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Ecological life cycle of *Chaerophyllum procumbens* variety *shortii* (Apiaceae), a winter annual of the North American Eastern Deciduous Forest

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CAROL C. BASKIN[1,2], TRACY S. HAWKINS[1,3], AND JERRY M. BASKIN[1] ([1]Department of Biology, University of Kentucky, Lexington, KY 40506-0225, [2]Department of Agronomy, University of Kentucky, Lexington KY 40546-0091, [3]Center for Bottomland Hardwoods Research, P.O. Box 227, Stoneville, MS 38776) Ecological life cycle of Chaerophyllum *procumbens* variety *shortii* (Apiaceae), a winter annual of the North American Eastern Deciduous Forest. J. Torrey Bot. Soc. 131: 126–139. 2004.—Seed dormancy and germination, flowering, and biomass allocation patterns of the deciduous forest species *Chaerophyllum procumbens* var. *shortii* were investigated relative to its winter annual life cycle. It was determined that seeds had nondeep simple morphophysiological dormancy at maturity in late May. The physiological component of dormancy was broken during summer, and embryos grew (morphological component) in autumn if seeds were exposed to light. Seeds sown in late spring germinated only in autumn, but a few did not germinate until the second to seventh autumn, indicting the potential to form a small persistent seed bank. Vernalization was not required for flowering. In the field, plant growth and development occurred during autumn, winter, and early spring, and individual plants reached highest total plant biomass [0.28 ± 0.01 g (mean ± SE)] at flowering. Total plant biomass decreased from flowering to mericarp maturity. In two successive years, the proportion of total biomass allocated to roots (≤ 22.2 ± 2.9%) at five growth stages was less than that allocated to any other vegetative structure. Changes in biomass allocation during reproductive growth stages occurred only in above-ground structures. Although mass of reproductive structures was strongly correlated with plant vegetative mass, differences in slopes of the regressions between years indicated that between cohort differences in percent reproductive allocation were not completely accounted for by overall plant size.

Key words: biomass allocation, *Chaerophyllum procumbens*, ecological life cycle, seed dormancy, winter annual.

Numerous winter annuals occur in temperate eastern North America. Based on life cycle information and flowering period, the flora of northeastern USA and adjacent Canada described in *Gray's Manual of Botany* (Fernald 1950) contains 96 winter annuals (C. Baskin unpublished). This list includes native and introduced species in 57 genera and 23 families. The majority of these winter annuals grow in open, well-lighted habitats such as fields, lawns, waste places, and rock outcrops, and only a few, including *Chaerophyllum procumbens* (L.) Crantz, *Collinsia verna* Nutt., *Corydalis flava* (Raf.) DC., *Nemophila aphylla* (L.) Grumm., and *Phacelia ranunculacea* (Nutt.) Const. are found in mesic deciduous forests.

Although seed germination ecology has been investigated for *C. verna* (Baskin and Baskin 1983), *C. flava* (Baskin and Baskin 1994), *N. aphylla* (Baskin et al. 1993), and *P. ranunculacea* (Baskin et al. 1993), no such studies have been done for *C. procumbens*. Of these five species of woodland winter annuals, only *C. verna* has received much attention with regard to autecology. Population genetics, demography, seed banks, and breeding system of *C. verna* have been investigated by Kalisz (1989, 1991), Kalisz and McPeek (1992, 1993) and Kalisz et al. (1999). As a further contribution to understanding the biology of winter annuals in mesic deciduous forests, we investigated seed germination ecology, life cycle phenology, flowering requirements, and biomass allocation of *C. procumbens*.

The geographic range of *Chaerophyllum procumbens* extends from New York, Michigan, Wisconsin, and Iowa south to Florida, Alabama, and Oklahoma (Fig. 1). Two varieties of *C. procumbens* have been named, and plants used in our study keyed easily to *C. procumbens* (L.) Crantz var. *shortii* T. & G. Variety *shortii* is distinguished from the typical variety by lack of a constriction near the top of the mericarp and densely pubescent (*vs.* glabrous) mericarps (Steyermark 1963).

Seed dormancy and germination have been investigated for the weedy, eastern North Amer-

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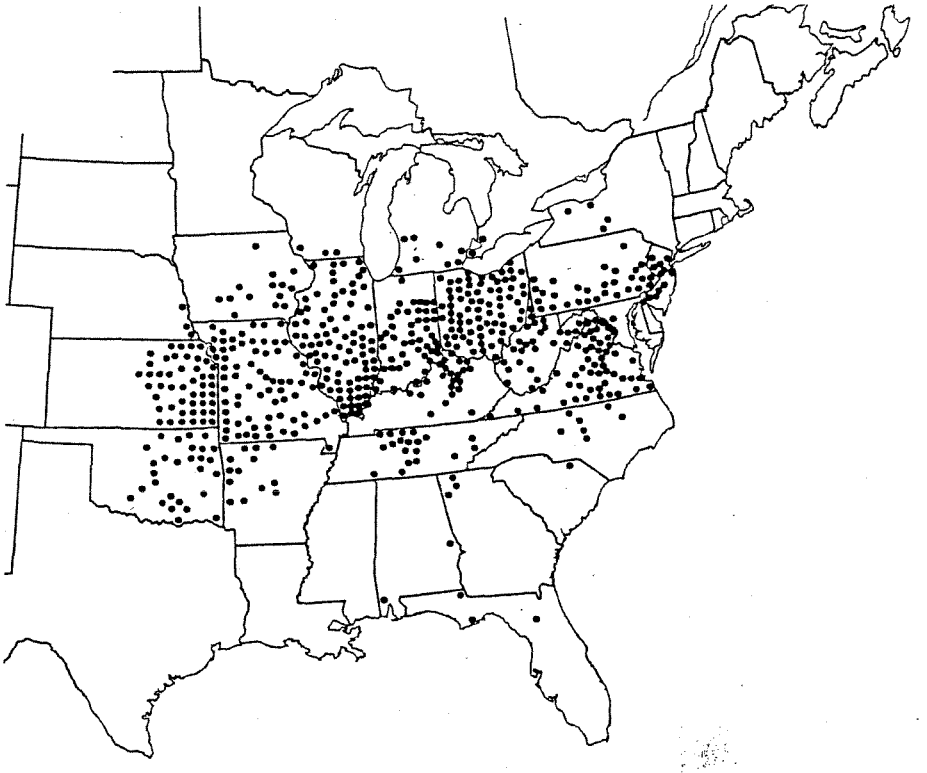

Fig. 1. Geographical distribution map for *Chaerophyllum procumbens* based on specimen information provided by the following herbaria (abbreviations according to Holmgren et al. 1990) AUA, DOV, GA, IA, KY, MO, NK, TROY, UNA, WIS or published reports in Deam (1940), Steyermark (1963), Radford et al. (1968), GPFA (1977), Mohlenbrock and Ladd (1978), Strausbaugh and Core (1978), Harvill et al. (1981), Hough (1983), Voss (1985), Smith (1988), Rhoads and Klein (1993), Cooperrider (1995), Chester et al. (1997), Oldham (1999), Weldy et al. (2002), and Wunderlin and Hansen (2002).

ican native winter annual *Chaerophyllum tainturieri* Hook. (Baskin and Baskin 1990a). Seeds of this species have underdeveloped (small) embryos, i.e., morphological dormancy, and the embryos also have a physiological inhibiting mechanism of germination, i.e., physiological dormancy. Consequently, seeds have morphophysiological dormancy (MPD). Physiological dormancy was broken in *C. tainturieri* seeds during exposure to high summer temperatures, and morphological dormancy was broken (embryos grew) if seeds were exposed to light. That is, morphological dormancy could not be broken until after physiological dormancy was broken. If seeds were not exposed to light in autumn, low temperatures of late autumn and winter induced the seeds back into physiological dormancy. Consequently, seeds did not have the potential to germinate until the subsequent autumn after physiological dormancy had been broken during summer (Baskin and Baskin 1990a).

Our preliminary examination of seeds of *C. procumbens* var. *shortii* (hereafter called *C. procumbens*) showed that the embryo was underdeveloped. Thus, it seemed reasonable that seeds of this species also had one of the eight known levels of MPD (Baskin and Baskin 1998). Since *C. tainturieri* grows in open, often-disturbed habitats (Fernald 1950), we wanted to know if seeds of *C. procumbens*, which grows in stable woodland habitats, also have nondeep simple MPD. Thus, experiments were designed to determine the dormancy breaking and germination requirements of this species, and results were compared to those for *C. tainturieri*.

Struik (1965) included *C. procumbens* in her comparative growth pattern analysis of native annual, biennial, and perennial forest herbs in southern Wisconsin. However, she was unable to determine biomass allocation to reproduction at mericarp maturity, and dry weight allocation patterns in her study largely were limited to root-shoot ratios. Thus, to supplement Struik's work, studies on growth habit, phenology, and

Table 1. Total monthly precipitation (mm) recorded at Bluegrass Airport, Lexington, Kentucky, for the duration of biomass allocation studies, September 2000–April 2002, (NOAA 2000–2002) and the 25-year average, 1949–1974, for Lexington, Kentucky (Hill 1976).

Month	2000 Cohort	2001 Cohort	25 Yr. Average
September	125.2	27.7	67.3
October	27.2	34.5	53.8
November	37.1	46.2	85.3
December	110.0	65.3	91.9
January	63.5	112.0	100.3
February	95.0	31.5	86.9
March	54.9	202.4	121.9
April	42.9	101.9	98.3
TOTAL	558.8	621.5	705.7

biomass allocation patterns were done in a naturally-occurring population of *C. procumbens* growing in a deciduous forest in north-central Kentucky.

Materials and Methods. STUDY SITE. All material was collected from, and observations made on, plants of *C. procumbens* growing in a second-growth, mesic deciduous forest in Fayette County, Kentucky, near the Kentucky River, in Braun's (1950) Western Mesophytic Forest Region. The soil association at the site is Fairmount-McAfee-Rock Land (Sims et al. 1968). Bedrock is Ordovician Lexington limestone (Black 1967). The Fairmont series is on sloping to steep topography, and the soils are shallow, rocky, and clayey. Soils are somewhat excessively drained, and pH is neutral to slightly alkaline. The McAfee series is on gently sloping to moderately steep topography, and the soils are silty loams and silty clay loams. They are shallow to moderately deep, well drained to excessively well drained, and slightly to moderately acid (Sims et al., 1968). Average annual temperature for the region is 12.8°C with the lowest mean monthly temperature occurring in January (0.8°C) and the highest mean monthly temperature in July (24.4°C) (Hill 1976). Average annual precipitation is 1130 mm and is fairly evenly distributed throughout the year; July (122.7 mm) is the wettest month and October (53.8 mm) the driest (Hill 1976). Total monthly precipitation during the phenology and biomass allocation studies are given in Table 1.

SEED GERMINATION ECOLOGY. Freshly-matured mericarps (hereafter called seeds) were collected, and seeds were allowed to dry for a few days in the laboratory, after which they were used in germination studies.

Germination tests were performed in light- and temperature-controlled incubators at a 14-hr daily photoperiod (ca. 40 μmol m^{-2} s^{-1}, 400–700 nm, of cool white fluorescent light) or in constant darkness at alternating temperature regimes (12/12 hr) of 15/6, 20/10, 25/15, 30/15, and 35/20°C. These temperature regimes approximate mean daily maximum and minimum air temperatures in north central Kentucky during the growing season (Wallis 1977): March and November, 15/6; April and October, 20/10; May, 25/15; June and September, 30/15; and July and August, 35/20°C. In each incubator, the photoperiod extended from 1 hr before the high temperature period began to 1 hr after it ended. Seeds were incubated on white quartz sand moistened with distilled water in 10 cm-diameter Petri dishes, and three replications of 50 seeds each were used for each test condition. Dishes containing seeds to be incubated in light were wrapped with plastic film to reduce loss of water, and those to be incubated in darkness were wrapped with plastic film and two layers of aluminum foil. Final germination percentages were determined after 15 days, and protrusion of the radicle was the criterion of germination. Details of a variety of experiments are given below.

Germination Phenology. Seeds sown on soil and exposed to natural seasonal temperature changes in a nonheated greenhouse were monitored for germination. Three replications of 200 seeds each (collected on 29 May 1978) were sown on soil in small flats on 1 June 1978 and covered with about 5 cm of dead oak leaves. The soil used in this study (and those described below) was a 3:1 volume/volume mixture of limestone-derived topsoil and river sand. The flats were kept under a bench in a nonheated greenhouse in Lexington, Kentucky. This greenhouse had no heating or air-conditioning, and windows were kept open all year. Continuous thermograph records were made inside a standard weather house located on the floor of the greenhouse. To simulate typical soil moisture conditions occurring in the habitat, the soil was watered to field capacity once each week during summer (1 May–31 August) and daily during the remainder of the year, unless it was frozen (in winter). Each week, the leaves were lifted, and seeds with an emerged radicle were counted

as germinated and removed from the flats. The study was terminated on 1 January 1983.

In a second study of germination phenology, three replications of 300 seeds each (collected on 21 May 1986) were sown on soil in flats in the greenhouse on 23 May 1986, covered with about 5 cm of dead oak leaves, and watered and monitored as described above until 1 January 1994.

Dormancy Break. To document rate of dormancy break, temperature requirements for germination in light were determined at monthly intervals for seeds previously exposed to natural temperature regimes in the nonheated greenhouse. Seeds were collected on 29 May 1978, and on 1 June a subsample was tested for germination in light at 15/6, 20/10, 25/15, 30/15, and 35/15°C. On 1 June, the remainder of the seeds was placed in a fine-mesh nylon bag on soil in a small flat and covered with about 5 cm of dead leaves. The flat was placed under a bench in the greenhouse and watered to field capacity each day. On 6 July, 2 August, and 1 September 1978, 750 seeds were arbitrarily removed from the bag to test for germination in light at the five temperature regimes.

In a second study, seeds were collected on 31 May 1984, and on 4 June a subsample was tested for germination in light at the five temperature regimes. On 4 June, the remainder of the seeds was placed in a bag in the greenhouse as described above, and on 3 September 1984 these seeds were tested for germination in light at the five temperature regimes.

Light Requirement for Germination. To determine if light is required for germination in autumn, seeds were tested for germination in light and in darkness at 15/6, 20/10, 25/15, 30/15, and 35/20°C before and after burial at high summer temperatures. Seeds were collected on 20 May 1987, and 3 days later a subsample of the fresh seeds were tested for germination in light and in darkness at the five alternating temperature regimes; this test was terminated after 15 days. On 23 May 2000, the remaining seeds were placed in a fine-mesh nylon bag and buried to a depth of 7 cm in soil in a 15-cm-diameter clay pot with drainage holes. The pot was kept under a bench in the greenhouse until 25 September 1987. From 23 May to 31 August, the soil was watered to field capacity once each week, and from 1–25 September it was watered daily. Seeds were buried under natural summer temperature regimes so that physiological dormancy in the embryos would be broken. On 25 September, the bag of seeds was removed from the soil in complete darkness and cut open and the seeds poured into a dish. A "pinch" of 50–60 seeds was placed in each of the 15 Petri dishes to be incubated in darkness (three replications × five temperature regimes), and the dishes were wrapped with plastic film and aluminum foil. Thus, seeds were not exposed to any light from the time they were buried until the end of the germination test. Using fluorescent room light, 50 seeds were placed into the 15 Petri dishes to be incubated in light (three replications × five temperature regimes); seeds were arbitrarily selected. Seeds were incubated in light and in darkness at 15/6, 20/10, 25/15, 30/15, and 35/20°C for 15 days.

Phenology of Embryo Growth. The purpose of this study was to determine when embryos grow in seeds exposed to natural temperature regimes. Seeds were collected on 21 May 1986, and 2 days later they were placed in a fine-mesh nylon bag on soil in a small flat and covered with about 5 cm of dead oak leaves. The flat was placed under a greenhouse bench and watered daily. Embryos were excised from 50 arbitrarily-selected seeds on 23 May, 1 June, 1 July, 1 August, and 1 September 1986 with a single-edge razor blade, and the length of each embryo was measured using a dissecting microscope equipped with a micrometer.

Light Requirement for Embryo Growth. The purpose of this experiment was to determine if light is required for embryo growth before and after burial at high summer temperatures. Seeds were collected on 20 May 1987, and 3 days later 50 seeds were placed in each of 15 Petri dishes on Whatman No. 1 filter paper moistened with distilled water. Eight of the dishes were wrapped with plastic film, and seven were wrapped with plastic film and two layers of aluminum foil. All dishes were placed in the 25/15°C incubator. After 8 hr, embryos were excised from the seeds in one of the dishes incubated in light and measured. At 2-day intervals for 14 days, embryos were excised from 50 seeds incubated in light and from 50 seeds incubated in darkness, and measured.

Also, on 23 May 1987 about 1000 seeds were placed in a fine-mesh nylon bag and buried 7 cm deep in soil in a 15-cm-diameter clay pot. The pot was kept under a bench in the greenhouse until 25 September, at which time seeds were exhumed. Seeds were exposed to high

summer temperatures to promote the breaking of physiological dormancy. The soil was watered to field capacity once each week from 1 May to 31 August and daily thereafter. On 25 September 1987, the bag of seeds was removed from the pot in complete darkness and cut open and seeds poured into a dish. A pinch of 50–60 seeds was placed on moist filter paper in each of seven dishes, which were wrapped individually with plastic film and aluminum foil. In light, 50 seeds each were placed in eight additional dishes. Embryos were excised from seeds incubated in light and in darkness at 25/15°C after 0, 2, 4, 6, 8, 10, 12, and 14 days and measured, as previously described. If seeds had germinated at time embryo measurements were made, length of the embryo was recorded as 4.6 mm (see results of phenology of embryo growth).

ECOLOGICAL LIFE CYCLE. *Effect of Vernalization on Flowering.* To determine if vernalization is required for flowering, seedlings of *C. procumbens* that germinated in a greenhouse flat in late September 1979 were transplanted to individual 10 cm-diameter pots (one plant/pot) filled with soil in the nonheated greenhouse. On 9 October 1979 (nonvernalized control), 1 and 15 November 1979, 1 and 15 December 1979, 1 and 15 January 1980, 1 and 15 February 1980, and 1 March 1980, 15 plants each were transferred from the nonheated greenhouse to a heated greenhouse and kept there until 31 March 1980, at which time all plants had flowered. An additional set of 15 plants was retained in the nonheated greenhouse (thus exposed to the full winter vernalization period). The number of hours that various sets of plants were exposed to vernalizing temperatures (0.5–10°C) was calculated from the thermograph records. In the heated greenhouse, mean daily maximum and minimum weekly temperatures between 9 October 1979 and 31 March 1980 were 30.2 and 16.6°C, respectively. All plants in both greenhouses were watered as needed to keep the soil moist, and they were checked weekly for open flowers. This experiment was repeated in part during 2000–2001: 15 plants received zero hours of vernalization and 15 full vernalization.

Life Cycle and Biomass Allocation Phenology. Observations on the life cycle of *C. procumbens* were recorded at 2- to 4-week intervals from September 2000 to April 2002. In the biomass allocation study, plants chosen at random in the field were harvested at four phenology stages, and this harvesting chronology was completed for two successive annual cohorts. Harvesting stages were as follows:

a) "Fall juvenile" described plant morphology in November. Plants had cotyledons + two leaves.

b) "Spring rosette" was the first harvest of the second growing season, when plants had produced five to six mature leaves in a rosette form.

c) "Flowering" referred to the peak flowering period.

d) "Late-Fruiting" was identified by signs of plant senescence (i.e., yellowing leaves). This stage occurred at mericarp maturity and preceded seed dispersal.

Given that growth periods and length of life cycle may vary between years, it was decided that use of phenology stages for between-cohort comparisons would be more precise than comparisons based on time units.

Ten individuals were harvested at each of the four growth stages. During field harvest, each plant was separated into leaves (blade + petiole), roots, stems, and umbels (pedicels + rays + flowers/fruits). Individual structures for each of the 10 plants were placed in separate paper bags, labeled, and taken to the laboratory, where they were oven-dried at 70° C for 48 hr, then weighed to the nearest 0.1mg. Biomass allocation for each plant was calculated by dividing dry weight of the plant structure by total plant dry weight.

Seedling biomass data were obtained from greenhouse specimens. Seeds were germinated on soil in metal flats in a non-temperature controlled greenhouse and harvested at the seedling stage of development (two cotyledons). Fifteen seedlings were harvested from the flats, separated into root-hypocotyl and shoot sections and dried at 70° C for 48 hr. Biomass allocation for each seedling was calculated by dividing dry weight of a seedling structure by total seedling dry weight.

Biomass Analysis. Each plant was considered a replicate. The square root of biomass allocation percentages were arcsine transformed for analysis, then back-transformed for presentation. One-way analysis of variance (ANOVA) was used to compare biomass allocation percentages between cohorts and regression analysis to test for linear relationships between reproductive mass and vegetative mass. The SAS procedures GLM and REG were used to perform statistical analyses (SAS 2001).

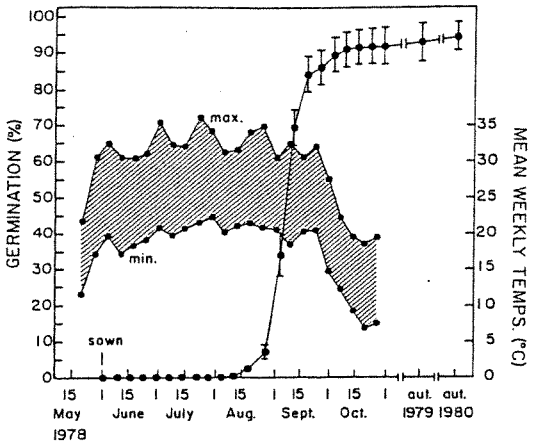

Fig. 2. Cumulative germination percentages (mean ± SE) of *Chaerophyllum procumbens* seeds sown in the nonheated greenhouse in Lexington, Kentucky, on 1 June 1978. Hatched area represents mean daily maximum and minimum weekly temperatures. Aut. = autumn.

Results. SEED GERMINATION ECOLOGY. *Germination Phenology.* Germination of *C. procumbens* seeds sown in the greenhouse on 1 June 1978 began the first week of August and ended the third week of October (Fig. 2). The peak of germination was between 27 August and 11 September 1978, when 374 (62%) of the 600 seeds germinated. Mean daily maximum and minimum temperatures for this 16-day period were 31.8 and 19.5°C, respectively. A total of 550 (92%) of the 600 seeds germinated in autumn 1978. In September and October 1979, eight additional seeds germinated, and in September and October 1980 seven more germinated. No germination occurred in spring of any year.

Seeds of *C. procumbens* sown in the greenhouse on 23 May 1986 germinated in the autumns of 1986–1993. Cumulative germination percentages (mean ± SE) were: 1986, 36.2 ± 6.1; 1987, 42.0 ± 4.3; 1988, 50.9 ± 2.5; 1989, 59.0 ± 6.0; 1990, 60.2 ± 6.7; 1991, 60.3 ± 6.7; 1992, 60.3 ± 6.7; and 1993, 60.4 ± 6.8.

Dormancy Break. Mean daily maximum and minimum weekly temperatures to which seeds were exposed in the nonheated greenhouse in summer 1978 are shown in Figure 2. In 1984, mean maximum/minimum temperatures were: May, 24.8/13.0; June, 31.2/18.7; July, 30.8/19.1; August, 28.9/18.0; and September, 24.6/12.9°C.

Seeds collected in both 1978 and 1984 were dormant at maturity in late May and consequently did not germinate at any test condition during June (Table 2). In July and August 1978, little or no germination occurred in the exhumed seeds regardless of the temperature regimes at which they were tested, indicating that the breaking of physiological dormancy requires a long period of time. Seeds came out of dormancy in the greenhouse during summer, and they germinated to 30–81% and to 90–100% at 15/6, 20/10, and 25/15°C in September 1978 and 1984, respectively. However, seeds germinated to only 0–8% at 30/15 and 35/20°C in both years.

Light Requirement for Germination. Freshly matured seeds were dormant and consequently did not germinate either in light or darkness (Table 3). In September (after physiological dormancy was broken), however, seeds germinated to 35–75% in light and to 15–25% in darkness at 15/6, 20/10, and 25/15°C but to only 0–4% in light and darkness at 30/15 and 30/20°C.

Phenology of Embryo Growth. Embryos in freshly-matured seeds were less than 0.5 mm in

Table 2. Germination percentages (mean ± SE) of *Chaerophyllum procumbens* seeds stored in a fine-mesh cloth bag on moist soil under 5 cm of dead oak leaves in the nonheated greenhouse for 0, 1, 2, and 3 months in 1978 and for 0 and 3 months in 1984 and incubated in light at five alternating temperature regimes for 15 days.

Date test began	Seed age (mos.)	Temperature regime (EC)				
		15/6	20/10	25/15	30/15	35/20
FIRST STUDY						
1 June 1978	0	0	0	0	0	0
6 July 1978	1	0	0	0	0	0
2 Aug. 1978	2	2 ± 0	12 ± 0	0	0	0
1 Sept. 1978	3	30 ± 1	81 ± 4	78 ± 5	8 ± 1	0
SECOND STUDY						
4 June 1984	0	0	0	0	0	0
3 Sept. 1984	3	90 ± 1	100	100	1 ± 1	0

Table 3. Germination percentages (mean ± SE) of *Chaerophyllum procumbens* seeds buried in soil in the nonheated greenhouse for 4 months and then incubated in light and in darkness at five alternating temperatures regimes for 15 days.

Date test began	Seed age (mos.)	Incubated in	Temperature regime (EC)				
			15/6	20/10	25/15	30/15	35/20
23 May	0	Light	0	0	0	0	0
		Dark	0	0	0	0	0
25 Sept.	4	Light	35 ± 1	63 ± 2	75 ± 2	2 ± 1	0
	4	Dark	16 ± 3	25 ± 8	15 ± 1	4 ± 1	0

length, and during May, June, and July 1986 they grew very little (Table 4). During August, embryo length more than doubled, and by 15 September all seeds remaining in the bag under the leaves in the greenhouse had germinated. Mean length of embryos at the time the radicle started to split the seed coat was 4.6 mm.

Light Requirement for Embryo Growth. Embryos in freshly matured seeds did not grow in either light or darkness in May 1987 (Fig. 3). However, in September (after physiological dormancy was broken) embryos grew in all seeds incubated in light, and 37 out of 50 seeds had germinated in light by day 14. In darkness, embryos grew in only 10 of 50 seeds, and all 10 of them germinated.

ECOLOGICAL LIFE CYCLE. *Effect of Vernalization on Flowering.* Plants of *C. procumbens* did not require vernalization to flower (Table 5). In the first experiment, the first nonvernalized plant to flower in the heated greenhouse did so on 7 January 1980 and the last one on 28 January 1980. In general, for plants moved to the heated greenhouse there was a decrease in time to beginning of flowering and in time before all plants in the cohort flowered with an increase in number of hours of vernalization. All plants in the nonheated greenhouse that were to receive the full winter vernalization period (last hours of vernalization were recorded on 9 May 1980) died. In the second experiment, first and last flowering dates for nonvernalized plants were 30 November 2000 and 28 December 2000, respectively. First and last flowering dates for plants exposed to the full winter vernalization period were 13 March 2001 and 7 April 2001, respectively.

Table 4. Growth of embryos (mean length ± SE) of *Chaerophyllum procumbens* seeds stored in a fine-mesh cloth bag on moist soil under 5 cm of dead oak leaves in a nonheated greenhouse.

Date measured	Embryo length (mm)
23 May 1986	0.47 ± 0.01
1 June 1986	0.53 ± 0.01
1 July 1986	0.56 ± 0.01
1 August 1986	0.59 ± 0.01
1 Sept. 1986	1.36 ± 0.01
15 Sept. 1986	all germinated

Life Cycle and Biomass Allocation Phenology. In north-central Kentucky, *C. procumbens* germinates in September and October, and plants overwinter with cotyledons and one or two leaves. Following the overwintering period, plants grow and develop into rosettes of five to six leaves. Flower buds are initiated by mid-March, plants begin to bolt in early April, and flowering occurs from mid-April to early May. Mericarps ripen and are dispersed by the end of May, by which time the entire plant has senesced.

Percent total dry weight allocated to roots was highest at fall and spring rosette growth stages and was significantly greater in the 2001 (21.6 ± 1.3 and 22.2 ± 2.9%, respectively) than in the

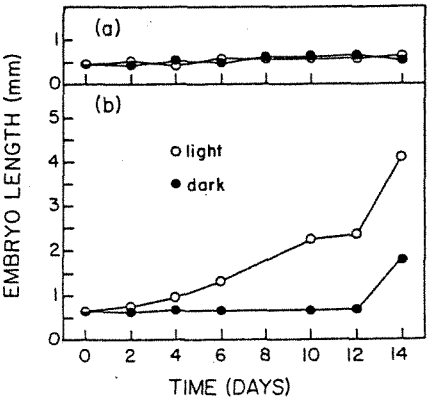

Fig. 3. Growth of embryos (mean length in millimeters; all SEs ranged from 0.01 to 0.05 mm) in seeds of *Chaerophyllum procumbens* incubated in light and in darkness at 25/15°C for 14 days starting on (a) 23 May 1987 and (b) 25 September 1987.

Table 5. Flowering of *Chaerophyllum procumbens* plants following exposure to various periods of vernalization in a nonheated greenhouse in Lexington, Kentucky. All surviving plants flowered.

Date moved to heated greenhouse	Hours of vernalization	Date first plant flowered	Date last plant flowered	Number of days to flowering	Number plants surviving and flowering
FIRST STUDY					
9 October 1979 (nonvernalized control)	0	7 January 1980	28 January 1980	90–111	15
1 November 1979	169	31 December 1979	28 January 1982	61–79	15
15 November 1979	411	31 December 1979	3 March 1980	46–108	15
1 December 1979	540	7 January 1980	11 February 1980	38–73	15
15 December 1979	773	21 January 1980	4 February 1980	37–51	15
1 January 1980	1002	28 January 1980	25 February 1980	28–59	15
15 January 1980	1173	4 February 1980	18 February 1980	20–34	13
1 February 1980	1356	18 February 1980	25 February 1980	18–25	11
15 February 1980	1439	3 March 1980	10 March 1980	16–23	11
1 March 1980	1629	17 March 1980	31 March 1980	17–31	7
Control (exposed to full winter vernalization period)	2217				0
SECOND STUDY					
30 September 2000 (nonvernalized)	0	30 November 2000	28 December 2000	61–89	15
Control (exposed to full winter vernalization period)	1588	13 March 2001	7 April 2001	164–189	15

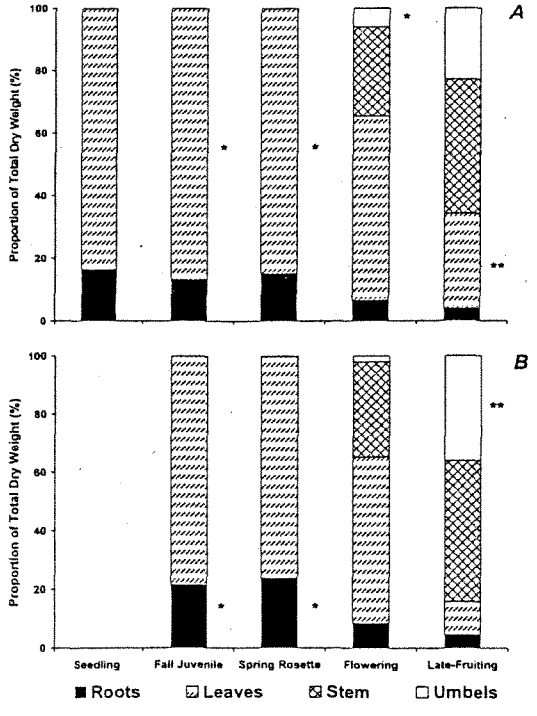

Fig. 4. Biomass allocation phenology for the 2000 (A) and 2001 (B) cohorts of *Chaerophyllum procumbens*. All SEs ≤ 2.89. Asterisk(s) indicate(s) significantly greater biomass allocation to a plant structure of 2000 or 2001 cohort (* $P < 0.05$; ** $P < 0.001$).

2000 (13.4% ± 1.1% and 15.2 ± 1.1%, respectively) cohort. Biomass allocated to roots then decreased to less than 7.0% of total plant dry weight by the end of the life cycle for both cohorts (Fig. 4). During the flowering and late-fruiting growth stages, significant differences in percent allocation occurred only in aboveground structures. Biomass allocation differences between cohorts at late-fruiting was greatest in percent dry weight allocated to reproductive structures and to leaves (Fig. 4). Reproductive allocation was significantly less in the 2000 (22.7 ± 0.4%) than in the 2001 (36.0 ± 0.9%) cohort.

Mean total plant dry weight increased from the seedling to flowering growth stages. Spring rosettes of the 2000 cohort were significantly heavier than those of the 2001 cohort (Fig. 5). However, between spring rosette and flowering growth stages total plant dry weight increased four-fold in the 2000 cohort and eight-fold in the 2001 cohort, resulting in no significant difference in mean total dry weight (0.28 ± 0.01 g) between cohorts at flowering. Between flowering and late fruiting, total plant dry weight decreased 49% in the 2000 cohort and 24% in the 2001 cohort (Fig. 5), apparently due to loss of mass in roots and leaves (Fig. 6).

Reproductive mass at late-fruiting was strongly correlated with vegetative mass (Fig. 7).

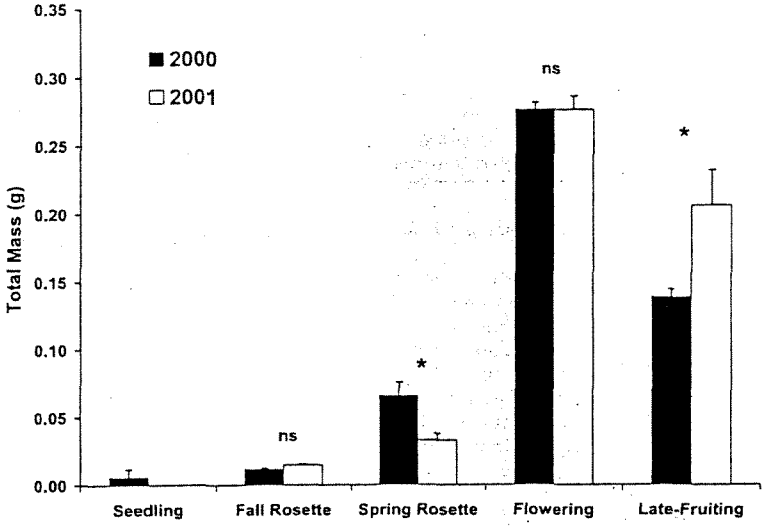

Fig. 5. Mean total dry mass (± SE) phenology for 2000 and 2001 cohorts of *Chaerophyllum procumbens*. Asterisk indicates a significant difference between cohorts ($P < 0.05$, ANOVA), and ns indicates no significant difference.

Slopes of the regression for the 2000 (0.259 ± 0.041) and the 2001 (0.684 ± 0.055) cohorts were significantly different ($P = 0.0044$). Intercepts of the regression for the 2000 (0.005 ± 0.004) and the 2001 (−0.003 ± 0.007) cohorts did not differ significantly ($P = 0.6839$).

Discussion. SEED GERMINATION ECOLOGY. Eight levels of MPD have been distinguished based on level of physiological dormancy (deep, intermediate, or nondeep), various temperature treatments (warm and/or cold stratification) required for completion of germination, temperature requirements for embryo growth, and responses of seeds to gibberellic acid (Baskin and Baskin 1998). Five levels of MPD are called simple, and three are called complex. In the simple levels of MPD, embryos grow only at high (≥15°C) temperatures, while in the complex levels embryos grow only during cold stratification.

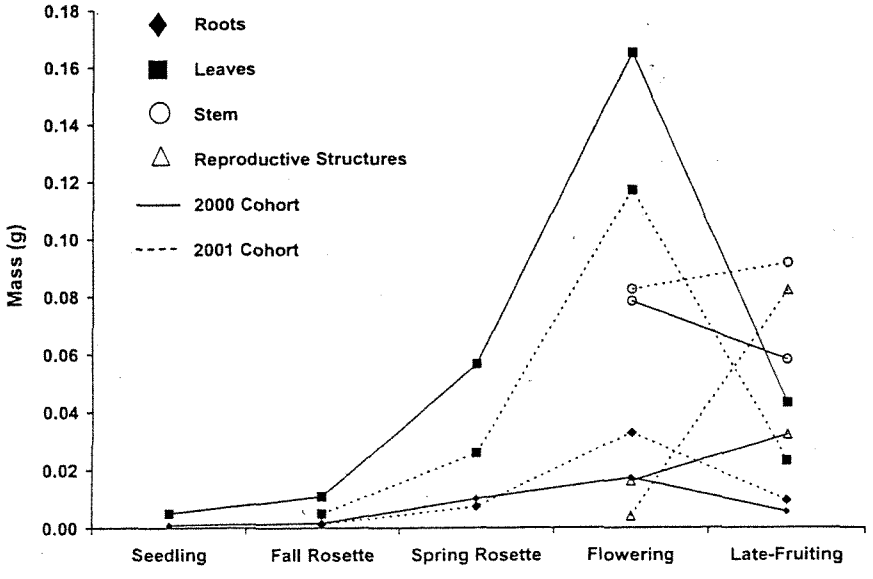

Fig. 6. Mean dry mass phenology for plant structures of 2000 and 2001 cohorts of *Chaerophyllum procumbens*.

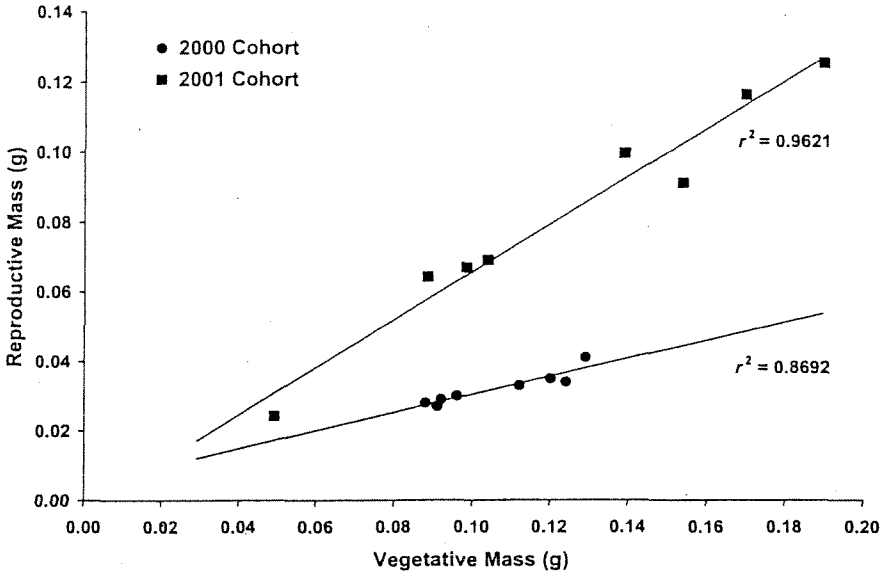

Fig. 7. Relationship between reproductive mass and vegetative mass at late-fruiting harvest for 2000 (•) and 2001 (■) cohorts of *Chaerophyllum procumbens*.

In four of the five levels of simple MPD, seeds require exposure to summer (high), autumn (intermediate), and winter (low) temperature conditions before they will germinate in spring. In contrast, seeds of some species with nondeep simple MPD require only summer temperature conditions and then germinate in autumn, while seeds of other species with nondeep simple MPD require only winter temperature conditions and then germinate in spring.

Seeds of *C. procumbens* have MPD when they mature in spring. Like seeds of various winter annuals with fully developed embryos (Baskin and Baskin 1986, 1990b) and those of *C. tainturieri* (Baskin and Baskin 1990a) with underdeveloped embryos, physiological dormancy in seeds of *C. procumbens* was broken during summer (Table 2). Further, also like *C. tainturieri*, embryo growth occurred in seeds of *C. procumbens* in late summer-autumn. Thus, relatively high temperatures were required for loss of both physiological and morphological dormancy, and seeds of *C. procumbens*, like those of *C. tainturieri*, germinate in autumn after being exposed to summer temperatures. Thus, seeds of *C. tainturieri* and *C. procumbens* have nondeep simple MPD.

Although embryos in freshly-matured seeds are slightly less than 0.5 mm in length, they are about 4.6 mm in length at the time the radicle begins to emerge. However, little embryo growth occurs until late summer and early autumn, after physiological dormancy is broken (Table 4). In the greenhouse, the peak of germination for seeds sown on 1 June 1978 was in late August and early September, when the daily temperature regime was about 32/20°C (Fig. 2). In contrast, seeds that had been allowed to come out of physiological dormancy in the greenhouse germinated to high percentages in light at 15/6, 20/10, and 25/15 but not at 30/15 and 35/20°C (Table 2). The reason for little or no germination occurring in the incubator at 30/15°C and high germination occurring in the greenhouse at 32/20°C may be due to the number of hours of high temperatures that seeds received each day. In the incubator, seeds, for example, were exposed to 30°C for 12 hr each day, while the thermograph records show that seeds in the greenhouse were exposed to temperatures of 30°C or higher for only about 6 hr each day.

The time required for embryo growth and thus for the breaking of morphological dormancy is relatively short. A few seeds that were incubated in light at 25/15°C in September had fully elongated embryos after 10 days, and about 75% of the embryos had grown to full length after 14 days (Fig. 3). Once an embryo begins to grow, it continues to elongate until the tip of the radicle is pushed from the seed coat and the seed is germinated. Since May temperatures (25/15°C) are optimal for embryo growth and since

embryos grow rapidly at favorable temperatures, seeds would germinate in May if the embryos did not have physiological dormancy. Thus, if seeds that fail to germinate in autumn (due to lack of light) did not enter physiological dormancy in late autumn and winter, temperatures in May would be suitable for embryo growth and thus germination. Although May temperatures promoted the break of physiological dormancy in seeds of *C. tainturieri*, 3–4 months of exposure to high temperatures were required for loss of physiological dormancy to occur (Baskin and Baskin 1990a). Thus, although seeds of *C. procumbens* are exposed to temperatures in May that are suitable for both the breaking of physiological dormancy and embryo growth, germination would not occur because there is insufficient time in May for physiological dormancy to be broken. Germination of freshly matured seeds of *C. procumbens* continuously incubated in light at 25/15°C did not reach 10% until the 60th day (Baskin and Baskin unpublished data). Exposure of *C. procumbens* seeds to the high temperatures of June, July, and August (30/15 to 35/20°) would promote the breaking of physiological dormancy, but these temperatures would be too high for embryo growth and germination.

At the end of summer, a high percentage of the *C. procumbens* seeds required light for germination, and this also was true for those of *C. tainturieri* (Baskin and Baskin 1990a). However, seeds of *C. tainturieri* exposed to light in June did not germinate in darkness in September, while those exposed to light in July germinated in darkness in September (Baskin and Baskin 1990a). These data indicate that: (1) embryos can respond to light at supraoptimal temperatures for germination when seeds are starting to come out of physiological dormancy in summer; and (2) the light stimulus is retained until physiological dormancy is fully broken and temperatures are favorable for germination in autumn. It is not known if seeds of *C. procumbens* can be light stimulated in summer and then germinate in darkness in autumn.

The light requirement for embryo growth in seeds of *C. procumbens* and of *C. tainturieri* is similar to that in seeds of *Apium graveolens* L. (Apiaceae), which have only morphological dormancy (Jacobsen and Pressman 1979). In seeds of *A. graveolens*, a light-induced stimulus from the embryo causes breakdown of endosperm, which apparently makes stored food reserves available for embryo growth. Jacobsen and Pressman (1979) suggested that the stimulus coming from the embryo is a gibberellin.

Germination of a few seeds the seventh autumn after they were sown in the nonheated greenhouse suggests that *C. procumbens* has the ability to form a long-lived or persistent seed bank (sensu Grime 1981). Decreased germination in darkness, as compared to light, in autumn (Table 3) is one factor contributing to the formation of a soil seed bank. However, some seeds do germinate in darkness in autumn. Consequently, a soil seed bank would eventually be depleted by *in situ* germination, unless it is replenished by the addition of seeds.

ECOLOGICAL LIFE CYCLE. In the germination phenology studies in the greenhouse, seeds of *C. procumbens* germinated only in autumn, indicating that the taxon is an obligate winter annual. This conclusion about the life cycle is corroborated by field observations; no newly germinated seedlings have been found at the population site in spring. Autumn germination means that growth and development of plants occur while light levels are high at the soil surface. In fact, by the time the tree canopy closes in early May plants have flowered and green seeds have reached their full length. If seeds did not germinate until March or April, plants would have only a few weeks of maximum light for growth and development before canopy closure. Thus, an obligate vs. facultative type of life cycle for this winter annual may be viewed as an adaptation to its winter-deciduous forest habitat. Like the perennial spring ephemerals that occur in temperate deciduous forests of the Northern Hemisphere (Sparling 1964, 1967; Goryshina 1980; Kawano et al. 1982), *C. procumbens* completes the photosynthetically-active phase of its annual life cycle during the time the deciduous trees are leafless.

The response of *C. procumbens* to varying amounts of vernalization was similar to that of most other winter annuals. In a study on the effect of vernalization on flowering of winter annuals, Baskin and Baskin (1974) found that 48 of 50 species did not require a low temperature pretreatment to flower. In naturally-occurring *C. procumbens* populations subjected to vernalizing temperatures, a decrease in number of days to flowering means an increase in number of days in which to complete reproduction before canopy closure.

The growth habit of *C. procumbens* was characterized by accumulation of biomass in both

above- and below-ground plant structures during open-canopy conditions (Fig. 6). All plant structures showed an increase in mass until harvesting at the peak of flowering. Decrease in total biomass from flowering to late-fruiting was due mainly to loss of mass in roots and leaves, and this was concurrent with canopy closure. Such phenology might suggest that the decrease in photosynthetic photon flux density (PPFD) associated with canopy closure in spring exerts a negative effect on biomass accumulation and initiates plant senescence. However, plants of *C. procumbens* in our vernalization studies received no reduction in PPFD at reproductive growth stages, and yet after flowering they senesced rapidly. Thus, time of senescence appears to be genetically predetermined.

Struik (1965) reported 45% dry weight allocation to roots in juveniles of *C. procumbens* growing in southern Wisconsin. This is twice the highest percent root allocation (22.2 ± 2.9%) recorded for *C. procumbens* harvested during our study. This rather large difference may be explained by plant response to differing ecological conditions. The Wisconsin population was confined to bottomland forests, where plants experienced repeated submergence by flooding in autumn. As the water level finally receded, fall juvenile plants then initiated regrowth of aerial organs (Struik 1965). During our study period, plants did not experience disruption in growth of aerial structures, nor were they flooded.

Although biomass allocation patterns were statistically significant between cohorts during juvenile growth stages, the most obvious differences were at late-fruiting. Mean allocation to leaves in the 2001 cohort (11.2 ± 0.4%) was about one third that of the 2000 cohort (30.2 ± 0.8%). Mean reproductive allocation was more than one-third greater in the 2001 cohort (36.0 ± 0.9%) than that in the 2000 cohort (22.7 ± 0.4%). Generally, variation in reproductive allocation in annual plants is relatively low, and variation in reproductive output (measured as the weight of infructescences) often is associated with plant size (Bazzaz et al. 2000). In the case of *C. procumbens*, this trend was not observed. Mean reproductive output in the 2001 cohort (0.077 ± 0.011 g) was 2.4 times greater than in the 2000 cohort (0.032 ± 0.001 g). However, mean vegetative mass was only 1.2 times greater in the 2001 cohort (0.134 ± 0.017 g) than in the 2000 cohort (0.109 ± 0.005 g). In other words, the difference in percent reproductive allocation between cohorts was not completely accounted for by differences in plant size. This is further supported by comparing the linear relationship between reproductive mass and vegetative mass for each cohort (Fig. 7). Samson and Werk (1986) suggested that if slope or intercept of reproductive mass vs. vegetative mass regressions change among environments, differences in allocation may be the result of extrinsic factors and not solely related to differences in plant size. Thus, differences in slopes of the regressions ($P = 0.0044$) between the two cohorts suggest some level of plasticity in reproductive allocation in *C. procumbens* (Fig. 7). This variation in reproductive allocation in response to ecological factors may be explained, in part, by differences in amount and distribution of precipitation (Table 1). Although precipitation at the study site in March (54.9 mm) and April (42.9 mm) 2001 (reproductive growth stages of the 2000 cohort) was evenly distributed, the total amount for both months (97.8 mm) was less than one-half the 25-year average (220.2 mm) for these months. In March (202.4 mm) and April (101.9 mm) 2002 (reproductive growth stages of the 2001 cohort) rainfall was unevenly distributed, but the total amount for both months (304.3 mm) was considerably greater than the 25-year average (220.2 mm). This was particularly true for March 2002, when rainfall was about 40% greater than the 25-year average.

The autecology of *C. procumbens* reflects adaptations of this winter annual to the mid-latitude deciduous forest environment. Seed dormancy breaking requirements ensure that seedling establishment begins with opening of the forest canopy (i.e., fall senescence of deciduous leaves). Juvenile plants are winter-green, remaining above leaf litter and accumulating biomass during high-light and low-temperature conditions. Vernalization decreases time to flowering, thus increasing time for completion of reproductive growth stages prior to canopy closure. Although environmental stress, such as low amounts of precipitation, may reduce reproductive output, the resulting decrease in seeds available for fall germination may be somewhat compensated for by the ability of *C. procumbens* to form a small persistent seed bank.

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