Amer. J. Bot. 71(5): 687–692. 1984.

GERMINATION ECOPHYSIOLOGY OF THE WOODLAND HERB OSMORHIZA LONGISTYLIS (UMBELLIFERAE)[1]

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ABSTRACT

Osmorhiza longistylis is an herbaceous perennial that grows in woodlands of eastern and central North America. In northcentral Kentucky seeds ripen in early to mid July, and dispersal begins in September and October. Although most of the seeds are shed during late autumn and winter, some remain on the dead shoots for up to 18 months. Seeds are dormant at maturity due to an underdeveloped embryo. Embryos grew at low (5 C) temperatures, but only after seeds were given a period of warm (30/15 C) stratification. With an increase in the length of the warm treatment, there was an increase in the number of embryos that grew to full length during a 12-wk period at 5 C and an increase in the percentage of seeds that germinated. Seeds given 12 wk of warm stratification required more than 8 wk at 5 C to overcome dormancy. Embryos in freshly-matured seeds averaged 0.60 mm long, but those in seeds given 12 wk warm plus 12 wk cold stratification averaged 8.86 mm. Lengths of embryos of seeds kept moist at 30/15 and 5 C for 24 wk averaged 0.63 and 0.89 mm, respectively. Regardless of age and dispersal time, imbibed seeds must be exposed to high (i.e., summer or autumn) and then to low (i.e., winter) temperatures before they will germinate. Consequently, germination occurs only in spring.

OSMORHIZA LONGISTYLIS (TORR.) DC. is an herbaceous, polycarpic perennial that grows in rich woods and thickets (Fernald, 1950; Steyermark, 1963) from Nova Scotia, the Gaspe Peninsula and southern Quebec and Ontario to Georgia, west to Texas, New Mexico, Colorado and Alberta (Constance and Shan, 1948; Lowry and Jones, 1979). In northcentral Kentucky the flowering shoot is produced during April, and the peak of flowering is in early May. Mericarps (hereafter called seeds) are ripe in early to mid July, and seeds germinate in February and March. Germinating seeds produce both roots and shoots the same spring.

As part of a broader investigation of the germination ecology of herbaceous species of mesic woodland habitats, we began making phenological observations and attempting to germinate seeds of *O. longistylis* in 1976. We observed that 1) seeds gave no germination at simulated spring habitat temperatures after receiving 0–16 wk of moist chilling (cold stratification); 2) seeds have rudimentary or underdeveloped embryos (Martin, 1946) (i.e., embryos are minute but cotyledons are distinguishable); and 3) although seed dispersal begins in September and October and most of them are shed during late autumn and winter, some remain on the plants for up to 18 months after maturation.

These results and observations raised a number of questions which are addressed in this paper. What environmental conditions are necessary to break dormancy in *O. longistylis*? If seeds germinate in the habitat in spring, after they have been exposed to low stratifying temperatures during late autumn and winter, but fail to germinate in the laboratory after they have been stratified at 5 C in a refrigerator, some other treatment, either alone or in combination with cold stratification apparently is required to overcome dormancy. For example, seeds may require warm stratification prior to cold stratification as do seeds of *Panax ginseng* C. A. May. (Grushvitzky, 1967). What environmental conditions are required for embryo growth? In seeds of species such as *Fraxinus nigra* Marsh. (Steinbauer, 1937) and *F. excelsior* L. (Villiers and Wareing, 1964) and *P. ginseng* (Grushvitzky, 1967), the underdeveloped embryos grow during warm stratification but germination does not occur until after seeds with fully elongated embryos have been cold stratified. On the other hand, in seeds of *Heracleum sphondylium* L. (Stokes, 1952a), *Tulipa tarda* Stapf (Nikolaeva, 1977) and *Frasera caroliniensis* Walt. (Threadgill, Baskin and Baskin, 1981) the underdeveloped embryos do not require warm stratification and grow while seeds are being cold stratified. Finally, how does an extended dispersal period influence the timing of germination of *O. longistylis* seeds in a given seed crop? Do seeds become nondormant when they remain on the dead flowering shoots for extended periods of time, or must they undergo

[1] Received for publication 18 July 1983; revision accepted 5 December 1983.

TABLE 1. *Cumulative germination percentages ($\bar{x} \pm SE$) of* Osmorhiza longistylis *seeds planted on soil in the non-temperature-controlled greenhouse on various dates*

No. of springs after planting	Yr. matured							
	1977	1979	1979	1979	1979	1980	1980	1980
	Date planted							
	7-3-77	9-12-79	11-3-79	1-2-80	3-15-80	7-15-81	9-7-81	12-20-81
1	78 ± 10	61 ± 3	5 ± 2	0	0	55 ± 4	45 ± 2	0
2	88 ± 8	84 ± 2	77 ± 6	64 ± 1	69 ± 5	67 ± 5	57 ± 3	56 ± 8
3	89 ± 8	87 ± 3	83 ± 9	72 ± 2	82 ± 6			
4	89 ± 8	88 ± 3	84 ± 9	73 ± 2	82 ± 6			

the full set of dormancy breaking treatments after they are dispersed?

In the only previous study on seed germination in *O. longistylis* that we are aware of, Howard (1915) obtained no germination either of freshly-matured seeds or of seeds that had been air dried for 1 month in the laboratory, but 40% of the seeds collected on July 5 and planted out-of-doors germinated the following spring. In the only other report that we have found on seed germination in the genus *Osmorhiza,* Struik (1965) obtained no germination of unstratified *O. claytoni* (Michx.) C. B. Clarke seeds. Seeds stratified at 5 C and below 0 C for 6 wk and then exposed to room temperature germinated to 1 and 4%, respectively, and seeds kept dry at 5 C for 6 wk, then exposed, on a moist substrate, to room temperature germinated to 5%.

METHODS—*Germination—Phenology:* Seeds of *O. longistylis* were planted on soil in a non-temperature-controlled greenhouse on the various dates given in Table 1 to simulate different dispersal times. Seeds were collected from *O. longistylis* plants growing in a deciduous forest in southeastern Fayette County, Kentucky, 1–2 days prior to each planting date. Three replications of 300 seeds each were used each time, except for 20 December 1981, when three replications of only 100 seeds each were planted. Seeds were placed on soil (3:1 v/v mixture of top soil and sand) in small flats and covered with dead oak leaves. The flats were kept under a bench in a greenhouse with no heating or air-conditioning and the windows open all year; temperatures were recorded continuously with a thermograph. During summer (1 May to 31 August) the soil was watered to field capacity once each wk, and during the remainder of each yr the soil was watered daily, except on days during winter when it was frozen. All flats were examined at 7-day intervals, and if seedlings were present they were counted and removed.

Warm followed by cold stratification: In this study the effect on germination of freshly-matured seeds of warm stratification followed by cold stratification was tested. Seeds were collected on 23 July 1979, and the experiment was started 3 days later. Three replications of 50 seeds each were used for each treatment and control. Seeds were placed on moist sand in 9-cm Petri dishes, and all dishes were covered with plastic film. Seeds were given warm stratification treatments of 0 to 24 wk at a (12/12 hr) daily thermoperiod of 30/15 C followed by cold stratification treatments at a constant temperature of 5 C for 0 to 24 wk. The various lengths of time that seeds were subjected to the two treatments are given in Table 2. After the stratification treatment was completed, seeds were tested for germination at thermoperiods of 15/6, 20/10 and 30/15 C. Germination tests were terminated after 15 days of incubation, and protrusion of the radicle was the criterion for germination.

The 30/15-C thermoperiod approximates mean daily maximum and minimum monthly air temperatures in northcentral Kentucky during June, July, August and September; 20/10 C during October and April and 15/6 C during November and March (Hill, 1976). Seeds were cold stratified at 5 C because this temperature is near-optimal for many seeds that require chilling to break dormancy (Stokes, 1965). In Kentucky temperatures during December, January and February often are between 0 and 10 C (Hill, 1976), and this is the effective range for cold stratification (Crocker and Barton, 1957; Stokes, 1965). The daily thermoperiods were obtained by using temperature- and light-controlled incubators, and the 5-C regime by using a refrigerator equipped with a fluorescent light and a time clock. Seeds were exposed to a 14-hr daily photoperiod throughout the study. At the alternating temperature regimes, the daily photoperiod extended from 1 hr before to 1 hr after the daily high temperature period.

TABLE 2. *Germination percentages ($\bar{x} \pm SE$) of* Osmorhiza longistylis *seeds given warm and cold stratification for various periods of time*

Weeks		Test temperatures (C)		
Warm	Cold	15/6	20/10	30/15
0	0	0	0	0
0	12	0	0	0
0	24	0	1 ± 1	0
2	12	29 ± 4	24 ± 4	13 ± 5
4	12	35 ± 1	20 ± 3	23 ± 3
6	12	39 ± 7	19 ± 7	39 ± 1
8	12	57 ± 3	43 ± 4	33 ± 2
10	12	66 ± 6	59 ± 6	49 ± 9
12	0	0	0	0
24	0	0	0	0
12	2	0	0	0
12	4	0	0	0
12	6	0	0	0
12	8	0	0	5 ± 2
12	10	31 ± 1	25 ± 2	38 ± 0
12	12	77 ± 6	74 ± 10	35 ± 5
12	14	89 ± 5*	87 ± 7*	56 ± 15*

* 25% of the seeds germinated while at 5 C.

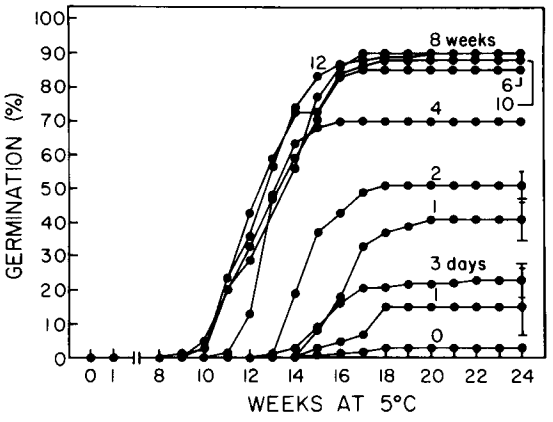

Fig. 1. Cumulative germination percentages of *Osmorhiza longistylis* seeds given 0–12 wk of warm stratification and then placed at 5 C for 24 wk. Standard errors are given for final germination means, if ≥5%.

The light source was 20-W cool white fluorescent tubes, and photon flux density at seed level was 20 μmol m^{-2} s^{-1} (400–700 nm).

In a second experiment, freshly-matured seeds of *O. longistylis* were collected on 17 July 1981, and placed on moist sand in Petri dishes 2 days later. Experimental conditions were the same as those previously described. Seeds were given warm stratification periods of 0, 1 and 3 days and 1, 2, 4, 6, 8, 10 and 12 wk and then transferred to 5 C where each set of seeds remained for a total of 24 wk. During the 24-wk period, germination counts were made at weekly intervals. Standard errors were calculated for final germination percentages.

A third experiment was conducted to determine whether or not seeds that remain undispersed for a year after maturation require warm plus cold stratification to break dormancy. Seeds produced during 1980 were collected on 15 July 1981, and the next day they were placed on moist sand. Experimental conditions were the same as those previously described. Seeds were given 12 wk of warm stratification at 30/15 C followed by 12 wk of cold stratification at 5 C and then tested for germination at 15/6 and 20/10 C for 15 days. Controls were given only 12 and 24 wk of warm stratification or 12 and 24 wk of cold stratification.

Embryo growth—To determine the requirements for embryo growth, freshly matured seeds were subjected to various temperature regimes, and at regular intervals embryos were excised and measured. Seeds were collected on 23 July 1979, and 3 days later the embryos from 50 seeds were measured. At 2-wk intervals 50 embryos each were excised and measured for seeds placed at 1) 30/15 and 5 C for 36 wk; 2) 30/15 C for 12 wk and then moved to 5 for 0–12 wk; and 3) 30/15 C for 0–12 wk and then moved to 5 C for 12 wk. Additionally, seeds were given 12 wk at 5 C followed by 12 wk at 30/15 C and then moved back to 5 C for 0–12 wk. When seeds were placed at 5 C the second time, embryo measurements were made at 2-wk intervals for 12 wk. Controls remained at 30/15 C. Embryos were dissected from seeds using a razor blade and measured using a dissecting microscope equipped with a micrometer; mean lengths and standard errors were calculated.

Embryo measurements also were made for seeds collected in the field on various dates to determine whether or not they grow if seeds remain undispersed for extended periods of time. Seeds produced in 1980 were collected on 23 July 1980, 15 July 1981, and 20 December 1981. The next day after each collection was made, seeds were allowed to imbibe on moist filter paper for 24 hr in the 30/15-C incubator, and then 50 embryos were excised and measured.

RESULTS—*Germination—Phenology:* Regardless of planting date, seeds germinated only in spring, and the germination season extended from mid February to mid April, with the peak occurring in March. Mean daily maximum temperatures in the greenhouse for each March from 1978–1983 were 13.9, 16.5, 12.3, 13.7, 16.8 and 15.9 C, respectively, and mean daily

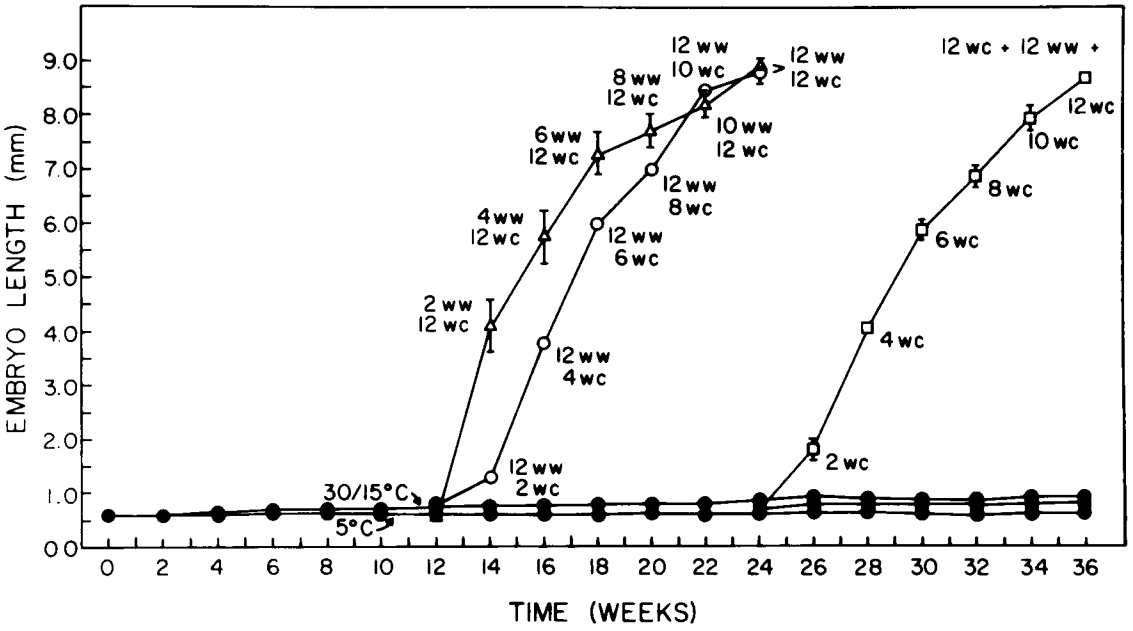

Fig. 2. Embryo lengths ($\bar{x}$ ± SE, if ≥0.2 mm) of freshly-matured *Osmorhiza longistylis* seeds incubated at 30/15 C (warm stratification) and/or 5 C (cold stratification) for various periods of time.

minimum temperatures each March were 1.8, 5.7, 2.2, 2.8, 4.0 and 5.5 C, respectively. Mean daily maximum and minimum temperatures in the greenhouse for each month from 1978–1982 are given in Baskin and Baskin (1983, 1984b). Regardless of age, seeds planted in July and September germinated to 45–78% the first spring (Table 1). On the other hand, seeds planted in November, January, March and December germinated to only 0–5% the first spring but to 56–77% the second spring. Very few, or no, seeds germinated in the third spring in any of the plantings. Thus, if seeds received high temperatures (i.e., summer or autumn) immediately after they were planted and then low temperatures (i.e., winter), they germinated the first spring. However, if seeds received low (winter) temperatures immediately after planting, they did not germinate until the second spring, after they had received high summer and then low winter temperatures.

Warm followed by cold stratification: Warm plus cold stratification was required to break dormancy in seeds of *O. longistylis* (Table 2). Two weeks of warm stratification followed by 12 weeks of cold stratification caused 13–29% of the seeds to germinate. With increases in the length of the warm stratification period, up to and including 12 wk, germination of seeds cold stratified for 12 wk increased. After seeds were given a warm stratification treatment of 12 wk, they required more than 8 wk of cold stratification to germinate at 15/6, 20/10 and 30/15 C. Seeds that were cold stratified for 14 wk germinated to 25% while they were at 5 C and to an additional 64, 62, and 31% at 15/6, 20/10 and 30/15 C, respectively.

Seeds not only came out of dormancy at 5 C, but those receiving 6–12 wk of warm stratification germinated to 85–90% after 16–18 wk at 5 C (Fig. 1). With an increase in the length of the warm stratification period up to 6 wk, there was a distinct increase in rate and final percentage of germination.

Seeds that remained undispersed for 1 yr after maturation also required warm plus cold stratification to come out of dormancy. Those given 12 wk warm plus 12 wk cold stratification germinated to 97 and 95% at 15/6 and 20/10 C, respectively. Seeds given 12 and 24 wk of warm stratification or 12 wk of cold stratification gave no germination at 15/6 and 20/10 C, while those given 24 wk of cold stratification, germinated to 1 and 0%, respectively.

Embryo growth—Embryos of freshly-matured seeds were 0.60 mm long, and they grew very little when seeds were kept continuously at 30/15 or 5 C; after 36 wk those at 30/15 C were 1.00 mm long while those at 5 C were 0.70 mm (Fig. 2). Embryos elongated if seeds were given warm plus cold stratification, but they failed to grow if seeds were given cold stratification first and then a warm stratifica-

tion. In the latter case, embryos grew only when seeds were given a second period of cold stratification. In seeds given various periods of warm stratification and then 12 wk of cold stratification, embryo length increased with an increase in the length of the warm stratification period. After seeds were at 30/15 C for 12 wk and then were transferred to 5 C, embryos grew at an average rate of 0.66 mm per wk, with the greatest growth rates (1.1 mm/wk) occurring between wk 2 and 6.

Embryos grew only a very little while seeds were attached to dead, upright flowering shoots for 12 and 18 months in the field. Embryo lengths of seeds that matured in 1980 and were collected on 23 July 1980, 15 July 1981 and 20 December 1981 averaged 0.60 ± 0.01, 0.70 ± 0.01 and 0.73 ± 0.01 mm, respectively.

TABLE 3. *Effect of increased length of warm stratification on 1) embryo growth at 5 C, and 2) germination of seeds subsequently cold stratified for 12 wk and tested at 15/6 C*

Weeks		% Embryos fully elongated	% Germination at 15/6 C
Warm	Cold		
0	12	0	0
2	12	22	29
4	12	42	35
6	12	44	39
8	12	52	57
10	12	70	66
12	12	82	77

DISCUSSION—Underdeveloped embryos occur in several dozen plant families (Martin, 1946; Grushvitzky, 1967) in both tropical and temperate zones. Grushvitzky's (1967) work on representatives of many families including Magnoliaceae, Annonaceae, Schisandraceae, Ranunculaceae, Fumariaceae, Papaveraceae, Nandinaceae, Berberidaceae, Paeoniaceae, and Araliaceae showed that embryo growth occurs after seeds are dispersed and generally at high (15–20 C) temperatures over a period of 2–4 months. After the embryos are fully elongated, germination of tropical species takes place immediately, but in most temperate zone species the seeds must be cold stratified before they will germinate. Grushvitzky (1967) believes that postembryonic growth is an ancient feature of primitive angiosperms and the requirement for subsequent cold stratification is a later adaptation of these seeds to a climate with alternations of winter and summer. As research continues on the germination characteristics of temperate zone species with underdeveloped embryos it is becoming increasingly apparent that there is a second group of species, not mentioned by Grushvitzky, in which embryos grow at low but not at high temperatures. In *Heracleum sphondylium* (Stokes, 1952a), *Tulipa tarda* (Nikolaeva, 1977) *Frasera caroliniensis* (Threadgill, Baskin and Baskin, 1981) and *Stylophorum diphyllum* (Michx.) Nutt. (Baskin and Baskin, 1984a) the only requirement for embryo growth and subsequent germination is a long period of cold stratification. Since seeds of *O. longistylis* require warm followed by cold stratification for embryo growth, *O. longistylis* does not fit into either of the two groups of species with underdeveloped embryos known to occur in temperate regions. *Osmorhiza longistylis* is unlike species in the first group in that embryos grow at low rather than at high temperatures, and it is unlike members of the second group in that warm stratification is required before embryos will grow during cold stratification.

The quantitative effects of warm stratification on subsequent embryo growth and germination of *O. longistylis* seeds at 5 C are illustrated not only by increases in rates and final percentages of germination but also by the number of embryos that elongated fully. Since embryos averaged 8.2 and 8.9 mm long after seeds received 12 wk of warm stratification plus 10 and 12 wk of cold stratification, respectively, we considered an embryo to be fully elongated if it was ≥8.5 mm long. There is a positive correlation between increased length of the warm stratification period, number of embryos that grew to full length at 5 C and the percentages of seeds that germinated at 15/6 C after receiving 0–12 wk of warm plus 12 wk of cold stratification (Table 3). The large standard errors (Fig. 2) for embryos excised from seeds receiving 0–12 wk warm plus 12 wk cold stratification are explained by the fact that within each set of seeds some embryos had grown very little, or none, while others were fully elongated.

In *Fraxinus nigra* (Steinbauer, 1937) and *F. mandshurica* Rupr. (Asakawa, 1956, 1968) embryos were dormant and gradually came out of dormancy and elongated at 20–25 C; however, cold stratification was required before seeds would germinate. During cold stratification of *F. nigra* seeds, food reserves of the endosperm were depleted, and starch, soluble carbohydrates and proteins increased in the embryos (Steinbauer, 1937). In both species of *Fraxinus* the growth potential of the embryos increased during cold stratification, and seeds germinated when they were placed at 20–30 C (Steinbauer, 1937; Asakawa, 1968). In *Heracleum sphondylium,* embryos elongated com-

pletely when seeds were cold stratified at 2 C for 8–12 wk, but in seeds incubated at 15 C embryo growth stopped after 6 wk when they were only half their potential length (Stokes, 1952a). Growth of embryos in seeds at 15 C ceased because food reserves in the embryo were exhausted, while at low temperatures storage proteins were converted into soluble nitrogenous compounds and transferred from the endosperm to the embryo (Stokes, 1952b, 1953). These data from studies on *F. nigra, F. mandshurica,* and *H. sphondylium* and the quantitative effects of warm stratification on subsequent embryo growth of *O. longistylis* at 5 C suggest that *O. longistylis* embryos may become nondormant at high temperatures and grow after seeds are placed at low temperatures where endosperm food reserves are made available.

The long dispersal period of *O. longistylis* seeds coupled with special temperature requirements to break dormancy spreads germination of a given seed crop over several years. Also, at any point in time there are seed reserves at a population site both attached to the dead flowering shoots and on the soil. A high percentage of the seeds dispersed or collected and planted in July immediately after maturation can germinate the following spring, 8 months after maturity. However, in the greenhouse (Table 1) some freshly matured seeds planted in July did not germinate until the second or third spring after planting, when they were 20 and 32 months old, respectively. Seeds collected and planted 18 months after maturation were 32 months old before any of them germinated. A few seeds that matured in July 1979 and were collected and planted in the greenhouse in September and November 1979 and in January 1980 did not germinate until the spring of 1983, 44 months after maturation.

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