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VEGETATION DYNAMICS IN CENTRAL EUROPEAN FOREST ECOSYSTEMS (NEAR-NATURAL AS WELL AS MANAGED) AFTER STORM EVENTS

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Abstract: All over the world forests and woodlands are damaged or reset to initial stages by fire, insect outbreaks or storms. In Central Europe storm events are the most important natural disturbances affecting stand structures of both natural and managed forests and yet only a few studies exist on long-term forest development following the destruction of the tree layer by a storm. This paper presents a permanent plot study established in 1988 in the Bavarian Forest National Park (SE Germany) on areas, where the tree layer had been destructed by a storm on August 1, 1983. The records concerning (1) floristic composition (spermatophytes, pteridophytes, bryophytes, lichens) and cover degree, (2) location and shape of each tree higher than 1 meter (height, diameter at breast height) including position of fallen trees and (3) number of seedlings and saplings were taken in 1988, 1993 and 1998. Two windfall areas, situated next to each other in the same broad and flat valley bottom on wet soils under local cold climate conditions (potential as well as recent vegetation: *Calamagrostio villosae-Piceetum bazzanietosum*) were analyzed, one of them with completely free development after the storm event ("untouched"), the other with dead wood cleared off after the event, but thereafter with free development ("cleared"). The vegetation analysis separated two major trends in vegetation dynamics: (1) On the cleared plots with intensive soil-surface disturbance (removal of the damaged wood) the species composition changed towards pioneer herb vegetation (*Rubus* sp.), and pioneer forest species (here: birch, *Betula pendula* and/or *B. pubescens*) established. Subsequently, vegetation dynamics leading towards clusters of forest ground-layer species composition took place. (2) In untouched stands, where soil-surface disturbances were restricted to pit-and-mound-system created by uprooted trees, the patchiness of forest vegetation increased and a regeneration of mainly terminal tree species (here: Norway spruce, *Picea abies*) started. Stand development for the next 100 years was simulated using the model FORSKA-M. The model is individual-based and includes competition for light, soil water, and nutrients. The simulations suggest that floristic structures of cleared and untouched plots, respectively, will remain different for several decades, but within one century, the floristic structure becomes rather similar. Major processes in forest ecosystems which can be used to improve forest management and nature conservation practices have been identified based on the results of the case study.

INTRODUCTION

Storm events are the most important natural large-scale disturbances that affect stand structures of both natural and managed forests in Central Europe. Two unusually large storms occurred during the 1990s in Central Europe, the first one at the early beginning of the decade, the second one at the end of it: (1) the storms "Vivian" and "Wiebke" (February 28 to March 1,

Table 1. The 1990 and 1999 storm events in Central Europe. Databasis: HUSS 1991, KÖNIG et al. 1995, HOLENSTEIN 1994, SCHUMACHER (1995), ANONYMOUS (2000).

Storm event	Country affected	Dead wood (million m^3)	Factor annual cut
Vivian/Wiebke (28.2.–1.3.1990)	Switzerland	4.9	1.1
	(Southern) Germany	65	2.0
	Czech Republic / Slovakia	11.3	0.6
	Great Britain	6.0	1.5
	Belgium	5.5	1.8
	Austria	4.8	0.3
	Central Europe	100–120	
Lothar 26.12.1999	(W)-France	114.6	~ 4
	Switzerland	12.3	2.6 (...10)
	Germany		
	Baden-Württemberg	23.5	2.4–3 (...)
	Bayern	4.3	0.4
	Austria	0.5	0.04
	Central Europe	~ 155	

1990) threw down more than 100 million m^3 of wood with the centre of damage in southern Germany, Switzerland, and the (today) Czech Republic, and (2) storm "Lothar" (December 26, 1999) centred in western France, Switzerland, and southwestern Germany, throwing down more that 150 million m^3 of wood (Table 1). In many areas the total annual timber harvest was thrown down in a few hours. In some countries, counties or forest districts the damage corresponded up to 2, 3, 4 or 10 times the annual allowable cut.

Besides the large-scale storms, smaller storm events frequently affect forest stands at local levels. For example on August 1, 1983 a storm hit the Bavarian Forest National Park in southeastern Bavaria, Germany (Fig. 1a). Including some smaller windfall events in the following years this local storm threw down about 173 hectares of forests and destroyed about 70,000 m^3 of timber (representing about 1.6% of the total stock volume of the forests of the park).

In Europe only a few forests, which also tend to be very small, allow for a study of the long-term forest dynamics after natural disturbances, because for several centuries nearly all forests have been more-or-less intensively managed. With the current preference for nature-oriented forest management there is increasing interest in, and need for, understanding the natural vegetation dynamics following natural disturbances in European forests. After the storm events of 1990, scientific programs aimed at developing recommendations for future forest management practices were initiated to analyse developments of important ecosystem components including plants, animals, fungi, and stand structures (Switzerland: SCHÖNENBERGER et al. 1995; SW Germany: FISCHER 1998, Europe: FISCHER & MÖSSMER 1999). The most valuable places in Central Europe to study natural forest dynamics without direct influence of forestry are the national parks. The Bavarian Forest National Park is the oldest German national park, covered nearly completely with forests; the forests in the core area of the National Park have been unmanaged since the establishment of the park in 1970.

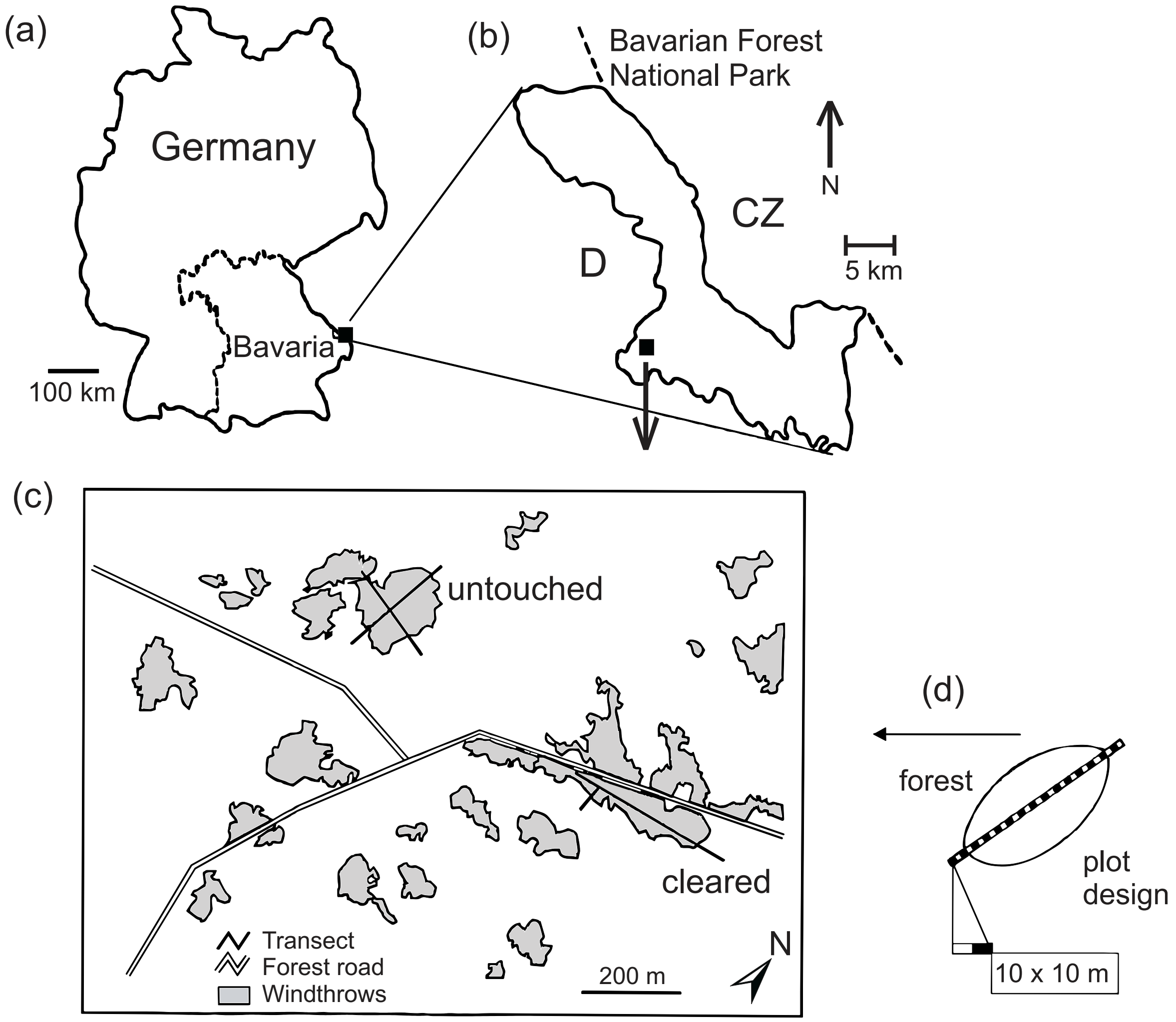

Fig. 1. Location of the Bavarian Forest National Park in Germany (a), study area within the national park (b), spatial correspondence of the permanent plot transects (c), general design of a permanent transect (d).

The storm event in the Bavarian Forest National Park created a unique opportunity to investigate natural vegetation dynamics with little human interaction.

Especially spruce (*Picea abies*) forests of wet and cold valley bottoms (potential natural vegetation: *Calamagrostio villosae-Piceetum*) were affected by the storm event on August 1, 1983. Destructed forest stands within the core protection zone of the national park were left untouched to develop without human interference ("untouched"). Outside this zone storm-effected areas in the national park were cleared of timber but not replanted ("cleared"). To observe and analyse vegetation dynamics following the storm event a set of permanent plots was established in 1988. Three inventories were carried out in 1988, 1993, and 1998. Although 15 years of observation (storm event in 1983, last record in 1998) is a comparatively short time when compared with the life span of a tree, this study can be seen as one of the very few studies on forest ecosystem dynamics on large plots available in Central Europe to cover a period of more than one decade (KLOTZ 1996).

This paper presents an overview of the investigation of the major developments and ecological trends from 1988 to 1998 and suggests a perspective of the future development of the forest stands.

LOCATION

The mountain ridge "Bavarian Forest" is situated in the southeastern part of Germany (Fig. 1a). The bedrock consists of metamorphic materials, mostly granite and gneiss. The climate tends to be sub-continental with long and rather cold winters and relatively warm and rainy summers (annual precipitation about 1100 to 1500 mm). While the highest mountain of the national park (Mount Rachel) reaches an elevation of 1453 m, the elevation of the broad and relatively flat valleys is between 700 and 900 m.

The slopes of the mountains are covered by mixed beech forests (*Fagus sylvatica*, *Abies alba*, *Picea abies*). The broad and flat valley bottoms have wet soils and a relatively cold climate (mean annual temperature 5° to 6 °C, snow cover 5 to 6 months, every month of the year with at least a few nights of frosts; PETERMANN & SEIBERT 1979). They are covered with forests dominated by Norway spruce. The potential natural vegetation is *Calamagrostio villosae-Piceetum bazzanietosum* ("valley-bottom-spruce-forest"). Because of the remote location of the mountain ridge the impact of man was relatively short (about 200 years), and in general the potential natural vegetation was maintained up to the present day.

The two windfall areas under investigation, cleared and untouched, are the largest of a group of storm-felled areas in a wide and flat depression at an altitude of about 750 m. They are situated next to each other (Fig. 1b, 1c) under very similar site conditions (see above). In both cases the forests blown down in 1983 consisted of a stand mosaic with spruce that was aged 40, 55 and 135 years, respectively. The dominating Norway spruce in both cases is accompanied by a few individuals of *Betula pendula / B. pubescens* and *Sorbus aucuparia*.

METHODS

Design of permanent plots

A set of permanent plots arranged as transects with plots of 10 × 10 meters each (Fig. 1d) was established in 1988. Each transect starts in undisturbed spruce forests, then crosses the area destructed by storm and ends in undisturbed forest again (FISCHER et al. 1990). Altogether 76 permanent plots were established, 33 of them in the forest district "Hochfallen" (cleared area including surrounding reference forest) and 43 of them in the forest district "Hahnenfalz" (area remained untouched after the storm, including the surrounding reference forest).

The standard records included (1) the species composition (spermatophytes, pteridophytes, bryophytes, lichens) and cover degrees of each species (phyto-sociological relevés according to the Braun-Blanquet-approach), (2) location and shape of all tree individuals higher than 1 meter, including height, diameter at breast height, tree location, fallen trees as well as pit-and-mound-systems created by uprooted trees, and (3) the number of all seedlings and all saplings smaller than 1 meter.

Phyto-sociological analysis

Phyto-sociological relevés from each plot (untouched after the storm; cleared after the storm; surrounding forest stands) and each year (1988, 1993, 1998) are presented in a frequency table (tree, shrub and field layer species) including mean cover degrees (mean of the cover degree values presented below; e.g. "100^{51}" means: species present in 100% of the plots, mean cover degree 51%; Table 2). These data were additionally evaluated by multivariate analysis (detrended correspondence analysis, DCA: using the program PCORD, McCune & Mefford 1999); cover degrees of species were considered and cover degree codings were converted into cover degree values (0.5, 2.0, 4.0, 8.75, 18.75, 37.5, 62.5 and 87.5% respectively; tree species as well as mosses were excluded from this inventory); transformations and down-weighting of rare species were not applied.

Nomenclature of vascular plants follows Wisskirchen & Haeupler (1998).

Simulation model FORSKA-M

FORSKA-M is a forest succession model, which originally was developed for the simulation of stand dynamics of boreal forests (Prentice et al. 1993). It is an individual-based model. Forest stand development is simulated based on the processes of growth, regeneration, and mortality of individual trees. Each tree is characterized by the following parameters: height, diameter at breast height, position of crown, age and species affiliation. In the model, trees compete for light, and thus tree growth depends on the resulting light conditions. Soil water and soil nutrient conditions as well as climatic parameters are implemented.

The model includes a vertical representation of individual tree crowns, but it does not consider real distributions of trees on the respective plot, i.e. it assumes a spatially homogeneous forest structure. Several improvements of the model as well as the parameterization of Central European tree species have been carried out and documented elsewhere (Lasch et al. 1999, Lindner 2000). Because some processes are modelled stochastically, 30 simulation runs have been aggregated for each plot. Site conditions were estimated based on average conditions described in Kennel (1998), using soil profile information from a digital soil map (BÜK 1000; Federal Institute for Geosciences and Natural Resources). Climate data were interpolated to local conditions using the method of Erhardt et al. (2001) and the climate data set of the Climate Research Unit of East Anglia, UK. Daily data were generated from the monthly means using the C2W weather generator (Bürger 1997). Simulation runs over a period of 100 years were initialized with the 1998 inventory of all trees above 1 meter of height. Some tree parameters that were not included in the measured data were estimated using methods described in Lindner (2000). In a second simulation experiment, regeneration below 1 meter of height was also considered. The model was initialized with the tree inventory of the year 1998 as before and run for 10 years. It was assumed that 10 % of the mapped seedlings and saplings of the year 1998 would have survived these 10 years and grown up above the height threshold. The diameter of the sapling in-growth was set to 1 cm with a height of 1.3 m in the case of individual saplings or up to 5 height cohorts of 1.0–1.4 m in the case of very dense regenerations. The model was then run another 90 years to produce comparable results to the first simulation experiment.

RESULTS

15 years of documented vegetation dynamics

The first results from the permanent plot study have been published by Fischer et al. (1990) and Fischer & Jehl (1999). Table 2 presents the floristic composition of the tree as well as the shrub and field layers of the cleared and untouched windfalls and the surrounding forests in the years 1988, 1993 and 1998.

Table 2. Frequency (main figures) as well as mean cover degree (exponents) of the vegetation of untouched and cleared plots, respectively, as well as the surrounding forests not effected by storm (forest 1 and forest 2), grouped into overstory and understory tree layer (tree layer 1 and 2), shrub layer, and different ecological strata of the field layer.

	Forest 1			Untouched			Forest 2			Cleared		
	1988	1993	1998	1988	1993	1998	1988	1993	1998	1988	1993	1998
Number of relevés	6	10	10	12	24	24	5	10	10	7	14	14
Tree layer 1												
Picea abies	100^{51}	100^{39}	100^{51}	25^{8}	21^{8}	75^{5}	100^{49}	100^{40}	100^{41}	14^{19}	14^{11}	36^{8}
Betula pendula/pubescens	17^{1}	.	.	8^{4}	4^{2}	58^{7}	60^{13}	20^{19}	20^{14}	.	.	86^{17}
Fagus sylvatica	.	.	.	.	.	.	20^{9}	10^{9}	.	.	.	.
Sorbus aucuparia	.	.	.	.	.	.	.	.	.	.	.	21^{2}
Salix caprea	.	.	.	.	.	.	.	.	.	.	.	14^{2}
Tree layer 2												
Picea abies	83^{4}	100^{8}	80^{5}	25^{4}	50^{6}	21^{5}	40^{3}	50^{5}	50^{8}	29^{2}	21^{2}	7^{9}
Betula pendula/pubescens	.	.	.	.	4^{4}	8^{2}	20^{2}	10^{9}	.	.	.	29^{24}
Sorbus aucuparia	.	.	.	.	.	.	.	.	10^{2}	.	.	21^{2}
Fagus sylvatica	.	.	.	.	.	.	.	10^{2}	.	.	.	.
Shrub layer												
Picea abies	33^{2}	90^{2}	60^{2}	83^{5}	88^{7}	100^{7}	100^{8}	90^{13}	90^{18}	57^{1}	71^{2}	100^{4}
Sorbus aucuparia	.	.	.	17^{1}	17^{1}	33^{1}	100^{1}	50^{1}	60^{1}	57^{1}	57^{1}	36^{1}
Betula pendula/pubescens	17^{4}	.	20^{3}	58^{2}	79^{7}	100^{8}	.	10^{1}	10^{4}	100^{3}	100^{28}	100^{15}
Salix caprea	.	.	.	17^{1}	8^{1}	13^{1}	.	.	.	14^{1}	21^{1}	14^{1}
Abies alba	.	20^{1}	.	.	33^{3}	.	80^{1}	.	.	.	.	.
Sambucus racemosa	.	.	.	8^{1}	.	8^{1}	.	.	.	.	7^{1}	.
Populus tremula	.	.	.	.	8^{1}	17^{1}	.	.	.	.	.	21^{1}
Fagus sylvatica	.	.	.	.	.	.	.	20^{1}	.	.	.	.
Forest species												
Vaccinium myrtillus	100^{1}	100^{1}	100^{3}	100^{3}	100^{3}	100^{11}	100^{37}	100^{26}	100^{31}	71^{1}	86^{2}	86^{2}
Calamagrostis villosa	100^{19}	100^{6}	100^{7}	92^{25}	88^{22}	96^{26}	60^{4}	70^{7}	80^{4}	100^{35}	100^{30}	100^{53}
Deschampsia flexuosa	83^{10}	90^{10}	80^{6}	92^{10}	92^{12}	88^{4}	60^{1}	40^{1}	20^{1}	14^{1}	7^{1}	14^{1}
Dryopteris carthusiana	50^{1}	50^{1}	40^{1}	100^{1}	96^{2}	96^{1}	40^{1}	30^{1}	30^{1}	100^{1}	100^{2}	100^{1}
Maianthemum bifolium	50^{1}	40^{1}	30^{1}	8^{1}	.	4^{1}	20^{1}	20^{1}	20^{1}	.	7^{1}	7^{1}
Vaccinium vitis-idaea	17^{1}	10^{1}	10^{2}	67^{1}	67^{2}	71^{2}	60^{1}	60^{1}	60^{2}	.	.	.
Athyrium felix-femina	.	.	.	.	38^{1}	33^{1}	.	10^{1}	10^{1}	.	36^{1}	21^{1}
Dryopteris dilatata	.	.	.	.	71^{2}	67^{1}	.	10^{1}	10^{1}	.	21^{1}	.
Lycopodium annotinum	.	.	.	.	.	.	20^{1}	20^{1}	20^{1}	.	36^{1}	7^{1}
Trientalis europaea	.	.	.	.	.	.	.	10^{1}	10^{1}	14^{1}	14^{1}	14^{1}
Gymnocarpion dryopteris	.	.	.	.	29^{1}	33^{1}	.	.	.	.	7^{1}	.
Carex pilulifera	.	.	.	.	.	.	.	20^{1}	10^{1}	.	.	.
Oxalis acetosella	.	.	.	.	.	.	.	.	.	14^{1}	.	.
Anemone nemorosa	.	.	.	.	.	.	.	.	.	.	7^{1}	.

Pioneer forest species												
Betula pendula/pubescens	50^{1}	40^{2}	40^{2}	100^{2}	92^{3}	92^{2}	20^{1}	30^{2}	30^{2}	100^{2}	93^{3}	71^{2}
Populus tremula	.	.	.	25^{1}	21^{1}	13^{1}	.	.	.	29^{1}	.	14^{1}
Salix caprea	.	.	.	25^{1}	17^{1}	8^{1}	.	.	.	43^{1}	.	7^{1}
Sambucus racemosa	.	.	.	.	8^{1}	.	.	.	.	14^{1}	7^{1}	7^{1}
Pioneer species												
Rubus idaeus	$33^{\mathbf{1}}$	$10^{\mathbf{1}}$	$10^{\mathbf{1}}$	$67^{\mathbf{1}}$	$92^{\mathbf{2}}$	$92^{\mathbf{2}}$	.	$10^{\mathbf{1}}$	.	$100^{\mathbf{18}}$	$100^{\mathbf{13}}$	$86^{\mathbf{1}}$
Epilobium angustifolium	.	.	.	83^{2}	83^{1}	83^{1}	.	10^{1}	.	100^{1}	100^{1}	57^{1}
Carex muricata agg.	17^{1}	.	.	33^{1}	33^{2}	42^{1}	.	.	.	71^{1}	14^{1}	.
Epilobium montanum	.	.	.	17^{1}	.	.	.	.	.	.	.	.
Wet soil indicators												
Carex canescens	17^{1}	10^{1}	10^{1}	75^{4}	58^{2}	63^{1}	.	.	.	71^{1}	14^{1}	7^{1}
Carex echinata	.	.	.	67^{1}	54^{1}	54^{1}	.	.	.	43^{1}	14^{1}	14^{1}
Juncus effusus	.	.	.	58^{1}	54^{1}	50^{1}	.	.	.	86^{1}	43^{1}	29^{1}
Phegopteris connectilis	.	.	10^{1}	17^{1}	13^{1}	8^{1}	.	.	.	.	.	7^{1}
Carex brizoides	.	.	.	.	.	.	.	.	.	29^{6}	21^{4}	43^{5}
Epilobium palustre	.	.	.	.	.	.	.	.	.	14^{1}	7^{2}	7^{1}
Carex nigra	.	.	.	.	4^{9}	4^{1}	.	.	.	.	.	.
Viola palustris	.	.	.	.	.	.	.	.	.	.	7^{1}	7^{2}
Petasites albus	.	.	.	.	.	.	.	.	.	14^{1}	.	.
Stellaria alsine	.	.	.	.	.	.	.	.	.	14^{1}	.	.
Equisetum sylvaticum	.	.	.	.	.	.	.	.	.	.	.	7^{1}
Myosotis scorpidioides agg.	.	.	.	.	.	.	.	.	.	.	.	7^{1}
Saplings of trees and shrubs												
Picea abies	100^{1}	100^{2}	100^{2}	100^{1}	100^{2}	100^{3}	100^{1}	100^{2}	100^{4}	86^{1}	100^{1}	100^{3}
Abies alba	.	20^{1}	20^{1}	8^{1}	4^{1}	4^{1}	60^{1}	90^{1}	100^{1}	.	7^{1}	7^{1}
Fagus sylvatica	17^{1}	20^{1}	10^{1}	.	13^{1}	8^{1}	.	30^{1}	.	.	7^{1}	7^{1}
Sorbus aucuparia	.	10^{1}	.	25^{1}	29^{1}	13^{1}	60^{1}	90^{1}	90^{1}	14^{1}	29^{1}	43^{1}
Frangula alnus	.	.	.	.	.	.	.	.	10^{1}	.	.	.
Tilia platyphyllos	.	.	.	.	.	.	.	.	10^{1}	.	.	.
Pinus sylvestris	.	.	.	.	.	.	.	.	.	.	14^{1}	.
Miscellaneous												
Galium saxatile	33^{1}	40^{1}	20^{1}	17^{1}	38^{2}	42^{2}	.	.	10^{1}	14^{2}	7^{2}	14^{1}
Urtica dioica	.	.	.	8^{1}	.	.	.	.	.	14^{1}	7^{1}	7^{1}
Circaea alpina	.	.	.	.	.	.	.	.	.	14^{1}	7^{1}	7^{1}
Carex sp.	.	.	.	.	.	.	20^{1}	.	.	29^{1}	.	.
Galeopsis pubescens	.	.	.	.	.	.	.	.	.	29^{1}	7^{1}	.
Chaerophyllum hirsutum	.	.	.	.	.	.	.	.	.	14^{1}	.	7^{1}
Taraxacum officinale agg.	.	.	.	8^{1}	.	.	.	.	.	.	.	.
Trifolium sp.	.	.	.	.	4^{1}	.	.	.	.	.	.	.
Prenanthes purpurea	.	.	.	.	.	4^{1}	.	.	.	.	.	.
Hypericum maculatum	.	.	.	.	.	.	.	.	.	14^{1}	.	.
Veronica officinalis	.	.	.	.	.	.	.	.	.	14^{1}	.	.
Ranunculus repens	.	.	.	.	.	.	.	.	.	.	7^{1}	.
Galeopsis bifida	.	.	.	.	.	.	.	.	.	.	.	14^{1}

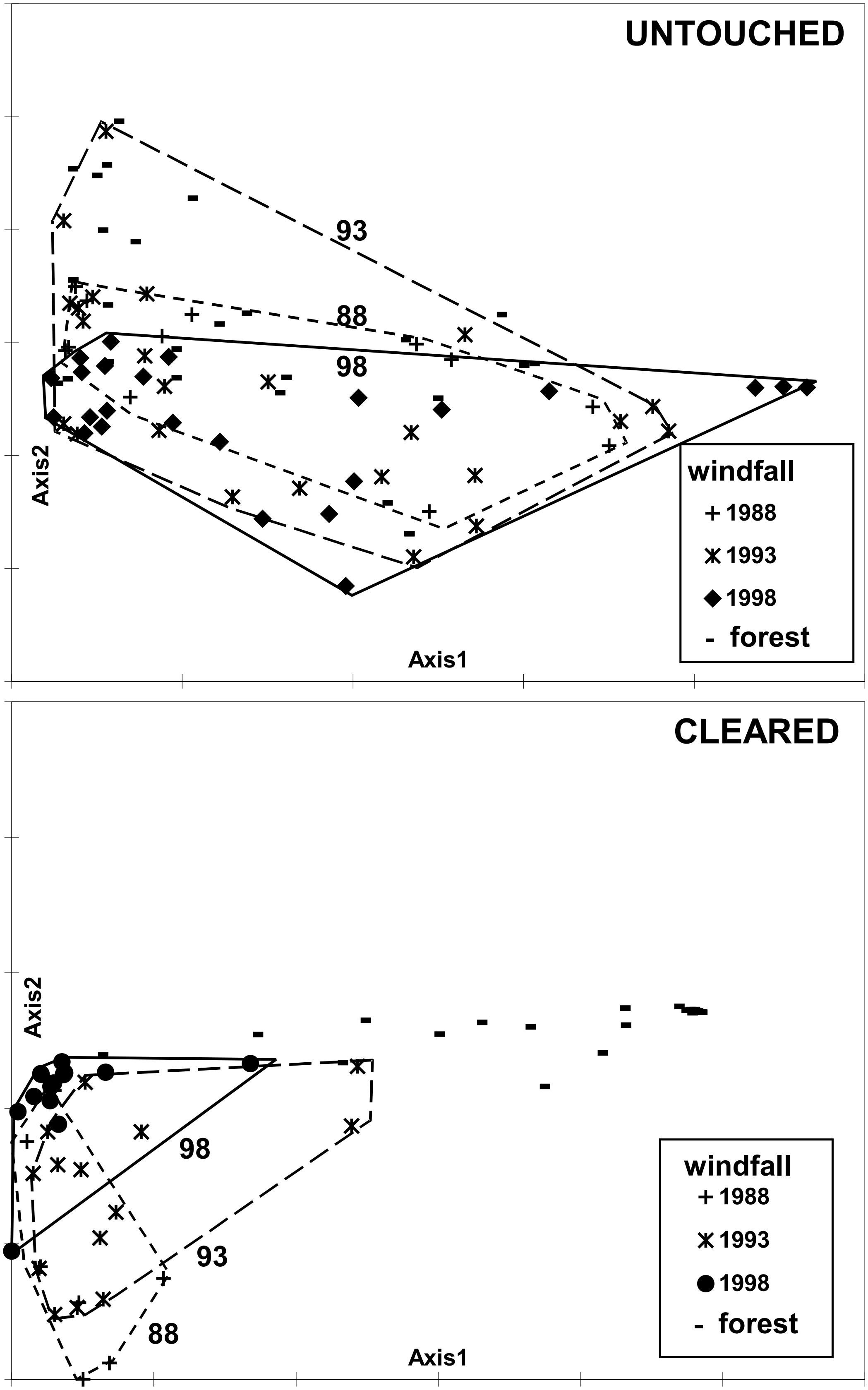

Fig. 2. DCA of all the records of untouched and cleared plots from 1988, 1993 and 1998 (clusters of each of the three years with borders) as well as of the surrounding forests. All data were calculated together, but for better presentability are organized into separate graphs (axis scaling identical in both plots).

Five years after the storm event, in 1988, raspberry (*Rubus idaeus*) was one of the dominant species on the cleared areas (see Table 2). Thus, the vegetation could be classified as a pioneer community typical for clear-cuts in managed forests, called *Rubetum idaei*. During the following 5 years, young trees (mostly genus *Betula*, *B. pendula* as well as *B. pubescens*, young individuals of both species hard to distinguish) started to establish (at first in the field layer, later growing into the shrub and tree layer). Fifteen years after the storm event birch reached up to 8 meters in height. Below the developing tree layer, *Rubus idaeus* as well as the clear-cut species decreased rapidly (birch pioneer forest). Spruce individuals started to occur in the undergrowth (mostly with less than 1 meter in height). Within a period of 15 years a successional change in the sense of a "sequence of plant communities" (FISCHER & KLOTZ 1999) from a clear-cut community to a pioneer (birch) woodland community took place, a sequence well known from European managed forest stands after harvesting (clear-cut) procedures (e.g. DIERSCHKE 1988).

Conversely, *Rubus idaeus* never became dominant on plots which remained untouched after the storm. Only small quantities of this species could be located, of which most of the plant individuals were restricted to the pit-and-mound-system created by uprooted trees. Individuals of birch (*Betula*) settled on these places as well. In general, during the 15 years of observation birch developed smaller cover degrees than spruce, because the latter species was already present with saplings in the forest stands prior to the disturbance. Spruce individuals are now dominating the young forest stands (see FISCHER & JEHL 1999).

In order to describe the different trends of vegetation dynamics, a detrended correspondence analysis (DCA) was carried out. Fig. 2 expresses the development of the floristic composition of the field layer (without tree saplings) from all the cleared and untouched plots as well as from the surrounding reference forest of 1988, 1993 and 1998. All the records from untouched plots are completely mixed in the diagram (Fig. 2, top). Neither an aging trend 1988 → 1993 → 1998 nor a structural trend (windfall area → surrounding forest) can be seen. On the other hand, the clusters of records of the cleared plots (Fig. 2, bottom) are partially separated from the clusters of the reference forest, and a time sequence 1988 → 1993 → 1998 can be seen. This sequence in the first place is reflecting a decrease in the cover degree of *Rubus idaeus* since 1988 as described above (see Table 2).

Bringing together ground-layer and tree-stand development these observations indicate a "successional" trend with the developmental steps "*Rubus*-pioneer-shrub" and "*Betula*-pioneer-forest" on the cleared plots, and regeneration of a spruce tree layer on untouched plots. This leads to varying future development pathways of the areas under investigation after the storm event: birch-dominance for several decades on cleared plots and continuing spruce-dominance on untouched plots. Nevertheless between all individual plots there is a relatively high degree of floristic variation (but within the association *Calamagrostio villosae-Piceetum*).

Modelling the tree stand development

Fifteen years is a comparatively short observation period to analyze forest dynamics. Therefore the model FORSKA-M was applied as an analysis tool that offers the possibilities (1) to outline the potential future developmental trends of forest stands, (2) to analyze the influence of different starting positions (e.g. to use only trees larger than 1 meter for

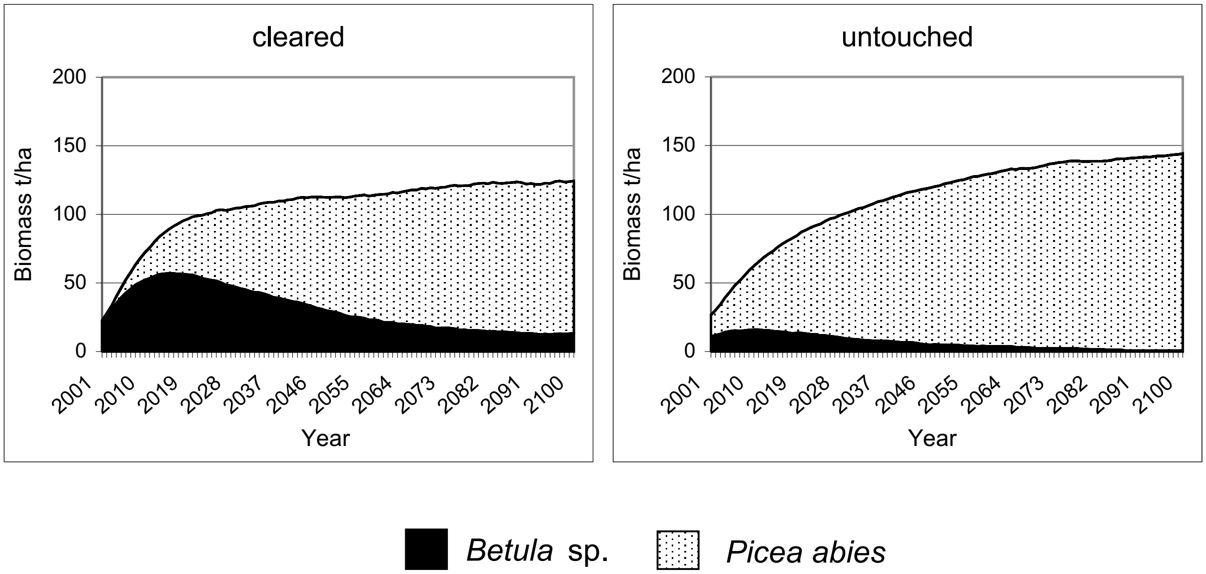

Fig. 3. Comparison of the simulated development of the tree stands (starting with the trees higher than 1 m in 1998) of the cleared (left) and untouched (right) plots within a 100-year-period. Each diagram represents the mean of 12 (cleared) and 24 (untouched) plots, respectively, based on 30 simulation runs per plot.

simulation, to gradually introduce the growing saplings), and (3) to analyze the influence of different environmental conditions (growing conditions, especially water availability) on the stand development. Thus, simulation models may help to analyze vegetation dynamics and understand the processes of vegetation development. Here the first two aspects are addressed.

At first the extrapolation of the stand situation of 1998 over the next 100 years based on the current environmental conditions is presented. Fig. 3 shows the simulated stand development in terms of the average biomass of all the untouched and cleared plots, respectively, when only trees larger than 1 meter (saplings ignored) in 1998 were considered. On the cleared sites, birch reaches its maximum biomass within the first 2 to 3 decades of the simulated period, and later its biomass decreases continuously. At the end of the 100-year simulation period birch is replaced by spruce as the dominant species. However, birch is still a remarkable element of the tree layer in 2050 (comprising about 1/3 of the total biomass) and in 2100 (about 15% of the biomass). In contrast, on untouched plots birch is outcompeted by spruce within 3 to 4 decades, and within less than 100 years it disappears completely.

The second simulation experiment included the seedlings and saplings less than 1 m high in 1998. It produces very similar results (Fig. 4). There was no effect on simulated stand composition and only a slight increase of total simulated biomass could be observed when seedlings and saplings were included in the simulation experiment.

DISCUSSION

Storm events are well-known components of forest ecosystems in many parts of the world. Recent large-scale destructions of forest stands were reported e.g. by KNIGHT (1994) from Wyoming (6,000 ha of destructed forest at "Teton Wilderness", blown down in 1987), by HAN JINXUAN et al. (1995) from the Chang-Bai-Mountains in NE China (27.8.1986; 9,600 ha; about 2-million m^3 of damaged wood) and by LÄSSIG & MOCALOV (2000) from Russia (July 1975; Perm-region, central Ural mountains; about 261,000 ha of forest, about 22 million m^3 of

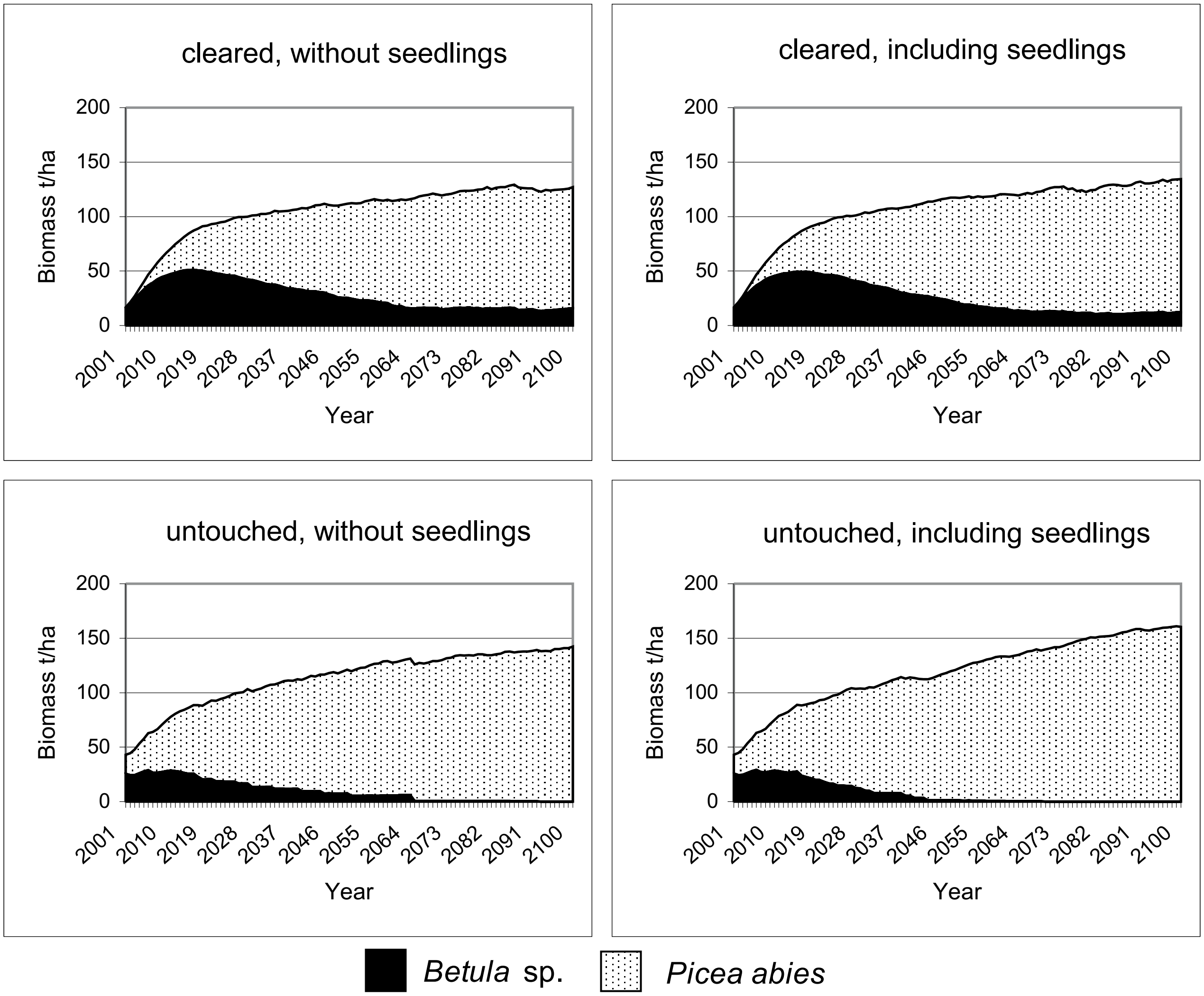

Fig. 4. 100-year simulation using only trees larger than 1 m in 1998 (left) and with additional tree regeneration smaller than 1 m (right), on cleared (above) and untouched plots (below); average of three plots each.

damaged wood). Long-term observations of the natural regeneration of such disturbed forest stands are rare, because (1) usually the destructed areas are cleared and replanted within a short time, and (2) the natural regeneration of the forests usually involves long periods.

The presented study on storm-effected forests in the Bavarian Forest National Park covers 1.5 decades after the disturbance event; this is a rather short time for studying forest dynamics, but a rather long period compared with other plot-based vegetation studies in forests (detailed records of the ground vegetation as well as tree layer) in Central Europe (e.g. DIERSCHKE 1988) and one of the very few in Central Europe dealing with unmanaged forests. It should be noted, however, that there are some restrictions concerning the interpretation of the results: (1) The plot system covers only a limited spectrum of site conditions and of forest types of Central Europe (*Calamagrostio villosae-Piceetum*, subtype *bazzanietosum*). (2) Because of its location in a remote border area in the mountain ridges separating Germany and the Czech Republic (in former times separating Bavaria and Bohemia) forest utilization at this site began rather late and only extensive timber extraction has been undertaken; that means that the forests in the national park generally are closer to natural conditions then in many other managed forests in Central Europe. (3) A long-term permanent plot study needs to repeat the field measurements in time intervals; therefore the number of plots has to be limited and the methods of recording simple to enable repeated observations. (4) The study has to use windfalls, which were created by storm (and not by scientists), therefore the comparability of the stands under observations may be limited (see the remarkable degree of floristic variance between the single plots). Therefore the results of such a field study cannot be generalized without some careful considerations. Nevertheless, the permanent plot study presented here offers valuable insights to understand better natural forest dynamics in forest ecosystems of Central Europe, information that is urgently needed especially in areas that have been affected by the most recent storms (see TEUFFEL 2000).

In the presented case study 15 years after the destructive storm event, different trends of stand development became obvious, although the studied windfall areas were next to each other under very similar site conditions (the same association and sub-association) and had a similar tree-stand structure before the storm event. In the following we try to identify the driving forces of vegetation development after the storm-induced stand disturbance.

Plots with a sequence of different plant communities (succession) are characterized by soil-surface disturbances caused by the removal of timber and subsequent clearing of the area: Buried seeds from the soil seed-bank become exposed to light and are stimulated to germinate; anemochorous species find open space for germination. Species present on the cleared plots, which are known to persist in the soil seed-bank for decades or centuries, are e.g., *Rubus* sp. div. and *Juncus* sp. div. (cf. survey of soil seed-bank studies in FISCHER 1987; general survey of longevity of seeds in soil in THOMPSON et al. 1997). ULANOVA (2000a) showed that in boreal forests of the central Russian Plain, species like *Rubus idaeus*, *Juncus effusus* and *Epilobium angustifolium* are only able to regenerate on disturbed soils, e.g. created by uprooting trees or clearing procedure, and only during a short period after the disturbance (1 to 3 years). These species are favoured by the soil disturbance. Soil disturbance therefore increases biodiversity (see also ULANOVA 2000b). The same is true for species invading by air like *Betula pendula* and *B. pubescens*, which need open space to establish seedlings and saplings. In boreal spruce forests of the central Russian Plain, natural soil disturbance by uprooting is limited to 7 to 12% of the area, and in the Carpathian Mountains to 11 to 15% of the area (ULANOVA 1991). During the clearing procedure this disturbance effect is extended to much larger areas.

During the clearing procedure a lot of the existing saplings of the terminal tree species (*Picea abies*) are destroyed. On untouched places the saplings of the terminal species survive, whereas a soil seed-bank activation as well as the creation of open space for establishment of new species takes place only on restricted sites: the pit-and-mound-systems around the root plates of fallen trees. The described vegetation dynamics after storm events are therefore quite different from observations in forests strongly affected by fire disturbances (PLOCHMANN 1956, GOLDAMMER & FURYAEV 1996, BASKIN 1999); ground fire not only destroys the recent field layer vegetation but also the humus layer, creating large-scale open habitats for invading species.

The simulation of forest-stand development, starting with the 1998 situation on cleared and untouched areas 15 years after disturbance shows that the structural differences characterizing the actual forest stands will persist for several decades. Within one century, however, the floristic similarity of the tree layers of cleared and untouched stands increases: birch is completely outcompeted by spruce on areas untouched after the storm and significantly reduced on cleared areas, while spruce is tending to dominate both forest stands within several decades. The results of the simulation study (FORSKA-M) confirm the observed trends in vegetation dynamics and are in good agreement with the conclusions from the vegetation analysis presented above. The model thus is a useful tool to quantify the mid- and long-term development of storm-effected forest ecosystems. According to the model, the dissimilarity between the differently treated study areas (cleared and untouched) will disappear to a great extent in less than one tree generation.

We also used the simulation model to analyse the importance of seedlings and saplings, which 15 years after the storm event were smaller than 1 m, for the future tree-layer development. The results suggest that the growth advantage of the larger trees on the plot was big enough for them to dominate the stand structure over the next century. Consequently the the additional established saplings were only affecting stand density and the standing volume of the stands. This also indicates that the stem numbers in the tree layer in 1998 were sufficient to build almost fully stocked stands. The density of trees larger than 1 m on the six selected plots for this experiment ranged from 600 to 16,900 stems per ha. Further analysis is needed to investigate critical stem densities on the disturbed plots. It is conceivable that a model initialization with the much lower tree numbers of the inventories from 1993 or 1988 would lead to quite different results.

On the investigated plots, forest-stand development was exclusively regulated by spruce and/or birch, only two more tree species grew on some of the plots: *Populus tremula* and *Sorbus aucuparia*, the first covering a similar ecological niche as *Betula* (short-living tree, high seed productivity, anemochorous species, open space for germination needed), the second covering an ecological position between pioneer and terminal species. Both of them occur very sparsely and produce so little biomass, that they do not occur in the diagram of Fig. 3 although they were also included in the simulation run.

The results presented and discussed here stem from only two windfall areas in the Bavarian Forest National Park and thus could be considered of mere local relevance. Nevertheless, there are many indications that the results not only reflect local conditions, but that they also reveal general pathways of vegetation dynamics after storm events. The same vegetation differentiation was documented in Russian boreal forests (ULANOVA 2000b). In close-to-nature Minnesota *Quercus ellipsoidalis* forests, windfall disturbance did not result in major changes in species composition; *Rubus idaeus* increased after windthrow from individuals already growing there before the event (PALMER et al. 2000; it is one of the very few studies including not only tree-layer species but the total floristic composition). Soil disturbances resulting from mound/pit creations lead to exposure of buried seeds of shade-intolerant species in forests of Panama (PUTZ 1983). The low importance of pioneer trees was also reported from the very few and small pristine forests in southeastern Europe (Lower Austria, Western Carpathians, Croatia; ZUKRIGL et al. 1963, KORPEĽ 1995, MAYER et al. 1980).

The first pathway described above is characteristic for forests of Central Europe, which were managed with clear-cuts over several rotations (see SCHÖNENBERGER et al. 1995); the second is characteristic of forest stands without any direct impact of man, the so-called “pristine forests”. Such pristine forests disappeared nearly completely in Central Europe already centuries ago. Today, in two types of conservation areas in Germany, forest vegetation is on its way back to an unmanaged situation: (1) in national parks like the Bavarian Forest National Park, which is nearly completely covered with forests, and (2) in natural forest reserves. The purposes of these protected areas are the same: (a) the protection of forest vegetation by exclusion of any direct human impact, (b) scientific analysis of forest ecosystems, and (c) public education. These types of protected areas differ mainly in size: national parks are few in number (13 in Germany), but cover large areas, and forest nature reserves are numerous (about 650 in Germany), but much smaller in area. In both cases the scientific analysis of forest development should provide knowledge on how to optimize forest management practices towards a close-to-nature type of forestry.

One of the main results of the presented study from the Bavarian Forest National Park is that the creation of new ecological niches by soil-surface disturbance is of general importance for vegetation development and biodiversity after storm events. Under conditions without any direct influence of man, the size of such disturbances is rather small (they are restricted to the pit-and-mound-systems around the root plates of fallen trees), while in managed forests this disturbance-phase will be largely extended both in space and in time. However, at least under semi-natural conditions the differences in stand composition and biomass may become blurred during one century of forest stand development.

CONCLUSIONS

Some general conclusions concerning forest management as well as nature conservation can be drawn:

(1) Reducing the soil-surface disturbances during the harvesting procedure is a key to improving forest management, and this is increasingly considered by semi-natural forest management in Germany (see Burschel & Huss 1987).

(2) The physiognomic structure of forests growing on areas untouched after storm events vary widely during the first decades after the event. Such untouched spots within areas of intensive forestry increase the structural diversity of the area.

(3) Stand destruction by storms accelerates the development from managed forests with rather homogeneous stand structures to a mosaic-like structure that is characteristic for natural forests. Thus, from an ecological perspective forest dynamics initiated by storm events can also be seen as a chance rather than a disaster. This is especially true in national parks, which are still in the process of developing back from systems with long land-use influences to unmanaged ecosystems.

(4) Simulation models, especially individual-based models, may be used as tools for evaluating the long-term consequences of new forest management practices.

Observation and analysis of long-term vegetation development is needed to understand the processes driving vegetation dynamics (Prach et al. 2001). Especially in forests this demand is hard to realize because of the long life span of trees. Nevertheless, studying forest dynamics over medium- and long-term periods remains an important task for forest ecology.

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