



# Seasonal variability of biomass, total leaf area and specific leaf area of forest understory herbs reflects their life strategies



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## ABSTRACT

Seasonal variability of forest understory herbs is not well understood and there are almost no data about seasonal changes of individual plant biomass and specific leaf area (SLA) of this functional group, even though they are a crucial element of forest ecosystem plant biodiversity. The aim of the study was to characterize the seasonal variation of individual aboveground standing biomass, total leaf area and SLA of understory herbaceous species during a growing season. The study was conducted in the Czmoń Forest (W Poland; 52°15'N, 17°05'E) and covered 12 plant species, i.e. *Aegopodium podagraria*, *Alliaria petiolata*, *Anemone nemorosa*, *Anemone ranunculoides*, *Asarum europaeum*, *Corydalis cava*, *Ficaria verna*, *Galium aparine*, *Galeobdolon luteum*, *Hepatica nobilis*, *Maianthemum bifolium* and *Paris quadrifolia*. Plants were harvested 14 dates, between the 109th and 287th day of year. In all species there were statistically significant differences ( $p < 0.05$ ) in SLA and total leaf area among harvest dates and in individual plant biomass for all except two species (*A. ranunculoides* and *G. aparine*). Changes in SLA and total leaf area were related to changes in light conditions during the growing season. However, responses of the species studied to seasonal changes of light availability were different: those species which persisted through the whole sampling period differed from spring ephemerals, which resulted in different patterns of biomass production and SLA seasonal variation. In most cases, flowering individuals had lower SLA than vegetative plants, which may indicate that light availability is more important than light use efficiency for their generative propagation.

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## 1. Introduction

Although contribution of the understory to total plant biomass of forest ecosystems is relatively small (c.a. 1–2%), understory plants can have a 20-fold higher share of micro- and macroelement cycling (Yarie, 1980; Gilliam, 2007; Muller, 2014). Species composition and diversity of understory plant communities strongly depends on overstory species composition and canopy closure (Augusto et al., 2003; Barbier et al., 2008; Jagodziński and Oleksyn, 2009; Ampoorter et al., 2015). This impact of tree stands most frequently results from modification of nutrient cycling (Finzi et al., 1998a; Reich et al., 2005; Hobbie et al., 2006, 2007, 2010), pH (Finzi et al., 1998b; Dauer et al., 2007; Mueller et al., 2012), or light availability (Knight et al., 2008; Jagodziński and Oleksyn, 2009;

Niinemets, 2010; Mueller et al., 2016). Understory species richness and diversity is positively correlated with overstory species richness and diversity. However, some species of trees, due to high leaf area index, which limits the amount of light available to understory plants, limit the understory species richness and diversity (Mölder et al., 2008; Chmura, 2013). Understory species composition may also influence the density and survival rates of natural regeneration of canopy trees (Gilliam, 2007; Gilliam and Roberts, 2014), which is crucial for further tree stand species composition (Baraloto et al., 2005).

Functional diversity of plant species allows their coexistence in the same habitats and results from seasonal dynamics of light availability through the growing season. Some temperate deciduous forest understory plant species are adapted to higher light availability in the spring. The amount of light reaching the forest floor is highest in early spring when foliage of canopy trees has not yet developed. Species typical of early-spring (spring ephemerals) differ from summer-green and semi-evergreen species in relative biomass accumulation patterns (Rothstein and Zak, 2001) and

Abbreviations: DIFN, diffuse non-interceptance; SLA, specific leaf area.

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in photosynthesis rate (Lapointe, 2001; Neufeld and Young, 2014). These species are geophytes, storing carbohydrates in tubers or bulbs, which allows them to quickly develop foliage and efficiently use the period of increased light availability (Dafni et al., 1981; Rothstein and Zak, 2001; Neufeld and Young, 2014). When canopy foliage cover is at its maximum, the understory is dominated by species with other life strategies, most frequently hemicryptophytes (Ellenberg, 1988; Jagodziński et al., 2013; Gilliam and Roberts, 2014; Neufeld and Young, 2014), usually with summer-green leaves and lower light requirements (Ellenberg, 1988; Rothstein and Zak, 2001; Ellenberg and Leuschner, 2010; Neufeld and Young, 2014). Thus, seasonal dynamics of temperate deciduous forest understory shapes its functional and species diversity (Hunt and Cornelissen, 1997; Small and McCarthy, 2003; Gilliam, 2007; Muller, 2014). Geophytes compose 90% of understory plant community biomass production during their spring emergence, however hemicryptophytes, which are the most frequent life form of woodland herbaceous plant species, compose over 90% of understory plant community biomass during summer (Jagodziński et al., 2013). Seasonal dynamics of understory biomass production is poorly understood. For example, Tremblay and Larocque (2001) found that understory biomass differed statistically significantly among harvest dates only in one of the four types of forests studied. However, Rawlik et al. (2012) and Jagodziński et al. (2013) found that the difference between minimum and maximum understory plant biomass was almost tenfold during the growing season.

Opposite to the situation for trees and field or meadow plants, growth patterns and traits of which have been studied in detail, few forest understory species have been included in experimental sets of species (Poorter and Remkes, 1990; Hunt and Cornelissen, 1997; Poorter and De Jong, 1999; Rothstein and Zak, 2001; Curt et al., 2005; Ma et al., 2010; Wang et al., 2010), and most frequently these species were pooled with other herbaceous plants. The exceptions are invasive species of herbaceous plants, for example *Impatiens parviflora* or *I. glandulifera* (Perglová et al., 2009; Godefroid and Koedam, 2010; Chmura, 2014), for which detailed assessments of individual traits were done. Only Rothstein and Zak (2001) studied photosynthetic response of three forest herbs to find the differences among their life strategies. In most cases data on herbaceous plant biomass considers the plant community or populations of several species, and given values are expressed as biomass per area unit, not per individual. In our previous studies (Jagodziński et al., 2013; Rawlik et al., 2012) we studied seasonal variation in biomass standing crop of the understory of oak-hornbeam forest, and although we provided detailed data about net primary production of the most frequent species, we did not study the individual plant traits in detail. Surprisingly, our literature review also found that there is no information about differences in biomass and specific leaf area (SLA) between flowering and vegetative individuals of forest understory plant species.

At this time our knowledge about dynamics of foliage development and SLA during the growing season is scarce. Only Wilson et al. (2000) and Tremblay and Larocque (2001) found that there is variation in SLA of herbaceous understory species within the growing season. However, they did not study this phenomenon for individual species, but for the whole group of understory herbs. Thus, there is a clear lack of data about seasonal dynamics of SLA for forest understory herbaceous plants.

The aim of the study was to characterize the seasonal variation of individual aboveground standing biomass, total leaf area and SLA, during a growing season for 12 herbaceous plant species (which compose the understory of a deciduous forest), based on their life histories and ecological requirements. The secondary aim of the study was to assess the differences in parameters studied between flowering and vegetative individuals. We hypothesized that spring ephemerals would show different dynamics of

biomass and SLA than species which persist in the understory during the whole growing season, due to differences in morphology and ecology of these groups (Dafni et al., 1981; Lapointe, 2001; Small and McCarthy, 2003; Neufeld and Young, 2014). We also hypothesized that flowering individuals would have higher SLA than vegetative ones within the same species and time period. We stated this assumption because higher SLA is connected with higher leaf photosynthesis efficiency (Poorter and De Jong, 1999; Cornelissen et al., 2003; Wright et al., 2004).

## 2. Materials and methods

### 2.1. Study area

The study was conducted in the Czmoń Forest (Babki Forest District, W Poland; 52°15'N, 17°05'E). According to meteorological data from Babki Forest District, the mean annual temperature in 2004–2008 was 8.5 °C and mean annual precipitation was 507 mm. The study area is located in a deciduous forest complex, where the most abundant plant community is deciduous forest with *Quercus robur*, *Carpinus betulus*, which by the phytosociological approach is named *Galio sylvatici-Carpinetum* (Ellenberg, 1988; Ratyńska et al., 2010). Detailed descriptions of this plant community in close vicinity of the study area were given by Wiczyńska et al. (2013), Horodecki et al. (2014) and Rawlik et al. (2015).

### 2.2. Species studied

We studied 12 species of vascular plants, which are the most abundant in the understories of deciduous forests in Central Europe (Ellenberg, 1988): *Aegopodium podagraria*, *Alliaria petiolata*, *Anemone nemorosa*, *Anemone ranunculoides*, *Asarum europaeum*, *Corydalis cava*, *Ficaria verna*, *Galium aparine*, *Galeobdolon luteum*, *Hepatica nobilis*, *Maianthemum bifolium*, and *Paris quadrifolia*. These species differed by their ecological requirements and life-history traits (Table A.1).

### 2.3. Methods

In the study area four 50 × 50 m experimental plots were established. Plant biomass was assessed by the harvest method. Plants were harvested on 14 dates, between the 109th and 287th day of year (19-Apr-2013 to 04-Oct-2013), with two-week intervals, except for the second harvest, which was performed one week after the first. Plants were randomly selected within the experimental plots. A single stem was treated as a single individual, and individuals damaged by herbivores were excluded from the sample. Flowering plants were treated separately to assess the differences between flowering and non-flowering individuals. We planned to harvest 15 (or in sufficient conditions 30) individuals of each species at each harvest date, however due to their seasonal dynamics, the number actually harvested was limited (Table A.2). Moreover, we excluded from statistical analyses two harvests of *A. nemorosa* and *A. ranunculoides*, which occurred a month after their emergence.

To obtain information about changes of light availability over the spring (during foliage development) we measured canopy openness (diffuse non-interceptance, DIFN) using an LAI-2200 plant canopy analyzer (Li-Cor Inc., Lincoln, NE, USA). We followed methods described by Machado and Reich (1999) and Knight et al. (2008). Results of four to six series of 20 measurements at each date have been shown as means with 95% confidence intervals (Fig. 1).

All harvested individuals were packed into envelopes, unfolded and transported to the laboratory, and separated into biomass

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