

Regeneration-degeneration processes in the inland dune forests in protected areas of central Poland (Kampinos National Park)

Abstract

The aim of our study was to quantify the differences in the regeneration-degeneration processes in pine and mixed oak-pine forest habitats in the Kampinos Forest (central Poland). We investigated whether the regeneration rate depends on habitat type, whether there is a relationship between the bilberry (*Vaccinium myrtillus*) cover and the degree of community deformation, and which habitat type has been most invaded by alien plant species. Our results indicate that the constant loss of pine forest habitats, which has been observed since the 1970s, is continuing. The less deformed communities generally have more bilberry coverage, the stands in pine forest habitats are older and less deformed, and the stands in mixed oak-pine forest habitats are more susceptible to the spread of alien species, but are able to regenerate faster after a disturbance. These results are in line with observations from other parts of Poland and other European countries.

Keywords

Pine forests • mixed oak-pine forests • regeneration • inland dunes • Kampinos National Park • central Poland

© University of Warsaw – Faculty of Geography and Regional Studies

Anna Kowalska, Ewa Kołaczowska

Institute of Geography and Spatial Organisation
PAS, Poland
e-mail: aniak@twarda.pan.pl
e-mail: ekolaczka@twarda.pan.pl

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Introduction

Vegetation dynamics comprises (following Faliński 1986) two distinctly directional processes – succession and regression – as opposite, reversible processes consisting of irregular changes which occur at variable intervals, i.e. the fluctuation, degeneration and regeneration of phytocenoses, and strictly cyclic and periodical processes such as seasonality. As degeneration, regeneration and fluctuation do not lead to irreversible changes in the structure and function of phytocenoses and as they ensure their stability (permanence) they may be called the internal dynamics of the phytocenosis (Pawłowski & Zarzycki 1972). The terms degeneration and regeneration refer to the disintegration and reconstruction, respectively, of structures specific to a given phytocenosis under the influence of external factors (Faliński 1986).

The regeneration of forest communities depends on a number of different factors, including past land-use, habitat type, forest persistence (temporal habitat continuity) and stand age, as well as management practices. Forest persistence over time is the most important factor in community regeneration (Matuszkiewicz et al. 2013a). The floristic composition of recent, usually post-agricultural forests is very different from that of ancient forests (Peterken 1977; Rackham 1980; Dzwonko & Gawroński 1994; Wulf 2003; Matuszkiewicz et al. 2013b), because forest species' recovery is very slow. Forest floor plants have specific biological traits (including shade tolerance, low dispersal capacity, limited mobility outside the forest environment, and the requirement of specific soil conditions) and lack the ability to compete with common species with wider ecological amplitude (Brunet & von Oheimb 1998; Dzwonko & Loster 2001; Hermy & Verheyen 2007). Agricultural land use has persistent effects on soil properties, even after several decades

or centuries. Land cultivation brings about changes of the water balance, soil reaction and biochemical components (Verheyen et al. 1999; Dupouey et al. 2002; Flinn & Marks 2007).

The regeneration process in old-growth forests depends mainly on the management practices undertaken in the ecosystem, such as the introduction of plant species and the creation of clearings by felling trees, as well as animal grazing pressure (wild and livestock), the gathering of firewood and other activities (Kirby 2001; Zielony 2004a; Olofsson et al. 2005). These factors limit or promote the development of specific species and influence plant community structure and habitat conditions. The introduction of invasive alien plant species to a forest usually leads to aggregations of one dominant species and community degeneration (Tokarska-Guzik 2005). On the other hand, there are species which speed up the regeneration process, for instance bilberry *Vaccinium myrtillus* L. This is one of the most important components of the herb layer in the pine and mixed oak-pine forests of the northern hemisphere. It contributes significantly to biomass production and to the matter cycle of substances rich in elements that are important to forest ecosystems (Moszyńska 1983). The presence of bilberry prevents soil erosion (Gądziński 1967) and promotes the formation and accumulation of a humus layer (Grochowski 1976) and the renewal of tree species (Jäderlund et al. 1996), as well as the development of other underground species (Parlane et al. 2006).

Kampinos National Park is a good example of postglacial valley relief with different types of inland dunes. The forest habitats have a long history of change and are worthy of study. In the 1960s, pine forest habitats dominated the dune fields, but



Figure 1. Location of the Kampinos National Park and the study area (Krzywa Góra forest division) within the Park

thirty years later their area had been diminished by almost half. They were mostly replaced by mixed oak-pine forest habitats, a change that was difficult to explain (Solon 2003). With these changes in mind, the aim of the present study was to quantify the differences in the regeneration-degeneration processes in pine and mixed oak-pine forest habitats. We looked at whether the actual plant communities were consistent with potential natural vegetation types (the concept of potential natural vegetation introduces the idea of the expected state of mature vegetation in the absence of human intervention – Tüxen 1956), with regard to plant species composition and tree stand structure. We investigated: (i) whether the regeneration rate of a specific forest community depends on habitat type, as has been observed in other studies (Matuszkiewicz et al. 2013a); (ii) whether there is a relationship between bilberry cover and the degree of community deformation, and (iii) which habitat type is more exposed to degeneration caused by alien plant species.

Materials and methods

Study area

The study was conducted in the northern dune belt of the Kampinos National Park, in the Krzywa Góra division (1522 ha) (Fig. 1). The whole Park covers 38,500 ha and was established in 1959 to maintain the unique complex of inland dunes and wetlands with their landscape and biological diversity.

Parabolic and ridged dunes of different sizes dominate in the Krzywa Góra division. The dunes have been stabilized mainly by pine and mixed oak-pine forests (Fig. 2). Most of the stands are considered to be ancient forests, as they have persisted in the landscape for at least 200 years. Their existence is documented in the Topographic Map of the Polish Kingdom of 1839, and in subsequent maps of the area (Kowalska 2006). Only the current forest patches located along the southern and northern borders of the study area are growing on former agricultural lands, which have been assigned to the Park over the last few decades. Thus the Krzywa Góra division may be considered a model subject for studying dynamic processes in pine and mixed oak-pine forests. The pine forests are represented by two phytosociological

associations: *Peucedano-Pinetum* W.MAT. (1962) 1973 and *Leucobrio-Pinetum* W.MAT. (1962) 1973¹. They have been considered together due to the frequent coexistence of their characteristic species on the edge of their range. The mixed oak-pine forests are mainly represented by the *Quercus roboris-Pinetum* (W.MAT. 1981) J.MAT. 1988² association.

Data collection and analysis

The habitat type, the actual plant community phytosociological type and the degree of vegetation deformation were all diagnosed for each distinguished forest patch on the basis of vegetation field mapping conducted in summer and early autumn 2013. The community deformation was defined as the dissimilarity of a given forest patch in terms of species composition and vertical structure to the potential natural vegetation (*sensu* Tüxen 1956), phytosociologically, at the level of potential natural association (PNA). It was assessed using a seven-degree (0–6) ordinal scale, where 0 means no deformation and 6 means severe deformation, i.e. a community being beyond the scope of the potential natural association (Matuszkiewicz & Solon 2006) (Table 1).

¹The characteristic species combination of the *Peucedano-Pinetum* association consists of ChCl.: *Dicranum scoparium* HEDW., *Pleurozium schreberi* (WILLD. EX BRID.) MITT., *Hylocomium splendens* (HEDW.) SCHIMP., *Melampyrum pratense* L., *Ptilium crista-castrensis* (HEDW.) DE NOT., *Trientalis europaea* L., *Vaccinium myrtillus* L., *Vaccinium uliginosum* L., *Vaccinium vitis-idaea* L.; ChO.: *Pinus sylvestris* L., *Cladonia rangiferina* (L.) NYL., *Cladonia arbuscula* (WALLER.) FLOTOW, *Dicranum polysetum* EHRH. EX F. WEBER ET D. MOHR.; ChAll.: *Chimaphila umbellata* (L.) W. P. C. BARTON, *Diphysastrum complanatum* (L.) HOLUB, *Monotropa hypopitys* L. S. STR., *Pyrola chlorantha* SW.; DAss.: *Peucedanum oreoselinum* (L.) MOENCH, *Convallaria majalis* L., *Polygonatum odoratum* (MILL.) DRUCE, *Pulsatilla patens* (L.) MILL., *Scorzonera humilis* L., *Solidago virgaurea* L. In comparison, *Leucobrio-Pinetum* is poorer in plant species but is characterized by a great abundance of *Leucobrium glaucum* (HEDW.) ÅNGSTR., *Deschampsia flexuosa* (L.) TRIN., *Hyponum cupressiforme* HEDW. and *Fagus sylvatica* L. (DAss.). The latter is an alien species in this part of Poland (Matuszkiewicz 2001).

²Elements of the *Vaccinio-Piceetalia* order dominate in its characteristic species combination, but species of the *Quercus-Fagetea* class (*Carex digitata* L., *Carpinus betulus* L., *Corylus avellana* L., *Euonymus verrucosa* SCOP., *Melampyrum nemorosum* L., *Melica nutans* L., *Mycelis muralis* (L.) DUMORT., *Quercus petraea* (MATT.) LIEBL., *Quercus robur* L., *Viola reichenbachiana* BOREAU) are constantly observed. Pine and oak co-dominate in the stand but oak *Quercus robur* has greater significance (Matuszkiewicz 2001).

Table 1. The seven-degree scale of vegetation deformation used in the field study (according to Matuszkiewicz & Solon 2006)

Degree of deformation	Characteristics
0	<i>No deformation</i> – actual community resembles perfectly a particular potential natural association (Matuszkiewicz JM 2001) in terms of floristic composition and stand and undergrowth structure (presence of very old trees and dead wood), without alien species and soil ground cover transformation.
1	<i>Minimal deformation</i> – as above, but characteristic species composition represented in at least 80%.
2	<i>Slight deformation</i> – floristic composition is consistent with characteristic species composition, with small gaps and few species alien to the association (50–80% of characteristic species). Stand structure may be changed in terms of age and composition (equal-age of trees; gaps in the stand; absence of typical, secondary species; greater cover of additional species) or overdeveloped undergrowth.
3	<i>Significant deformation</i> – floristic composition and stand and undergrowth structure distinctly depart from the PNA (only one typical species in the stand; typical species only in the undergrowth, domination of ecologically/geographically alien or additional species; 35–50% of characteristic species composition).
4	<i>Big deformation</i> – there are big gaps in characteristic species composition (presence of 20–35% of species) and stand structure significantly changed.
5	<i>Very big deformation</i> – community is hardly identified (under 20% of characteristic species).
6	<i>Severe deformation</i> – vegetation beyond the scope of potential natural association.

The forest patches established in pine and mixed oak-pine forest habitats were also compared with each other in terms of the stand age identified from the existing forest map. Additionally, each forest patch was characterised by the percentage of bilberry cover (a projection of leaved heads of shrubs expressed in percentage terms) and the presence or absence of alien plant species (giant goldenrod *Solidago gigantea* AITON, black cherry *Prunus serotina* EHRH., black locust *Robinia pseudoacacia* L. and red oak *Quercus rubra* L.).

To explore the differences in the regeneration process across pine and mixed oak-pine habitats, the percentage share of forest patches classified to a certain deformation degree was calculated. Spearman's rank correlation test was used to examine the relationships between the stand age and the degree of deformation in each habitat type as well as to correlate the cover of bilberry with the degree of community deformation and the stand age. For these analyses, we selected mature stands, i.e. those aged over 50 years (according to the forest stand classification for Polish forests by Andrzejewski 1991).

Fisher's exact probability test was used to compare the frequency of occurrence of alien species in the habitat types, combined with the stand age categories.

The statistical analyses were carried out using the Statistica 7.1 software package.

Results

Pine and mixed oak-pine forest habitats cover 92% of the study area. The areal ratio of these habitats is 1:6 (198:1199 ha), with dominant mixed oak-pine forests surrounding pine forests (Fig. 2). This corresponds closely to the ratio calculated for the whole area of dune belts in the park, 1:5 (2450:14039 ha).

We distinguished 53 patches of pine forest and 295 patches of mixed oak-pine forest habitats in the studied division. A considerable amount of forest phytocoenoses in the mixed oak-pine forest habitats was beyond the scope of the PNA (category 6) – 45% (541 ha), compared to 36% (71 ha) in the pine forest habitats. Their stands were generally built by native species: Scots pine *Pinus sylvestris*, silver birch *Betula pendula* and/or English oak *Quercus robur* – but their structure was severely deformed (young or equal-aged trees, numerous gaps in the stand, co-domination of alien or additional species) and the species composition of the undergrowth was very limited

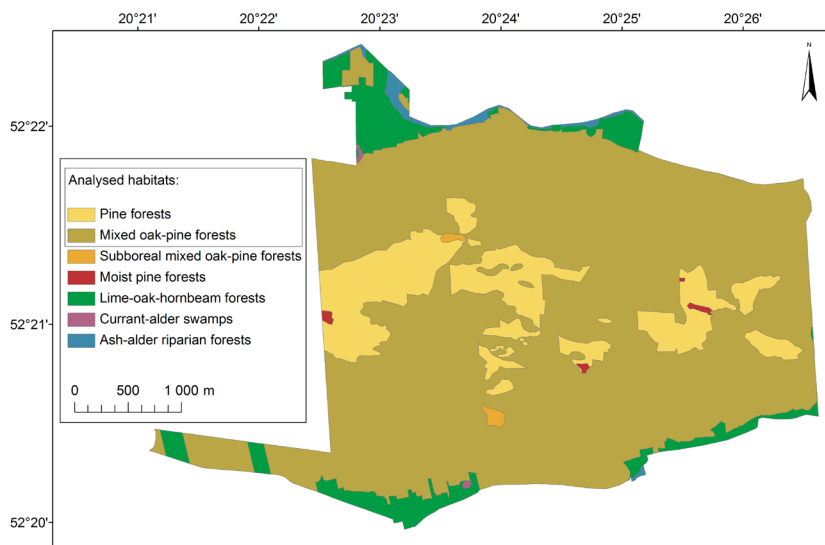


Figure 2. Distribution of potential natural vegetation (habitats) in the study area



Photo 1. Entirely deformed pine forest (6th degree of deformation)
Author: Ewa Kołaczowska



Photo 2. Well-developed pine forest (2nd degree of deformation)
Author: Ewa Kołaczowska

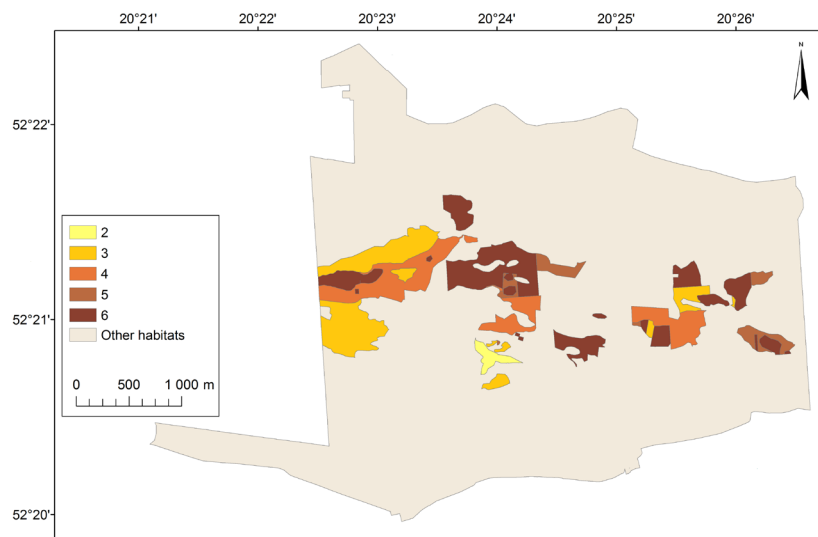


Figure 3. Deformation of the pine forest communities in the study area according to the seven-degree (0–6) scale of vegetation deformation (0 and 1 were not observed)

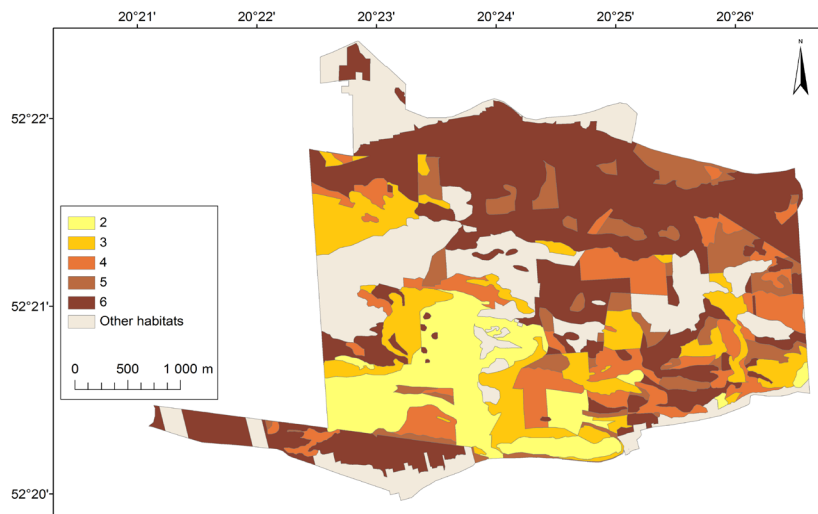


Figure 4. Deformation of the mixed oak-pine forest communities in the study area according to the seven-degree (0–6) scale of vegetation deformation (0 and 1 were not observed)

(Photo 1). These forest phytocoenoses were not sufficiently developed for them to be assigned to a certain phytosociological association. However, some patches – usually those with mature stands – were identified phytosociologically as examples of the *Dicrano-Pinion* W. Mat. 1962 alliance³.

Stands younger than 50 years accounted for 10% (124 ha) of mixed oak-pine forest habitats and 2.5% (5 ha) of pine forest habitats.

The most natural patches were located in the southern and middle parts of the study area, although no examples of undeformed communities (category 0), nor anything very similar (category 1), were observed in both habitat types. Well-developed phytocoenoses (2–4) accounted for 57% (127 ha) of pine forest habitats and 44% (658 ha) of mixed oak-pine forest habitats (Fig. 3, 4, 5, Photo 2).

There was no correlation between the degree of deformation and forest stand age (excluding the young stands) (Table 2). Although they were weakly negatively correlated in the case of the pine forest habitats (the patches with older stands resembled their

PNA more than those with younger stands), this relationship was not significant (Table 2). We found many examples of stands which were over 90 years old and were far from their potential natural state. The specific features of such stands in mixed oak-pine forest habitats suggest that they were former pine forests (Table 2).

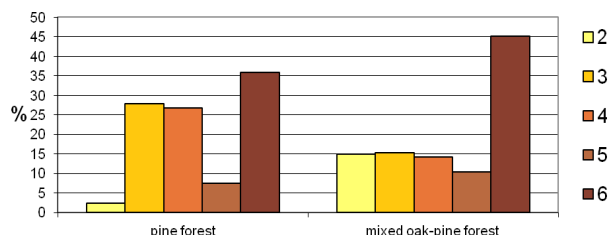


Figure 5. The percentage of pine and mixed oak-pine forests in the study area that have been deformed according to the seven-degree (0–6) scale of vegetation deformation (0 and 1 were not observed)

Table 2. Correlations between chosen ecological parameters of the phytocoenoses developed in the pine forest habitats PF and in the mixed oak-pine forest habitats MF; forest stands aged under 50 are not considered; $N_{PF} = 53$, $N_{MF} = 295$

Variables	Habitat type	Spearman r_s statistic	p (uncorr.)
Degree of deformation (0–6) vs. forest stand age (yrs)	PF	-0.250	0.071
	MF	-0.037	0.530
Degree of deformation (0–6) vs. cover of bilberry (%)	PF	-0.331	0.015
	MF	-0.211	<0.001
Forest stand age (yrs) vs. cover of bilberry (%)	PF	0.402	0.003
	MF	0.246	<0.001

Table 3. Frequency of occurrence of alien species in the forest patches. Test of the frequency difference between the forest categories (habitat type and stand age) according to Fisher's exact test: bold indicates the significance of the test between categories $p \leq 0.05$; PF – pine forest habitats, MF – mixed oak-pine forest habitats; young – stands aged 50 or less; old – stands aged over 50; * high frequencies of occurrence of giant goldenrod and black cherry in young pine forests result from a small number of patches

Name of alien plant species	Frequency of occurrence of alien species according to the habitat types and the stand age categories [%]				p value					
	young PF	old PF	young MF	old MF	young PF vs old PF	young PF vs young MF	old PF vs old MF	young MF vs old MF	young PF vs old MF	old PF vs young MF
giant goldenrod <i>Solidago gigantea</i>	25.0*	0.0	8.5	1.2	0.07	0.31	1.00	0.00	0.07	1.00
black cherry <i>Prunus serotina</i>	25.0*	0.0	18.2	6.5	0.07	0.56	0.06	0.00	0.29	1.00
black locust <i>Robinia pseudoacacia</i>	0.0	0.0	8.5	5.0	1.00	0.31	0.14	0.16	1.00	1.00
red oak <i>Quercus rubra</i>	0.0	0.0	3.6	7.1	1.00	0.16	0.06	0.16	1.00	1.00

³The alliances stand directly above the associations in the Braun-Blanquet phytosociological classification system.

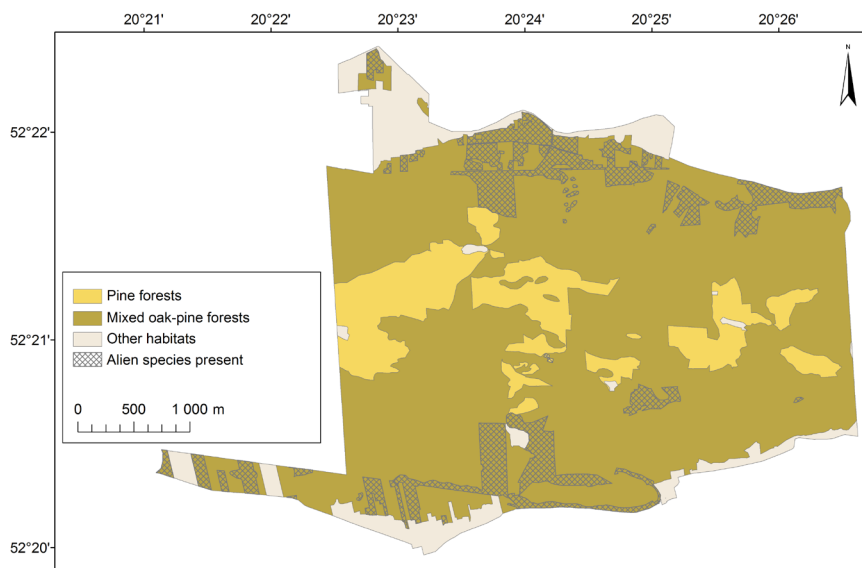


Figure 6. Distribution of alien species in the pine and mixed oak-pine forest habitats in the study area

We observed a general trend that the more natural the forest patch, the higher the bilberry *Vaccinium myrtillus* cover. This species is associated with ancient forests (Dzwonko & Loster 2001), and this study confirms its greater abundance under older stands in both habitat types. Moreover, this correlation is stronger for the pine forests than for the mixed oak-pine forests (Table 2).

One of the most important factors hindering the regeneration of the PNA in the studied area was the occurrence of alien plant species. The most frequently noted aliens were four invasive ones: giant goldenrod *Solidago gigantea* AITON, black cherry *Prunus serotina* EHRH., black locust *Robinia pseudoacacia* L. and red oak *Quercus rubra* L. They were concentrated mainly at the edge of the forest, in the vicinity of human settlements, along paths and other routes (Fig. 6). Overall, they were most abundant in mixed oak-pine forest habitats and in forest communities under 50 years old. The only exception was red oak which was more frequent in the older stands. However, significant differences occurred only for giant goldenrod and black cherry, between young and old communities of mixed oak-pine forest habitats (Table 3).

Discussion

The physiognomy of the analysed forest area, as well as the main reasons behind the deformation of the plant communities identified during the field study, indicated that the most important factors responsible for the current distribution of the forest habitat types are land management practices. This also explains why some of the patches on the maps have angular shapes.

According to Kobendzina (1979), mixed oak-pine forests had historically dominated the inland dunes in Kampinos Forest, until human pressures changed the habitat. Heymanowski (1975) reported that oak trees were intensively felled for the ship-building industry and military purposes in the second half of the 19th and beginning of the 20th centuries. Further regression of the mixed oak-pine forest habitats was caused by forest destruction as a result of both World Wars. Deforested sites were left un-restocked, which also often led to secondary migration of the dunes. Forest exploitation and the large scale logging of broadleaved trees promoted the faster growth of the extant Scots pine, and limited the admixture of deciduous species.

The distribution of pine forest and mixed oak-pine forest habitats has varied extensively over the past 50 years. Maps of the potential natural vegetation of Kampinos National Park, which depict its state in the mid-1960s (Matuszkiewicz 1966), at the beginning of the 1980s (Matuszkiewicz 1982), and finally in the mid-1990s (Solon 1994), show a decreasing area of pine forest habitats and an increasing area of mixed oak-pine forest habitats. Now, our research indicates that pine forest habitats are still in decline, most likely due to the regeneration of moister, more fertile habitats after the discontinuation of domestic livestock grazing in the forests, traditional litter raking in the Park in the late 1960s and early 1970s, as well as numerous oak plantings (Zielony 2004a). The transition from pine forests to mixed oak-pine forests has been described in the context of recovery processes from degradation in Poland (Dzwonko & Gawroński 2002; ed Matuszkiewicz 2007; Stefańska-Krzaczek 2010) and in Central Europe (Heinken 2008; Reinecke et al. 2014).

The stands in the pine forest habitats have in general a better developed vertical structure than those in the mixed oak-pine forest habitats. However, the latter seem to regenerate faster due to the fact that even the phytocoenoses with immature stands (less than 50 years old) were developed in accordance with the potential natural vegetation. Our results are also in line with the observations of Matuszkiewicz et al. (2013a), who found that forest communities regenerate faster in more fertile habitats. They also proved that bilberry has a significant influence on undergrowth structure, and that this species was more abundant in ancient and older forests than recent forests (north-eastern Poland). The same was observed during the present study in Kampinos Forest and by Góras & Orczewska (2007) in south-western Poland. Furthermore, our results are in line with other European studies (Sweden – Kardell 1980; Hedwall et al. 2013; Finland – Reinikainen et al. 2000; Germany – Jandt et al. 2011) showing that bilberry abundance increases with forest age but declines with tree density. This dwarf shrub decidedly prefers half-shade or moderate light under moderate canopy cover (Głowacki 1999; Ihalainen et al. 2002; Nielsen et al. 2007).

Alien species are not highly abundant in the Krzywa Góra division (often occurring singly in patches), and are generally more frequent in the more fertile, mixed oak-pine forest

habitats and in young stands, which is in accordance with other observations. It was found that non-natives are more abundant in communities with a high degree of disturbance (Pyšek et al. 1995), and also in those with higher nutrient availability (Davis et al. 2000). The most explicit example of the negative influence of alien plant species on the forest vegetation is the spread of black cherry which constrains the development of other native species (Otręba 2014; Zielony 2004b). Introduced by foresters, this species is easily dispersed by frugivorous birds and some mammals (Otręba & Mędrzycki 2009). The abundance of red oak is also associated with forest management. It was planted to improve habitat conditions, taking advantage of the fact that this species grows faster and is more tolerant of adverse climates, soil and light conditions than native oak species (Tomanek 1997). At present, red oak is rarely planted in Kampinos Forest, which is why it is more frequent in the older stands. The invasion of alien species is a common problem in other protected areas where they are chemically and mechanically controlled (Danielewicz & Maliński 1997; Dajdok et al. 2007; ed Matuszkiewicz 2007).

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