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Natural regeneration in the 'Czmoń' nature reserve (Wielkopolska Region)

Paweł Horodecki[1], Katarzyna Wiczyńska[1], Andrzej M. Jagodziński[1,2*]

[1] Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, 62–035 Kórnik, Poland; [2] Poznań University of Life Sciences, Department of Game Management and Forest Protection, Wojska Polskiego 71c, 60–625 Poznań, Poland.

*Tel. +48 61 8170033, fax: +48 61 8170166, e-mail: amj@man.poznan.pl

Abstract. The 'Czmoń' nature reserve (23.65 ha) was established in 1998 to protect one of the best-retained areas of natural oak-hornbeam forest (*Galio-Carpinetum*) in the center of the Wielkopolska Region. Apart from oak-hornbeam forest, the ash-elm riparian forest (*Querco-Ulmetum*) and alder riparian forest (*Fraxino-Alnetum*) are found in the reserve. These plant communities, both natural and degenerated as a consequence of previous forest management, have created the convenient conditions for assessment the phytocoenoses' regeneration potential. The aim of this study was to assess the age and species structure of woody species natural regeneration of the whole area of the nature reserve.

To achieve that target, during August and September 2012, 142 sample plots were established with the total area 3550 m^2 on which tree and shrub composition and densities were calculated.

Woody species regeneration created various diverse communities among individual sub-units, however oak-hornbeam forest species were predominant in the whole regeneration layer.

The character of a 'natural' forest was retained on a part of the stands. Moreover, regeneration in degenerated parts of the 'Czmoń' nature reserve stands is changing according to potential vegetation. Whereas, the establishment of gaps in the Scots pine stands using artificial regeneration was not worthwhile. The natural regeneration structure under the canopy layer of Scots pine stands unambiguously supports the claim that phytocoenoses can regenerate on their own. In spite of the oak regeneration being infrequent, all stands within the 'Czmoń' nature reserve retain substantial rejuvenation potential.

Key words: natural regeneration, phytocoenoses regeneration, oak-hornbeam forest.

1. Introduction

In the past, broadleaved forests were common in the lowland part of Poland. Due to the fertility of habitat, they were partially converted to cropland during the most intensive development of agriculture (Danielewicz, Pawlaczyk 2004a). Some oak-hornbeam forests were replaced by poorer forest communities through the introduction of fast-growing and less demanding tree species such as *Pinus sylvestris* (Olaczek 1974; Jaszczak et al. 2011). The resulting pure stands are characterised by a lower biological stability than mixed or deciduous stands (Dobrowolska 2006). Part of the oak-hornbeam forests that remained in Poland are deformed, which can be seen not only in changed species composition and structure of forest stands but also in a clear depletion of forest floor species composition (Danielewicz, Pawlaczyk 2004a; Woziwoda 2007). Many studies conducted in such transformed forest communities have allowed for better identification of the consequences of management of forest stands incompatible with the ecological requirements of individual tree species (Balcerkiewicz 1991; Łaska 1996). An interest in natural self-regulatory processes in transformed forest communities has

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also increased (Jaszczak et al. 2011). The stability and biodiversity of plant associations increases significantly favouring the natural regeneration (Dobrowolska 2006), and hence the emphasis is now on the use of regenerative forces of nature, trying to limit human impact on the environment. However, there are few examples of studies showing the regenerative potential of oak-hornbeam forests, including the degenerated ones (Sowa et al. 1993; Bobiec 2007; Miścicki 2012).

The 'Czmoń' nature reserve was created in 1998 to preserve one of the most natural fragments of oak-hornbeam forests, *Galio-Carpinetum*, in the centre of the Wielkopolska Region (Lisiewska, Król 2007). Tree stands growing there are characterised by relatively high diversity. This is the result of both spontaneous processes as well as management of varying intensity applied in this area in the past. The area of the reserve started to be informally protected in the late 80s of the last century, when silvicultural treatments were kept down to a minimum (Bernat 1989). Since then, the plant communities there, either natural or close to natural or degenerated to various degrees, have changed only due to spontaneous processes. Only the Scots pine stands growing on the oak-hornbeam habitats were rebuilt by introducing artificial regeneration in gap areas (Wiczyńska et al. 2013). Varying degrees of stand degeneration in the reserve and the natural regeneration processes taking place there make it an interesting subject of research.

The main objective of this study is to assess the condition, age structure and species composition of natural regeneration of trees and shrubs within the reserve. The data obtained also allow comparing the regenerative processes occurring in the well-preserved fragments of oak-hornbeam forests with the degenerated ones of Scots pine.

2. Materials and methods

The study area

The study was conducted in the 'Czmoń' nature reserve (52°09'06" N, 17°02'43" E), located 30 km south of Poznań, in the Śrem Commune (Fig. 1). According to the nature and forest regionalisation of Poland (Trampler et al. 1990), the reserve is located in the Land of the Wielkopolska-Pomerania (III), District of the Wielkopolska-Kujawy Lowland (7), and Mesoregion of the Wielkopolska Lake District (III.7.b), and in later terminology (Zielony, Kliczkowska 2012) in the Land of the Wielkopolska-Pomerania (III) and Mesoregion of the Śremska Basin (III.29). According to the physico-geographical regionalisation of Poland by Kondracki (2002), this area is located in the North European Plain Province, Subprovince of the Southern Baltic Lake District, Macroregion of the Warta-Oder Urstromtal and Mesoregion of the Śremska Basin. Administratively, the reserve is managed by the Babki Forest District.

The reserve is located on a flat area at an altitude of 76 m above sea level. This area is characterised by a relatively short and mild winter and predominant summer rainfall (Woś 1994). The average annual temperature for the decade 1988–1998 was 8.8°C, while the average annual rainfall was 556 mm. The growing season for this area takes an average of 220 days (Plan ochrony rezerwatu "Czmoń" 2006).

According to the data from the Preservation Plan for the 'Czmoń' nature reserve for 2006–2025 (Plan ochrony… 2006), the reserve can be divided into three habitat types: fresh forest site type associated with the *Galio sylvatici-Carpinetum betuli corydaletosum* (12.32 ha), moist forest site type associated with the *Querco-Ulmetum minoris* (9.60 ha) and alder-ash riparian forest site type associated with the *Fraxino-Alnetum* (1.35 ha). Later studies (Lisiewska, Król 2007) have also revealed the existence of dry-mesic oak forest community *Potentillo albae-Quercetum* in the north-eastern part of the reserve. According to information contained in the Preservation Plan for the 'Czmoń' nature reserve (2006),

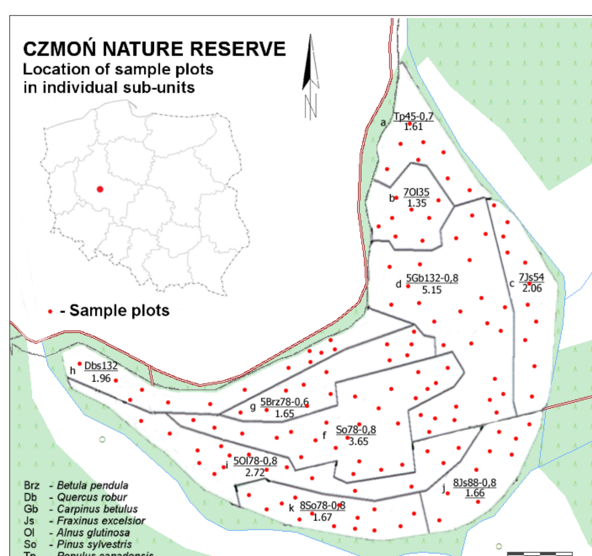

Figure 1. The location of sample plots established for structure analysis of natural regeneration of the 'Czmoń' nature reserve

grey-brown soils occur in 93% of the reserve area and mineral-muck soils, found in the northern parts, in an area of 1.35 hectares.

Stands within the reserve are not homogeneous (Table 1): 10 different sub-units were identified in terms of stand and site conditions. In the sub-units 92 d and h, according to the potential habitat, there is a very well-preserved oak-hornbeam forest, with the dominance of hornbeam and oak in the upper stand. In the sub-units c, i and j, the upper layer of the stand is dominated by riparian species (*F. excelsior*, *A. glutinosa*), and species composition corresponds to the potential vegetation (Plan ochrony… 2006). In the subunits a and g, tree stands are dominated by alien or inappropriate species (*P.* × *canadensis* and *P. sylvestris*), as forest communities in the recovery phase of development. The regeneration process also occurs in the sub-unit b, where alder, ash and hornbeam increasingly move to the second floor of the stand. Forest communities occurring in the sub-units f and k are described in the Preservation Plan for the 'Czmoń' nature reserve (Plan ochrony… 2006) as a degenerated form of oak-hornbeam forest. This is due to the dominance of Scots pine in the upper storey. In the last two sub-units (f and k), gaps were established with the artificial regeneration to accelerate the rebuilding process of tree stands (Wiczyńska et al. 2013).

Methods of research

In order to determine the structure of natural regeneration in the reserve, there were a set of 142 sample plots with an area of 25 m^2 (5×5 m) each (Fig. 1). The number of plots on which natural regeneration was studied varied according to the size of the sub-unit, stand diversity within it and the diversity of the state of natural regeneration of trees and shrubs. The selection of plots has been guided by the principle of proportionality, i.e. if the sub-unit seedlings and saplings were estimated to occupy 20% of the area – the same percentage of the study plots were located within, if gaps occupied 5% of the area – the same numbers of plots were located in gaps. The study was conducted in August and September 2012.

Within each area of research, the state of natural regeneration of the species of trees and shrubs as well as age-height categories was defined. The following were distinguished:

– seedlings (this year plants),
– one-year-old and
– two-year-old and older plants (up to 0.5 m).

Trees and shrubs with a height of 0.5 m to 1.3 m were classified separately. In addition, within each area dead trees and shrubs were counted.

Inside the gaps established to rebuild pine stand in two sub-units (f and k), 20 study plots were located. The condition of regeneration was defined in an analogous manner as in the regeneration analysis of the rest of the area, adding two further categories:

– plants higher than 1.3 m,
– plants topped during cleanings.

In further analyses, the density of natural regeneration in gaps was calculated as the actual number of regeneration minus the number of seedlings of a given species introduced artificially.

3. Results

During the assessment of regeneration within the area of research in the 'Czmoń' nature reserve, 28 species of trees and shrubs in this layer of the forest were found. The presence of natural regeneration of *Acer campestre*, *A. platanoides*, *A. pseudoplatanus*, *Alnus glutinosa*, *Betula pendula*, *B. pubescens*, *Carpinus betulus*, *Cornus sanguinea*, *Corylus avellana*, *Euonymus europaea*, *Fagus sylvatica*, *Frangula alnus*, *Fraxinus excelsior*, *Padus avium*, *P. serotina*, *Pinus sylvestris*, *Populus alba*, *P. tremula*, *Quercus petraea*, *Q. robur*, *Rhamnus cathartica*, *Salix caprea*, *Sambucus nigra*, *Sorbus aucuparia*, *Tilia cordata*, *Ulmus glabra*, *U. laevis* and *Viburnum opulus* has been reported. Natural regeneration of *B. pubescens*, *P. alba*, *P. tremula* and *S. caprea* was observed only within the four gaps established in the Scots pine stands being rebuilt.

Average density of natural regeneration of trees and shrubs to a height of 1.3 m was 59 935 individuals per ha, and less than 1.5% of them were dead (artificial regeneration in gaps within Scots pine stands were excluded from the analysis; Table 2). Amongst all the species, the most frequent were ash, sycamore, hornbeam and common dogwood. In turn, the least regenerating species were sessile oak, beech, silver birch, alder buckthorn, black cherry and small-leaved linden.

Due to the existence of three habitat types in the reserve (see Introduction section) and the associated diversity of forest stands (Table 1), the state of natural regeneration (species composition, density and the proportion of dead individuals) in each sub-unit differed significantly.

In the sub-unit a (1.61 ha), elm-oak riparian habitat was found. The dominant regeneration group were trees and shrubs older than one year with a height up to 0.5 m

Table 1. The description of stands in the 'Czmoń' nature reserve (data in columns 2–4 after Plan ochrony… 2006; in columns 5–9 after Wiczyńska et al. 2013)

Sub-unit (area, ha)	Forest site type	Potential vegetation	Age of A1	Mean DBH of A1 (cm)	Mean height of A1 (m)	Density of trees of given layer (ind. ha^{-1}) A1 Upper storey	A2 Lower storey	B Shrubs and undergrowth
1	2	3	4	5	6	7	8	9
a (1.61)	Lw	F-U	46	35.4; 74.5	24.5	*P. canadensis* (219), *F. excelsior* (10)	-	*C. sanguinea* (7781), *F. excelsior* (695), *C. avellana* (924), others (1639)
b (1.35)	OlJ	F-A	36	20.0	19.5	*A. glutinosa* (1040)	-	*C. sanguinea* (3538), *P. avium* (890), *A. glutinosa* (621), others (284)
c (2.06)	Lw	F-U	55	29.7; 26.3; 26.9	24.1	*F. excelsior* (117), *B. pendula* (111), *A. glutinosa* (11)	*C. betulus* (100), *A. pseudoplatanus* (28), *T. cordata* (22), others (29)	*C. avellana* (2411), *A. pseudoplatanus* (456), *C. sanguinea* (339), others (174)
d* (5.15)	Lśw	G-C	133	52.7; 40.0; 46.7	26.8	*Q. robur* (58), *F. excelsior* (17), *C. betulus* (10), others (5)	*C. betulus* (232), *A. pseudoplatanus* (7), *Q. robur* (2), others (2)	*A. pseudoplatanus* (698), *C. betulus* (218), *C. avellana* (185), others (26)
f** (3.65)	Lśw	G-C	79	28.1; 28.4; 30.0	25.7	*P. sylvestris* (464), *P. abies* (8), *B. pendula* (8), others (15)	*C. betulus* (124), *P. sylvestris* (73), *A. pseudoplatanus* (34), others (69)	*C. avellana* (1335), *C. betulus* (462), *C. sanguinea* (194), others (140)
g (1.65)	Lw	F-U	79	31.3; 29.0; 27.7	26.0	*B. pendula* (155), *P. sylvestris* (135), *A. pseudoplatanus* (45), others (34)	*C. betulus* (135), *P. sylvestris* (18), *A. pseudoplatanus* (18), others (39)	*C. avellana* (1830), *A. pseudoplatanus* (1188), *C. sanguinea* (630), others (243)
h (1.96)	Lw	G-C	133	48.9; 32.0; 27.9	25.1	*Q. robur* (178), *B. pendula* (6), *P. sylvestris* (4), others (6)	*C. betulus* (304), *Q. robur* (4), *A. glutinosa* (6)	*C. avellana* (2830), *C. sanguinea* (1611), *C. betulus* (144), others (159)
i (2.72)	Lw	F-U	79	32.5; 32.9; 38.5	28.0	*F. excelsior* (91), *A. glutinosa* (84), *B. pendula* (15), others (13)	*A. glutinosa* (97), *C. betulus* (32), *A. pseudoplatanus* (12), others (5)	*C. avellana* (3118), *C. sanguinea* (1701), *A. pseudoplatanus* (170), others (236)
j (1.56)	Lw	F-U	89	34.2; 47.6; 42.1	28.5	*F. excelsior* (200), *Q. robur* (20), *A. pseudoplatanus* (4), others (8)	*C. betulus* (80), *A. pseudoplatanus* (36)	*C. avellana* (3744), *C. sanguinea* (560), *P. avium* (216), others (344)
k** (1.56)	Lśw	G-C	79	29.5; 33.0; 25.4	26.0	*P. sylvestris* (303), *B. pendula* (118), *C. betulus* (53), others (13)	*C. betulus* (118), *A. pseudoplatanus* (13), *B. pendula* (13)	*C. avellana* (4368), *A. pseudoplatanus* (368), *C. sanguinea* (303), others (13)

* data based on five sample plots from 'oak-hornbeam' part of sub-unit d

** excluding the gap areas in Scots pine stands

Abbreviations: Lśw – fresh broadleaved forest site type; Lw – moist broadleaved forest site type; OlJ – alder-ash forest site type; F-U – *Ficario-Ulmetum*; F-A – *Fraxino-Alnetum*; G-C – *Galio-Carpinetum*

Table 2. Mean densities of natural regeneration (±SE) of particular tree and shrub species growing on the whole nature reserve area (ind. ha^{-1}; excluding artificial regeneration in gap areas in Scots pine stands)

Species	Density (ind. ha^{-1})		Share of dead trees and shrubs (%)
	total	dead specimens	
F. excelsior	18908 ±8037	214 ±70	1.1
A. pseudoplatanus	13805 ±4056	338 ±169	2.5
C. betulus	10131 ±4528	12 ±7	0.1
U. laevis	1719 ±825	11 ±11	0.7
A. glutinosa	360 ±360	0	0.0
P. sylvestris	109 ±109	6 ±6	5.3
A. platanoides	60 ±50	0	0.0
Q. robur	54 ±20	0	0.0
U. glabra	47 ±47	15 ±15	30.8
A. campestre	45 ±40	0	0.0
T. cordata	9 ±9	0	0.0
B. pendula	8 ±6	0	0.0
F. sylvatica	4 ±4	0	0.0
Q. petraea	2 ±2	0	0.0
C. sanguinea	8382 ±2632	129 ±28	1.5
E. europaea	4618 ±2102	48 ±34	1.0
P. avium	1124 ±312	74 ±30	6.6
C. avellana	418 ±44	24 ±21	5.8
R. cathartica	45 ±45	0	0.0
V. opulus	40 ±23	0	0.0
S. aucuparia	16 ±11	0	0.0
S. nigra	14 ±8	0	0.0
P. serotina	9 ±9	0	0.0
F. alnus	8 ±5	0	0.0

(40%; Table 3), while the least frequent were seedlings. In this sub-unit, the most frequent was common dogwood, which accounted for over 51% of the total juvenile trees and shrubs growing here. The share of all shrub species recorded in this part of the reserve (*C. sanguinea*, *E. europaea*, *P. avium*, *C. avellana*, *R. cathartica*) accounted for approximately 62% of the species composition of regeneration (Table 4). The second most numerous species in the regeneration was *C. betulus*, and the third – occurring in a small percentage in the upper stand – *F. excelsior*. The lack of hornbeam and significant share of ash (63%) among seedlings are worth noting. The regeneration of *Q. robur*, *A. pseudoplatanus* and *A. campestre* was least frequent in this sub-unit. No seedlings of alien species *P. × canadensis* were recorded.

The sub-unit b, with a total area of 1.35 hectares, was covered by alder stand on alder-ash riparian habitat; however, the proportion of alder in the natural regeneration did not exceed 3% (Table 4). The most abundant species in the natural regeneration of this sub-unit were: *F. excelsior*, *A. pseudoplatanus* and *C. betulus*. The most numerous age group for these species was two-year-old individuals and older. Here, likewise in the sub-unit a, the least regenerated were also oak and field maple. Approximately 19% of natural regeneration consisted of shrubs – mainly *C. sanguinea* – 15% (20 800 ind. ha^{-1}) and *E. europaea* – 2% (2 850 ind. ha^{-1}). Share of *P. avium*, *C. avellana* and *F. alnus* together did not exceed 2% of total regeneration. Total density of juvenile trees and shrubs in the sub-unit b was higher than in the other sub-units of the nature reserve (Table 3).

Table 3. Density of natural regeneration of trees and shrubs in the particular sub-units of the nature reserve (ind. ha^{-1}; divided into age-height categories)

Sub-unit	Density of natural regeneration				
	total	seedlings	one-year-old plants	two-year-old plants and older, lower than 0.5 m	two-year-old plants and older, higher than 0.5 m
	ind. ha^{-1}	%			
a	45 300	15.1	18.2	40.1	26.6
b	136 600	17.9	4.7	69.7	7.7
c	46 036	21.2	14.0	47.9	16.9
d_1*	118 273	5.8	38.9	44.1	11.2
d_2*	28 800	0.7	0.3	51.7	47.2
f	61 457	4.4	13.9	72.1	9.7
g	67 233	19.8	3.3	56.5	20.4
h	32 831	3.2	6.2	78.9	11.7
i	23 882	13.6	8.0	53.8	24.6
j	25 200	0.5	2.6	57.8	39.0
k	56 300	5.7	15.6	64.1	14.6

***** d_1 – values based on 22 sample plots from ‘oak-hornbeam’ part of the sub-unit d; d_2 – values based on 4 sample plots from ‘alder’ part of the sub-unit d

Table 4. Density of natural regeneration (±SE) of various tree and shrub species (in total) in the particular sub-units of the nature reserve (ind. ha^{-1}) and their share (%) in the total natural regeneration density of a given sub-unit. Value of 0.0 is included in the range of (0; 0.05)

Sub-unit	Species	Density of natural regeneration						
		total	share of species	share of dead specimens	seedlings	one-year-old plants	two-year-old plants and older, lower than 0.5 m	two-year-old plants and older, higher than 0.5 m
		(ind. ha^{-1})	%					
1	2	3	4	5	6	7	8	9
a	*C. betulus*	9100 ±5443	20.1	0	0	48.4	50.5	1.1
	F. excelsior	7450 ±3512	16.4	0	63.1	12.8	23.5	0.7
	A. campestre	400 ±200	0.9	0	25.0	25.0	50.0	0
	A. pseudoplatanus	250 ±199	0.6	0	20.0	0	80.0	0
	Q. robur	200 ±107	0.4	0	0	25.0	75.0	0
	Shrubs (5 species)	27900	61.6	1.3	7.2	9.9	40.3	42.7
b	*F. excelsior*	88350 ±44297	64.7	0.3	18.1	1.0	80.1	0.8
	A. pseudoplatanus	9150 ±6804	6.7	0	2.2	0	95.6	2.2
	C. betulus	8850 ±5450	6.5	0	1.7	39.0	59.3	0
	A. glutinosa	3600 ±2729	2.6	0	95.8	2.8	1.4	0
	U. laevis	1050 ±845	0.8	0	23.8	61.9	14.3	0
	Q. robur	100 ±100	0.1	0	0	0	100	0
	A. campestre	50 ±50	0.0	0	0	0	100	0
	Shrubs (5 species)	25450	18.6	0.4	17.5	5.3	39.7	37.5

1	2	3	4	5	6	7	8	9
c	*A. pseudoplatanus*	14582 ±3431	31.7	3.7	5.5	3.2	58.1	33.2
	F. excelsior	10982 ±5027	23.9	6.0	78.1	12.3	8.3	1.3
	C. betulus	7636 ±2214	16.6	0	0.5	49.5	45.2	4.8
	U. laevis	5527 ±3727	12.0	0	0	5.9	91.4	2.6
	A. platanoides	509 ±259	1.1	0	0	7.1	85.7	7.1
	U. glabra	473 ±318	1.0	30.8	7.7	38.5	53.8	0
	F. sylvatica	36 ±36	0.1	0	0	100	0	0
	Shrubs (5 species)	6291	13.7	4.0	5.2	4.0	54.9	35.8
d_1	*C. betulus*	56255 ±27498	47.6	0.0	0.2	73.3	25.8	0.7
	A. pseudoplatanus	32655 ±6140	27.6	1.2	0.3	1.7	71.7	26.3
	F. excelsior	25891 ±7756	21.9	0.5	24.3	14.6	47.8	13.3
	T. cordata	109 ±75	0.1	0	0	0	83.3	16.7
	Q. robur	55 ±30	0.0	0	33.3	0	66.7	0
	A. platanoides	36 ±36	0.0	0	0	0	50.0	50.0
	B. pendula	18 ±18	0.0	0	100	0	0	0
	Shrubs (5 species)	3255	2.8	1.1	10.1	14.0	53.6	22.3
d_2	*A. pseudoplatanus*	15200 ±5571	52.8	0.7	0	0.7	38.2	61.2
	F. excelsior	4600 ±3672	16.0	0	4.3	0	95.7	0
	C. betulus	2400 ±1532	8.3	0	0	0	95.8	4.2
	U. laevis	700 ±574	2.4	0	0	0	57.1	42.9
	Shrubs (3 species)	5900	20.5	0	0	0	33.9	66.1
f	*F. excelsior*	20571 ±11467	33.5	2.6	6.3	17.1	76.0	0.7
	A. pseudoplatanus	17714 ±4928	28.8	1.1	2.6	10.6	81.8	5.0
	U. laevis	7457 ±4249	12.1	1.5	0.0	13.4	69.3	17.2
	C. betulus	5257 ±2531	8.6	0.0	0.0	30.4	69.0	0.5
	P. sylvestris	1086 ±1086	1.8	5.3	78.9	15.8	5.3	0
	A. platanoides	29 ±29	0.0	0	0	0	100	0
	Q. robur	29 ±29	0.0	0	0	100	0	0
	Shrubs (6 species)	9314	15.2	2.1	0.9	3.4	57.1	38.7
g	*A. pseudoplatanus*	40633 ±10339	60.4	4.3	1.6	1.2	72.0	25.2
	F. excelsior	18267 ±9995	27.2	0.7	68.1	5.5	23.0	3.5
	U. laevis	1300 ±553	1.9	0	12.8	7.7	66.7	12.8
	C. betulus	733 ±255	1.1	0	0	63.6	36.4	0
	A. platanoides	33 ±33	0.0	0	0	0	100	0
	Q. robur	33 ±33	0.0	0	0	100	0	0
	Shrubs (6 species)	6233	9.3	3.7	1.1	2.1	53.5	43.3
h	*F. excelsior*	4308 ±2605	13.1	2.1	18.6	8.6	57.9	15.0
	A. pseudoplatanus	2031 ±999	6.2	1.5	0	0	81.8	18.2
	C. betulus	831 ±682	2.5	7.4	0	0	77.8	22.2
	B. pendula	62 ±42	0.2	0	50.0	50.0	0	0
	Q. robur	31 ±31	0.1	0	0	100	0	0
	Shrubs (5 species)	25569	77.9	2.3	0.8	6.3	82.6	10.3
i	*F. excelsior*	6118 ±2085	25.6	3.5	51.5	4.2	40.4	3.8
	A. pseudoplatanus	4235 ±1276	17.7	5.6	0.6	2.8	72.8	23.9
	C. betulus	1976 ±1076	8.3	0	0	65.5	34.5	0
	U. laevis	1247 ±1128	5.2	0	1.9	3.8	18.9	75.5
	Q. petraea	24 ±24	0.1	0	0	0	100	0
	Shrubs (5 species)	10282	43.1	4.3	0.5	1.8	61.8	35.9
j	*A. pseudoplatanus*	12489 ±2718	49.6	2.1	0.7	2.1	59.8	37.4
	F. excelsior	1422 ±554	5.6	0	3.1	6.3	68.8	21.9
	C. betulus	1156 ±459	4.6	3.8	0	23.1	65.4	11.5
	Shrubs (5 species)	10133	40.2	3.5	0	0.4	53.1	46.5
k	*C. betulus*	17800 ±15590	31.6	0	0.6	37.6	61.8	0
	F. excelsior	9000 ±2553	16.0	1.1	24.4	13.3	54.4	7.8
	A. pseudoplatanus	7000 ±2877	12.4	0	5.7	0	87.1	7.1
	U. laevis	500 ±500	0.9	0	0	80.0	20.0	0
	Q. robur	100 ±100	0.2	0	0	100	0	0
	Shrubs (5 species)	21900	38.9	0.9	2.3	1.8	63.9	32.0

* d_1 and d_2 – as in Table 3

In the sub-unit c (2.06 ha), comprising of ash-elm riparian forest site type, the average density of natural regeneration was 46 036 ind. ha^{-1}. Half of this number consisted of two-year-old and older plants to a height of 0.5 m (Table 3). The most numerous were *A. pseudoplatanus*, followed by *F. excelsior*, *C. betulus* and *U. laevis*. Shrubs in the natural regeneration were dominated by *C. sanguinea* (7%), *E. europaea* (4%) and *P. avium* (2%; Table 4). In the lowest layer of the forest, in addition to the listed species, five other woody plant species were present (three tree species and two species of shrubs), and although their overall density slightly exceeded 1 300 ind. ha^{-1}, their presence itself is worth noting, since the regeneration of *U. glabra* and *F. sylvatica* in the lowest layer of the forest could be found only in this part of the reserve.

In the sub-unit d (5.15 ha), covering the largest part of the reserve (about 22%), there is mainly an oak-hornbeam stand, and also a small patch of alder stand in the north-east, which was omitted from further analysis.

More than 55% of natural regeneration in this oak-hornbeam forest consisted of two-year-old plants and older (up to 1.3 m in height), while seedlings amounted to only 6% (Table 3). Of the twelve species of trees and shrubs recorded in the regeneration layer of this 'oak-hornbeam' part of the sub-unit d, three typical of oak-hornbeam stand species, i.e. *C. betulus*, *A. pseudoplatanus* and *F. excelsior* (often found in the most fertile and humid habitats), accounted for over 97% of total regeneration (Table 4). The density of other tree species typical of oak-hornbeam habitat (*T. cordata*, *Q. robur*, *A. platanoides*) did not exceed a total of 200 ind. ha^{-1}. The density of shrubs (*C. sanguinea*, *E. europaea*, *P. avium*, *C. avellana*, *S. nigra*) did not exceed 3% of the total woody plant species density in the regeneration of sub-unit d.

In the sub-unit f, there is a degenerated oak-hornbeam site type of *Galio sylvatici-Carpinetum* (dominated by artificially established Scots pine stand). Total density of natural regeneration here was 61 457 ind. ha^{-1}, of which 83% were young trees of *F. excelsior*, *A. pseudoplatanus*, *U. laevis*, *C. betulus*, *A. platanoides* and *Q. robur* (Table 4). The regeneration was dominated by two-year-old trees or older and not higher than 0.5 m (72%). Among the shrubs recorded in this sub-unit, the most numerous were *C. sanguinea*.

In order to rebuild the Scots pine stand, two gaps were created with artificial regeneration. In 2010, in each gap (0.3 ha), seedlings of pedunculate oak (initial density of 5 700 ind. ha^{-1}) and sessile oak (830 ind. ha^{-1}), lime (830 ind. ha^{-1}), hornbeam (620 ind. ha^{-1}), sycamore (580 ind. ha^{-1}) and ash (330 ind. ha^{-1}) were planted. Apart from those species listed above, in 2012 trees and shrubs of natural origin were also recorded, and their density (Table 5) indicates a high potential for regeneration. It is noteworthy that in the created gaps the density of seedlings and one-year-old plants of most desirable broadleaved species was relatively low, not exceeding 400 ind. ha^{-1} overall. In addition, there was a very high density of Scots pine regeneration, which is an undesirable species for this habitat.

In the sub-unit g, over 60% of natural regeneration consisted of individuals of *A. pseudoplatanus*, and 27% of *F. excelsior* (Table 4). The density of the other tree species did not exceed a total of 2 100 ind. ha^{-1}. The proportion of hornbeam was extremely small, compared with other parts of the reserve (1%), although this species is predominant in the lower storey of tree layer (Table 1). In the sub-unit g, like in the previously discussed sub-units, the most numerous age group were two-year-old and older trees and shrubs. The lack of regeneration of dominant species in the upper stand – *B. pendula* and *P. sylvestris* – is noteworthy.

The regeneration in sub-unit h (1.96 ha) was strongly dominated by the juveniles of *E. europaea* making up over 71% of all trees and shrubs recorded in this layer. The best regenerated tree species here was *F. excelsior* (Table 4) with age structure consisting mostly of the two-year-old and older plants (73%). Among the relatively numerous juveniles of *A. pseudoplatanus* and *C. betulus*, there were no plants younger than two-year-old at all. The amount of pedunculate oak individuals in the regeneration was marginal (31 ind. ha^{-1}).

Ash and sycamore were the dominant species in the natural regeneration of the sub-unit i (2.72 ha) in the oak-elm site type (Table 4). Despite the large share of alder in the upper storey, no trail of its regeneration was found here. There were no young pedunculate oak trees either. However, there was, though scarce, regeneration of sessile oak (24 ind. ha^{-1}); actually, it was the only place in the reserve where it was recorded on the study plots. The share of shrubs in the natural regeneration was 43%, and the total density of 10 282 ind. ha^{-1}, of which the majority were *C. sanguinea* (3 294 ind. ha^{-1}), *E. europaea* (3 224 ind. ha^{-1}) and *P. avium* (3 082 ind. ha^{-1}). Other shrub species (*C. avellana* and *S. nigra*) did not exceed a total of 700 ind. ha^{-1}.

The density of natural regeneration in sub-unit j (1.56 ha) was 25 200 ind. ha^{-1} (Table 3), half of which was due to *A. pseudoplatanus* (Table 4). Among shrubs, the most frequent was common dogwood with the share of the

Table 5. Density of natural and planted regeneration (±SE) of various tree and shrub species in the gap areas established in Scots pine stands (ind. ha^{-1}) and their share in the total regeneration's density (living and dead) of a given sub-unit

Sub-unit	Species	Density of natural and planted regeneration								
		total	share of species	share of dead specimens	seedlings	one-year-old plants	two-year-old plants and older, lower than 0.5 m	two-year-old plants and older, higher than 0.5 m	older plants, higher than 1.3 m	cut plants
		(ind. ha^{-1})	%							
1	2	3	4	5	6	7	8	9	10	11
f	*P. sylvestris*	114520 ±41087	75.2	29.2	0	0.3	90.2	3.0	0	6.5
	A. pseudoplatanus	12960 ±4797	8.5	0	0	0.3	33.0	36.1	3.1	27.5
	C. betulus	4800 ±864	3.2	0	0	2.5	36.7	42.5	10.0	8.3
	F. excelsior	3960 ±3305	2.6	2.0	1.0	6.1	38.4	48.5	2.0	4.0
	B. pendula	3640 ±1198	2.4	1.1	0	0	6.6	29.7	7.7	56.0
	C. avellana	3160 ±1792	2.1	0	0	0	5.1	19.0	1.3	74.7
	Q. robur	2920 ±820	1.9	0	0	0	19.2	79.5	1.4	0
	U. laevis	2400 ±2356	1.6	0	0	0	5.0	45.0	33.3	16.7
	C. sanguinea	1320 ±798	0.9	0	0	6.1	45.5	42.4	3.0	3.0
	T. cordata	720 ±278	0.5	0	0	0	0	38.9	33.3	27.8
	B. pubescens	520 ±231	0.3	0	0	0	7.7	46.2	0	46.2
	Q. petraea	440 ±256	0.3	0	0	0	18.2	81.8	0	0
	S. aucuparia	360 ±242	0.2	0	0	0	11.1	11.1	66.7	11.1
	E. europaea	200 ±123	0.1	0	0	0	60.0	40.0	0	0
	P. tremula	120 ±120	0.1	0	0	66.7	0	0	33.3	0
	P. avium	80 ±53	0.1	0	0	0	50.0	50.0	0	0
	P. serotina	40 ±40	0.0	0	0	0	0	0	0	100
	S. caprea	40 ±40	0.0	0	0	0	0	0	0	100
	S. nigra	40 ±40	0.0	0	0	0	0	100	0	0
k	*C. betulus*	23480 ±11672	30.7	0	0.2	1.2	63.7	30.5	1.5	2.9
	A. pseudoplatanus	20680 ±5770	27.0	0.6	0	0	12.8	23.4	19.3	44.5
	C. sanguinea	13160 ±4298	17.2	0	0	0.3	6.1	22.2	51.4	20.1
	P. sylvestris	7760 ±5463	10.1	1.0	0	0.5	97.4	1.5	0	0.5

1	2	3	4	5	6	7	8	9	10	11
	C. avellana	2800 ±888	3.7	0	0	0	10.0	14.3	2.9	72.9
	E. europaea	2360 ±959	3.1	0	0	0	30.5	62.7	3.4	3.4
	F. excelsior	2040 ±1186	2.7	0	0	2.0	41.2	54.9	2.0	0
	S. nigra	1040 ±322	1.4	11.5	0	0	7.7	42.3	15.4	34.6
	T. cordata	1000 ±255	1.3	0	0	0	0	48.0	36.0	16.0
	Q. robur	680 ±274	0.9	0	0	0	58.8	41.2	0	0
	B. pendula	560 ±392	0.7	0	0	0	0	35.7	0	64.3
	P. avium	440 ±193	0.6	0	0	0	0	90.9	9.1	0
	P. tremula	200 ±200	0.3	0	0	0	20.0	60.0	0	20.0
	U. laevis	160 ±88	0.2	0	0	0	25.0	50.0	25.0	0
	A. platanoides	120 ±85	0.2	0	0	0	0	66.7	0	33.3
	P. alba	40 ±40	0.1	0	0	0	100	0	0	0
	R. cathartica	40 ±40	0.1	0	0	0	0	0	100	0

regeneration accounting for more than 20%. In the regeneration of sub-unit j juveniles from this or previous year was a group formed less numerous than in other sub-units of the reserve (Table 3).

The sub-unit k represents the degenerated form of oak-hornbeam site type, covered by Scots pine. Likewise, in the sub-unit f, two canopy gaps were also established here for regeneration in 2010, each with an area of 0.3 ha. Within the gaps, the following species were planted: *Q. robur* (2 380 ind. ha^{-1}), *C. betulus* (1 930 ind. ha^{-1}), *A. pseudoplatanus* (1 000 ind. ha^{-1}), *T. cordata* (830 ind. ha^{-1}), *F. excelsior* (500 ind. ha^{-1}), *A. platanoides* (170 ind. ha^{-1}) and *Q. petraea* (70 ind. ha^{-1}). Analysis of the state of trees and shrubs regeneration in gaps found negligible density of seedlings and one-year-old plants (less than 440 ind. ha^{-1}, of which 82% were broadleaved species). The young generation of hornbeam and sycamore in this sub-unit accounted for the biggest part of natural regeneration (Table 5). In turn, Scots pine being dominant in the stand surrounding the gaps regenerated poorly compared with pines in sub-unit f. Its share was just over 10% of all trees and shrubs in the lowest layer of the forest. Beside the gaps, the density of Scots pine natural regeneration was 56 300 ind. ha^{-1} (Table 3), of which the largest group was two-year-old and older plants. The most numerous species present in the regeneration were *C. betulus* and *C. sanguinea*, while the least numerous were *Q. robur* (Table 4).

4. Discussion

The total average density of natural regeneration of all species throughout the nature reserve reaches 60 000 ind. ha^{-1}; thus, it greatly exceeds the recommended density for tree planting (Modrý et al. 2004; Zasady hodowli lasu 2012). The most important species typical for oak-hornbeam site type represent almost 75% of the total young trees and shrubs recorded. *F. excelsior* regenerates most frequently among all the species listed in the reserve (nearly 32% of the total regeneration). Chwistek (2007) studying the structure of the species composition of forests in the Ojcowski National Park, including the oak-hornbeam site type, demonstrated a similar share of ash, amounting to almost 26% of the regeneration. This author reported only regeneration not higher than 0.5 m, excluding one-year-old seedlings from the analysis. Taking into account only the groups of plants analysed by Chwistek (2007), it was found that the share of the young generation of ash in total regeneration recorded in the reserve was just over 33% (11 523 ind. ha^{-1}). The results obtained by Modrý et al. (2004) on natural regeneration in the 120-year-old stand of beech with an admixture of hornbeam and sycamore showed in turn a slightly higher density of ash. Average density of ash in the cited studies was estimated at 27 000 ind. ha^{-1}, which accounted for 18% of the total natural regeneration recorded. On the other hand, Bobiec (2007) in a community of *Tilio-Carpinetum* in the Białowieża Forest, both in gaps and under the canopy, found only a trace share (on average less than 3%) of ash in regeneration. Noteworthy is the fact that a significant proportion of ash juveniles do not promote to the higher layers of undergrowth. This problem has been also noted in the studies of Chwistek (2007) and Miścicki (2012) who demonstrated a small share of this species passing into the upper layers of the stand. Also, within the reserve, the share of ash in the undergrowth (here above 1.3 m in height) is only 3% (Wiczyńska et al. 2013). This reflects the relatively rapid dieback of ash in the ground layer and low undergrowth, which may be due to unfavourable light conditions for juveniles of this species, which are known to be moderate light-demanding (Faliński, Pawlaczyk 1995). The share of older ash individuals in the studied layers (64%) indicates an 'expectation' of juveniles for better conditions for growth. The cause of dieback of ash saplings here is rather not the ash dieback disease, identified in the end of the last century and caused by the fungus *Chalara fraxinea* (e.g. Schumacher et al. 2010; Kowalski, Kraj 2012), as the share of dead individuals of ash in its total regeneration within the reserve is only 1%.

Juveniles of *A. pseudoplatanus* in the 'Czmoń' nature reserve account for more than 23% of the total regeneration, although its share in the upper storey is only slightly over 4% (Wiczyńska et al. 2013). The seedlings and saplings of sycamore are observed in each of the sub-units, whereas mature trees are only in seven of them. Light conditions in the reserve are sufficient for the development of the young generation of sycamore, which is considered a moderately shade-tolerant species (Boratyński, Filipiak 1999; Saniga, Balanga 2008; Szwagrzyk et al. 2012). It is also worth paying attention to the high density of this species in Scots pine stands growing in the reserve (in the sub-unit f – 17 700 ind. ha^{-1}, and in the sub-unit k – 7000 ind. ha^{-1}). Such an arrangement can also be seen in Pomerania where the expansion of sycamore or maple was noticed in Scots pine stands (Danielewicz, Pawlaczyk 2004b). Gieruszyński (1961), studying the development dynamics of the yew reserve, noted that among the broadleaved, riparian and alder habitats reported there, sycamore has the largest successional dynamics. Emborg (1998), in turn, considered the mass emergence of sycamore quite undesirable from the point of view of creating competition for the regeneration of the target species.

Regeneration of hornbeam is on average 17% of the total number of young trees and shrubs in the study area; however, in certain sub-units its share varies considerably. The best conditions for the development of hornbeam are in the sub-unit d, where the species represents almost 48% of the total regeneration, while the least frequently (1.1% share) it occurs in the sub-unit g. The presence of hornbeam in the upper layers of the stand does not have to affect the density of young trees of this species. For example, in the sub-units h and d, where the share of individuals of *C. betulus* in the second floor of the stand is equal (Wiczyńska et al. 2013), the regeneration densities of this species differs nearly twenty-fold (Table 4). Random distribution of seedlings, reflecting the distribution of seeds reaching the forest floor by barochory and secondarily by zoochory (Faliński, Pawlaczyk 1993), together with the random establishment of study plots, may have little impact on the assessment of the density. Dobrowolska (2006) in her studies of natural regeneration under the canopy of Scots pine trees growing on a fertile forest habitat showed that the amount of hornbeam seedlings was 200 750 ind. ha^{-1}, which accounted for almost 89% of the total natural regeneration. The density of hornbeam seedlings demonstrated by the cited author was almost 20 times higher than the density of the regeneration of hornbeam in the 'Czmoń' nature reserve – both the average for the whole of the reserve, as well as average for only the two sub-units with the dominance of Scots pine in the upper storey (f and k). Considering the analysis of the data for the sub-unit d – one of the best preserved fragments of oak-hornbeam forest (*Galio-Carpinetum*) in Wielkopolska Region (Żukowski, Jackowiak 1992 after Lisiewska, Król 2007) – it turns out that the density of hornbeam juveniles in this sub-unit, although accounting for almost 48% of the total regeneration, is over four times smaller than the density evidenced by Dobrowolska (2006). The reasons for such a numerous regeneration of hornbeam demonstrated by Dobrowolska (2006) should be ascribed to both favourable microhabitat conditions as well as regenerative abilities of the habitat under the Scots pine trees. The data obtained in studies conducted on less fertile sites (e.g. Mirschel et al. 2011) show a much lower density of hornbeam in the natural regeneration.

Of the remaining species desired in oak-hornbeam communities, only *U. laevis* is characterised by a noticeable density of juveniles in the layer of natural regeneration. The share of this species in the total number of young trees recorded in the reserve is less than 3%.

The regeneration of *A. platanoides*, *Q. robur* and *T. cordata* represents 0.2% of the total number of regeneration. The low density of regeneration of linden and maple can be explained by an insignificant number of mature trees of these species in the upper stands. However, the small amount of juvenile oak, though its dominancy in the tree layer is in a large part of the reserve, is an anxious issue. Oak has a different life strategy from hornbeam. According to Faliński and Pawlaczyk (1993), Danielewicz and Pawlaczyk (2004a), and Paluch (2012), a constant presence in the oak-hornbeam stands, oak trees owe individual's durability, allowing for the emergence and development of natural regeneration even at a low probability of obtaining reproductive success in subsequent years. Moreover, oak is a hardly regenerated tree species (Lorimer et al. 1994; Harmer et al. 2005; Bobiec, Jaszcz 2010), what may be caused by its high sensitivity to the deficiency of water and nutrients in the upper soil levels (Modrzyński et al. 2006; Mirschel et al. 2011). Emborg et al. (1996) note a general lack of significant success of oak regeneration nowadays. In the case of the 'Czmoń' nature reserve, the lack of mass regeneration of oak can be explained by the fact that fragments of forest stands with a high proportion of oak have not yet entered a terminal phase (Plan ochrony… 2006; Wiczyńska et al. 2013), in which treefall gaps could create favourable conditions for the development of oak seedlings (Saniga, Balanga 2008; Bobiec, Jaszcz 2010), as well as a significant share of hornbeam in the upper storey in most of the sub-units, which according to Zerbe (2002) and Paluch and Bielak (2009) may inhibit the regeneration of light-demanding species. There is no doubt that oak – one of the most important hardwood species in Poland (Dobrowolska 2006; Ceitel 2006) – should be treated with special attention in the process of rebuilding the stand using natural regeneration (Mirschel et al. 2011). In protected areas, preparation of the soil, recommended in order to enhance opportunities for the regeneration of oak (Nilsson et al. 1996; Löf et al. 1998; Harmer et al. 2005), is at odds with the idea of protection. In the case of nature reserves, in order to increase oak regeneration, the living conditions of birds, which play an important role in the dispersal of acorns (Mosandl, Kleinert 1998; Götmark et al. 2005; Danielewicz, Pawlaczyk 2006; Mirschel et al. 2011; Paluch 2012), can be improved in their neighbourhood.

In the sub-units f and k, in order to rebuild Scots pine stands, it was decided to establish four gaps for regeneration in a total area of 1.2 hectares. Some researchers recommend such prescriptions even in reserves (e.g. Jakubowska-Gabara 1992). In 2010, seedlings of desired hardwood species were planted in the clear-cut gaps (see Results section). In comparison of state, species and age structure of the regeneration within the gaps and the natural regeneration in the rest of the sub-units (4.01 ha) should lie the answer to the question of whether felling the stand and introducing artificial regeneration was justified. In parts of the sub-units f and k under the canopy closure, the total average density of the most desirable broadleaved species (*F. excelsior*, *A. pseudoplatanus*, *C. betulus*, *U. laevis, Q. robur* and *A. platanoides*) is 42 729 ind. ha^{-1} and constitutes almost 73% of the total regeneration in these sub-units. The age and species structure do not differ in these sub-units from the average for the whole of the reserve. Götmark et al. (2005) claim that the appearance of the regeneration of deciduous trees in stands with the dominance of coniferous species is natural. This is confirmed by Zerbe (2002) who argues that pine stands growing on fertile sites species with smaller trophic requirements reduce its share, giving way to a more demanding deciduous species. In his opinion, it is associated with an increase in the nutrient content of organic soil layers, which in turn is the result of natural regeneration of soil after the cessation of tree felling in the stand. This thesis is in accordance with the findings of Czerepko (2004) who even says that conditions start to recover in the direction of potential habitat almost right after the introduction of Scots pine stand.

The total number of young trees and shrubs found in the gaps of the study plots was estimated to an average of 114 400 ind. ha^{-1} (including individuals over 1.3 m high and the ones topped during early cleanings in 2011), of which a maximum of 7 900 ind. ha^{-1} was derived from planting. Such a large number is mainly due to Scots pine representing more than 53% of the total regeneration (61 140 ind. ha^{-1}). For comparison, the proportion of juveniles of this species in parts of the sub-units f and k under the canopy closure does not exceed 1%. Furthermore, only 6% of the natural regeneration of *P. sylvestris* recorded within the gaps is higher than 0.5 m, suggesting that the density of seedlings of this species had been negligible before the gaps were created. Apart from the pine seedlings, the species structure of natural regeneration can be considered similar to that of sub-unit d (in the 'oak-hornbeam' part; Table 4). However, considering the actual number of regeneration, it should be noted that the density of juveniles of species typical of oak-hornbeam stand in the gaps is relatively small compared with the density of regeneration in other parts of the stand (five times smaller than in the 'oak-hornbeam' part of sub-unit d and twice smaller than the average in the part of the sub-units f and k under the canopy closure). Within the gaps the lack of natural regeneration of small-leaved linden and oaks is noteworthy: pedunculate and sessile, of which the average density is lower than the number of seedlings introduced artificially.

Looking at these results, it can be concluded that clear-cutting fragments of the Scots pine stand (as in group shelterwood system) and setting the artificial regeneration within the gaps created favourable conditions for the germination of seeds of Scots pine – an undesirable species in the oak-hornbeam habitat. Removing trees to create these openings does not seem to be justified. This is confirmed by the rapid development of natural regeneration of oak-hornbeam species within the gaps. The structure of tree regeneration in the fragments of forest with Scots pine suggests that the community regeneration towards the potential vegetation appropriate to oak-hornbeam site type can be successfully obtained through spontaneous processes. According to some authors, the restoration of potential vegetation is very likely to happen without human intervention (e.g. Keczyński 2007). This occurs already in the second generation of the forest; thus, Karczmarski and Kunz (2010) are doubtful of the sense of performing any silvicultural treatments in the reserves. According to other authors, vegetation can return to the state consistent with habitat only after exclusion of degenerating factors (Mąkosa 1991; Czerepko 2004).

Spatial diversity of vegetation in the forests of the temperate climate creates a unique microclimate, significantly affecting the state of the regeneration process (Podlaski 2010). The 'Czmoń' nature reserve, despite the varying degree of stand degeneracy, creates generally good conditions for natural regeneration of the forest. It is indicated by a significant share of oak-hornbeam species in each layer of the forest. In the protected tree stands, species diversity may be far greater than that in the commercial forests (Graae, Heskjær 1997). This in turn can have a huge impact on the dynamics of phytocoenoses recovery in the reserve. It is also assumed that the lack of juvenile oaks in the layer of regeneration is temporary. After the stands in the reserve enter a terminal phase, through the treefall gaps, the access of light to the forest floor will increase, which in turn will create more convenient conditions for the growth and development of oak seedlings (Danielewicz, Pawlaczyk 2006; Dobrowolska 2006; Bobiec, Jaszcz 2010).

5. Conclusions

The 'Czmoń' nature reserve is a place in which there are favourable conditions for the observation of spontaneous regeneration processes of degenerated phytocoenoses and development of these close to natural conditions. Analysis of the state and structure of natural regeneration in this reserve allows drawing the following conclusions:

– Dynamic processes of transformation in all degenerated phytocoenoses in the 'Czmoń' nature reserve progress towards the desired oak-hornbeam potential vegetation, and naturally occurring self-regulatory processes in degenerated forest communities are sufficient to rebuild the stands that compose species incompatible with habitat conditions;

– Rebuilding tree stands in the reserve is unnecessary, as evidenced by the abundance and species structure of natural regeneration, which was recorded in artificially established gaps in Scots pine stands;

– The small proportion of ash juveniles in the upper layer of undergrowth, although is the most frequently regenerating tree species found in the reserve, occurring in all layers of the forest, may be due to the high density of natural regeneration of other species of trees and shrubs, and hence increased competition for limited resources (space and light);

– As a result of extensive forest management kept in the reserve until recently, and therefore preserving the full stand density in the oak-hornbeam part of the reserve, the prevailing light conditions here, due to the lack of naturally occurring gaps, are detrimental to the natural regeneration of oaks, though its small density appears to be temporary.

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Translated by: Maria Łysik

Contributions

All authors have made substantial contributions to conception of the study, data acquisition, analysis and interpretation of results and drafting the manuscript. P.H. and K.W. collected field data, prepared data basis and conducted statistical analyses of the data, P.H. wrote the initial draft of the manuscript, AMJ designed the study and the manuscript, provided critical comments, and contributed additional expertise to enhance the initial draft. All authors read and approved the final manuscript.