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Effect of phenology, nutrient availability and windthrow on flowering of *Allium ursinum* – results from long-term monitoring and experiments

Einfluss von Phänologie, Nährstoffverfügbarkeit und Windwurf auf das Blühverhalten von *Allium ursinum* – Ergebnisse aus langfristigen Beobachtungen und Experimenten

Steffi Heinrichs[1, *], Hartmut Dierschke[2], Thomas Kompa[1] & Wolfgang Schmidt[1]

[1]*Department Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany;*
[2]*Department Vegetation and Phytodiversity Analysis, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany*
[*]*Corresponding author, e-mail: sheinri@gwdg.de*

Abstract

Allium ursinum, a dominant herb layer species in nutrient rich, deciduous forests of Central Europe, has considerably expanded in the past decades. As this species mainly relies on regeneration by seeds, we wanted to analyse if and how the timing of phenological phases, climatic factors and resource availability correlated with flowering intensity as a potential factor for its success. We recorded annual inflorescence numbers in a population of the Göttinger Wald from 1981 until 2017 and conducted phenological observations across the same time span. In addition, inflorescences were counted in a fertilization experiment contrasting a control with a nitrogen, a phosphorus and a nitrogen + phosphorus fertilization variant from 2010 to 2017. To investigate the effect of disturbance, inflorescence numbers were counted two to four years after a local summer storm in the southwestern foothills of the Harz Mountains in different disturbance categories after windthrow.

Our results demonstrate that the length of the growing period for *A. ursinum* was a strong predictor of the number of inflorescences produced in the following year from 1981 to 2017. Climatic factors that had a significant effect on inflorescence numbers were all linked to growing period length. The effect of an increasing trend in growing period length on inflorescence numbers of *A. ursinum*, was, however, not directly obvious through an increasing flowering intensity with time. Instead, an exceptionally long growing period in 1991 synchronized the flowering behaviour of the population leading to years with a very high flowering intensity. These recurrent high flowering years may have facilitated the expansion of *A. ursinum* e.g., by increasing the probability of successful seedling establishment or of an accidental dispersal by ungulates. Results of the fertilization experiment indicate that atmospheric nitrogen deposition alone does not lead to an increase in inflorescence numbers. Highest numbers were recorded with a combined application of nitrogen and phosphorus. Inflorescence numbers also benefited from an increase in light availability after windthrow but decreased in the third year after disturbance. Nevertheless, the high reproductive effect after disturbance might enable the persistence of this closed forest specialist against other competitors.

Overall our results indicate that recurrent high flowering years induced by long growing periods and a high resource availability including light, phosphorus and nitrogen may have influenced the successful expansion of *A. ursinum* in the past decades and can explain new occurrences and the efficient gap filling in already *A. ursinum*-rich stands.

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Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Central European deciduous forests with nutrient- and base-rich soils and a sufficient water supply in spring are often characterised by dense carpets of *Allium ursinum* L. from March until June (ELLENBERG & LEUSCHNER 2010, OBORNY et al. 2011). These species poor stands have been shown to be very stable in their extent in the past (ERNST 1979) and were characterized by a distinct distribution pattern, with densely colonised patches of varying sizes next to uncolonised patches without clear differences in site conditions (SCHMUCKER 1934, WINTERHOFF 1963, MORSCHHAUSER et al. 2009, SCHMIDT 2009). Several authors, though, reported a considerable expansion and a closure of the distribution gaps in the last decades in parts of temperate Europe (e.g., KIRBY et al. 2005, BÖHLING 2008, HEINRICHS et al. 2012, DIERSCHKE 2013, BECKER et al. 2017), implying an increase in reproductive success. *Allium ursinum* is a strong interspecific competitor that can supress species diversity and tree species regeneration (LANGE & KANZOW 1965, ERNST 1979, GRIME et al. 1988, DIACI et al. 2012). Its dynamics can therefore largely influence the composition of temperate forest understories in the future underlining the importance to identify potential drivers of its success.

Allium ursinum is one of the first species which sprouts in early spring. In the Göttinger Wald most of its vegetative development is completed in the ensuing months March and April. In late April to early May, with the beginning of tree foliation, the species starts to flower, with leaves already showing signs of die back. After seed maturity in late June, *A. ursinum* disappears (ERNST 1979, DIERSCHKE 1989a, EGGERT 1992). Thus, *A. ursinum*, like other spring ephemerals, relies on a short period of high irradiance for carbon assimilation (BETHKE et al. 1965, KRIEBITZSCH 1992a, LAPOINTE 2001, ROUTHIER & LAPOINTE 2002). During this period, it can reach photosynthetic rates comparable to sun plants (TUTIN 1957, KRIEBITZSCH 1992b, ROTHSTEIN & ZAK 2001) and assimilates in this short period enough carbohydrates to ensure its survival in subsequent years.

In contrast to many other clonal forest herbs, including other *Allium* species (NAULT & GAGNON 1993), *A. ursinum* regenerates prevalently by seeds (TUTIN 1957). This implies a very high investment into reproductive biomass (41% in total and 7% specifically for seeds; EGGERT 1992), that is why individual plants often have a negative resource budget which prevents flowering in the following year. Despite this, EGGERT (1992) recorded a relatively constant mean inflorescence number across 80 permanent plots in an *A. ursinum* population from 1982 to 1984. Similarly, SCHMIDT (1988) observed constant numbers of 53 to 57 inflorescences per m² between the years 1983 and 1986 across 8 permanent plots for another population. Within single plots inter-annual fluctuations occurred indicating a reproductive trade-off of individuals (INGHE & TAMM 1988). Within the population, large individuals not flowering in the year before resumed flowering and maintained a stable flowering population (ERNST 1979). These stable patterns can be disrupted by an unusual shortening of the growing period as shown by SCHMIDT (1988). A rapid canopy closure and an early die back of *A. ursinum*-leaves in 1986 led to a synchronised steep decline in inflorescence numbers across all plots in the following year. The time was too short for sufficient carbon as-

similation (IDA & KUDO 2008). The sensitivity of growth and reproduction to the timing of canopy closure was verified for several spring ephemerals (KRIEBITZSCH 1992a, SUNMONU & KUDO 2014, KIM et al. 2015) including *A. tricoccum* (DION et al. 2017). As the starting conditions for spring species in late winter/early spring and the time of canopy closure have been shown to be influenced by global climate change (RUTISHAUER & STUDER 2007, BERTIN 2008, FU et al. 2015, GÜSEWELL et al. 2017), the timing of phenological phases might have directly affected the flowering intensity of *A. ursinum* and its potential reproductive success in the last decades.

Contrasting site conditions have also been shown to influence inflorescence numbers of *A. ursinum*. ERNST (1979) proposed light availability (for bulb diameter) and phosphorus supply (for flowering) as being most important for the reproductive success of this species. Atmospheric nitrogen deposition is mentioned as another potential driver of its expansion (BÖHLING 2008, SCHMIDT 2009, BECKER et al. 2017). For the spring geophyte *Narcissus pseudonarcissus*, differences in canopy cover and nutrient availability following forest management determined among plot variation in flowering intensity (BARKHAM 1980).

In the present study, we aimed to examine the role of phenology, climate variables and resource availability on flowering of *A. ursinum*. We related annual inflorescence numbers sampled per m² and monitored for 37 years (1981 to 2017) within a population to the timing of phenological phases and climate variables of the previous year. We concentrated on the year before flowering, as it is decisive for the reproductive status in the following year as flowering initials are already formed in late summer to autumn (NAULT & GAGNON 1993). We expected a positive impact of the length of the growing period for *A. ursinum* on next year's inflorescence numbers, but also wanted to know if direct climatic variables may explain flowering intensity better. We also assessed the effect of nitrogen, phosphorus and a combined fertilizer addition on inflorescence numbers between 2010 and 2017. ERNST (1979) detected a decrease in the phosphate content of leaves by 60% prior to flowering. We therefore assumed a positive effect of phosphorus fertilization on inflorescence numbers. By investigating the interaction between growing period length and fertilizer application, we further examined if a long growing period can enhance a potential positive effect of high resource availability. To investigate the impact of an increased light intensity after disturbance, we used data sampled on permanent plots after windthrow. We assumed that an increase in the availability of light (and nutrients) enhances the allocation to generative reproduction.

2. Material and methods

2.1 *Allium ursinum* life cycle

Even though *A. ursinum* is a bulbiferous clonal plant, regeneration by seed is prevalent. The seeds germinate in the first (~ 16%), but mainly in the second year (~ 61%) after production (OBORNY et al. 2011). In the third year of seedling growth, the development of contractile roots, moving bulbs into deeper soil layers, reduces the risk of desiccation. Now nutrients can become limited (ERNST 1979). In the fifth year, both vegetative and sexual reproduction start. Vegetative propagation is characterized by the formation of daughter bulbs connected to the mother in the first year and leading to densely packed bulbs. Daughter bulbs can reach the size of the mother bulb rapidly and are able to develop an inflorescence already in the second year. This is an advantage compared to bulbs developing from seeds (OBORNY et al. 2011). Despite this, investment into sexual reproduction is nearly twice as high as into vegetative reproduction (EGGERT 1992), presumably to maintain genetic diversity and to increase the

distance of the dispersal to the mother plants (25 cm up to 50 cm depending on the height of the stalk). Regeneration by seeds reduces intraspecific competition with older individuals facilitating the survival of seedlings and promoting the formation of dense and pure, but genetically diverse, stands (MORSCHHAUSER et al. 2009). The majority of plants within a population belongs to the juvenile phase (78.6%; EGGERT 1992). The rest is able to reproduce, though less than 2% form daughter bulbs. ERNST (1979) assigned 55 to 93% of individuals of being in the first or second year of life, while 2 to 33% were 5 years or older.

Insects are the main pollinators, but self-pollination occurs frequently (TUTIN 1957, GRIME et al. 1988). Seed production of *A. tricoccum* was not limited by pollinator activity (NAULT & GAGNON 1987). This indicates that the reproductive success of *A. ursinum* is not susceptible to fluctuations in pollinator abundance as seen for other spring ephemerals in light of global climate change (KUDO et al. 2008, KUDO & IDA 2013). Despite this, seed production is generally low with only 9.7 seeds found in 14.1 flowers per inflorescence (EGGERT 1992). Senescence starts in the 7th year with a maximum longevity of up to 10 years (OBORNY et al. 2011).

2.2 Study area

Data was sampled primarily in a beech forest on limestone located close to the city of Göttingen, Central Germany in a plateau area at altitudes of 420 m (study area Göttinger Wald; N 51°32‘, E 10°03‘). The study area comprised about 11 ha and is characterised by a suboceanic-submontane climate, with a mean annual temperature of 7.4 °C and an annual precipitation sum of 709 mm (PANFEROV et al. 2009). Mean annual temperatures in the study area have increased by 0.5 °C in the last two decades compared to the long-term mean (HEINRICHS & SCHMIDT 2015). The shallow soils (rendzina, terra fusca) have a good base and nutrient supply and are rarely affected by drought (MEESENBURG et al. 2009). The plateau is covered with a typical beech forest on limestone. The aboveground layer is largely dominated by *A. ursinum* in spring (*Hordelymo-Fagetum lathyretosum*, *Allium*-variant, DIERSCHKE 1989b, SCHMIDT 2009). After the abandonment of coppice management in the 19th century, the beech forest was managed as high forest (today ca. 145 years old). Since 1970, no major harvesting operations have taken place. Management ceased completely in 1980 with the establishment of a permanent research area for the University of Göttingen (SCHMIDT 2009).

Data from windthrown sites were collected in two areas in the southwestern foothills of the Harz Mountains (study areas Hainholz (N 51°41‘, E 10°16‘) and Nüllberg (51°40‘, E 10°19‘), ca. 40 km east of Göttingen). Both areas were affected by a local summer storm in June 1997 (KOMPA & SCHMIDT 2005, BRUELHEIDE & LUGINBÜHL 2009). The windthrown sites in the Hainholz were left to natural development, whereas the areas in Nüllberg were cleared of all stems. The mean annual temperature is 7.6 °C; the annual precipitation sum is 800 mm. Compared to the Göttinger Wald, temperature and precipitation show a larger fluctuation within the year due to a higher continentality. Both areas are formed on Upper Permian dolomite and covered with loess. Their soils are predominantly rendzina-brown soils. The loess layer is thicker in the Hainholz area, consequently the soils are deeper and have a better water supply compared with those at Nüllberg. Plant community in the Hainholz area can be classified as *Hordelymo-Fagetum typicum* and *circaeetosum*, *Allium*-variant, in Nüllberg as *Hordelymo-Fagetum lathyretosum* (DIERSCHKE 1989b, KOMPA & SCHMIDT 2005).

2.3 Data sampling

To monitor inflorescence numbers in a population across time, permanent plots (1 m²) were established in 1981 (n = 8) and 1982 (n = 11) in the Göttinger Wald in spots dominated by *A. ursinum* (Fig. 1a, b). Plots already dominated by the study species were chosen to avoid a strong effect of differences in population density on inflorescence numbers. The 19 plots were not monitored continuously from 1981 to 2017. In each year, however, at least three plots were sampled (minimum of three plots sampled in 2003, 2005, 2007–2009, maximum of 19 plots sampled in 1983–1986, 1989, 1991 and 1993). From 2010 to 2017, seven plots were continuously sampled.

Fig. 1. Study sites for counting inflorescence numbers of *A. ursinum*. a/b) Permanent study site in the Göttinger Wald research area; **a)** *A. ursinum*-beech forest in the area of a permanent quadrat in May 2011 (mean 77.6 inflorescences/m²); **b)** detailed view of a 1 m² permanent plot in May 2015 (mean 40.4/m²; photos: H. Dierschke); c/d) study site of the fertilization experiment in the Göttinger Wald, **c)** in late May 2010 with few flowering stems of *A. ursinum* (mean 0.8/m²); **d)** same study site in mid May 2015 with an intermediate number of flowering stems (mean 31.3/m²; photos: W. Schmidt); e/f) Hainholz; **e)** *A. ursinum* in a nearly undisturbed forest site in May 2001 (mean 68.7/m²); and **f)** in a windthrown site in May 2000 (mean 343.8/m²; photos: T. Kompa).

Abb. 1. Untersuchungsflächen zur Bestimmung der Zahl der Blütenstände von *A. ursinum*. a/b) Ökosystem-Forschungsfläche Göttinger Wald; **a)** *A. ursinum*-Buchenwald im Bereich einer Daueruntersuchungsfläche im Mai 2011 (im Mittel 77,6 Blütenstände/m²); **b)** Nahaufnahme eines 1 m²-Dauerquadrats im Mai 2015 (im Mittel 40,4/m²; Fotos: H. Dierschke); c/d) Untersuchungsfläche des Düngungsversuchs im Göttinger Wald; **c)** wenige Blütenstände Ende Mai 2010 (im Mittel 0,8/m²); **d)** die gleiche Untersuchungsfläche Mitte Mai 2015 mit einer durchschnittlichen Zahl an Blütenständen (im Mittel 31,3/m², Fotos: W. Schmidt); e/f) Hainholz; **e)** *A. ursinum*-Blüte in einer weitgehend ungestörten Waldfläche im Mai 2001 (im Mittel 68,7/m²); und **f)** in einem Flächenwurf im Mai 2000 (im Mittel 343,8/m²; Fotos: T. Kompa).

In each year inflorescence numbers were counted per sampled 1 m² when leaf development was at a maximum (between end of April and beginning of May) using a 1 m x 1 m frame subdivided into 16 25 cm x 25 cm quadrats. Cover values were estimated parallel to inflorescence counting.

Within the studied site and in the surroundings (including forest edges) phenological observations were continuously conducted from 1981 until 2017 by recording the start of different phenological phases. For our investigation, the time span between the start of the *Acer platanoides-Anemone nemorosa*-phase (phase 2; start of spring) and the *Cornus sanguinea-Melica uniflora*-phase (phase 6; start of early summer) defined the growing period for *A. ursinum* (see characterisation of the different phenological phases in Supplement E1; DIERSCHKE 1982, 1989a).

Climate variables from 1981 to 2017 were measured in the weather station Göttingen (Deutscher Wetterdienst DWD) ca. 8 km away from the study area. The weather station is located at 167 m a.s.l. (before 1993 at 173 m a.s.l.). Due to the higher elevation of the study plots, the air temperature is generally 1–2 °C lower and the precipitation 30–70 mm higher compared to the data of the weather station (PANFEROV et al. 2009). Of particular interest were the climate variables of three three-month periods: 1) January to March, 2) February to April, 3) April to June that define different developmental stages of *A. ursinum* (ERNST 1979, EGGERT 1992, see Table 1). From 1981 to 2017 mean temperatures from January to June fluctuated between a minimum of 4.5 °C in 1987 and a maximum of 9.6 °C in 2007. Precipitation sums for the same time period fluctuated between 169 mm (1996) and 540 mm (1981).

Table 1. Overview of time periods considered and predictor variables used in three linear regression models to describe inflorescence numbers of *A. ursinum* from 1981 to 2017. We always tested the effect of the previous year (prev) on inflorescence numbers.

Tabelle 1. Überblick über die betrachteten Zeitspannen und Einflussvariablen in drei unterschiedlichen linearen Regressionsmodellen zur Beschreibung der Zahl der Blütenstände von *A. ursinum* von 1981 bis 2017. Es wurde stets der Effekt des Vorjahres (prev) auf die Zahl der Blütenstände untersucht.

Predictor variable	Description [unit]
Relevant time periods	
Jan–Mar	January to March with below ground sprouting and beginning of aboveground leaf expansion of *A. ursinum*
Feb–Apr	February to April with main aboveground development of *A. ursinum*
Apr–Jun	April to June with flowering, senescence and the beginning growth of new inflorescence initials below ground
1) Phenology-model	
$Start_{prev}$	Annual starting day of the growing period of *A. ursinum* defined as the start of phenological phase 2 (*Acer platanoides-Anemone nemorosa*-phase) [day of year]
End_{prev}	Annual end of the growing period of *A. ursinum* defined as the start of phenological phase 6 (*Cornus sanguinea-Melica uniflora*-phase) [day of year]
GP_{prev}	Length of the growing period of *A. ursinum* between the start of phenological phase 2 and the start of phenological phase 6 [number of days]
2) Temp/Prec-model	
T_{prev}	Mean annual air temperature [°C]
$Prec_{prev}$	Precipitation sum [mm]
3) Frost/Heat-model	
$Frost_{prev}$	Last day with minimum temperature < 0°C in late winter and early spring [day of year]
Ice_{prev}	Last day with maximum temperature < 0°C in late winter and early spring [day of year]
$dFrost_{prev}$	[Number of days] with minimum temperature < 0°
$dSummer_{prev}$	[Number of days] with maximum temperature > 25 °C

To analyse the effect of nutrient addition on inflorescence numbers, we used data from a fertilization experiment established within the same research area of the Göttinger Wald in 1997 in an *A. ursinum*-rich *Hordelymo-Fagetum lathyretosum* (for details see SCHMIDT 2009). The experiment consists of a control (unfertilized) and three fertilization variants (Nitrogen (N)-fertilization: 100 kg N/ha; Phosphorus (P)-fertilization: 30 kg P/ha; Nitrogen + Phosphorus (NP)-fertilization: 100 kg N and 30 kg P/ha) applied annually since 1998. Each variant is repeated on four 25 m^2-plots. From 2010 to 2017 in each of the 25 m^2-plots three 1 m^2 subplots were randomly positioned to count inflorescences at the time of maximum leaf development and for concurrent cover estimation. Inflorescences were not counted before 2010 (Fig. 1c, d).

The effect of disturbance on flowering intensity was investigated using a total of 24 permanent 1 m^2-plots established in 1999, two years after a local summer storm in 1997 in the study areas Hainholz and Nüllberg. The permanent plots represented three different disturbance categories based on disturbance area and structure: 1) nearly undisturbed sites with no direct disturbance but with light reaching the plots from adjacent disturbed areas (Fig. 1e); 2) gaps with single root plates and/or lying stems and a canopy cover of more than 20%; 3) thrown sites with root plates and lying stems and a canopy cover < 20% (Fig. 1f). Inflorescence numbers and cover values were recorded from 1999 until 2001 using a 1 m x 1 m frame. Plots were unequally distributed across years and disturbance categories (see results). Relative irradiance was measured above the herb layer at a height of 50 cm for every permanent plot in May 2000 with LI-190 Quantum Sensors (Licor, Nebraska, USA) on overcast days with diffuse light conditions. The relative irradiance was calculated as the ratio of photosynthetic active radiation within the forest sites to photosynthetic active radiation at an open area nearby (maximum distance 1 km).

2.4 Data analyses

To determine changes in the growing period for *A. ursinum,* in inflorescence numbers and in cover from 1981 to 2017, we used the Mann–Kendall test and Sen-Slope, a non-parametric regression analysis, to identify trends in time series. For each year, we used mean numbers of available plots for inflorescence numbers and cover.

We built linear regression models to determine phenological and climatic variables that best explain next year's inflorescence numbers (see Table 1): 1) A first model tested the effect of the start, end and length of the growing period for *A. ursinum* as defined by phenological observations (Phenology-model). 2) A second model analysed the influence of mean temperatures and precipitation sums of the three different time periods (see Table 1) on inflorescence numbers (Temp/Prec-model). 3) Occasional extreme environmental events may have a greater effect than average conditions across periods (BARKHAM 1980). We therefore analysed the effect of early and late frost events by including the last ice (Ice) and frost day (Frost) in late winter/early spring as well as the number of frost days (dFrost) in the periods Jan–Mar and Apr–Jun. Warm temperatures induce a fast canopy closure and *A. ursinum* die back. We therefore also included the number of days with temperatures > 25 °C (dSummer) into the model. Across years, these high temperatures occurred from April onwards only (Frost/Heat-model).

Variables were tested in separate models as phenological phases are directly influenced by climatic variables, mainly temperatures. In addition, mean temperatures were largely correlated with extreme values of frost and heat. For each model, we included current cover of *A. ursinum* as predictor variable to account for an effect of population density on current inflorescence numbers as well as the inflorescence number of the previous year to account for a reproductive trade-off.

An effect of fertilization was analysed annually from 2010 to 2017 using ANOVA with plot as random effect (function lme of the R-package nlme; PINHEIRO et al. 2017). Differences between fertilization variants were tested with the post-hoc Tukey-test (function glht of the R-package multcomp; HOTHORN et al. 2008). To assess if a long growing period enhanced an effect of nutrient addition across years, we conducted an ANCOVA using inflorescence numbers as response variable, growing period of the previous year as a continuous co-factor and plot as a random effect.

For regression models, we evaluated the best combination of variables explaining inflorescence number based on Akaike Information Criterion (with correction for a finite sample size; AICc) also considering simple interactions between variables (PEARSE et al. 2014). The AICc is a measure of relative fit of a statistical model based upon observed data with the best model having the smallest AICc. When two models were equal (AICc < 2), we chose the model with less parameters included (BURNHAM & ANDERSON 2002).

Data collected on plots after windthrow were compared between disturbance categories and study areas using ANOVA followed by Tukey-test when the data was normally distributed, or the Kruskal-Wallis-H-test followed by Dunn's test when normality was lacking. Differences between years were analysed using the paired Wilcoxon signed-rank-test.

Statistical significance was assumed at $p < 0.05$ if not otherwise stated.

3. Results

From 1981 to 2017, we found an average inflorescence number per m² of 40.0 (± 4.7 SE) with a minimum of 0.86 (±0.46 SE) in 2010 and a maximum of 109.5 (±5.8 SE) in 1998. Inflorescence numbers were relatively constant from 1981 to 1991 (with the exception of 1987) ranging from 30 to 45. Inter-annual fluctuations occurred afterwards with a continuous change of high and low flowering years (Fig. 2a). In almost every high flowering year, mean inflorescence numbers exceeded values counted before 1991. Maximum inflorescence numbers with more than 140/m² were recorded on permanent plots in 1992 (143/m²), 1998 (145/m²) and 2013 (146/m²), while in 1994, 2001, 2007, 2012 and 2014 at least one of the surveyed plots showed no flowering stalks at all (see also Supplement E2).

3.1 Predictors for long-term inflorescence numbers

Because of the strong inter-annual fluctuations after 1992, we detected no long-term trend in inflorescence numbers (Sen-Slope = 0.076, $\tau = 0.021$, $p = 0.865$). A long-term trend was also not detectable for the estimated cover (Sen-Slope = 0.051, $\tau = 0.068$, $p = 0.565$; Fig. 2a). The growing period for *A. ursinum* showed a trend for a slight elongation from 1981 to 2017 (Sen-slope = 0.227, $\tau = 0.227$, $p = 0.052$; Fig. 2b). The shortest growing period was observed in 1987 with 41 days and the longest in 1991 with 78 days. During the first ten years of monitoring (1981 to 1990), the mean length was 51.5 days. From 2008 to 2017, the mean length was 57.2 days ($t = -1.769$, $p = 0.089$). A longer growing period can mainly be explained by a significantly earlier start (i.e., an earlier start of the *Acer platanoides-Anemone nemorosa*-phase) across the years (Sen-slope = -0.400, $\tau = -0.269$, $p = 0.021$), while the end (i.e., the start of the *Cornus sanguinea-Melica uniflora*-phase) changed similarly, but to a lesser extent (Sen-slope = -0.218, $\tau = -0.173$, $p = 0.142$; Fig. 2b). The earliest start was in 1990 at day 72 (March 13th), the latest start in 1987 at day 118 (April 28th).

The longest growing period in 1991 with 78 days was followed by a peak in inflorescence numbers in 1992 (Fig. 2c). Afterwards, a regular change of high and low flowering years occurred. This suggests that the long growing period in 1991 was the decisive factor for inducing a masting behaviour in *A. ursinum*. In the recent past (2015–2017), intermediate inflorescence numbers were counted, presumably indicating a beginning de-synchronization. A synchronized behaviour of the population becomes obvious at the single plot level (see Supplement E2). Despite a large range in inflorescence numbers across plots, high and low flowering years were synchronized in 1987 and from 1992 onwards.

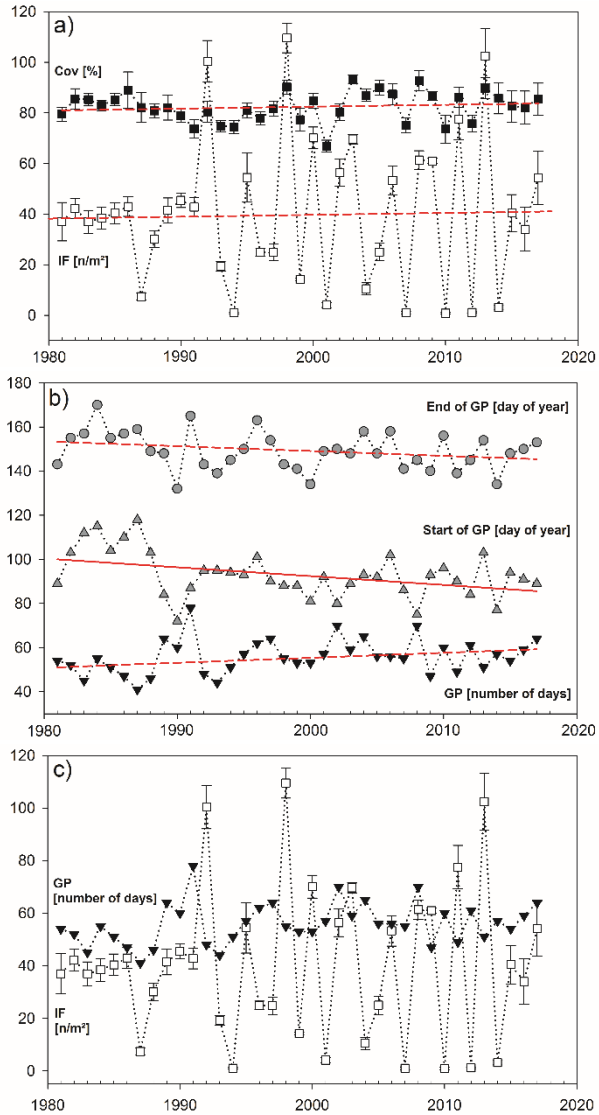

Fig. 2. Long-term dynamics of *A. ursinum* (1981 to 2017): **a)** inflorescence numbers (IF in n/m²; white quadrates) and cover (Cov in %, black quadrates), **b)** start (grey triangles), end (grey circles) and length of the growing period (GP; black triangles), and **c)** inflorescence numbers (white quadrates) directly contrasted to the growing period (black triangles). IF and Cov are mean values of a different amount of 1 m² plots during the observation period. Error bars represent standard error, red lines the calculated Sen slope. The solid line shows a significant trend (see text for numbers).

Abb. 2. Langzeitliche Dynamik von *A. ursinum* (1981 bis 2017): **a)** Zahl der Blütenstände (IF in n/m²; weiße Quadrate) und des Deckungsgrads (Cov in %; schwarze Quadrate), **b)** Beginn (graue Dreiecke), Ende (graue Kreise) und Länge der Vegetationsperiode (schwarze Dreiecke) und **c)** Zahl der Blütenstände (weiße Quadrate) direkt der Länge der Vegetationsperiode (schwarze Dreiecke) gegenübergestellt. IF und Cov sind Mittelwerte von einer in den Jahren des Untersuchungszeitraums unterschiedlichen Zahl von Dauerquadraten. Fehlerbalken zeigen den Standardfehler, die roten Linien den errechneten Sen-Slope. Eine durchgezogene Linie zeigt einen signifikanten Trend an (s. Text für detaillierte Zahlen).

Table 2. Results of the linear regression models of the three categories predicting inflorescence numbers from 1981 to 2017. For each category, the current cover (Cov) of *A. ursinum* and the inflorescence numbers of the previous year (IF_{prev}) were included to account for density effects and a reproductive trade-off. We always tested the effect of the previous year (prev) on inflorescence numbers. Shown is the best combination of predictor variables in each model category based on model comparisons. For considered predictor variables and abbreviations see Table 1. * all three models were highly significant with $p < 0.001$.

Tabelle 2. Ergebnisse der linearen Regressionsmodelle zur Beschreibung der Zahl der Blütenstände von 1981 bis 2017. In jedem Modell wurde auch der aktuelle Deckungsgrad von *A. ursinum* (Cov) sowie die Blütenstandszahl des Vorjahres (IF_{prev}) als Maß für die Dichteabhängigkeit bzw. ein negatives Ressourcen-Budget berücksichtigt. Es wurde stets der Effekt des Vorjahres (prev) auf die Zahl der Blütenstände untersucht. Dargestellt ist jeweils die beste Kombination an Variablen pro Modell-Kategorie basierend auf Modellvergleichen. Alle berücksichtigten Variablen und ihre Abkürzungen finden sich in Tabelle 1. * alle drei Modelle waren hoch signifikant mit $p < 0{,}001$.

Predictor	Estimate (SE)	F-value$_{(df)}$	*p*-value	R^2_{adj}*	AICc
1) Phenology-model				0.591	320.836
GP_{prev}	1.720 (0.429)	$28.685_{(1,32)}$	< 0.001		
Cov	1.294 (0.610)	$13.595_{(1,32)}$	< 0.001		
IF_{prev}	-0.395 (0.118)	$11.280_{(1,32)}$	0.002		
2) Temp/Prec-model				0.615	320.387
T_{prev}(Jan-Mar)	6.818 (1.700)	$6.158_{(1,31)}$	0.019		
T_{prev}(Apr-Jun)	-13.775 (4.028)	$27.592_{(1,31)}$	< 0.001		
Cov	1.807 (0.566)	$18.875_{(1,31)}$	< 0.001		
IF_{prev}	-0.311 (0.115)	$7.334_{(1,31)}$	0.011		
3) Frost/Heat-model				0.639	319.990
$dSummer_{prev}$	-1.546 (0.615)	$10.019_{(1,30)}$	0.004		
$dFrost_{prev}$(Apr-Jun)	1.811 (0.908)	$16.511_{(1,30)}$	< 0.001		
$dFrost_{prev}$(Jan-Mar)	-0.914 (0.208)	$21.195_{(1,30)}$	< 0.001		
Cov	1.633 (0.592)	$12.876_{(1,30)}$	0.001		
IF_{prev}	-0.284 (0.112)	$6.411_{(1,30)}$	0.017		

All tested models predicted inflorescence numbers significantly and with a similar predictive power (Table 2). In all models, we detected a positive effect of species density expressed by estimated cover values and a negative effect of previous inflorescence numbers indicating a reproductive trade-off on inflorescence numbers. In the phenology model, a long growing period positively influenced inflorescence numbers in the following year. The Temp/Prec-model revealed a negative effect of high temperatures in Apr-Jun on next year's inflorescence numbers probably due to an earlier canopy closing reducing directly the length of the growing period. Warmer temperatures from Jan–Mar had a positive effect on next year's flowering intensity as they induced an earlier start of the vegetation. Precipitation was not an important predictor for inflorescence numbers. The Frost/Heat-model is as well linked to the growing period. Many frost days in Jan-Mar delayed the start of the growing period for *A. ursinum* (dFrost(Jan–Mar) vs. Start: $r_{Pearsson} = 0.602$, $p < 0.001$), while many days > 25 °C induced an earlier end of the growing period (dSummer vs. End: $r_{Pearsson} = -0.442$,

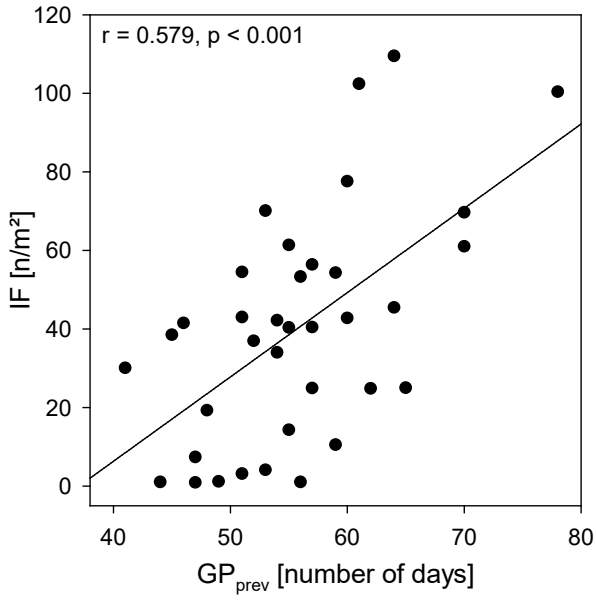

Fig. 3. Scatterplot of the relationship between the length of the growing period in the previous year (GP_{prev}) and inflorescence numbers (IF) of *A. ursinum* from 1981 to 2017.

Abb. 3. Streudiagramm der Beziehung zwischen der Länge der Vegetationsperiode im Vorjahr und der Zahl der Blütenstände von *A. ursinum* zwischen 1981 und 2017.

p = 0.007). Thus, both variables had a direct effect on the length of the growing period and reduced next year's inflorescence numbers. Positive were late frost events (Apr–Jun) for flowering in the following year.

The significant negative effect of previous inflorescence numbers on current numbers is the result of the masting behaviour of the investigated population that started in 1992. A negative relationship between previous and current inflorescence numbers was not present from 1982 to 1991 (see Supplement E3), while the length of the growing period had a positive effect on subsequent inflorescence numbers before and after 1992 (Supplement E3). Thus, the length of growing period for *A. ursinum* as defined by the start of different phenological phases is the most important single predictor for the flowering intensity in the following year as it combines climatic factors that influence the starting conditions of the understorey vegetation in spring as well as the time of canopy closure (Fig. 3). The induced masting behaviour, however, decouples flowering intensity and vegetation period length in low flowering years when stored resources after flowering in the year before are depleted and no new flowering initials were formed.

3.2 Fertilization effect on inflorescence numbers

In five out of the eight investigated years, the NP variant had highest inflorescence numbers with a significant difference to the N variant in five years, to the control in four years and to the P variant in three years (Table 3). Significantly higher numbers after NP fertilization were detected in high (2011, 2013), intermediate (2016) and low flowering (2012, 2014) years. Results were similar when corrected for the cover of *A. ursinum* that was highest for the NP variant across years (except for 2012; see Supplement E4).

Table 3. Mean inflorescence numbers/m² (IF plus standard error) in four fertilization variants (Control, N = Nitrogen, P = Phosphorus, NP = Nitrogen+Phosphorus) from 2010 to 2017 (*n* = 4 plots per variant). Given is also the growing period length for the year before counting (GP_{prev}). Different lowercase letters indicate significant differences among variants per year. Highest numbers per year are written in bold when a significant difference to at least one other variant was detected.

Tabelle 3. Mittlere Zahl an Blütenständen/m² in vier Düngungsvarianten (Kontrolle, N = Stickstoff, P = Phosphor, NP = Stickstoff und Phosphor) von 2010 bis 2017 (*n* = 4 Plots pro Variante). Angegeben ist auch die jeweilige Vegetationsperiodenlänge des Vorjahres (GP_{prev}). Unterschiedliche Buchstaben markieren signifikante Unterschiede zwischen den Düngungsvarianten innerhalb eines Jahres. Die höchsten Zahlen pro Jahr sind fett markiert, wenn der Unterschied zu mindestens einer anderen Düngungsvariante signifikant war.

Year	GP_{prev}	Mean IF (SE)			
		Control	N	P	NP
2010	47	0.6 (0.1)ab	**1.2 (0.3)a**	0.5 (0.1)b	1.1 (0.2)a
2011	60	69.8 (8.5)a	63.7 (2.6)a	81.5 (3.0)b	**96.7 (6.5)c**
2012	49	1.3 (0.3)a	2.1 (0.8)ac	3.6 (1.2)bc	**4.2 (0.8)b**
2013	61	102.3 (7.8)ab	92.5 (7.1)a	107.0 (12.4)ab	**121.8 (7.7)b**
2014	51	5.3 (0.8)ab	2.4 (0.7)a	8.6 (1.0)b	**13.3 (2.1)c**
2015	57	32.2 (3.7)a	33.2 (2.5)a	32.3 (5.4)a	30.3 (3.3)a
2016	54	35.2 (7.6)a	38.4 (7.3)a	37.5 (6.6)a	**53.5 (2.1)b**
2017	59	48.8 (5.3)a	52.4 (1.9)a	46.7 (3.4)a	58.2 (1.6)a

Table 4. Comparison of regression models linking the fertilization variants (Fert) and previous year growing period length (GP_{prev}) to predict inflorescence numbers/m² (IF). Plot was included as random effect. The best model is represented by the smallest AICc-value. Models are equal when $\Delta AICc \leq 2$. *Goodness of fit based on fixed effects only (function sem.model.fits, R package piecewiseSEM; Lefcheck [2015]).

Tabelle 4. Vergleich von Regressionsmodellen, die die Düngungsvarianten und die Länge der Vegetationsperiode im Vorjahr zur Beschreibung der Zahl der Blütenstände/m² (IF) in Beziehung setzen. Plot wurde als Zufallseffekt berücksichtigt. Das beste Modell wird durch den kleinsten AICc-Wert repräsentiert. Modelle sind gleichwertig, wenn der $\Delta AICc \leq 2$ ist. *Güte der Anpassung nur basierend auf festen Effekten (Funktion sem.model.fits, R Paket piecewiseSEM; Lefcheck [2015]).

Model	K	AICc	ΔAICc	Weights	Marginal R²*
1 IF = Fert x GP_{prev} + Fert x GP_{prev}^2	14	3162.43	0	0.52	0.800
2 IF = Fert + GP_{prev} + GP_{prev}^2	8	3162.55	0.125	0.48	0.793
3 IF =Fert x GP_{prev}	10	3250.36	87.929	0.00	0.741
4 IF = Fert + GP_{prev}	7	3252.15	89.726	0.00	0.735

When relating the length of the growing period for *A. ursinum* from 2009 to 2016 to inflorescence numbers from 2010 to 2017, we detected a quadratic relationship across fertilization variants that explains inflorescence numbers much better than linear models (Table 4). Even though there was a slightly larger increase in inflorescence numbers with increasing length of the growing period on the NP compared to the other fertilization variants (Fig. 4), the interaction term did not increase the overall fit of the quadratic model significantly ($\Delta AICc \leq 2$; Table 4).

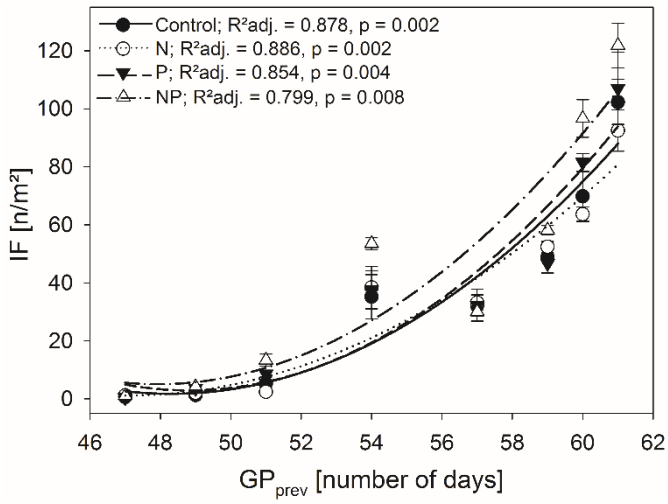

Fig. 4. Relationship of inflorescence numbers (IF) in four fertilization variants from 2010 to 2017 and previous year growing period length (GP_{prev}). Quadratic regressions show results of Model 1 in Table 4.

Abb. 4. Beziehung der Zahl der Blütenstände (IF) in den vier Düngungsvarianten von 2010 bis 2017 und der Länge der Vegetationsperiode im Vorjahr (GP_{prev}). Quadratische Regressionen zeigen die Ergebnisse von Modell 1 in Tabelle 4.

3.3 Effect of windthrow on inflorescence numbers

On the permanent plots affected by windthrow, inflorescence numbers followed a light gradient, with lowest numbers in the nearly undisturbed sites and highest numbers in the thrown sites (Fig. 5). Inflorescence numbers in the nearly undisturbed sites were much higher compared to the Göttinger Wald presumably due to differences in light availability.

A further contrast to the Göttinger Wald is the steady decrease in inflorescence numbers in both study areas and in all disturbance categories from 1999 to 2001. In the fourth year after the storm (2001) only one quarter to one third of inflorescences could be recorded compared to the second year (1999). The steepest decrease was detected in the thrown sites. In contrast, the shrub layer cover steadily increased in gaps and thrown sites from 1999 to 2001 (Table 5). The cover of *A. ursinum* remained relatively constant in all disturbance categories throughout the observation period.

Inflorescence numbers were significantly higher in the Hainholz area compared to the Nüllberg area across years and disturbance categories, except for the nearly undisturbed sites in 2001 (Fig. 5).

4. Discussion

We found that the length of the growing period for *A. ursinum* is a good single predictor for inflorescence numbers in the following year across a time series of 37 years. The significant predictors found in the Temp/Prec- and Frost/Heat-model were also related to the growing period with low temperatures in Jan-Mar inducing a later start and high temperatures in Apr-Jun inducing an earlier end. For spring geophytes, flowering in the subsequent year is

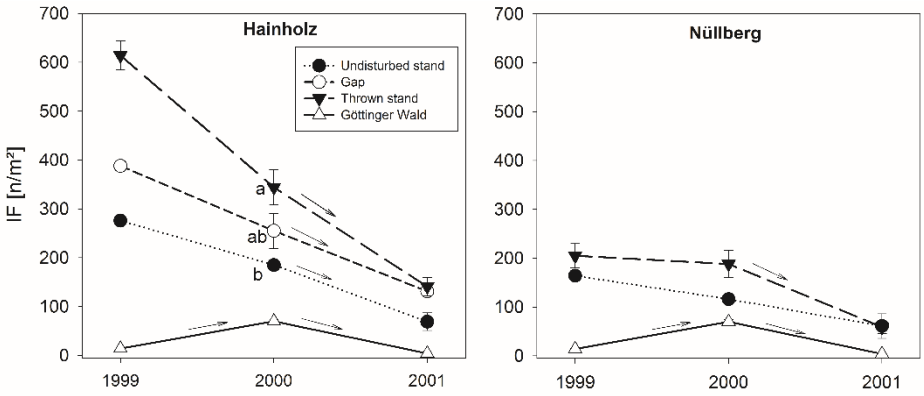

Fig. 5. Mean inflorescence numbers (IF) of *A. ursinum* in three different disturbance categories in Hainholz and Nüllberg. Permanent 1 m² plots were sampled from 1999 to 2001. Arrows indicate a significant increase or decrease in IF between years; different lowercase letters mark significant differences between disturbance categories. For a comparison, IF-values determined on the permanent plots of the Göttinger Wald are also specified for 1999 to 2001. Values of the Göttinger Wald (n = 11) were significantly lower compared to Hainholz and Nüllberg for all years and disturbance categories. For sample sizes see Table 5. Due to the low sample size in 1999, the comparisons of the annual means of the plots Hainholz and Nüllberg were only restricted on 2000 and 2001.

Abb. 5. Mittlere Zahl der Blütenstände (IF) von *A. ursinum* in drei Störungskategorien in Hainholz und Nüllberg. Dauerflächen von 1 m² wurden von 1999 bis 2001 erfasst. Pfeile zeigen einen signifikanten Anstieg oder Rückgang der IF zwischen Jahren. Unterschiedliche Buchstaben zeigen signifikante Unterschiede zwischen den Störungskategorien. Als Vergleich wurde auch die Zahl der Blütenstände im Göttinger Wald für die Jahre 1999 bis 2001 aufgeführt. Die Werte im Göttinger Wald (n = 11) waren signifikant geringer im Vergleich zum Hainholz und Nüllberg für alle Jahre und Störungskategorien. Für die unterschiedliche Flächenanzahl siehe Tabelle 5. Durch geringe Flächenzahlen im Jahr 1999 beschränkt sich der Vergleich der jährlichen Mittelwerte der Untersuchungsgebiete im Hainholz und Nüllberg nur auf die Jahre 2000 und 2001.

initiated when the size of the bulb and consequently the amount of reserves stored in the bulbs reaches a certain threshold (BARKHAM 1980, NAULT & GAGNON 1993, SCHMID et al. 1995, ISAGI et al. 1997). Then flowering initials will be formed. This is closely linked to season length and time for assimilation. Thus, beneficial for flowering is an early start followed by cooler temperatures that delay leaf senescence and canopy closure and thereby extent the growing period (YOSHIE 2008, BERNATCHEZ & LAPOINTE 2012). Late frost events, a positive predictor for inflorescence numbers in the following year, can also extend the growing period. We found, however, no significant correlation between late frost events and the end of the growing period for *A. ursinum* (dFrost(Apr–Jun) vs. End: $r_{Pearson}$ = 0.243, p = 0.153). Thus, late frost events may have affected the resource budget indirectly by preventing seed set in frost damaged flowers. Frost damage of flowers was rarely observed on the studied plots. It was, however, particularly obvious in 1991 after strong frost in late April. NAULT & GAGNON (1993) observed that 30–35% of *A. tricoccum* individuals remained flowering in the following year when previous seed set was unsuccessful compared to only 2% after a year with high seed production. CRONE et al. (2009) demonstrated a positive effect of flower removal on next year's flowering for a perennial legume.

Table 5. Cover of *A. ursinum*, of the herb layer in spring and summer, and of the shrub layer in summer on permanent plots sampled from 1999 to 2001 in three disturbance categories in the study areas Hainholz and Nüllberg. The relative light availability was determined in May 2000. Different lowercase letters indicate significant differences between disturbance categories; significant higher values comparing the year 2000 and 2001 are printed in bold. Due to the low sample size in 1999, the comparisons of the annual means of the plots Hainholz and Nüllberg were only restricted on 2000 and 2001.

Tabelle 5. Deckungsgrade von *A. ursinum*, der Krautschicht insgesamt im Frühjahr und Sommer und der Strauchschicht im Sommer auf Dauerflächen von 1999 bis 2001 in drei Störungskategorien nach Windwurf in den Gebieten Hainholz und Nüllberg. Der relative Lichtgenuss wurde im Mai 2000 bestimmt. Unterschiedliche Buchstaben markieren signifikante Unterschiede zwischen den Störungskategorien; signifikant höhere Werte für den Vergleich der Jahre 2000 und 2001 sind fett markiert. Durch geringe Flächenzahlen im Jahr 1999 beschränkt sich ein Vergleich der jährlichen Mittelwerte der Flächen Hainholz und Nüllberg auf die Jahre 2000 und 2001.

	Undisturbed site			Gap			Thrown site		
	1999	2000	2001	1999	2000	2001	1999	2000	2001
Hainholz	*n* = 1	*n* = 3	*n* = 3	*n* = 1	*n* = 3	*n* = 3	*n* = 2	*n* = 9	*n* = 9
Cover [%]									
A. ursinum	75	75±5	73±7	85	80±6	82±3	78±8	65±7	71±7
Herb layer (Spring)	90	80±5	78±7	95	92±6	90±3	93±3	94±4	91±2
Herb layer (Summer)	15	17±3a	15±0a	45	23±2ab	37±13ab	65±25	70±8b	68±7b
Shrub layer	0	0	0	10	32±16	52±26	14±2	28±10	**51±12**
Light [%]	-	6±3a	-	-	55±4b	-	-	77±4c	-
Nüllberg	*n* = 1	*n* = 3	*n* = 3	-	-	-	*n* = 2	*n* = 6	*n* = 6
Cover [%]									
A. ursinum	60	55±13	62±17	-	-	-	70±10	44±7	53±8
Herb layer (Spring)	70	65±8a	70±12				83±8	**94±2b**	87±4
Herb layer (Summer)	25	17±8a	28±13				60±15	**84±5b**	69±9
Shrub layer	0	0	0a				0	31±16	**62±15b**
Light [%]	-	8±2a	-				-	81±5b	-

Phenological observations conducted across the whole study period underline the consistent trend of a premature starting of early phenological phases across temperate regions in the last decades (RUTISHAUER & STUDER 2007, GÜSEWELL et al. 2017). The delayed response of later phases (FU et al. 2015) resulted in a slight, but not significant, increase in growing period length for *A. ursinum* and other spring ephemerals (GÜSEWELL et al. 2017). The increasing trend in growing period length, however, did not induce a similar increasing trend of flowering intensity of *A. ursinum* with time. Instead, we found that an exceptionally long growing period in 1991 synchronized the flowering behaviour of the population leading to a clear biennial pattern and to years with a very high flowering intensity exceeding numbers recorded before 1991. The recurrent change of high and low flowering years, though, averted a clear increasing trend with time despite a positive effect of growing period length on inflorescence numbers.

According to NAULT & GAGNON (1993), resource availability and the regulating effect of season length can determine reproductive synchrony. The long growing period in 1991 with 78 days and late frost events in the same year seem to have had a positive effect on the resource budget of most adult individuals within the population. This led to synchronized

flowering in the following year and a depletion of resources preventing flowering in the year after (SALA et al. 2012) independent of growing period length. Our results support other findings that plant species with an alternate-year reproduction of individuals can produce patterns of masting following slight environmental variations (PIOVESAN & ADAMS 2001, CRONE & RAPP 2014, KOENIG & KNOPS 2014, PEARSE et al. 2014). The induced masting pattern might have resulted in lower seed predation and better dispersal (CRONE & RAPP 2014) contributing to an *A. ursinum* expansion. Moreover, season length was found to have a positive effect on juvenile growth rate and bulb division rate indicating that individuals can reach the flowering stage faster contributing to high inflorescence numbers. NAULT & GAGNON (1993) also demonstrated that flowering individuals tend to produce daughter bulbs in the following year linking sexual and vegetative reproduction (HERBEN et al. 2015). Daughter bulbs can flower in their second year and can therefore contribute to maintain the biennial masting pattern that lasted more than 20 years in the investigated *A. ursinum* population.

High atmospheric nitrogen depositions in Central European deciduous forests have been found to be responsible for a more frequent masting of *Fagus sylvatica* in recent years (SCHMIDT 2006, MUND et al. 2010). MIYAZAKI et al. (2014) identified nitrogen as the key regulator of mast flowering in *Fagus crenata*. The masting behaviour of *A. ursinum* in our study was independent of fertilization. The same is true for the positive effect of growing period length on inflorescence numbers that was not significantly different between fertilization variants (SMAILL et al. 2011). However, we found that fertilization with combined nitrogen and phosphorus increased inflorescence numbers in low-, medium- and high flowering years compared to no fertilization or single fertilizer variants. The importance of phosphorus, in particular for flowering, is supported by a strong depletion of phosphorus in the leaves before flowering begins, while the depletion of nitrogen only starts with the seed formation (ERNST 1979). An effect of a different phosphorus and nitrogen supply on vitality and small-scale distribution of *A. ursinum* was also shown by TRÉMOLIÈRES et al. (2009). In a French riparian forest the occurrence of *A. ursinum* was either limited by nitrogen (frequently flooded areas) or by phosphorus (unflooded areas). In the Göttinger Wald, very dense and vital *A. ursinum* carpets were found in an area that was used in ancient times as a refuge fort where people and their livestock took shelter in times of danger (WINTERHOFF 1963, SCHMIDT & HEINRICHS 2017). The soils in this area are characterised by a higher phosphorus and nitrogen content compared to other areas in the Göttinger Wald (SCHMIDT 1970). The results also show that atmospheric nitrogen depositions cannot have facilitated the expansion of *A. ursinum* (BÖHLING 2008) by an increased sexual reproduction if phosphorus supply was limited.

While the Göttinger Wald study site was largely undisturbed, the plots sampled after windthrow demonstrate how flowering intensity can be influenced by an increase in light and nutrient availability after disturbance (BARKHAM 1980). In the two study areas affected by windthrow in 1997 (Hainholz and Nüllberg), we recorded inflorescence numbers that largely exceeded numbers of the Göttinger Wald, even in nearly undisturbed sites that were affected by adjacent disturbed areas. Although *A. ursinum* is known to be susceptible to high temperatures and low air humidity (DIACI et al. 2012), the higher soil water content after the loss of the tree layer and the partly available protective structures of the thrown stems (in the uncleared Hainholz area) may have even increased air humidity and facilitated reproduction. BARKHAM (1980) found a peak in flowering intensity of *Narcissus pseudonarcissus* in the third year after intensive forest management operations followed by a steep decline. A similar pattern was observed for *A. ursinum* with a steady decline from 1999, the second year

after windthrow, to 2001. This was caused by a reduction in light availability as natural tree regeneration, mainly *Fraxinus excelsior* and *Fagus sylvatica*, rapidly developed in the gaps and thrown sites, and by root competition from regenerating trees, shrubs (*Rubus ideaus*) and herbaceous species (*Carex sylvatica*, *Lamium galeobdolon*, *Cirsium arvense*, *Stachys sylvatica* and *Mercurialis perennis*) that expanded after the disturbance (BARKHAM 1980, KOMPA & SCHMIDT 2005). As cover values of *A. ursinum* remained relatively constant, our results indicate that the reduced resource availability three to four years after disturbance solely affected the allocation of resources to sexual reproduction. However, the high reproductive success early after disturbance was particularly important for this relatively short-lived forest plant to persist against other competitors (ERNST 1979, GRIME et al. 1988, ERIKSSON 1989, EGGERT 1992, MORSCHHAUSER et al. 2009, OBORNY et al. 2011). As we detected a decreasing trend in flowering in both study areas after disturbance, neither site management after windthrow nor the different site conditions seem to have affected the change in inflorescence numbers. The decrease in inflorescence numbers on nearly undisturbed plots cannot be clearly explained by our data. The reduction of light availability following canopy closure may have been one reason. *Fagus sylvatica* as the main tree species shows a high plasticity and is able to close small gaps very rapidly (SCHRÖTER et al. 2012). Furthermore, the short period of investigation precludes a clear evaluation if, or in which way, impacts of windthrow and inter-annual fluctuations interfere.

5. Conclusions

Our results demonstrate that the length of the growing period for *A. ursinum* - from leaf foliation to leaf die back - was a strong single predictor for inflorescence numbers in the following year across three decades. Phenological observations support the trend towards an advancement of early phenological phases and longer growing periods in the last decades. For *A. ursinum*, the growing period length mainly functioned as a decisive factor to induce masting behaviour. An exceptionally long growing period in 1991 positively affected the resource budget of most adult individuals of a population, induced a high flowering intensity and synchronized individual flowering behaviour within the population across the following 20 years. The increasing length of the growing period over time supported the maintenance of this masting behaviour by increasing carbon assimilation, juvenile growth and the formation of daughter bulbs that can contribute to flowering already in the second year.

The induced masting pattern may have facilitated the observed expansion of this species in different ways: 1) In contrast to *A. tricoccum*, where inflorescences showed a high mortality (NAULT & GAGNON 1993), ERNST (1979) showed a strong relationship between flowering, seed production and seedling establishment for *A. ursinum*. Thus, high inflorescence numbers can have resulted in a high seedling establishment. 2) *A. ursinum* showed a successful seedling establishment even at high densities indicating low intraspecific competition and an efficient gap filling (MORSCHHAUSER et al. 2009). 3) A synchronised flowering (and an assumed synchronised high seed production) may enable a long-distance dispersal by browsers. Although seed dispersal by ants or ungulates was poorly valued by several authors (ERNST 1979, VON OHEIMB et al. 2005, OBORNY et al. 2011), humid and productive soils with *A. ursinum* attract ungulates and are often over-browsed (KLÖTZLI 1965, ELLENBERG 1988). A high seed density might increase the probability of an accidental dispersal by these browsers. In addition, gastropods may function as dispersal agents for *A. ursinum*, as has

been demonstrated for two other temperate forest herbs (*Anemone nemorosa*, *Asarum europaeum*; TÜRKE et al. 2012). Although the latter species were swallowed more frequently, seeds of *A. ursinum* were also found in gastropod feces (TÜRKE & WEISSER 2013).

Thus, recurrent high flowering years supported by longer growing periods and a high resource availability including light, phosphorus and nitrogen have influenced the successful expansion of *A. ursinum* in the past decades and can probably explain new occurrences of this species in ruderal phosphorus-rich woodlands (H. Haeupler, personal communication) and the efficient gap filling in already *A. ursinum*-rich stands.

Erweiterte deutsche Zusammenfassung

Einleitung – *Allium ursinum* kann in Mitteleuropa im Frühjahr die Krautschicht sommergrüner Laubwälder auf nährstoffreichen, ausreichend wasserversorgten Standorten beherrschen. Der Bärlauch war in der Vergangenheit jedoch durch markante Verbreitungslücken zwischen dichten Beständen gekennzeichnet. In den letzten Jahrzehnten wird vermehrt eine Ausbreitung von *A. ursinum* und ein Schluss dieser Lücken beobachtet. Da der Bärlauch sich, im Gegensatz zu anderen Frühjahrsgeophyten, überwiegend über Samen vermehrt, deutet dies auch auf eine erhöhte generative Reproduktion hin. Ziel der vorliegenden Studie war es, in verschiedenen Buchenwäldern die Rolle von Phänologie, Klimavariablen und Ressourcenverfügbarkeit auf die Blühintensität von *A. ursinum* über einen Zeitraum von 37 Jahren (1981 bis 2017) zu untersuchen. Beginn und Länge verschiedener phänologischer Phasen im Frühjahr definieren die Wachstumsperiode von *A. ursinum* und haben möglicherweise Einfluss auf die Anzahl der Infloreszenzen. Diese Phänophasen können wiederum von veränderten Temperaturen infolge des Klimawandels beeinflusst werden. Deshalb wurde neben der Phänologie auch der langzeitige Einfluss verschiedener klimatischer Variablen analysiert. Zusätzlich wurde zwischen 2010 und 2017 mit Hilfe eines Düngungsversuchs im selben Wald der Einfluss erhöhter Stickstoff- und Phosphorversorgung auf das Blühverhalten untersucht. Erfasste Blütenstandszahlen nach einem Windwurf sollten außerdem Hinweise auf einen möglichen Einfluss erhöhter Lichtverfügbarkeit geben.

Material und Methoden – *Allium ursinum* hat im Vergleich zu anderen Frühlingsgeophyten einen eigenartigen Lebenszyklus. Die Art gehört zu den am frühesten austreibenden Pflanzen in Laubwäldern, kommt aber von den Frühblühern am spätesten zur Blüte, nämlich erst bei beginnender Seneszenz unter dem sich schließenden Laubdach der Bäume. Bei der Vergilbung verlagern sich die Reservestoffe in die Erneuerungszwiebeln, wo schon ab Sommer Anlagen für neue Blüten und Sprosse und Tochterzwiebeln gebildet werden. Für die Blüten- und Fruchtbildung wird das Stoffreservoir stark in Anspruch genommen, so dass die Pflanzen im nächsten Jahr meist steril bleiben. Dafür können andere Pflanzen aus dem Nachwuchs zur Blüte kommen, denn mit den im Juni reichlich ausgestreuten Samen gibt es nach der Keimung im Herbst bis Frühjahr (meist im 2. Jahr nach der Samenbildung) reichlich Nachwuchs. So bestehen dichte *A. ursinum*-Bestände aus einem Nebeneinander unterschiedlich alter Individuen, offenbar ohne stärkere intraspezifische Konkurrenz. Auch vegetative Vermehrung durch Tochterzwiebeln trägt zur Verjüngung bei, ist allerdings weniger wichtig als bei anderen Frühlingsgeophyten.

Die vorliegenden Daten stammen überwiegend von einer Ökosystem-Forschungsfläche der Universität Göttingen im Göttinger Wald (Abb. 1a, b). Hier wurden in den Jahren 1981 und 1982 in einem Kalkbuchenwald (*Hordelymo-Fagetum lathyretosum*) weit verteilt 19 1 m²-Flächen angelegt, in denen zwischen 1981 und 2017 jährlich die Anzahl der Infloreszenzen von *A. ursinum* sowie sein Deckungsgrad erfasst wurden. Die eingerichteten Flächen waren vollständig von *A. ursinum* bedeckt, um einen Einfluss sich ausbreitender Bestände auf die Zahl der Blütenstände pro Flächeneinheit zu minimieren. Die Zahl der jährlich untersuchten Dauerquadrate variierte über den gesamten Beobachtungszeitraum zwischen drei und 19 Flächen. – In der Forschungsfläche (einschließlich der Waldränder) wurden über den gleichen Zeitraum phänologische Beobachtungen durchgeführt, um den Beginn sich ablösender phänologischer Phasen während der Vegetationsperiode zu ermitteln. Der Anfangszeitpunkt bestimmter Phänophasen definierte dabei auch die Vegetationsperiode von *A. ursinum*. Für unsere Untersuchungen war die Zeitspanne zwischen dem Beginn der *Acer platanoides-Anemone nemorosa*-Phase (Phase 2:

Frühlingsbeginn) und der *Cornus sanguinea-Melica uniflora*-Phase (Phase 6: Frühsommerbeginn) entscheidend (s. Anhang E1; DIERSCHKE 1982, 1989a). Für den gleichen Zeitraum wurden zusätzlich Klimadaten aus der Wetterstation Göttingen des Deutschen Wetterdienstes ausgewertet. – Im Bereich der Forschungsfläche Göttinger Wald wurde 1997 zudem ein Düngungsversuch angelegt, der aus einer Kontrolle und drei Düngungsvarianten bestand: Seit 1998 erfolgt Stickstoffdüngung mit 100 kg N/ha; Phosphor-Düngung mit 30 kg P/ha; Stickstoff + Phosphor-Düngung mit 100 kg N und 30 kg P/ha pro Jahr (Abb. 1c, d). Jede Variante wurde auf vier 25 m²-Flächen wiederholt. Von 2010 bis 2017 wurden in jeder Fläche die Blütenstände von *A. ursinum* in 3 x 1 m²-Unterflächen gezählt. – Nach einem lokalen Sturm, der im Sommer 1997 im südwestlichen Harzvorland örtlichen Windwurf verursachte, wurden in Buchenwäldern des Hainholzes und Nüllbergs außerdem von 1999 bis 2001 *A. ursinum*-Infloreszenzen auf insgesamt 24 1 m²-Flächen gezählt. Die Flächen verteilten sich auf unterschiedliche Störungskategorien vom weitgehend ungestörten Bestand bis zum Flächenwurf (KOMPA & SCHMIDT 2005; Abb. 1e, f). – Für die Datenauswertung wurden verschiedene statistische Verfahren und Modelle benutzt, vor allem für Beginn und Länge der Vegetationsperiode von *A. ursinum* und für verschiedene Klimavariablen in Bezug zu Zahlen der jährlichen Infloreszenzen. Als Vergleichszeiträume für Klimadaten wurden jeweils dreimonatige Perioden (Januar-März, Februar-April, April-Juni) herangezogen.

Ergebnisse – Die Langzeitzählung der Blütenstände im Göttinger Wald zeigte zunächst zwischen 1981 und 1991 relativ konstante Zahlen mit 30 bis 45 Blütenständen je m² und Jahr. Dann sorgte im Jahr 1991 eine ausgesprochen lange Vegetationsperiode von *A. ursinum* – 78 Tage vom Frühjahrsaustrieb bis zum Vergilben unter sich schließenden Baumkronen – für ein blütenreiches Jahr 1992 und eine folgende Synchronisation der Blühintensität aller Dauerquadrate; diese hielt fast 20 Jahre an (Abb. 2, Anhang E2) und drückte sich in einem (fast) jährlichen Wechsel blütenreicher und blütenarmer Jahre aus. Erst ab 2015 schwächte sich dieser deutliche Wechsel wieder ab. – Für die gesamte Untersuchungszeit erwies sich der Witterungsverlauf des Vorjahres als wichtigster Faktor für den Reproduktionsstatus des Folgejahres, insbesondere über Klimavariablen, die einen deutlich signifikanten Einfluss auf die Zahl der Blütenstände hatten. So konnte ein positiver Zusammenhang zwischen der Anzahl der Blütenstände und der Länge der Vegetationsperiode im vorausgegangenen Jahr festgestellt werden. Hohe mittlere Temperaturen im Zeitraum Januar-März (Verfrühung des Austriebs) hatten z. B. positive Effekte auf die Zahl der Infloreszenzen im Folgejahr. Dagegen wirkten sich viele Frosttage im Januar-März (Verspätung des Vegetationsbeginns) und auch sehr warme Bedingungen im April-Juni (früher Schluss des Kronendaches und rasche Vergilbung des Bärlauchs) negativ auf die Zahl der Blütenstände im Folgejahr aus. Obwohl die Vegetationsperiode für *A. ursinum* in den letzten Jahren früher begann als Anfang der 1980er Jahre und sich so die Vegetationsperiode im Durchschnitt leicht verlängerte, konnte aufgrund der starken interannuellen Schwankungen über die gesamte Beobachtungszeit kein positiver Trend der Zahl der Blütenstände über die Dauerquadrate festgestellt werden. Aufgrund der Synchronisation und des anhaltenden Trends einer längeren Vegetationsperiode konnten in blütenreichen Jahren jedoch im Mittel deutlich höhere Infloreszenzzahlen gezählt werden (z. B. 1998 oder 2013) als noch Anfang der 80er Jahre.

Der Düngungsversuch zeigte positive Effekte einer kombinierten Stickstoff- und Phosphor-Düngung auf die Zahl der Blütenstände. Dieser positive Effekt erhöhte sich jedoch nicht weiter, wenn die Vegetationsperiode im vorausgegangenen Jahr relativ lang war.

Nach Windwurf folgten die Blütenstandszahlen einem Störungsgradienten mit geringsten Werten im weitgehend ungestörten Bestand und den höchsten bei Flächenwurf. Bereits im dritten Jahr nach Windwurf nahm die Zahl der Blütenstände jedoch stetig ab, während der Deckungsgrad von *A. ursinum* konstant blieb, auch unter einer sich deutlich entwickelnden Konkurrenzvegetation.

Diskussion – Unsere Ergebnisse zeigen, dass von 1981 bis 2017 die Länge der Vegetationsperiode von *A. ursinum* im Vorjahr (vom Austrieb bis zum Vergilben) eine stark positive Wirkung auf die Zahl der Blütenstände hatte. Ein signifikanter Einfluss verschiedener klimatischer Faktoren bestätigt die Bedeutung der Länge der oberirdischen Wachstumszeit. Für Frühlingsgeophyten wird die Blühintensität durch die Menge gespeicherter Reservestoffe im Vorjahr gesteuert, die wiederum von der Länge der Assimilationszeit abhängt. Phänologische Beobachtungen in Mitteleuropa zeigen für die letzten Jahr-

zehnte überall einen Trend zu verfrühtem Beginn der Vegetationsperiode unter Einfluss des Klimawandels, was unsere Untersuchungen bestätigen. Doch trotz einer früher beginnenden und teilweise länger andauernden Vegetationszeit in den letzten Jahren zeigten die Blütenstände des Bärlauchs keine signifikante Zunahme mit der Zeit, sondern reagierten durch Synchronisation auf die veränderten Umweltbedingungen. Eine ausgesprochen lange Vegetationsperiode im Jahr 1991 mit positivem Effekt auf die Nährstoffspeicherung induzierte diese Synchronisation des Blühverhaltens aller untersuchten Dauerquadrate und führte zu einem rhythmischen Auftreten wiederholter blütenreicher und -armer Jahre. Maximal wurden 146 Blütenstände pro m² in einem blütenreichen Jahr (2013) gezählt, was die Zahlen vom Beginn des Beobachtungszeitraums deutlich übersteigt (siehe Anhang E2). Das verstärkte Auftreten dieser blütenreichen Jahre könnte die Ausbreitung und Verdichtung von *A. ursinum* im Göttinger Wald (DIERSCHKE 2013) begünstigt haben, z. B. durch die erhöhte Wahrscheinlichkeit einer erfolgreichen Keimung und Etablierung oder einer zufälligen Samenausbreitung durch das Schalenwild. Außerdem mag die verlängerte Vegetationszeit die Wuchsrate der Jungpflanzen und die Bildung von Tochterzwiebeln positiv beeinflusst haben, die bereits im zweiten Jahr zur Blüte kommen und den Blührhythmus verstärken können. – Unsere Ergebnisse zeigen außerdem, dass Stickstoffdepositionen allein nicht zu einer erhöhten Zahl an Blütenständen führen, aber sich in Kombination mit einer guten Phosphor-Versorgung positiv auf die Zahl der Blütenstände auswirken können. – Der hohe Blütenreichtum nach Störung durch Windwurf deutet darauf hin, dass sich die Lichtverfügbarkeit ebenfalls positiv auf die Zahl der Blütenstände auswirkt, was möglicherweise dazu beiträgt, dass der Waldspezialist *A. ursinum* auch bei mehr Licht dem hohem Konkurrenzdruck hochwüchsiger Offenlandarten zumindest kurzfristig gewachsen ist.

Insgesamt zeigen die Ergebnisse, dass wiederholte blütenreiche Jahre aufgrund einer verlängerten Vegetationszeit sowie einer hohen Ressourcenverfügbarkeit von Licht, Phosphor und Stickstoff die Ausbreitung von *A. ursinum* begünstigen können.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Short characterisation of phenological phases.

Anhang E1. Kurze Charakterisierung der phänologischen Phasen.

Supplement E2. Number of inflorescences in the 19 1 m² plots from 1981 to 2017 in the Göttinger Wald research area.

Anhang E2. Zahl der Blütenstände in den 19 1 m²-Flächen von 1981 bis 2017 in der Forschungsfläche des Göttinger Waldes.

Supplement E3. Scatterplots of the relationships between a) the length of the growing period in the previous year and inflorescence numbers and b) between inflorescence numbers in the previous year and current inflorescence numbers from 1982 to 1991 and from 1993 to 2017.

Anhang E3. Streudiagramme der Beziehung zwischen a) der Länge der Vegetationsperiode im Vorjahr und der Zahl der Blütenstände und b) zwischen der Zahl der Blütenstände im Vorjahr und der aktuellen Zahl der Blütenstände von 1982 bis 1991 und von 1993 bis 2017.

Supplement E4. Mean cover values of *A. ursinum* and mean inflorescence numbers (in n/m²) extrapolated to a cover value of 100% in four fertilization variants from 2010 to 2017.

Anhang E4. Mittlerer Deckungsgrad von *A. ursinum* und mittlere Zahl der Blütenstände (in n/m²) extrapoliert auf einen Deckungsgrad von 100 % in vier Düngungsvarianten von 2010 bis 2017.

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Heinrichs et al.: Effect of phenology, nutrient availability and windthrow on flowering intensity of *Allium ursinum* – results from long-term monitoring and experiments

Supplement E1. Short characterisation of phenological phases.

Anhang E1. Kurze Charakterisierung der phänologischen Phasen.

Short characterisation of phenological phases 1 to 6 in beech forests on limestone, defined according to the start of flowering of different phenological species groups (following DIERSCHKE 1982) and with special consideration of *Allium ursinum*:

1 *Corylus-Leucojum*-Phase

At the first beginning of spring only few plant species are flowering. In beech forests on limestone these species are *Daphne mezereum* and *Leucojum vernum,* and *Hepatica nobilis* towards the end of this phenological phase.

Below the protective beech litter layer *Allium ursinum* starts its development. Shoots reach above the litter layer at the end of this phenological phase and the first leaves start to grow.

2 *Acer platanoides-Anemone nemorosa*-Phase

The beginning of spring is characterised by the flowering of *Acer platanoides* and *Fraxinus excelsior* in the tree layer and a first flowering peak in the herb layer. Below the still open canopy *Anemone nemorosa*, *A. ranunculoides*, *Corydalis cava*, *Ranunculus ficaria*, *Gagea lutea*, *Mercurialis perennis*, *Primula elatior* and *Pulmonaria obscura* are flowering.

During this phase *A. ursinum* shows a rapid vegetative development with the growth of the first two leaves. The laterally originating flower buds become visible. The beginning of this phase marks the beginning of the (aboveground) growing period of *A. ursinum*.

3 *Prunus avium-Ranunculus auricomus*-Phase

During this phase the leaves of tree and shrub species start to unfold and *Prunus* species are flowering. Flowering in the herb layer is at a maximum with *Euphorbia amygdaloides*, *Lathyrus vernus*, *Oxalis acetosella*, *Ranunculus auricomus* and *Viola reichenbachiana* joining the already flowering species.

With its big leaves, *A. ursinum* can dominate the herb layer but it is especially susceptible to frost events during this phase. Inflorescence stems grow rapidly.

4 *Fagus-Lamium galeobdolon*-Phase

This phase is characterised by the leaf unfolding and flowering of *Fagus sylvatica*. For the understorey, the transition from high irradiance to deep shade in the following phases begins. The first early flowering species start to die back and other species begin flowering. These species are *Cardamine bulbifera*, *Carex sylvatica*, *Lamium galeobdolon*, *Ranunculus lanuginosus* and *Stellaria holostea*.

The thick flowering buds of *A. ursinum* can now reach heights of up to 50 cm; towards the end of this phase the two week long flowering period of *A. ursinum* begins.

5 *Sorbus aucuparia-Galium odoratum*-Phase

During this phase, full shade is reached for the understorey in the beech forest and most spring species rapidly disappear. A last flowering peak in the understorey begins with *Arum maculatum*, *Galium odoratum*, *Geranium robertianum*, *Polygonatum multiflorum*, *P. verticillatum* and *Sanicula europaea*.

A. ursinum particularly dominates the flowering aspect of the herb layer during this phase. At the same time, its leaves begin to die back.

6 *Cornus sanguinea-Melica uniflora*-Phase

With the starting of summer during this phase, the flowering time of most species in the beech forest is finished. Some grasses, such as *Melica uniflora* and *Milium effusum*, are still flowering; the same is true for *Phyteuma spicatum* and *Veronica montana*.

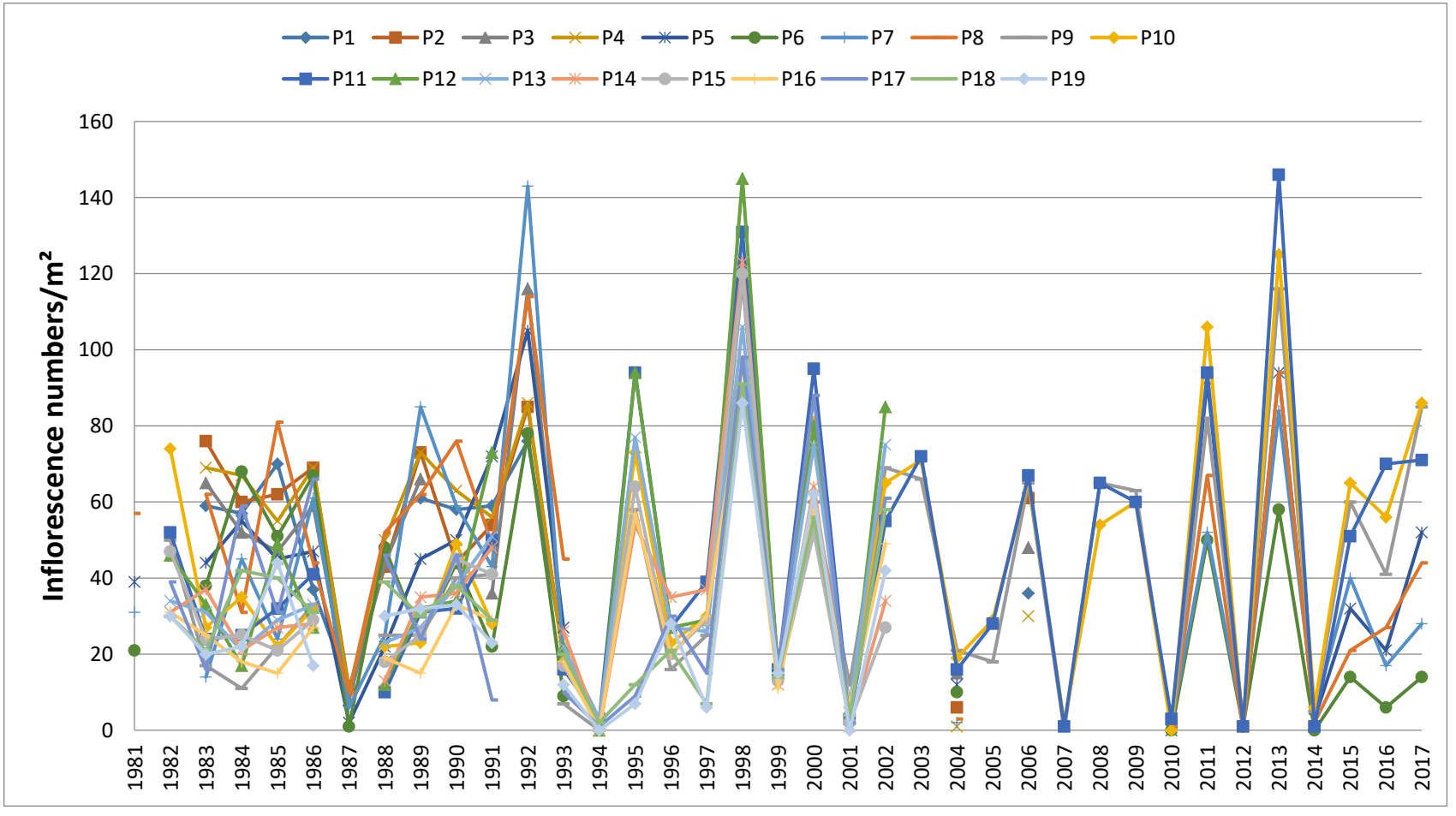
During this phase *A. ursinum* rapidly disappears, leaving behind its yellowed seed heads that distribute seeds at the end of this phenological phase. The start of this phase marks the end of the growing period of *A. ursinum*.

In the following summer and autumn phases, *A. ursinum* has disappeared from aboveground but below ground it starts the development of new leaf and flowering initials. In late autumn, up until the following spring the seeds germinate.

Heinrichs et al.: Effect of phenology, nutrient availability and windthrow on flowering intensity of *Allium ursinum* – results from long-term monitoring and experiments

Supplement E2. Number of inflorescences in 19 1 m² plots (P1-P19) from 1981 to 2017 in the Göttinger Wald. No plot was sampled in each year.

Anhang E2. Zahl der Blütenstände in den 19 1 m²-Flächen (P1-P19) von 1981 bis 2017 im Göttinger Wald. Keine Fläche wurde in jedem Jahr erfasst.

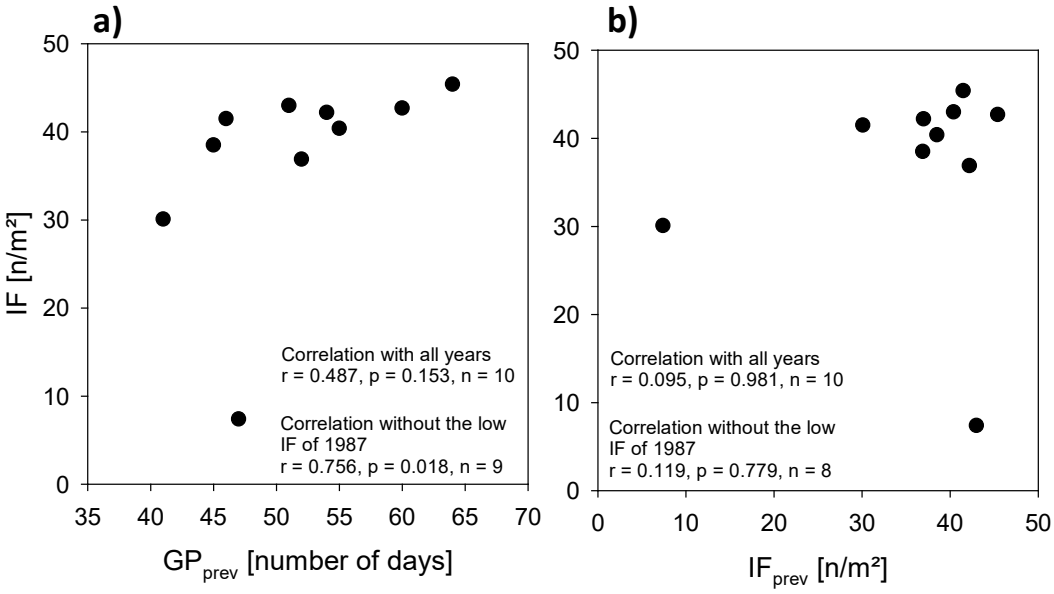


Heinrichs et al.: Effect of phenology, nutrient availability and windthrow on flowering intensity of *Allium ursinum* – results from long-term monitoring and experiments

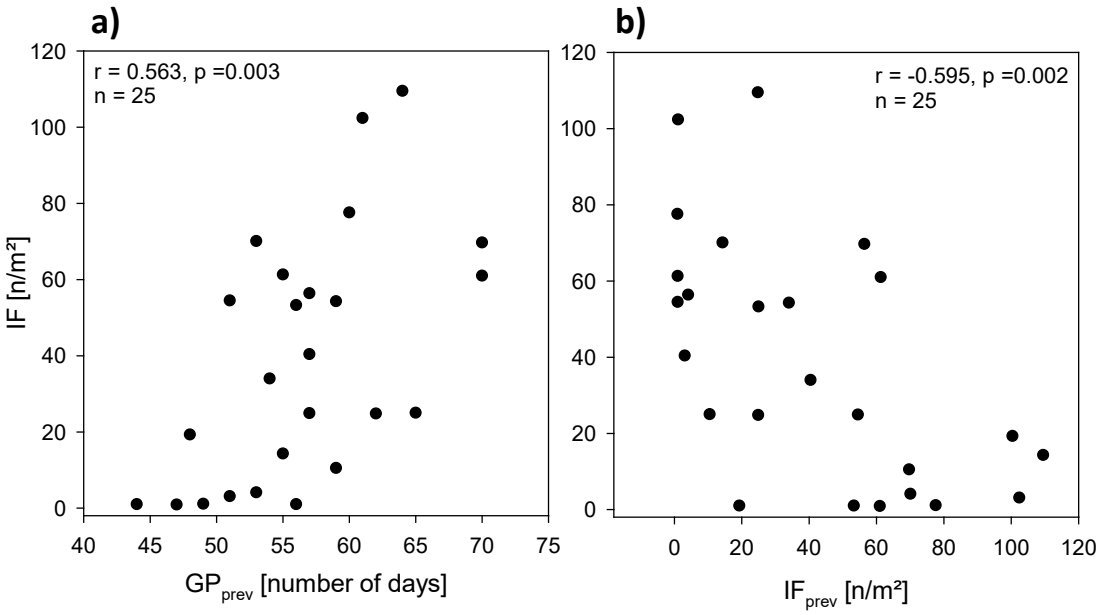
Supplement E3. Scatterplots of the relationships between a) the length of the growing period in the previous year (GP_{prev}) and inflorescence numbers (IF) and b) between inflorescence numbers in the previous year (IF_{prev}) and current inflorescence number (IF) from 1982 to 1991 and from 1993 to 2017.

Anhang E3. Streudiagramme der Beziehung zwischen a) der Länge der Vegetationsperiode im Vorjahr (GP_{prev}) und der Zahl der Blütenstände (IF) und b) zwischen der Zahl der Blütenstände im Vorjahr (IF_{prev}) und der aktuellen Zahl der Blütenstände (IF) von 1982 bis 1991 und von 1993 bis 2017.

1982 to 1991



1993 to 2017



Heinrichs et al.: Effect of phenology, nutrient availability and windthrow on flowering intensity of *Allium ursinum* – results from long-term monitoring and experiments

Supplement E4. Mean cover values of *A. ursinum* and mean inflorescence numbers (in n/m²) extrapolated to a cover value of 100 % in four fertilization variants from 2010 to 2017. *Different lowercase letters indicate significant differences among variants per year (based on mixed effect models with plot as random effect). Highest numbers per year are written in bold when a significant difference to at least one other variant was detected.

Anhang E4. Mittlerer Deckungsgrad von *A. ursinum* und mittlere Zahl der Blütenstände (in n/m²) extrapoliert auf einen Deckungsgrad von 100 % in vier Düngungsvarianten von 2010 bis 2017. *Unterschiedliche Kleinbuchstaben zeigen signifikante Unterschiede zwischen Varianten pro Jahr (basierend auf Gemischten Modellen mit Plot als Zufallseffekt). Die höchsten Zahlen pro Jahr sind in Fettdruck geschrieben, wenn ein signifikanter Unterschied zu mindestens einer Variante ermittelt wurde.

	Cover [%]				Extrapolated inflorescence numbers [n/m²]			
Year	Control	N	P	NP	Control	N	P	NP
2010	66.3 (7.2)ab	60.8 (6.0)a	71.7 (2.3)b	**74.2 (3.4)b**	1.0 (0.2)a*	**2.1 (0.3)b**	0.6 (0.1)a	1.5 (0.4)ab
2011	79.0 (5.5)ac	76.3 (2.4)a	85.0 (3.4)bc	**90.5 (4.7)b**	87.9 (9.4)ac	83.7 (1.7)a	97.0 (5.8)bc	**106.8 (4.4)b**
2012	75.4 (6.4)ab	70.8 (1.6)a	**82.5 (1.4)b**	81.7 (6.7)b	1.8 (0.5)a	2.9 (1.1)a	4.4 (1.5)ab	**5.5 (1.7)b**
2013	88.4 (4.0)a	81.7 (2.5)b	88.4 (3.9)a	**94.4 (2.2)a**	114.9 (4.7)ab	112.1 (5.6)a	120.3 (10.5)ab	**128.9 (7.1)b**
2014	87.6 (5.2)ab	80.7 (5.9)a	90.0 (2.8)b	**95.5 (1.1)b**	6.1 (0.9)ac	3.0 (0.8)a	9.6 (1.2)bc	**14.0 (2.0)b**
2015	85.6 (3.7)ab	83.3 (1.5)a	86.7 (2.5)ab	**90.0 (1.5)b**	37.4 (3.2)a	39.6 (2.6)a	37.3 (6.0)a	33.9 (4.1)a
2016	77.5 (7.5)a	75.4 (4.3)a	81.5 (4.8)ab	**87.1 (1.0)b**	43.7 (6.4)a	50.2 (8.0)ab	44.9 (5.9)a	**61.0 (2.7)b**
2017	85.2 (5.2)ab	85.4 (2.7)ab	80.2 (4.6)a	**89.2 (1.6)b**	57.3 (4.9)a	61.1 (1.6)a	57.4 (3.0)a	65.1 (2.5)a

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Autor(en)/Author(s): Heinrichs Steffi, Dierschke Hartmut, Kompa Thomas, Schmidt Wolfgang

Artikel/Article: Effect of phenology, nutrient availability and windthrow on flowering of Allium ursinum – results from long-term monitoring and experiments 111-134