POPULATION BIOLOGY OF \textit{ALLIUM UR SINUM} \\
IN NORTHERN GERMANY

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\textbf{SUMMARY}

(1) The population biology of four \textit{Allium ursinum} stands was studied in a beech-wood on calcareous soil and in a mixed \textit{Carpinus-Fagus} woodland on a pseudo-gley soil in northern Germany from 1968 to 1977.

(2) Under laboratory conditions germination of \textit{Allium ursinum} seeds occurred after a dormancy period at 15-20 °C followed by stratification at 4 °C for at least 30 days. In the field, germination is restricted to the late winter and early spring.

(3) Development of leaves and inflorescences is also dependent on low temperature.

(4) Sexual and vegetative reproduction of \textit{A. ursinum} first occurs in the fourth year, and lasts no longer than the eighth year.

(5) A population of \textit{Allium ursinum} has four dominant phases of mortality: at the embryo stage, autolysis of seeds during dormancy and stratification, mortality of individuals as they move to lower soil layers by means of contractile roots, and the phase of ageing (after 7-8 years).

(6) The existence of pure stands of \textit{Allium ursinum} is discussed in relation to the concept of \textit{Allium} as an \textit{r}-strategist amongst \textit{K}-strategists, and to possible allelochemical and mechanical effects of the dying leaves.

(7) The mineral-element content of different organs of \textit{A. ursinum} is related to the life cycle of the individual plant. The significance of high nitrate concentration in the leaves of \textit{Allium} in spring is discussed.

\textbf{INTRODUCTION}

Despite the great emphasis upon woodland ecosystems during the International Biological Programme (Reichle 1970), very little attention has been paid to the population ecology of the plants of the ground flora of deciduous woodland (Tamm 1948, 1972; Persson 1975; Hutchings & Barkham 1976). Any scheme of management for the ground vegetation of woodland requires a knowledge of the population dynamics of the component herbaceous species. In species-rich deciduous woodlands, one of these species is \textit{Allium ursinum} L., a perennial member of the Liliaceae. \textit{Allium ursinum} can cover large areas as pure stands, and these stands provide interesting material for plant-population studies in the field, because casual observation has revealed very large numbers of seedlings growing amongst the mature plants (Schmucker & Drude 1934). Any attempt to explain the pure stands has been restricted to studies of the interaction of leaf extracts of \textit{Allium} with the growth of cultivated plants on artificial substrates (Lange & Kanzow 1965), rather than in relation to the chemical properties of woodland soils and the viability and
reproductive strategy of this species. The present paper reports observations and experiments on the population biology of Allium stands.

STUDY SITE

The study site is located in the Teutoburg Forest, near Brochterbeck, West Germany (52°14'N, 7°43'E), at an altitude of 55–115 m. Three populations of Allium ursinum growing within 1 km of each other in an Asperulo-Fagetum woodland on rendzina soil were studied—one on a north-facing slope, one on a plateau and one on a south-facing slope. The fourth population occurs on a plateau within a Stellario-Carpinetum, on a pseudo-gley soil which is flooded once or twice in spring (March) or summer (July, August) after heavy rains. The approximate areas covered by each population within the Asperulo-Fagetum were 4600 m² on the north-facing slope, 500 m² on the plateau and 2000 m² on the south-facing slope; the fourth population within the Stellario-Carpinetum covered nearly 600 m². The soils are characterized by a high pH (7.5 ± 0.5), a cation-exchange-capacity of 28.4 m-equiv. per 100 g soil, and a base-saturation of 96.4% (Ernst 1978). True replication within each population is not possible under woodland conditions, because of the temporal and spatial variation in both the chemical properties of the soils (Frankland, Ovington & Macrae 1963; Ernst 1978) and the flux and quality of light (Federer & Tanner 1966; Schulze 1972).

METHODS

Field studies

All populations were monitored from 1968 to 1977. Population structure and population dynamics were analysed by investigating germination, flowering, number of ovules and mature embryos, seed production, leaf area, bulb growth, rooting behaviour and numbers of individual plants. For the determination of longevity, 100 seedlings and 100 flowering individuals in each of the stands were marked in 1968, to try and trace the behaviour of individuals through the life cycle. A second experiment was started in 1970, to determine the mortality rate. In each of the three populations within the Asperulo-Fagetum, three subpopulations, each covering 3 x 1 m, were created as follows: field plots with an additional margin of 50 cm all round were cleared of existing vegetation except for flowering plants of Allium ursinum. The flowering plants (equivalent to embryo counts of 3720, 4860 and 12 170 for the three subpopulations) were left until seed dispersal and were then also removed. In order to prevent loss of seeds by predation by birds, the plots were then covered with wire netting up to January 1971, when seeds started to germinate. In this and the following years all seedlings of invading species were removed from the plots, so that the development of even-aged subpopulations of Allium could be monitored. A similar experiment, on the north-facing slope only, was started in 1971, and terminated in 1977 when the seasonal-biomass distribution among roots, bulbs, leaves and reproductive organs was measured from 5 March to 13 August.

Dynamics of undisturbed subpopulations in all four areas were analysed by counting numbers of flowering and non-flowering individuals in three permanent 1-m² plots per stand of each population from 1971 to 1977. The development of bulbs and leaf area in relation to ageing of the individuals was investigated by transplanting freshly-germinated seeds of Allium ursinum into two plots on the north-facing slope and two plots on the
south-facing slope of the Asperulo-Fagetum in March 1969. A proportion of the plants was excavated from the plots each year in late May—in the first two years 100 individuals per plot, from the third to the sixth year twenty individuals per plot, and in the seventh year up to ten individuals per plot—when more than 50% of the Allium plants in the neighbourhood in undisturbed plots were starting to fruit. In 1977 the population structure in each of the stands was analysed. Germinating seeds were collected in February and March, and the rest of the subpopulation was collected in May by excavating 3 x 1 m undisturbed plots, for the determination of bulb diameter, rooting depth, number of leaves, leaf area and the number of inflorescences.

**Germination experiments**

Germination experiments in replicated sets of fifty seeds (collected immediately after shedding) were carried out on moist filter paper in closed Petri-dishes, filled with distilled water, in the dark in temperature-controlled incubation chambers. The Petri-dishes were initially kept for 4 months at temperatures of 5, 10, 15 or 20 °C, after which they were transferred to another temperature (300 seeds per treatment) and kept there for a further 4 months. Seeds which had germinated were counted weekly, and then removed from the experiment. At the end of the experiment, ungerminated seeds were opened, incubated for 8–12 h in a solution of 1% 2,3,5-triphenyltetrazolium chloride (Schubert 1967), and examined under a microscope for viability of the embryos.

**Experiments on leaf development**

In order to study the influence of temperature on the development of leaves, 600 bulbs each of age-class 1, 3 or 5/6 years were excavated in August. The bulbs were grown in a mixture of sand and peat at the following temperature regimes:— One set (100 individuals) of each age-class was kept at room temperature (15-20 °C); all the other sets were kept at 4 °C. After 1 and 2 months, a further 100 individuals of each age-class were transferred to a temperature regime of 18 °C day/10 °C night and 12 h light (1500 lux). After 4 months, two further sets of the different age-classes were transferred to temperatures of 10 °C and 15 °C respectively, so that only one set remained at 4 °C for the whole period of the experiment.

**Allelochemical effects**

To test the suggested allelochemical effects of Allium ursinum on other plants (Lange & Kanzow 1965), freshly-cut leaves of Allium ursinum were added (2.5 kg m⁻²) to three stands of Mercurialis perennis L. and Glechoma hederacea L. twice a year (March and May) for 2 years. The stands of Mercurialis and Glechoma were on the plateau of the Asperulo-Fagetum. In the third year the biomass of treated and control plots (3 x 1 m) was measured in early May (Glechoma) and in July (Mercurialis).

**Chemical analysis**

Biomass, as used here, refers to the weights of plants after drying to constant weight at 105 °C. After wet digestion (HNO₃/HClO₄), the mineral elements were determined by atomic-absorption spectrophotometry in the usual way, with the exception of phosphorus and nitrate which were measured colorimetrically (Ernst 1976). Total nitrogen was analysed by burning in a pure oxygen stream with a N-microrapid azotometer (Merz 1970).
RESULTS

Life history

Seeds of *Allium* are shed in June and July, the exact time depending on the general weather conditions and on the aspect of the stand. A cold spring and summer, as well as a north-facing aspect, delay shedding of seeds for 2–3 weeks. The seeds fall to the ground directly beneath the capsules. Up to 75% of the fruiting stalks, however, are prostrate before the seeds ripen, so that the dispersal distance depends mostly on the height of these stalks; the mean height for the four populations was 22.4 ± 5.7 cm (Table 1).

<table>
<thead>
<tr>
<th>Population</th>
<th>Number of stalks</th>
<th>Height of stalks</th>
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</thead>
<tbody>
<tr>
<td>I</td>
<td>73</td>
<td>18.6 ± 3.0</td>
</tr>
<tr>
<td>II</td>
<td>102</td>
<td>20.1 ± 3.5</td>
</tr>
<tr>
<td>III</td>
<td>113</td>
<td>27.0 ± 6.2</td>
</tr>
<tr>
<td>IV</td>
<td>48</td>
<td>24.0 ± 5.5</td>
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</table>

In typical stands, wind at ground level was unable to move the heavy (5.4 ± 0.7 mg), smooth, elliptic seeds. The mean dispersal distance of seeds from one fruiting individual may be not more than 2.5 m over a 20-year period. Heavy rains and animals may occasionally assist dispersal, especially in *Allium* stands in lowland forests and on steep hillsides. However, the generally-supposed dispersal by ants (van der Pijl 1972) could not be detected, even though seeds were exposed experimentally along ant tracks. Only two out of one-thousand seeds were removed more than 10 cm, and these were moved less than 24 cm. This observation supports the criticism of myrmecochory of *Allium ursinum* by Schmucker & Drude (1934) and Brezinsky (1963). The low capacity for seed dispersal over large distances is one of the reasons for the crowded appearance of *Allium* stands.

In the field, germination occurs in the winter and early spring (January to April), and the species exhibits a dormancy mechanism. As indicated by laboratory experiments (Table 2), exposure of seeds to temperatures of 15–20 °C for several months is necessary for germination. Thereafter, a cold storage for at least 2 months gives reasonable germination. Less than 5% of seeds kept constantly at 5 °C germinated. None of the seeds which had failed to germinate after 8 months contained a viable embryo, as tested by the reaction with 2,3,5-triphenyltetrazolium chloride.

<table>
<thead>
<tr>
<th>Initial temperature (°C)</th>
<th>Final temperature (°C)</th>
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<tbody>
<tr>
<td></td>
<td>20</td>
</tr>
<tr>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>15</td>
<td>—</td>
</tr>
<tr>
<td>10</td>
<td>—</td>
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<tr>
<td>5</td>
<td>—</td>
</tr>
</tbody>
</table>
PLATE 1. Development of bulbs and leaves of *Allium ursinum* at different temperature regimes in a glasshouse: 30 days at 4 °C followed by 90 days at 18 °C day/10 °C night (30d); 60 days at 4 °C followed by 60 days at the higher temperature regime (60d); and 90 days at 4 °C followed by 30 days at 18/10 °C (90d).

(Facing p. 350)
In the first year, the seedling has only one leaf, with an area of 65–200 mm². The development of a bulb from the lowest part of the leaf petiole starts in March or April, but is very limited during the first growing season; no contractile roots appear, so that the young bulb of the seedling remains near the soil surface in the rooting zone of *Anemone nemorosa* L. or *Galium odoratum* (L.) Scop. At the end of the growing season (June/July), leaves of the seedlings turn yellow at the same time as those of the adults. By August all leaves are decomposed. The summer dormancy of the bulb lasts to the beginning of October, as earlier indicated by Rubat du Mérac (1951); then some new small roots start to grow, and from September to December new leaves are developed, but remain within the bulb. After a second period of dormancy the leaves start sprouting in February or March.

The development of leaves is strongly influenced by storage temperature of the bulbs. At room temperature (15–20 °C) no further development of the 2-mm-long leaves within the bulb occurred. At 4 °C for 1 month, leaves grew up to 9 mm, dependent on the bulb size, but in any case they remained within the bulb; at this stage a transfer to 18 °C day/10 °C night did not promote any further growth during the following 3 months. Bulbs kept at 4 °C for a further month, however, showed continued development, the leaves breaking through the bulb and growing up to 15 mm in length. Exposure of this stage to 18 °C day/10 °C night once again slowed down further growth, whereas growth continued unchecked at 4 °C (Plate 1). Only after a cold treatment at 4 °C for 3 months was good leaf growth and inflorescence development achieved. Further growth was more rapid at temperatures of 10 °C and above than at a constant temperature of 4 °C. These experimental results are in good accordance with field observations that during mild winters, with maximum soil temperatures in December and January of 10 °C or above and average soil temperatures of 8 °C, the development of leaves and inflorescences is not more advanced than in cold winters when soil temperatures remain near freezing point.

In the experimental populations there was a doubling of the biomass of the bulbs and roots every year from the second to the fifth year, and a sharp increase in the leaf area (Fig. 1). During the third year contractile roots are developed, and these may bring about a movement of the bulbs from the soil surface to the deeper soil layers—up to 27 cm below the soil surface, dependent on soil resistance. This movement of the bulbs creates a less fertile environment for the plant roots in the A₁, A₂ or B₁ horizons (Ernst 1978). Bulb growth under a dense forest canopy was considerably lower than under the relatively open canopy of the *Stellario-Carpinetum*, the reduction being comparable with the differences in light-compensation points of plants under unshaded and shaded conditions (Lieth & Ashton 1961). The bulbs in an open *Stellario-Carpinetum* receiving 65% of the incident solar radiation were 5-5 times as heavy as those in an *Asperulo-Fagetum* on a south-facing slope (40% solar radiation), and these were twice as heavy again as those in an *Asperulo-Fagetum allietosum* on a north-facing slope receiving only 6% of the solar radiation. However, one further factor, soil structure, may also account for the vigorous bulb growth in the *Stellario-Carpinetum*, because transplant experiments of bulbs from the two woodland types indicated better bulb growth in the sandy pseudo-gley of the *Stellario-Carpinetum* than in the stony rendzina of the *Asperulo-Fagetum*. Vegetative reproduction, indicated by serial bulbs, can start in the fifth year, but it is normally restricted to very few plants (0.1–7.2% of this age-class). Every plant which has more than two leaves develops at least one daughter bulb (Table 3), which generally remains in contact with the parent plant. The daughter bulb produces two leaves and an inflorescence in the second year, mostly of the same size as those of the parent bulb. Sexual reproduction
starts sometimes in the fourth year, but more generally in the fifth year, and ends in the seventh, or exceptionally in the eighth year. The longevity of the plants was independent of the diameter of the bulbs in the experimental stands, perhaps because each individual bulb lives only 1 year and is the product of the second leaf (Fig. 2).

Reproductive allocation, biomass distribution and turnover of minerals

As Harper (1977) emphasized, 'the cost of reproduction cannot really be measured without knowing what is the relevant currency'. It seems that in Allium ursinum the amount of light may be the relevant currency (with regard to the bulb diameter), and perhaps also phosphorus, as may be concluded from the high rate of its redistribution (see later). In Fig. 3 the proportional distribution of dry matter in plants during the sixth growing season in the experimental population on the north-facing slope is plotted as a function of time. Maximum development of leaves was reached 3 months after emergence from the bulb, whereas maximum reproductive allocation was found just
before the disappearance of all above-ground parts. At the end of the season the greater increase of the root biomass compared with that of the bulbs is characteristic for *Allium ursinum* (Kojic 1966). Biomass of roots, however, decreased again during autumn and winter, because some of the roots, but not the bulbs, were decaying. The reproductive allocation, estimated as the ratio of dry weight of all reproductive organs to the total above-ground dry weight, varied from 0.47 to 0.70, the highest value being for the more mature plants. The seed-reproductive allocation, estimated as the ratio of seed dry weight to total above-ground biomass, varied from 0.19 to 0.58, including plants from outside the experimental plots.

The standing crop of *Allium ursinum* growing in a pure stand is dependent on the distribution of age-classes within the population, on the density of the population, and on its abiotic environment. The greatest biomass is contributed by individuals which are 5 years old or more; these plants have at least two leaves, with a large leaf area, and mostly one inflorescence (Table 4). The standing crop in the five stands studied varied from 23.5 to 560.0 g m⁻² in the middle of May, when the individuals were flowering and had their greatest leaf development.

During the life cycle, total biomass of individuals increased from 5.4 mg as seed to 7600 mg dry weight in mature plants after 6 years. In juvenile plants there is only a slight increase in the biomass of the bulb each year, compared with the relatively large increase in leaf biomass. Three-year-old plants have nearly 50% of the biomass in leaves, and
Population biology of Allium ursinum

FIG. 3. Percentage distribution of dry matter in the different plant organs of Allium ursinum in the sixth year, over the period from 5 March to 13 August 1977, in an even-aged experimental population on a north-facing slope in an Asperulo-Fagetum. At each sampling twenty individuals were measured.

only in plants which have reached the reproductive phase is the growth of bulb and roots more stimulated than that of the leaves.

In Allium ursinum the roots of the seedlings are restricted to the L and A₁ horizons of the soil, where the amounts of available macronutrients such as potassium, phosphorus and nitrate-nitrogen are high, due to bioaccumulation by leaf litter and a high mineralization rate (Ernst 1978). In plants of reproductive age (5–8 years) the roots are concentrated in the less fertile A₂ horizon; these nutritional consequences of bulb movement, however, seem to be without any effect on the plant itself. The leaves of mature individuals contain more nitrogen than those of juveniles, and the nitrogen concentration of roots and bulbs

TABLE 4. The standing crop (g m⁻²) in selected stands of Allium ursinum in an Asperulo-Fagetum in relation to the age-composition of the population (percentage of total individuals in each age-class); harvesting was carried out in the middle of May, when the standing crop was at a maximum

<table>
<thead>
<tr>
<th>Stand</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age of individuals</td>
<td>1–2 years</td>
<td>3363</td>
<td>2800</td>
<td>2378</td>
<td>720</td>
</tr>
<tr>
<td>Number of individuals per m²</td>
<td>23.5</td>
<td>55.8</td>
<td>105</td>
<td>270</td>
<td>560</td>
</tr>
</tbody>
</table>
Table 5. Mean nitrogen concentration (% dry weight, with standard error) of different plant organs of *Allium ursinum* during the life cycle, for a population growing in an *Asperulo-Fagetum*; all values, except for the seeds, are given for the time of flowering of mature individuals; three replicates were analysed per age-class and organ.

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seed</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.26 ± 0.02</td>
<td>3.49 ± 0.09</td>
<td>3.30 ± 0.17</td>
</tr>
<tr>
<td>Flowers</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.59 ± 0.11</td>
<td>2.83 ± 0.19</td>
<td>2.71 ± 0.13</td>
</tr>
<tr>
<td>Inflorescence stalk</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.83 ± 0.07</td>
<td>0.79 ± 0.09</td>
<td>0.79 ± 0.14</td>
</tr>
<tr>
<td>Leaves</td>
<td>5.02 ± 0.10</td>
<td>5.45 ± 0.08</td>
<td>5.49 ± 0.29</td>
<td>5.60 ± 0.11</td>
<td>6.51 ± 0.17</td>
<td>6.40 ± 0.03</td>
<td>6.37 ± 0.17</td>
</tr>
<tr>
<td>Bulbs</td>
<td>2.83 ± 0.49</td>
<td>1.78 ± 0.32</td>
<td>1.88 ± 0.46</td>
<td>2.25 ± 0.05</td>
<td>2.15 ± 0.15</td>
<td>2.13 ± 0.23</td>
<td>2.10 ± 0.13</td>
</tr>
<tr>
<td>Roots</td>
<td>1.51 ± 0.17</td>
<td>1.58 ± 0.08</td>
<td>1.67 ± 0.10</td>
<td>1.59 ± 0.11</td>
<td>1.67 ± 0.23</td>
<td>1.93 ± 0.18</td>
<td>1.71 ± 0.22</td>
</tr>
</tbody>
</table>
does not vary significantly throughout the life cycle (Table 5). The annual loss of mineral elements in flowers, seeds and leaves is within the range reported from other plants, the precise value depending on the particular mineral element and species concerned. In Allium ursinum the amounts of calcium, magnesium, zinc, phosphorus and nitrogen returned each year by the above-ground biomass are 89, 86, 79, 76, and 72%, respectively of the total amount in the plant. Up to 50% of the iron, sodium, potassium and manganese is lost, so that a relatively high turnover of these elements also is realized by Allium ursinum.

Nevertheless, in all plants there is some redistribution of mineral elements from the leaves to other parts of the plant (Fig. 4). Before flowering the phosphate content of the leaves decreases by 60%, whereas the nitrate content is not lowered until the development of the seeds in early June, when there is a reduction of 67%. In contrast to sodium, potassium, manganese and chloride, which show no significant redistribution or accumulation, the concentration of calcium in the leaves increases nearly four times (382%) between first emergence and senescence.

![Graph showing mineral concentrations](image)

**Fig. 4.** Variation of mineral-nutrient concentrations of leaves of Allium ursinum during the growing season from March to June. Each point is the mean of three subsamples from three stands in an Asperulo-Fagetum.

**Allelochemical effects**

The addition of fresh-cut leaves of Allium ursinum to each of three pure stands of Mercurialis perennis and Glechoma hederacea had no effect on biomass production of the treated plants compared with those on control plots. The standing crop of the treated plots of Mercurialis perennis was 263.7 ± 47.2 g m⁻² against 275.3 ± 36.5 g m⁻² on the control plots, whereas Glechoma hederacea produced 131.7 ± 23.2 g m⁻² on the treated plots and 120.9 ± 25.7 g m⁻² on the control plots.
Population structure and dynamics

Mean density within the four populations studied varied from 320 plants per m² to 3350 plants per m². As seen from Table 6, population IV of the Stellario-Carpinetum had a high percentage (43.1) of reproductive individuals in 1977, whereas in all the other stands young plants (first to third year) dominated, and flowering individuals comprised 16.8% or less of the total population. However, this population structure varied widely from year to year, as demonstrated by the plant densities in the permanent plot (Fig. 5). In these populations, which were monitored from 1971 to 1977, the percentage of flowering individuals was almost independent of climatic conditions. The population on the south-facing slope increased within 3 years by a factor of three, after a flower and seed explosion between 1971 and 1973. The other two populations in the Asperulo-Fagetum decreased over the same period, and the increase in numbers of flowering individuals was delayed until 1976 and 1977 respectively. The population dynamics of Allium ursinum in the Stellario-Carpinetum was different, perhaps because in this area the annual flooding in spring/summer removed most of the seeds and young seedlings, so that an increase in reproduction was not reflected in the number of individuals.

TABLE 6. Age-structure and flowering behaviour of four populations of Allium ursinum in 1977, based on measurements of bulb diameter, leaf area, number of leaves and flowering behaviour; population I was on a south-facing slope, population II on a plateau, and population III on a north-facing slope of an Asperulo-Fagetum, population IV was on a plateau in a wet Stellario-Carpinetum, and population V was on a plateau in a Fagetum near Göttingen (the last according to Schmucker & Drude (1934))

<table>
<thead>
<tr>
<th>Population</th>
<th>Individuals per m²</th>
<th>Individuals per age class (year)</th>
<th>% of flowering plants in the population</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>3351</td>
<td>864 2030 355 59 43</td>
<td>3.0</td>
</tr>
<tr>
<td>II</td>
<td>576</td>
<td>80 416 33 15 32</td>
<td>8.2</td>
</tr>
<tr>
<td>III</td>
<td>709</td>
<td>105 363 122 47 72</td>
<td>16.8</td>
</tr>
<tr>
<td>IV</td>
<td>320</td>
<td>45 120 17 14 124</td>
<td>43.1</td>
</tr>
<tr>
<td>V</td>
<td>2297</td>
<td>1903 331 63</td>
<td>2.7</td>
</tr>
</tbody>
</table>

Population development

Each flower of Allium ursinum contains three ovules; the number of flowers per inflorescence varies from three to twenty-nine, with a mean of 13.7 ± 5.4 (based on more than 500 inflorescences). In years without late snow or frost all flowers expand fully and are pollinated. The curve of mortality/age ($q_x$) shown in Fig. 6 is constructed from three experimental subpopulations, with 3720, 4860 and 12 170 embryos respectively in 1970. The mortality rate is given by

$$q_x = \frac{L_x - L_{x+1}}{L_x},$$

where $L_x$ is the number of individuals at age $x$ and $L_{x+1}$ is the number of these individuals surviving to age $x + 1$. Figure 6 shows a mortality pattern with three peaks. The first peak is the mortality of ovules and embryos, which is very high (45.9 ± 20.4%), being followed by a further increase of mortality during the dormancy and stratification of the seeds—72.3 ± 5.6% of the seeds produced died during summer, autumn and winter.
through autolysis, the seed coat remaining undisturbed. This mortality is independent of density, and occurred also in the germination experiments in the laboratory (where the embryos of the non-germinated seeds were found to be dead—Table 1). A low rate of mortality is found during the 2 years of the seedling stage (21.2 ± 11.2%), but the rate of mortality increases again during the phase of bulb movement, mainly as a result of attacks of nematodes, so that only 0.7–10.6% of the seedlings reach the reproductive stage. The final increase in mortality is due to ageing.

**DISCUSSION**

As for other species of the herb layer in deciduous woodlands (Kojic 1966; Morgan 1971; Wigham 1974), the main growth and reproduction of *Allium ursinum* occur during the very short period between the onset of favourable growing conditions in early spring and the closure of the overhead canopy. In contrast to most plant species of the herb layer, however (Mukerji 1936; Knight 1964; Morgan 1971; Wigham 1974; Persson 1975; Hutchings & Barkham 1976), sexual reproduction is much more important than vegetative reproduction to the success of *Allium* populations. Nevertheless, the mortality risk of the seed population of *Allium ursinum* is as high as for the vegetative propagules of *Mercurialis perennis* (Hutchings & Barkham 1976). Even under apparently ideal conditions, less than 50% of the available ovules develop into seeds—the same percentage as in *Hyacinthoides non-scripta* (L.) P.Chd. (Knight 1964) and in *Baccharis halimifolia* L. grown in the shade (Westman, Panetta & Stanley 1975). Nevertheless, the mean number of seeds may reach 10 000 per m², as already recorded for a population in Göttingen.
Forest by Schmucker & Drude (1934). Most workers have suggested a high germination rate (Schmucker & Drude 1934; Ellenberg 1963). In the sampled stands, however, there was a very high seed mortality between the time of shedding (June/July) and the time of germination (January/April), due to autolysis; this is in contrast to the situation in most perennial herbaceous plants, where the high mortality rate for any year's seed crop is normally attributable to predation and competition (Rabotnov 1969). As in other vernal herbs—e.g. Eranthis hiemalis (L.) Salisb. (Frost-Christensen 1974) and Hyacinthoides non-scripta (Thompson & Cox 1978)—germination occurred in response to a high temperature (20 °C) followed by a low (5–10 °C) temperature.

The further development of the Allium population through time illustrates the exceptional situation in which, within monospecific stands, the dominance hierarchy does not lead to a removal of the smallest individuals (first- and second-year group), in contrast to other natural monocultures of perennial but rhizomatous species such as Chamaenerion angustifolium (L.) Scop. (van Andel & Rozema 1974) and Mercurialis perennis (Mukerji 1936). According to Yoda et al. (1963), White & Harper (1970) and Harper 1977 (p. 183), the power equation $w = Kd^{-1.5}$, where $w =$ mean weight per plant, $d =$ plant density and $K =$ a constant, should apply generally to even-aged populations with self-thinning. If the relation between the mean weight of Allium plants and their density in the experimental plots with even-aged individuals is examined, however, the gradient which the population follows as it proceeds from the seedling stage to reproductive adults is $-3.2$; a slightly different gradient of $-2.9$ was found in stands of Allium ursinum that were not even-aged. Both values far exceed the $-1.5$ predicted by the power equation.
In all cases when redistribution of matter between parts of the plant occurs at different times of the year, the power equation will not allow for the development of perennating organs which are reformed each year. The present results for *Allium ursinum*, as well as those for shoots of *Mercurialis perennis* (Hutchings & Barkham 1976), roots and stolons of *Chamaenerion angustifolium* (van Andel 1975) and tillers of *Lolium perenne* L. (Kays & Harper 1974), all point to the inapplicability of the $-1.5$ power equation to herbaceous perennials.

At present, the ecological basis of the maintenance of pure stands of *Allium* within stable communities is uncertain. With respect to the four consistent features of 'competitive' species (Grime 1973), only the tendency to deposit a dense layer of (heavy) litter (up to 1 cm in depth) is shown by *Allium ursinum*, so that its competitive index is 5-0; this means a medium competitive ability, so that a high species-diversity (more than twenty species per m$^2$) in *Allium* stands should be expected instead of monoculture. Even if we look to the modification of Grime's hypothesis by Newman (1973), that 'when competition for light is intense species-diversity tends to be low', *Allium ursinum* still appears later, disappears earlier and is smaller than other species in deciduous woodlands.

Hutchings & Barkham (1976) suggested that persistence of rhizomatous perennials in pure stands (e.g. *Mercurialis perennis*) is the result of such a thorough and efficient exploitation of the habitat resources that entry of competitors is prevented. However, the development of clones of *Chamaenerion angustifolium* in clearings (van Andel 1975), and its subsequent disappearance in developing woodlands by invasion of tree seedlings, does not conform to this suggestion. Moreover, *Allium ursinum* is not a rhizomatous perennial, yet still manages to establish stable monocultures.

A further ecological factor, the production of allelochemicals—isothiocyanates or organic disulphides in *Allium ursinum* (Kjaer 1958)—has been shown to have a strong effect only on tomatoes grown in sand (Lange & Kanzow 1965). Decaying leaves of *Allium ursinum* were without any effect on the natural vegetation of the beechwoods studied (stands of *Mercurialis perennis* and *Glechoma hederacea*). This finding is in accord with the negligible growth reduction of tomatoes in a 'standard' soil with extracts of *Allium* leaves. The persistence of pure stands of *Allium ursinum* may be due, therefore, mainly to other factors, for example, the reproductive strategy in the light of the concept of $r$- and $K$-selection (Moore 1976). According to Gadgil & Solbrig (1972), the ratio of reproductive to vegetative biomass should be greater in an environment which imposes a high degree of density-independent mortality. This would imply that plants in open habitats should have higher $r$-values than those in less open habitats (Abrahamson & Gadgil 1973; Gaines *et al.* 1974; Harper 1977). A comparison of the reproductive strategy of *Allium ursinum* with that of other woodland herbs—e.g. *Mercurialis perennis, Hyacinthoides non-scripta, Narcissus pseudonarcissus* L. (Mukerji 1936; Knight 1964; Kojic 1966; Hutchings & Barkham 1976), *Anemone nemorosa* L. and *Polygonatum multiflorum* (L.) All.—shows that *Allium* exceeds all other species of the herb layer in its seed production and establishment of seedlings. The vegetative reproduction, however, is low. This is in contrast to other bulb-geophytes, e.g. *Narcissus pseudonarcissus*, where the establishment by daughter bulbs is high in comparison to that of seedlings (J. P. Barkham, personal communication). In addition, *Allium ursinum* has extremely limited centrifugal dispersal of seeds—approximately 22.4 cm per annum; the *Allium* stands in the Göttingen Forest have remained nearly constant in their extent over a period of 25 years (Schmucker & Drude 1934; Winterhoff 1963). *Allium ursinum* might be characterized as an $r$-strategist among $K$-strategists in a so-called stable environment. Furthermore,
its longevity of 8 years (this paper) or c. 10 years (Rimbach 1897) is low in comparison to that of Polygonatum multiflorum (c. 35 years) and Anemone nemorosa (25-30 years), even if the geographical situation may strongly influence the age of a plant (Persson 1975). A further possible factor promoting monospecific stands is the mechanical suppression of young seedlings of other plant species during the phase of senescence of leaves of Allium ursinum.

In this manner Allium ursinum may reduce the diversity of the herbaceous layer in deciduous woodlands; however, it also improves the nutrient budget of these ecosystems during the spring. Greatest losses of nutrients in deciduous forest ecosystems occur during spring, when run-off is high and the influence of summer-green plants on water balance and nutrient uptake is low (Likens et al. 1970). During this period nitrate concentrations in soils and streams are higher than in summer (Muller & Bormann 1976; Ernst 1978). Allium ursinum, with its well-developed rooting system during winter and spring, is very efficient in nitrate accumulation, especially when adults are growing in the lower and less fertile soil horizons. The enormous nitrate pool in the leaves (Ernst 1978) is immediately made available to summer-green plants when leaves of Allium decay, without any action by nitrifying bacteria being involved.

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REFERENCES

Population biology of Allium ursinum


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