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The Ecological Life Cycle of Cryptotaenia canadensis (L.) DC. (Umbelliferae), a Woodland Herb with Monocarpic Ramets

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ABSTRACT: *Cryptotaenia canadensis* is an herbaceous species of mesic and wet mesic forests and floodplains of eastern North America. The peak of flowering is in late May, and seeds ripen in late August and early September. Seeds have underdeveloped embryos and require cold stratification to come out of dormancy; thus, they have deep morphophysiological dormancy (MPD). In a nonheated greenhouse embryo length increased more than 85% (from 1.6-3.0 mm) during winter, and seeds germinated from early March to late April. Plants do not require vernalization for flowering, and in the greenhouse they can flower within 10 weeks after germination in spring. Thus, plants have the potential to behave as summer annuals. In the field, however, flowering is delayed until the 2nd year, or later. Vegetative propagation in *C. canadensis* occurs by the production of offshoots (ramets) at the base of the stem. The ramets are monocarpic. Ramet buds are formed during early May, but they do not produce leaves and roots until late August and early September. Many ramets behave as winter annuals, growing during autumn, overwintering, and then growing, flowering, setting seeds and dying the following growing season. Any ramets that fail to reach the critical size for flowering remain vegetative throughout the growing season and survive to the next growing season.

INTRODUCTION

Among the herbaceous species of the mesic deciduous forests of eastern North America, there are annuals, biennials and perennials that reproduce only sexually (seeds), and perennials that reproduce both sexually and vegetatively (*e.g.,* bulbs, corms and rhizomes). Members of the Umbelliferae (*e.g., Chaerophyllum procumbens* (L.) Crantz, *Cryptotaenia canadensis* (L.) DC., *Erigenia bulbosa* (Michx.) Nutt., *Osmorhiza clayontii* (Michx.) C. B. Clarke and *O. longistylis* (Torr.) DC.) are frequent components of the herb layer of mesic woodlands, and except for *C. canadensis* all of them reproduce by seeds only. *Cryptotaenia canadensis,* the subject of this study, differs from other woodland Umbelliferae as well as herbaceous woodland dicots in other plant families, because it reproduces via both seeds and monocarpic ramets. The purpose of this study was to investigate the ecological life cycle of *C. canadensis*. In this study, we determined: (1) the requirements for dormancy breaking and germination of seeds; (2) when ramets are produced; (3) age of plants (*i.e.,* ramets as well as plants derived from seeds) when they flower; and (4) if vernalization is required for flowering.

Cryptotaenia DC. is a small genus native to eastern North America, Eurasia and Africa (Hiroe and Constance, 1958). The only member of the genus in eastern North America is *C. canadensis*. This herbaceous species is found in rich woods, thickets and woodland margins and along stream banks from Quebec and New Brunswick to Manitoba S to Georgia, Alabama, Arkansas and Texas (Fernald, 1950; Gleason. 1952; Radford *et al.,* 1968). *Cryptotaenia canadensis* also occurs in Japan (Hiroe and Constance, 1958), where it is cultivated as a vegetable (Hiroe and Constance, 1958). Although Hiroe and Constance (1958) called the *Cryptotaenia* species in Japan *C. canadensis,* Hara (1962) considers it to be *C. japonica* Hassk. because of differences in numbers of involucral and involucellal bracts and of flowers per umbellule. *Cryptotaenia* is one of 34 herbaceous genera in mesic deciduous forests of eastern North America that exhibits an Arcto-Tertiary pattern of distribution (Li, 1952; Wood, 1971). In N-central Kentucky flowering shoots of *C. canadensis* begin to elongate in mid-April, and buds are visible in

early May. The flowering season extends from mid-May to mid-June, with the peak occurring in late May. Seeds (mericarps) develop during summer, ripen in late August and early September, fall from the plant mostly in September and October and germinate in March and April.

Information about the ecological life cycle of *Cryptotaenia canadensis* is sparse. Seeds have underdeveloped (linear) embryos (Martin, 1946), which means that the embryo is small in relation to the amount of endosperm in the seed. The species has been described as a hemicryptophyte (*e.g.,* Cain, 1945; Buell and Wilbur, 1948; Leblanc, 1963), and reported dates of earliest flowering range from 23 May in Michigan (McWilliams and Ludwig, 1972), to 6 June in Ohio (Wolfe *et al.,* 1949). Daubenmire (1936) reported that the species flowers in early summer and has functional leaves during early, mid and late summer.

MATERIALS AND METHODS

Germination phenology. —Seeds were exposed to near-natural daily and seasonal temperature changes to determine the time of the year when they germinate. Mature ripe seeds were collected on 10 September 1978 and on 16 September 1979 from a population growing in a mesic deciduous forest in Fayette Co., Kentucky. Eight days after each collection, three replications of 300 seeds each were sown on soil in 32 x 22 x 9 cm metal flats and covered with oak leaves. The flats were placed under a bench in a nontemperature-controlled greenhouse (no heating or air-conditioning and windows were kept open all year). Temperatures were recorded continuously with a thermograph, and mean weekly maximum and minimum temperatures were calculated from the data. Flats containing seeds sown in 1978 were kept in the greenhouse until 1 July 1981, and those containing seeds sown in 1979 were kept until 1 July 1982. To simulate moisture conditions that could occur in the field, the soil was watered daily from 1 September to 30 April, except on days during winter when it was frozen, and once each week from 1 May to 30 August. Each week the leaves were lifted, and seeds with an emerged radical were counted as germinated and removed from the flats.

Germination requirements. —A preliminary experiment conducted in the autumn and winter of 1978-1979 showed that seeds required cold stratification to overcome dormancy and that warm prior to cold stratification was not necessary. Therefore, we conducted experiments to determine (1) how much cold stratification was required to break seed dormancy and (2) the temperature and light requirements for germination of stratified seeds. Germination requirements were determined using seeds collected on 16 September 1979. Seeds were placed on moist sand in 5.5-cm petri dishes on 24 September 1979, and three replications of 50 seeds each were used for each test condition. Seeds were moist-cold stratified for 0, 42, 70 and 98 days in light (14-hr daily photoperiod of 20 μmol m^{-2} s^{-1}, 400-700 nm) or darkness at a constant temperature of 5 C. Germination tests were conducted in temperature- and light-controlled incubators at alternating (12/12 hr) temperature regimes of 15/6, 20/10, 25/15, 30/15 and 35/20 C. These temperature regimes approximate the mean daily maximum and minimum monthly air temperatures in N-central Kentucky for March, 15/6; April, 20/10; May, 25/15; June and July, 30/15; August, 35/20; September, 30/15; October, 20/10 and November, 15/6 C (Hill, 1976). Seeds received either 14 hr of cool white fluorescent light (20 μmol m^{-2} s^{-1}, 400-700 nm) each day, or they were in continuous darkness. Seeds stratified in light were tested in light and darkness, and those stratified in darkness were tested in darkness and light. All dishes were wrapped with plastic film, and those incubated in darkness were wrapped additionally with two layers of aluminum foil. The daily photoperiod extended from 1 hr before to 1 hr after the daily high temperature period. Germination tests were terminated after 15 days for all seeds, except those receiving no stratification and tested in light. These seeds were kept at their respective thermoperiods until the end of the experiment (113 days). Germination data were analyzed using a 4-way ANOVA.

Phenology of embryo growth.—Seeds were exposed to near-natural daily and seasonal temperature changes, and the time of year when the embryos elongated within the seeds was determined. Seeds were collected on 11 September 1985 and placed in a fine-mesh nylon bag on soil in a flat and covered with leaves to simulate field conditions. The flat was placed under a bench in the nontemperature-controlled greenhouse and watered daily, except on days during winter when the soil was frozen. On 11 September 1985 and the 1st and 15th day of each month until 1 March 1986, 50 seeds were removed from the bag. Embryos were excised from the 50 seeds with a razor blade and measured using a dissecting microscope equipped with a micrometer; mean lengths and standard errors were calculated.

Phenology of seedlings and ramets.—On 5 April 1981, 50 newly germinated seedlings and on 10 June 1980, 50 flowering plants were marked with wire rings in a 5 x 10 m area in a mesic deciduous forest in Fayette Co., Kentucky. At 2- to 4-week intervals until August 1982, the seedlings were checked for survival, number of leaves and flowers, and the other plants were checked for production of ramets. After ramets appeared, they were checked for number of leaves, flowers, production of ramets and senescence.

Flowering.—The objective of this experiment was to determine if plants require vernalization for flowering. On 16 September 1979, one ramet was collected in the field from each of 80 plants that flowered during the summer of 1979. Each plant was placed in a 15 x 15 cm (diam x depth) pot in the nontemperature-controlled (nonheated) greenhouse. On 8 October, 1 November, 1 December 1979 and on 1 January and 1 February 1980, 15 plants were moved to a heated greenhouse, where temperatures were 20-30 C during the day and 15-20 C at night. Fifteen plants were retained in the nonheated greenhouse throughout the study. From the thermograph records in the nonheated greenhouse, we calculated the number of hours that each group of plants was exposed to temperatures between 0.5 and 10 C (Fig. 2). These temperatures generally are optimal for vernalization of most species, but effective temperatures can range from a few degrees below 0 to a few above 10 C (Leopold, 1964). Plants were watered daily and examined weekly for flowering until the study was terminated on 18 August 1980.

RESULTS

Germination phenology.—In the nontemperature-controlled greenhouse, seeds of *Cryptotaenia canadensis* germinated only in spring (Fig. 1). Eighty-one percent of the seeds sown in 1978 germinated in the spring of 1979, and 82% of those sown in 1979 germinated in the spring of 1980. The germination season extended from early March to late April, with 73 and 60% of the germination in 1979 and 1980, respectively, occurring the last 2 weeks of March. Mean daily maximum and minimum temperatures during this period in 1979 were 19.5 and 9.6 C, respectively, and in 1980 they were 14.5 and 5.4 C, respectively. An additional 3.9 and 2.0% of the seeds sown in 1978 and 1979, respectively, germinated the 2nd spring after sowing. No seeds germinated the 3rd spring after sowing.

Germination requirements.—Seeds were dormant at maturity and required cold stratification before they would germinate (Table 1). Germination increased significantly with an increase in length of the stratification period from 42 to 98 days (Table 2). The incubation (test) temperature of stratified seeds had a significant effect on germination; 15/6 and 20/10 C were the optimal thermoperiods. Seeds stratified in light tended to have higher germination than those stratified in darkness. However, this effect of stratification light environment depended on both incubation light environment and incubation temperature, resulting in significant interactions between all these factors. The positive effect of stratification in the light on germination was strongest if seeds were incubated in the dark and/or incubated at higher than optimal temperatures. For seeds incubated in the light at optimal temperatures there was no apparent effect of stratification light environment.

Phenology of embryo growth.—On 15 September 1985, embryos in the freshly matured

seeds were 1.6 ± 0.04 mm (mean ± SE) long, and on 1 March 1986 they were 3.0 ± 0.08 mm. They elongated 0.7 mm from 15 September to 15 February and another 0.7 mm between 15 February and 1 March. Embryos were not measured on 15 March because most of the seeds in the bag had germinated.

Phenology of seedlings and ramets. —Seedlings marked on 5 April were in the cotyledon stage, and 2 weeks later they had cotyldeons plus one leaf. By mid-May, the cotyledons were dead, but most seedlings still had only one leaf. However, a few had two leaves. All seedlings had two leaves by early June, and by late September they had 3-4 leaves. At the end of October, only 13 of the 50 seedlings were alive and by late November only eight were alive. All leaves died during winter, and new ones began to expand in March 1982. By early May, only four plants were alive and they had 1-3 leaves. One of these plants flowered in June 1982; the other three died during the summer of 1982 without flowering.

On 10 June 1980, flowering plants had from 1-3 buds at the base of the stem, and these buds were 2-4 mm long. In late August and early September the buds began to grow, and each one produced 2-3 leaves and 3-4 roots. Thus, by mid- to late September each senescing flowering plant had 1-3 offshoots (ramets) attached to the base of its stem. The ramets remained attached to the parent plant until it died in late September and early October. Almost all the leaves on the ramets died during winter, but small unexpended ones were present under the leaf litter. Leaf growth resumed in early March 1981, and by early April ramets had 1-4 leaves. Bolting began in mid-April, and ra-

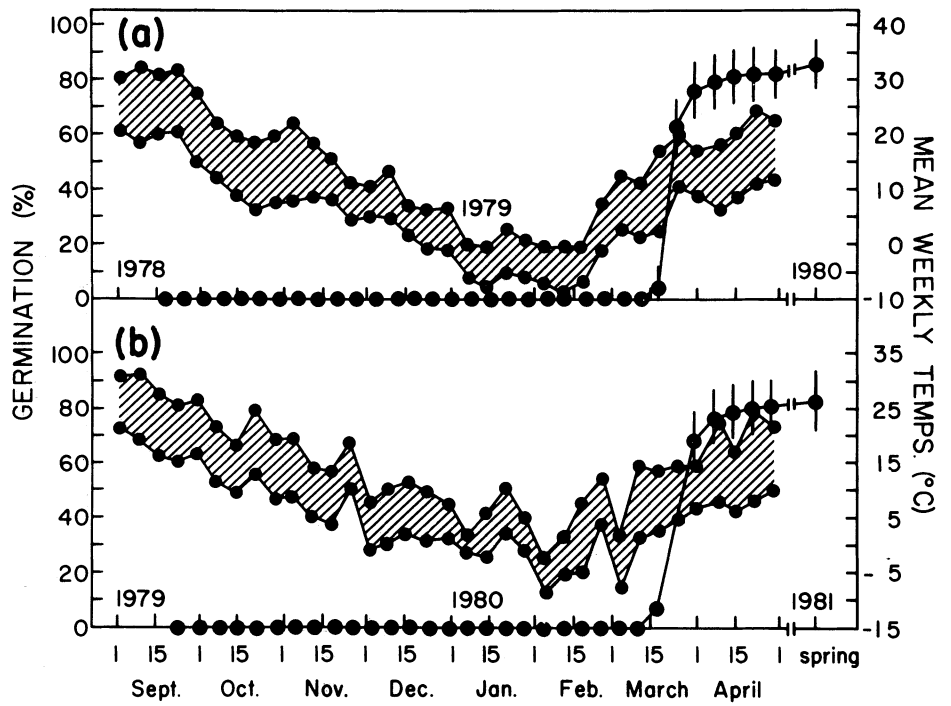

Fig. 1.—Germination phenology of *Cryptotaenia canadensis* seeds sown on soil in the non-heated greenhouse on (a) 18 September 1978 and (b) 23 September 1979. No additional seeds germinated the third spring after sowing. Lines represent cumulative germination curves and hatched areas represent mean weekly maximum and minimum temperatures in the greenhouse. Bars are ± 1 SE

mets had flower buds by mid-May. In most cases where three ramets were growing very close to each other (*i.e.,* derived from the same parent plant), usually only one flowered, and the nonflowering ramets had 1-2 green leaves all summer. New buds appeared at the base of the flowering stems in early May, and on 10 May 1981 they were 2-3 mm in length. These buds developed into new ramets in the autumn of 1981.

Flowering.—Vernalization is not required for flowering; however, vernalized plants flowered sooner than those not vernalized (Fig. 2).

DISCUSSION

A first step in understanding the ecological life cycle of a species is to determine the environmental conditions necessary for completion of each stage of the life cycle. In *Cryptotaenia canadensis,* low winter temperatures are required to break seed dormancy; therefore, seeds become nondormant during winter and germinate in early spring. If seeds receive light during winter and/or spring, they germinate to high percentages in light and darkness in early spring. Since seeds can be light-stimulated during stratification and retain the ability to germinate in darkness at higher temperatures, the light requirement for germination may be fulfilled during winter, and seeds can germinate in darkness in spring. On the other hand, if seeds are in darkness during winter, they can be light-stimulated in spring. Seeds not receiving light in winter or spring germinate to low percentages, and this may explain why some seeds covered with leaves in the nonheated greenhouse did not germinate until the 2nd year. Although stratified seeds can germinate to high percentages at May (25/15) and June (30/15 C) thermoperiods, germination at these temperatures is probably of little ecological consequence. In the field,

TABLE 1.—Germination (mean ± SE) percentages of *Cryptotaenia canadensis* seeds stratified at 5 C for 0, 42, 70 and 98 days and incubated at various thermoperiods

Days of strat.	Strat. in	Incubated in	Days of incubation	Incubation temperatures (C)				
				15/6	20/10	25/15	30/15	35/20
0		light	15	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
0		light	113	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
0		dark	15	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
42	light	light	15	0 ± 0	17 ± 2	3 ± 2	1 ± 1	0 ± 0
42	dark	light	15	1 ± 1	11 ± 3	1 ± 1	1 ± 1	0 ± 0
42	light	dark	15	0 ± 0	71 ± 7	29 ± 1	14 ± 4	0 ± 0
42	dark	dark	15	0 ± 0	5 ± 2	0 ± 0	3 ± 2	0 ± 0
70	light	light	15	54 ± 8	75 ± 2	25 ± 8	11 ± 5	0 ± 0
70	dark	light	15	51 ± 4	79 ± 3	5 ± 3	2 ± 1	0 ± 0
70	light	dark	15	86 ± 5	78 ± 3	35 ± 3	23 ± 3	1 ± 1
70	dark	dark	15	13 ± 2	13 ± 2	9 ± 2	1 ± 1	0 ± 0
98	light	light	15	91 ± 1	87 ± 2	38 ± 4	20 ± 4	0 ± 0
98	dark	light	15	98 ± 2	86 ± 4	22 ± 6	11 ± 2	0 ± 0
98	light	dark	15	95 ± 2	93 ± 6	87 ± 2	59 ± 5	0 ± 0
98	dark	dark	15	18 ± 1	25 ± 3	4 ± 1	6 ± 0	0 ± 0

seeds germinate in March and April before mean daily maximum and minimum temperatures reach 25/15 and 30/15 C. Some of the light environment x temperature interactions of germination occur because 25/15 and 30/15 C are too high for optimal germination, and seeds are more sensitive to light received at 5 C than at higher temperatures.

During cold stratification, the underdeveloped embryos in the seeds double in length. Seeds with underdeveloped embryos that require cold stratification before they will germinate have deep morphophysiological dormancy (MPD) (Nikolaeva, 1977). Of the 40 (including *Cryptotaenia canadensis*) herbaceous woodland species that have been studied (Pickett, 1913; Barton, 1936, 1939, 1944; Barton and Schroeder, 1942; Baskin and Baskin, 1983a,b, 1984a,b, 1985a,b,c, 1986a,b), 30 have deep MPD, and nine do not have it. Seeds of *Isopyrum biternatum* (Raf.) T. & G. have underdeveloped (rudimentary) embryos, but they exhibit morphological, not morphophysiological, dormancy (Baskin and Baskin, 1986b).

The presence of deep MPD in seeds of *Cryptotaenia canadensis* is significant from two points of view: (1) Of the 34 herbaceous genera in mesic deciduous forests in eastern North America that exhibit an Arcto-Tertiary pattern of distribution, 18 (including *Cryptotaenia*) have deep MPD; three do not have deep MPD and 13 have not been stud-

TABLE 2.—Summary of analysis of variance for germination of stratified seeds of *Cryptotaenia canadensis*. Nonstratified seeds were not included in the analysis. Days = length of stratification period; Stratification = light environment during stratification; Incubation = light environment during incubation period; Temperature = temperature during incubation period

Source of variation	Sum of squares	df	Mean square	F	Significance
Days	8912.68	2	4456.34	682.67	P<.001
Stratification	4971.76	1	4971.76	761.63	P<.001
Days x strat.	659.48	2	329.74	50.51	P<.001
Incubation	5.69	1	5.69	.87	n.s.*
Days x incub.	510.81	2	255.41	39.13	P<.001
Strat. x incub.	3414.76	1	3414.76	523.11	P<.001
Days x strat. x incub.	504.54	2	252.70	38.65	P<.001
Temperature	16857.42	4	4214.35	645.60	P<.001
Days x temp.	5496.54	8	687.07	105.25	P<.001
Strat. x temp.	1538.80	4	384.70	58.93	P<.001
Days x strat. x temp.	739.97	8	92.50	14.15	P<.001
Incub. x temp.	1238.20	4	309.55	47.42	P<.001
Days x incub. x temp.	1692.30	8	211.54	32.41	P<.001
Strat. x incub. x temp.	1408.24	4	352.06	53.93	P<.001
Days x strat. x incub. x temp.	724.46	8	90.56	13.87	P<.001
Error	783.33	120	6.53		

*n.s. = not significant at P<.05

ied. Based on embryo size, however, there is a good chance that six of the 13 unstudied genera have deep MPD. Thus, deep MPD appears to be an ancient type of seed dormancy, and it is found in *C. canadensis*. (2) Underdeveloped embryos are prevalent in the Umbelliferae (Martin, 1946), but not all seeds with underdeveloped embryos have deep MPD. According to seed dormancy characteristics, the Umbelliferae with underdeveloped embryos can be divided into three categories. *Heracleum sphondylium* L. (Stokes, 1953), *Osmorhiza longistylis* (Baskin and Baskin, 1984b), *C. canadensis, Perideridia americana* (Nutt.) Reichenb. and *Sanicula canadensis* L. have deep MPD. Seeds of *Chaerophyllum procumbens* (L.) Crantz are dormant, but they require high (summer) temperatures to break dormancy. Consequently, embryos elongate and seeds germinate in autumn. Seeds of *Conium maculatum* L. and *Pastinaca sativa* L. exhibit morphological dormancy. That is, the embryo must grow before seeds will germinate, but neither warm nor cold stratification is required. Consequently, embryos grow and seeds germinate over a wide range of temperatures immediately after seeds are dispersed.

Although low winter temperatures are required to break seed dormancy in *Cryptotaenia canadensis,* vernalization is not required for flowering. Thus, *C. canadensis* has the potential to flower and set seeds in the same year it germinates. The main effect of low winter temperatures on plants of *C. canadensis* is that it kills expanded leaves and retards growth of unexpended leaves. Plants from newly germinated seeds grew rapidly and flowered within 10 weeks after germination in spring in the greenhouse, and those in the field grew slowly and did not flower until at least their 2nd year. Thus, it appears that initiation of flowering is size-dependent. The fact that the species does not flower the same year it germinates in mesic forests gives some indication of the stressfulness of this habitat.

If a monocarpic species is to persist in a habitat where few seedlings survive, the production of ramets is a necessity. The persistence of *Cryptotaenia canadensis* in mesic

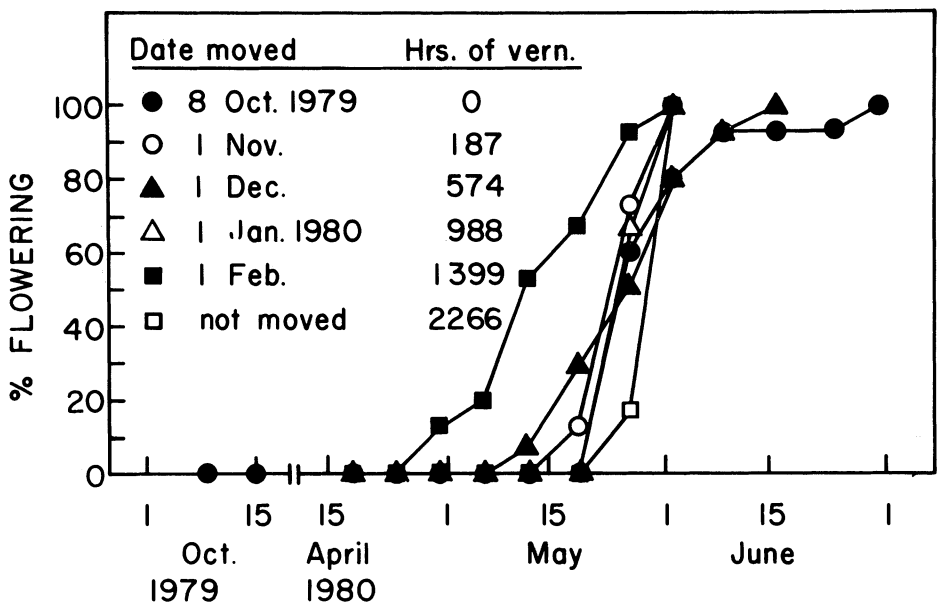

Fig. 2.—Cumulative flowering percentages of *Cryptotaenia canadensis* plants moved from the nonheated to the heated greenhouse on various dates and of plants that remained in the nonheated greenhouse

forests appears to be possible because the species produces ramets. Other species that have the same method of genet perennation as *C. canadensis* include two Umbelliferae, *Anthriscus sylvestris* (L.) Hoff. (Holm, 1925) and *Peucedanum palustre* (L.) Moench (Harvey and Meredith, 1981) and a composite *Boltonia decurrens* (T. & G.) Wood (Schwegman and Nyboer, 1985). It is not known if seedling survival is also low in natural habitats of the latter three species.

In addition to being much larger than a seedling when it becomes independent of the parent plant, the ramet has two periods of growth (autumn and spring) whereas the seedling has only one (spring) before the next flowering season begins. Thus, ramets reach the critical size for flowering during their 1st year of growth, whereas seedlings do not. Seedlings have the potential to reach flowering size before the onset of the flowering season, but this potential is not realized in the forest habitat. Ramets, then, may exhibit a winter annual life cycle. They are produced in autumn, overwinter and flower, set seeds and die the following growing season.

The ecological life cycle of *Cryptotaenia canadensis* is like that of many perennial herbaceous woodland species since its seeds have deep MPD and require cold stratification to become nondormant. The ramets of *C. canadensis* are like woodland annuals in that they are monocarpic. However, unlike the woodland annuals, *C. canadensis* perennates *via* production of ramets.

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