Plant Ecology and Evolution 144 (3): 321–326, 2011
doi:10.5091/plecevo.2011.638

REGULAR PAPER

Germination ecology of *Sison amomum* (Apiaceae) at the northern edge of its distribution range on the European mainland

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Background and aims – *Sison amomum* reaches the north-western limit of its distribution on the European mainland as a rare species in a very small area in western Belgium. For conservation management it is important to know different aspects of life history such as seed longevity, phenology of germination and survival of seedlings.
Methods – Germination requirements in field and laboratory conditions were analyzed in detail. Survival of seedlings in winter conditions was recorded.
Key results – Most seeds germinated soon after dispersal in autumn. Eighty percent of the autumn seedlings survived winter conditions and grew up to flowering plants in the 2nd and 3rd calendar year. Buried seeds survived till next spring, but later on very few seeds were able to germinate after exhumation, thus no persistent seed bank was formed. In fresh seeds, the underdeveloped embryo (embryo to seed ratio = c. 0.35) immediately started to grow in light conditions at low temperatures (5, 10°C and alternating 20/10°C); when the critical E:S ratio of 0.82 was reached after two to four weeks, the radicle protruded. In darkness and at 20 or 23°C growth of the embryo was very slow and very few seeds germinated.
Conclusions – The small seeds of *S. amomum* are morphologically dormant, and germinate very soon in light at lower temperatures. No persistent seed bank is formed. Based on life history characteristics revealed in this study, we propose a mowing of the grasslands in late autumn to protect this threatened plant. Well timed mowing reduces the biomass and decreases the competition, while still allowing seed set and dispersal of *S. amomum*.

Key words – biennial, conservation, embryo growth, germination, seed dormancy, *Sison amomum*, winter annual.

INTRODUCTION

The winter-annual or biennial herb *Sison amomum* L. is distributed in Southern and Western Europe, Asia Minor and North Africa (Hegi 1926). In the British Isles it is found up to 53°30'N (Tutin et al. 1968). On the European mainland the north-western limit of its distribution is reached in Belgium, where it is growing in a small area in the vicinity of Poperinge (50°51'N 2°44'E). This area is part of a region on the French-Belgian border of c. 1200 km^2, between the rivers Aa and IJzer, where *S. amomum* is rather frequent and quite isolated from southern populations. Further southwards *S. amomum* is only rather frequent in Normandy, at a distance of more than 200 km from the northern populations in Belgium, and it is very rare between both regions (Delvosalle et al. 2009).

Van de Vijvere (1957) first described the presence of *S. amomum* in Belgium and Zwaenepoel & Vanhecke (1995) more recently reinvestigated its distribution. *Sison amomum* was only found in *Arrhenateretum* grasslands along roadsides. In 1995, the number of locations was reduced to a few dozen, thus *S. amomum* may be regarded as a threatened species in Belgium (Cosijns et al. 1994, Van Landuyt et al. 2006). Additionally, peripheral populations are important targets for conservation. These peripheral populations often differ genetically and morphologically from more central populations (Lesica & Allendorf 1995). Maintaining the genetic variability present throughout the range of a species is essential, especially when considering future conditions with climate change (Hampe & Petit 2005). In the planning of conservation management for protection of threatened plants, it is important to know different aspects of life history, such as seed longevity, phenology of germination and temperature requirements and survival of seedlings.

Apiaceae generally have seeds with an underdeveloped embryo and show morphophysiological dormancy (Martin 1946, Baskin & Baskin 1998). In most species the embryo grows at lower temperature in autumn and winter and seedlings emerge in spring. However, within the Apiaceae much variation in germination ecology exists and investigation of individual species is necessary. As far as we know, only one study has been performed with *S. amomum* seeds: Roberts (1979) showed that in England most seeds germinated in the autumn of sowing and the following spring, but some seeds persisted until the second year and a few for longer periods.

In order to know different aspects of life history of the threatened *S. amomum*, we performed a detailed study of its germination phenology in natural conditions, temperature requirements for germination, survival of buried seeds, a possible seasonal cycle of dormancy and survival of seedlings. Possible practical management advices for protection of this rare plant are discussed.

MATERIALS AND METHODS

Seeds (mericarps) of *S. amomum* were collected in September 2006 in Watou, Poperinge (50°51'N 2°37'E) and sown in the botanical garden in Leuven. Mature fruits for the experiments were harvested in September 2008 and 2009 and most experiments were started with fresh seeds within two weeks after harvest. Some fruits were stored dry at room temperature (c. 20°C) for different periods as mentioned in the Results.

Dimensions and mass of 100 mericarps were determined. To estimate the standard error, this sample was visually divided into ten size classes, and the total weight of each group of ten seeds was determined. The dimensions of the mericarps were determined individually and averaged for the ten size classes.

Phenology of germination

Seeds were sown outdoors on 1 Oct. 2008 in three plastic pots (diameter 20 cm) filled with sandy loam and dug in to the normal soil level in an open unshaded place. In each pot, 200 seeds were spread over the surface. The pots were covered with a net to prevent bird disturbance and a molluscicide was applied. Emerged seedlings were counted and removed on the dates mentioned in the Results section.

Survival of seedlings during winter

Since most seeds germinated in autumn, within 6–8 weeks after sowing, we investigated whether seedlings survived the winter. On three small plots (50 × 50 cm) in a garden near Leuven, 200 seeds were sown on 1 Oct. 2009. Seedlings were counted on 1 Dec. 2009 and marked with a toothpick. The surviving seedlings were counted on 1 Apr. 2010. Daily maximum and minimum temperatures at a depth of 2 cm in the soil were recorded.

Germination experiments

In standard germination tests, 100 seeds were placed in Petri dishes (diameter 9 cm) on filter paper (MN400) moistened with distilled water. All tests were performed in triplicate. The seeds were incubated at different temperature regimes and different light conditions. We imposed constant temperatures of 5, 10 and 20°C and daily alternating temperatures of 12 h at 20°C and 12 h at 10°C. Half of the Petri dishes were kept in total darkness (in wooden boxes) and half of the Petri dishes at a 12 h photoperiod. Light was provided by fluorescent tubes (Philips TLD80) with a photon irradiance of 36 µmol $m^{-2}s^{-1}$ (400–700 nm). Germinated seeds were counted after four weeks or at different times, mentioned in the Results section. Fresh seeds were used within two weeks after harvest. Other seeds were stored dry for three or twelve months at room temperature (c. 20°C) or pretreated in wet conditions in darkness at 5 and 20°C for three months.

Table 1 – **Percentage emergence of *Sison amomum* seeds sown on 14 Oct. 2008 in field conditions.**
Mean ± SE; n = 3.

Date of observation	Emerged seedlings
15 Nov. 2008	46.6 ± 3.5
1 Dec. 2008	15.3 ± 2.0
1 Apr. 2009	6.5 ± 0.7
1 Jun. 2009	1.3 ± 0.4
1 Sep. 2009	0.2 ± 0.2
1 Dec. 2009	2.5 ± 0.5
Total percentage emerged	72.5 ± 4.7

Embryo growth

Embryo growth was studied in fresh seeds incubated at 5, 10, 23°C and alternating 20/10°C in light and in darkness (see above) during ten weeks. Every week twenty seeds were selected and cut in half under a dissecting microscope. Lengths of the embryo and the seed were measured with an ocular micrometer and the E:S ratio was calculated. The critical E:S ratio, i.e. the E:S ratio at the moment of germination, was determined as the average E:S ratio of twenty seeds with a split seed coat, but no radicle protrusion. Since we wanted to measure the embryo growth inside the seed and not the radicle growth after germination, this critical E:S ratio was applied to seeds that had germinated during the ten weeks of incubation.

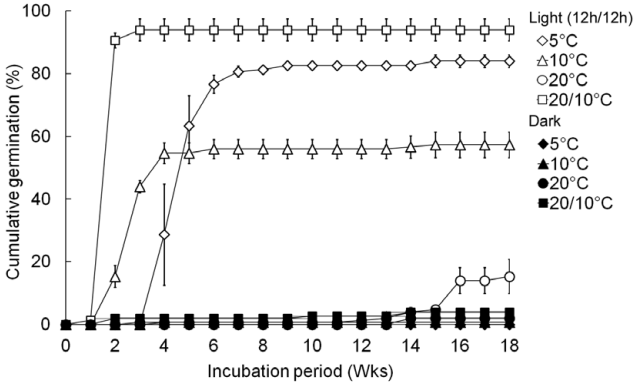

Figure 1 – Cumulative germination percentage of *Sison amomum* seeds incubated at 5°C, 10°C, 20°C or at 20/10°C (12 h/12 h) in a 12 h photoperiod or in darkness. Error bars ± SE; n = 3.

Table 2 – **Percentage germination during 4 weeks in different conditions for fresh seeds and seeds after different pretreatments**. RT: room temperature; - not tested. Means (± SE) followed by different letters within the incubation condition (capital letters) or within pretreatment (lower case letters) are significantly different ($P < 0.05$), Tukey's multiple comparisons test ($n = 3$).

Incubation condition		Pretreatment				
Temperature (°C)	Light	Fresh	3 months moist at 5°C	3 months moist at 20°C	3 months dry at RT	12 months dry at RT
5	Light	28.7 ± 16.2 Aab	-	40.4 ± 13.6 Ab	-	91.3 ± 3.7 Bb
	Dark	0 Aa	-	-	-	4.3 ± 1.4 Aa
10	Light	54.7 ± 3.3 Ab	71.7 ± 4.4 Bc	89.9 ± 3.1 Cc	92.5 ± 1.4 Cc	82.7 ± 2.2 BCb
	Dark	0.7 ± 0.7 Aa	6.0 ± 0.7 Ba	0.7 ± 0.7 Aa	27.4 ± 1.7 Ca	0.3 ± 0.3 Aa
20	Light	0.7 ± 0.7 Aa	1.4 ± 0.7 Aa	96.5 ± 0.5 Bc	90.8 ± 3.3 Bc	86.0 ± 4.2 Bb
	Dark	0 Aa	0 Aa	-	28.5 ± 6.1 Ba	4.0 ± 1.5 Aa
20/10 (12/12h)	Light	94.0 ± 3.5 Ac	84.1 ± 2.9 Ac	91.8 ± 1.4 Ac	91.0 ± 0.6 Ac	92.7 ± 0.7 Ab
	Dark	2.0 ± 1.2 Aa	27.2 ± 37.7 Bb	97.8 ± 2.2 Dc	72.3 ± 2.6 Cb	7.3 ± 4.1 Aa

Burial experiments

Each of 180 nylon bags were filled with 100 seeds mixed with sand. On 14 Oct. 2008 the nylon bags were buried at a depth of 7 cm in pots filled with soil. These pots were buried at soil level at an open sunny place. Each pot contained four bags. Starting on 15 Nov. 2008, two pots were exhumed every two or three months and the content of each bag was spread on moistened filter paper in Petri dishes. This manipulation was carried out in a dark room under green safe light. Germination was tested in four different conditions: at 23°C and at alternating temperatures of 20/10°C in a 12 h photoperiod and in continuous darkness (see above) during four weeks.

Statistical analyses

A two-way ANOVA was performed to test for significant effects of temperature and light condition during incubation on final germination percentage and on final embryo size of fresh *S. amomum* seeds. To test whether final germination percentages were significantly different in separate excavation events in the burial experiment, we analyzed the data using a one-way ANOVA followed by Tukey's multiple comparisons test within each incubation condition. Similarly we tested for significant effects of incubation condition within pretreatment and of pretreatment within incubation condition on final germination percentage. All germination data were arcsine transformed prior to analysis.

RESULTS

The length and width of *S. amomum* seeds was 2.1 ± 0.01 mm (mean ± SE) and 1.2 ± 0.01 mm, respectively. Mean mass of the mericarps was 1.2 ± 0.01 mg.

Phenology of germination

More than half of the seeds germinated within 1.5 months after sowing in autumn (table 1). No seedlings appeared during winter and 6.5 ± 0.7% germinated in early spring. Very few seeds germinated in the next months. In total 72.5 ± 4.7% of the seeds sown had germinated after one year.

Survival during winter

In the three garden plots, only 19.0 ± 5.8% had germinated on 1 Dec. 2009. Of these seedlings 80.5 ± 4.2% survived the winter of 2009–2010. Mean soil temperatures at a depth of 2 cm were 3.5°C in December 2009, 0.7°C in January and 2.8°C in February 2010. Afterwards 50.0 ± 13.6% of the surviving seedlings developed into plants that started to flower on 20 Jul. 2010. The remaining plants had only rosette leaves and would probably flower in 2011.

Germination at different temperatures

Germination of fresh seeds at different temperature regimes and light conditions was followed during eighteen weeks (fig. 1). In a light photoperiod nearly all seeds germinated within two weeks at alternating temperatures 20/10°C and germination was slower at constant temperatures of 10 and 5°C. At the end of the experiment few seeds had germinated at 20°C and in darkness at all temperature conditions.

In a second experiment, seeds were pretreated during three months at 5°C and at 20°C in moist conditions or stored dry at room temperature (c. 20°C) for three months or one year (table 2). Final germination percentages were significantly affected ($P < 0.05$) by pretreatments in all conditions, except for seeds incubated at 5°C in darkness and seeds incubated at 20/10°C in light. After dry storage nearly all seeds germinated even at 10 and 20°C in light conditions. Even in dark conditions 27 and 28% germinated at respectively 10 and 20°C, and 72% at alternating temperatures of 20/10°C. After three months of moist incubation at 20°C, germination was enhanced at 10 and 20°C in light conditions and germination was nearly complete in dark conditions at 20/10°C. Pretreatment at 5°C had small effects on germination, but enabled some germination in darkness at 20/10°C.

Table 3 – Germination percentage of exhumed seeds after 1 to 26 months of burial.
Germination was tested at 20/10 and 23°C in light and in darkness. Percentage was based on the initial number of buried seeds. Values (mean ± SE) followed by different letters within temperature and light condition are significantly different (P < 0.05), Tukey's multiple comparisons test (n = 2).

Month of exhumation	20/10°C		23°C	
	light	dark	light	dark
November 2008	83.0 ± 4.0 c	3.0 ± 0.5 ab	0.5 ± 0.5 a	0.5 ± 0.5 a
January 2009	73.0 ± 12.0 c	32.5 ± 13.5 b	20.0 ± 15.0 b	9.0 ± 7.0 b
March 2009	17.5 ± 6.5 ab	5.5 ± 0.5 ab	6.5 ± 0.5 ab	8.5 ± 0.5 b
May 2009	2.5 ± 2.5 a	0.0 a	0.0 a	0.0 a
August 2009	32.0 ± 8.0 b	13.5 ± 13.5 ab	2.5 ± 2.5 ab	0.0 a
November 2009	0.0 a	0.0 a	0.0 a	0.0 a
January 2010	0.0 a	0.0 a	0.0 a	0.0 a
March 2010	0.0 a	0.0 a	0.0 a	0.0 a
May 2010	1.5 ± 1.5 a	0.0 a	0.0 a	0.0 a
August 2010	0.0 a	0.0 a	0.0 a	0.0 a
November 2010	0.0 a	0.0 a	0.0 a	0.0 a

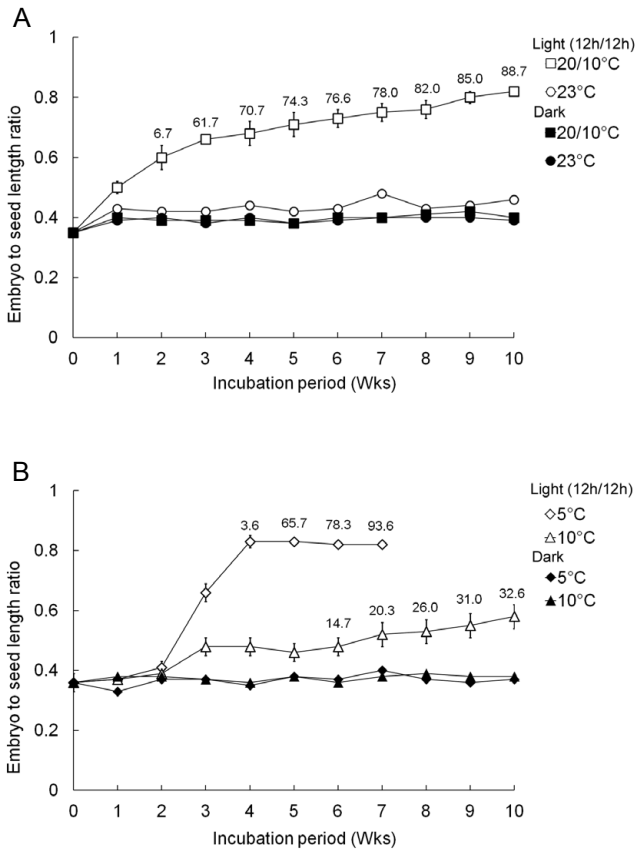

Figure 2 – Growth of the embryo expressed as embryo to seed length ratio during ten week incubation at: A, 20/10°C (12h/12h), 23°C; B, 10°C and 5°C in a 12 h photoperiod or in darkness. Numbers next to symbols represent germination percentages. Error bars ± SE.; n = 20.

Growth of embryo in controlled conditions

The initial mean E:S ratio in fresh seeds was about 0.35 (fig. 2). Embryo growth was significantly affected (P < 0.001) by light and temperature conditions and a significant interaction effect ($F_{1,3}$ = 43.87; P < 0.001) was observed for these two factors. Embryos started to grow immediately during incubation in light at alternating temperatures of 20/10°C; some attained the critical E:S ratio of 0.82 ± 0.01 after three weeks, resulting in high germination percentages. In light at 5°C embryo growth was slower but present in nearly all seeds and this resulted in nearly complete germination after 6–7 weeks. At 10°C in light the mean embryo length increased, but germination was not completed after ten weeks. At 23°C embryos grew very little and no germination occurred in ten weeks. Also in dark conditions at all temperatures regimes, embryo growth was absent or very slow and no germination was observed.

Burial experiment

Seeds exhumed from the soil germinated to the highest percentage at 20/10°C in light after one to four months of burial (table 3). This indicates that most buried seeds survive autumn and winter. In the bags exhumed in March after the first winter a dozen of germinating seeds were observed and discarded. During burial some seeds were able to germinate in dark conditions in the soils in early spring after the first winter. After three months of burial some seeds were able to germinate at 23°C in light and darkness and in darkness in alternating temperatures. Longevity of seeds in soil was limited, since after one year practically no seed germinated in all conditions, with the exception of a very few survivals in May of the second year.

DISCUSSION

More than half of the seeds of *S. amomum* germinate shortly after dispersal in autumn and an important fraction of the remaining seeds germinate in the following spring. Only a few other examples of Apiaceae are known where the seeds are capable of immediate germination (e.g. Lhotská 1978, Baskin & Baskin 1990a, Cochrane & Probert 2006). Most Apiaceae growing in temperate climates require stratification at lower temperature and germinate in spring (Grime et al. 1981, Baskin & Baskin 1998, Vandelook 2009).

Germination in autumn exposes seedlings to cold winter temperatures. The sensitivity of *S. amomum* seedlings to frost might be the reason for its absence in continental regions of Europe (Hegi 1926, Delvosalle et al. 2009). We have measured the survival of seedlings in only one winter period and found c. 80% survival. In the rather cold winter of 2009–2010, the mean temperature of 1.8°C was lower than normal in Belgium (3.5°C) (KMI: Royal Metereological Institute). During the cold periods the seedlings were covered by snow. We do not know how harmful freezing periods are without a snow cover.

In controlled conditions, embryos started to grow immediately in light at all temperatures, except at constant 23°C and they needed some time to grow to full size, *c*. two weeks at 20/10°C and c. four weeks at 5°C. Following this period of growth the radicle emerged through the fruit coat. Therefore, like all Apiaceae studied so far, seeds of *S. amomum* have an underdeveloped embryo at dispersal and seeds are classified as morphologically dormant (Baskin & Baskin 2004). Besides morphological dormancy, most species of Apiaceae require a supplementary treatment to break a physiological component of dormancy. This pretreatment may be a period of relatively high temperature or a long stratification at lower temperatures. While germination percentages generally increased after moist and dry storage, dormancy of *S. amomum* is certainly not deep, since more than half of the seeds germinated in field experiments within six weeks after sowing and embryos started to grow immediately in some controlled conditions.

Seeds of *S. amomum* are relatively small compared to other Apiaceae. A study of 460 Apiaceae growing in different habitats and climatic regions revealed a mean mass of 5.47 ± 0.37 mg (mean ± SE) for these seeds and a mean length of 3.85 ± 0.10 mm (F. Vandelook, unpubl. results). The light requirement of *S. amomum* seeds might be related to their small dimensions, since it is known that smaller seeds in general require light for germination (Milberg et al. 2000, Jankowska-Blaszczuk & Daws 2007). Germination of *S. amomum* is nearly complete in light conditions at 20/10°C and 5°C, while germination in darkness is very low and in nearly all conditions lower than in light. Seed germination of most Apiaceae is indifferent to light, only a few species are known in which embryo growth and therefore also germination are stimulated by light (e.g. Baskin & Baskin 1990b, Pons 1991, Vandelook et al. 2008). Although seeds of *S. amomum* are relatively small and responsive to light for germination, they do not form a persistent seed bank. Very few seeds germinated from the bags exhumed after a burial period of more than eleven months. Roberts (1979), however, found a few seeds surviving for up to five years.

While 62% of seeds spread on the soil surface germinated in autumn, buried seeds did not germinate *in situ* in this season, presumably because of the absence of light. Nearly all buried seeds survived during autumn and winter since high germination percentages were observed in exhumed seeds at 20/10°C in light. In the bags exhumed in March (after five months burial), about 10% of the seeds had germinated in the soil. This germination in the soil does show that germination in darkness is possible after some months of burial. Seeds exhumed after three months of burial germinated up to 30% in darkness at 20/10°C.

Germination of fresh seeds was optimal at alternating temperatures of 20/10°C and was also high at lower temperatures of 5 and 10°C, indicating that germination is possible in field conditions in autumn. Optimal germination at lower temperature is a characteristic of Mediterranean plants (Thanos et al. 1989). It is remarkable that the Mediterranean *S. amomum* conserves this property in its northern populations. Very few fresh seeds germinated at 20°C and in darkness in all conditions. After dry storage germination occurred in a wider temperature range up to 20 and 23°C, and even in darkness germination was possible. For unknown reasons the germination percentage in darkness was high after three months storage and low after one year storage (table 2). The increase in range of conditions over which the cold-stratified and the dry-stored (three months) seeds could germinate to high percentages indicates the presence of nondeep physiological dormancy (and thus some morphophysiological dormancy) in at least some of the seeds.

Based on the knowledge of life history, some management advices may be proposed to protect the threatened *S. amomum* in Belgium. As already suggested by Zwaenepoel & Vanhecke (1995), late mowing (second half of October to November) and removal of the mowing litter may be the best management practice of *Arrhenateretum* grasslands with *S. amomum*. In this season *S. amomum* has produced ripe fruits that easily separate from the mother plant. Mowing in the autumn may create some gaps in the vegetation where the seedlings can develop in the same season. Mowing and removal of the mowing litter in general reduce the amount of biomass and decrease the competition for *S. amomum*. It is important to protect the existing populations of *S. amomum*, since there is very little chance that *S. amomum* reappears from the seed bank after local extinction.

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Manuscript received 19 Jan. 2011; accepted in revised version 14 Jun. 2011.

Communicating Editor: Renate Wesselingh.