Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieża Primeval Forest, Poland

Dries P.J. Kuijper, Bogumiła Jędrzejewska, Bogdan Brzeziecki, Marcin Churski, Włodzimierz Jędrzejewski & Henryk Żybura

Abstract

Question: What are the main driving factors in 70 years of natural dynamics in tree recruitment in the Białowieża National Park?

Location: Białowieża National Park, Poland, is one of the least disturbed temperate, lowland forest systems in Europe.

Methods: We tested whether fluctuations in large herbivore populations, changes in climate and openness of the forest explained compositional dynamics. Tree recruitment (to size class DBH ≥ 5 cm) was measured on permanent transects (in total, 14.9 ha) six times between 1936-2002. These data were related to existing data on ungulate density, climatic parameters and estimates of forest openness collected during the same period.

Results: Total recruitment of all tree species combined was negatively correlated with total ungulate density and red deer density. The variation in response between species was related to the preferences of herbivores; the more preferred forage species (especially *Carpinus betulus*) were positively and the less preferred species negatively related to herbivore density. Total tree recruitment rates were not related to climatic parameters and openness of the forest. Only *Alnus glutinosa* recruitment was significantly related to climatic parameters, and *Ulmus glabra* related to forest openness, but there were no predictable patterns in recruitment among species in relation to these factors.

Conclusion: The present study indicated that changes in large herbivore density have played an

important role in driving patterns in tree recruitment and species composition during the last 70 years in Białowieża National Park. In contrast to other studies, increasing herbivore numbers were associated with higher recruitment of preferred and browsing-tolerant species. Periodical crashes in ungulate numbers, whether human-induced or caused by natural factors, may offer windows of opportunity for regeneration of a range of tree species and facilitate more diverse and dynamic forest development.

Keywords: Browsing impact; European bison; Red deer; Roe deer; Temperate deciduous forest; Top-down effects; mouse.

Introduction

Recruitment of trees in mature forest typically depends on the formation of gaps in the tree canopy (e.g. Runkle 1981; Faliński 1986; Bobiec 2007). Most tree species profit from the enhanced light availability and show higher growth and recruitment inside canopy gaps. As trees differ in their tolerance to low light conditions, the formation of gaps or increase in openness of a forest is predicted to result in a shift in the recruitment process towards the more light-demanding species (Brzeziecki & Kienast 1994; Bobiec 2007).

Next to light conditions, foraging by large herbivores can also be an important factor regulating both total recruitment rate and species composition of recruited trees in temperate forests (Ammer 1996; Van Hees et al. 1996; Kriebitzsch et al. 2000; Scott et al. 2000). In the long term, browsing may prevent successful regeneration of some species into the tree canopy and alter the structure and dynamics of forest ecosystems (Mladenoff & Stearns 1993; Long et al. 2007). The effects of browsing are expected to strongly depend on the tree species, due to selectivity of the ungulate species. Several studies from temperate forest systems showed that ungulate browsing reduced the proportion of highly palatable species during the recruitment process (Horsley et al. 2003; Modry et al. 2004; Long et al. 2007). However, also

Kuijper, D.P.J. (corresponding author, dkuijper@zbs.bialowieza.pl), Jędrzejewska, B. (bjedrzej@zbs.bialowieza.pl), Churski, M. (mchurski@zbs.bialowieza.pl) & Jędrzejewski, W. (wjedrzej@zbs.bialowieza.pl): Mammal Research Institute, Polish Academy of Sciences, ul. Waszkiewicza 1c, 17-230 Białowieża, Poland. Brzeziecki, B. (bogdan_brzeziecki@sggw.pl) & Żybura, H. (khl@sggw.pl): Warsaw University of Life Sciences, Forestry Faculty, Department of Silviculture, ul. Nowoursynowska 159, 02-776 Warszawa, Poland.
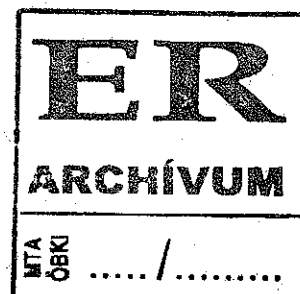
the reverse has been reported, in which preferred forage species increased in relative abundance (Tilghman 1989; Van Hees et al. 1996). A possible mechanism for such an increase in abundance of preferred species in the presence of herbivores is that preferred species are also those most tolerant to browsing. How herbivory affects tree species composition typically depends on the balance between selectivity of the herbivores and tolerance to browsing (Augustine & McNaughton 1998).

Whereas light conditions and herbivore pressure are expected to influence tree recruitment on a relatively short time scale, climatic changes are a major factor affecting abundance and distribution of tree species over longer time scales. Obviously, climate has played a dominant role on a geological time scale in determining tree species abundances (see for example Mitchell & Cole 1998). However, the more recent rapid changes in climate have also been suggested to affect tree recruitment of certain species and result in range expansion or contraction, for example, affecting altitudinal distribution in mountainous habitats (Höfgaard et al. 2009; Lenoir et al. 2009; Landhausser et al. 2010; Mátyás 2010). Species that are at the borders of their ecological or geographical range are predicted to be the first affected.

Studying the relative influence of the above-mentioned factors on tree regeneration processes is difficult in Europe because temperate forest systems where natural tree stand dynamics can be observed are rare. In particular, in European temperate forests, forestry practices strongly influence species composition and stand dynamics. The Białowieża Primeval Forest (Poland and Belarus) is an exception to this. The entire forest belongs to the most extended and natural temperate forest complexes still found in the Central European lowlands. Since 1921, the least disturbed and most valuable central parts of this forest were declared a national park, in which all human intervention, such as hunting and wood exploitation, was prohibited. Surprisingly, the tree stand composition since then has shown large changes, as described in detail by Bernadzki et al. (1998). The main change has been a shift from dominance of coniferous species (*Picea abies* and *Pinus sylvestris*) towards deciduous species. Several hypotheses have been proposed as possible explanations for this shift. Changes in climate and fluctuations in herbivore numbers occurring throughout this period have been proposed as likely factors explaining these patterns (Bernadzki et al. 1998). However, Bernadzki et al. (1998) did not test whether these factors are related

to the observed changes in tree species composition. Since tree regeneration depends largely on the formation of gaps, structural changes in forest openness may also have played a role in explaining these patterns.

In the present study, we analysed the roles of changes in climate, herbivore number and forest openness in explaining the observed shifts in tree species composition. In contrast to the study of Bernadzki et al. (1998), who described changes in species composition of the tree stand, we used patterns of recruitment of tree species as these are more likely to respond directly to fluctuations of driving factors. The three proposed potential driving factors are predicted to result in different patterns in the recruitment of different tree species, which led us to test three hypotheses. When *herbivory is the main driving factor*, changes in the recruitment rate of tree species towards taller size classes should be related to (sudden) changes in herbivore density, mainly because browsing is most intense on small and young trees (Renaud et al. 2003); recruitment of trees should be inversely related to herbivore density. The preferred species are predicted to experience a large impact, whereas a lower impact is expected on less preferred species (Horsley et al. 2003; Modry et al. 2004; Long et al. 2007). However, the opposite pattern may occur depending on tolerance to browsing of the preferred species (Augustine & McNaughton 1998). When *climate change is the main driving factor*, long-term changes in mean annual temperature or temperature amplitude, January or July temperature, should be correlated with a shift in the ratio of recruitment of typical boreal to Atlantic tree species. The Białowieża Primeval Forest is located in the transition zone between the boreal and temperate zones (Faliński 1986); hence a trend to increases in annual temperatures will provide more favourable growing conditions for temperate broadleaf deciduous species relative to typical boreal species (i.e. *Picea abies* and *Pinus sylvestris*). Likewise, long-term changes in precipitation may lead to a shift in the ratio between tree species associated with dry soils compared to those of wetter soils. Lastly, when *changes in the forest openness are the driving factor*, tree recruitment rate should be related to tree density or basal area, indicating available regeneration space. Light-demanding early successional species (such as *Betula* spp., *Populus tremula*) are predicted to show the quickest response to increased openness relative to species that can tolerate low light levels (such as *Acer platanoides* and *Tilia cordata*; Faliński 1986).

Methods

Description of study site

The Białowieża National Park (BNP) is situated in eastern Poland (52°45'N, 23°50'E). Initially, the park covered 47.5 km² and in 1996 its was enlarged to 105 km². The BNP is situated in the centre of the Białowieża Primeval Forest (BPF), which covers 1450 km², of which 600 km² belongs to Poland and the remaining 850 km² to Belarus.

The mean altitude is 165 m a.s.l. and the total altitudinal range is 68 m. During the study period (1936-2002) the mean annual air temperature was 7.0°C, with the coldest month in January (average −4.6°C) and the warmest month in July (average 18.2°C). Mean annual precipitation is 631 mm (1948-1999) and snow cover lasts for an average of 92 days. Within the BNP different forest types can be distinguished (with dominant trees in brackets): coniferous forest (*Pinus sylvestris, Picea abies*), mixed coniferous forest (*Pinus sylvestris, Picea abies* and *Quercus robur*), mixed deciduous forest (*Picea abies, Quercus robur, Tilia cordata* and *Carpinus betulus*), deciduous forest (*Quercus robur, Tilia cordata, Carpinus betulus* and *Acer platanoides*), black alder bog forest (*Alnus glutinosa, Betula pubescens*), streamside alder–ash forest (*Alnus glutinosa* and *Fraxinus excelsior*). These forest types, based on phytosociological units, are arranged along an ecological gradient of soil fertility and water availability. Coniferous forest can be found on the most well-drained, nutrient-poor soils. Deciduous forest and flood-plain forest both occur on productive soils rich in organic matter but differing in water supply. During some periods of the year, flood-plain forests are inundated. Mixed coniferous and mixed deciduous forests occupy transitional parts of the soil fertility gradient. For a detailed description of the phytosociological units, see Faliński (1986).

Measuring recruitment of trees

In 1936, five permanent transects were established in the BNP by Professor T. Włoczewski, Forestry Faculty of Warsaw University of Life Sciences. These transects consisted of areas of varying width (40-60 m) and length (200-1380 m), running across the main topographical zones and representing the variability in soil fertility and water availability and diversity of forest stands. The total sampled area amounts to 14.9 ha. The locations of transects were selected in such a way as to cover the range of abiotic conditions and main forest types encountered in the BNP. The five transects are spread out over the BNP and the distance between them ranged from 0.5 km to 4.0 km. These transects were monitored in 1936, 1955-1959, 1968-1972, 1981-1983, 1991-1993 and in 2002. During each monitoring period, each tree with a DBH (diameter at breast height) of at least 5 cm was identified and its spatial location mapped. DBH was measured to the nearest mm with calipers in two directions (N-S and E-W). The places of measurement were marked on the bark of the tree and subsequently renewed at consecutive recordings. The mapping of individual trees, in combination with the marking, allowed determination of recruited trees (all unmarked trees with DBH $\geq$ 5 cm) in the time between two monitoring periods. Tree recruitment in this study is thus defined as the number of trees entering the size class DBH $\geq$ 5 cm within a given time interval. In the present study, the total number of recruited trees, summed for all transects, was determined for each monitoring period. As the interval between the monitoring periods differed, the recruitment rate was calculated as the number of recruits per year per hectare for the time before each monitoring period.

The number of recruiting trees in the period 1916-1936 was indirectly assessed, based on experience from later measurement periods and on growth rates observed in this area (Koop 1989). It was assumed that the recruits in that period were trees that at the moment of the first measurement (1936) were in size class DBH 5-15 cm. To prevent over-estimation of recruitment rate, a period of 20 years was used to calculate recruitment rates. The choice for a 20-year lag period was based on the relationships by Koop (1989) between diameter and age of dominant trees inside the BNP. These relations showed that species reach a DBH 5 cm in 5-10 years (*Populus tremula*), 15-20 years (*Quercus robur, Picea abies, Tilia cordata*) or 20-25 years (*Carpinus betulus*). Hence, a 20-year period would allow most species to reach size class DBH 5-15 cm.

As a proxy for forest openness we used basal area, defined here as the area of a given section of land that is occupied by the cross-section of tree trunks and stems at breast height. There was no significant change in basal area during the study period ($r^2 = 0.022$, $F_{1,4} = 0.068$, $P = 0.811$), with values between 35.6 and 38.6 m² ha⁻¹ (Bernadzki et al. 1998). Also, tree density did not increase or decrease with time ($r^2 = 0.22$, $F_{1,5} = 1.156$, $P = 0.343$), with values between 664 and 830 trees ha⁻¹ (Bernadzki et al. 1998). Both factors combined indicate that no trend in forest openness occurred during the study period.

However, we excluded tree density as an independent measure of forest openness as it is directly affected by tree recruitment, which was used as a dependent variable in subsequent analyses (see *Statistical analyses and hypotheses testing*).

Long-term changes in ungulate populations

Population dynamics of all browsing ungulates (European bison *Bison bonasus*; moose *Alces alces*; red deer *Cervus elaphus*; roe deer *Capreolus capreolus*; non-native fallow deer *Dama dama*) were analysed in the BPF in the period 1798-1993 by Jędrzejewska et al. (1997). In the present study, we updated this information with more recent annual assessments of ungulate density from the period 1994-2002 (Jędrzejewski et al. 2002 and unpublished data). Annual densities of all species of ungulates show large fluctuations related to periods of intense hunting of ungulates or their main predators, the wolf (*Canis lupus*) and lynx (*Lynx lynx*) (Jędrzejewska et al. 1996, 1997; Jędrzejewski et al. 1996). Most ungulates reached maximum density in 1914 as a result of management practices, including severe predator control and supplementary winter-feeding of ungulates. This period was followed by a sharp decrease in numbers due to intensive culling during the First World War (Jędrzejewska et al. 1997). All ungulates were greatly reduced, and the European bison, fallow deer and moose were eradicated (Jędrzejewska et al. 1997), but only fallow deer never returned. Since 1936, most species of ungulates have shown a gradual increase in number related to better protection and regulation of hunting in the BPF. In 1936-2002, red deer was a dominant species in the ungulate community, especially in the old growth forests of BNP (Jędrzejewska et al. 1997; Jędrzejewska & Jędrzejewski 2005).

Selection of tree species by browsing ungulates

To determine the selection of tree species as forage by ungulates, data from two previous studies carried out in the BNP were used (Table S1). Both studies (Miścicki 1996; Zielski 1998) determined the proportion of trees, in height class 0.3-1.3 m, from which the last-year leader shoot had been browsed, based on a large number of sampled trees ($N > 7000$) throughout the BNP. Sampled trees were located on either 460 evenly spaced plots of 20 m² (Miścicki 1996) or on one of the permanent transects used in the present study (1360 m×40 m, Zielski 1998), where all present trees were recorded. These measurements were collected in spring and summer and included both recent and older browsing marks. Hence, both summer and winter browsing is included in these figures. As it is difficult to distinguish between browsing marks of different ungulates, these numbers show browsing for all ungulates combined. We calculated the proportion of each occurring tree species in the sample and the proportion of each species in the total number of trees including only trees with browsing marks. Based on these figures, we calculated the Jacob's selectivity index (Jacobs 1974) as $D = (r - p)/r + p - 2rp)$, where r is the proportion of each tree in the sample of browsed trees and p is the proportion of each species in the entire sample. This index varies between -1 least selected to 1 most selected species, as a result of browsing by all ungulate species combined. We calculated this index separately for each tree species within each study and then calculated the mean per tree species based on these two figures. In general, the ranking of species was very similar in both studies, with *Picea* and *Alnus* the least selected, and *Ulmus* and *Carpinus* the most selected species.

Meteorological data and tree species response to climate

Records on temperature were obtained from the meteorological station in Białowieża. This station has operated since 1948. Data from the beginning of the 20th century were obtained from Jędrzejewska et al. (1997). Data were available for January, July and annual temperatures, which are average temperatures of those months and of the year, temperature amplitude (difference between January and July temperature) for the period 1930-1998 and annual precipitation for 1948-2000. These numbers give an indication of the severity of the winter (January is the coldest month), temperature at the peak of the growing season (July) and annual rainfall; all being parameters that potentially influence growth conditions for trees. The temperature amplitude is typically larger in more continental climates compared to an oceanic climate.

Statistical analyses and hypotheses testing

To test our hypotheses of whether herbivory, climate or canopy openness was the main driver in determining tree recruitment we used two approaches. First, we correlated recruitment rates of each individual tree species and the summed recruitment of all trees with herbivore density, climatic parameters or basal area. Second, we tested if recruitment rates were related to herbivore den-

sity, climatic factors and basal area using ranks of tree species and taking all tree species into account.

For the first approach, we used the average density of moose, red deer, roe deer and the summed density of all these species combined in the coinciding periods that tree recruitment was measured. Tree recruitment was not correlated with bison density separately, as bison used the forest compartments of the BPF close to the reintroduction areas and started to use the Białowieża National Park only from 1989 onwards (Krasińska & Krasiński 1997). The effects of climate were tested by correlating tree recruitment with average temperature in January and July, annual temperature and annual temperature amplitude (difference between average January and July temperature) of the coinciding period in which tree recruitment was measured. Lastly, to test for the effects of forest openness, we used basal area measured on transects during each monitoring period. Pearson's correlation coefficients were used as the data were normally distributed. As we carried out multiple significance tests (for each tree species separately), we additionally performed a binomial probability test for each of the studied variables. We tested whether the occurrence of significant relationships between tree species and the variable is larger than expected by chance (0.05% chance of incorrectly finding a significant relation).

As it takes time for trees to reach DBH 5 cm, the observed recruitment rate can be the result of (un)-favourable growing conditions in preceding periods. To investigate this, in the afore-mentioned correlations we also included a lag period in the response of tree recruitment. Recruitment of trees during one period was correlated with ungulate densities, climatic parameters or basal area during the preceding 10-year period, and the 10-year period before the preceding period. This allowed 10- to 20-year lag periods in the response of tree recruitment to these factors. The choice of a 10-20-year lag period was again based on relationships between DBH and age of the dominant species inside the BNP established by Koop (1989), which showed that most species reach a DBH of 5 cm within 10-20 years. In combination with the fact that the interval between measurements on the transects monitored in the present study was 9-20 years, we believe that including a time lag of 10-20 years in our analyses provided sufficient time for most species to be able to reach the size class DBH 5 cm.

For the second approach we related the Pearson's correlation coefficients (PC) to rank numbers of tree species. To test for the role of herbivory, we used the PC of each species with total ungulate den-

sity and related this to their Jacob's selectivity index. To relate the response of tree species to climate we used a ranking of species with a temperature index and a soil moisture index based on Brzeziecki & Kienast (1994). The temperature index indicates whether the distribution of tree species is associated with cooler or warmer climates and ranges from 1 (coldest, more boreal climate) to 4 (warmest, more oceanic climate). The soil moisture index ranges between 1 and 5 and indicates whether the location of tree species is associated with dry (1) or wet soils (5). To relate the response of species to forest openness, we used species ranks on the basis of their shade tolerance, ranging between 1 (shade intolerant) and 5 (shade tolerant). For further details see Brzeziecki & Kienast (1994), for clarity we reversed the shade-tolerance ranking used by Brzeziecki & Kienast (1994) from low to high tolerance. For all ordinal independent variables (all indices except for Jacob's selectivity index) we used Spearman's rank correlations to test for significance of the relations.

When herbivory is the main driving factor, tree species that are highly preferred by herbivores are expected to show low recruitment rates in periods of high herbivore density, whereas tree species that are least preferred would show the opposite pattern (Fig. 1). As a result, a negative relation between the correlation coefficients of each species with herbivore density and their preference ranking (preferred species with highest rank) is predicted. However, the opposite pattern may evolve when trees that are preferred by herbivores are also the most tolerant to browsing and react through rapid regrowth. When climate is the main driving factor, recruitment rates of thermophilous species would be most positively correlated with annual temperature, in contrast to species adapted to colder climates, or species associated with wet soils would be most positively correlated to precipitation (Fig. 1). Finally, when forest openness is important, recruitment rates of shade-tolerant species will be most positively correlated with basal area. As herbivory directly influences growth rates and climatic parameters and openness indirectly, the time frame at which effects are expected may differ. Fluctuations in herbivore density are predicted to lead to more rapid responses in recruitment rates than changes in climatic parameters (Fig. 1).

Results

Patterns of tree recruitment rate

All tree species could be divided in four distinct groups based on high positive inter-specific
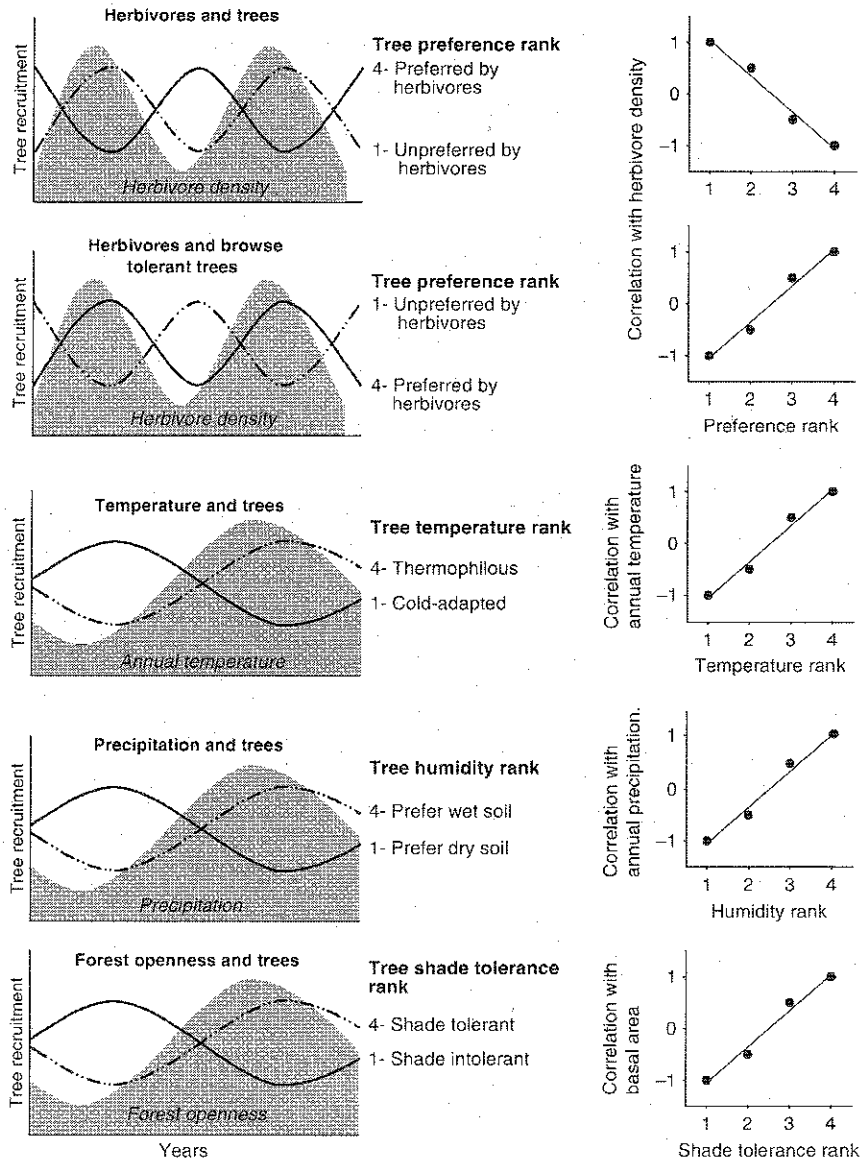
Fig. 1. Predicted patterns of tree recruitment when large herbivores, climatic parameters or forest openness are the main driving factors. Graphs in the left panel illustrate how tree recruitment (lines) coincides with fluctuations in driving factors (grey areas) over time. The recruitment of trees in response to these fluctuations is predicted to depend on their ranking of preference as food for herbivores (when herbivory is the main factor), temperature or humidity ranking (when climate is main factor) or shade-tolerance ranking (when forest openness is the main factor). For simplicity, the patterns of tree recruitment of only the two most extreme ranking species are shown. Scales are indicative of the different time frames in which effects are expected. As a result, graphs in the right panel show that the strength of the relationships between tree recruitment and each driving factor depends on tree rankings for different tree species.

correlations (Table 1). One group consisted of *Picea*, *Quercus* and *Acer* with highest recruitment only in the earliest period (1916-1936), after which they declined (Fig. 2). The second group consisted of *Betula*, *Populus* and *Salix* and showed high recruitment rates in the first two monitoring periods (1916-

1936 and 1937-1957), after which their recruitment rates declined sharply. Trees in the third group had low recruitment rate in the earliest period followed by a peak in recruitment in 1937-1957 (*Fraxinus, Tilia*) or in 1958-1970 (*Ulmus*), after which recruitment rate declined. The last group consisted of two

Table 1. Pearson's correlation coefficients (r) between tree recruitment rates (number of recruits ha^{-1} year^{-1}) of different tree species. Significant relationships are in bold with asterisks indicating significance level: *$P<0.05$, **$P<0.01$, ***$P<0.001$, #marginally significant at $P = 0.055$ ($n = 6$ periods). Three groups can be distinguished based on positive inter-specific correlations; 1, *Betula, Populus, Salix*, 2, *Pinus, Quercus, Picea, Acer*, 3, *Tilia, Ulmus, Fraxinus*. The fourth group consists of species that were not positively correlated with any of the other species (*Carpinus, Alnus*). See text for further details.

Species	Populus	Salix	Pinus	Quercus	Picea	Acer	Tilia	Ulmus	Fraxinus	Carpinus	Alnus
Betula	0.99***	0.89*	0.60	0.65	0.75	0.53	0.33	-0.07	0.46	-0.90*	0.05
Populus	1	0.91*	0.57	0.63	0.73	0.51	0.38	-0.01	0.51	-0.91*	0.01
Salix		1	0.18	0.25	0.38	0.11	0.71	0.23	0.76	-0.76	-0.21
Pinus			1	0.98***	0.98***	0.99***	-0.52	-0.50	-0.29	-0.65	0.45
Quercus				1	0.99***	0.98***	-0.41	-0.33	-0.14	-0.75	0.33
Picea					1	0.96**	-0.32	-0.37	-0.08	-0.80#	0.34
Acer						1	-0.55	-0.42	-0.29	-0.63	0.45
Tilia							1	0.71	0.94**	-0.28	-0.60
Ulmus								1	0.80#	-0.17	-0.71
Fraxinus									1	-0.52	-0.65
Carpinus										1	0.17
Alnus											1

species with a different pattern to all other species: *Alnus glutinosa* had both a high recruitment rate at the beginning (1916-1936) and at the end of the study period (1993-2002) and *Carpinus betulus* showed increasing recruitment rates during the study period (Fig. 2). When all species of recruited trees were summed, the highest total recruitment rate occurred during 1916-1936.

Tree recruitment rates in relation to ungulate density, climate and forest openness

Periods with highest recruitment rates for most tree species and total tree number coincided with, or occurred directly following, the period with lowest average total ungulate density (Fig. 2).

The summed recruitment rate of all tree species combined was negatively correlated to total ungulate density ($r = -0.89$, $n = 6$, $P = 0.017$) and red deer density ($r = -0.91$ $n = 6$, $P = 0.012$) occurring in that period. Recruitment of three tree species was significantly correlated to red deer density, which was higher than expected by chance (binomial probability test, $P = 0.015$). Recruitment rates were significantly negatively correlated with red deer density for *Betula* spp. ($r = -0.87$, $n = 6$, $P = 0.024$) and *Populus tremula* ($r = -0.87$, $n = 6$, $P = 0.026$, Table 2). An exception to this general picture was *Carpinus betulus*, which was the only species that showed a positive correlation between recruitment rate and red deer density ($r = 0.82$, $n = 6$, $P = 0.046$), and a marginally significant correlation with total ungulate density ($r = 0.82$, $n = 6$, $P = 0.055$). When taking a lag period into account, a weaker response of tree recruitment to ungulate density was observed

(Table 2). Only *Carpinus betulus* ($r = 0.83$, $n = 6$, $P = 0.041$) and *Fraxinus excelsior* ($r = -0.87$, $n = 6$, $P = 0.023$) showed, respectively, positive and negative relationships to total ungulate density in the preceding period. Summed recruitment rate was not correlated to ungulate density (neither to each ungulate species nor to their summed density) in the preceding period nor to ungulate density before that period (Table 2).

Recruitment rate of only one species, *Alnus glutinosa*, was significantly correlated with average January temperature ($r = 0.84$, $n = 6$, $P = 0.04$) and annual temperature amplitude ($r = -0.903$, $n = 6$, $P = 0.014$) in the coinciding period. None of the other tree species or summed recruitments showed a significant relation with any of the climatic parameters (Table 3). Finding one significant relation is not higher than that expected by chance (binomial probability test, $P = 0.431$), hence these relations should be treated with care. Also, no significant relations where found between recruitment rates of individual species or all species combined with either average January, July, annual temperature or annual temperature amplitudes when taking a 10- or 20-year lag period into account (Table 3).

Recruitment rates of all species combined were not correlated to basal area ($r = 0.43$, $n = 6$, $P = 0.391$, Table 4). One species, *Fraxinus excelsior*, showed a significant correlation with basal area, but in the opposite direction to what could be expected: an increase in recruitment with increasing basal area ($r = 0.906$, $n = 6$, $P = 0.013$). Again, the finding of one significant relation is not different from what would be expected based on chance alone (binomial probability test, $P = 0.431$).
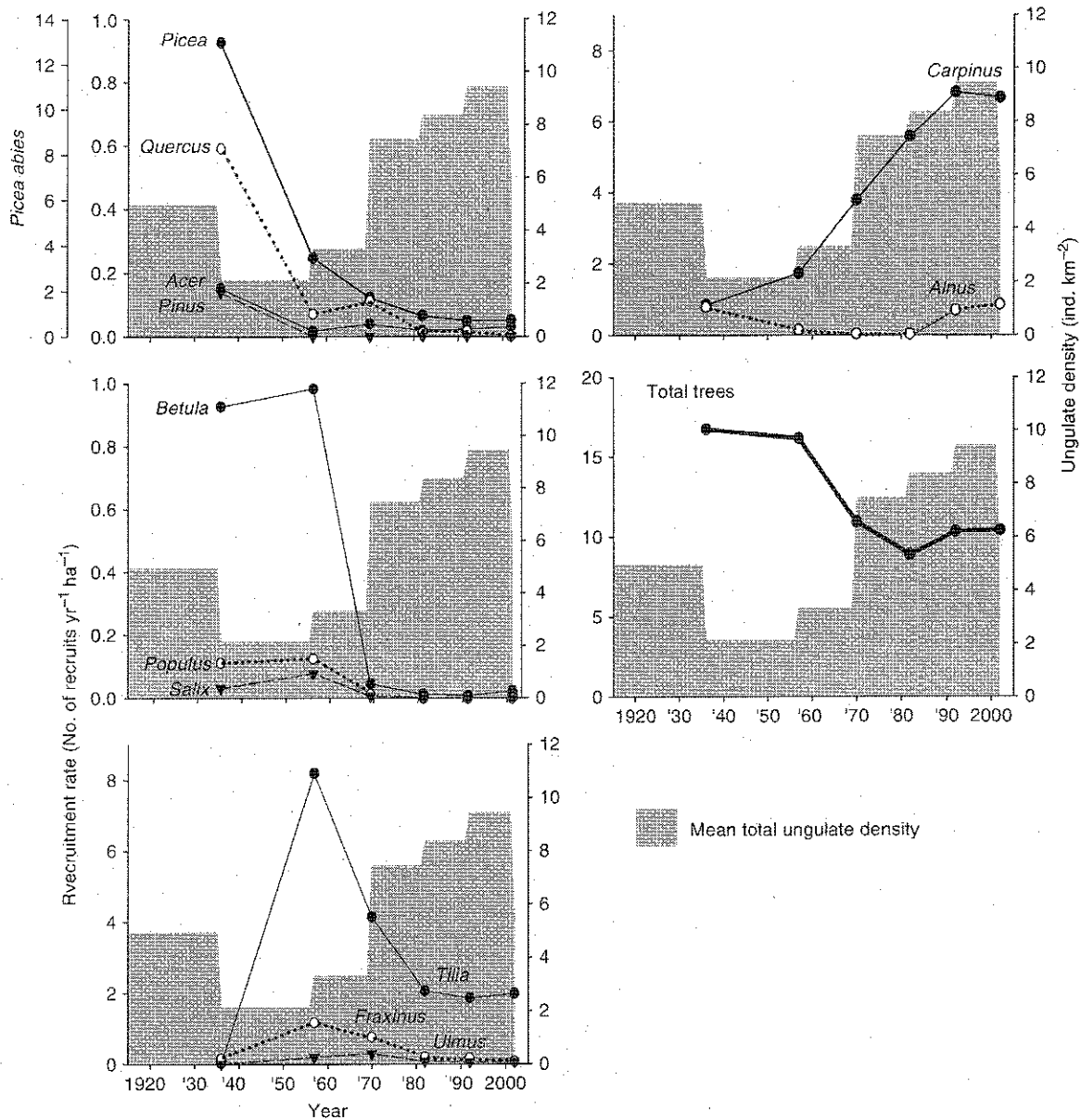
Fig. 2. Tree recruitment rates for all occurring tree species and mean density of all wild browsing ungulates (red deer, roe deer, bison, moose). Patterns are shown separately for the four groups of tree species that can be distinguished based on positive inter-specific correlations (Table 1): species showing high recruitment only during the first measuring period (*Picea abies, Quercus robur, Acer platanoides, Pinus sylvestris*), high recruitment during first and second period (*Betula* spp., *Populus tremula, Salix caprea*), high recruitment only during second measuring period (*Tilia cordata, Fraxinus excelsior, Ulmus glabra*), and the remaining group with a different pattern (*Carpinus betulus, Alnus glutinosa*). The total recruitment of all trees combined is also shown.

Tree recruitment rates in relation to ranking of species

Recruitment rates of tree species that were selected by large herbivores were most positively related to total ungulate density, whereas the oppo-

site was true for less preferred species ($r = 0.64$, $n = 11$, $P = 0.034$, Fig. 3a). No relation was found between the temperature index of tree species and the correlation these species showed with average annual temperature ($r_S = 0.344$, $n = 12$, $P = 0.274$, Fig. 3b), July temperature ($r_S = 0.344$, $n = 12$,

Table 2. Pearson's correlation coefficients (r) between tree recruitment rate (number of recruits ha^{-1}yr^{-1}) and mean density of ungulate species and summed total ungulate density per 10-year interval in Białowieża Primeval Forest (from Table 1). Total recruitment is the summed recruitment for all tree species. The relation between total tree recruitment and ungulate density with a one and two period lag in response are also included. Asterisks indicate significance level: *$P<0.05$, #marginally significant at $P = 0.055$ ($n = 6$ and $n = 5$ with 20-year lag period). Tree species are listed from most to least preferred by large herbivores based on Jacob's selectivity index (see Table S1).

Tree species	Jacob's selectivity index	Red deer	Roe deer	Moose	All wild ungulates
Carpinus betulus	0.18	0.82*	0.59	0.76	0.80#
Ulmus glabra	0.08	0.05	0.42	− 0.41	0.13
Tilia cordata	0	− 0.19	0.10	− 0.35	− 0.15
Fraxinus excelsior	− 0.01	− 0.32	0	− 0.52	0.26
Betula pubescens & B. pendula	− 0.02	− 0.87*	− 0.75	− 0.62	− 0.88*
Populus tremula	− 0.08	− 0.87*	− 0.72	− 0.64	− 0.87*
Acer platanoides	− 0.31	− 0.63	− 0.55	− 0.44	− 0.63
Quercus robur	− 0.32	− 0.68	− 0.56	− 0.49	− 0.68
Pinus sylvestris	− 0.34	− 0.64	− 0.61	− 0.38	− 0.65
Alnus glutinosa	− 0.40	− 0.27	− 0.36	0.09	− 0.26
Picea abies	− 0.52	− 0.76	− 0.67	− 0.51	− 0.76
Salix caprea	–	− 0.71	− 0.56	− 0.57	− 0.71
Total recruitment		− 0.91*	− 0.71	− 0.68	− 0.89*
Total recruitment (10-year lag)		− 0.70	− 0.70	0.46	− 0.66
Total recruitment (20-year lag)		− 0.19	0.03	0.92*	− 0.02

Table 3. Pearson's correlation coefficients (r) between tree recruitment rates and January, July and annual temperature, annual temperature amplitude and annual precipitation in Białowieża Primeval Forest. Total recruitment is the summed recruitment for all tree species. The relation between total tree recruitment and climate with a 10- and 20-year lag in response are included. Asterisks indicate significance level: *$P<0.05$, #marginally significant at $P = 0.055$ ($n = 6$ for temperature data and $n = 5$ for precipitation). Correlation with precipitation could not be carried out for *Pinus* as no regeneration occurred in the period for which precipitation data were available. Sample size is smaller with a 10- and 20-year lag period in precipitation (respectively $n = 4$ and $n = 3$) and correlation was not performed in the last case. Tree species are ranked according to their temperature index, from species associated with colder (1) to warmer (4) climates. The soil moisture index indicates whether the species is associated with dry (1) or wet (5) soils. Both indices are based on Brzeziecki and Kienast (1994), see text for further detail.

Tree species	Temp. index	Mean temperature			Temp. amplitude	Soil moisture index	Precipitation
		January	July	Annual			
Picea abies	1	− 0.16	− 0.28	− 0.40	0.05	4	− 0.14
Pinus sylvestris	1	− 0.02	− 0.15	− 0.24	− 0.10	1	–
Betula pubescens & B. pendula	3	− 0.36	− 0.38	− 0.53	0.33	1	− 0.15
Fraxinus excelsior	3	− 0.73	− 0.66	− 0.74	0.77	5	− 0.18
Tilia cordata	3	− 0.53	− 0.40	− 0.48	− 0.62	2	− 0.19
Populus tremula	3	− 0.40	− 0.42	− 0.57	− 0.38	2	− 0.16
Salix caprea	3	− 0.47	− 0.42	− 0.55	0.49	3	− 0.16
Ulmus glabra	3	− 0.64	− 0.58	− 0.66	0.66	5	− 0.22
Acer platanoides	4	− 0.01	− 0.16	− 0.28	− 0.12	4	0.42
Alnus glutinosa	4	0.84*	0.71	0.62	− 0.90*	5	− 0.59
Carpinus betulus	4	0.61	0.65	0.81#	− 0.56	4	0.02
Quercus robur	4	− 0.16	− 0.30	− 0.41	0.04	4	− 0.22
Total recruitment	− 0.30	− 0.36	− 0.54	0.25			− 0.39
Total recruitment (10-year lag)	− 0.09	0.41	0.02	0.09			0.19
Total recruitment (20-year lag)	0.28	0.70	0.26	− 0.15			

$P = 0.273$), January temperature ($r_S = 0.447$, $n = 12$, $P = 0.145$) or temperature amplitude ($r_S = − 0.412$, $n = 12$, $P = 0.183$). The soil moisture index of tree species was also not related to the correlation these species had with average precipitation ($r_S = − 0.459$, $n = 11$, $P = 0.156$, Fig. 3c). Similarly, no pattern was observed when plotting species accord-

ing to their shade-tolerance index ($r_S = 0.275$, $n = 12$, $P = 0.387$, Fig. 3d).

Discussion

Despite the natural development of old growth forests of Białowieża National Park, Bernadzki

Table 4. Pearson's correlations between tree recruitment rate (number of recruits ha^{-1}yr^{-1}) and basal area (m^2 ha^{-1}). Total recruitment is the summed recruitment for all species. The relation between total tree recruitment and basal area with a 10- and 20-year lag in response is also included. Asterisks indicate significance level: *$P<0.05$, **$P<0.01$, ***$P<0.001$, #marginally significant at $P = 0.055$ ($n = 6$ and $n = 5$ with 20-year lag period). Species are ranked according to their shade-tolerance index, from shade intolerant (1) to shade tolerant (4). Indices are based on Brzeziecki and Kienast (1994), see text for further details.

Tree species	Shade tolerance	Basal area
Alnus glutinosa	1	− 0.79
Betula spp.	1	− 0.13
Pinus sylvestris	1	− 0.65
Populus tremula	1	− 0.07
Salix caprea	1	0.24
Fraxinus excelsior	2	0.84
Quercus robur	2	− 0.52
Carpinus betulus	3	− 0.05
Picea abies	3	− 0.53
Ulmus glabra	3	0.98*
Acer platanoides	4	− 0.58
Tilia cordata	4	0.79
Total recruitment		− 0.12
Total recruitment (10-year lag)		− 0.74
Total recruitment (20-year lag)		− 0.60

et al. (1998) showed that large changes have occurred during the last century in tree stand composition. The present study demonstrated that patterns in recruitment rates of tree species were related to fluctuations in large herbivore density throughout this period. Climatic changes and changes in forest openness seemed of lesser importance in driving changes in tree recruitment and species composition to tree stands during this time frame.

Herbivory as a driving factor

The diet of large herbivore species in the Białowieża Forest is composed to an important extent of woody material (Dzięciołowski 1967; Morow 1976; Gębczyńska 1980), with bison as the species that did least browsing (Gębczyńska et al. 1991). As virtually all tree species are included in the ungulate diet during different parts of the year (see Borowski & Kossak 1972; Gębczyńska 1980; Gębczyńska et al. 1991; Borkowska & Konopko 1994), a relaxation in browsing pressure by the total ungulate community is expected to influence growth and survival of a large number of tree species. Indeed, highest total recruitment rate of trees (except *Carpinus betulus*) occurred within or directly after the period (1916-1936) in which a sharp decline in ungulate density

occurred. This decline in density followed a period with peak numbers of all ungulate species as a result of intensive game management (severe predator control, supplementary winter feeding and introduction of alien species), which occurred in 1900-1915 (Jędrzejewska et al. 1997). High ungulate numbers may have suppressed all tree regeneration. The response of trees to changes in ungulate density suggests important top-down effect of ungulates. We observed that including a time-lag of 10-20 years in the analyses did not improve but actually weakened the observed relations, suggesting that tree recruitment (into DBH 5 cm) is a rather rapid process, and trees had reached this size already between two consecutive measurements, with an average interval of 15 years, on the transect.

As total tree recruitment was correlated with red deer numbers and not with any other single ungulate species, this suggests that red deer played a dominant role. The variations in response among tree species to fluctuations in herbivore density were related to the preference for these tree species as food by herbivores. Tree species that were most preferred by herbivores were most positively related, whereas less preferred species were negatively related to herbivore density. *Carpinus betulus* was the most extreme is this respect and was the only species positively related to herbivore numbers, even though it was positively selected and comprised an important food plant, especially for red deer and roe deer (Gębczyńska 1980), the dominant browsers in the system.

This pattern can be explained in two ways. First, it may show that bottom-up effects are dominant in this system and the availability of preferred forage regulates the number of herbivores (Turkington et al. 2002). This is in accordance with Pettorelli et al. (2003), who suggested that the availability of *Carpinus betulus* as a main forage species is likely a key factor in the dynamics of roe deer populations. In that case, factors other than herbivores determine recruitment rates of trees, and herbivore populations are simply following these patterns. Alternatively, these patterns may be the result of herbivore top-down effects, where tree species that are preferred by herbivores also have higher tolerance to browsing (Augustine & McNaughton 1998). Periods with high ungulate density will then favour browse-tolerant tree species, whereas other species will be suppressed when they are also eaten. We believe that the observed changes in tree species composition are mainly the result of herbivore top-down effects for the following reasons. First, the most selected forage species in our study, *Carpinus*,
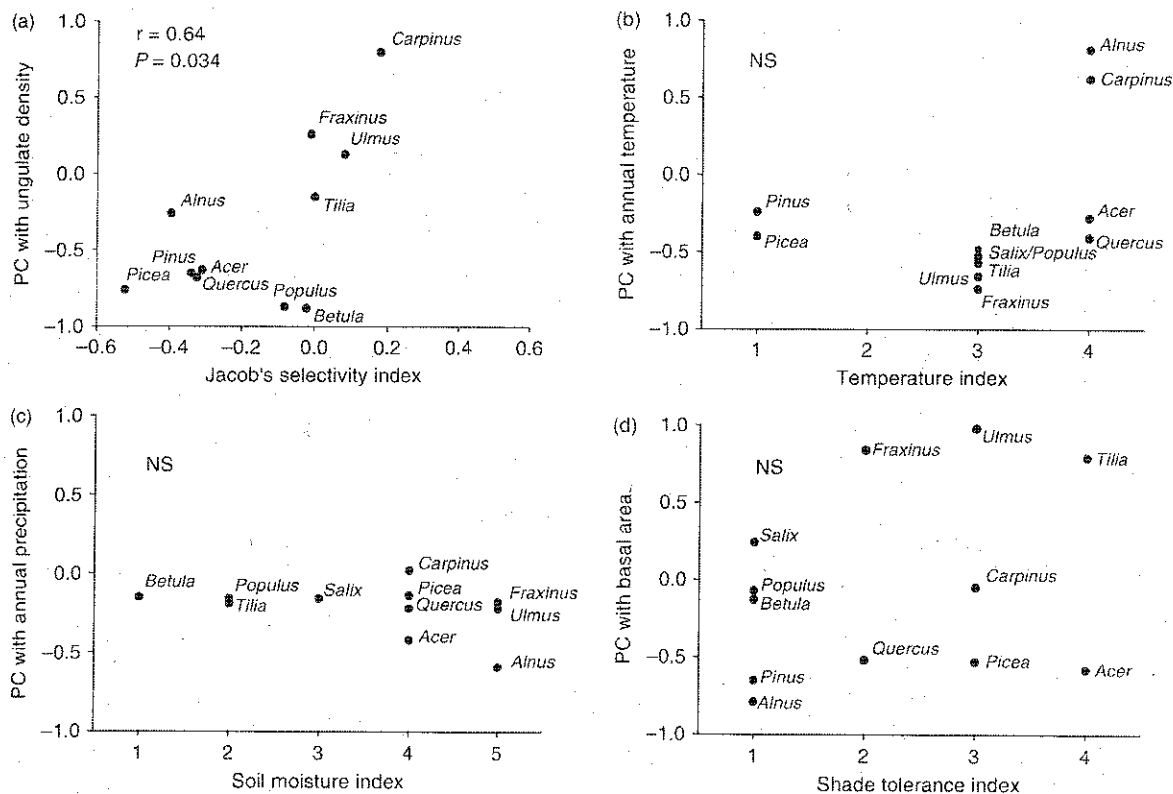
Fig. 3. Pearson's correlation coefficients (PC) of tree species recruitment rates with herbivore abundance (a), annual temperature (b), annual precipitation (c) and basal area (d) plotted against ranks of each tree species according to Jacob's selectivity index, temperature, soil moisture and shade-tolerance index. Sources of data are Tables 2-4. The significance of the relations are indicated in the figures based on Pearson's correlation coefficient (a) or Spearman's rank correlations (b-d).

also shows a high (possibly the highest) tolerance to browsing. In response to browsing of its apical shoot, *Carpinus* produces large numbers of lateral shoots and typically develops a bushy structure, which explains its wide use in hedgerows (see for example Croxton et al. 2004). The high (relatively to other species) browsing tolerance of *Carpinus*, is also illustrated in on-going studies that include detailed growth measurements of five tree species (*Carpinus, Quercus, Tilia, Picea, Acer*) that were planted on experimental plots (see Kuijper et al. 2009). *Carpinus betulus* is in all respects (increase in total and relative tree height, basal stem length, summed branch length) the fastest grower in the presence of herbivores, despite the fact that the amount of browsing (percentage of trees browsed) is similar in all species (D.P.J. Kuijper, unpublished data). Second, the strongest argument that the observed patterns are caused by herbivore top-down effects comes from a set of long-term (10 years) exclosures erected in BNP. These experiments illustrate that in the presence of herbivores, tree recruitment is strongly reduced, with more than three-fold higher overall tree recruitment rates inside exclosures compared to control plots. Moreover, species diversity is higher inside exclosures and the species composition is pushed towards a dominance of *Carpinus betulus* on control plots. This species is the most successful compared to other species and virtually the only one able to regenerate in the presence of herbivores (Kuijper et al. 2010). The higher relative recruitment of *Carpinus* in the presence of herbivores has also been observed in other studies (Kriebitzsch et al. 2000). Hence, the patterns observed in these exclosure studies, demonstrating a causal relationship with ungulates, fits with the findings of the present long-term correlative study. In the absence of ungulates (periods with low ungulate numbers), higher total recruitment occurred, whereas in the presence of ungulates (periods with high ungulate numbers), mainly one species could successfully regenerate – *Carpinus betulus*.

Although browsing tolerance seems an important factor explaining our results, in which in

general preferred species seem more tolerant, not all tree species conformed to these predictions. For example, whereas *Fraxinus, Tilia, Populus* and *Betula* had relatively similar selectivity indices, their response to changes in herbivore density showed large variation, from positive to strongly negative correlations with ungulate density (see Fig. 3a). This variance in response indicates that more factors are important in explaining inter-specific patterns of tree recruitment. One factor may be related to functional aspects of species that influence their tolerance to browsing. For example, variation in growth rate among species may influence the capacity for recovery after browsing (Herms & Mattson 1992; Bee et al. 2007). Tree species may also differ in resistance traits, such as chemical or physical defences against herbivory, which may influence tolerance to browsing (Herms & Mattson 1992) or selectivity of the herbivore. A second factor is local conditions where the species grow. In our study system, coniferous species occur in the most infertile parts of the forest system, whereas deciduous species dominate the most fertile parts. The availability of resources may influence the amount of resistance or tolerance traits in plants (Bryant et al. 1983; Mole 1994) or the cost of replacing tissue lost to herbivory (Coley et al. 1985). Hence, local growing conditions may cause large differences among species in their reaction to changes in herbivore pressure. Based on the present data set, we are unable to explore how important these factors are. But the general patterns that emerge from our rather crude analyses indicate that herbivores are an important factor driving overall changes in tree recruitment and species composition.

Whereas experimental studies demonstrated the importance of herbivore top-down effects in shaping patterns of tree recruitment in the early stages of tree regeneration (Kuijper et al. 2010), the present study suggests that they may also affect the tree stand and influence long-term stand dynamics. Although we believe that the observed patterns are the result of dominating top-down effects of herbivores, this does not exclude that both bottom-up and top-down forces act simultaneously (Polis & Strong 1996) and that the observed patterns are the result of a combination of both of the above views.

Positive feedback of ungulate browsing?

An increase in palatable tree species as a result of increasing herbivore pressure, as observed in the present study, contrasts to findings from other studies in old-growth temperate deciduous forests, and the general idea that deer browsing favours the least preferred species because of heavy browsing of the preferred species (Horsley et al. 2003; Modry et al. 2004; Long et al. 2007). The normally observed reduction of preferred young trees, together with a shift towards less palatable species, can decrease the quality of the area as wildlife habitat (Tilghman 1989; Horsley et al. 2003). In contrast, the present study suggests that the long-term effects of herbivory lead to a shift in species composition that increases the quality of wildlife habitat. *Capinus betulus* is an important food plant, especially for the browsing ungulates in the system (Gębczyńska 1980). Hence a shift in species composition towards this preferred forage species, together with constant tree density or basal area (see also Bernadzki et al. 1998), likely results in more profitable foraging conditions and may increase the carrying capacity of the system for these ungulates (Pettorelli et al. 2003). Several factors might explain these contrasting findings. The tree composition might first of all be related to the lower ungulate density in our study area compared to other studied systems. High ungulate densities might prevent these positive feedbacks from occurring. The differences in ungulate density between areas may reflect dissimilarities in hunting management or productivity of study systems. In addition, the presence of large carnivores (wolf and lynx) in the Białowieża Forest, which are absent in most other studied temperate forest systems, might influence these contrasting findings. On the one hand, their combined predation has top-down effects on deer populations and prevents a rapid increase in numbers (Jędrzejewski et al. 2002; Jędrzejewska & Jędrzejewski 2005); on the other hand, their presence can alter behaviour, habitat choice and spatial distribution of ungulate species (Creel et al. 2005; Fortin et al. 2005; Frair et al. 2005). Recent studies suggest that these indirect effects of carnivores might be as important (Schmitz et al. 1997) or even more important in influencing herbivore–plant interactions as their direct lethal effects on population density (Creel & Christianson 2008). Both factors might prevent too intense browsing on preferred forage species in the present study area. At lower deer densities or lower concentration in preferred foraging habitats (Kuijper et al. 2009), the positive feedback mechanism of deer browsing on the abundance of their forage plants might be visible, but disappears when deer density or concentration increases in the absence of predator control (see also Kuijper et al. 2010).

Climate change and forest openness had less influence on tree recruitment

In the present study covering 70 years, no significant relations were found between total recruitment rate of all trees and climatic parameters, even when taking a lag period of 10-20 years into account. Since strong relations were found for total recruitment rate and total ungulate density and red deer density, this indicates that climatic parameters are not a major factor in explaining overall recruitment rates. A significant relation with climatic parameters was found for only one species, *Alnus glutinosa*. The positive relation with January temperature and negative relation with temperature amplitude indicate that this species recruits better in periods with milder climatic conditions. Similarly, *Carpinus betulus* recruitment was marginally significantly positively related to annual temperature. Since, significant relations between individual species were found both in relation to ungulate density and climatic parameters, these two factors might drive shifts in species composition in the pool of regenerating trees. However, the patterns in species recruitment, by ranking species according to climatic preferences, did not show predictable shifts in species composition. Species that are associated with milder climates did not, in general, show higher recruitment in milder periods than typical boreal species. This contrasts to the ranking of species according to herbivore selectivity, indicating a weaker role of climate relative to herbivory.

Climate and herbivore density might also interact with one another. In the present study we could not test for the interaction between these factors due to the low number of data points (five to six periods). However, using a longer time-scale Jędrzejewska & Jędrzejewski (2005) illustrated that population fluctuations of bison and wild boar were mainly shaped by changes in annual temperature. Annual temperature explained a negligible fraction of the variation in population density in red deer and roe deer. The population dynamics of these two main browsers of the system were shaped through predators and human activities (hunting). Although climate changes have played a major role in determining forest composition and species abundances throughout Europe since the last glacial period (Brewer et al. 2002; Lacourse 2009), they did not seem to have played a dominant role in determining patterns of recruitment during the last 70 years in the Białowieża Forest.

Similarly, despite the fact that gap formation is a crucial factor affecting tree recruitment on a small scale, at the scale of these transect (14.9 ha) it did not seem to be an important factor driving the observed changes in tree recruitment and species composition. The constant values of basal area and tree density observed during the study period indicate that no large changes occurred in forest openness and hence available regeneration space.

Other possible driving factors

Apart from the above studied factors, Bernadzki et al. (1998) mentioned two other likely factors influencing the observed compositional dynamics of trees. First, successional replacement might drive changes in tree stand composition (Faliński 1986). Changes in recruitment rates of tree species and tree stand composition should then reflect the successional order of species. In the present study, typical early successional species (*Populus, Salix* and *Betula*; Faliński 1986) showed a peak in recruitment rate in the period 1937-1957. However, typical late-successional species (Faliński 1986), such as *Picea, Quercus* and *Acer*, showed highest recruitment in the preceding (1916-1936) or in the coinciding (*Tilia cordata*) period.

Only one late-successional species, *Carpinus*, showed increasing recruitment rates during the study period. Similarly, both early- and late-successional tree species decreased in abundance in the tree stand in the period 1936-2002 (Bernadzki et al. 1998), with only two late-successional species increasing, *Carpinus* and *Tilia*. The observed patterns of tree recruitment and changes in tree stand composition make it unlikely, therefore, that competitive replacement is an important driving factor in the observed changes in species composition.

Second, the observed changes can be related to a recovery from human exploitation in the centuries before establishment of the national park in 1921. Until the mid-19th century, small-scale multipurpose forest utilization was predominant, such as selective cutting, bee-keeping, potash, tar and charcoal burning (Jędrzejewska et al. 1997; Samojlik 2005, 2006). These activities, together with frequent unintentional fires, had an important influence on the forest dynamics and tree species abundances (Samojlik & Jędrzejewska 2004; Samojlik 2005, 2006). Since the beginning of the 19th century, fire protection regimes have strongly reduced the number of unintentional fires, and the traditional use of forests has been abandoned (Samojlik & Jędrzejewska 2004). Given the longevity of trees, which can reach up to 350-500 years for *Quercus, Pinus* and *Ulmus* (Faliński 1986; Brzeziecki &

Kienast 1994), the effects of human impact in the 19th century may still be visible in the species composition of old tree stands during the 20th century. Similarly, the openness of the forest might have been affected by human exploitation. However, we believe the observed patterns in tree recruitment are not consistent with the recovery hypotheses for the following reasons. First, we observed sudden changes in recruitment rates during the study period that are not likely to result from impacts that occurred in the 19th century, but more likely to events occurring in the few previous decades. Second, the data on basal area and tree density do not indicate that the forest was more open at the beginning of the study period. Both values show little variability with time (Bernadzki et al. 1998). Third, the consistently increasing recruitment rates of only one species, *Carpinus*, do not fit with the idea of a forest becoming more closed after recovery from human impact. In that case, we would expect that other shade-tolerant species (*Tilia, Acer, Ulmus*) would show increased recruitment (Faliński 1986).

The most recent exploitation for timber at the beginning of the 20th century occurred outside the area that was later assigned as national park (Faliński 1988; Jędrzejewska et al. 1997). Although some cutting inside the BNP occurred in 1910 (Faliński 1988), this did not affect tree stands at the locations of the permanent transects in the present study.

Conclusion

Although several factors, including climate and changes in human exploitation of the forest, might have influenced tree stands in Białowieża Primeval Forest during the last centuries (Faliński 1986; Mitchell & Cole 1998), the present study suggests that during the last 70 years changes in ungulate density have played an important role in shaping recruitment rates of trees and affecting species composition of the regenerating trees. Increasing herbivore numbers seem to have shifted the tree recruitment towards preferred and browsing-tolerant species, coinciding with a long-term change in tree stand composition from a *Picea*-dominated stand towards a *Carpinus*- and, to a lesser extent, a *Tilia*-dominated tree stand (Bernadzki et al. 1998). Periodical crashes in ungulate number, whether human-induced or caused by natural factors (see Gulland et al. 1993; Takatsuki et al. 1994), may therefore offer windows of opportunity for regeneration of various tree species and hence maintain tree stand diversity. This contrasts to the aims of game management

observed throughout Europe. As game is often managed to maintain constant numbers, patterns of natural forest regeneration can be effectively prevented and the development of even-aged, single species stands is predicted. Management that allows ungulate populations to fluctuate, as is observed in many little-disturbed ecosystems (i.e. Coulson et al. 2004; Ogutu & Owen-Smith 2005), might allow more natural and diverse forest development.

References

Ammer, C. 1996. Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. *Forest Ecology and Management* 88: 43–53.

Augustine, D.J. & McNaughton, S.J. 1998. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62: 1165–1183.

Bee, J.N., Kunstler, G. & Coomes, D.A. 2007. Resistance and resilience of New Zealand tree species to browsing. *Journal of Ecology* 95: 1014–1026.

Bernadzki, E., Bolibok, L., Brzeziecki, B., Zajaczkowski, J. & Żybura, H. 1998. Compositional dynamics of natural forests in the Białowieża National Park, northeastern Poland. *Journal of Vegetation Science* 9: 229–238.

Bobiec, A. 2007. The influence of gaps on tree regeneration: a case study of the mixed lime–hornbeam (*Tilio-Carpinetum* Tracz. 1962) communities in the Białowieża Primeval Forest. *Polish Journal of Ecology* 55: 441–455.

Borkowska, A. & Konopko, A. 1994. The winter browse supply for moose in different forest site-types in the Biebrza valley, Poland. *Acta Theriologica* 39: 67–71.

Borowski, S. & Kossak, S. 1972. The natural food preferences of the European bison in seasons free of snow cover. *Acta Theriologica* 13: 151–169.

Brewer, S., Cheddadi, R., de Beaulieu, J.L. & Reille, M. 2002. The spread of deciduous *Quercus* throughout Europe since the last glacial period. *Forest Ecology and Management* 156: 27–48.

Bryant, J.P., Chapin, F.S. & Klein, D.R. 1983. Carbon nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40: 357–368.

Brzeziecki, B. & Kienast, F. 1994. Classifying the life-history strategies of trees on the basis of the Grimian model. *Forest Ecology and Management* 69: 167–187.

Coley, P.D., Bryant, J.P. & Chapin, F.S. 1985. Resource availability and plant antiherbivore defense. *Science* 230: 895–899.

Coulson, T., Guinness, F., Pemberton, J. & Clutton-Brock, T. 2004. The demographic consequences of releasing a population of red deer from culling. *Ecology* 85: 411–422.

Creel, S. & Christianson, D. 2008. Relationships between direct predation and risk effects. *Trends in Ecology and Evolution* 23: 194–201.

Creel, S., Winnie, J. Jr., Maxwell, B., Hamlin, K. & Creel, M. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86: 3387–3397.

Croxton, P.J., Franssen, W., Myhill, D.G. & Sparks, T.H. 2004. The restoration of neglected hedges: a comparison of management treatments. *Biological Conservation* 117: 19–23.

Dzięciołowski, R. 1967. Food of the red deer in an annual cycle. *Acta Theriologica* 12: 503–520.

Faliński, J.B. 1986. *Vegetation dynamics in temperate lowland primeval forests: ecological studies in Białowieża forest*. Dr. W. Junk Publishers, Dordrecht, NL.

Faliński, J.B. 1988. Succession, regeneration and fluctuation in the Białowieża forest (NE Poland). *Vegetatio* 77: 115–128.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. 2005. Wolves influence elk movements: behaviour shapes trophic cascade in Yellowstone National Park. *Ecology* 86: 1320–1330.

Frair, J.L., Merrill, E.H., Visscher, D.R., Fortin, D., Beyer, H.L. & Morales, J.M. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology* 20: 273–287.

Gębczyńska, Z. 1980. Food of the roe deer and red deer in the Białowieża Primeval Forest. *Acta Theriologica* 40: 487–500.

Gębczyńska, Z., Gębczyński, M. & Martynowicz, E. 1991. Food eaten by free-living European bison in Białowieża forest. *Acta Theriologica* 36: 307–313.

Gulland, F.M.D., Albon, S.D., Pemberton, J.M., Moorcroft, P.R. & Clutton-Brock, T.H. 1993. Parasite-associated polymorphism in a cyclic ungulate population. *Proceedings of the Royal Society of London Series B - Biological Sciences* 254: 7–13.

Herms, D.A. & Mattson, W.J. 1992. The dilemma of plants, to grow or to defend. *Quarterly Review of Biology* 67: 283–335.

Hofgaard, A., Dalen, L. & Hytteborn, H. 2009. Tree recruitment above the treeline and potential for climate-driven treeline change. *Journal of Vegetation Science* 20: 1133–1144.

Horsley, S.B., Stout, S.L. & DeCalesta, D.S. 2003. White-tailed deer impact on the vegetation dynamics of a Northern hardwood forest. *Ecological Applications* 13: 98–118.

Jacobs, J. 1974. Quantitative measurements of food selection. *Oecologia* 14: 413–417.

Jędrzejewska, B. & Jędrzejewski, W. 2005. Large carnivores and ungulates in European temperate forest ecosystems: bottom-up and top-down control. In: Ray, J.C., Redford, K.H., Steneck, R.S. & Berger, J. (eds.) *Large carnivores and the conservation of biodiversity*. pp. 230–245. Island Press, Washington, DC, US.

Jędrzejewska, B., Jędrzejewski, W., Bunevich, A.N., Miłkowski, L. & Krasiński, Z.A. 1997. Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th century. *Acta Theriologica* 42: 399–451.

Jędrzejewska, B., Jędrzejewski, W., Bunevich, A.N., Miłkowski, L. & Okarma, H. 1996. Population dynamics of wolves *Canis lupus* in Białowieża Primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847–1993. *Mammal Review* 26: 103–126.

Jędrzejewski, W., Jędrzejewska, B., Okarma, H., Schmidt, K., Bunevich, A.N. & Miłkowski, L. 1996. Population dynamics (1869–1994), demography and home ranges of the lynx in Białowieża Primeval Forest (Poland and Belarus). *Ecography* 19: 122–138.

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B., Selva, N., Zub, K. & Szymura, L. 2002. Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). *Ecology* 83: 1341–1356.

Koop, H. 1989. *Forest dynamics. SILVI-STAR: a comprehensive monitoring system*. Springer Verlag, Berlin, DE.

Krasińska, M. & Krasiński, Z. 1997. Utilization of the Białowieża National Park by the European bison. *Parki Narodowe i Rezerwaty Przyrody* 16: 63–77 (in Polish with English summary).

Kriebitzsch, W.U., von Oheimb, G., Ellenberg, H., Engelschall, B. & Heuveldop, J. 2000. Development of woody plant species in fenced and unfenced plots in deciduous forests on soils of the last glaciation in northernmost Germany. *Allgemeine Forst und Jagdzeitung* 171: 1–10.

Kuijper, D.P.J., Cromsigt, J.P.G.M., Churski, M., Adams, B., Jędrzejewska, B. & Jędrzejewski, W. 2009. Do ungulates preferentially feed in forest gaps in European temperate forests? *Forest Ecology and Management* 258: 1528–1535.

Kuijper, D.P.J., Cromsigt, J.P.G.M., Jędrzejewska, B., Miścicki, S., Churski, M., Jędrzejewski, W. & Kweczlich, I. 2010. Bottom-up versus top-down control of tree regeneration in the Białowieża Primeval Forest, Poland. *Journal of Ecology*, 98: 888–899.

Lacourse, T. 2009. Environmental change controls postglacial forest dynamics through interspecific differences in life-history traits. *Ecology* 90: 2149–2160.

Landhausser, S.M., Deshaies, D. & Lieffers, V.J. 2010. Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. *Journal of Biogeography* 37: 68–76.

Lenoir, J., Gegout, J.C., Pierrat, J.C., Bontemps, J.D. & Dhote, J.F. 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). *Ecography* 32: 765–777.

Long, Z.T., Pendergast, T.H. & Carson, W.P. 2007. The impact of deer on relationships between tree growth and mortality in an old-growth beech–maple forest. *Forest Ecology and Management* 252: 230–238.

Mátyás, C. 2010. Forecast needed for retreating forests. *Nature* 464: 1271–1271.

Mladenoff, D.J. & Stearns, F. 1993. Eastern Hemlock regeneration and deer browsing in the Northern Great-Lakes region – a reexamination and model simulation. *Conservation Biology* 7: 889–900.

Miścicki, S. 1996. Forest regeneration and its damage by herbivorous ungulates in the Białowieża National Park. In: Paschalis, P. & Zajączkowski, S. (eds.) *Biodiversity protection of Białowieża Primeval Forest.* pp. 91–108. Warsaw University of Life Sciences, Warsaw, PL.

Mitchell, F.J.G. & Cole, E. 1998. Reconstruction of long-term successional dynamics of temperate woodland in Białowieża Forest, Poland. *Journal of Ecology* 86: 1042–1059.

Modry, M., Hubeny, D. & Rejsek, K. 2004. Differential response of naturally regenerated European shade-tolerant tree species to soil type and light availability. *Forest Ecology and Management* 188: 185–195.

Mole, S. 1994. Trade-offs and constraints in plant–herbivore defense theory – a life history perspective. *Oikos* 71: 3–12.

Morow, K. 1976. Food habits of moose from Augustów Forest. *Acta Theriologica* 21: 101–116.

Ogutu, J.O. & Owen-Smith, N. 2005. Oscillations in large mammal populations: are they related to predation or rainfall? *African Journal of Ecology* 43: 332–339.

Pettorelli, N., Dray, S., Gaillard, J.M., Chessel, D., Duncan, P., Illius, A., Guillon, N., Klein, F. & Van Laere, G. 2003. Spatial variation in springtime food resources influences the winter body mass of roe deer fawns. *Oecologia* 137: 363–369.

Polis, G.A. & Strong, D.R. 1996. Food web complexity and community dynamics. *American Naturalist* 147: 813–846.

Renaud, P.C., Verheyden-Tixiera, H. & Dumont, B. 2003. Damage to saplings by red deer (*Cervus elaphus*): effect of foliage height and structure. *Forest Ecology and Management* 181: 31–37.

Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62: 1041–1051.

Samojlik, T. 2005. A tree of many uses: the history of small-leaved lime (*Tilia cordata*) in Białowieża

Primeval Forest. *Rocznik Dedrologiczny* 53: 55–64 (in Polish with English summary).

Samojlik, T. 2006. The grandest tree – a history of Scots pine (*Pinus sylvestris* L.) in Białowieża Primeval Forest until the end of the 18th century. *Rocznik Dedrologiczny* 54: 7–27 (in Polish with English summary).

Samojlik, T. & Jędrzejewska, B. 2004. Utilization of Białowieża Forest in the times of Jagiellonian dynasty and its traces in the contemporary forest environment. *Sylwan* 148: 37–50 (in Polish with English summary).

Schmitz, O.J., Beckerman, A.P. & O'Brien, K.M. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78: 1388–1399.

Scott, D., Welch, D., Thurlow, M. & Elston, D.A. 2000. Regeneration of *Pinus sylvestris* in a natural pinewood in NE Scotland following reduction in grazing by *Cervus elaphus*. *Forest Ecology and Management* 130: 199–211.

Takatsuki, S., Suzuki, K. & Suzuki, I. 1994. A mass-mortality of Sika-deer on Kinkazan Island, Northern Japan. *Ecological Research* 9: 215–223.

Tilghman, N.G. 1989. Impacts of White-tailed deer on forest regeneration in Northwestern Pennsylvania. *Journal of Wildlife Management* 53: 524–532.

Turkington, R., John, E., Watson, S. & Seccombe-Hett, P. 2002. The effects of fertilization and herbivory on the herbaceous vegetation of the boreal forest in north-western Canada: a 10-year study. *Journal of Ecology* 90: 325–337.

Van Hees, A.F.M., Kuiters, A.T. & Slim, P.A. 1996. Growth and development of silver birch, pedunculate oak and beech as affected by deer browsing. *Forest Ecology and Management* 88: 55–63.

Zielski, M. 1998 *Wpływ zwierzyny na stan odnowień naturalnych w oddziale 288/289/318 Białowieskiego Parku Narodowego.* Report from Forestry Faculty, Warsaw University of Life Sciences, Warsaw (in Polish).

Supporting Information

Additional supporting information may be found in the online version of this article:

Figure S1. Annual precipitation, January, July and average annual temperature in Białowieża during the last century. Data on annual precipitation are available since 1948.

Table S1. Calculation of Jacob's selectivity indices of tree species (0.3–1.3 m) according to the proportion that had its leader shoot browsed based on two field studies with large sample sizes carried out in the Białowieża Primeval Forest. Both studies

were carried out in spring-summer, total sample size and number of sampled trees are indicated. The proportion of each tree species in the total sample and the proportion of each tree species in the sample including only trees with browsing marks are shown.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.