

## Changes in the stands of the Białowieża National Park from 2000 to 2015

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**Abstract.** The aim of the study was to characterise changes in the natural forest of the Białowieża National Park (BNP) Strict Reserve during a 15-year period. To allow for a more precise determination of the time course, overall duration and intensity of the observed changes, the 15-year period was further divided into shorter 2–7-year intervals. Taken together, the Strict Reserve forest stands cover 4584 hectares and they constitute the oldest part of the Białowieża Forest placed under protection in 1921.

The measurements were carried out in 2000, 2002, 2004, 2011 and 2015 on 160 permanent sample plots, which are systematically distributed throughout the BNP Strict Reserve. During those 15 years, the volume of merchantable timber and the tree density fluctuated only slightly, because the reduction in standing volume due to a spruce and ash decline was compensated for by an increase in the standing volume of lime, hornbeam and alder. The volume increment and tree loss fluctuated slightly, but were nevertheless similar throughout the whole period between 2000 and 2015. The number of trees in the regeneration layer increased. The number of hornbeam trees in this layer increased continuously throughout the whole measurement period, while the number of maple trees started to increase in the second half. All together only five tree species growing in the BNP Strict Reserve progressed from the regeneration layer to the canopy layer in significant numbers. As a result, a gradual decrease in species diversity of forest stands may be expected.

The rather stable, average volume of merchantable timber in the BNP Strict Reserve may be due to the fact that, in a forest with diverse habitats and high species richness, only a few stands are subjected to strong disturbances in a given period of time. Repeated measurements during a relatively short period of time allowed the detecting some fairly quick changes occurring in natural lowland forests.

**Keywords:** increment, ingrowth, loss, regeneration, standing volume, Strict Reserve, tree species

### 1. Introduction

National parks began to be established at the beginning of the twentieth century in Europe. Their borders contain the most valuable fragments of nature that have been least transformed by humans. The largest proportion of protected areas in the temperate zone consists of forest ecosystems. The value of these forests and the desire to ensure their unrestricted development meant that they became the object of observation and research.

The study of natural forests evolved with the introduction of representative (statistical) methods to forestry. This enabled large areas to be measured, the accuracy of the results

to be assessed as well as statistical analysis methods to be used to compare distant objects or the same ones studied at different times. The introduction in the 1960s of permanent sample plots (Schmid-Haas 1989) proved to be particularly useful. For example, they enabled measurements to be taken on decreasing occurrences of trees or the non-invasive determination of growth. In Poland, this method was first used in 1969 to study a forest reserve (Rutkowski et al. 1972). Before 2005, when the large-scale forest inventory was started, permanent sample plots were used to measure forests in national parks – initially their fragments (e.g. Dziewolski 1980), then reserves and experimental study subjects (e.g. Przybylska 1977). At the end of the 1980s, these experimen-

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tal plots began to be used to measure the state and dynamics of forests throughout the national parks (Chwistek 2007).

The lack of continuity in research, the use of different measurement methods and problems with data storage resulted in insufficient knowledge about the processes occurring in natural forests. For this reason, papers appeared, suggesting a common system of performing research on natural forests (Koop 1989), and attempts were made to coordinate them and define their scope in European countries (Parviainen et al., 2000).

One of the best-preserved natural forests – not only in Poland but throughout the temperate climate zone – is the Strict Forest Reserve of the Białowieża National Park (BNP). It was placed under protection in 1921 as one of the first in Europe. Since its inception, numerous studies have been carried out there, yet for a long time, they did not provide information on the status and development of the entire forest area. The first results on the stands of the BNP were obtained after the measurements were taken in 1989–1990 by the Bureau of Forest Management and Forest Geodesy in Białystok (Michalczyk 2001).

Permanent sample plots hold a special place in the studies of BNP forest stands, with their records of identified trees with diameter at breast height (DBH)  $\geq 5$  cm. They were founded in 1936 by Prof. Tadeusz Włoczewski, measured again around 1957, and since then, measured at approximately 10-year intervals (Bernadzki et al. 1998). They were selected with the intention of having the entire diversity of the BNP stands represented. These measurements are a unique resource illustrating the changes occurring in the natural forest over a period of 80 years and are used in contemporary researches (e.g. Bernadzki et al. 1998; Kuijper et al. 2010b; Bolibok 2014; Brzezicki et al. 2016). The disadvantage of these research plots is the subjective choice of the forest fragments being observed and the lack of representation of marsh forests (Miścicki 2012). According to Jaroszewicz et al. (2016), even the total area of the transects (15.44 ha) was too small to observe the life cycle of the types of forests present in the BNP.

In 1999, BNP employees established a network of permanent sample plots. They were used to characterise the status and, after repeated measurements in 2009, the dynamics of the forest stands. The outcome of these results was ‘The report on the dynamics of the forest ecosystems in the Białowieża National Park’ (Brzezicki et al. 2010).

In measuring the status and dynamics of the forest, it is usually assumed that the period between successive measurements of permanent sample plots is 10 years. Sometimes shorter periods are used (e.g. Chwistek 2007, 2010), allowing one to explore the relatively rapid changes taking place in the forest. Since about 1995, easily recognisable changes were being observed in BNP stands that were, amongst others, the consequence of dying spruces during bark beetle infestation (Michalski et al., 2004) or ash dieback.

These facts influenced the choice of the following research aim: to determine the changes in the status and dynamics of the natural forest in the BNP Strict Reserve in relatively short periods of time (ranging 2–7 years). It was assumed that this will provide more accurate information on the timing of a given phenomenon, its duration and intensity. The study covered the period from 2000 to 2015.

## 2. Study subject

The study subject covered the forest stands of the BNP Strict Reserve. Its total area is 4,747 ha, of which 4,584 ha are occupied by forest stands. Their coordinates are (52°45'N, 23°52'E). These stands are located in the temperate climate zone, transitioning from the predominance of (depending on the given year) continental conditions over Atlantic ones, sometimes influenced by boreal characteristics (Faliński 1986). The mean annual values of the most important climatic features are air temperature of 6.8°C (−4.7°C in January, 17.8°C in July), precipitation of 641 mm and duration of snow cover at 92 days. The terrain of the BNP Strict Reserve is flat – the difference in height is 23 m and the average height above sea level is 158 m. It is located outside the naturally occurring ranges of silver fir (*Abies alba*), European beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*) and sycamore (*Acer pseudoplatanus*).

## 3. Methods

Data consisted of measurement results were collected from 160 permanent sample plots. A team led by the author performed these measurements in August months of 2000, 2002, 2004, 2011 and 2015. Measurement points set by BNP staff in 1999 were used as sample plot centres, which formed a network of an average size of 267 × 1,067 m, with the long side oriented to the azimuth of 0°. In the case of three BNP areas with no measurement points, own ones were set by the author in 2000.

On each of the measurement occasions, concentric sample plots were identically measured. Each consisted of five concentric circles with an area of 5.31 m<sup>2</sup> (within which all trees of at least two years of age were measured – regardless of size), 20 m<sup>2</sup> (measurement of trees with height  $h \geq 0.3$  m), 50 m<sup>2</sup> (measurement of trees with DBH  $\geq 2.0$  cm), 200 m<sup>2</sup> (measurement of trees with DBH  $\geq 12.0$  cm) and 500 m<sup>2</sup> (measurement of trees with DBH  $\geq 36.0$  cm). The location of individual trees, including those from the regeneration layer, was determined in relation to the sample plot centre. The magnetic azimuth at the left edge of the trees and the distance to the site where they grew were used for this. This enabled the identification of the trees during subsequent measurements. On this basis, changes in their size and status (living, dead, exceeded the threshold measurement)

were determined. The species was identified, and the DBH of each tree included in the sample (or its height if  $h \leq 1.3$  m) was measured. The relationship between height and DBH of the trees of a given species was calculated based on the data from 2015. Then, in the 500 m<sup>2</sup> area of each sample plot, the height of all trees with DBH of  $\geq 7.0$  cm was measured.

All BNP Strict Reserve forest stands formed one interpretation unit, with regard to the separate data for the overstorey layer and the regeneration layer. The merchantable volume of the sampled trees was calculated using formulas currently used in Polish forest management planning (Bruchwald et al., 2000). The lower threshold measurement of DBH and the calculation of the merchantable timber volume (categorised as the overstorey layer) was 8.0 cm. To determine the amount of the regeneration layer, two characteristics were used: the density of trees and the total tree height per area unit.

Calculating the dynamics of the standing volume was carried out according to the methods provided for concentric sample plots (Miścicki, Nowicka 2007). ‘Ingrowth’ – that is, trees that were measured for the first time in a given period, because their DBH exceeded the thresholds of 12.0 or 36.0 cm from the time of the previous measurement – and ‘exceedance’, that is, trees that exceeded the thresholds of DBH in the given period but were measured in both periods, were taken into account.

The empirical distribution of most variables (a quantity in the sample plot referenced to an area of 1 ha) had a positively skewed distribution. In such a case, before beginning the statistical analysis, the data was square root transformed. The repeated measures ANOVA was used to compare the mean values obtained from the permanent sample plots. In cases

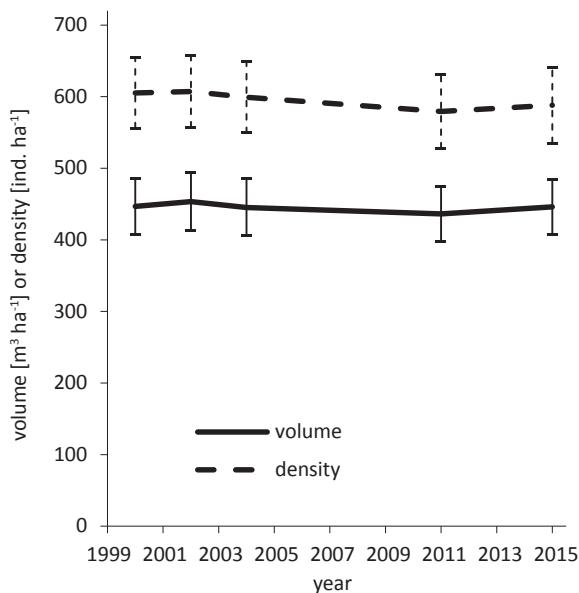
of static characteristics, calculations were made for five occasions. In the case of dynamic characteristics (e.g. current increment of volume), calculations were made for three periods: 2000–2004, 2004–2011 and 2011–2015. The post hoc multiple comparison of the study subjects (the state of a given characteristic at individual occasions or periods) was performed using Tukey’s honest significant difference test.

The tree species composition of BNP forest stands between two selected moments was compared using Morisita’s Index as modified by Horn (1966).

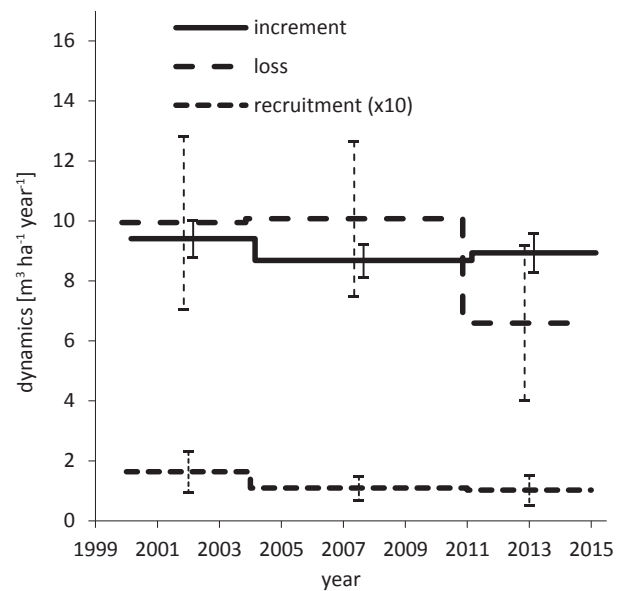
## 4. Results

The average standing volume of the stands (merchantable volume of trees with DBH  $\geq 8.0$  cm) was stable between 2000 and 2015 years (Fig. 1). It was subject to small fluctuations in a range of 20 m<sup>3</sup> ha<sup>-1</sup> ( $p > 0.05$ ). In 2015, the average standing volume of the stands was  $446 \pm 38$  m<sup>3</sup> ha<sup>-1</sup> and the same as at the beginning of the measurements. The mean density of trees (with DBH  $\geq 8.0$  cm) was also stable over the period of 2000–2015 ( $p < 0.05$ ) (Fig. 1). Its slight fluctuation had a similar trend to that observed for the average standing volume, except that over 15 years, the density of trees (amounting to  $588 \pm 53$  trees ha<sup>-1</sup> in 2015) slightly decreased.

In 2000–2015, the current volume increment of the forest stands averaged  $8.96 \pm 0.34$  m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup>. The differences in its quantity in the individual shorter periods were not large (Fig. 2); however, they were significant ( $p = 0.036$ ). The largest increase was in 2000–2004 and differed signifi-



**Figure 1.** Standing volume and tree density in individual measurement periods in 2000–2015 (error value at  $p = 0.05$ )



**Figure 2.** The current volume increment, volume of loss and ingrowth (multiplied by 10) in individual periods in 2000–2015 (error value at  $p = 0.05$ )

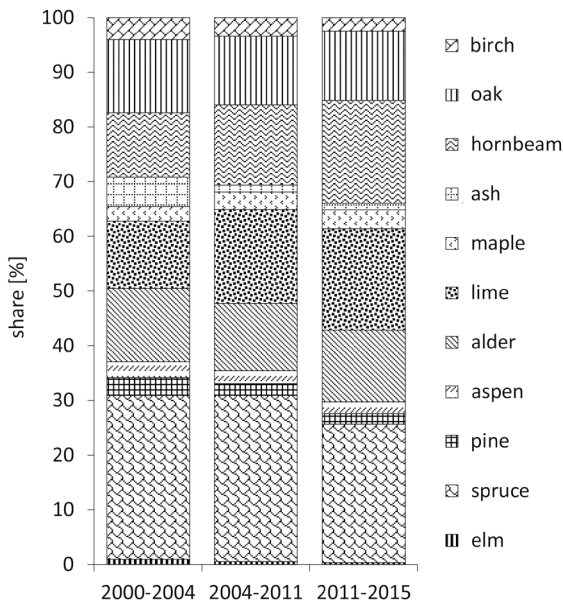
cantly from that of 2004–2011, which was the smallest ( $p = 0.028$ ). In the whole period of 2000–2015, spruce represented the largest part of the current volume increment (29%). Species with a high proportion of increment also included small-leaved lime (*Tilia cordata*) (16%), hornbeam (*Carpinus betulus*) (15%), black alder (*Alnus glutinosa*) (13%) and pedunculate oak (*Quercus robur*) (13%). The individual shorter periods did not differ much because of the share of tree species in the current volume increment (Fig. 3). However, trends towards changes in the share of tree species in the volume increment were noticed: a decrease in the case of spruce, ash, Scots pine (*Pinus sylvestris*), silver birch (*Betula pendula*) and downy birch (*Betula pubescens*) and wych elm (*Ulmus glabra*) (rarely field elm *Ulmus minor*), whilst an increase in the case of lime and hornbeam. The share of other species (oak, alder, maple) in the volume increment remained at a similar level throughout the whole period.

The volume of trees growing from the regeneration layer into overstorey layer (in excess of the DBH threshold of 8.0 cm in a given period) was small, on an average  $0.12 \pm 0.03 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$  in 2000–2015. In successive shorter periods, it slightly decreased ( $p < 0.05$ ) (Fig. 2). In the period 2000–2015, only six species grew into overstorey layer, with hornbeam accounting for 46% of the volume increment. Ingrowth of spruces (18% of share), limes (13%) and alders (12%) was present in each of the shorter observation periods. In 2011–2015, the ingrowth of birches (10% in the whole study period) was not noted but the ingrowth of elm was recorded (1%).

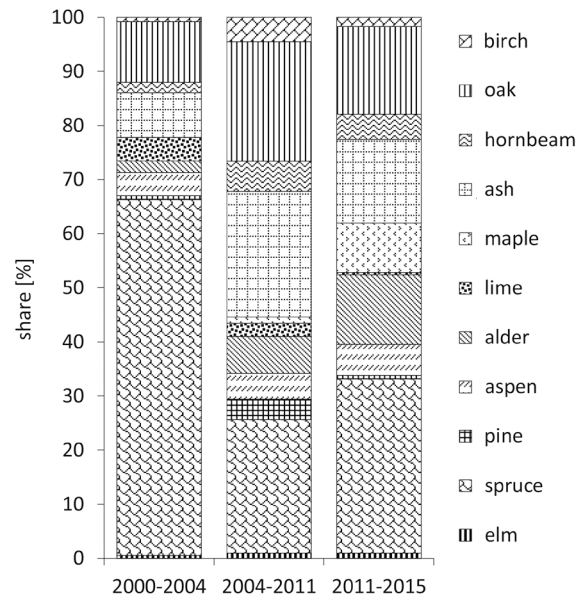
From 2000 to 2015, the average volume of loss (trees that died and the difference in ingrowth volume and exceedance of

DBH = 12.0 cm and DBH = 36.0 cm – a total average of  $-0.22 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ ) was  $9.13 \pm 1.59 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ , similar to the sum of the current volume increment and ingrowth volume in the same period. It had a greater fluctuation than the volume increment (Fig. 2), but there were no significance differences in the mean values. In 2000–2015, a significant proportion of volume loss occurred for three species: spruce (37%), oak (18%) and ash (17%). Hornbeam (4%) and especially lime (2.5%) were represented to a small extent in the group of dead trees. Individual shorter periods differed in the proportion of species represented in volume loss (Fig. 4). This reflected the periodic fluctuations of the decay intensity of some species: spruce following the spruce bark beetle infestation in 2000–2004 (and, to a lesser extent, in the period of 2011–2015), ash in 2004–2011 (and also in 2011–2015, but then seemingly less intensively due to the reduction in the volume of living trees), oak in 2004–2011 and alder and maple in 2011–2015.

Despite the overall stable standing volume of the stands, there were changes in the volume of individual tree species in the period of 2000–2015 (Fig. 5). In 15 years, the standing volume of ash ( $p < 0.001$ ), spruce ( $p = 0.011$ ) and aspen (*Populus tremula*) ( $p = 0.033$ ) decreased significantly, although each of them experienced a short period of a slight increase. Ash was such a species whose volume decreased to the greatest extent – both in relation to its initial state or the difference between the initial and final standing volume. Since 2002, a slight decrease in the average volume of pedunculate oak had been observed ( $p > 0.05$ ). The tree species with a stable standing volume in the period of measurements ( $p > 0.05$ ) were Scots pine, maple, silver and downy birch and wych elm. However, in the case of

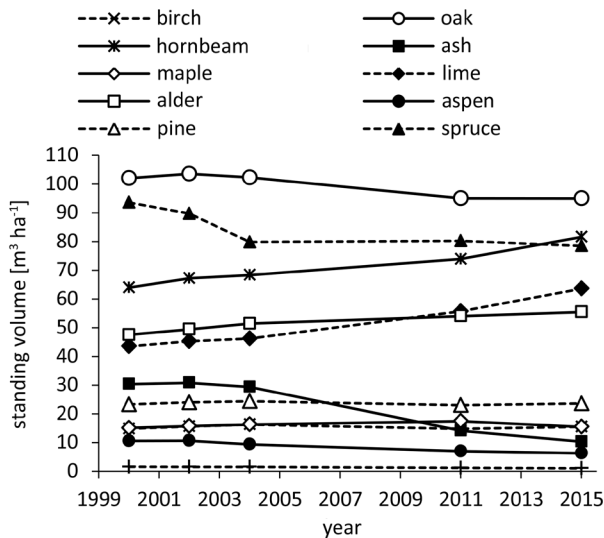


**Figure 3.** The share of tree species in current volume increment in individual periods in 2000–2015

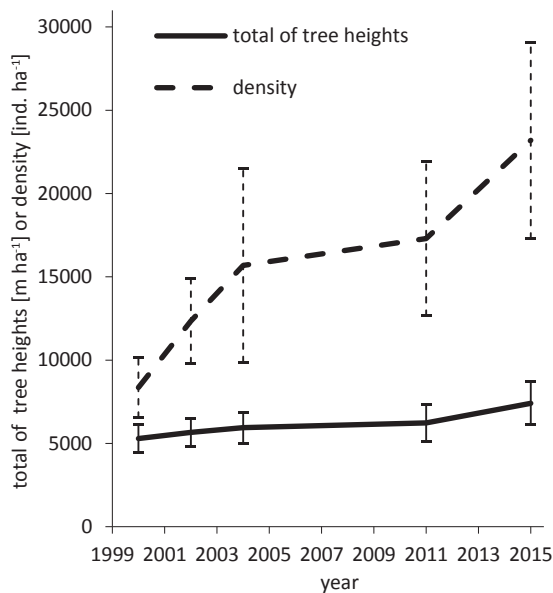


**Figure 4.** The share of tree species in volume loss in individual periods in 2000–2015

the least abundant species, a relatively large increase (although impossible to confirm statistically) (downy birch – about 40%) or decrease (wych elm – about 35%) was observed in the standing volume. Over the 15-year period, the standing volume of lime ( $p < 0.001$ ), hornbeam ( $p < 0.001$ ) and alder ( $p = 0.001$ ) was continually increasing. The volume of lime increased to the greatest extent in relation to its initial state as well expressed by the difference in standing volume. Despite the observed chang-



**Figure 5.** Changes in the standing volume of individual tree species in the overstorey ( $dbh \geq 8.0$  cm) in 2000–2015



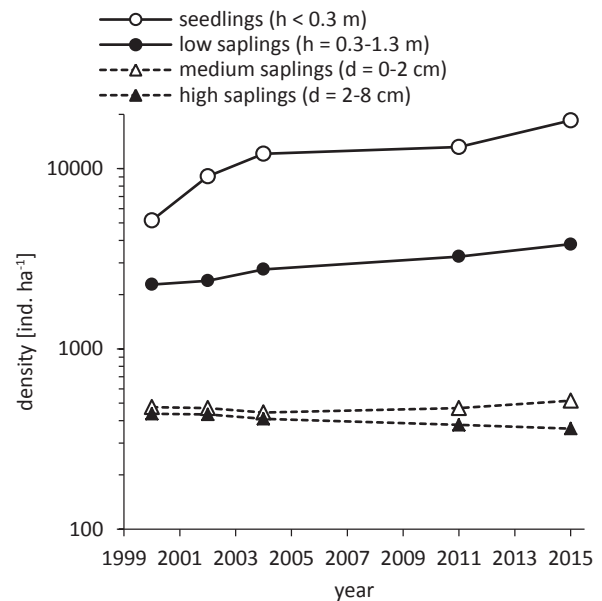
**Figure 6.** Tree density and the total tree height of the regeneration layer in individual measurement periods in 2000–2015 (error value at  $p = 0.05$ )

es, there was a little variation in the species composition of the BNP Strict Reserve stands. The Morisita's Index of similarity of the species structure between 2000 and 2015 was 0.975.

The regeneration layer (trees with  $DBH < 8.0$  cm or height  $h \leq 1.3$  m) in the period 2000–2015 was more dynamic than that of the overstorey ( $DBH \geq 8.0$  cm). The total tree height – illustrating the overall amount of regeneration – was continually increasing ( $p < 0.001$ ) and was 40% higher after 15 years ( $7,408 \pm 1,305$  m ha<sup>-1</sup>) than that at the beginning of the measurements (Fig. 6).

An even more significant change occurred in the tree density of the regeneration layer (Fig. 6). It was continually increasing ( $p < 0.001$ ) in the 15-year period. In 2015, it amounted to  $23,152 \pm 5,903$  ind. ha<sup>-1</sup>, which was almost three times more comparing with the initial state. This increase in the tree density of the regeneration layer was due to the change in the number of low saplings ( $h = 0.3–1.3$  m) ( $p < 0.001$ ), but most of all, of seedlings ( $h < 0.3$  m) ( $p < 0.001$ ) (Fig. 7). The density of medium saplings ( $DBH = 0.1–1.9$  cm) was subject to small fluctuations ( $p > 0.05$ ), and that of high saplings ( $DBH = 2.0–7.9$  cm) slightly decreased ( $p > 0.05$ ).

There were significant changes in the quantity of certain tree species of the regeneration layer in the period of 2000–2015. The only species whose total height significantly decreased was birch (both downy birch and silver birch) ( $p = 0.002$ ) (Fig. 8a and 8b). The amount of aspen significantly fluctuated ( $p < 0.001$ ) after the period of increasing in total height, a significant number of trees began dying around 2008. Smaller fluctuation occurred in the case of spruce (marginally significant,



**Figure 7.** The density of seedlings, low, medium and high saplings in individual measurement periods in 2000–2015

$p = 0.066$ ). The amount of its regeneration increased during the period of intensive dying of mature trees as a result of the spruce bark beetle infestation (in 2000–2004), but later returned to its initial state. The total height of hornbeam ( $p = 0.021$ ), maple ( $p < 0.001$ ), alder ( $p = 0.005$ ) and elm ( $p = 0.005$ ) all increased. Hornbeam constituted the predominant species of the regeneration layer over the entire period, 2000–2015. In the period of measurements, the amount of maple rapidly increased. It was initially a species representing only a medium share of the regeneration layer, but after 2008, it became the second species in terms of total tree height. The amount of alder increased in the period of 2011–2015 and elm in the period of 2002–2004, thereafter remaining at a similar level. The average total height of pine, oak, ash and lime remained at similar levels ( $p > 0.05$ ). Oak, and especially pine, had sparse regeneration. Although the total height of lime was stable during the period of measurement, in terms of its share was the second to fourth species of the regeneration layer in individual measurement periods. The species composition of the regeneration layer of the BNP Strict Reserve stands expressed by total tree height experienced a slightly greater change than the species composition of the overstorey (expressed by volume). The Morisita's Index of similarity of the regeneration layer species structure in 2000 and 2015 was 0.937.

## 5. Discussion

Between 2000 and 2015, five measurements were made of 160 permanent sample plots evenly distributed over the BNP Strict Reserve stands. Repeated measurements conducted in relatively short periods of time enabled recognition of

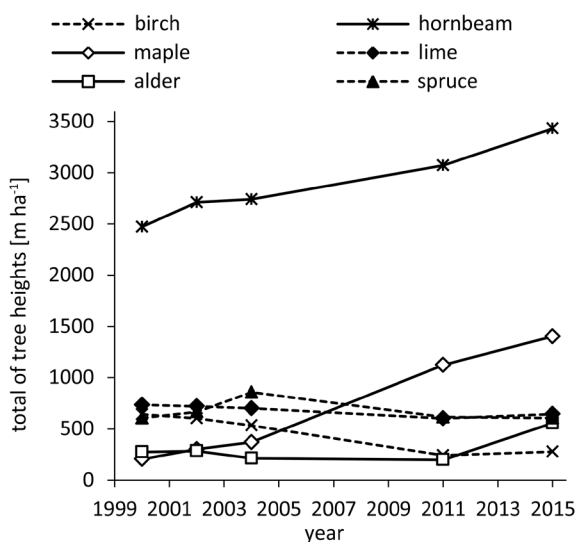
some quite rapidly occurring changes in the state of a natural lowland forest, including the time a given phenomenon began occurring, its duration and intensity. In the case of phenomena exhibiting small fluctuations, results of repeated measurements proved their stability.

Amongst the most important phenomena observed as a result of the fairly often repeated measurements are

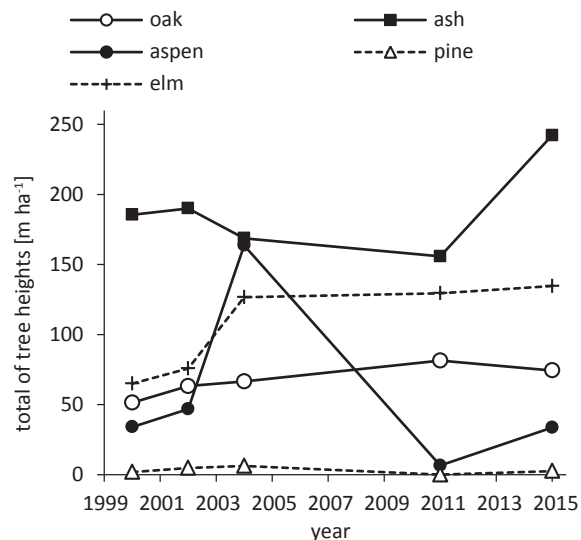
- the periodic dieback of spruce, mainly due to spruce bark beetle infestation,
- the dieback of ash infected by the *Chalara fraxinea* fungus,
- the periodic dying of alder (probably in response to drought),
- the increasing amount of alder regeneration (probably as the result of new habitats emerging during the periods of drought),
- the increase in the intensity of dying maples,
- the increasing amount of maple regeneration,
- the periodic dying of young aspens (mainly from offshoots) following fungal diseases,
- the continuous increase in the amount of hornbeam regeneration,
- the presence of a group of tree species significantly increasing their share as well as groups of species reducing their share in the standing volume.

Some of these phenomena occurred not only in the BNP but also in the entire Poland (or even over larger areas), whilst some others occurred on a regional scale. Others are probably associated with the specific structure of the BNP Strict Reserve stands.

The intensive declining of spruce because of the spruce bark beetle infestation in 2000–2004 took place in both the



**Figure 8a.** The total height of the most frequent tree species in the regeneration layer in individual measurement periods in 2000–2015



**Figure 8b.** The total height of the less frequent tree species in the regeneration layer in individual measurement periods in 2000–2015

BNP stands and managed stands of the Białowieża Forest (Michalski et al. 2004). According to the available data (Miścicki 2012), the volume of dead spruce tree trunks in this period in the BNP Strict Reserve stands was 81,000 m<sup>3</sup>. In relation to the total standing volume, this was much more than in the managed stands or in the natural reserves in the rest of Białowieża Forest (122,000 m<sup>3</sup> according to the unpublished data from the Białowieża, Browsk and Hajnówka forest districts). However, in 2012–2015, according to the data used in this study, mortality of spruces in the BNP was smaller than that in the managed stands or nature reserves of the Białowieża Forest (approximately 333,000 m<sup>3</sup>, according to unpublished data from the Białowieża, Browsk and Hajnówka forest districts). This could be explained by the fact that in the BNP Strict Reserve, a significant portion of trees susceptible to spruce bark beetle feeding were killed during the earlier infestation of 2000–2004.

Ash dieback was recorded in Poland in 1992 (Turczański 2016). A significant intensification of the disease, most noticeable in its first phase on young trees, affected the BNP a little later, in 1999. The results of this study showed that by 2002, the volume increment of ash still outweighed losses. However, the later severity of the disease was high. In subsequent years, the volume of ash was continuously decreasing, reaching one-third of its quantity in 2015 from 13 years earlier. It remains an open question whether the numbers of ash in the BNP Strict Reserve will decrease in the future to the level of, for example, wych elm. A positive phenomenon identified during the study period was the stable presence of ash in the regeneration layer. However, the transition of young trees of this species to the regeneration layer may be difficult because of the impact of herbivorous hoofed mammals. Ash is one of the most often browsed tree species (Miścicki 1996).

Another phenomenon worthy of wider discussion is the significant increase in the quantity of Norway maple in regeneration layer. This phenomenon is similar to the one observed after World War I (Paczoski 1930), although in 2000–2015, there was not a simultaneous increase in the amount of young limes. Increasing quantity of maple of the regeneration layer in hornbeam habitat occurred much earlier in reserves located in Warsaw. This is evidenced by the fact that the maple became very numerous, and even the dominant species, not only amongst seedlings and low saplings but also amongst medium saplings, high saplings and in the understory of the stands (Fiedoruk 2015; Pelc 2016; Przypaśniak 2016). The explanation of this phenomenon may be the assumption that the increasing amount of regenerating maple is associated with global warming. The gradual movement of the optimum temperature zone for this species from west to east could explain why this species emerged so numerously in the regeneration layer only recently in the BNP. However, as in the case of the ash, the increased density of younger generation maples does not guarantee a fu-

ture significant presence in the overstorey. An obstacle may be that the maple is a species frequently browsed by ungulates and is sensitive to such damage (Kuijper 2010a).

An important result of this work is the information that the average standing volume (and thus probably the biomass) of the BNP Strict Reserve forest stands experienced only minor fluctuations in the 15-year period. This result can be referenced to data presented in the work of Brzeziecki et al. (2016) on changes in the basal area of the trees in the stands of this area during the period of 1936–2012. This parameter reached its highest value in 1957 and thereafter was subject to small fluctuations. Although it is difficult to convert basal area to standing volume without additional data, the fairly strong correlation between these characteristics in a given forest allows to presume that the average standing volume remained at a similar level over a long period of time. It should be emphasised that in the period of 2000–2015, the average standing volume of the BNP Strict Reserve stands experienced only minor fluctuations, despite the emergence of significant disturbances: the decline of spruces following the spruce bark beetle infestation (in 2000–2004, amounting to approximately 20% compared to its volume in 2000) and the ash decay (about 75% compared to its volume in 2000). In 2005, some parts of the BNP Strict Reserve stands were destroyed by a hurricane, but at the scale of the entire Reserve, this turned out to be a minor disturbance.

In interpreting the stability of average standing volume, it should be remembered that the BNP Strict Reserve forest is a mosaic of different stands (patches). This mosaic reflects different habitat conditions, variability in species composition and age of trees. Additionally, the long period of protection probably contributed to the establishment of a fairly regular age structure of the trees in the entire forest. Shugart (1984) concluded that a state of pseudo-equilibrium (equilibrium in a statistical sense) at the landscape scale is achieved when disturbances in the forest are small in relation to its area, and the age structure of trees is complete and stable. Whittaker and Levin (1977) similarly determined that the effect of disturbances, which some of the patches forming the mosaic structure are subjected to, can be neutralised in a sufficiently large landscape (forest) by the lack of disturbances in other patches. We must, therefore, conclude that in a forest of a small area, it is possible that relatively large disturbances may appear. An example of this may be the change in the standing volume of the ‘Beech Mountain’ (‘Bukowa Góra’) Strict Protected Area of 128 ha, located in the Roztocze National Park. In 1974, a storm damaged about one-third of the standing volume (Gazda, Miścicki 2016). Since then, no major disturbances have been reported and the average standing volume has steadily increased, after 30 years surpassing the amount from before the disaster.

Jaroszewicz et al. (2016) critically assessed the appropriateness of studying the structure of the forest in the BNP Strict Reserve with five transects ranging from 1.20 to 5.22 ha used in the research of Brzeziecki et al. (2016). They stressed, amongst other things, that stands consisting of coniferous species can be totally destroyed in areas much larger than those of the transects, subsequently leading to the emergence of seedlings all at once in that area. Indeed, this example shows the danger of having a phenomenon be disproportionately represented – especially as a consequence of a disturbance occurring in a vast area. However, the transects in question contain a mosaic of habitats. Assuming the theory of Whittaker and Levin (1977), it can be concluded that the chances of having a disturbance impacted on the entire area at once is small.

Using the example of spruce, the species experiencing the greatest level of disturbance in 2000–2015, it should be noted that different DBH classes were attacked by the spruce bark beetle to varying degrees (Miścicki 2012). Seidl et al. (2007) reported, amongst others, that soil moisture, the share of spruce in a stand, their age and basal area affect the intensity of the dieback of this species. Spruce occurs in almost all habitats of the BNP Strict Reserve, although its proportion varies. During the spruce bark beetle infestation, the structure of the stands was changed in different ways, depending on the proportion of spruce and the trees that died. This means that different dynamics of the stands may exist in the BNP Strict Reserve, similar to those described, amongst others, by Shorohova et al. (2009): even-aged stands established after a disturbance, stands established from the cohort emerging after subsequent stages of the disturbance, medium-scale regeneration in the form of patches in areas where the trees died, small-scale regeneration in the gaps created after the death of small groups of trees.

Probably only a forest fire over a large area could lead to the over-representation of disturbed areas within Włoczewski's study sites. Bobiec (2002) emphasised that most of the forests in the BNP Strict Reserve grow in 'non-flammable' habitats, and only damage caused by wind or insect infestation may be the factors significantly affecting the structure of the forest. The danger of incorrect report on the scale of the phenomena taking place in the forest is greatly reduced in studies using numerous, evenly distributed sample plots covering the entire area of the BNP Strict Reserve.

## 6. Conclusions

- Assessment of changes in the BNP Strict Reserve stands was conducted using measurements at relatively short time intervals on 160 permanent sample plots. This enabled recognition of changes in many characteristics of the forest stands.

- The relatively short periods of time between measurements revealed that some phenomena in the natural forest occur relatively quickly or are subject to significant variability. The most important examples in the BNP Strict Reserve were the fluctuation in the total volume of dying spruces, the fast pace of ash dieback and the increase in the total height of maples in the regeneration layer.

- The limited species number of high saplings and the fact that only five species growing from the regeneration layer into the overstorey layer indicate that a gradual reduction in the tree species diversity of the BNP Strict Reserve stands should be expected.

## Conflict of interest

The author declares that no potential conflicts of interest exist.

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