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Zbigniew MACIEJEWSKI

Roztoczański National Park, ul. Plażowa 2, 22-470 Zwierzyniec

LONG-TERM CHANGES IN THE ABUNDANCE AND MASS OF THE MAIN TREE SPECIES IN BEECHWOOD AND FIR FOREST COMMUNITIES OF ROZTOCZAŃSKI NATIONAL PARK (EAST-CENTRAL POLAND)

ABSTRACT: Work was done in 1993, in the strict reserve within Roztoczański National Park (East-Central Poland), on 4 permanent research plots representing the associations *Dentario glandulosae-Fagetum* Klika 1927 em. Mat. 1964, *Abietetum polonicum* (Dziub. 1928 Br.-Bl. et Vlieg. 1939) and *Querco roboris-Pinetum* Mat. W. 1981. Comparisons with studies from 1968 and 1978 revealed significant changes in stand structure, namely increases in the abundance and proportion by mass of beech *Fagus sylvaticus* and hornbeam *Carpinus betulus*, and a decline among fir *Abies alba* and the other species of major importance in the associations studied. The rate of the observed changes had increased markedly in the most recent period of study.
KEY WORDS: natural forests, species composition, stand structure, beech *Fagus sylvatica*, hornbeam *Carpinus betulus*.

1. INTRODUCTION

Research on permanent plots within natural forest has, for the last several decades, revealed considerable ongoing changes in structure and species composition (Peterken and Jones 1987, Stephens and Ward 1992). In mountainous areas, the species most often showing proportional declines within stand composition are fir *Abies alba* and Norway spruce *Picea abies*. These are being replaced by broadleaved species, among which the greatest dynamics is being shown by beech *Fagus sylvatica* (Vyskot 1981, Dziewolski 1987, 1990, 1992, Dziewolski and Skawiński 1988). In turn, in Białowieża Primeval Forest – the largest natural complex in lowland Europe – the declining species are spruce and Scots pine *Pinus sylvestris*, while limes *Tilia* and hornbeam *Carpinus betulus* are rapidly increasing their representation in the stand

composition (Sokołowski 1991, Kowalski 1993). Some studies have shown the directions and rates of these changes to be dependent on habitat type and the corresponding type of plant community (Leak 1987, Danielewicz 1991, Jaworski and Karczmarski 1990, 1991, Michalik 1991, Sokołowski 1991). In different cases, the dynamics of stands have been found to be influenced to a considerable degree by unfavourable atmospheric phenomena acting over large areas (e.g. droughts and the invasions of foliophages or fungal diseases commonly associated with them) (Peterken and Jones 1987, Busing et al. 1988, Stephens and Ward 1992); by strong winds (Hibbs 1983); by ice storms (De Steven et al. 1991) or by climatic fluctuations (Steijlen and Zackrisson 1987). These disturbances most often appear randomly and unpredictably, and lead to abrupt changes in the original direction of development of forests.

Stands in the area studied (Roztoczański National Park, E-C Poland) are "foothill" communities of Carpathian beechwoods and fir forest made up of species presenting considerable long-term changes, i.e. the beech, fir and spruce characteristic of mountain areas, and the hornbeam, oak and pines typical of lowlands. The aforementioned communities occupy more than 34% of the studied area of forest. Fir, spruce and beech are all at the limits of their natural ranges in this region known as the Roztocze Plateau (latitude 49°50', 50°48' N longitude 22°19', 24°10' E). This limit is determined by habitat conditions, and particularly by temperature and precipitation which limit possibilities for growth and development of the trees. The Roztocze Plateau is a significant boundary line in Europe, being the point at which the last fading influence of the Atlantic climate is to be felt. A clearly continental climate predominates in areas further east (Szafer 1977).

It was to be anticipated that the long-term changes described in the introduction are also occurring in the study area, though research on stand dynamics has not hitherto been done on the Roztocze Plateau, which constitutes, as mentioned, a zone of separation of different climates and of the natural ranges of different forest species. The aim of the study was to determine the trends and rates of changes in selected forest associations of Roztoczański National Park, as well as the trends of main tree species dynamics making up these communities.

2. STUDY AREA AND METHODS

Lying in the western part of the Central Roztocze (Fig. 1), Roztoczański National Park was established in 1974. Its coordinates are 50°31' to 50°40' N and 22°53' to 23°07' E. The current area is 8481.76 ha, of which 805.11 ha is under strict protection. The main subjects of protection are natural forest communities, along with elements of flora and fauna which are rare, or even described as new to science from the Park itself. Of the 19 forest associations distinguished here, the greatest areas (Fig. 1) are taken by: *Dentario glandulosae-Fagetum* (25% of the Park), *Leucobryo-Pinetum* Mat. W. 1981 (18%) and *Abietetum polonicum* (8%). Large areas (together 31% of the Park) are also occupied by secondary commu-

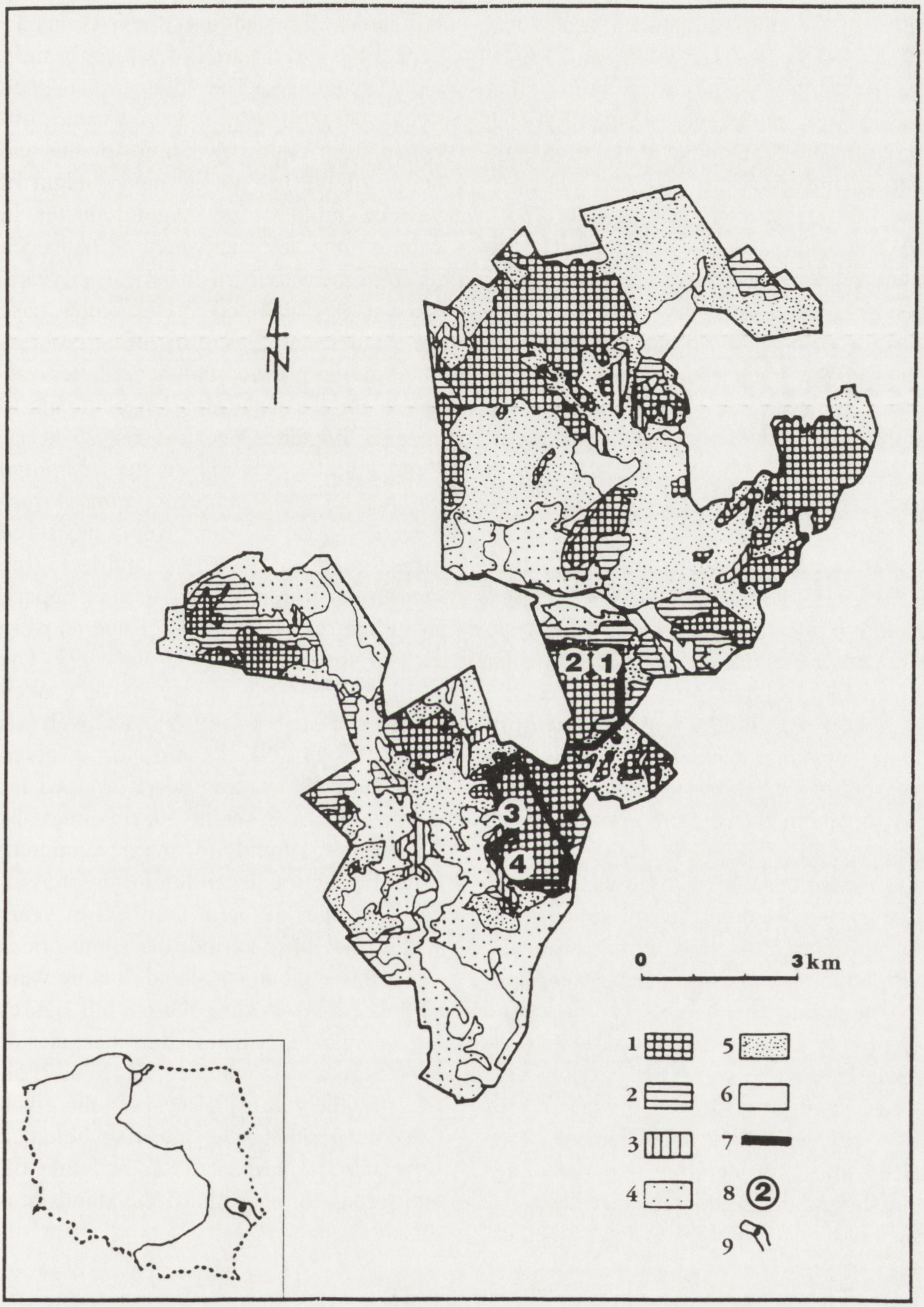

Fig. 1. Map of the forest communities of The Roztoczański National Park (from: Izdebski et al. 1992), generalized: 1 – *Dentario glandulosae-Fagetum*, 2 – *Abietetum polonicum*, 3 – *Querco roboris-Pinetum fagetosum*, 4 – *Leucobryo-Pinetum*, 5 – Substitute communities from Querco-Fagetea and Vaccinio-Piceetea classes, 6 – the others communities, 7 – borders of strict reserves, 8 – sample plots, 9 – outline of Roztocze Region in Poland (insert) and localisation of Roztocze

nities of the classes *Querco-Fagetea* and *Vaccinio-Piceetea* (Izdebski et al. 1992).

Research was done in 1993, on 4 half-hectare plots established in 1968 in the area brought under strict protection subsequently (from 1974 onwards, Fig. 1). Protection dates back to 1957, when a forest reserve was established to take in natural fragments representing the remnants of a formerly-extensive complex of primaeval fir and beech forest. Most of the study area is located in plateau at between 250 and 345 m a.s.l. Differences in altitude are of up to 90 m. Detailed descriptions of the area are in Izdebski (1964) and Izdebski et al. (1992).

Breast-height diameters over 7 cm were measured for all the trees in this category, which were numbered. Measurements were made in two perpendicular directions. Heights were also measured and recorded. In the case of trees of higher diameter classes, the height was measured twice to avoid mistakes. In the case of inclined trees, the distance of the departure of trunks from the vertical was also measured, while in the case of bent or curved specimens it was height plus the distance of maximum distortion within the curve. These results were used in calculating the heights of trees. The lengths of trunks, and breast-height diameters, were also recorded for fallen dead trees whose degree of decomposition still permitted measurement. Also taken into consideration were saplings and stumps left after trees had been cut. Stand volume in 1993 was determined using tables for standing trees (Czuraj et al. 1960), as the sum of values for individual specimens. The volume of snapped trees was defined by reducing values obtained from tables by a ratio for the real height of the tree to the mean height of trees of similar breast-height diameter. In contrast, the size class method had been used for measurements from earlier years. The results obtained in the latter case were not exact, owing to the large class intervals employed, but nevertheless allowed for the determination of trends to changes in stands over the last 25 years. Plots 1 and 2 (Fig. 1), in the *Abietetum polonicum* and *Dentario glandulosae-Fagetum* associations, were measured three times – in 1968, 1978 and 1993 (the measurement referred to in this paper), while the remaining plots (3 and 4) were measured twice – in 1968 and 1993. The results from 1968 and 1978 were taken from Izdebski (1969), as well as Płaksej (1979). Results for a given stand in different years were grouped for diameter classes set at 10 cm intervals. To determine trends for the development of particular species in the different associations, over different numbers of years within the study period, the annual rates of change in abundance and volume were calculated by dividing the overall figures for the changes (expressed as increases or decreases in abundance and stand volume) by the number of years in the given research period. The values so obtained were used as measures of the scale of, and trends to, changes in the stands studied.

3. RESULTS

3.1. LONG-TERM CHANGES IN THE ABUNDANCE AND MASS OF TREE SPECIES

Changes in abundance mainly concerned the young generation of trees. However, analysis of them provides for predictions of the directions of stand de-

velopment, as well as the likely length of time that a given species will persist in the forest association. In turn, changes in volume (mass of wood) mainly relate to middle and older age classes, allowing for the establishment of current trends in stand development.

3.1.1. Fir

This species declined in abundance on all plots. The greatest decline, to only one-eighth of the previous level, occurred in the *Querco roboris-Pinetum fagetosum* association, where the fall in the proportion of trees of this species was of as much as 61% (Fig. 2). The loss of individual trees per year was of almost 60 ha^{-1}(Table 1), equating to a fall of 2.4%. A high rate of decline was also noted for fir in the *Abietetum polonicum* association (Fig. 3), with the mean figure for the loss being of almost 19 trees ha^{-1}, or 1.4%. In both cases, it was mainly the youngest trees that died (saplings, and those of size class II). The relatively limited rate of change in abundance noted in *Dentario glandulosae-Fagetum* was linked to the lack of any young-generation firs on plots, as well as to the small number of older individuals.

The rate of decline of fir was significantly greater in the years 1978–93 than previously (Table 1, Figs. 3 and 4). In *Abietetum polonicum*, the number of dying fir trees was greater by 7 per year, while in *Dentario glandulosae-Fagetum* it was actually lower, albeit with the proportion of individual stand trees of this species nevertheless declining. The study plots with *Dentario glandulosae-Fagetum* and *Querco roboris-Pinetum* show a total lack of fir seedlings and younger saplings, while on plot 4 there are no firs smaller than diameter class 41–50 cm.

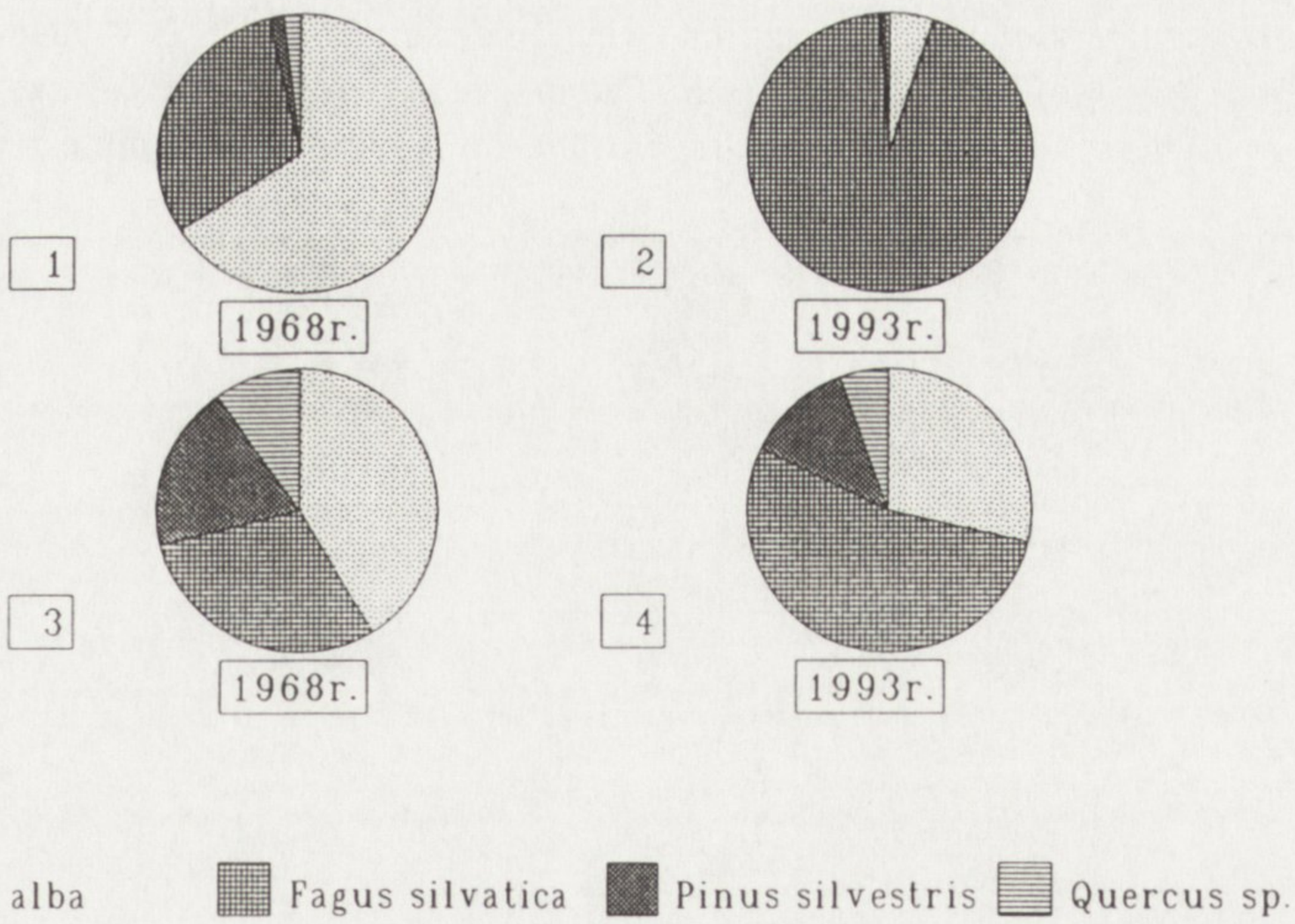

Fig. 2. Percentage contribution of investigated tree species in total number of trees (1, 2) and in total volume of forest stand (3, 4) in the *Querco roboris-Pinetum fagetosum* plant association in 1968 and 1993 years

Volume increments for fir were only noted in *Abietetum polonicum* (of 76 m^3 ha^{-1}), and even then the proportion of stand volume taken by the species was 6% lower than in 1968 (Fig. 3). On the other plots the volume fell markedly, with the greatest decline being on plots representing the *Dentario glandulosae-*

Table 1. Yearly rate of change in density and volume of respective tree species

Plant association	Years	Species											
		Abies alba		*Fagus silvatica*		*Carpinus betulus*		*Picea excelsa*		*Pinus silvestris*		*Quercus* sp.	
		A	B	A	B	A	B	A	B	A	B	A	B
A.-p.	68–78	–14.6	+4.3	+46.0	–0.2	+3.6	–0.2	–17.8	–0.1				
	78–93	–21.8	+2.2	+31.2	+3.0	+16.6	+0.1	–5.0	+0.1				
	68–93	–18.8	+3.1	+37.2	+1.7	+12.4	0.0	–9.8	0.0				
D.g.-F. no. 3	68–78	–9.0	–11.5	+5.0	+0.7	–98.2	+1.1						
	78–93	–3.1	–15.3	–0.7	+2.1	–27.4	+2.1						
	68–93	–5.4	–13.8	+1.5	+1.6	–55.6	+1.9						
D.g.-F. no. 1	68–93	–1.4	–2.9	–38.6	+5.1	–44.2	+1.3						
Q.r.-P.f.	68–93	–59.8	–0.3	+129.0	+6.3					–0.5	0.0	–1.1	0.3

A – changes in total numbers of trees during one year [individuals. ha^{-1}], B – changes in total volume of trees during one year [m^3 ha^{-1}], *A.-p.* – *Abietetum polonicum*, *D.g.-F.* – *Dentario glandulosae-Fagetum*, *Q.r.-P.f.* – *Querco roboris Pinetum-fagetosum*, no – number of sample plot (Fig. 1)

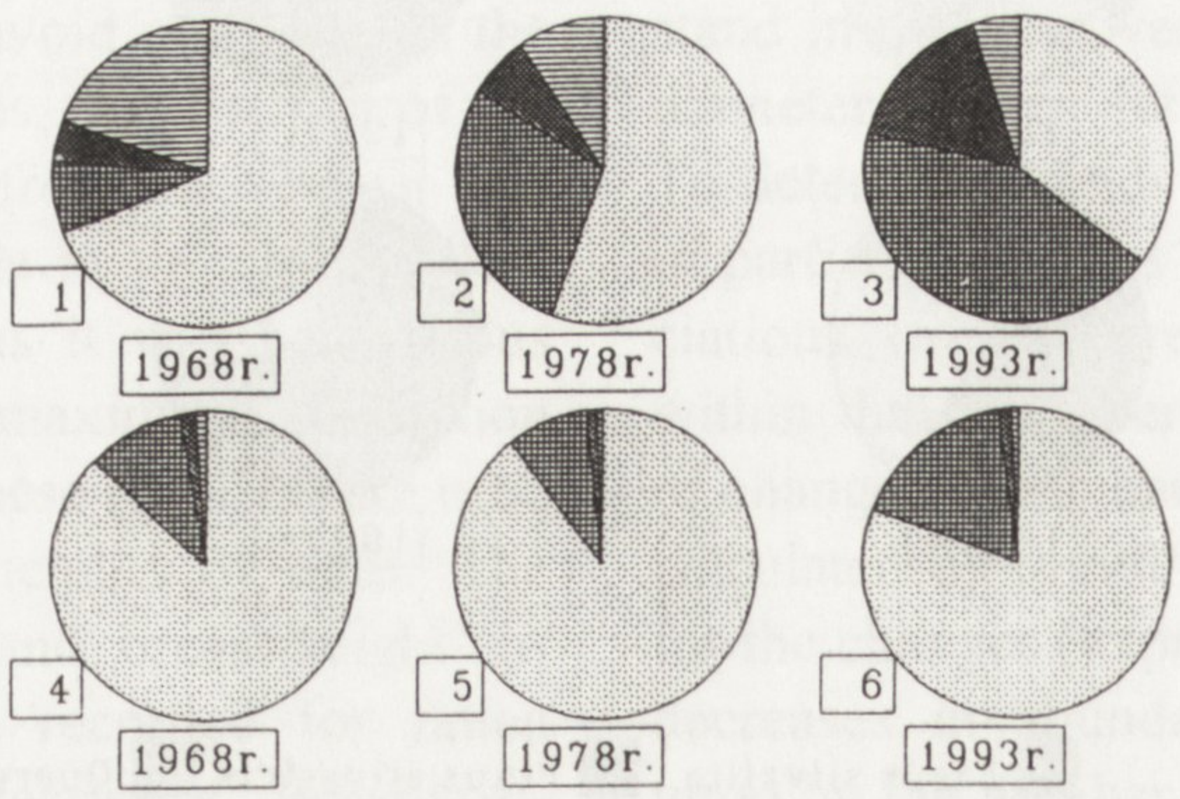

Fig. 3. Percentage contribution of investigated tree species in total number of trees (1, 2, 3) and in total volume of forest stand (4, 5, 6) in the *Abietetum polonicum* plant association in 1968 and 1978 and 1993 years

Fagetum association. On plot 2, the decline in the volume of standing fir was of 344 m^3 ha^{-1}. This reduced the proportion of stand volume taken by the species by 42% as compared with 1968 (Fig. 4). The rates of decline in volume were of almost 12 m^3 per ha per year in the first period, and more than 15 m^3 in the second (Table 1). Changes in the proportion of the species were almost four times more

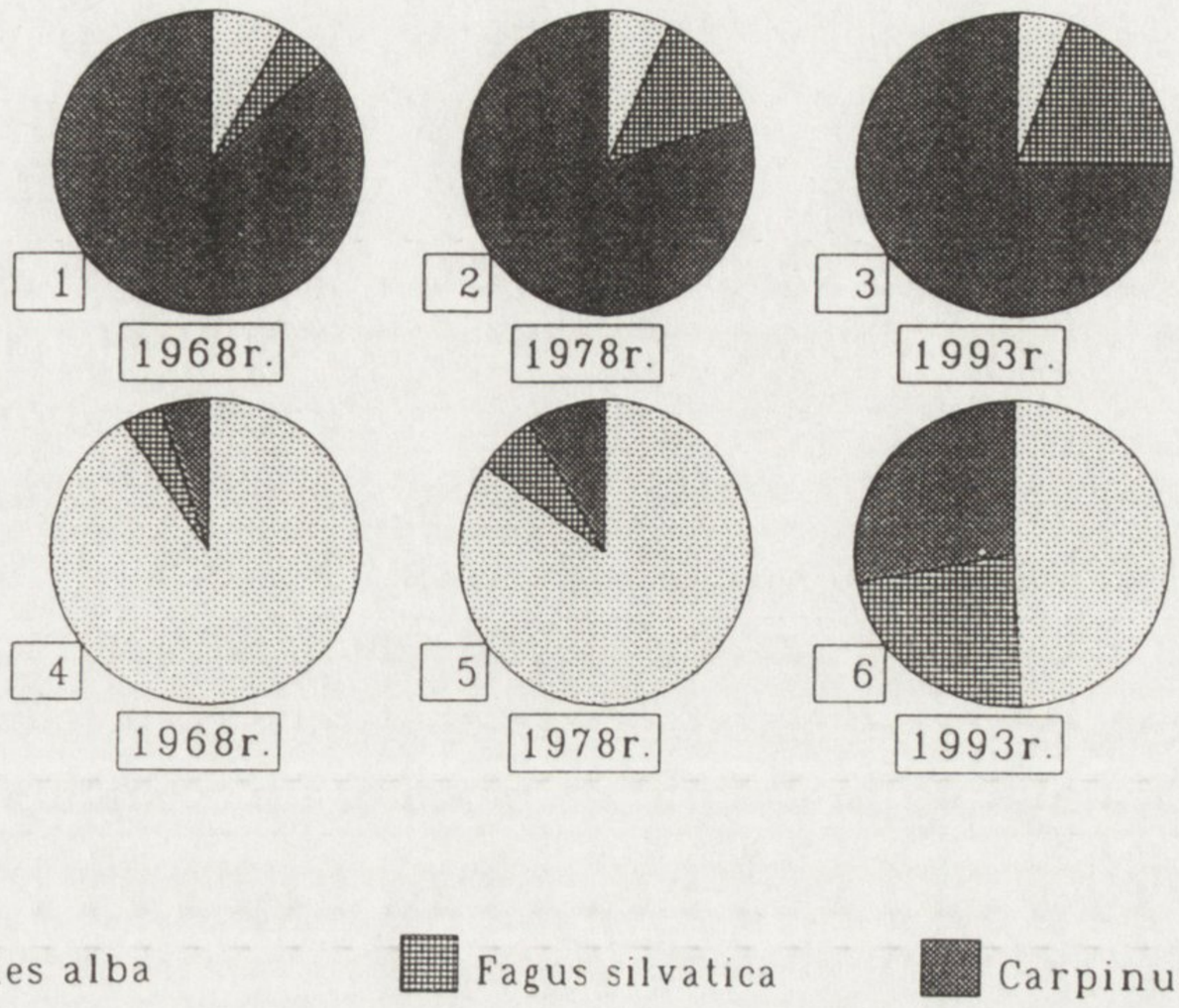

Fig. 4. Percentage contribution of investigated tree species in total number of trees (1, 2, 3) and in total volume of forest stand (4, 5, 6) in the *Dentario glandulosae-Fagetum* plant association (sample plot no 2) in 1968 and 1978 and 1993 years

rapid in the second period than the first, and reached 2.4% per year. An equally high rate of change, albeit with a relatively limited decline in volume of 73 $m^3\ ha^{-1}$, was noted on plot 4 (Fig. 1). A relatively limited decline was noted in the *Querco roboris-Pinetum fagetosum* association, where there were relatively large numbers of dead standing firs (96% of the number alive). However, the trees dying here were those of smaller diameter, so the loss of mass was compensated for by increments in older trees.

Overall, the data cited point to an ongoing process of fir regression. This even occurred in the association optimal to the species, i.e. *Abietetum polonicum.* Here an initial increase in the proportion of fir has been followed more recently by a clear decline, in spite of what is still a considerable increase in mass. This points to the limited vitality of fir in this association in comparison with that of beech. Also attesting to the poor condition of firs is the intensive dieback affecting most of the diameter classes (with numbers of dead standing trees being between 36 and 96% of the numbers left alive), as well as the major representation of this species among dead trees on all plots. It was clear on the plots measured three times that the rate of decline of the species was considerably greater in the second period of study, i.e. in the years 1978–93.

3.1.2. Beech

On plots representative of *Abietetum polonicum* and *Querco roboris-Pinetum fagetosum*, beech showed clear trends towards increased abundance and increased proportional representation among trees of all species (Figs. 2 and 3). The rate of the change is particularly high in the latter community, with c. 130 young individuals per ha joining the undergrowth in the course of a year and thereby increasing the proportion of stand trees that were of this species by 2.5% (Table 1). The increases were more limited in *Abietetum polonicum* association (at +37 individuals per ha per year and, +1.5%). Nevertheless, there is clear expansion of the species in both communities, though plots measured three times do indicate a recent

slowing-down in the increases for the abundance of beech and for the share taken by it (Table 1).

The *Dentario glandulosae-Fagetum* association witnessed a large decline in the abundance of beech on plot 4 (mainly in saplings), and a limited downward trend on plot 2. In the face of rapid increases in the volume and share taken by the species, the decline in abundance results from natural self-thinning in young trees. In all the associations studied there was an increase in volume and in the proportion taken by beech among all species. The greatest changes concerned *Querco roboris-Pinetum fagetosum* (Fig. 2), as well as *Dentario glandulosae-Fagetum* on plot 4 (Fig. 5), where there were the greatest numbers of trees in the middle and higher size classes. A considerable increase in the volume and share of beech occurred, also in the *Abietetum polonicum* association in the last period 44 $m^3\ ha^{-1}$ and 9%. In this last habitat the first period of research was characterized by a weak downward trend for the volume and share taken by beech. However, in the second period, the proportion increased there rapidly at 0.6% per year (about 9% in the whole second period), or a rate of change close to that noted for plots with *Dentario glandulosae-Fagetum*. The sizes and rates of changes in both volume and abundance show that this is currently the most dynamic species in the studied associations within Roztoczański National Park. In addition, on all plots there was an increase in the number of size classes of beech, attesting to good diameter increments among both old specimens and the young generation of trees. There is a very clear process of the passage of trees into higher diameter classes in successive years of measurement (the advancement of trees from class to class), while dead trees only appeared in the last year, mainly in the undergrowth and the lowest diameter classes accounting for between 1.4 and 12% of the number of living trees. The onset of the expansive phase for the species in *Abietetum polonicum* and *Querco roboris-Pinetum* came in the 1960s, as attested to by high abundance and rates of increase in abundance in the first period of research. In turn, the intensive increases in the volume and volume share of beech came at the end of the 1970s.

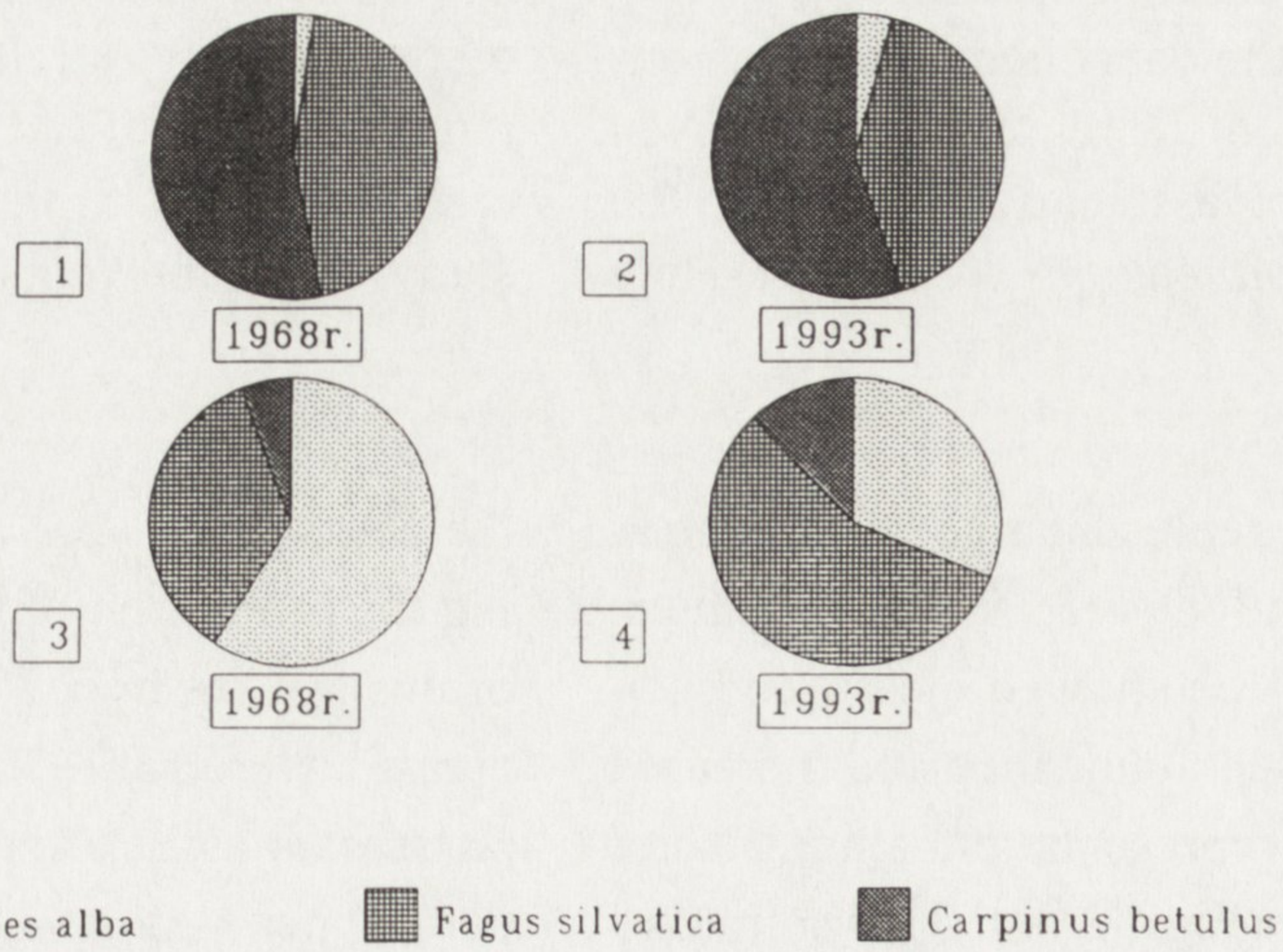

Fig. 5. Percentage contribution of investigated tree species in total number of trees (1, 2) and in total volume of forest stand (4, 5) in the *Dentario glandulosae-Fagetum* plant association (sample plot no 4) in 1968 and 1993 years

3.1.3. Hornbeam

An increase in abundance for this species (more than fourfold) was only noted in *Abietetum polonicum*. The rates of increase in abundance and in the proportion of stand trees of this species were markedly greater in the second period (Table 1). This points to strong expansion of hornbeam into this community. In contrast, in the *Dentario glanduolsae-Fagetum* on plot 2 (Fig. 1), the abundance and proportion of hornbeam declined quickly, especially in the first period of study (by 98 individuals year^{-1}). As with beech, the decline in abundance results from natural processes in stand development. The other plot representing this association (no. 4) was characterized by a rather lower rate of decline in abundance and in share – 44 individuals year^{-1} (Table 1). This probably reflects the greater age of trees on this plot, and hence the earlier onset of the process of intensive self-thinning. In contrast, the plot representing *Querco roboris-Pinetum fagetosum* had had single trees in the undergrowth in 1968, but now has none. The greatest increases in the volume and share of hornbeam occurred in *Dentario glanduolsae-Fagetum* (Figs. 4 and 5), with the rates being greater than those noted for beech in the case of plot 2 (Table 1, Fig. 2), despite a much larger decline in abundance. At the same time, the rate increased rapidly in both species. In contrast, on plot 4, the rates of growth in volume and in the share taken by hornbeam are rather lower than on the previous plot – a fact linked to the smaller number of trees of the species. The hornbeam dynamics in *Abietetum polonicum* is better characterized the change in abundance, on account of the low age of the trees. As with beech, there was an increase in the number of size classes for hornbeam in successive years of measurement. Dead trees were only noted in 1993, in the lowest diameter classes, and the number was equivalent to between 5 and 12% of the number of living specimens.

3.1.4. Spruce

In the first period of study, abundance of spruce declined at a considerable rate and volume at a rather lower rate. Changes in the share taken by this species in stands were of a similar nature. In the second period, there was a slower rate of decline in abundance, and signs of a limited increase in volume and in the share of volume taken by the species (Table 1). At the same time, the ratio of dead to living trees was high (with the former equivalent to 89% of the latter). Also attesting to unfavourable changes in the dynamic for spruce was its retreat from *Querco roboris-Pinetum fagetosum* and *Dentario glandulosae-Fagetum* (plot 4), where it had been found in the undergrowth back in 1968.

3.1.5. Other species

It is mainly on the plot with *Querco roboris-Pinetum fagetosum* that pine and oak co-dominate in the stand. However, both species are showing there a downward trend from the points of view of both absolute abundance and the share taken among all species, with volume showing limited fluctuation (Fig. 2, Table 1). The proportion of dead trees is very high, being equivalent to 54% and

100% of the numbers of living trees. However, the deaths are occurring among the higher diameter classes and the plot shows a complete lack of any young generation of these species, in spite of the periodic appearance of seedlings.

3.2. CHANGES IN FOREST COMMUNITIES ASSOCIATED WITH THE LONG-TERM CHANGES IN SPECIES ABUNDANCE

The data presented point to a relationship between the trends and rates of the ongoing changes and the habitats and corresponding plant communities occurring on the plots.

3.2.1. The *Abietetum polonicum* association

There is a clear decline in the abundances of, and shares taken by, both fir and spruce, with a coincident increase among species more demanding in terms of trophic conditions like beech and hornbeam. As a result, a stand in which the coniferous species – fir and spruce – initially prevailed to the extent of 88% of all trees, has come to be dominated by the broadleaved species now taking a 60% share (Fig. 3). These changes in stand composition by species point to the weakening and retreat of fir, and to its replacement by beech, whose share has increased from 7 to 43% (Fig. 3). The process intensified after 1978, with the trends to changes being the reverse in the earlier period. As changes in abundance mainly involved the trees of lowest diameter, the contribution of fir and spruce in terms of volume showed only a limited decline, with an increase in the role of beech (Fig. 3). The diminished share taken by firs may reflect the weakening of the species on the one hand, and the large increment in mass achieved by broadleaved species – mainly beech – on the other. These changes may in turn result from the eutrophication of the habitat and from climatic changes favouring the latter species (K o w a l s k i 1992). Study of the plant communities of the National Park (I z d e b s k i et al. 1992) reveal that, in conditions of the progressing eutrophication of habitats, *Abietetum polonicum* in its typical form may be transformed into the fertile variant *A. p. circaeaetosum*, and in turn into a community with hornbeam (the sub-association *Tilio-Carpinetum abietosum*).

3.2.2. The *Dentario glandulosae-Fagetum* association

Plot 2 (Fig. 1) showed a decline in the abundance and shares taken by both fir and hornbeam, with increases noted for beech. In spite of this, stand composition by species did not change greatly (Fig. 4). The dominant species in terms of numbers of trees remained hornbeam. The stand volume declined by nearly a half. This resulted from a large fall in the volume of fir in the stand (of 344 m^3 ha^{-1}) which could not be compensated for by volume increments among the mainly young generations of other species. In this case, the dieback of trees was augmented by the major role played by strong winds and rain. In December 1974 and January 1975 these felled or broke most of the old fir trees. Forest compartment No 102, in which the discussed study plot was located, lost 158 fir trees with a volume of 611 m^3 to the wind. Gales are a relatively frequent phenomenon in this region, and one which

brings major losses, especially among firs. Most vulnerable are old stands growing on hilltops, i.e. the most frequent places of occurrence of *Dentario glandulosae-Fagetum*. As a consequence of this, dynamic of the association often assumes a character similar to the "catastrophic" type (Szwagrzyk 1988). Firs suffered particularly badly in the winds of 1974, because in this beech forest association they were at the time the only species with leaves. This combined with the problem of rain-saturated soil unable to give sufficient support to the roots. However, the considerable (229 m^3 ha^{-1}) decline in the volume of fir after 1974 attests to the fact that wind damage is not the main factor behind the decline of the species. More important causes are those inherent in changes in the environment, or in the stand itself. The studies of Michalik (1991), Jaworski and Karczmarski (1990, 1991) have shown that it is from Carpathian beechwoods specifically that the strongest declines in fir have been noted.

In contrast, two other species – beech and hornbeam (Fig. 4) are showing an increase in volume and in share within the stand. This trend has intensified markedly in the last 15 years as a result of the growth of the young generation of trees that were formerly only present in advance regeneration. As a result of the changes in volume among the different species over 25 years, the stand on this plot has changed from being an almost pure fir forest (in which 91% of trees were of this species, or an even higher percentage than the 87% in *Abietetum polonicum*) to being a multi-species one in which broadleaved trees prevail. The trends and rates of changes in volume associated with the abundance and share of hornbeam in the stand point to the very strong position of this species in *Dentario glandulosae-Fagetum*. Hornbeam is a constant element of this association in the region, and a beech forest community with a large share of hornbeam was termed *Fagetum zamosciense* by Sławiński (1946).

There was a decline in the abundance of all the main species on plot 4 (Fig. 1), albeit with almost no changes in the shares taken by them within the stand (Fig. 5). Overall stand volume increased from 361 m^3 ha^{-1} in 1968 to 448 m^3 ha^{-1} in 1993. The trends of changes for the species are as on plot 2 (Fig. 5), except for the fact that fir has shown a smaller fall in volume and share, because the species either died off or was felled even before the research period (the forestry management assessment from 1946 showed fir to be the main species, accounting for 40% of stand volume). However, the higher values for the volume and share of beech result from the larger number of old specimens of the species growing here and experiencing strong increments in volume considerably exceeding those for young hornbeam trees. In 1968, fir dominated in the stand composition by species, but by 1993 the decided dominants were broadleaves accounting for 69% of all trees.

To sum up, both beech and hornbeam may be considered to show similar dynamics in the association under discussion. However, in the face of the much greater number of young, well-developing hornbeam trees, it may be expected that this species will come to determine the character of the association in the near future. The frequent appearance of hornbeam in these beech forest associations may be linked with managemental mistakes made in the past, notably the excessive felling of beeches, with the retention of old hornbeams able to fill the gaps with their seedlings. Attesting to this is the presence of stumps of cut trees within the research plot.

3.2.3. The *Querco roboris-Pinetum fagetosum* association

From the point of view of changes in abundance and volume, this association is showing a clear expansion of beech, mainly at the expense of the self-thinning of firs, as well as of the other main species (Fig. 2), which were not able to find appropriate conditions for growth and development in the community by 1993. As with the plots described above, so in this case too the coniferous species fir and pine were dominant at the beginning of the research period, accounting for 68% of the stand in terms of the number of trees and 60% in terms of volume. However, the latest studies suggest that beech is now the dominant species from both points of view (Fig. 2). Hornbeam was not noted in 1993, but had occurred as single individuals in the undergrowth in 1968. The overall resource of timber in the stand increased, mainly as a result of considerable increments in the volume of beech, as set against a limited decline for fir. However, along with the former species, the latter remains a determinant of the dynamics of the association.

4. DISCUSSION

The following factors exert a significant influence on the dynamics of the stands studied:

a) the natural development of the stands over time – over their full development cycle, natural forests successively pass through the growing-up, optimal and destruction stages. As part of the stages, the developmental phases are identified like the regeneration, ageing and dieback phases (Korpel 1989, Jaworski 1991). In the different stages and phases of development dominance is gained by different biological processes that often act in opposition to one another. In the dieback phase, the death of old specimens create ecological conditions favourable to the emergence and development of a young generation of trees (the regeneration phase). It is thus in this dieback phase that the greatest numbers of trees per unit area are present. By the growing-up stage, the young generation has already become a thicket or consists of pole trees, and these are then subject to a process of intensive mortality of the weakest trees as a result of competition (Szymański 1986). It is first and foremost in this way that it is possible to account for the large declines noted in the number of beeches and hornbeams of lower diameter classes in the plots with *Dentario glandulosae-Fagetum*, as well as the appearance of a large young generation of trees in *Abietetum polonicum* and *Querco roboris-Pinetum fagetosum*. In the latter case, the old stand found itself in the destruction phase earlier as a result of the high grading attested to by the presence of stumps, the action of strong winds or else the self-thinning of old pines. The dominance of beech in the stand and the consequent strong shading of the forest floor did not allow for the development of a young generation of the light-demanding Scots pine, in spite of the fact that seedlings of this species appeared. In turn, the lack of seedlings and saplings of fir in *Dentario glandulosae-Fagetum* may result from the natural process of species replacement ongoing there (Jaworski and Zarzycki 1983).

b) Processes of stand regeneration (Faliński 1991). The stands of the Reserves were brought under strict protection following utilization (felling and

grazing). These processes led to changes in stand structure, species composition and the share taken by different species in the stand. This is clear from the coniferous forest associations, which are losing light-demanding or moderately light-demanding species like Scots pine and oaks respectively. The stand in the *Abietetum polonicum* association has a structure similar to that of beech/fir stands managed by way of a selective felling system. In many plots, diameter breast height distribution of hornbeams may attest to the partial cutting of the species in the past, with no more than single seed trees left with a view to the future creation of a subcanopy layer formed from this species.

c) climate change. The currently-prevalent climatic warming (Kowalski 1991, Trepińska 1994) is changing the environmental conditions for trees through: an increase in mean air temperatures, particularly in the winter period; an extension of the growing season; changes in the distribution of precipitation through the year and the eutrophication of habitats. These changes may provoke changes in distributional ranges of certain tree species (Kienast and Brzeziecki 1993), with some being favoured while others are weakened or eliminated (Kowalski 1991, Xu 1993, Siwecki 1994). Involving as it does the elevation of the mean temperatures for winter months, the warming exerts a great influence on the vitality of spruce, whose proper development requires a minimum of 4 months with temperatures below 0°C (Obmiński 1977).

In the conditions typical for the forests of Roztoczański National Park, these changes may be favouring the development of species like hornbeam (Kowalski 1993) or beech, and their expansion into coniferous forest communities, as well as leading to the weakening and elimination of spruces and old fir trees. In their youth (c. 150 years ago), the latter would have developed in completely different ecological conditions shaped by the so-called "little ice age" (Trepińska 1994).

d) the effects of earlier human interference. Contributing to the appearance of a large young generation of hornbeam was human management activity entailing the thinning of stands with a view to obtaining natural regeneration amongst beeches and firs. In the face of the rarity of abundant fruiting among fir and beech on the one hand, and the frequent fruiting, presence of old specimens and specific life strategy of hornbeam (Faliński and Pawlaczyk 1993) on the other, it was in fact the latter species which came to dominate in the gaps which appeared. Favourable changes in the habitat combined with the dieback of fir to favour the further development of hornbeam and its attainment of a competitive advantage over beech. However, in the light of references to the expansion of this species in a variety of stands (Danielewicz 1991), including ones that are not cut (Włoczewski 1972, Kowalski 1993), it should be presumed that human activity is only accelerating the expansion of hornbeam in the area, while the main causes of the observed changes are disturbances resulting from changes to the climate and soil. Palynological research by Ralska-Jasiewiczowa (1993) also attests to the increasing role of hornbeam in broadleaved forest communities subject to various kinds of disturbance.

e) the eutrophication of forest habitats. This process may result from both climatic change (Billett 1993, Kowalski 1993) and the deposition of air pollutants (Brożek 1986, Greszta 1987, Bucking 1992). Although the Park is some distance from large centres

of industry, the level of deposition of air pollution is relatively high (Maciejewski 1995). This is particularly the case for dusts, whose deposition exceeds 45 tones per km^2, albeit with calcium carbonate being the main chemical constituent. According to Tobolski (1976), the so-called climatic optimum (mesocratic stage) saw a forest dominated by oak develop on poor, lime-free sands of fluvial origin, on the sands of coastal dunes and on detritus gyttjas and on wood peats. This attests to a strong link between climate and soil fertility.

The eutrophication of habitats is leading to marked changes in the Park's plant associations (Izdebski et al. 1992). It is favouring the development of such more-demanding species as beech and hornbeam. At the same time, the relatively high level of air pollution is weakening sensitive species like fir, spruce and Scots pine. Soil studies done at various sites with fir in southern Poland (including Central Roztocze) show the species to develop better in poor habitats, like mixed forest on podsolic soils with moder or mor humus that is acidic throughout the profile and has high exchangeable acidity, than in more fertile, more alkaline habitats such as upland forest (Januszek 1988).

f) catastrophic atmospheric phenomena, such as the heavy falls of wet snow and storms linked with hurricane winds, that occur relatively frequently in the area of the Park. These accelerate the decline of an old stand, ensuring that those aged 180–200 years have permanent gaps in the canopy and are entering the regeneration phase. Moreover, in some phytocoenoses of the *Dentario glandulosae-Fagetum* association these have contributed to the almost total elimination of old firs from the stand. The occurrence of heavy rain and strong winds in winter may also be a result of climate change.

5. CONCLUSIONS

1. The species showing the greatest long-term dynamics since the 1960s is beech, which has increased in relative abundance and volume in all the forest associations studied. It is also rapidly expanding into coniferous forest associations.

2. A rather more limited dynamics is being shown by hornbeam in the associations studied. This species develop well in *Dentario glandulosae-Fagetum* and *Abietetum polonicum*.

3. Fir is declining in all the forest associations studied, though the highest rates of change in abundance and volume characterize *Dentario glandulosae-Fagetum*, where the species is hardly present at all in younger age classes. In coniferous forest associations, normal development is only being shown by fir trees of greater size.

4. The remaining species studied – spruce, Scots pine and oak – are showing a tendency to disappear from the studied associations, with declines in abundance and share of the stand in terms of volume.

5. Rates of change are different for the different forest associations, and are dependent on the phase of stand development. In the cases of fir, beech and hornbeam, the rate of change was markedly higher in the last period of study.

6. A major role in the dynamics of the forest associations of Roztoczański National Park is played by catastrophic atmospheric phenomena like the storms

associated with strong winds and heavy falls of wet snow that occur relatively frequently in this part of Poland.

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6. SUMMARY

The aim of the study was to determine the trends and rates of changes to the structure and species composition of stands in selected forest associations. Research was done in 1993, on 4 permanent plots representing Carpathian beech forest *Dentario glandulosae-Fagetum*, upland mixed fir forest *Abietetum polonicum* and continental oak-pine forest with beech *Querco roboris-Pinetum fagetosum*, and located in the strictly-protected part of Roztoczański National Park (Fig. 1).

The results reveal significant and rapid changes in the stands. The directions and rates of change depend on the prevailing association and on the stage of stand development. The species showing the greatest dynamic is beech, which has increased its share in terms of numbers or volume in all the associations studied (Figs. 2–5), and is expanding rapidly into coniferous forest. A more limited dynamic is being shown by hornbeam, which is developing well in Carpathian beech forest (Figs. 4 and 5) and fir forest (Fig. 3), but which has disappeared completely from the continental oak-pine forest, where it had been present as single specimens in 1968. Fir is decreasing in all the associations studied (Figs. 2–5), but most rapidly in *Dentario glandulosae-Fagetum* (Table 1), where individual of younger age classes hardly now occur at all. Other species, like Scots pine, oak and spruce, are showing limited downward trends in the associations studied, with their abundance, or share of stand volume, decreasing (Figs. 2 and 3). The rate of these changes was greater in the later period of study (Table 1).

The dynamics of the studied stands are much influenced by processes associated with the natural development of the forest, by regeneration processes, and also by catastrophic atmospheric phenomena. However, changes in stand composition on the scale noted are probably caused by the eutrophication of forest habitats and climate change.

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