Seasonal dynamics of shoot biomass of dominant clonal herb species in an oak–hornbeam forest herb layer

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Abstract Seasonal fluctuations of light availability, nutrient concentrations, and moisture affect plant population traits like density, standing biomass, and flowering. We analyzed seasonal changes of density and shoot biomass of the four most frequent herb species growing in an oak–hornbeam forest community, i.e., *Anemone nemorosa*, *Ficaria verna*, *Galeobdolon luteum*, and *Galium odoratum*. In 2010 and 2011 plant biomass was harvested from 7 to 10 randomly situated square sample plots (0.36 m²) in the homogeneous oak–hornbeam forest community every week in the spring and every two weeks in the summer and autumn. The highest abundance of *Anemone nemorosa* reached over 1000 shoots per m², of *Ficaria verna* 459.5 shoots per m², of *Galium odoratum* 83.6 shoots per m², and of *Galeobdolon luteum* 98.4 shoots per m² (means for 2010 and 2011, based on all sample plots). We did not observe negative correlation between density and shoot biomass. Growth rates of vegetative shoot biomass amounted to 0.857 mg day⁻¹ for

Anemone nemorosa, 0.467 mg day⁻¹ for *Ficaria verna*, 0.722 mg day⁻¹ for *Galium odoratum*, and 0.448 mg day⁻¹ for *Galeobdolon luteum* (means for 2010 and 2011). Spring ephemerals had much higher densities of shoots than summer-greens. Summer-greens reached higher biomass of individual shoots than spring ephemerals. Flowering shoots constituted only 4, 2, and 11% of all shoots for *A. nemorosa*, *F. verna*, and *G. odoratum*, respectively. More resource availability resulting in high shoot biomass did not translate to higher share of flowering shoots.

Keywords Plant biomass · Plant density · Clonal plants · Oak–hornbeam forest · Seasonal dynamic

Introduction

Central European oak–hornbeam forest association is a stable, self-organized, and spontaneous ecosystem which occurs in areas without human intervention and disturbances. This forest association is characterized by low ratio of gross primary production to standing crop, a ratio of gross primary production to respiration close to zero, and plants that have long and complex life cycles, usually representing a K-type strategy (Morin 2009). Nevertheless, this static view of the ecosystem obscures processes that contribute to dynamic stability. One example of natural changes

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in deciduous forest associations in the temperate zone is seasonal fluctuations of vegetation cover. During the year many changes may occur, e.g., in light conditions, temperature, moisture, net primary production, or foliage development stage (Abraitienė and Marozas 2011; Eliáš 1984; Jagodziński et al. 2016). The herb layer, the lowest layer of forest association, is dependent, among other factors, on seasonal dynamics of climate and the tree layer in deciduous, and to a lesser extent in mixed forests (Krotoska 1961). Spring ephemerals like *Anemone nemorosa* and *Ficaria verna* grow, assimilate, bloom, and bear fruits before full development of leaves and canopy closure, and then all shoots die within a short period (Lapointe 2001). Aboveground shoots of these plant species have short life cycles, but belowground organs store products of assimilation for future development the next spring. Therefore, spring ephemerals can successfully compete with seedlings and annual herbs (Chapin et al. 1990; Suzuki and Stuefer 1999). However, some other plant species growing in oak–hornbeam forest, e.g., *Galeobdolon luteum* and *Galium odoratum*, represent a different adaptation strategy to changes in light conditions. Summer-green species such as *G. luteum* and *G. odoratum* are able to effectively assimilate CO₂ at low light intensity, and their daily net primary production rate is lower in comparison with spring ephemerals, but production lasts much longer during the growing season. The highest biomass of summer-green species is observed in late summer or even in early autumn (Bierzichudek 1982). The number of herb species which are able to grow under an oak–hornbeam forest canopy is lower than the number of species in open areas (e.g., meadows, canopy gaps in deciduous forests, etc.). In general, forest associations have lower herb species diversity (31–56 species at 1600 m²; Decocq 2000) in comparison with meadows (77–89 plant species at 25 m²; Škornik et al. 2008) and open areas (50–90 species at 1000 m²; Weibull et al. 2003). Most of the herb layer species in an oak–hornbeam forest are perennials, while annuals are rare. The dominance of perennial plant species in the flora of this forest association is caused, among other factors, by reduced life expectancy of seeds and much higher probability of seedling death (Bierzichudek 1982). Annuals appear mostly in gaps and forest borders. Aboveground shoots of forest perennials mostly live less than one year. In this way, they resemble annuals but in contrast they have

belowground storage organs that store much more energy needed for growth and survival during early spring phenological stages of growth, than do seeds. Energy captured during photosynthesis and stored belowground is used for growth and development of plant organs and to survive periods of unfavorable environmental conditions. An individual can bloom when it has accumulated a sufficient pool of energy and resources (Dafni et al. 1981). On the other hand, summer-green herb species have smaller storage organs. These plants are characterized by low photosynthesis ratio, high carbon dioxide assimilation ratio, low light compensation point, durable, thin or low density leaves (to capture more photons), and low respiration ratio (Reich et al. 2003). Both groups (spring ephemerals and summer-green plants) are usually clonal plants. Clonality is an adaptation of plants to live in heterogenous environments with regard to water, nutrient, or light conditions (Antos and Zobel 1984). Clonal plants can share water, nutrients, and products of photosynthesis between ramets (individuals) and due to physiological integrity among ramets, can form a crop of individuals even when soil or light conditions are unfavorable (Chesson and Peterson 2002).

Net primary production of the herb layer is negatively correlated with canopy closure (Axmanová et al. 2011; Nabuurs 1996). Results obtained by Axmanová et al. (2011) do not indicate that herb layer net primary production is correlated with nutrient concentrations in soils in Central European oak forests. These results indicate that light is the most limiting resource in deciduous forests, while nutrient concentration is sufficient for growth and development of herbaceous plants. Competition between plants for environmental resources determines population traits like density, shoot mass, and biomass distribution. For example, a negative correlation between density and shoot mass of individuals was observed by Enquist et al. (1998). Increasing densities of plants cause increasing plant association biomass, but above a certain level association biomass starts decreasing (Chu et al. 2008; Stoll et al. 2002). However, in natural associations, these relationships are more complex because various species can use different environmental resources in a complementary fashion.

In clonal plants only a part of the shoots create flowers. In general, number of flowers are correlated to resource availability. Plants growing in favorable

conditions create more flowers (Iason and Hester 1993). In the case of insect-pollinated species, the availability of pollinators may be a limiting factor (Brown and Mitchell 2001; Pleasants 1980; Sargent and Ackerly 2008; Waser 1978). That may suggest that number of flowering shoots may be an adaptation to the availability of pollinators, while large number of flowering shoots may be a waste of resources.

The aims of the study were to compare dynamics of shoot biomass, density, and share of flowering shoots of two spring ephemerals and two summer-greens which dominate the herb layer of oak–hornbeam deciduous forest over two consecutive growing seasons. We take into account growth ratio of each species, relationship between density and shoot biomass, and relationship between shoot biomass and share of flowering shoots. We hypothesized that shoots of spring ephemerals would have higher growth ratio than summer-greens due to shorter period needed for shoot development. Furthermore, we suppose that shoot biomass will be negatively correlated with shoot density, and shoot biomass will be positively correlated with the share of flowering shoots. Numerous publications consider relationships between biodiversity, plant density, vegetation cover, biomass, or shoot biomass (Chu et al. 2008; Loreau et al. 2001; Naeem et al. 1996; Stoll et al. 2002). Most of the cited studies are focused on *Poaceae* and annual plants, but seasonal patterns are neglected or rarely addressed. Thus, our study provides rare evidence from natural associations of clonal plants, while addressing an interesting question about how these relationships are shaped in clonal species. The novelty of this study is comparisons among biomass, density, and dynamics of the share of flowering shoots, of herbaceous clonal plants occurring in the natural association of oak–hornbeam forest during two growing seasons.

Material and methods

The study was conducted in an oak–hornbeam forest association (*Stellario holostea*–*Carpinetum betuli*). The research site (12 ha) was located in the Różańsko Forest District (NW Poland, 52°52′30″ N, 14°45′22″ E). The research site is adjacent to the riparian forest on the northeast side and thus we excluded this part from the analysis. The research area was located on a slight slope with SW exposure. Stand species

composition of well-preserved *Stellario holostea*–*Carpinetum betuli* association (Rawlik et al. 2012) is composed mostly of beech *Fagus sylvatica* (70%), hornbeam *Carpinus betulus*, oak *Quercus robur*, and sycamore *Acer pseudoplatanus* (Plan Urządzenia Lasu 2006). Additional description of the study site is given by Rawlik et al. (2012). Mean annual temperature during 1971–2010 was 8.8 °C and annual sum of precipitation was 541 mm. During the field work (2010–2011) mean annual temperature was 8.8 °C and annual sum of precipitation was 615 mm, based on data from Gorzów Wielkopolski meteorological station (Central Statistical Office 2011, 2012).

The dynamics of aboveground shoot biomass of the four most frequent plant species in the herb layer over the growing season is presented in this paper. Two of them are spring ephemerals (*A. nemorosa*, *F. verna*) and two are summer-green species (*G. luteum*, *G. odoratum*). Plant density and biomass were determined from March 20 to October 30, 2010 (21 times) and March 19 to November 12, 2011 (24 times). During the spring 2010 and 2011, plants were harvested every 7 days, and during summer and autumn, every two weeks. In 2010, we collected plants from 7 to 9 randomly selected places (replications) and ten places in 2011. Plant material was collected from randomly located sample plots within the whole research site characterized by homogenous conditions, with respect to topography and vegetation. We excluded only places where plants were collected during a previous sampling. We included sample plots even when all of the studied species were not present. A single sample at each time consisted of a collection of plants from the area limited by a metal frame (0.6 × 0.6 m). All living plants that grew within the frame were collected by cutting them at the soil surface. Number of shoots, separated by species and blooming or non-blooming status, was determined immediately after harvest. The collected plant material of each species studied was placed into separate envelopes with labels. In the case of *Galeobdolon luteum*, we did not distinguish blooming and non-blooming shoots due to low density of blooming shoots. Individuals rooted outside the frame, but having some parts inside the frame, were not taken into account. Individuals which were rooted inside the frame but had some parts outside the frame were wholly included in the data.

The collected samples were 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 with 0.0001 g accuracy (BP 210 S, Sartorius, Göttingen, Germany; <https://www.sartorius.dataweigh.com>). In cases where samples were stored before biomass measurement in the laboratory, the plant material was dried again for one day. Thirty randomly selected shoots were chosen and biomass was measured from each sample plot. If within the sample plot less than 30 shoots of a particular herb species were collected, all shoots were weighed. Shoots were weighted separately to obtain individual biomass for each shoot. Thus, if we collected ten sample plots, the possible maximal number of weighed shoots was 300, so we had 300 replications of individual shoot biomass for each time of collection for each species. In total, we measured 17,189 shoots. In the table and figure, we used median values due to skewness of results. We used Kruskal–Wallis tests ($p < 0.05$) to obtain statistically significant differences between species. Shapiro–Wilk tests were done to estimate a distribution of the traits analyzed. Statistical analyses were carried out in Statistica 10.0 software.

Based on the data obtained, we calculated (a) maximal shoot biomass as mean of maximums from 2010 and 2011, and as maximal shoot biomass, we used the median value from the time when shoot median biomass was the highest; (b) maximal shoot density as mean of maximums from 2010 and 2011, and as maximal shoot density, we use the value from the time when shoot average density was the highest, based on 7–10 sample plots; (c) shoot life expectancy was the period in days during the growing season when aboveground shoots were observed and collected; (d) period of shoot biomass increment was the time in days from beginning of growing season to the term when shoot biomass obtained its peak; (e) growth ratio was the quotient of maximal shoot biomass by period of shoot biomass increment; (f) share of blooming shoots was the quotient of generative shoot density to total shoot density in the term of maximal shoot density (sum of vegetative and generative).

Results

Dynamics of biomass growth (increment) differed between spring ephemerals and summer-green herb species (Fig. 1). In fact, aboveground shoots of spring ephemerals were characterized by shorter life cycles than summer-green species; presence of summer-green species shoots were observed for almost all of the growing seasons. The highest growth ratio of vegetative shoots was observed for *A. nemorosa* – $0.857 \text{ mg day}^{-1}$, a lower value was observed for *G. odoratum* – $0.722 \text{ mg day}^{-1}$, and growth ratios almost two-times lower were observed for *F. verna* – $0.467 \text{ mg day}^{-1}$ and *G. luteum* – $0.448 \text{ mg day}^{-1}$. Thus, these results show no difference in growth ratio between the spring ephemerals and summer-green species. The spring ephemerals had lower maximal shoot biomass in comparison with summer-greens, which grew longer (Table 1).

For three of the species, biomass of blooming shoots was higher than vegetative shoots in all terms (Fig. 1). For example, maximal biomass (over growing season, based on median value) of *A. nemorosa* blooming shoots was twice as high as biomass of vegetative shoots. The highest differences were found for *F. verna*—maximal blooming shoot biomass was 4.4 times higher than biomass of vegetative shoots (Table 1). *G. odoratum* blooming shoots had almost 40% higher biomass than vegetative shoots (Table 1). Density of blooming shoots of *G. luteum* was very low within the study site and blooming shoots occurred very rarely within the sample plots.

Vegetative shoots of *A. nemorosa* were more numerous than blooming shoots. Consequently, blooming shoots had a low share of total population biomass. For instance maximal density of blooming shoots was 74 per m^2 . Maximal density of vegetative shoots was 1046 per m^2 . Density of blooming shoots was fourteen times lower than that of vegetative shoots. The highest average biomass of vegetative shoots was 42 mg, whereas the highest biomass of blooming shoots was 85.8 mg (Table 1). Biomass of the vegetative shoots increased sharply between March to the beginning of May (Fig. 1). Daily growth ratio for vegetative shoots was $0.857 \text{ mg day}^{-1}$. The blooming shoots grew rapidly from the beginning of the growing season to the end of April. Daily growth ratio was $1.907 \text{ mg day}^{-1}$ per blooming shoot. After rapid growth ratio, shoots of *A. nemorosa* reached

Fig. 1 Changes of median shoot biomass of four herb layer species: *Anemone nemorosa*, *Ficaria verna*, *Galium odoratum*, and *Galeobdolon luteum* over 2010 and 2011 growing seasons.

Medians based on values of shoot biomass of shoots collected from 7 to 10 sample plots. Points represent median values and the vertical lines show interquartile ranges

their highest individual biomass, and then the biomass decreased immediately to total disappearance of this species from the herb layer. In brief, *A. nemorosa* shoots grew for ca. 50 days, and after the next ca. 50 days their density diminished to less than 5% of the highest density observed during the growing season.

Aboveground shoots of *F. verna* were observed from March to the first half of June (80 days). Maximal density of vegetative shoots during the above-mentioned periods was 449.4 m^{-2} . Maximal density of blooming shoots reached 10.1 m^{-2} . The vegetative shoot biomass increased until the end of

Table 1 Selected characteristics of analyzed plant populations

	<i>Anemone nemorosa</i>		<i>Ficaria verna</i>		<i>Galium odoratum</i>		<i>Galeobdolon luteum</i>
	Vegetative	Blooming	Vegetative	Blooming	Vegetative	Blooming	Vegetative
Max shoot biomass (median value) [mg] ^a	42.0 b	85.8 c	17.4 a	75.9 cd	106.5 cd	145.8 d	90.6 c
Max shoot density [shoots m ⁻²] ^b	1046.0	74.0	449.4	10.1	62.2	21.4	98.4
Shoot life expectancy [days] ^c	119	77	80	49	231	182	224
Period of shoot biomass increment [days] ^d	49	46	38	46	154	133	210
Growth ratio [mg day ⁻¹] ^e	0.857	1.907	0.467	1.686	0.722	1.102	0.448
Share of blooming shoots [%] ^f	3.8		1.9		10.6		–

Values in the table are means from 2010 and 2011. In the case of *Galeobdolon luteum* only vegetative shoots are distinguished. Kruskal–Wallis tests ($p < 0.05$) were performed for maximal shoot biomass

^aFirstly we obtained maximal median in a given time (based on maximal 300 shoots collected on 7–10 sample plots) in years 2010 and 2011, then we calculated an average based on medians from 2010 and 2011

^bFirstly we obtained averages of density in a given time (based on 7–10 sample plots), next we used maximal values from 2010 and 2011 to present mean values in the table

^cShoot life expectancy was the period in days during the growing season when aboveground shoots of species were observed and collected

^dPeriod of shoot biomass increment was the time in days from beginning of growing season to the term when shoot biomass obtained its peak

^eGrowth ratio was the quotient of maximal shoot biomass by period of shoot biomass increment

^fShare of blooming shoots was the quotient of generative shoot density to total shoot density in the terms of maximal shoot density (sum of vegetative and generative)

April, when it reached the highest values during the growing season (17.4 mg). For blooming shoots the highest biomass was observed at the beginning of May (75.9 mg). Biomass of blooming shoots of *F. verna* was similar to *A. nemorosa* blooming shoots. Daily individual biomass growth ratio of *F. verna* vegetative shoots in March and April was 0.467 mg day⁻¹. However, blooming shoots of *F. verna* grew 1.686 mg day⁻¹ (Table 1).

Galium odoratum shoots were observed during entire growing seasons. Biomass of vegetative shoots (Fig. 1) increased continuously, but the date with highest shoot biomass could not be determined. The highest vegetative shoot biomass was observed in the August–September period. Maximal average density was 62.2 per m² for vegetative shoots and 21.4 per m² for blooming shoots. The highest biomass was 106.5 for vegetative shoots and 145.8 mg for

blooming shoots. Taking into account values observed in individual sample plots, it was found that the highest density was 328 vegetative shoots per m² and 139 blooming shoots per m² (the highest values from two growing seasons).

Aboveground shoots of *Galeobdolon luteum* were present in the herb layer for entire growing seasons. Biomass dynamic of aboveground shoots (Fig. 1) shows continuous growth during both growing seasons. The highest biomass value of current year shoots was observed during September–November, thus shoots developed for 168 days in 2010 and 238 days in 2011 (Fig. 1). The maximal shoot biomass increased to 90.6 mg. Maximal density of *G. luteum* shoots was 98.4 shoots per m².

We did not find any relationship between density of blooming shoots and biomass of vegetative shoots for any herb species studied. Also, we did not find any

relationship between density of vegetative shoots and shoot biomass. However, density of blooming shoots was positively correlated with density of vegetative shoots for all species analyzed. Individual biomass of blooming shoots was positively correlated with the individual biomass of vegetative shoots.

Discussion

In nutrient-rich deciduous forests light is the factor limiting biomass production of the herbaceous layer (Axmanová et al. 2011; Elemans 2003). Plant species occurring in these environments represent two general adaptations: spring ephemerals in which aboveground organs grow for a short period of the year when they can use light before canopy closure, and summer-greens which grow throughout the whole growing season and are adapted to limited light under the tree canopy. Aboveground organs of spring ephemerals *Anemone nemorosa* and *Ficaria verna* grow up through the end of June, and after that plants fall into dormancy as storage organs. For example, in eastern North American maple–beech forest the spring ephemeral *Erythronium americanum* occurs up to the beginning of June (Tremblay and Larocque 2001), similarly, in oak–beech–hornbeam forest in the Netherlands, the spring ephemeral *Allium ursinum* reaches peak biomass during a two-week period of May (Werger and Laar 1985). The biomass peak in the herb layer of non-degraded floodplain forest was observed at the end of May, and spring ephemerals were largely responsible for that (Czapiewska et al. 2019).

We hypothesized that the spring ephemerals *Anemone nemorosa* and *Ficaria verna* will have greater growth ratios than the summer-greens *Galeobdolon luteum* and *Galium odoratum*. In fact, the greatest growth ratio was observed for *Anemone nemorosa*, but growth ratio for *Ficaria verna* was lower than the growth ratio for *Galium odoratum* and quite similar to *Galeobdolon luteum*. Both spring ephemerals reached lower shoot biomass than summer-greens. That suggests that low shoot biomass, rather than high growth ratio, is an adaptation to short growth period. However, due to high densities of spring ephemerals, they are responsible for the whole herb layer biomass peak, and they had a dominant share of herb layer biomass (Rawlik et al. 2012).

Literature data confirm that a negative relationship exists between plant density and individual biomass (Damgaard et al. 2002; Franco and Kelly 1998; White and Harper 1970). Not all authors have concurred that the correlation is described by a $-3/2$ regression coefficient in logarithmic scales (Weller 1987). Our results do not confirm existence of this relationship. In cases of the analyzed species, we do not recognize a correlation between density and individual shoot biomass. We suggest that this observation is caused by natural conditions under which research occurs. Natural populations aim to achieve optimal density and biomass rather than extreme values of density or biomass. In natural populations effects of other species are also significant, but they are neglected in experimental data sets.

Specimens with high biomass have greater seed production because it is bound to energetic effort. When fertility of a population is limited, genetic variance inside the population is also limited (Weiner and Thomas 1986). We have studied populations in which the shares of blooming shoots were relatively small. Generative shoots had higher biomass for all analyzed species. For example, the most visible differences occurred in spring ephemerals, whereas the least differences occurred in the *G. odoratum* population. Moreover, the share of blooming shoots was much higher in *G. odoratum* than spring ephemerals. Size hierarchy, which determines blooming of the largest specimens, is observed in many plant populations (Weiner 1985).

Biomass designation for blooming is a high-risk investment. Plants designate more resources for blooming in optimal site conditions and sufficient nutrient concentrations than in poor habitats. Production of flowers and seeds require limiting nutrients and products: nitrogen, phosphorus, and lipids (Bloom et al. 1985). We expected to obtain a positive correlation between shoot biomass and number of flowering shoots per area. High average shoot biomass indicates favorable site conditions and sufficient amounts of nutrients and light (Müller et al. 2000; Vermeer and Berendse 1983), and thus should translate to numerous flowering shoots (Iason and Hester 1993) but we did not observe those correlations in our study. In three of the species (*A. nemorosa*, *F. verna*, and *G. odoratum*), the number of flowering shoots were a specific portion of all shoots and the number of flowers showed no dependence on shoot biomass

indicating site richness. These observations suggest that number of flowering shoots in genets is evolutionarily determined and benefits from favorable site conditions are used in other ways. A possible explanation is sharing the resources among shoots due to physiological integration of ramets (Antos 1988; Chesson and Peterson 2002).

We observed right skewness in shoot biomass distribution. Thus, we observed low numbers of shoots with high biomass and numerous shoots with low biomass. Asymmetric, right skewness in distribution of shoot biomass might be considered as an effect of competition for light. Competition for soil resources causes a symmetric distribution of shoot biomass (Schwinning and Weiner 1998). Competition for light is precisely described by a competition model based on a relationship between plant size and resource use. Larger specimens shade smaller ones, and larger specimens also absorb more light and grow faster, increasing the size difference. Large shoots limit growth of small shoots but small shoots do not limit growth of large ones, hence that type of competition is called one-sided competition (Weiner and Thomas 1986). Skewness of biomass distribution is clearer in crowded populations (Weiner 1985; Weiner and Damgaard 2006).

All of the species studied are insect pollinated (Klotz et al. 2002). Pollination by insects is bound to many plant population traits. Plant density should be high so that insects can transfer pollen among flowers. In cases of non-clonal plants it was demonstrated that high densities are related to high numbers of cross pollination. A similar relationship was also found for genets of clonal plants (Charpentier 2002; Söber et al. 2009). In the clonal plant species studied here, genetic variability of whole genets is transferred to the next generation by blooming shoots. Additionally, blooming shoots may be genetically identical to many vegetative shoots (Eriksson 1993; Stehlik and Holderegger 2000). Clonal plants are adapted to existence in small populations, which are usually not attractive for pollinators, and large numbers of flowers cause higher attractiveness for pollinators. That phenomenon is not beneficial when a population has a few genets (Whigham 2004). Many papers indicate existence of competition among plants for pollinators (Brown and Mitchell 2001; Pleasants 1980; Sargent and Ackerly 2008; Waser 1978). It is possible that high density of blooming plants is not beneficial, due to the

limited number of pollinators. The best pollination effectiveness requires strictly determined density of flowers (Stout et al. 1998). Production of large numbers of flowers without guarantee of pollination is a waste of resources. It seems that right skewness of shoot biomass distribution and low number of blooming shoots is unfavorable for the population. On one hand, number of blooming shoots is limited by resources, but on the other hand the number of flowers may be an adaptation for availability of pollinators. Therefore, the share of blooming shoots is balanced by site resource availability and pollination effectiveness.

In the case of vegetative shoots, we did not observe higher growth ratio in spring ephemerals than in summer-greens. The highest growth ratio was observed for spring ephemeral *Anemone nemorosa*— 0.9 mg day^{-1} , lower ratios were observed for summer-green *Galium odoratum*— 0.7 mg day^{-1} and for spring ephemeral *Ficaria verna*— 0.5 mg day^{-1} . The lowest growth ratio was observed for summer-green *Galeobdolon luteum*— 0.4 mg day^{-1} . In the case of blooming shoots, spring ephemerals *Anemone nemorosa* and *Ficaria verna* had higher growth ratios (1.9 and 1.7 mg day^{-1} , respectively) than summer-green *Galium odoratum* (1.1 mg day^{-1}). This shows that summer-greens can grow as fast as spring ephemerals even under unfavorable light conditions during tree canopy closure. Due to longer period of growth the summer-greens reach larger shoot biomass than the spring ephemerals. Thus, small shoot biomass characterizes spring ephemerals rather than high growth ratio. Spring ephemerals reach high densities, which translate to dominance in total biomass of the herb layer. Although summer-greens reach higher shoot biomass than spring ephemerals, they reach lower densities, and thus the peak of biomass is lower than for spring ephemerals. The share of blooming shoots was low in spring ephemerals, nearly 4% for *Anemone nemorosa* and 2% for *Ficaria verna*, while densities reached 74 per m^2 for *Anemone nemorosa* and 10 per m^2 for *Ficaria verna*. For *Galium odoratum*, the share of blooming shoots was over 10% and density reached $21 \text{ blooming shoots per m}^2$. In the case of *Galium odoratum*, high share of blooming shoots may be caused by low density of all shoots, yielding the number of flowers is necessary to attract pollinators. On the other hand, spring ephemerals had low shares of blooming shoots with densities similar to summer-

greens. This suggests that the number of blooming shoots is an adaptation to availability of pollinators.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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