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Seed Morphology, Germination Phenology, and Capacity to Form a Seed Bank in Six Herbaceous Layer Apiaceae Species of the Eastern Deciduous Forest

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ABSTRACT

We compared seed mass, seed morphology, and long-term germination phenology of three monocarpic (M) and three polycarpic (P) Apiaceae species of the herbaceous layer of the Eastern Deciduous Forest. Seeds (mericarps) of the six species differed considerably in mass, shape, and ornamentation. Mean seed masses were ranked *Cryptotaenia canadensis* (M) < *Thaspium barbinode* (P) < *Sanicula canadensis* (M) < *S. gregaria* (P) < *Osmorhiza claytonii* (P) < *S. trifoliata* (M). Germination peaks occurred in the first or second spring following sowing. Germination of a few seeds was delayed until the sixth year. Regardless of seed mass or morphology, each species has the potential to form a (modified) Type III or (modified) Type IV persistent soil seed bank. Occurrence of a germination peak in the first or in the second year following seed maturity was related to time of dispersal in autumn and to type of seed dormancy.

INTRODUCTION

Cryptotaenia canadensis (L.) DC., *Osmorhiza claytonii* (Michx.) Clarke, *Sanicula canadensis* L., *S. gregaria* Bickn., *S. trifoliata* Bickn., and *Thaspium barbinode* (Michx.) Nutt. (Apiaceae) are frequent components in the herbaceous layer throughout a large portion of the deciduous forest of eastern North America (Hawkins 2003). *Cryptotaenia canadensis* and *S. canadensis* are biennials (monocarpic), and *S. trifoliata* is a facultative biennial (Hawkins 2003), therefore also a monocarpic species. *Osmorhiza claytonii, S. gregaria*, and *T. barbinode* are polycarpic perennials. Fruits of *C. canadensis* ripen in late August and early September and fall from the mother plants in September and October (Baskin and Baskin 1988, Hawkins 2003). Dispersal of *O. claytonii, S. canadensis*, and *S. trifoliata* seeds begins in August and can last for 1 yr or longer, with mature mericarps retained on dead, upright stems (Hawkins 2003). Dispersal of seeds of *S. gregaria* begins in August and lasts into September. However, unlike *S. canadensis* and *S. trifoliata*, seeds are not retained on the mother plant for an extended period of time. Hawkins (2003) found that most seeds of *T. barbinode* remained attached to the infructescences when dead shoots fell to the ground at the end of the growing season in October.

The fruit of the six study species, and of Apiaceae in general, is a schizocarp consisting of two mericarps that separate at maturity. In some species, including *C. canadensis* and *O. claytonii*, the mericarps remain attached to the mother plant by a slender stalk of tissue called the carpophore. The mericarp is the unit of dispersal and of germination. Morphology and size of mericarps differ considerably among the four genera included in our study (Table 1).

The potential for a species to form a persistent seed bank has been shown to be correlated with seed mass and morphology. Thompson and Grime (1979) reported that, generally, small seeds with smooth seed coats have a higher probability of forming a persistent soil seed bank

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Table 1. Morphology and size of mericarps of the six Apiaceae study species (Murley 1946, Radford et al. 1968, Gleason and Cronquist 1991)

Species	Morphology	Size
Cryptotaenia canadensis	linear-oblong, with ribs, often curved, not winged, stylopodium slender, glabrous, suborbicular in x-sec	5–8 mm long
Osmorhiza claytonii	narrowly ellipsoid, with ribs and appressed bristles, not winged, stylopodium present, not pubescent, pentagonal in x-sec	15–22 mm long
Thaspium barbinode	ellipsoid, slightly flattened dorsally, with ribs, winged, stylopodium absent, carpophore absent, glabrous, subreniform in x-sec (with wings excluded)	4–6 mm long
Sanicula gregaria	subglobose with obsolete ribs, slightly flattened, densely covered with hooked bristles in rows and not bulbous at base, stylopodium lacking, carpophore absent, semicircular to semireniform in x-sec	3–5 mm long
Sanicula canadensis	subglobose with obsolete ribs, slightly flattened dorsally, densely covered with hooked bristles with swollen base in distinct rows, stylopodium lacking, carpophore absent, semicircular to semireniform in x-sec	2–5 mm long
Sanicula trifoliata	ovoid with obsolete ribs, slightly flattened dorsally, densely covered with hooked bristles, bases not bulbous, stylopodium lacking, carpophore absent, semicircular to semireniform in x-sec	6–8 mm long

(seeds remain viable in the habitat for 1 yr or longer) than do large seeds with projections on the seed coat. Further, Thompson et al. (1993) found that compact seeds/fruits weighing less than 3 mg form persistent seed banks, whereas non-compact seeds/fruits weighing more than 3 mg form transient seed banks (seeds remain viable in the habitat for 1 yr or less).

As a contribution to the seed ecology of these six species, about which little information is available, we addressed the following two questions: (1) Is there a relationship between seed mass/morphology and the potential to form a persistent seed bank?; and (2) What is the contribution of germination phenology and seed dormancy to formation of seed banks? Since all six species used in our investigation belong to the same taxonomic family, phylogenetic constraint should not be a major concern about any differences among the taxa.

METHODS

Seed Source

Seeds used in this study were collected in September 1999 and in September 2000 from plants growing in a second growth forest in the Breathitt County (Kentucky) tract of University of Kentucky's Robinson Forest, which is located in the Eastern Rugged Area of the Cumberland Plateau in Braun's (1950) Mixed Mesophytic Forest Region. Hawkins (2003) and Hawkins et al. (2005) provide a detailed description of the physical environment and vegetation of the area in which seeds were collected.

Seed Mass

Ten replications of 50 seeds each of *Cryptotaenia canadensis, Osmorhiza claytonii, Sanicula canadensis, S. gregaria, S. trifoliata*, and *Thaspium barbinode* were air-dried in the laboratory for approximately 1 wk, then weighed to the nearest 0.1 mg. The SAS procedure GLM was used to perform analysis of variance (ANOVA) and Tukey (HSD) tests for comparison of seed masses (SAS Institute 2001).

Germination Phenology and Potential to Form a Seed Bank

Three replications of 100 seeds of *C. canadensis, O. claytonii, S. canadensis, S. gregaria, S. trifoliata*, and *T. barbinode* were sown on the surface of greenhouse soil mix in metal flats on 7 October 1999 and covered with approximately 5 cm of dead oak leaves. Sown seeds were exposed to near-natural seasonal temperature changes in a nontemperature-controlled greenhouse (Baskin and Baskin 1985) at the University of Kentucky in Lexington and monitored for germination. Continuous thermograph records were made inside a standard weatherhouse located in the greenhouse (Figure 2a). To simulate soil moisture conditions that could occur 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 the soil was frozen (in winter). At 2-week intervals until 15 May 2003 and in spring 2004, 2005, and 2006, leaves were lifted from soil in the flats, and any seeds with an emerged radicle were counted as germinated and removed from the flats. Then, the leaves were placed back onto the soil.

In a repeat of the germination phenology study, three replications of 150 seeds of *O. claytonii* were sown on 2 September 2000, and three replications of 100 seeds of *C. canadensis, S. canadensis, S. gregaria, S. trifoliata*, and *T. barbinode* were sown on greenhouse soil mix in metal flats in the greenhouse on 18 November 2000. Watering and monitoring regimes were the same as those described above.

RESULTS

Seed Mass

Seed mass ranked in order of increasing mean (±SE rounded to nearest 0.1) was *Cryptotaenia canadensis* < *Thaspium barbinode* < *Sanicula canadensis* < *S. gregaria* < *Osmorhiza claytonii* < *S. trifoliata* (Figure 1).

Germination Phenology and Potential to Form a Seed Bank

Germination of seeds of *O. claytonii, S. canadensis*, and *T. barbinode* occurred in February–April, *S. trifoliata* in February–May, *C. canadensis* in March–April, and *S. gregaria* in March–May. Based on germination peak the six species can be divided into three general germination phenology categories: 1) early- (October; except September for *O. claytonii*) and late-sown (November; except October for *O. claytonii*) seeds germinated the first spring after sowing (*C. canadensis*; Figure 2b); 2) early-sown seeds germinated the first spring, whereas late-sown seeds germinated the second spring (*O. claytonii, S. canadensis, S. gregaria*; Figures 2c, d, e); and 3) both early- and late-sown seeds germinated the second spring (*S. trifoliata, T. barbinode*; Figures 2f, g). Following the germination peak, one to several seeds of both sowing dates for all six species germinated each spring through 2003 (Figures 2b–g). For one or both sowing dates, a few seeds (≤ 10%) germinated in spring prior to the germination peak (Figures 2c, e, f, g).

Cryptotaenia canadensis, O. claytonii, and *S. gregaria* seeds sown in 1999 and in 2000 did not germinate beyond 2003. However, one to five seeds each of *S. canadensis* and *T. barbinode* germinated in 2004, 2005, and 2006. For *S. trifoliata* seeds sown in October 1999, 11, three, and zero seeds germinated in 2004, 2005, and 2006, respectively. Fifteen, zero, and two seeds of this species sown in November 2000 germinated in 2004, 2005, and 2006, respectively. Combining these data with those shown in Figures 1b–g, it can be seen that germination of a small percentage of *C. canadensis, O. claytonii*, and *S. gregaria* can be delayed until the fourth spring and of *S. canadensis, S. trifoliata*, and *T. barbinode* until the sixth spring.

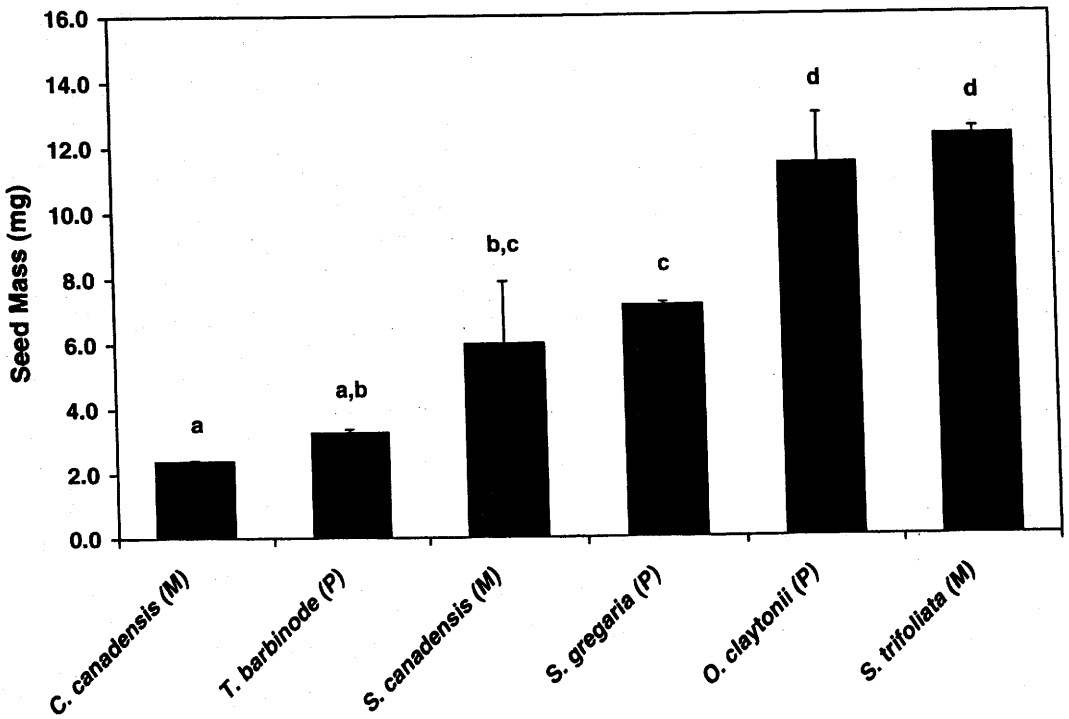

Figure 1. Mean (±SE) seed masses for six Apiaceae species. Seed masses with the same letter are not significantly different (P > 0.05). M = monocarpic, P = polycarpic.

DISCUSSION

Struik (1965) reported a mean seed mass of 0.7 mg for forest biennials and of 4.1 mg for forest herbaceous perennials. In our study, mean seed mass for biennials (*Sanicula canadensis* and *S. trifoliata*) and of two of the three polycarpic perennials (*Osmorhiza claytonii* and *S. gregaria*) was greater than that reported by Struik (1965). *Cryptotaenia canadensis, O. claytonii*, and *S. gregaria* were included in Hendrix and Sun's (1989) comparative study of seed mass of seven Apiaceae species. The results of our study are consistent with those of Hendrix and Sun in that the hierarchy of seed mass was *O. claytonii* > *S. gregaria* > *C. canadensis*. However, Hendrix and Sun reported mean (±SD) seed masses of 1.22 ± 0.47 mg and 7.23 ± 1.22 mg for *C. canadensis* and *O. claytonii*, respectively, which are considerably less than those for these two species in our study. Umbel position in *C. canadensis* and in *O. claytonii* has a significant effect on seed mass (Hendrix and Sun 1989); therefore, the discrepancy between mean seed masses in our study and those of Hendrix and Sun may be related to umbel position.

Regardless of seed mass and morphology, germination of a few seeds of *Cryptotaenia canadensis, Osmorhiza claytonii*, and *Sanicula gregaria* was delayed until the fourth year after sowing and a few seeds of *S. canadensis, S. trifoliata*, and *Thaspium barbinode* until the sixth year. Thus, the six species have the potential to form a (primarily short-lived) persistent seed bank (Thompson et al. 1997, Walck et al. 2005). Thompson and Grime (1979) described two types of persistent seed banks. In Type III, a high percentage of seeds germinates in autumn soon after dispersal, and a small reserve of viable seeds remains ungerminated for 1 yr or longer. In Type IV, a low percentage of seeds germinates in autumn soon after dispersal, and a large reserve of viable seeds remains ungerminated for 1 yr or longer. In neither Type III nor Type IV is germination shown to occur in spring, which is what happens in all six Apiaceae

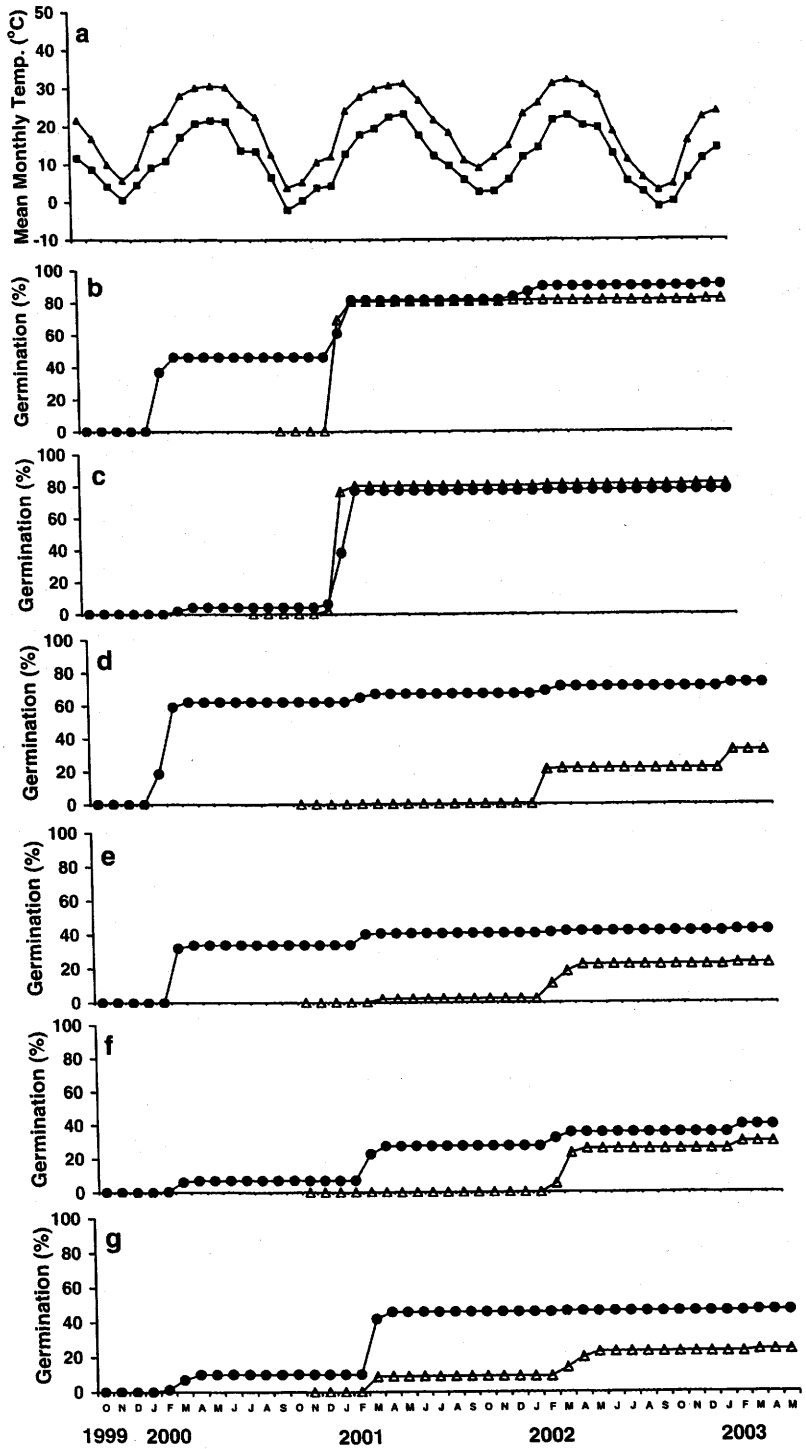

Figure 2. (a) Mean monthly minimum (■) and maximum (▲) temperatures in a nontemperature-controlled greenhouse in Lexington, Kentucky, and germination phenologies for (b) *Cryptotaenia canadensis*; (c) *Osmorhiza claytonii*; (d) *Sanicula canadensis*; (e) *Sanicula gregaria*; (f) *Sanicula trifoliata*; and (g) *Thaspium barbinode* seeds (all SEs ≤ 7.1%) sown in 1999 (●) and 2000 (△).

species included in our study. If the seed bank models are modified so that germination is advanced forward by approximately 6 mo (i.e. from autumn to spring), seeds of *C. canadensis* formed a fairly distinct (modified) Type III seed bank, and those of *S. trifoliata* and *T. barbinode* a fairly distinct (modified) Type IV seed bank.

In *O. claytonii, S. canadensis*, and *S. gregaria*, early-sown seeds formed a (modified) Type III seed bank and late-sown seeds a (modified) Type IV seed bank. Type of persistent seed bank in these three species appears to be linked to time of dispersal, as has been shown for *Osmorhiza longistylis* (Torr.) DC. (Baskin and Baskin 1984) and *O. claytonii* (Baskin and Baskin 1991). At least in the two *Osmorhiza* species, this is explained by the fact that the seeds have nondeep complex morphophysiological dormancy (MPD) (Baskin and Baskin 2004). In other words, these seeds have an underdeveloped embryo and require warm followed by cold stratification to come out of dormancy and germinate (Baskin and Baskin 1984, 1991). Consequently, a high percentage of seeds dispersed in late summer or early autumn germinates the following spring, whereas those dispersed thereafter do not germinate until at least the second spring following dispersal. In their natural habitat, seeds of *O. longistylis* (Baskin and Baskin 1984) and *O. claytonii* (Hawkins 2003) can remain attached to mother plants up to 18 mo following maturity in July. If these seeds are dispersed in the last 2–3 mo of the long dispersal period, they do not germinate until at least the third spring following maturation, i.e. not until they are imbibed and exposed to a warm-cold stratification sequence.

Germination phenology patterns of the three *Sanicula* species suggest that their seeds also have nondeep complex MPD. Similarly, a relatively small percentage of the October-sown seeds of *T. barbinode* germinated in their first spring, whereas many more seeds germinated the second spring. These data suggest that *T. barbinode* also might have nondeep complex MPD, since those that germinated the second spring were exposed to a warm-cold temperature sequence. This dormancy break requirement differs from the congener, *T. pinnatifidum* (Buckl.) A. Gray. *Thaspium pinnatifidum* seeds have deep complex MPD, requiring only cold stratification for dormancy-break (Baskin et al. 1992). Seeds of *C. canadensis* also have deep complex MPD (Baskin and Baskin 1988). As such, most *C. canadensis* seeds produced in autumn of one year germinate the following spring, and only a small percentage of them persist ungerminated in the seed bank for ≥ 1 yr.

Thompson et al. (1993) and Funes et al. (1999) found that for some plant species, seed size and shape are good predictors of seed persistence in soil. Although seeds of the six Apiaceae species in our study differed considerably in seed size, shape, and ornamentation (ribs, wings, spines), there was no obvious relationship between these traits and potential to form a seed bank. The type of persistent seed bank formed was related to kind of MPD and, for those species with nondeep complex MPD, also to time of seed sowing (dispersal).

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