

Seasonal changes in the understorey biomass of an oak-hornbeam forest *Galio sylvatici-Carpinetum betuli*

Andrzej M. Jagodziński^{1,2✉}, Katarzyna Pietrusiak², Mateusz Rawlik², Sławomir Janyszczek³

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;

³ Poznań University of Life Sciences, Department of Botany, Wojska Polskiego 71c, 60–625 Poznań, Poland.

✉ Tel. +48 61 817 00 33, fax: +48 61 817 00 33, e-mail: amj@man.poznan.pl

Abstract. We studied seasonal changes in the understorey biomass of an oak-hornbeam forest association *Galio sylvatici-Carpinetum betuli*. Samples were collected weekly during the most dynamic period of herbaceous layer development (April–May 2010), and every two weeks for the remainder of the growing season (June–October). Samples were collected from 10 randomly selected localities of 0.36 m² within the plant community. The plants harvested were separated by species, then oven-dried and weighed. There were statistically significant differences in aboveground understorey biomass during the time between harvests. For example, the lowest plant biomass (produced in 2010 and previous years) was found on April 3rd (37.2 kg/ha), whereas the two highest were on May 1st (308.1 kg/ha) and June 12th (337.6 kg/ha). The lowest biomass of plants produced in 2010 was on April 3rd (13.0 kg/ha) and the highest was on May 1st (259.8 kg/ha). When biomass of particular herbaceous plant species were analyzed, there was no one clearly dominant species. For example, from March 20th to May 22nd the biomass of *Ficaria verna* was the highest at ca. 36% of the total herbaceous layer plant biomass (range: 14.5–51.0%). During the next harvesting period (June–October), there were a few dominant herbaceous plant species, e.g. *Geranium robertianum*, *Stachys sylvatica*, *Impatiens parviflora*, *Dryopteris dilatata*, *Dryopteris carthusiana*, *Dryopteris filix-mas*, and *Maianthemum bifolium*.

Key words: plant biomass, herbaceous layer, oak-hornbeam forest association, geophytes, seasonal changes

1. Introduction

The aim of research on productivity and quantitative changes in plant biomass during the growing season is, in addition to the assessment of the amount of organic matter produced in a given time by plants, monitoring the flow of matter and energy flow in the ecosystem. An important aspect of the carried out research is to obtain information on the potential productivity of plant communities (Kaźmierczakowa 1971; Parzych, Sobisz 2010). According to many researchers, the production of understorey biomass is a good indicator of soil fertility (Chapin 1980; Gilliam 1988; Gilliam, Roberts 2003).

The studies on forest productivity rarely provide a detailed analysis of the potential productivity of herbaceous layer. The research results so far have

shown that the share of understorey biomass in relation to the total aboveground biomass of the forest ecosystem is small (about 1–2%), but the importance of it in the context of macro- and micronutrient cycle is disproportionately higher (Yari 1980; Muller 2003; Gilliam 2007). For example Kaźmierczakowa (1971) showed that the annual biomass production in an oak-hornbeam forest association *Tilio-Carpinetum stachyetosum* amounts to approximately 11.3 t/ha, of which the production of understorey biomass is about 20%, despite the fact that during the period of the most intensive growth of herbs its biomass is only 0.7% of the maximum total biomass of the community. Today, this type of research is becoming particularly important in the context of validation of mathematical models, which generally ignore the “contribution” of undergrowth

plant in the fixation of CO₂ from the atmosphere (Dixon et al. 1994; Widén 2002).

In temperate climate, the standing biomass and production of understorey biomass depend on the growing season. This is particularly evident in deciduous and mixed forest stands. In spring, when trees are still leafless, ample light reaches the forest floor. This enables the rampant development of geophytes (Rothstein, Zak 2001; Small, McCarthy 2002; Rawlik et al. 2012). The substances accumulated in the geophytes underground storage organs enable their dynamic growth in early spring, before the development of tree leaves and other competing plants (Dafni et al. 1981). The emergence of foliage in woody plants limits the access of light to the lower layers of the forest, affecting the conditions in the ground vegetation. This limitation results in inhibition of geophytes growth, followed by their gradual decay. Then, their place is taken by summer plants, which have a less dynamic development (Barbier et al. 2008).

The aim of this study was to investigate the seasonal variability of aboveground biomass of undergrowth plants in oak-hornbeam forest association *Galio sylvatici-Carpinetum betuli*.

2. Materials and Methods

Study area

The study area has been located in the Syców Forest District (RDSF in Poznań), Forestry Wioska (latitude and longitude coordinates for the center of the plot: 51°17'56" N, 17°44'4" E). According to the forest regionalization, the study area is in the Land of Silesia, Wrocław District and Mezonegion of Oleśnicka Plain (Trampller et al. 1990).

According to the data contained in the forest stand and soil report (BULiGL 2000), the area of the Syców Forest District is located in the transition zone between the lowlands and the highlands belt. In the warmest month – July – the average temperature is 19°C, and in January – the coldest month – 1.5°C. A characteristic feature of this area is a rapid drop in temperature, occurring mainly in May. Average annual temperature ranges from 8.0°C to 8.5°C. Total annual precipitation ranges from 500 to 600 mm, with 65% of it due to summer rainfall. Around the Ostrzeszowskie Hills, characteristics of continental climate can be observed and the length of the growing season in this area lasts 210 days (BULiGL 2000).

Plant material was collected in compartments 82c and 82g, which are part of the forest complex acting as

a protective forest, located near the city park in Syców. By placing the study plot in a managed forest on the outskirts of the park, it was relatively little exposed to penetration by humans.

The range of the designated study area did not cover the whole area of compartments 82c and 82g, but only parts of them (2.24 ha). In the compartment 82c there is a 65-year-old stand of *Fraxinus excelsior* (share – 60%, average diameter at breast height – 33 cm, average height – 26 m), the additional species are *Quercus robur* (share – 30%, average diameter at breast height – 31 cm, average height – 25 m) and *Acer pseudoplatanus* (share – 10%, the average diameter at breast height – 32 cm, average height – 25 m), and there also occur single trees of *Tilia platyphyllos*, *T. cordata*, *Betula pendula*, and *Carpinus betulus*. 70% of the study area is covered by undergrowth, which is composed of *C. betulus*, *Corylus avellana*, *A. pseudoplatanus*, *Sorbus aucuparia*, *Sambucus nigra*, and *Padus avium*. In compartment 82g, the dominant species is *Q. robur* at the age of 140 years, with an average diameter at breast height of 53 cm and an average height of 29 m and 50% share in the species composition. Less abundant tree species within the site are *T. cordata*, *Fagus sylvatica*, and *C. betulus*. Understorey covers about 70% of the area and is composed of the same species as in compartment 82g. According to the data contained in the forest management plan (BULiGL 2010) forest stand type in surveyed areas is identified as fresh forest (strongly fresh variant), developed on acid brown soils. Ground cover is defined as herbaceous. The ground vegetation in the growing season is very rampant mostly due to the spring plants. The study area is crossed by 1 m wide ditch, which is partially drained during the summer. The presence of this stream generates a specific microclimate in a narrow strip along its banks, enabling the development of plants with higher moisture requirements.

Phytosociological classification of community

In June 2010, 10 phytosociological relevés were made, documenting all physiognomically distinguishable variants of the studied forest stand, using the classic Braun-Blanquet method. Phytosociological abundance scale according to Barkman et al. (1964) was applied. Relevés are summarized in the phytosociological table (tab. 1). Syntaxonomic classification was adopted after Matuszkiewicz W. (2007), while the subassociation classification was based on the paper of Matuszkiewicz J.M. (2001). We followed the plant nomenclature adopted by Rutkowski (2006).

Table 1. Phytosociological table for oak-hornbeam forest *Galio sylvatici-Carpinetum betuli*. Explanations: zn. – minimal cover (1-4%), phytosociological scale according to Barkman (Barkman et al. 1964) – 2a: 5.1-12.5%, 2b: 12.6-25.0%, 2m: numerous seedlings covering less than 5%.

Succesive no. of relevé	1	2	3	4	5	6	7	8	9	10	No. of occurrences	Constancy		
Relevé no.	1	10	2	5	9	4	8	7	6	3				
Date: d-m-y	04-06-2010													
Humus layer type	mull	mull	moder	mull	mull	mull	mull	mull	mull	mull				
Cover of tree layer (a1+a2) in %	80	95	90	70	70	95	50	50	80	90				
Cover of tree layer (a1) in %	80	20	65	65	45	35	15	50	50	50				
Cover of tree layer (a2) in %		80	25	10	60	75	45	5	50	30				
Cover of shrub layer (b) in %	zn.	5	zn.	zn.	20	zn.	50	20	10	10				
Cover of herb layer (c) in %	80	40	50	70	35	10	60	60	60	40				
Cover of moss layer (d) in %	0	zn.	zn.	zn.	0	zn.	zn.	zn.	5	zn.				
Area of relevé in m ²	150	150	120	300	200	300	150	150	300	200				
No. of species in relevé	32	20	35	30	26	18	33	32	33	34				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Ch. All. Carpinion betuli</i> (lok. Ch. Ass. <i>Galio sylvatici-Carpinetum</i>)														
<i>Carpinus betulus</i>	a1	4.4	2b.3	2b.3	2a.	.	.	.	3.3	.	2b.1	6	III	
<i>Carpinus betulus</i>	a2	.	5.4	.	2a.3	4.4	5.4	3.3	1.1	4.4	3.2	8	IV	
<i>Carpinus betulus</i>	b	.	1.2	r	+2	2b.3	+	2b.3	2a.1	2a.1	1.3	9	V	
<i>Carpinus betulus</i>	c	1.1	+	2m.2	+	+	.	2a.	1.1	+	2a.1	9	V	
<i>Carpinus betulus</i> s.	c	.	+	+1	+	r	2m.1	.	+	r	r	8	IV	
<i>Dactylis polygama</i>	c	+2	+2	r	.	r	4	II	
<i>Corylus avellana</i>	b	.	.	+	.	.	2b.3	.	2a.3	+	.	5	III	
<i>Corylus avellana</i>	c	.	.	r	.	.	.	r	.	.	.	2	I	
<i>Ch. All. Fagion sylvaticae</i>														
<i>Fagus sylvatica</i>	b	+2	r	.	r	.	.	3	II	
<i>Fagus sylvatica</i> juv.	c	.	.	r	r	+	r	4	II	
<i>Fagus sylvatica</i> s.	c	.	.	.	r	+	r	3	II	
<i>Ch. O. Fagetalia sylvaticae</i>														
<i>Acer pseudoplatanus</i>	a1	.	2a.3	.	2b.	+2	.	.	2b.3	2b.3	.	5	III	
<i>Acer pseudoplatanus</i>	a2	2a.1	.	.	.	1	I	
<i>Acer pseudoplatanus</i>	b	.	1.2	.	.	1.1	+	2a.1	2b.1	+	2a.3	7	IV	
<i>Acer pseudoplatanus</i> juv.	c	1.1	2b.1	.	1.1	r	1.1	2b.1	1.1	+	2a.1	10	V	
<i>Acer pseudoplatanus</i> s.	c	.	1.1	+	+	+	2m.1	.	+	2m.1	r	8	IV	
<i>Viola reichenbachiana</i>	c	+	+	+2	+	.	r	.	r	+2	r	8	IV	
<i>Adoxa moschatellina</i>	c	.	+3	.	+3	r	.	r	+	2b.1	r	7	IV	
<i>Atrichum undulatum</i>	d	.	+2	.	+2	.	+3	+3	+3	1.3	+2	7	IV	
<i>Impatiens noli-tangere</i>	c	1.2	.	r	3.1	1.1	.	2b.1	.	.	r	6	III	
<i>Milium effusum</i>	c	+2	2a.2	.	+	r	.	.	+	.	1.3	6	III	
<i>Stachys sylvatica</i>	c	.	.	.	+3	1.3	2	I	

1	2	3	4	5	6	7	8	9	10	11	12	13	14
Ch. Cl. <i>Querc-Fagetea</i>													
<i>Fraxinus excelsior</i>	a1	.	.	.	2a.	1.2	2a.	2a.3	1.3	3.1	2b.1	7	IV
<i>Fraxinus excelsior</i>	b	r	.	.	1	I
<i>Fraxinus excelsior s.</i>	c	+2	r	+	+	+	2m.1	.	r	.	.	7	IV
<i>Fraxinus excelsior juv.</i>	c	+	+	r	r	1.1	r	+	+	1.1	r	10	V
<i>Acer platanoides</i>	a1	.	.	3.3	.	.	1.1	.	.	.	2b.1	3	II
<i>Acer platanoides</i>	a2	1.1	.	2b.1	.	.	.	2	I
<i>Acer platanoides</i>	b	1.2	.	.	.	+	.	r	r	+	.	5	III
<i>Acer platanoides juv.</i>	c	+	+	+	+	r	+	r	+	+	r	10	V
<i>Acer platanoides s.</i>	c	.	.	+	+	.	2m.1	.	r	r	+	6	III
<i>Poa nemoralis</i>	c	+2	1.2	+2	1.2	.	.	+	+	r	+	8	IV
<i>Aegopodium podagraria</i>	c	1.3	.	.	.	1.2	2	I
<i>Euonymus europaeus</i>	c	.	r	.	.	r	.	+	r	r	.	5	III
Ch. Cl. <i>Artemisietea vulgaris</i>													
<i>Galium aparine</i>	c	1.2	r	r	1.1	.	r	+2	+	1.3	r	9	V
<i>Allaria petiolata</i>	c	r	r	.	+2	+2	.	+	+2	+	.	8	IV
<i>Impatiens parviflora</i>	c	4.4	2a.1	2b.1	.	1.1	1.1	.	2b.1	2b.1	2a.1	8	IV
<i>Geranium robertianum</i>	c	3.4	r	1	.	+	.	1.1	+2	+	.	7	IV
<i>Chaerophyllum temulum</i>	c	+1	.	r	.	.	.	r	r	.	.	4	II
<i>Chelidonium majus</i>	c	+2	.	r	.	r	4	II
<i>Glechoma hederacea</i>	c	+2	+	.	1.3	4	II
<i>Galeopsis pubescens</i>	c	.	.	.	1.3	.	.	.	+2	+2	.	3	II
<i>Geum urbanum</i>	c	+1	.	.	r	.	.	+2	.	.	.	3	II
<i>Urtica dioica</i>	c	+2	+2	.	.	.	2	I
<i>Rubus idaeus</i>	c	+2	.	2b.3	.	.	.	2	I
Accompanying species													
<i>Quercus robur</i>	a1	.	.	5.3	1.1	3.4	2a.2	2a.3	.	.	.	5	III
<i>Quercus robur</i>	c	.	r	r	r	.	r	r	r	.	.	6	III
<i>Aesculus hippocastanum</i>	a1	2b.3	1	I
<i>Aesculus hippocastanum</i>	a2	.	.	2b.3	1	I
<i>Aesculus hippocastanum juv.</i>	c	.	.	r	.	r	2	I
<i>Aesculus hippocastanum s.</i>	c	r	2	I
<i>Robinia pseudoacacia</i>	a2	.	.	+	2	I
<i>Robinia pseudoacacia juv.</i>	c	.	.	.	r	r	.	3	II
<i>Tilia platyphyllos juv.</i>	c	.+	.	+	.	r	+	r	r	.	.	6	III
<i>Rubus fruticosus (sp. coll.)</i>	c	.	r	+2	1.2	r	r	.	+	r	+	8	IV
<i>Dryopteris carthusiana</i>	c	r	.	+	r	.	+	+2	r	+2	1.1	8	IV
<i>Oxalis acetosella</i>	c	+2	.	+2	+3	.	+3	.	1.3	.	+	6	III
<i>Moehringia trinervia</i>	c	r	.	r	+	.	+	.	+	+2	+	7	IV
<i>Maianthemum bifolium</i>	c	+2	+	2b.3	.	+2	.	.	.	r	r	6	III
<i>Padus avium</i>	b	+	.	.	1	I
<i>Padus avium</i>	c	.	.	r	r	+	.	r	+	.	.	6	III
<i>Prunus serotina</i>	c	r	.	.	r	r	r	4	II
<i>Athyrium filix-femina</i>	c	+	.	+	+	3	II
<i>Sambucus nigra</i>	b	+	.	+	r	3	II
<i>Sambucus nigra</i>	c	.	r	.	r	+	.	.	.	+	.	4	II
<i>Tilia sp. s.</i>	c	.	+	.	r	.	r	.	.	r	.	4	II
<i>Brachythecium rutabulum</i>	d	.	.	r	r	.	.	.	r	.	.	4	II
<i>Rubus caesius</i>	c	.	.	+2	.	.	.	+2	.	.	.	3	II
<i>Ulmus laevis</i>	c	r	.	r	.	.	r	3	II
<i>Crataegus monogyna</i>	c	.	.	.	r	.	r	.	.	.	r	3	II

Sporadic species

Ch. All. *Carpinion betuli* (lok. Ch. Ass. *Galio sylvatici-Carpinetum*): *Tilia cordata* b 1 (r), 8 (r), *T. cordata* c 8 (r);

Ch. Cl. *Quercu-Fagetea* (incl. Ch. O. *Fagetalia sylvaticae*, Ch. All. *Fagion sylvaticae*, Ch. All. *Alno-Ulmion*): *Ulmus minor* b 1 (r), *U. minor* c 5 (r), *Plagiomnium undulatum* d 9 (1), *Acer campestre* c 3 (r), *Populus tremula* c 3 (r), *Dryopteris filix-mas* 3 (+), 10 (r), *Ribes spicatum* b 6 (r), *R. spicatum* c 7 (r), 9 (+), *Scrophularia nodosa* 7 (r), 8 (r), *Carex digitata* 9 (+), *Anemone nemorosa* 9 (r), *Carex sylvatica* 10 (r), *Crataegus laevigata* 7 (r);

Ch. Cl. *Artemisieta vulgaris*: *Lamium maculatum* 1 (2a).

Accompanying species: *Stellaria media* 10 (r), *Sorbus aucuparia* b 1 (+), 10 (r), *S. aucuparia* c 3 (r), *Tilia platyphyllos* b 6 (r), 9 (+), *Ajuga reptans* 1 (+), 7 (1), *Dryopteris carthusiana* 3 (1), 7 (r), *Geum rivale* 6 (r), 10 (r), 4 (r), *Lysimachia vulgaris* 5 (r), 7 (+), *Poa trivialis* 1 (r), 9 (r), *Scleropodium purum* d 3 (r), 10 (r), *Dicranella heteromalla* d 4 (r), 8 (r), *Fraxinus pennsylvanica* a1 10 (2), *Picea abies* a1 3 (2a), *Quercus rubra* 9 (r), *Robinia pseudoacacia* s., *Mycelis muralis* 8 (+), *Viola canina* 7 (+), *Betula pendula* a1 9 (+), *B. pendula* a2 3 (+), *Polytrichum formosum* d 10 (r).

Plant collection and lab works

Understorey biomass was determined by the plant material collected from the study plots from March 20 to October 2, 2010 (in 18 terms). From March 20 to May 29 the plants were harvested every 7 days, and then every 14 days. The frequency of material collection was initially greater in order to register the dynamic changes taking place in the undergrowth in the spring. This is particularly important in the case of associations in which geophytes can be observed.

At each time, the material was collected from 10 randomly placed frames (repetitions), under relatively uniform topographic conditions, marking sample points on a simplified map and avoiding their overlapping in the following harvest dates. A single sample consisted of a collection of plants from the area limited by a square metal frame with dimensions of 0.6×0.6 m (0.36 m²). While choosing locations of sample plots, trodden paths, dense clumps of natural regeneration, piles of woody debris, and places of wild boar rooting were avoided. All plants (including woody plants of height up to 0.5 m) that grew within the frame were collected by cutting them flush with the surface of the ground using scissors and shears. Individuals growing outside of the frame, but having some parts inside, were not taken into account. However, those plants which grew within the frame, i.e. in the area of the sample, were cut and whole of it was treated as a part of the collection sample. It has been assumed that inside the frame the parts of plants growing outside it balance the sticking out fragments of individuals growing in the sample area. The plants were separated by identifying the species. The collected material was placed into the separated appropriately identified envelopes. During fieldwork, the biomass of woody plants and herbaceous perennials produced

in 2010 was separated from that produced in previous years. In order to assess changes in herbaceous biomass produced during the growing season of 2010, both biomass of woody plants (seedlings) and herbaceous biomass produced before 2010 were excluded from the collected biomass. Due to the fact that in some places the collection of plant material was composed solely of woody plants, the number of samples included in the analysis ranged from 7 to 10.

The collected material was transported to the Institute of Dendrology of the Polish Academy of Sciences in Kórnik, where it was dried at 65°C to constant weight (at least 7 days) in forced-air dryers (ULE 600, Memmert GmbH + Co.KG, Germany), and then weighed. The total mass from each of the collected samples was determined for each species separately with accuracy of 0.001 g using weights BP 210 S and Mettler Toledo PG 1003-S.

Statistical analysis

Statistical differences between the weights of plants in the analyzed harvest dates were determined using one-way analysis of variance (ANOVA), and the mean values were compared using the Tukey's test. Hereinafter we use abbreviations SE and CV for standard error and coefficient of variation, respectively. The weight of plants of each species was related to the whole collection period, even if the species did not appear in all of the collected samples. Regardless of the number of samples in which the species occurred, the average weight was calculated as though it was present in each collected sample. For statistical analyzes the JMP software was used (SAS Institute, Cary, NC, USA).

3. Results

Phytosociological relations

Based on phytosociological relevés made on the experimental plot, the presence of oak-hornbeam forest in two subassociations was diagnosed: *Galio sylvatici-Carpinetum typicum* and *Galio sylvatici-Carpinetum corydaletosum*, All. *Carpinion betuli*, O. *Fagetalia sylvaticae*, Cl. *Quercu-Fagetea* (tab. 1).

On the study area, plant species diversity is faint and plant community exhibits features of severe impoverishment. There are no characteristic species in the strict sense for *Galio sylvatici-Carpinetum*; therefore, assigning the studied area to this community is determined mainly by a significant quantitative share of *Carpinus betulus* and the presence of *Dactylis polygama*, recognized as a characteristic species of the *Carpinion betuli* association. Another species attributed to this plant association is *Corylus avellana*, but its connections with the oak-hornbeam forests in the Greater Poland region are hardly visible; this species is common here in the ash and alder riparian forests. Additional feature which contributes to recognition of the studied plant community as oak-hornbeam forest, is a very small proportion of species characteristic for other types of mesotrophic forests: riparian (All. *Alno-Ulmion*) and beech (All. *Fagion*) forests.

It is problematic to assign the studied plant patches to plant subassociation. Due to the topographical and hydrological situation (located in the valley of a few streams and high water table) it should be expected that the studied patches represent the most humid variant of an oak-hornbeam forest - *G.s.-C. corydaletosum*; however, in the studied patches very few geophytes occurred, and their range was limited to the closest vicinity of the stream. The described area also lacked distinctive species of other subassociations of oak-hornbeam forest, such as poor acid oak-hornbeam forest *G.s.-C. polytrichetosum* and dry oak-hornbeam forest *G.s.-C. lathyretosum*. Thus, on the basis of a floral composition, these patches need to be assigned to a typical subassociation *Galio sylvatici-Carpinetum typicum*. It should be noted that it is impossible to determine whether such phytocoenosis formation is only the result of habitat, or the lack of distinctive species is due to observable floristic impoverishment, which may be the result of anthropopression (periodically strong thinning, grazing and even eradication of plants due to collection for decorative purposes). Such interactions are very likely in the woods adjacent to the park complex located near urban areas. The anthropopression supposition is

also supported by the fact that in the undergrowth the geophytes, which are not associated with humid habitats and which are generally abundant in typical variant of hornbeam forest, such as *Anemone nemorosa*, *Adoxa moschatellina*, and even *Hepatica nobilis*, which also occurs frequently in dry oak habitats, are very poorly represented. These floristically poor forms of oak-hornbeam forests, probably of anthropogenic origin, are known from the whole Polish lowland, and the most striking example in spring geophytes is the poor Grabina oak-hornbeam forest reserve in the Wielkopolska (Greater Poland) National Park (Balcerkiewicz et al. 1992).

Apart from a clear depletion of flora, the studied forest community bears no visible signs of other forms of degeneration of plant communities. The only clear anthropogenic trace is the presence of a few individuals of an alien tree species on the periphery of the tree stand – *Aesculus hippocastanum* – and a single occurrence of two other invasive species: *Padus serotina* and *Impatiens parviflora*. The last two of these species in the study area are relatively sparse.

Dynamics of understorey biomass

The material collected throughout the growing season includes 57 species of both herbaceous (33 species) and tree (24 species) plants. Additionally, among the collected plant material four species of mosses have been found: *Atrichum undulatum*, *Brachythecium rutabulum*, *Polytrichum formosum*, *Pseudoscleropodium purum*.

Average mass of plants (produced in 2010 and earlier) differ significantly between terms of collection ($p=0.0006$, tab. 2). The smallest biomass was recorded on April 3 (37.2 kg/ha), while the highest one on June 12 (337.6 kg/ha), May 1 (308.1 kg/ha), May 15 (280.0 kg/ha) and May 8 (279.5 kg/ha).

By analyzing changes in solely herbaceous biomass produced during the growing season of 2010, a statistically significant difference between them could be observed at different times of collection ($p=0.0007$, tab. 2). The smallest mass of herbs was observed on April 3 (13.0 kg/ha), while the largest on May 1 (259.8 kg/ha), June 12 (246.5 kg/ha) and May 15 (245.4 kg/ha).

The most commonly reported species in the growing season were: *Oxalis acetosella* (in 18 collections), *Moehringia trinervia* (17), *Geranium robertianum* (16), *Impatiens parviflora* (14), *Maianthemum bifolium* (13), and *Viola reichenbachiana* (13). Although these species were found in many of the analyzed periods, their share in the total biomass of herbaceous plants was not high. For example, the average share of *Oxalis acetosella* was 2%, of *Moehringia trinervia* – 3%, *Geranium robertianum*

Table 2. Mean biomass of all plants (herbaceous and woody species, produced in the year 2010 and previous years) and herbaceous plants (produced in the year 2010).

Date of biomass harvesting	Day of year	Plant biomass (kg/ha)					Biomass of herbaceous plants (kg/ha)						
		min.	max.	mean	SE	CV (%)	min	max.	mean	SE	CV (%)		
20.03.	79	19,2	469,1	105,4	ab	42,2	126,7	1,8	108,7	33,1	ab	11,2	101,8
03.04.	93	2,9	87,9	37,2	b	8,6	73,0	0,0	34,5	13,0	b	3,7	91,1
10.04.	100	81,0	792,3	214,9	ab	8,6	108,7	26,8	436,5	110,5	ab	37,9	108,4
17.04.	107	91,5	505,1	219,1	ab	42,3	61,0	4,5	351,4	169,7	ab	34,5	64,3
24.04.	114	18,9	573,0	210,5	ab	59,6	89,5	1,8	549,7	173,3	ab	61,2	111,7
01.05.	121	28,7	449,4	308,1	a	44,3	45,4	89,8	384,1	259,8	a	37,0	42,7
08.05.	128	28,7	695,6	279,5	ab	61,0	69,1	16,1	569,3	226,0	ab	54,5	76,2
15.05.	135	22,6	731,1	280,0	ab	67,4	76,1	83,8	662,0	245,4	a	63,3	77,4
22.05.	142	30,8	654,7	182,4	ab	61,2	106,1	1,1	572,9	129,1	ab	55,1	134,8
12.06.	163	30,5	821,6	337,6	a	76,3	71,5	0,1	794,8	246,5	a	76,8	98,6
26.06.	177	83,1	482,6	253,3	ab	41,7	52,0	51,6	362,2	147,9	ab	29,5	63,0
10.07.	191	72,4	381,4	188,4	ab	38,7	65,0	15,6	377,4	130,1	ab	41,4	100,7
24.07.	205	41,0	363,8	219,0	ab	41,8	60,3	4,1	358,4	128,2	ab	39,3	96,8
07.08.	219	31,7	230,6	124,4	ab	21,8	55,5	2,4	230,6	79,5	ab	27,8	105,0
21.08.	233	22,3	220,7	121,6	ab	26,3	68,5	0,4	218,0	64,3	ab	29,5	121,4
04.09.	247	10,9	454,3	123,6	ab	45,9	117,5	1,1	344,9	64,8	ab	42,0	183,2
18.09.	261	13,7	644,1	119,9	ab	63,5	167,4	7,3	600,1	146,0	ab	83,9	151,9
02.10.	275	10,0	254,2	97,0	ab	24,1	78,6	3,8	216,1	42,6	ab	25,2	167,7
ANOVA		<i>F P</i>					<i>F P</i>						
<i>P>F</i>		2,7129 0,0006					2,6858 0,0007						

and *Impatiens parviflora* – both 6%, *Maianthemum bifolium* – 8%, and *Viola reichenbachiana* – 4% (tab. 3).

In the analyzed periods, different numbers of herbaceous species within the samples (from 9 to 22, tab. 3) were reported. Analysis of the share of each species in the understorey biomass indicated the dominance of just a few of them, but their dominance has been changing in the course of growing season. For example, biomass of *Ficaria verna* predominated in 8 of 18 collection periods (from March 20 to May 22, with the exception of May 1, when it was a co-dominant species), and its presence was recorded nine times in total. Average weight of *F. verna* from all terms in which it was recorded, amounted to 48.2 kg/ha and ranged from 5.5 kg/ha to 88.4 kg/ha. The average share of biomass for this species was 36.0% and oscillated between 14.5 and 51.0% during the growing season (tab. 3). Distinctive group of plants, i.e., ferns *Athyrium filix-femina*, *Dryopteris filix-mas*, *Dryopteris carthusiana*, were reported only in 1-4 terms; nevertheless, the share of their biomass in the total weight of herbaceous plants collected in a given term was very high. For example, the average share of the mass of *Athyrium filix-femina* (recorded only on September 4)

was 52.2%, the average share of biomass of *Dryopteris filix-mas* (recorded on three dates: May 8, August 7, and September 18) was 33.4%, while that of *Dryopteris carthusiana* (recorded four times: March 20, April 17, July 10, and October 2) was 25.9%.

The obtained results allow us to trace the changes in biomass of individual species in the growing season (tab. 3). For example, the biomass of *Oxalis acetosella*, a species present in all harvest dates, reached its maximum value on May 15 (8.4 kg/ha), accounting for 3.4% of the total mass of plants collected on that date. The greatest share of this species (7.6%) in total herbaceous biomass was recorded on March 20. The average weight of *Moehringia trinervia* was 3.2 kg/ha (range from 0.01 to 16.6 kg/ha). The average share of biomass of this species was 3.0% and ranged from 0.02% (on August 7) to 14.7% (on March 20). Slightly less frequently recorded species was *Impatiens parviflora*. Its biomass ranged from 0.7 kg/ha (on September 18) to 39.8 kg/ha (on June 12) and averaged 9.7 kg/ha. The share of *Impatiens parviflora* with respect to the total biomass ranged from 0.5% (September 18) to 16.2% (June 12).

Table 3. Mean plant biomass (kg/ha) of the particular herbaceous species and percent biomass of individual plant species by harvest period in relation to the total herbaceous plant biomass harvested on a given date (%).

Species	Plant biomass (kg/ha) and biomass share in total understorey biomass (%)																				
	20.03.	03.04.	10.04.	17.04.	24.04.	01.05.	08.05.	15.05.	22.05.	12.06.	26.06.	10.07.	24.07.	07.08.	21.08.	04.09.	18.09.	02.10.			
<i>Adoxa moschatellina</i>	0,46 (3,58)	15,14 (13,70)	18,97 (11,17)	3,03 (1,75)	48,14 (18,53)	9,73 (4,31)	27,32 (11,14)	11,98 (9,28)	3,42 (1,39)	4,32 (2,92)	0,32 (0,25)										
<i>Aegopodium podagraria</i>	1,60 (1,44)		1,86 (1,07)				6,33 (4,90)	1,11 (0,45)	2,21 (1,49)	8,46 (6,50)	5,06 (5,14)	6,59 (6,37)			0,16 (0,24)	9,38 (6,42)					
<i>Ajuga reptans</i>	2,40 (7,24)				11,19 (4,31)	34,66 (15,34)	28,98 (11,81)	10,50 (8,13)	1,20 (0,49)	11,42 (7,72)	2,52 (1,94)	3,37 (2,63)				1,65 (2,54)					
<i>Alliaria petiolata</i>	1,15 (3,46)	0,71 (0,64)		0,72 (0,42)	5,49 (2,11)	2,57 (1,14)	0,35 (0,14)	1,79 (1,39)	0,06 (0,02)	1,42 (1,09)	0,41 (0,32)						0,32 (0,22)				
<i>Anemone nemorosa</i>	2,32 (17,89)	5,16 (4,67)	16,56 (9,76)	4,26 (2,46)	37,14 (14,30)	9,09 (4,02)	2,81 (2,18)														
<i>Athyrium filix-femina</i>																		36,44 (56,20)			
<i>Chaerophyllum temulum</i>				1,65 (0,95)					27,54 (11,17)	7,09 (4,80)			0,01 (0,02)								
<i>Chelidonium majus</i>	1,43 (1,29)				4,83 (1,86)															0,29 (0,68)	
<i>Dactylis polygama</i>									5,89 (2,39)					7,10 (8,92)							
<i>Dryopteris carthusiana</i>	2,15 (6,49)			7,77 (4,58)								37,74 (29,00)								27,01 (63,46)	
<i>Dryopteris dilatata</i>						5,13 (2,09)			11,11 (4,51)	35,47 (23,97)			35,80 (27,92)	10,10 (12,70)	7,59 (11,80)					1,49 (3,51)	
<i>Dryopteris filix-mas</i>																				25,62 (32,23)	
<i>Ficaria verna</i>	15,92 (48,05)	5,51 (42,44)	55,56 (50,28)	79,49 (46,83)	88,41 (51,03)	37,74 (14,53)	55,73 (24,66)	76,16 (31,04)	18,95 (14,68)												
<i>Galeopsis pubescens</i>																				0,63 (0,48)	
<i>Galium aparine</i>			3,64 (3,30)	0,97 (0,57)	1,60 (0,93)	7,13 (2,75)	0,34 (0,14)	2,34 (1,81)	0,40 (0,16)	0,10 (0,07)											
<i>Geranium robertianum</i>		0,45 (0,41)	0,92 (0,54)	9,74 (5,62)	4,20 (1,62)	8,47 (3,74)	26,58 (10,83)	7,16 (5,55)	50,83 (20,62)	16,78 (11,34)	5,95 (4,57)	7,33 (5,72)	2,72 (3,42)	6,07 (9,43)	1,21 (1,87)	0,24 (0,16)	2,21 (5,20)				

<i>Geum urbanum</i>	0,64 (1,94)	0,06 (0,03)	1,31 (0,58)	0,58 (0,24)	12,05 (9,33)	7,88 (3,20)	3,40 (4,28)	14,63 (22,74)	4,25 (6,55)									
<i>Glechoma hederacea</i>			13,76 (6,09)	4,65 (1,90)	0,04 (0,03)	16,04 (6,51)	3,02 (2,32)	1,69 (1,32)	0,02 (0,02)									
<i>Impatiens noli-tangere</i>		0,11 (0,07)	0,02 (0,01)	0,07 (0,03)	2,14 (0,87)	1,50 (1,02)												
<i>Impatiens parviflora</i>		1,12 (0,66)	6,96 (4,02)	7,57 (2,91)	11,97 (5,55)	39,81 (16,15)	10,69 (7,23)	17,42 (13,38)	8,60 (6,71)	2,81 (3,53)	3,17 (4,94)	1,55 (2,38)	0,72 (0,49)					
<i>Lamium maculatum</i>		28,23 (16,63)	32,19 (18,58)	3,51 (1,42)	17,53 (13,67)					30,67 (21,00)								
<i>Lysimachia nummularia</i>							18,93 (23,80)											
<i>Maianthemum bifolium</i>	1,61 (12,43)	9,61 (5,66)	15,18 (8,76)	29,19 (11,24)	5,78 (2,56)	9,31 (3,80)	16,14 (6,55)	15,31 (10,35)	14,62 (11,23)	16,15 (12,59)	1,49 (2,30)	1,32 (0,90)						
<i>Milium effusum</i>			20,92 (8,05)	18,27 (8,09)	35,86 (14,61)	23,34 (15,78)	16,48 (12,67)	5,53 (4,31)	22,67 (35,24)	2,56 (3,94)	4,58 (3,14)	3,52 (8,28)						
<i>Moehringia trinervia</i>	4,88 (14,73)	1,43 (1,02)	2,01 (1,82)	1,77 (1,04)	16,62 (6,40)	4,75 (2,10)	7,21 (2,94)	7,87 (6,10)	2,16 (0,88)	1,73 (1,33)	0,23 (0,18)	0,01 (0,02)	0,33 (0,77)					
<i>Mycelis muralis</i>		0,09 (0,68)	0,10 (0,06)	2,31 (0,94)														
<i>Oxalis acetosella</i>	2,51 (7,56)	0,04 (0,28)	5,48 (4,96)	1,32 (0,78)	1,60 (0,62)	1,56 (0,69)	8,43 (3,44)	1,18 (0,91)	2,17 (0,88)	4,31 (2,91)	0,11 (0,09)	0,18 (0,14)	2,22 (2,79)	1,60 (2,49)	0,42 (0,65)	0,08 (0,05)	1,90 (4,45)	
<i>Poa nemoralis</i>	2,36 (7,14)		12,67 (11,47)	1,23 (0,71)	22,68 (8,73)	21,30 (9,42)	6,11 (4,73)	15,69 (12,24)										
<i>Poa trivialis</i>					0,06 (0,02)										0,12 (0,08)			
<i>Stachys sylvatica</i>					50,38 (20,44)	8,31 (5,62)	18,60 (14,30)	9,12 (7,11)										
<i>Urtica dioica</i>	1,44 (11,11)				11,37 (8,80)								1,28 (1,99)					
<i>Viola canina</i>				5,30 (2,04)											0,67 (1,03)			
<i>Viola reichenbachiana</i>	1,12 (3,39)	0,07 (0,56)	6,64 (6,01)	3,00 (1,77)	3,54 (1,57)	2,41 (0,98)	2,27 (0,92)	5,53 (3,73)	1,10 (0,84)	5,50 (8,56)	13,89 (21,43)	7,62 (5,21)	0,09 (0,20)					
Day of year	79	93	100	107	114	121	128	135	142	163	177	191	205	219	233	247	261	275
Number of species	9	9	12	12	17	16	18	16	16	22	15	15	14	13	9	13	13	9

4. Discussion

The study results showed statistically significant differences in the understorey biomass between the periods of material collection. Among the published studies on seasonal changes in understorey biomass in forest communities there are some which have shown a strong correlation between the date of harvest and the amount of biomass produced (e.g. Kaźmierczakowa 1971; Rawlik et al. 2012), as well as those which have demonstrated the lack of such a relationship (e.g. Tremblay, Larocque 2001). The amounts of understorey biomass may vary significantly in different plant communities at the same time. This is confirmed, for example, by the work of Kubiček and Jurko (1975), who determined the understorey biomass in August 1973 in Little Carpathians in Slovakia in five different forest communities varying in terms of trophic and moisture conditions. In *Luzulo-Fagetum* association, herbaceous biomass amounted to 41 kg/ha (excluding mosses), in *Dentario-Fagetum* – 364 kg/ha, in *Aceri-Carpinetum* – 476 kg/ha, in *Carici pilosae-Carpinetum* – 691 kg/ha, while in *Stellario-Alnetum* – 1364 kg/ha. On the other hand, in plant communities formed mainly by shrubs and mosses, standing biomass can take much greater value. For example, research of Sobisz and Parzych (2010) carried out in the Słowiński National Park shows that the understorey biomass in plant community of *Vaccinio uliginosi-Betuletum pubescentis* is 4745 kg/ha (of which 24% is the biomass of mosses), while in other plant community such as *Empetro nigri-Pinetum* it is 3393 kg/ha (of which 29% is the biomass of mosses).

The course of changes in understorey biomass (total and produced in 2010) in the growing season in the studied patches of *Galio sylvatici-Carpinetum betuli* is similar. Undergrowth biomass increases rapidly in early spring, reaches its maximum values in May and mid-June, and then decreases markedly. Maximum total biomass (including woody plants) is approximately 300 kg/ha, while the maximum herbaceous biomass produced during the analyzed growing season stands at around 250 kg/ha.

Comparison with the literature data shows that the states of understorey biomass in oak-hornbeam communities can be very diverse. For example, in oak-hornbeam forest of *Tilio-Carpinetum stachyetosum*, Kaźmierczakowa (1971) observed the highest values of undergrowth biomass in early July (in 1965 – 660 kg/ha, and in 1967 – 270 kg/ha). A significant difference in amounts of biomass between the investigated years was most likely caused by pathogenic fungi in the second turn of research. In the oak-hornbeam forest investigated by us, the highest weight of all plants was

recorded on June 12 and it amounted to 337.6 kg/ha, while the highest herbaceous biomass was produced on May 1, 2010 (259.8 kg/ha). Differences in the periods of maximum biomass occurrence may result from the species composition of ground vegetation, especially from the characteristics of growth and development of the dominant species. It is well illustrated by the oak-hornbeam forest described by Kaźmierczakowa (1971), in which the dominant species in terms of weight were *Aegopodium podagraria*, *Stellaria holostea*, *Galium odoratum*, and *Ranunculus lanuginosus*, i.e. species that grow rapidly after the end of flowering of the spring geophytes and that contribute to the easily observable effect of late-spring “greening” of the forest floor, which is very characteristic for the oak-hornbeam and riparian forests. In the oak-hornbeam forest in the Syców Forest District, however, there was no single species that would dominate throughout the whole growing season. The periodically largest share in the total weight of the plants has been observed in *Ficaria verna* and *Impatiens parviflora*. The first species is an early spring geophyte, the only representative of this typical for oak-hornbeam forests group of species that was observed constantly in the study area. The second one is an invasive annual plant species, beginning its growth relatively late and reaching a maximum density in June and early July (Piskorz, Klimko 2002; Piskorz 2005). This species is probably responsible for the observed maximum of the biomass in this study plot in the middle of June (compare with fig. 1). We also recorded the occurrence of *Aegopodium podagraria* in the investigated area, but its share in the total biomass was significantly lower than the one observed by Kaźmierczakowa (1971).

Understorey biomass production rate during the growing season and dates when biomass reaches the maximum value in the given plant community may vary in successive years. For example, Banasik (1978) found the highest values of understorey biomass in the medium moist oak-hornbeam forest *Tilio-Carpinetum typicum* on July 14, 1967 (433.4 kg/ha) and on June 4, 1968 (445.5 kg/ha), and of standing biomass very close to the maximum were reported on May 26, 1967 (374.2 kg/ha) and May 3, 1968 (312.2 kg/ha). These values are much higher than those obtained by us in the plant community of *Galio sylvatici-Carpinetum betuli*, although the states of maximum biomass were observed later. In turn, in the moist oak-hornbeam forest *Tilio-Carpinetum stachyetosum*, with a much smaller coverage of ground vegetation, the highest state of biomass was noted already on April 23, 1968 (243.0 kg/ha) (Banasik 1978). Both the term and amount of biomass are similar to the results obtained in plant community of *Galio sylvatici-Carpinetum betuli* in the

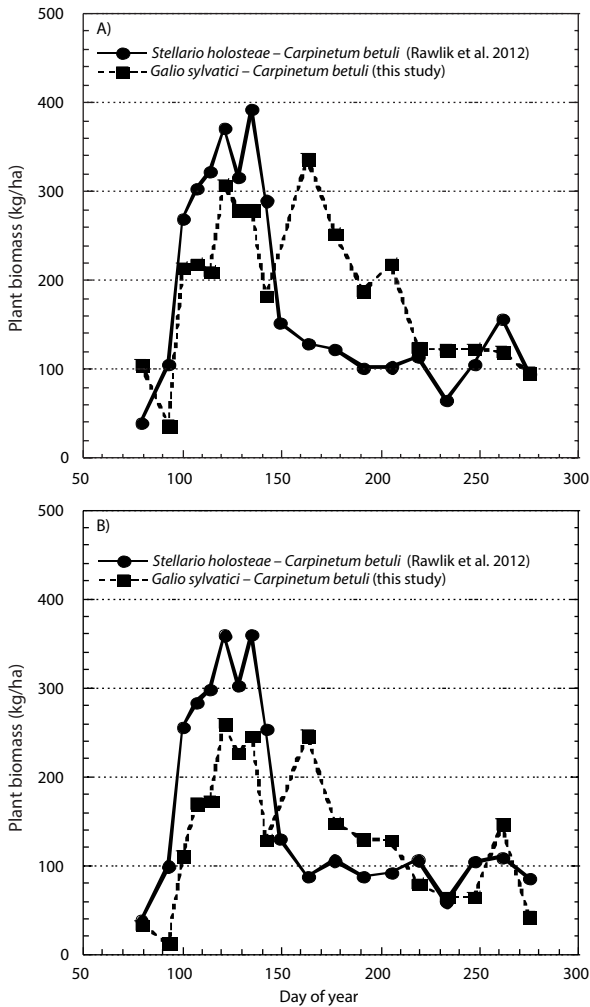


Figure 1. Changes in mean plant biomass of A) woody and herbaceous species produced in 2010 and previous years and B) herbaceous species produced in 2010 in two plant communities: *Stellario holosteeae-Carpinetum betuli* and *Galio sylvatici-Carpinetum betuli* over the growing season.

Syców Forest District. Research carried out by Traczyk and Traczyk (1967) shows that in forest communities with a significant share of geophytes the maximum values of understorey biomass are recorded in June-July. These authors noted undergrowth biomass in the community of *Tilio-Carpinetum* at two dates: April 28 (121.6 kg/ha) and July 8 (338.2 kg/ha).

Comparison of the results presented in this paper with data of Rawlik et al. (2012) from the area of the Różańsko Forest District indicates that the maximum biomass of understorey in *Galio sylvatici-Carpinetum betuli* takes place at the same time as in the community of *Stellario holosteeae-Carpinetum betuli* (end of April to mid-May, fig. 1). Both total understorey biomass, i.e. including

woody (seedlings) and herbaceous plants (produced in 2010 and earlier, fig. 1A), as well as herbaceous biomass produced in 2010 (fig. 1B), were significantly higher in patches of *Stellario holosteeae-Carpinetum betuli* studied by Rawlik et al. (2012) than in patches of *Galio sylvatici-Carpinetum betuli* in Syców during the period of maximum plant biomass in both communities. It is worth noting the fact that in the second decade of May the state of biomass in the oak-hornbeam forest *Galio sylvatici-Carpinetum betuli* is still higher than the one recorded at the same time in the community of *Stellario holosteeae-Carpinetum betuli* (until the end of July). The maximum herbaceous biomass produced in 2010 was recorded in the community of *Galio sylvatici-Carpinetum betuli* on May 1 (259.8 kg/ha), while in the community of *Stellario holosteeae-Carpinetum betuli* it was on May 15 (378.4 kg/ha) (Rawlik et al. 2012). It can be assumed that the differences observed in Syców are caused by a high share in the undergrowth of an annual neophyte *Impatiens parviflora*, which reaches its maximum development in late spring and summer (Piskorz, Klimko 2002; Piskorz 2005). The presence of this species can also cause the reduction in biomass of other oak-hornbeam forest species, including the taxa determining the maximum biomass in spring in typical oak-hornbeam forests (Balcerkiewicz et al. 1996).

Floristic characteristics indicate differences in the herbaceous species composition of both communities. In the ground vegetation of oak-hornbeam in Syców there are quite numerous plant species of the class *Artemisietea vulgaris*, which are not typical for deciduous forests, and their presence may be due to the location of research area in the vicinity of the city park, and thus increased anthropoppression. The undergrowth of oak-hornbeam forest in Różańsko species in classes other than *Quercus-Fagetea* have not been found (Rawlik et al. 2012). The ground flora in Różańsko is rather dominated by one species of geophytes, i.e. *Anemone nemorosa*, which reached the highest share in total plant biomass on April 10 (85% biomass), and the highest value of biomass on May 1 (258.23 kg/ha, 75.4% of the total biomass). In the plant community of *Galio sylvatici-Carpinetum betuli* the dominant species in spring was *Ficaria verna*; however, the prevalence of this species is not as clear as in the community of *Stellario holosteeae-Carpinetum betuli*. The maximum weight of this species in patches of *Galio sylvatici-Carpinetum betuli* was reached on April 24 and was 88.4 kg/ha, which accounted for 51% of the total mass of plants in this period of collection. A similar, though slightly lower, share of *Ficaria verna* in the total mass was recorded on March 20. Therefore both communities are marked by early spring geophytes domination,

but the species are different and have different habitat requirements. In the ground vegetation of an oak-hornbeam forest *Stellario holostea-Carpinetum betuli* after the period of geophytes dominance, the plant weight reduces significantly. After the withering of geophytes, the summer species start to dominate: *Galeobdolon luteum* and *Galium odoratum*. In this period in the ground vegetation of oak-hornbeam forest *Galio sylvatici-Carpinetum betuli* the species noticed without any marked dominance were more.

The development of ground flora is significantly influenced by tree species composition, especially the share of deciduous trees, which determines the changing light conditions in the studied phytocoenosis. In early spring, when the trees have not yet developed leaves, the forest floor gets more light, of which spring plants take advantage. In the investigated oak-hornbeam forest the highest average biomass of herbaceous plants was recorded on May 1, when the undergrowth was dominated by geophytes. In communities where geophytes are not so numerous, the highest state of biomass is generally observed in June and July in the case of dicots, while in the case of monocots – in mid-September (Każmierczakowa 1971).

5. Summary

The study results showed statistically significant differences in the state of understorey biomass during the growing season. The smallest total biomass of an understorey layer (including woody plants) was recorded on April 3 (37.2 kg/ha), while the highest on June 12 (337.6 kg/ha), May 1 (308.1 kg/ha), May 15 (280.0 kg/ha) and May 8 (279.5 kg/ha). Taking into consideration only herbaceous biomass produced during the analyzed growing season, the lowest biomass was found on April 3 (13.0 kg/ha), while the highest on May 1 (259.8 kg/ha), June 12 (246.5 kg/ha) and May 15 (245.4 kg/ha). The data indicate that although the share of herbaceous biomass expressed as a percentage of total aboveground biomass of the forest community is small, the rate of biomass production is important in the macro- and micronutrient cycle in the ecosystem. The greatest amounts of biomass and the rate of its production in oak-hornbeam forest *Galio sylvatici-Carpinetum betuli* were found in early spring, when the access of light to the forest floor is not limited by the developed leaves of the trees. Geophytes play an important role in the increased biomass production in spring, as they produce large amounts of biomass in a relatively short period of time.

Acknowledgment

We would like to thank the reviewers for insightful and valuable comments, which were used in the final version of the article.

References

- Balcerkiewicz S., Brzeg A., Kasprowicz M. 1992. Roślinność rezerwatów ścisłych Wielkopolskiego Parku Narodowego, in: Przyroda Wielkopolskiego Parku Narodowego. (ed. L. Kaczmarek, B. Walna). Materiały z konferencji naukowej. Uniwersytet im. Adama Mickiewicza w Poznaniu, Stacja Ekologiczna w Jeziorach, pp. 91–96.
- Balcerkiewicz S., Brzeg A., Kasprowicz M. 1996. Roślinność rezerwatu “Pod Dziadem” w Wielkopolskim Parku Narodowym. *Badania Fizjograficzne nad Polską Zachodnią – seria B*, 45: 79–120.
- Banasik J. 1978. Sezonowy rozwój i produkcja netto runa w dwóch płatach lasu grądowego Puszczy Niepołomickiej. *Studia Naturae – seria A*, 14: 67–134.
- Barbier S., Gosselin F., Balandier P. 2008. Influence of tree species on understorey vegetation diversity and mechanisms involved – A critical review for temperate and boreal forests. *Forest Ecology and Management*, 254(1): 1–15.
- Barkman J.J., Doing H., Segal S. 1964. Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. *Acta Botanica Neerlandica*, 13: 394–419.
- BULiGL 2000. Operat siedliskowo-glebowy dla Nadleśnictwa Syców wg stanu na 01.01.2000 na okres obowiązywania od 01.01.2000 do 31.12.2009. Biuro Urządzania Lasu i Geodezji Leśnej w Brzegu. Maszynopis w Nadleśnictwie Syców.
- BULiGL 2010. Plan Urządzania Lasu dla Nadleśnictwa Syców wg stanu na 01.01.2010 na okres obowiązywania od 01.01.2010 do 31.12.2019. Biuro Urządzania Lasu i Gospodarki Leśnej w Brzegu. Maszynopis w Nadleśnictwie Syców.
- Chapin F.S. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, 11: 233–260.
- Dafni A., Cohen D., Noy-Mier I. 1981. Life-cycle variation in geophytes. *Annals of the Missouri Botanical Garden*, 68(4): 652–660.
- Dixon R.K., Brown S., Houghton R.A., Solomon A.M., Trexler M.C., Wisniewski J. 1994. Carbon pools and flux of global forest ecosystems. *Science*, 263: 185–190.
- Gilliam F.S. 1988. Interactions of fire with nutrients in the herbaceous layer of a nutrient-poor Coastal Plain forest. *Bulletin of the Torrey Botanical Club*, 115(4): 265–271.
- Gilliam F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience*, 57: 845–858.
- Gilliam F.S., Roberts M.R. 2003. The herbaceous layer in forests of eastern North America. New York. Oxford University Press. ISBN: 0-19-514088-5.
- Każmierczakowa R. 1971. Ekologia i produkcja runa świetlistej dąbrowy i grądu w rezerwach Kwiatkówka i Lipny Dół na Wyżynie Małopolskiej. *Studia Naturae*, 15: 1–107.

- Kubiček F., Jurko A. 1975. Estimation of the above-ground biomass of the herb layer in forest communities. *Folia Geobotanica et Phytotaxonomica*, 10: 113–129.
- Matuszkiewicz J.M. 2001. Zespoły leśne Polski. Warszawa. WN PWN. ISBN: 83-01-13401-1
- Matuszkiewicz W. 2007. Przewodnik do oznaczania zbiorowisk roślinnych Polski. Warszawa. PWN. ISBN: 978-83-01-14439-5.
- Muller R.N. 2003. Nutrient relations of the herbaceous layer in deciduous forest ecosystems, w: The herbaceous layer in forests of eastern North America. (red. F.S. Gilliam, M.R. Roberts). New York. Oxford University Press, pp. 15–37. ISBN: 0-19-514088-5.
- Parzych A., Sobisz Z. 2010. Biomasa i produkcja pierwotna netto roślin runa w wybranych zespołach leśnych Słowińskiego Parku Narodowego. *Ochrona Środowiska i Zasobów Naturalnych*, 42: 72–83.
- Piskorz R. 2005. The effect of oak-hornbeam diversity on flowering and fruiting of *Impatiens parviflora* DC. *Roczniki Akademii Rolniczej w Poznaniu – Botanica Steciana*, 373(9): 187–196.
- Piskorz R., Klimko M. 2002. Fenologia *Impatiens parviflora* DC. w silnie prześwietlonym gradzie środkowoeuropejskim na lokalnym stanowisku w Wielkopolskim Parku Narodowym. *Roczniki Akademii Rolniczej w Poznaniu – Botanika*, 347(5): 135–144.
- Rawlik M., Jagodziński A.M., Janyszek S. 2012. Sezonowe zmiany stanu biomasy w runie lasu grądowego *Stellario holosteae-Carpinetum betuli*. *Leśne Prace Badawcze*, 73(3): 221–235.
- Rothstein D.E., Zak D.R. 2001. Photosynthetic adaptation and acclimation to exploit seasonal periods of direct irradiance in three temperate, deciduous-forest herbs. *Functional Ecology*, 15: 722–731.
- Rutkowski L. 2006. Klucz do oznaczania roślin naczyniowych Polski niżowej. Warszawa. PWN. ISBN: 978-83-01-14342-8.
- Small C.J., McCarthy B.C. 2002. Spatial and temporal variability of herbaceous vegetation in an eastern deciduous forest. *Plant Ecology*, 164: 37–48.
- Traczyk H., Traczyk T. 1967. Tentative estimation of the production of herb layer. *Ekologia Polska*, 15(46): 823–835.
- Trampler T., Kliczkowska A., Dmyterko E., Sierpińska A. 1990. Regionalizacja przyrodniczo-leśna na podstawach ekologiczno-fizjograficznych. Warszawa. PWRiL. ISBN: 83-913320-6-3.
- Tremblay N.O., Larocque G.R. 2001. Seasonal dynamics of understorey vegetation in four eastern Canadian forest types. *International Journal of Plant Sciences*, 162(2): 271–286.
- Widén B. 2002. Seasonal variation in forest-floor CO₂ exchange in a Swedish coniferous forest. *Agricultural and Forest Meteorology*, 111: 283–297.
- Yarie J. 1980. The role of understorey vegetation in the nutrient cycle of forested ecosystems in the mountain hemlock biogeoclimatic zone. *Ecology*, 61: 1498–1514.