopy is turned over about once every 160–180 yr, with high nutrient sites being turned over faster.

The long-term decrease of stand density was not associated with a proportional increase in stand biomass, as would be expected from self-thinning theory (Table 4). In none of the stands did the long-term log biomass versus log density plot reach the theoretical slope of -0.5 . In most cases, the long-term loss of individuals resulted in a strong (*Eriophorum* site)

Table 3. Inventory parameters for experimental sites^a

Site Bonitet Area	Year	Species composition	Age, (yr)	Dbh (cm)	Height, (m)	Wood volume (m ³ ha ⁻¹)	Wood biomass (t _{dw} ha ⁻¹)	Stand density (ind. ha ⁻¹)	
<i>Eriophorum</i> Bonitet V 0.258 ha	1972	65% <i>Picea</i>	151	13.4	13.4	105	47.3	1018	
		26% <i>Betula</i>	104	17.3	16.6	40	19.5	213	
		9% <i>Pinus</i>	108	35.3	21.0	16	6.3	16	
	Total		135			161	73.1	1247	
	1988	16% <i>Picea</i>	128	10.8	11.9	12	5.4	178	
		59% <i>Betula</i>	120	19.6	17.6	43	20.9	171	
25% <i>Pinus</i>		124	38.2	21.3	18	7.1	16		
Total		122			73	33.4	365		
<i>Sphagnum</i> 0.285 ha Bonitet IV	1972	83% <i>Picea</i>	150	18.5	19.3	266	108.9	1035	
		15% <i>Betula</i>	108	20.7	21.8	45	20.5	133	
		Total		141			311	129.3	1168
	1988	86% <i>Picea</i>	169	22.5	22.7	322	132.1	733	
		14% <i>Betula</i>	124	23.2	22.6	51	23.2	116	
		Total		162			373	155.3	849
<i>Vaccinium</i> Bonitet III 0.318 ha	1972	57% <i>Picea</i>	107	18.5	22.0	248	94.2	823	
		35% <i>Populus</i>	92	29.8	30.6	151	56.0	145	
		8% <i>Betula</i>	102	24.1	28.8	36	16.4	60	
	Total		101			435	166.6	1028	
	1988	47% <i>Picea</i>	128	21.6	23.1	214	81.3	506	
		44% <i>Populus</i>	108	38.0	33.2	202	74.9	113	
9% <i>Betula</i>		102	27.6	30.0	39	17.8	47		
Total		117			455	174.0	666		
<i>Oxalis</i> 0.238 ha Bonitet I	1972	91% <i>Picea</i>	115	26.1	24.7	447	169.9	655	
		5% <i>Populus</i>	86	65.0	33.0	22	8.2	4	
		4% <i>Betula</i>	121	25.7	25.6	18	8.2	29	
		<1% <i>Ulmus</i>	44	n.m.	n.m.	<1	0.3	4	
		Total		114			476	182.4	692
	1988	85% <i>Picea</i>	136	26.6	27.6	337	128.3	370	
		8% <i>Populus</i>	102	74.0	36.1	32	11.9	4	
		6% <i>Betula</i>	137	32.1	29.1	23	10.5	21	
		1% <i>Ulmus</i>	60	12.5	10.7	1	0.5	4	
		Total		133			397	151.1	399
	<i>Dryopteris</i> Bonitet Ia 0.368 ha	1972	78% <i>Picea</i>	87	23.2	25.4	392	149.0	714
			18% <i>Populus</i>	78	27.2	29.5	94	34.9	114
4% <i>Betula</i>			72	19.6	24.6	18	8.2	52	
Total			85			504	192.1	880	
1988		77% <i>Picea</i>	113	28.3	29.8	402	152.8	457	
		19% <i>Populus</i>	94	33.7	34.7	99	36.7	68	
	4% <i>Betula</i>	88	25.6	27.8	18	8.2	27		
Total		108			519	197.7	552		
<i>Tilia</i> 0.671 ha Bonitet I	1972	76% <i>Picea</i>	134	28.7	26.3	293	111.3	331	
		20% <i>Populus</i>	101	37.8	31.4	76	28.2	42	
		4% <i>Betula</i>	117	37.1	31.1	16	7.3	10	
	Total		127			385	146.8	383	
	1988	72% <i>Picea</i>	152	31.8	28.9	236	89.7	201	
		25% <i>Populus</i>	117	47.1	35.4	82	30.4	28	
3% <i>Betula</i>		133	42.1	35.5	7	3.2	3		
Total		143			325	123.3	232		

^aDbh, Diameter at 1.3 m; ind./ha, individuals per ha (Pugachevskii, 1992). Wood density for *Picea* was 450 kg m⁻³, *Eriophorum* site; 410 kg m⁻³, *Sphagnum* site; 380 kg m⁻³, all other sites (Karpov, 1973; 1983). Wood density for *Populus* was 0.371 kg m⁻³ (Trendlenburg and Mayer-Wegelin, 1955) Species composition was expressed as % of cover. N.m., not measured Species: *Picea abies*, *Pinus sylvestris*, *Betula pendula*, *B. pubescens*, *Populus tremula*, *Ulmus scabra*.

Table 4. Yearly changes in stand density ($\Delta n/\text{yr}$), change in density as related to the average stand density (%), and change in biomass as related to changes in density ($\Delta \log B/\Delta \log n = \text{slope of self-thinning line}$) for the period between 1992 and 1988^a

Site	Loss of individuals [$\Delta n/\text{yr}$ (%)]		Change in biomass per change in density ($\Delta \log B/\Delta \log n$)		Change in stand age per year ($\Delta \text{age yr}^{-1}$)	
	<i>Picea</i>	Total stand	<i>Picea</i>	Total stand	<i>Picea</i>	Total stand
<i>Eriophorum</i>	-52.5 (-5.2%)	-55.1 (-4.4%)	2.10	0.64	-2.1	-0.8
<i>Sphagnum</i>	-18.9 (-1.8%)	-19.9 (-1.7%)	-0.71	-1.00	1.2	1.3
<i>Vaccinium</i>	-19.8 (-2.4%)	-22.6 (-2.7%)	0.28	-0.10	1.2	1.0
<i>Oxalis</i>	-17.8 (-2.7%)	-18.7 (-2.6%)	0.43	0.32	1.3	1.2
<i>Dryopteris</i>	-16.1 (-2.2%)	-20.5 (-2.3%)	-0.05	-0.10	1.0	1.4
<i>Tilia</i>	-8.1 (-2.5%)	-9.4 (-2.5%)	0.41	0.36	1.1	1.0

^aUnder conditions of competition for light a slope of -0.5 is to be expected.

or a lesser (*Tilia*, *Oxalis*, *Vaccinium* sites) absolute loss in biomass. At the *Dryopteris* site biomass remained constant (1972–1988), and only at the *Sphagnum* site did the biomass increase between 1972 and 1988 more than expected from the -0.5 slope of a self-thinning line. Following the rule of Eichhorn (1904) the deviation from the self-thinning line indicates the presence of harvest or disturbances. The response of all species was in a similar direction but less strong than that of *Picea* alone. *Betula* and *Populus* changed less over time, but these individuals were also younger (Table 3).

The long-term trend of stand density and thinning, as described by either the self-thinning rule or the Eichhorn rule, does not allow insight into the processes that lead to tree death. On plotting the logarithm of stem biomass versus log stand density (Fig. 5A) it becomes apparent that the change of stand density and biomass is very irregular. There were periods, e.g. at the *Dryopteris* and the *Sphagnum* sites, when stand density and the associated increase in biomass followed the expected slope of the self-thinning rule of -0.5 . However, these periods were interrupted by unpredicted large losses of biomass and/or individuals, which may be followed by periods of "recovery," similar to what has been observed after fire (Wirth et al., 1999). In some cases recovery was very fast (biomass increased after loss in density: *Dryopteris* and *Sphagnum* sites); in others recovery balanced the continuing loss of individuals (biomass remains constant as predicted by the Eichhorn rule: *Tilia* site) or the forest continues to lose biomass and density (*Eriophorum* site). The variation in response shows that neither

the Eichhorn rule, which was established for managed forest, nor the self-thinning rule of natural vegetation is generally applicable in natural forest and under all conditions.

In the period under observation, events between 1972 and 1976 affected the *Tilia*, *Dryopteris* and *Sphagnum* sites, and with some delay also the *Eriophorum* and *Dryopteris* sites. Events between 1984 and 1986 affected the *Tilia*, *Oxalis* and *Dryopteris* sites. The *Sphagnum* site was affected again between 1988 and 1990. In the following we will try to identify the causes for these periodic events of tree death.

Tree death was mainly associated with wet and dry years (Schmidt-Vogt, 1989a,b), with wet years causing death of fine roots due to waterlogging. If a wet year is followed by a dry year, the effect of drought is accentuated, because the root system cannot reach or follow the water table. In this case, drought can result in a weakening of tree vitality over the years, and this may attract insects and other diseases, which may finally result in tree death. We observed oscillations of tree mortality which seem to be triggered by climatic events, but the response depended on site conditions and on the past history. The wet *Eriophorum* sites showed a higher loss of trees than the other sites in the dry year of 1972. Following this dry year most other sites, especially *Oxalis*, showed increasing tree death with some delay because recovery in tall trees is slow, and weakening attracts other diseases. The very wet year of 1976 following dry years in 1972 and 1975 initiated a cascade of tree death at the *Eriophorum* site, which led to a major collapse of this stand. A wave of tree death was initiated at all sites by a

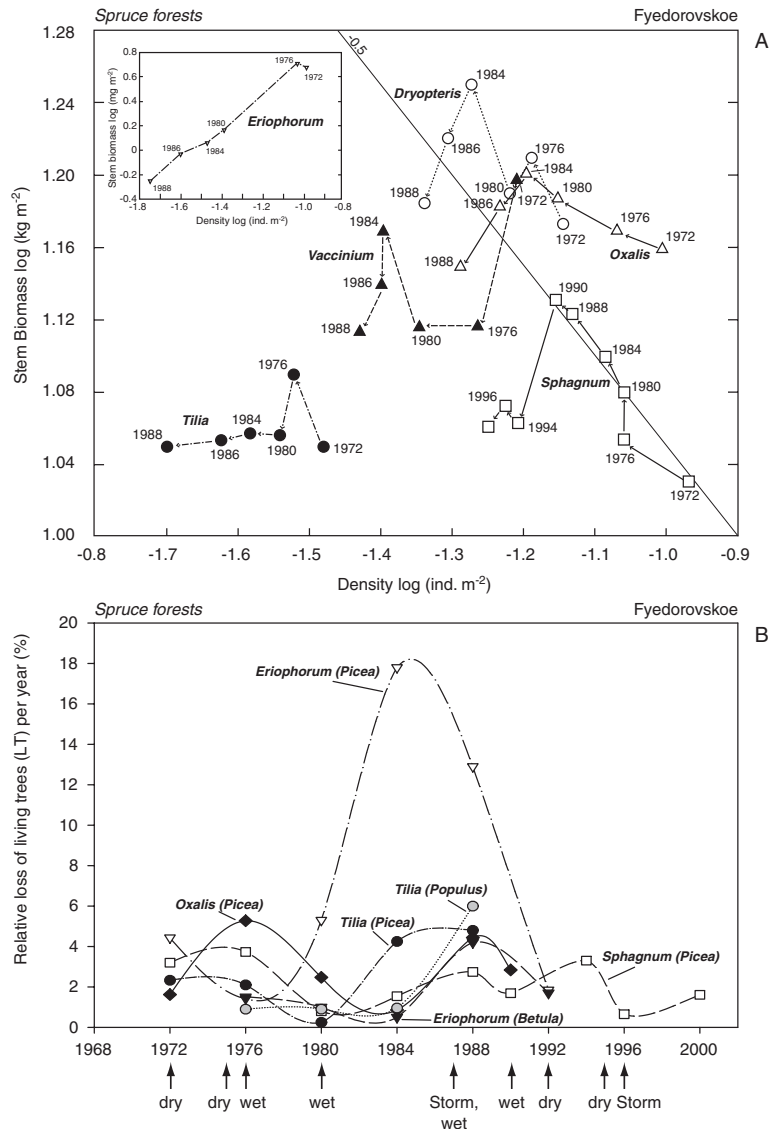


Fig. 5. (A) Log (biomass of stems) (wood + bark, kg m^{-2}) as a function of log (stand density) (number of individuals m^{-2}) for the experimental sites. The trend over time is indicated by the year. The theoretical slope of a self-thinning process (-0.5) is indicated by a line. (B) Relative changes of living tree species, $(L_{T+1} - L_T)/L_T$, as related to the year of observation.

storm in a wet year of 1987 because root systems were damaged by the movement of trees in heavy wind. The resulting response may be similar to drought. The very wet year of 1990 had little effect on tree losses, but the 1992 drought caused increasing death at the *Sphagnum* site, which at that time remained the only site under investigation.

The decrease in density did not occur at the same rate in all size classes of the tree population. In most sites, more younger than older trees were lost. Thus, the average age of *Picea* plots increased by factor of 1.1–1.3 yr per yr. An exception is the *Eriophorum* site, where preferentially old trees died and the average age of *Picea* decreased. Only in the *Dryopteris* site did the

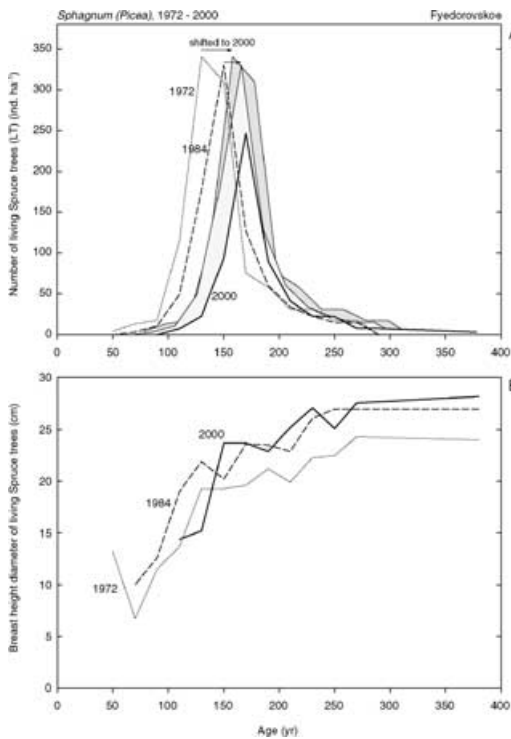


Fig. 6. (A) Age distribution of trees at the *Sphagnum* site in 1972 and in 2000. For comparison, the age distribution of 1972 was shifted 18 yr to match 2000. (B) Breast height diameter of living spruce trees as a function of the age of the individual tree age class in the years 1972 and 2000.

average age of *Picea* increase by 16 yr over the 16 yr period of observation.

The *Sphagnum* site is taken as an example to demonstrate the change in the age structure of the surviving stand (Fig. 6A). In 1972 the largest cohort of trees was 130 yr old, while average age was 150 ± 30 yr. The distribution was slightly left-centered. Twenty-eight yr later, in yr 2000, the largest cohort of trees was 170 yr old and average age was 181 ± 35 yr. This demonstrates that a larger fraction of young and rather than old trees died over the 28 yr period. The change in age structure affected the distribution of breast height diameters (Fig. 6B). In 1972 a cohort of young trees existed with relatively high Dbh. Breast height diameter then increased linearly with age, and a plateau of 24 cm was reached at age 270 yr. In 2000 the initial cohort of young trees with large diameters had disappeared; in fact all trees died that were younger than 80 yr in 1972. Also in year 2000, Dbh increased with age and

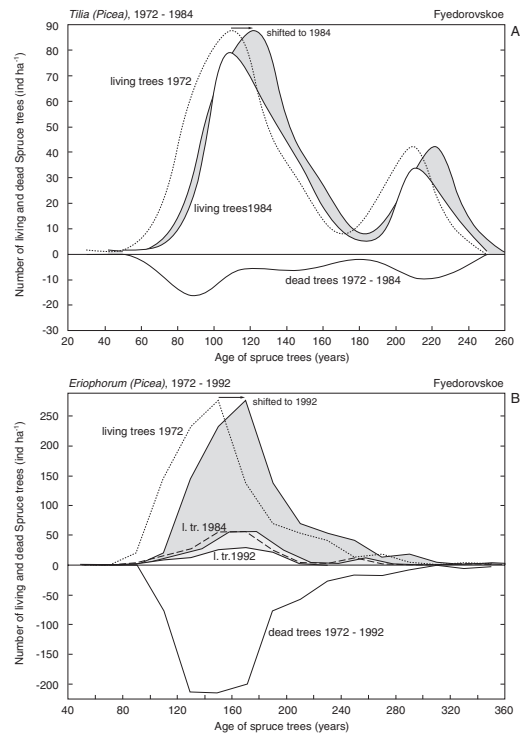


Fig. 7. Age distribution of living trees in different years of observation for (A) the *Tilia* site and (B) the *Eriophorum* site.

reached a plateau at age 270 yr, but this plateau had a diameter of 27 cm. The 1984 curve showed a parallel shift to 1972, and the same plateau as 2000. This shows that the change of the relation of age-dependent Dbh over time does not represent growth, but it is determined by the loss of cohorts of specific age classes.

The change in age structure with time was similar for the other sites (Fig. 7). One extreme is the *Eriophorum* site, in which almost all trees died, and only few old trees survived. The *Tilia* site, which showed very little recovery in the "thinning-plot" of Fig. 5, consists of two cohorts of trees, one at an average age of 210 yr and the other at an average age of 120 yr. In this case, in both populations, more older than younger trees died, especially in the period 1972–1976.

Drought and excessive water emerge as the two main factors that determine stand density. In Fig. 8 we show tree mortality in relation to the amplitude of the yearly change in soil water (see also Fig. 4). The amplitude of yearly soil water changes was

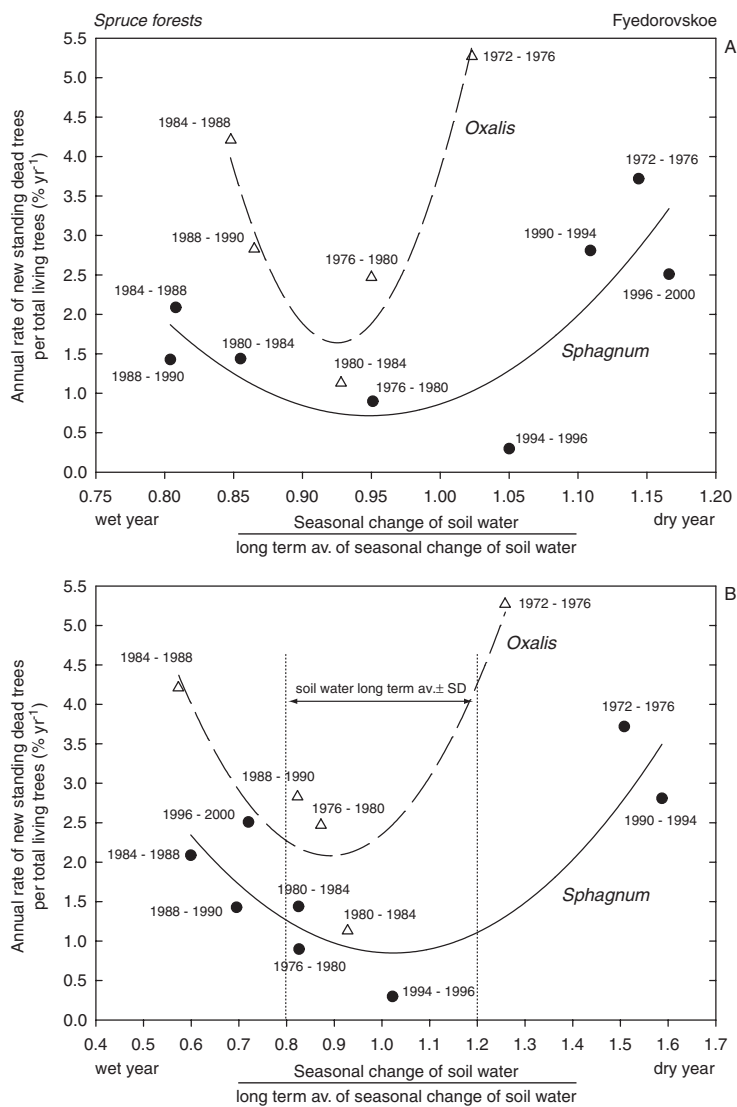


Fig. 8. Relative annual rate of death of spruce trees (dead trees/total live trees) as a function of the average soil water content in the 0–0.2 m soil layer. (A) Mean soil water content amplitude during 2–4 yr periods. (B) Extreme soil water content amplitude during the same period.

scaled according to the long-term average change in soil water. Mortality was low in years with average climate conditions. However, mortality significantly increased in wet and in dry years, when the seasonal amplitude of soil water changes were above or below the long-term average. The figure does not distinguish between mortality as caused by water stress directly and mortality caused by insects as a consequence of a

weakening of trees. Both factors contribute to mortality in these stands.

In contrast to the effect of drought on stand density, which eliminates smaller diameter trees, wind primarily affects larger trees and thus affects mainly biomass and to a lesser extent stand density. The 1987 storm caused a decrease of biomass and stand density at the *Dryopteris*, *Oxalis* and *Tilia* sites. The effects were

not consistent across all sites because a change in density prior to a climatic event may make the stand more vulnerable (*Eriophorum* site) or more resilient to climate extremes.

5.3. The fate of standing dead trees

The result of changes in living trees is the production of dead trees. These remain either as standing dead trees for an unknown period of time before they fall to the forest floor. Standing dead trees originate from drought and associated insect damage, while wind results in uprooting or breakage of living trees and of damage by falling neighboring trees. Each of these cohorts of trees has its own dynamic of decay which makes it difficult to interpret the total number of dead trees at a site without knowledge of their history.

The *Sphagnum* and the *Oxalis* sites carried about 120–160 standing dead trees ha^{-1} (Fig. 9, dashed line) which had died before 1972 (most likely in the 1963 drought). It took >20 yr until this group fell to the forest floor. A new large cohort of standing dead trees was recorded in 1976 as a result of the 1972 drought, and lesser cohorts in the following years of census. The total number of standing dead trees at any one time follows from the falling of the different cohorts and the emergence of new cohorts. For instance, the total of 105 dead trees at the *Sphagnum* site in year 2000 resulted from tree death and falling of dead standing trees since 1984. Similar responses emerged at the *Tilia* and *Eriophorum* sites, but standing dead trees were falling to the ground at a more rapid rate at the wet site.

Figure 9 shows that over the period of observation the fraction of trees that reached the forest floor as living trees is generally small (<5% of the total number of lost canopy trees), except for 1984, where strong wind caused uprooting and breakage to an extent that 50% of the lost canopy trees reached the forest floor as live trees. A similar pattern emerged for the *Oxalis* site, where in 1984 not only a large number of live trees were felled by wind but also a larger number of dead standing trees were felled.

The mean residence time of standing dead trees can be determined from the persistence of the different cohorts of standing dead trees (Fig. 10). There is an apparent time lag between tree death and falling of the first standing dead trees, which may be due to the observation system, i.e. the census took place every 4 yr. From that point on, the falling of trees followed an negative exponential curve with $k = 0.149$ at the

Sphagnum site. Fifty percent of standing dead trees had fallen after 11 yr (including the time lag). This decay function was not as regular at the *Oxalis* site, where some cohorts (1980, 1984 and 1988) fell more rapid than other cohorts. This is in part due to the effect of strong winds in 1984. The average time for 50% of the standing dead trees to fall was 12 yr at that site. These values are twice as high as generally being used for carbon balance calculations (Alexeyev and Birdsey, 1994).

The dead trees on the forest floor can be detected for very long periods of time at various degree of decay. The decomposition rate constant (k_d , yr^{-1}) was calculated as $k_d = -\ln(M_t/M_0)/t$, where M_0 and M_t are the tree biomass before tree death and after a time t that the tree fell to the ground (Olson, 1963). The data shown in Fig. 10c indicate that decomposition cannot be described by a single equation. Following rapid decay in the first 10 yr ($k_{d1} = 0.0329$), the rate decreased to $K_{d2} = 0.0125$, probably due to a change in chemical composition of the remaining wood. The mean residence time for the total process is 42 yr, which is longer than predicted by a single “Olson-type” equation (Knohl et al., 2001: $t_{1/2}$ -18 yr, see also Krankina and Harmon, 2000; Harmon et al., 2000). Complete humification is predicted after 80 yr, which is close to field observations (Storoyenko, 1990; Storoyenko et al., 1992).

6. Discussion

Our data show that the thinning process in unmanaged forest ecosystems results from a combination of both a weakening of tree individuals by competitive processes and by disruptive climatic events (see also Vygodskaya et al., 1995). We may generalize that there is an interdependence between both in such a way that forest stands that experience strong competition are more prone to climatic extremes, and that thinning by climatic extremes relieves the competitive pressure in such a way that the self-thinning process is being stalled. In the period of reduced competition, the stand may also be resistant to the same climatic conditions that would otherwise cause a disruptive thinning event.

In the case of our study, the main climatic factors that altered stand density were waterlogging and drought, as well as strong wind. Drought seems to affect suppressed small and younger trees mainly. In this respect it acts like ground-fires (Wirth et al., 2002)

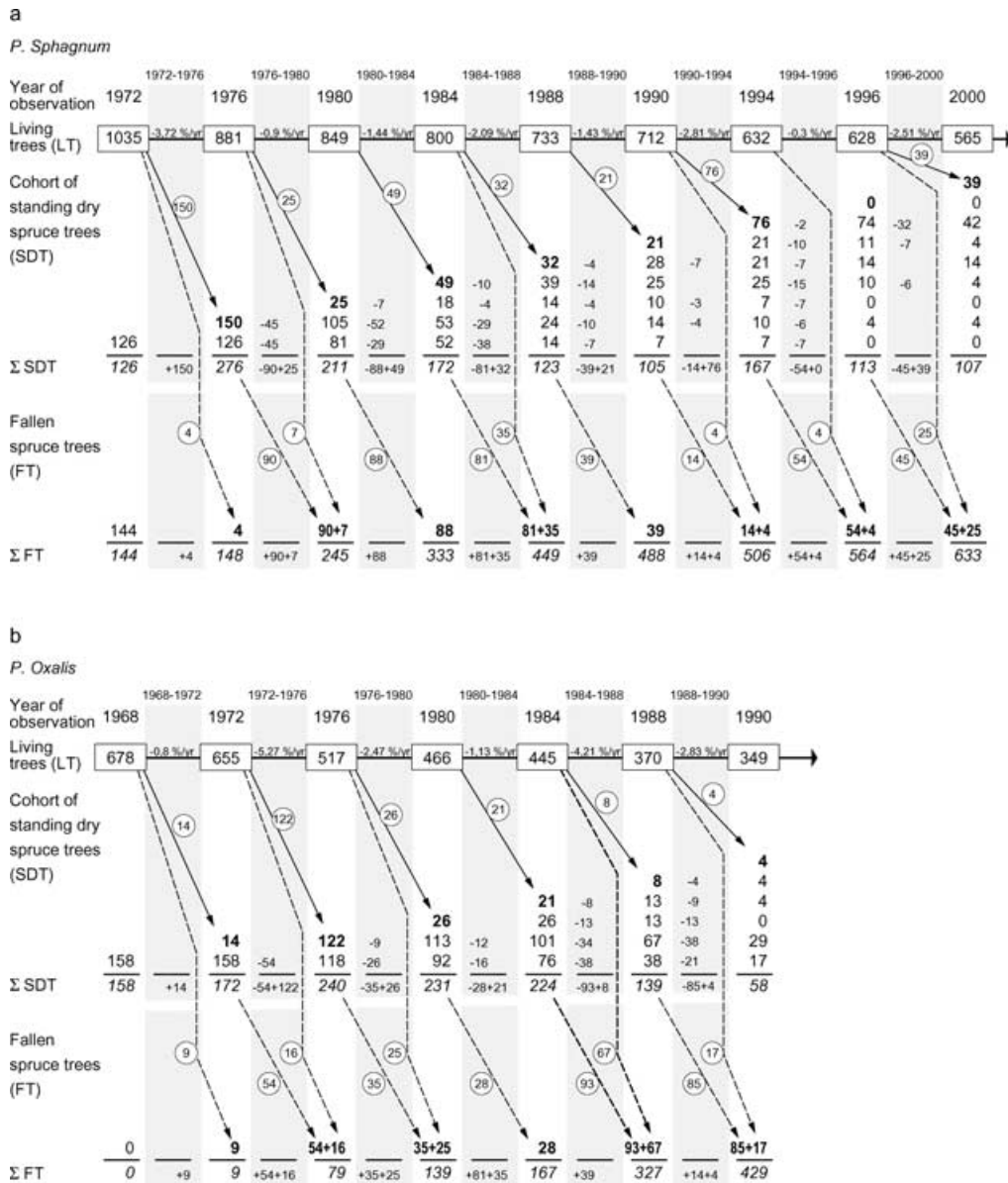


Fig. 9. Demography of living and dead spruce trees (A) for the *Sphagnum* site and (B) for the *Oxalis* site. Top: the year of observation, (second) the number of life trees (LT, numbers in boxes) and the relative rate of loss of living tree individuals. Center: the total number of standing dead trees (SDT), and the individual cohorts and their fate of falling to ground. Arrows indicate the number of trees moving from life to standing dead and fallen trees. Bottom: total number of dead trees on the ground at various stages of decay.

or thinning operations by forest management (Schulze et al., 1999). Thus soil water stress promotes the larger trees that generally have deeper root systems which are more resilient to changes in precipitation. How-

ever, there is a cut-off point in this process, where the canopy becomes opened and atmospheric turbulence starts to enhance the process of canopy collapse mainly by uprooting and breakage of trees. In this

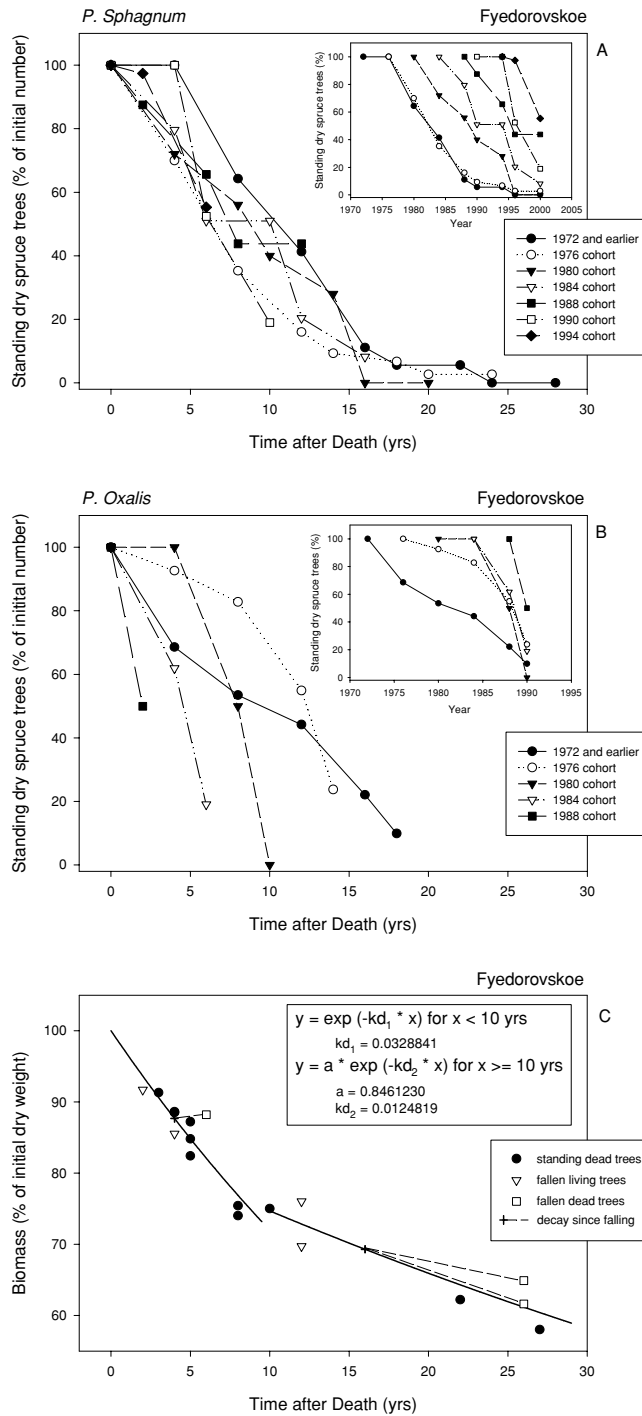


Fig. 10. Relative loss of standing dead spruce trees over time: 50% of a cohort is lost on average after 12 yr (mean residence time of standing dead trees).

case the tallest trees are also affected, but strong wind also affects mainly the subdominant canopy strata of a diameter class just at or below stand average (see Schmidt-Vogt, 1989a;b). Thus we observe that stand density is regulated by drought and waterlogging, and stand biomass by wind. The long-term result of these processes, which include density regulation, recovery by growth and extraction of biomass from the canopy by wind, is an almost constant stand biomass over a broad range of stand densities in spruce-dominated habitats [which was postulated by Eichhorn (1904) for managed forests]. The long-term development of stand biomass does not follow the theoretical self-thinning line in mature unmanaged forest. The examples presented by Westoby (1984) of self-thinning forests were plantations that were competing for light in a climate which apparently had no climatic extremes. This confirms earlier observations in natural unmanaged forest vegetation, where thinning is dominated not simply by stand internal competition but by external events (Wirth et al., 2002; Mund et al., 2001). Prediction made on wood extraction based on the self-thinning line may be taken with caution.

The oscillation of periods in which biomass aggregates in canopy trees and events which put biomass abruptly into the decomposer compartment makes inventory and flux studies difficult. One may envisage two stands, one acting as carbon sink, the other as carbon source, and both are different just by the way they responded to soil water stress: one stand may be in a phase of recovery from past damage and continue to aggregate carbon, while the other had a high biomass and stand density and responds with a strong decline of canopy trees. Thus the probability of climatic events becomes an essential parameter for interpretation of inventory or flux studies. This enforces the need for long-term observations, which have to cover at least the period of climate oscillations, which were in our case in the order of 16–28 yr. In addition it becomes clear that the study of selected compartments, such as stem biomass (IPCC-SRLULCF, 2000) as measure of a carbon sink, becomes extremely questionable. If biomass is exported from the live into the dead compartment, the time between dying and decomposition on the forest floor becomes important. In the case where trees remain as standing dead trees, as in the case of drought or insect damage, decomposition will be delayed by about a decade, but decomposition will start immediately in the case of uprooting and breakage by wind.

Besides oscillations of periods of damage and recovery, we present an example, the *Eriophorum* site, that thresholds exist which open the canopy to an extent that recovery is not possible and which lead to a canopy collapse. In the *Eriophorum* case, a single dry year followed by a wet year caused a decrease in stand density of about 50%. This opened the canopy such that a chain of wind events essentially eradicated this stand. Also the *Oxalis* plot was terminated in 1987 by heavy wind.

The more gentle case, namely the oscillation between disturbance and recovery, was observed in most other sites, and the question emerges if there is an optimum periodicity of climatic events that have a more than proportional effect on these stands. In our case, drought events occurred every 15–20 yr. The periodicity of strong wind events is more difficult to establish, because of a lack of long-term wind measurements, and because wind effects may be very local. In our study strong winds occurred every 4–6 yr in one or another, but regional heavy windthrow occurs with a periodicity of about 9–15 yr in the area under study. Our 16–28 yr observation is too short to answer the question if a shortening of the time between climatic extreme events, as predicted by global climate change, would increase forest damage. We observe that the effect of drought in communities that are sensitive to drought results in a recovery which lasts 10–14 yr. In that period stand density would still be below the level predicted by self-thinning. Additional dry years at higher frequency would not have a larger effect than a second drought in the period of recovery, because water may be sufficient for a leaf area below the self-thinning line. Thus the effect of climatic extremes, such as drought and waterlogging, may not increase with increasing frequency. It is possible that this frequency is then responsible for triggering threshold events such as observed in the *Eriophorum* or *Oxalis* community. In 1990 a regional assessment showed that 52% of the total forest area was affected by wind, i.e. showing >20% damage.

7. Conclusion

We may conclude that forest biomass and stand density can only be interpreted by periodic climatic extremes in which soil water stress regulates the density and storms the biomass. This leads to saw-tooth-like

responses of aggregation of carbon in canopies over periods of decades and extraction of C from the canopy on an annual or daily basis. The periodicity becomes important, in that it may trigger threshold events that lead to a chain of reactions that finally cause total destruction of the stand.

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