Life cycles and biomass allocation in seed- and ramet-derived plants of *Cryptotaenia canadensis* (Apiaceae), a monocarpic species of eastern North America

Tracy S. Hawkins, Jerry M. Baskin, and Carol C. Baskin

Abstract: Life cycles, survivorship, and biomass allocation for seed- and ramet-derived plants of *Cryptotaenia canadensis* (L.) DC. were studied to determine if variation existed between plant derivations, and how these attributes contribute to persistence of the species within a temperate forest habitat. Seed-derived plants behaved as biennials, reproducing both sexually and asexually in the second growing season. Ramet-derived plants reproduced sexually and asexually annually. Annual survivorship was greater for seed-derived juveniles; however, fewer seed-derived plants flowered than did ramet-derived plants. Biomass allocation for plants harvested at four growth stages over two complete life cycles was significantly different between plant derivations during vegetative growth stages. During reproductive growth stages, biomass allocation did not differ between ramet- and seed-derived plants harvested in the same year. Regressions showed a strong correlation between sexual reproductive mass and vegetative mass for both plant derivations, with no significant difference between slopes or intercepts. Ramet mass was less dependent on plant size, and differences between slopes and intercepts were not significant. Regressions of sexual versus asexual reproductive mass varied with year and cohort. Equivalent reproductive output in conjunction with temporal differences in life cycle phenologies between plant derivations optimize this species' ability to persist in its natural habitat.

Key words: allometry, Apiaceae, biomass allocation, *Cryptotaenia canadensis*, monocarpic.

Résumé : Afin de déterminer s'il existe une variation entre l'origine de la plante, et comment ces attributs contribuent à la persistance de l'espèce dans un habitat de forêt tempérée, les auteurs ont étudié les cycles vitaux, la capacité de survie et l'allocation de la biomasse, chez des plants de *Cryptotaenia canadensis* (L.) DC. dérivés de graines ou de ramettes. Les plantes provenant de graines se comportent en bisannuelles, se reproduisant à la fois sexuellement et asexuellement au cours de la deuxième saison de croissance. Les plantes issues de ramettes se reproduisent sexuellement et asexuellement tous les ans. La survie annuelle est plus élevée chez les jeunes plantes issues de graines; cependant moins de plantes issues de graines fleurissent, que ne le font celles issues de ramettes. L'allocation de la biomasse chez des plantes récoltées à quatre étapes au cours de la croissance, sur deux cycles vitaux complets, est significativement différente selon l'origine de la plante, au cours des stades végétatifs. Au cours des stades de croissance reproductive, l'allocation de la biomasse ne diffère pas entre les plantes provenant de graines ou de ramettes, sur une même année. Les régressions montrent une forte corrélation entre la masse reproductive sexuelle et la masse végétative pour les plantes des deux origines, sans qu'il y ait de différence significative entre les pentes et les interceptions. La masse de la ramette dépend moins de la dimension de la plante et les différences entre les pentes et les interceptions ne sont pas significatives. Les régressions entre masse reproductive sexuelle vs asexuelle varient selon l'année et la cohorte. Une productivité reproductive équivalente, en conjonction avec des différences temporelles dans les phénologies du cycle vital, optimise la capacité de cette espèce à persister dans ses habitats naturels.

Mots clés : allométrie, Apiaceae, allocation de biomasse, *Cryptotaenia canadensis*, monocarpie.

[Traduit par la Rédaction]

Received 24 November 2004. Published on the NRC Research Press Web site at http://canjbot on 21 May 2005.

T.S. Hawkins[1,2] and J.M. Baskin. Department of Biology, University of Kentucky, Lexington, KY 40506-0225, USA.
C.C. Baskin. Department of Biology, University of Kentucky, Lexington, KY 40506-0225, USA, and Department of Agronomy, University of Kentucky, Lexington, KY 40546-0321, USA.

[1] Corresponding author (e-mail: tracyhawkins@fs.fed.us).
[2] Present address: USDA Forest Service, P.O. Box 227, Stoneville, MS 38776, USA.

Can. J. Bot. **83**: 518–528 (2005)   doi: 10.1139/B05-031

Introduction

The theory of allocation asserts that a finite amount of resources is available to competing plant functions, which generally are categorized as growth, maintenance, and reproduction. These three functions are considered mutually exclusive; therefore, the amount of resources allocated to one function results in a simultaneous decrease in the amount allocated to other functions, i.e., trade-offs (Harper 1977). However, trade-offs between competing functions are not easily measured (Reznick 1985), partly because of complex relationships between structure and function throughout the life cycle of a plant (Bazzaz et al. 2000). For example, vegetative structures such as roots, stems, or leaves may contribute to several plant functions simultaneously (e.g., support, photosynthate accumulation and transport, and reproduction), and the degree of each contribution may vary at different points in time throughout a species' life cycle (Bazzaz et al. 2000). Further, plant size may affect acquisition and allocation of resources, resulting in variation of observed correlations between life history traits among individuals of a population (van Noordwijk and de Jong 1986).

Studies of biomass allocation in polycarpic perennials have contributed to further understanding of the dynamic relationship between plant structure and function. For example, reproductive–vegetative relationships may be influenced by environment (Ashmun et al. 1985; Biere 1995), genotype, or by interaction between environment and genotype (Reekie and Bazzaz 1987; Schmid and Weiner 1993). Biomass distributed between competing reproductive functions (sexual and asexual reproduction) may vary with genotype (Reekie 1991), nutrient availability (Biere 1995), and light and successional gradients (Ashmun et al. 1985; Jurik 1985). It also is known that biomass allocation patterns may differ between rhizome- and seed-derived plants of polycarpic species (Schmid and Bazzaz 1990; Schmid and Weiner 1993; Schmid et al. 1995) as a result of developmental effects (Schmid and Bazzaz 1990; Schmid and Weiner 1993) or of selective pressures favoring one mode of reproduction over the other (Schmid et al. 1995). In turn, these differences between plant derivations may reduce mortality and increase competitive ability of individuals within the population (Tripathi and Harper 1973; Zangerl and Bazzaz 1983; Stearns 1992).

Biomass allocation studies of these types are less extensive for monocarpic species that perennate the genet via asexual reproduction. In pseudoannuals (clonal plants in which ramets die at the end of the season, but hibernacles (dormant ramets) and seeds survive the winter), life cycle phenology, clonal propagation, and sexual reproduction have been investigated in *Circaea lutetiana* (Verburg and During 1998; Verburg and Grava 1998) and vegetative reproduction has been investigated in *Helianthus* ×*laetiflorus* (Verburg et al. 1996). Seasonal distribution of dry matter in plants of *Trientalis borealis* has been studied by Anderson and Loucks (1973), and response of *T. europaea* clonal offspring to nutrient gradients has been studied by Dong et al. (1997). In these pseudoannual species, sexual reproduction by seeds and clonal propagation of hibernacles by rhizomes or stolons occur in the same growing season. Toward the end of the growing season, the parent plant senesces, hibernacles are physiologically independent, and they remain dormant until emergence above the soil the following spring (Pitelka and Ashmun 1985). Given this life cycle phenology, clonal production of hibernacles often is compared with seed production (Dong et al. 1997) and not treated as clonal propagation as in polycarpic perennial species.

The purpose of this study was to augment existing knowledge of life cycle phenology and biomass allocation in monocarpic species by investigating *Cryptotaenia canadensis* (L.) DC., a groundcover herb of eastern North America. Its reproductive phenology differs from the pseudoannuals *C. lutetiana*, *H.* ×*laetiflorus*, *T. borealis*, and *T. europaea*. In *C. canadensis*, ramet emergence and vegetative growth and development occur in the first growing season (Baskin and Baskin 1988); whereas in the pseudoannuals, ramet emergence and subsequent growth is delayed until the second growing season. Three objectives of the study were to (*i*) describe in detail the ecological life cycle of *C. canadensis*, (*ii*) monitor survivorship of seed- and ramet-derived juveniles, and (*iii*) compare biomass allocation patterns and reproductive–vegetative relationships within and between ramet- and seed-derived plants.

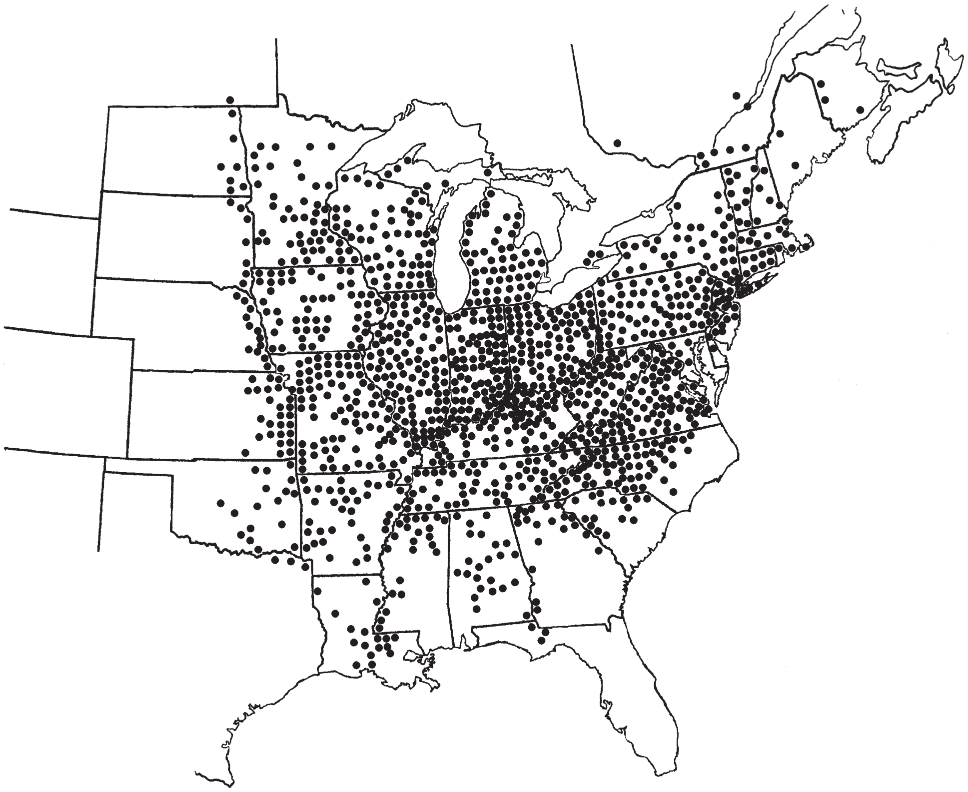
Materials and methods

Study species

Cryptotaenia canadensis (Apiaceae; common name: honewort or wild chervil) is a member of a small genus native to eastern North America, eastern Asia, and Africa (Hiroe and Constance 1958). During the growing season, this species has alternating ternately compound leaves on a slender stem with relatively few branches. Minute white flowers are produced on axillary and terminal compound umbels (Radford et al. 1968; Godfrey and Wooten 1981). *Cryptotaenia canadensis* reproduces sexually by seeds, which are dispersed in fall and germinate the following spring (Baskin and Baskin 1988). Baskin and Baskin (1988) noted asexual propagation via ramets produced at the base of the parent plant in early summer.

In eastern North America, the species grows in dry-mesic, mesic, wet-mesic, and wet deciduous forests (Braun 1940; Curtis 1959; Rogers 1981; Menges and Waller 1983; Menges 1986; McCarthy et al. 2001) and ranges from Quebec and New Brunswick to Manitoba, south to Georgia, Alabama, Arkansas, and Texas (Fig. 1; Radford et al. 1968; Gleason and Cronquist 1991). Intercontinental distribution of *C. canadensis* is unclear because of differences in taxonomic treatment of the genus. Based on morphological differences in leaflets, involucres, and calyx-teeth, Li (1952) considers the eastern North American – eastern Asian *Cryptotaenia* to be specifically distinct, i.e., *C. canadensis* in North America and *C. japonica* in Asia. Hara (1962) describes the disjuncts as "morphologically distinct geographic races", and Fernald (1950) treats the North American *Cryptotaenia* as taxonomically distinct from the east Asian *Cryptotaenia*. Hiroe and Constance (1958) and Gleason and Cronquist (1991), on the other hand, consider the American and Asian plants of *Cryptotaenia* a single species, and thus Wagner et al. (1999) report that *C. canadensis* (syn. *C.*

Fig. 1. North American distribution of *Cryptotaenia canadensis* s.l. based on specimen information from AUA, DOV, EK, GA, IA, KA, KY, LAF, LL, LO, LSU, LTU, NBM, NK, NLU, NMNH, MTMG, MISS, MO, QK, TEX, TROY, UNA, UNB, WIS, and WK (sensu Holmgren et al. 1990) and published reports from Deam (1940), Radford et al. (1968), Steyermark (1963), Great Plains Flora Association (1977), Mohlenbrock and Ladd (1978), Strausbaugh and Core (1978), Scoggan (1979), Harvill et al. (1981), Hough (1983), Voss (1985), Smith (1988), Ownbey and Morley (1991), Rhoads and Klein (1993), Cooperrider (1995), Chester et al. (1997), Magee and Ahles (1999), Hinds (2000), Weldy et al. (2002), and Wunderlin and Hansen (2002). Each symbol (●) represents one or more county records.



canadensis var. *japonica*, *C. japonica*) has escaped cultivation and become naturalized on most of the inhabited islands of Hawaii, where it grows from sea level to 400 m elevation. Tutin et al. (1968) report that *C. canadensis* has been naturalized in Austria. Presumably, this is material that was introduced from Asia.

Study site

This study was conducted in Robinson Forest, a second-growth mesic deciduous forest located in the Rugged Eastern Area (sensu Braun 1950) of the Appalachian Plateaus ecological (physiographic) region in Kentucky (Campbell 1997). Topography of Robinson Forest is characterized by long, narrow ridgetops and highly dissected slopes and deep coves, with elevations ranging from 244 to 426 m above sea level (Phillippi and Boebinger 1986). Bedrock is part of the Breathitt formation (Hinrichs 1978) of the Pottsville Series of the Lower and Middle Pennsylvanian System, and the soil association is Cloverlick–Shelocta–Cutshin (Hays 1998). The soils are deep to very deep, well drained with moderate permeability, and slightly to moderately acidic; all are found on side slopes and benches and in coves. Cloverlick soils are loamy-skeletal, mixed, mesic Umbric Dystrochrepts; Cutshin soils are fine-loamy, mixed, mesic Typic Haplumbrepts; and Shelocta soils are fine-loamy, mixed, mesic Typic Hapludults (Hays 1998).

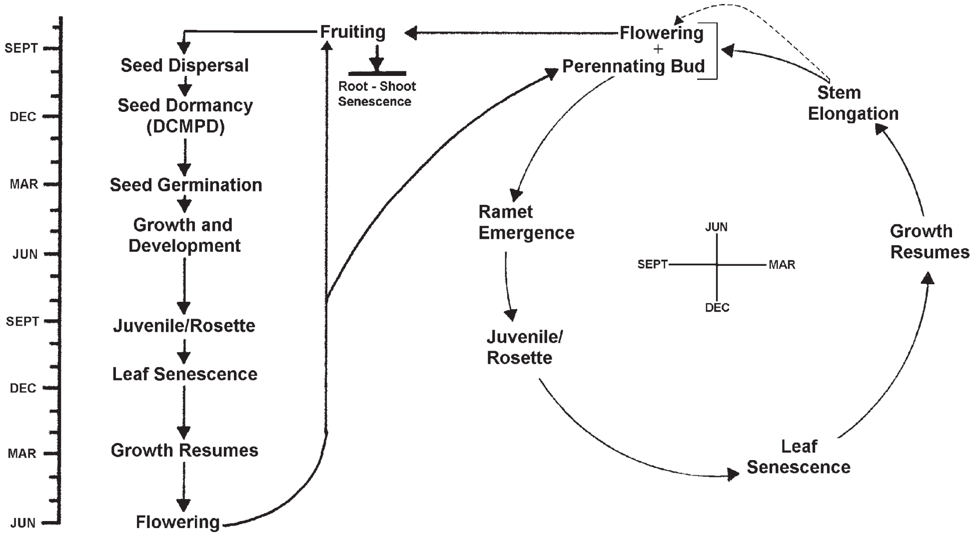
Mean annual temperature for the study area is 12.9 °C. Lowest temperatures occur in January (0.1 °C) and highest temperatures occur in July (24.3 °C). Mean annual precipitation is 1145 mm and is fairly evenly distributed throughout the year. July (127.3 mm) is the wettest month, and October (57.2 mm) is the driest (Hays 1998). During the study period (March 1999 through October 2002) mean monthly temperatures were near the 34-year (1951–1984) average, but total monthly precipitation varied considerably from the 34-year average and also between years. Total rainfall reported by the Jackson National Weather Station (approximately 15 km northwest of the study site) during March through October 1999, 2000, and 2001 was 642, 882, and 603 mm, respectively.

The *C. canadensis* population studied is located on a north slope (340°NNW) in Robinson Forest. Forest canopy is dominated by *Fagus grandifolia* and *Tsuga canadensis*, and the subcanopy is dominated by *Acer rubrum* and *Magnolia acuminata*. Associated groundcover herbs are *Adiantum pedatum*, *Impatiens capensis*, and *Monarda clinopodia*.

Life cycle phenology and survivorship

Fifty flowering plants of unknown derivation (seed derived vs. ramet derived) were marked on 29 August 1999, and 50 first-year seed-derived juveniles and ramet-derived

Fig. 2. Life cycle model for *Cryptotaenia canadensis* growing in a second-growth, mixed-mesophytic forest in Breathitt County, Kentucky. Broken line represents ≤10% of surviving population. DCMPD, deep complex morphophysiological dormancy (Baskin and Baskin 1988).



juveniles each were marked on 9 September 2000, with color-coded flags. Plants were monitored annually for survivorship, and life cycle observations were recorded monthly for three growing seasons.

Biomass allocation phenology

Plants to be harvested were marked on 29 August 1999 and on 9 September 2000. Observations of the *C. canadensis* population prior to initiation of our study indicated that length of life cycle may vary between years because of extended winter temperatures, early onset of fall temperatures, or uneven rainfall distribution. Further, ramet emergence was not synchronous between plants within the population. Therefore, it was determined that time of harvest based on plant morphology would provide more accurate comparisons within and between plant derivations, as well as comparisons between years. Plants were harvested in the field at four phenology stages, and this harvesting chronology was completed for two successive cohorts: 1999 and 2000 for ramet-derived plants and 2000 and 2001 for seed-derived plants. Harvesting stages were as follows.

(*i*) “Fall rosette” occurred in autumn of the first growing season prior to death of aerial organs. Rosettes had three to five leaves.
(*ii*) “Spring rosette” was the first harvest of the second growing season, when plants had produced three to four new leaves following the overwintering period.
(*iii*) “Flowering” refers to the peak flowering period.
(*iv*) “Late-fruiting” was identified by signs of plant senescence (i.e., yellowing leaves). This stage occurred at mericarp maturity and preceded seed dispersal.

At each growth stage, 10 ramet-derived and 10 seed-derived plants were harvested, the roots were gently washed free of soil, and each plant was separated into vegetative (roots, leaves, stems) and reproductive (pedicels + rays + flowers or fruits) structures. 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 h. Total dry mass was determined for each plant harvested. Biomass allocation for each plant was calculated by dividing the dry mass of the structure by total dry mass of the plant and multiplying the quotient by 100.

Plant biomass statistical analysis

Each plant was considered a replicate. The square root of biomass allocation percentages were arc-sine transformed before they were analyzed and were back transformed for presentation. A fixed-effects model one-way analysis of variance (ANOVA) was used to compare biomass allocation patterns and reproductive–vegetative relationships within and between ramet- and seed-derived plants harvested in the same year, and a two-way ANOVA for harvests in different years (Zar 1999). Regression analysis was used to evaluate the relationship between reproductive and vegetative dry mass. The SAS procedures GLM and REG were used to perform statistical analyses (SAS Institute Inc. 2001).

Results

Life cycle phenology and survivorship

The life cycle phenology of *Cryptotaenia canadensis* is illustrated in Fig. 2. Seeds germinated in early spring, and during the first growing season plants grew into rosettes of three to five leaves. In late autumn, all aboveground leaves senesced as a result of heavy frost, and the plants overwintered with small nonexpanded leaves that were covered by leaf litter from the forest canopy. Growth resumed in early spring of the second growing season, and plants flowered in early to mid-June. Fruit-set was complete by early July, and plants began senescing in August. Seeds were dispersed in September.

During the peak flowering period, a small perennating bud (ramet shoot bud) was produced at the base of the stem of the parent plant, followed by ramet root development. Time of appearance of ramet leaves above the soil surface varied from early August to late September, and emergence was not synchronous among plants in the population. Both above- and below-ground parts of the parent plants were dead by mid to late September, and thus the new ramets were independent. Rosettes overwintered, and subsequent growth, development, and reproduction of ramet-derived plants followed the same temporal sequence as seed-derived plants in the second growing season. In other words, seed-derived plants had a biennial life cycle and ramet-derived plants had an annual life cycle.

Only one ramet was produced per flowering plant in this study population. Survivorship (via vegetative ramets) for flowering plants of unknown derivation was 62% in 2000 and 41% in 2001 (Fig. 3). Following the first overwintering period, survivorship was 48% in the seed-derived genet and 40% in the ramet-derived genet. From 2001 through 2002, when all plants were products of asexual perennation, survivorship was 47% in the seed-derived genet, 25% in the ramet-derived genet, and 29% in the genet of unknown derivation. Not all surviving plants flowered each year, and those that remained vegetative neither produced ramets nor survived to the following year (Fig. 3).

Biomass allocation phenology

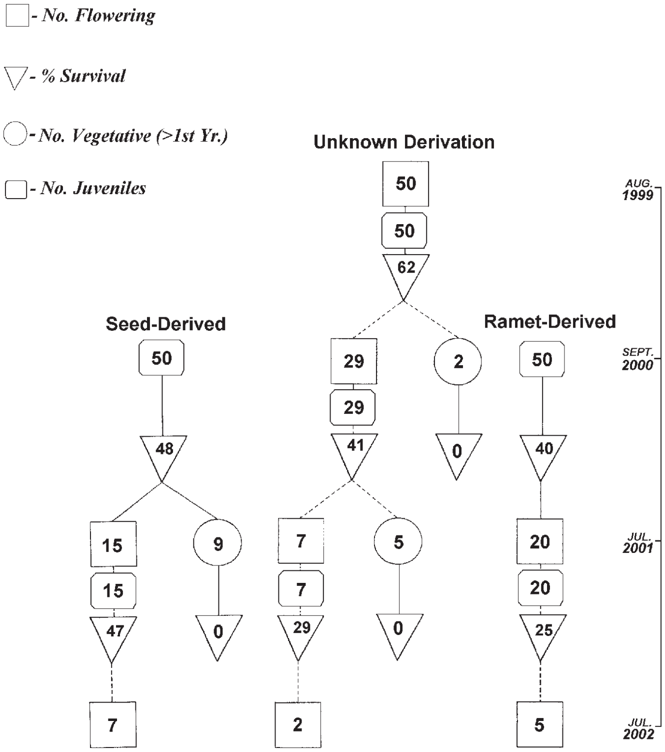
Differences in biomass allocation patterns between seed- and ramet-derived plants occurred during vegetative growth (fall and spring rosettes). Both cohorts (1999 and 2000) of ramet-derived fall rosettes allocated approximately two thirds (66.2%, 70.5%) of their total dry mass to leaves, and seed-derived fall rosettes (2000 and 2001 cohorts) allocated dry mass about equally between roots and leaves (Fig. 4). For ramet-derived plants, the proportion of total dry mass in roots and leaves remained the same from the fall rosette to the spring rosette life cycle stages. However, root allocation increased for seed-derived plants during this phenologic period (Fig. 4). Although mean total dry mass was the same between cohorts and plant derivations at the fall rosette stage, ramet-derived plants were significantly heavier than seed-derived plants at spring rosette harvests (Fig. 5).

At flowering, differences in biomass allocation patterns were not clearly identifiable by plant derivation, and by late-fruiting no significant differences existed between ramet- and seed-derived plants harvested in the same year (Fig. 6). Further, biomass allocated to asexual reproduction did not differ between either cohorts or plant derivation. Mean total dry mass was not significantly different between ramet- and seed-derived plants at either reproductive stage (Fig. 5).

Plant biomass comparisons

Reproductive–vegetative relationships fit a simple linear model. Sexual reproductive biomass was strongly correlated with vegetative biomass for both ramet-derived ($r^2 = 0.8081$) and seed-derived ($r^2 = 0.8125$) plants, and neither slopes ($p = 0.2665$) nor intercepts ($p = 0.5048$) were significantly different (Fig. 7A). Strength of the correlations between biomass of sexual reproductive structures and biomass of individual vegetative structures varied from moderate to strong. Biomass allocated to sexual reproductive structures was higher per gram of root than per gram of leaf or stem for both plant derivations (Table 1).

Fig. 3. Origin and survivorship to flowering of *Cryptotaenia canadensis* plants of unknown derivation (seed or ramet) and from seed- and ramet-derived juveniles. Broken line represents asexual reproduction.



Ramet biomass was less dependent on plant size (Fig. 7B) than was sexual reproductive biomass, and the correlation for ramet-derived plants ($r^2 = 0.6143$) was slightly weaker than that for seed-derived plants ($r^2 = 0.6823$). However, neither slopes ($p = 0.4247$) nor intercepts ($p = 0.2903$) were significant. The highest dry mass allocation to ramets per gram of root, leaf, or stem varied with harvest, and there was a great deal of year to year variation in the strength of the regression between ramets and individual vegetative structures (Table 1). The relationship between sexual reproductive structures and asexual reproductive structures differed with plant derivation and year of harvest. For example, dry mass of umbels versus dry mass of ramets showed a strong positive correlation ($r^2 = 0.8318$) in seed-derived plants of the 2000 cohort, but they were not correlated ($r^2 = 0.0082$) in the 2001 cohort (Fig. 8). Ramet-derived plants showed similar variation between cohorts.

Discussion

The life cycle of *Cryptotaenia canadensis* generally is described in taxonomic manuals (e.g., Radford et al. 1968; Gleason and Cronquist 1991; Magee and Ahles 1999) as perennial, and Williams and Guries (1994) refer to the species more specifically as a polycarpic perennial. According to Gibson (1961), *C. canadensis* is “a perennial semi-rosette herb, dying down yearly with perennial buds on more or less thick stock at ground level”. However, Baskin and Baskin (1988) showed that sexual and asexual reproduction occurred in the same growing season and that ramets were

Fig. 4. Biomass allocation to roots and leaves at fall and spring rosette stages for ramet- and seed-derived plants of *Cryptotaenia canadensis*. Within the same phenologic stage, plant structures (column segments) with different lowercase letters are significantly different between harvests ($p < 0.05$, ANOVA). All SE ≤ 3.50%.

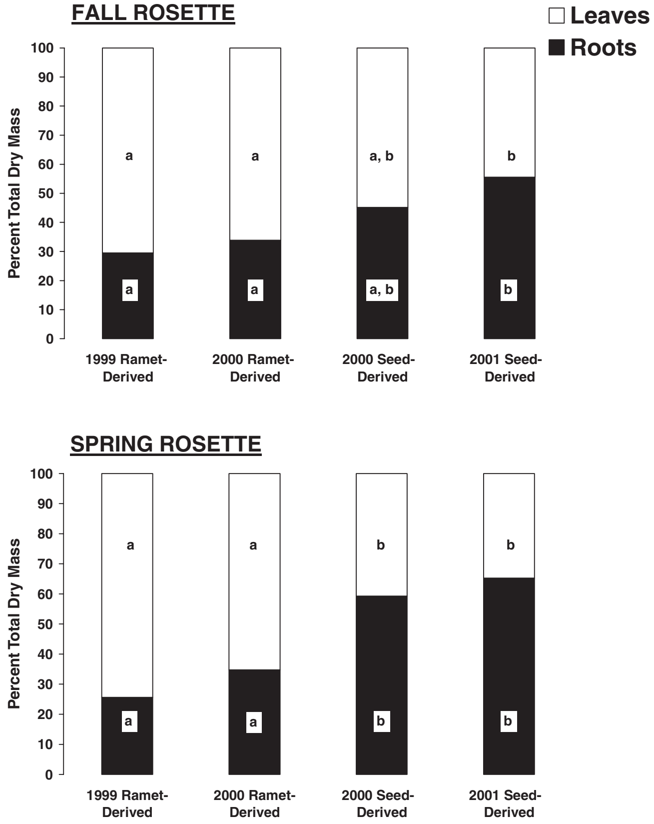


Fig. 5. Total dry mass (mean ± SE) of seed- and ramet-derived plants of *Cryptotaenia canadensis* at four phenologic stages. *, a significant difference ($p < 0.05$, ANOVA) in total dry mass between seed- and ramet-derived plants; ns, no significant difference.

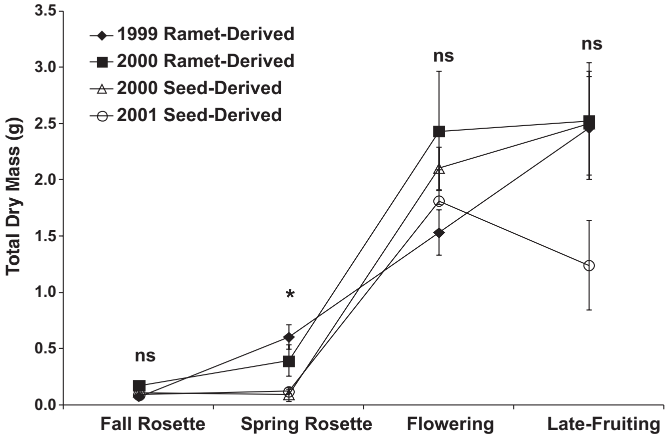
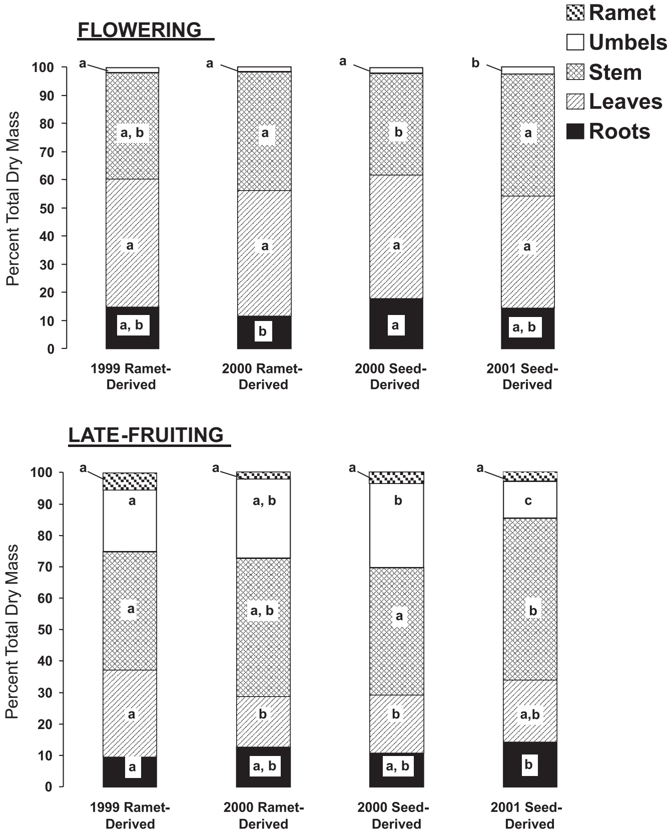


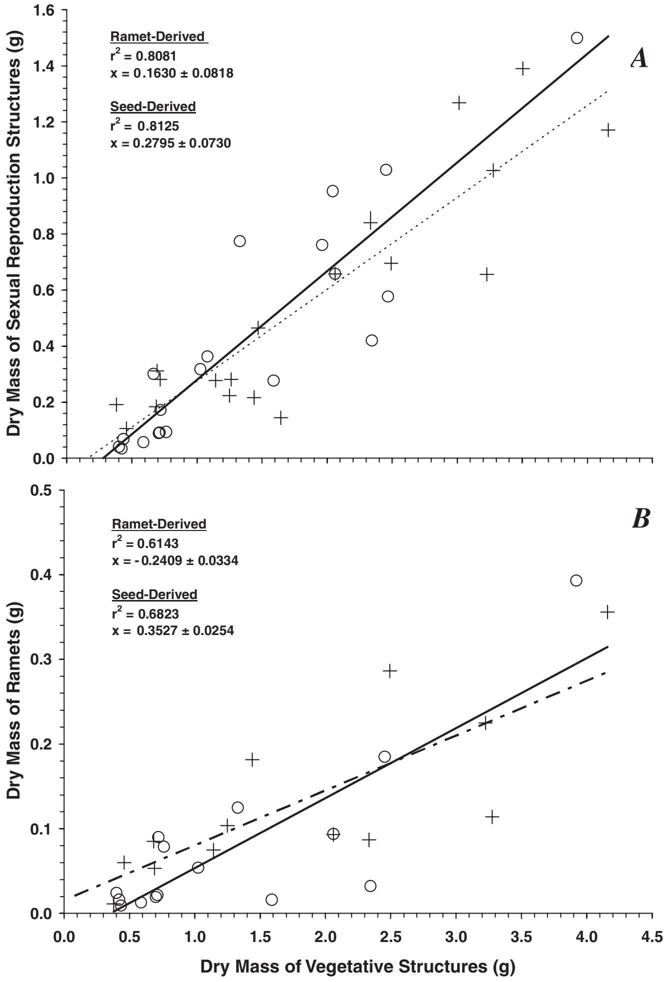
Fig. 6. Biomass allocation at flowering and late-fruiting phenologic stages for ramet- and seed-derived plants of *Cryptotaenia canadensis*. Within the same phenologic stage, plant structures (column segments) with different lowercase letters are significantly different between harvests ($p < 0.05$, ANOVA). All SE ≤ 3.20%.



monocarpic. Life cycle observations during this study supported that of Baskin and Baskin (1988) and showed how various life-cycle attributes distinguish *C. canadensis* from those of other “typical” perennial species. Polycarpic perennials often have a persistent rootstock (Holm 1925), and reproduction may or may not occur annually during the life span of the genet (Jurik 1985; Inghe and Tamm 1988; Biere 1995). Roots of *C. canadensis* do not persist after reproduction, and in naturally occurring populations, survivorship of the parent plant does not extend beyond the second growing season, regardless of whether the plant reproduces or remains vegetative (Fig. 2). Thus, seed-derived plants behave as biennials, but the genet persists via production of monocarpic ramets.

The mechanism of sexual and asexual reproduction in *C. canadensis* closely resembles that described for several pseudoannual species (Anderson and Loucks 1973; Kawano 1985; Dong et al. 1997; Verburg and During 1998; Verburg and Grava 1998). However, the life cycle phenology of *C. canadensis* differs from that of pseudoannuals in that its ramets begin growth and development in the season they are produced. This life cycle type seems to have been described only for the Asteraceae species *Boltonia decurrens* (Schwegman and Nyboer 1985) and the Apiaceae species *Anthriscus sylvestris* (Hansson 1993, 1996) and *Peucedanum palustre* (Harvey and Meredith 1981; Meredith and Grubb 1993). Descriptions by Holm (1925) suggest that plants of *Archemora rigida* (i.e., *Oxypolis rigidior*, Apiaceae) and

Fig. 7. Dry mass correlations between sexual reproductive structures and vegetative structures (A) and between ramets (asexual propagation) and vegetative structures (B) at late-fruiting harvest for ramet-derived (+, broken line) and seed-derived (○, solid line) plants of *Cryptotaenia canadensis*. There were no significant differences in slopes and intercepts in Figs. 7A ($p = 0.2665$, $p = 0.5048$, respectively) and 7B ($p = 0.4247$, $p = 0.2903$, respectively).



Prenanthes alba (Asteraceae) also may have this type of life cycle.

The proportion of total plant dry mass (11.9%–26.8%) allocated to sexual reproduction by plants of *C. canadensis* (Fig. 6) is higher than that reported for many polycarpic perennial species (Struik 1965; Pitelka 1977; Abrahamson 1979) and substantially higher than that in the pseudoannuals *C. lutetiana* (approx. 4%, Verburg and During 1998) and *T. borealis* (approx. 2%, Anderson and Loucks 1973). Hansson (1993, 1996) reported sexual reproductive allocation percentages ranging from 10.5% to 13.5% for *A. sylvestris*. However, these percentages represent only fruits and flowers, whereas reproductive allocation percentages in our study represent fruits and ancillary reproductive structures. In light of this, percent sexual reproductive allocation may well be comparable between plants of *A. sylvestris* and *C. canadensis*.

At late-fruiting harvests, ramet- and seed-derived plants of *C. canadensis* allocated 2.2%–5.4% total dry mass to ramets (Fig. 6). Direct comparison of these percentages with asexual reproductive allocation in pseudoannuals is difficult, if not impossible, because of differences in phenology between life cycle types. *Cryptotaenia canadensis* ramets emerge in the growing season in which they are produced and may contribute resources to their own growth. Hibernacles produced by pseudoannuals such as *C. lutetiana*, *T. borealis*, and *T. europaea* remain below ground throughout the first growing season, and it is not known when physiological independence is established.

Developmental effects (pattern of biomass partitioning influenced by plant derivation) were observed in vegetative and subsequent reproductive growth stages of seed- and rhizome-derived plants of *Solidago altissima* (Schmid and Weiner 1993). Differences in biomass allocation patterns between ramet- and seed-derived plants of *C. canadensis* primarily were restricted to vegetative growth stages. Seed-derived rosettes allocated more biomass to roots (Fig. 4), and ramet-derived spring rosettes were heavier than seed-derived spring rosettes (Fig. 5). However, at flowering and late-fruiting, when seed- and ramet-derived life cycle phenologies were temporally equivalent (Fig. 2), mean total plant mass did not differ between plant derivations (Fig. 5), and biomass allocation was not significantly different between ramet- and seed-derived plants of same-year harvests (Fig. 6). On the other hand, seed-derived juveniles had a higher percent survivorship to flowering than did ramet-derived juveniles, but a lower percentage of seed-derived plants reproduced in the second growing season (Fig. 3). Within the methodology of our study, it would be impossible to attribute these differences to developmental effects; however, it should not be completely ruled out and merits further investigation.

Reproductive–vegetative relationships in *C. canadensis* are size dependent (Figs. 7A, 7B) and not unlike those observed in the old-field polycarpic perennials *Aster lanceolatus* and *Solidago canadensis* (Schmid et al. 1995) and in the woodland pseudoannual *Circaea lutetiana* (Verburg and Grava 1998). Dry mass allocated to sexual reproduction and clonal propagation increased linearly with vegetative mass in seed- and rhizome-derived plants of *A. lanceolatus* and *S. canadensis* (Schmid et al. 1995). This relationship also was found in *C. lutetiana* (Verburg and Grava 1998), although reproductive output was not determined for seed-derived plants. Plants of the old-field perennials *A. lanceolatus* and *S. canadensis* derived from seeds showed a slightly weaker correlation between clonal mass and vegetative mass (Schmid et al. 1995) than did rhizome-derived plants. However, the correlation between clonal mass and vegetative mass was slightly stronger in seed- than in clonally derived plants of *C. lutetiana* (Verburg and Grava 1998) and was not significantly different between ramet- and seed-derived plants of *C. canadensis* (Fig. 7B).

Sexual reproductive dry mass correlated positively with dry mass of vegetative structures in both ramet- and seed-derived plants of *C. canadensis* (Table 1), with little between-year variation in correlations or slopes of the regressions. However, relationships between dry mass of

Table 1. Parameter estimates for the relationship between reproductive structures and vegetative structures for ramet- and seed-derived plants of *Cryptotaenia canadensis*.

Regression	Plant derivation*	Cohort	Slope ± SE[†]	r^2	N[‡]	$F_{[1, N-2]}$
Umbel × root	R	99	1.8266±0.4580a	0.6653	10	15.90
	R	00	2.6320±0.4649a	0.8003	10	32.06
	S	00	2.1246±0.3150a	0.8505	10	45.50
	S	01	2.2483±0.2991a	0.8760	10	56.52
Umbel × leaf	R	99	0.6088±0.2042a	0.5264	10	8.89
	R	00	1.4586±0.3410a	0.6957	10	18.29
	S	00	1.1565±0.2314a	0.7575	10	24.99
	S	01	0.8737±0.1244a	0.8605	10	49.34
Umbel × stem	R	99	0.5576±0.0779a	0.8649	10	51.21
	R	00	0.5439±0.0569a	0.9198	10	91.76
	S	01	0.6175±0.1205a	0.7665	10	26.26
	S	01	0.3516±0.0156a	0.9845	10	506.53
Ramet × root	R	99	0.5422±0.1430a	0.7056	8	14.38
	R	00	0.2690±0.7612a	0.0400	5	0.12
	S	00	0.5078±0.0988a	0.8684	6	26.39
	S	01	0.0097±0.1192b	0.0009	9	0.94
Ramet × leaf	R	99	0.1931±0.0579abc	0.7056	8	11.10
	R	00	–0.2815±0.4883a	0.0997	5	0.33
	S	00	0.3629±0.0389b	0.9561	6	87.18
	S	01	0.0292±0.0416ac	0.0661	9	0.05
Ramet × stem	R	99	0.1395±0.0447ab	0.6192	8	9.76
	R	00	0.0850±0.1488abc	0.1488	5	0.33
	S	00	0.1465±0.0545b	0.6439	6	0.05
	S	01	0.0047±0.0192c	0.0084	9	0.06

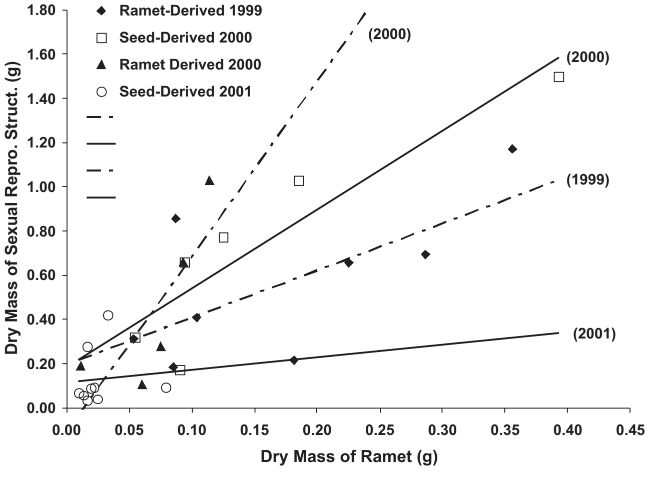
Note: df = 1.

*R, ramet-derived plant; S, seed-derived plant.

[†] Slopes followed by different lowercase letters are significantly different within a reproductive–vegetative mass comparison ($p < 0.05$, ANOVA).

[‡] If $N < 10$, one or more plants did not produce a ramet.

Fig. 8. Dry mass correlations between ramets (asexual propagation) and sexual reproductive structures at late-fruiting harvest for ramet-derived (broken line) and seed-derived (solid line) plants of *Cryptotaenia canadensis*.



asexual reproductive structures (ramets) and dry mass of vegetative structures were highly variable in both slope and strength of correlation (Table 1). Two factors may contribute to the latter result. (*i*) Ramet emergence occurs late in the growing season (Fig. 2), when the parent plant is nearing senescence and the ramet is contributing resources to its own growth. (*ii*) If the ramet is physiologically independent, or nearly so, accumulation and allocation of biomass reflect an independent response to environmental conditions.

Relationships between sexual and asexual reproduction varied with year and cohort. No direct trade-offs between the two modes of reproduction were observed in biomass allocation percentages (Fig. 6) or in structural dry mass relationships (Table 1), nor did plant derivation influence the correlations (Fig. 8). Division of resources between infructescences and rhizomes of *Agropyron repens* varied with habitat stress and nutrient availability but showed no direct trade-offs (Reekie 1991). Reekie (1991) concluded that these variations were related to costs associated with varying environments. Although the *C. canadensis* population in our study occurred in a mesic, seemingly homogeneous habitat, there were large differences in the correlations between sexual and asexual reproduction (Fig. 8). While timing of physiological independence of the ramet may influence these correlations, further investigation is required to determine causal factors for variations in this relationship.

Schmid et al. (1995) suggested that differences in how rhizome- and seed-derived plants of *A. lanceolatus* and *S. canadensis* allocated resources to reproduction was a bet-hedging strategy. Greater allocation to sexual reproduction and clonal growth by rhizome-derived plants relative to seed-derived plants minimized the risk of mortality rather than maximizing fitness (Schmid et al. 1995). A bet-hedging strategy was not observed in the *C. canadensis* population. Equivalent reproductive output by seed- and ramet-derived plants serves to minimize the effects of high seedling mortality (Baskin and Baskin 1988), as well as enhancing genetic variability. Further, ramet production in autumn somewhat compensates for seedling mortality in the first growing season, as well as delaying competition between sexually and asexually produced individuals. Lethal reproduction eliminates parent–sib competition and reduces future intraspecific competition. Within an ecological context, biomass allocation patterns and variation in life cycle phenologies between plant derivations optimize the ability of the species to persist in the temperate deciduous forest habitat.

Detailing the life cycle of *C. canadensis* and constructing biomass allocation phenologies over two growing seasons were critical to the interpretation of biomass allocation patterns in this species. The extent of variation in biomass allocation within, and differences in life cycles between plant derivations would not have been observed in a single season study. (*i*) The high proportion of total plant dry mass allocated to sexual reproduction would seem somewhat anomalous for a perennial life cycle. However, in comparison with a monocarpic life cycle, sexual reproductive allocation is within the range of that reported for other monocarpic species. A single-year, late-fruiting harvest could have under- or over-estimated mean percent reproductive allocation and misrepresented comparison of ramet- and seed-derived plants. (*ii*) Variability expressed in sexual–asexual and ramet–vegetative regressions were not likely to be the result of environmental stress within the parameters of this study and thus primarily can be attributed to timing of physiological independence of the ramet. (*iii*) Timing of life cycle events exerted an influence on biomass allocation patterns such that changes in environment (e.g., absence of vernalization, artificial growing conditions) that would alter this phenology may give results different from those found in naturally occurring populations of *C. canadensis*.

Acknowledgements

The authors thank Bev Benedict, Jessica DiCicco, Steve Ginzbarg, Curtis Hansen, Diana Horton, Lucille McCook, Robert Naczi, Sula Vanderplank, Troy Weldy, Michael Woods, and Wendy Zomlefer, who took time to provide distribution information for the study species.

References

Abrahamson, W.G. 1979. Patterns of resource allocation in wildflower populations of fields and woods. Am. J. Bot. **66**: 71–79.

Anderson, R.C., and Loucks, O.L. 1973. Aspects of the biology of *Trientalis borealis* Raf. Ecology, **54**: 798–808.

Ashmun, J.W., Brown, R.L., and Pitelka, L.F. 1985. Biomass allocation in *Aster acuminatus*: variation within and among populations over 5 years. Can. J. Bot. **63**: 2035–2043.

Baskin, J.M., and Baskin, C.C. 1988. The ecological life cycle of *Cryptotaenia canadensis* (L.) DC. (Umbelliferae), a woodland herb with monocarpic ramets. Am. Midl. Nat. **119**: 165–173.

Bazzaz, F.A., Ackerly, D.D., and Reekie, E.G. 2000. Reproductive allocation in plants. *In* Seeds: the ecology of regeneration in plant communities. 2nd ed. *Edited by* M. Fenner. CABI Publishing, Wallingford, UK. pp. 1–29.

Biere, A. 1995. Genotypic and plastic variation in plant size: effects on fecundity and allocation patterns in *Lychnis flos-cuculi* along a gradient of natural soil fertility. J. Ecol. **83**: 629–642.

Braun, E.L. 1940. An ecological transect of Black Mountain, Kentucky. Ecol. Monogr. **10**: 193–241.

Braun, E.L. 1950. Deciduous forests of eastern North America. Blakiston, Philadelphia, Penn.

Campbell, J. 1997. The Appalachian Plateaus of Kentucky: once the “Wasioto Wilderness” now the “Eastern Coalfield”. Kentucky News, Spring: 18–20.

Chester, E.W., Wofford, B.E., and Kral, R. 1997. Atlas of Tennessee vascular plants. Vol. 2. Angiosperms: Dicots. Available from the Center for Field Biology, Austin Peay State University, Clarksville, Tenn. Misc. Publ. No. 13.

Cooperrider, T.S. 1995. The dicotyledoneae of Ohio. Part II. Linaceae through Campanulaceae. The Ohio State University Press, Columbus, Ohio.

Curtis, J.T. 1959. The vegetation of Wisconsin. An ordination of plant communities. The University of Wisconsin Press, Madison, Wisc.

Deam, C.C. 1940. Flora of Indiana. Department of Conservation, Division of Forestry, Indianapolis, Ind.

Dong, M., During, H.J., and Werger, M.J.A. 1997. Clonal plasticity in response to nutrient availability in the pseudoannual herb, *Trientalis europaea* L. Plant Ecol. **131**: 233–239.

Fernald, M.L. 1950. Gray’s manual of botany. 8th ed. American Book Company, New York.

Gibson, D. 1961. Life-forms of Kentucky flowering plants. Am. Midl. Nat. **66**: 1–60.

Gleason, H.A., and Cronquist, A. 1991. Manual of the vascular plants of northeastern United States and adjacent Canada. 2nd ed. The New York Botanical Garden, Bronx, N.Y.

Godfrey, R.K., and Wooten, J.W. 1981. Aquatic and wetland plants of southeastern United States: Dicotyledons. University of Georgia Press, Athens.

Great Plains Flora Association (GPFA). 1977. Atlas of the flora of the Great Plains. Iowa State University Press, Ames, Iowa.

Hansson, M.L. 1993. *Anthriscus sylvestris* (L.) Hoffm. — an autecological study. Ph.D. dissertation, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Hansson, M.L. 1996. Biomass partitioning and its effect on reproduction in a monocarpic perennial (*Anthriscus sylvestris*). Response to nitrogen and light supply. Acta Bot. Neerl. **45**: 345–354.

Hara, H. 1962. Racial differences in widespread species, with special reference to those common to Japan and North America. Am. J. Bot. **49**: 647–652.

Harper, J.L. 1977. Population biology of plants. Academic Press, London.

Harvey, H.J., and Meredith, T.C. 1981. Ecological studies of *Peucedanum palustre* and their implication for conservation management of Wicken Fen, Cambridgeshire. *In* The biological aspects of rare plant conservation. *Edited by* H. Synge. John Wiley and Sons, Chichester. pp. 365–378.

Harvill, A.M., Bradley, T.R., and Stevens, C.E. 1981. Atlas of the Virginia flora. Part II. Dicotyledons. Virginia Botanical Associates, Farmville.

Hays, R.A., 1998. Soil survey of Breathitt County, Kentucky. Available from United States Department of Agriculture, Natural Resources Conservation Service, Washington, D.C.

Hinds, H.R. 2000. Flora of New Brunswick. Primrose Press, Fredericton, N.B.

Hinrichs, E.N. 1978. Geologic map of the Noble quadrangle, eastern Kentucky. Available from United States Geological Survey, Washington, D.C. Map No. GQ-1476.

Hiroe, M., and Constance, L. 1958. Umbelliferae of Japan. Univ. Calif. Publ. Bot. **30**: 1–144.

Holm, T. 1925. Hibernation and rejuvenation, exemplified by North American herbs. Am. Midl. Nat. **9**: 477–512.

Holmgren, P.K., Holmgren, N.H., and Barnett, L.C. 1990. Index herbariorum. Part I: the herbaria of the world. 8th ed. The New York Botanical Garden, Bronx, N.Y.

Hough, M.Y. 1983. New Jersey wild plants. Harmony Press, Harmony, N.J.

Inghe, O., and Tamm, C.O. 1988. Survival and flowering of perennial herbs. V. Patterns of flowering. Oikos, **51**: 203–219.

Jurik, T.W. 1985. Differential costs of sexual and vegetative reproduction in wild strawberry populations. Oecologia, **66**: 394–403.

Kawano, S. 1985. Life history characteristics of temperate woodland plants in Japan. The population structure of vegetation. *In* Handbook of vegetation science. Vol. 3. *Edited by* J. White. Dr. W. Junk Publishers, Dordrecht, The Netherlands. pp. 515–549.

Li, H.L. 1952. Floristic relationships between eastern Asia and eastern North America. Trans. Am. Philos. Soc. **42**: 371–429.

Magee, D.W., and Ahles, H.E. 1999. Flora of the northeast. A manual of the vascular flora of New England and adjacent New York. University of Massachusetts Press, Amherst.

McCarthy, B.C., Small, C.J., and Rubino, D.J. 2001. Composition, structure and dynamics of Dysarts Woods, an old-growth mixed mesophytic forest of southeastern Ohio. For. Ecol. Manage. **140**: 193–213.

Menges, E.S. 1986. Environmental correlates of herb species composition in five southern Wisconsin floodplain forests. Am. Nat. **115**: 106–117.

Menges, E.S., and Waller, D.M. 1983. Plant strategies in relation to elevation and light in floodplain herbs. Am. Nat. **122**: 454–473.

Meredith, T.C., and Grubb, P.J. 1993. *Peucedanum palustre* (L.) Moench. Biological flora of the British Isles. No. 179. J. Ecol. **81**: 813–826.

Mohlenbrock, R.H., and Ladd, D.M. 1978. Distribution of Illinois vascular plants. Southern Illinois University Press, Carbondale.

Ownbey, G.B., and Morley, T. 1991. Vascular plants of Minnesota: a checklist and atlas. University of Minnesota Press, Minneapolis.

Phillippi, M.A., and Boebinger, A. 1986. A vegetational analysis of three small watersheds in Robinson Forest, Eastern Kentucky. Castanea, **51**: 11–30.

Pitelka, L.F. 1977. Energy allocation in annual and perennial lupines (*Lupinus*: Leguminosae). Ecology, **58**: 1055–1065.

Pitelka, L.F., and Ashmun, J.W. 1985. Physiology and integration of ramets in clonal plants. *In* Population biology and evolution of clonal organisms. *Edited by* B.C. Jackson, L.W. Buss, and R.E. Cook. Yale University Press, New Haven, Conn. pp. 399–435.

Radford, A.E., Ahles H.E., and Bell, C.R. 1968. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill.

Reekie, E.G. 1991. Cost of seed versus rhizome production in *Agropyron repens*. Can. J. Bot. **69**: 2678–2683.

Reekie, E.G., and Bazzaz, F.A. 1987. Reproductive effort in plants. 3. Effect of reproduction on vegetative activity. Am. Nat. **129**: 907–919.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos, **44**: 257–267.

Rhoads, A.F., and Klein, W.M., Jr. 1993. The vascular flora of Pennsylvania: annotated checklist and atlas. American Philosophical Society, Philadelphia, Penn.

Rogers, R.S. 1981. Mature mesophytic hardwood forest: community transitions, by layer, from east-central Minnesota to southeastern Michigan. Ecology, **62**: 1634–1647.

SAS Institute Inc. 2001. The SAS system for Windows, release V8. SAS Institute Inc., Cary, N.C.

Schmid, B., and Bazzaz, F.A. 1990. Plasticity in plant size and architecture in rhizome-derived vs. seed-derived *Solidago* and *Aster*. Ecology, **71**: 523–535.

Schmid, B., and Weiner, J. 1993. Plastic relationships between reproductive and vegetative mass in *Solidago altissima*. Evolution, **41**: 61–74.

Schmid, B., Bazzaz, F.A, and Weiner, J. 1995. Size dependency of sexual reproduction and of clonal growth in two perennial plants. Can. J. Bot. **73**: 1831–1837.

Schwegman, J.E., and Nyboer, R.W. 1985. The taxonomic and population status of *Boltonia decurrens* (Torr. & Gray) Wood. Castanea, **50**: 112–115.

Scoggan, H.J. 1979. The flora of Canada. Part 4. Dicotyledoneae (Loasaceae to Compositae). National Museum of Natural Sciences Publications in Botany No. 7(4). National Museums of Canada, Ottawa, Ont.

Smith, E.B. 1988. An atlas and annotated list of the vascular plants of Arkansas. 2nd ed. University of Arkansas, Fayetteville.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, New York.

Steyermark, J.A. 1963. Flora of Missouri. Iowa State University Press, Ames.

Strausbaugh, P.D., and Core, E.L. 1978. Flora of West Virginia. 2nd ed. Seneca Books, Inc., Grantsville, W.V.

Struik, G.J. 1965. Growth patterns of some native annual and perennial herbs in southern Wisconsin. Ecology, **46**: 401–420.

Tripathi, R.S., and Harper, J.L. 1973. The comparative biology of *Agropyron repens* (L.) Beauv. I. The growth of mixed populations established from tillers and from seeds. J. Ecol. **61**: 353–368.

Tutin, T.G., Ball, P.W., Chater, A.O. et al. (*Editors*). 1968. Flora Europaea. Vol. 2. Rosaceae to Umbelliferae. Cambridge University Press, Cambridge, UK.

Van Noordwijk, A.J., and de Jong, G. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. Am. Nat. **128**: 137–142.

Verburg, R.W., and During, H.J. 1998. Vegetative propagation and sexual reproduction in the woodland understorey pseudo-annual *Circaea lutetiana* L. Plant Ecol. **134**: 211–224.

Verburg, R.W., and Grava, D. 1998. Differences in allocation patterns in clonal and sexual offspring in a woodland pseudo-annual. Oecologia, **115**: 472–477.

Verburg, R.W., Kwant, W., and Werger, M.J.A. 1996. Does plant size affect vegetative reproduction in a pseudoannual? Vegetatio, **125**: 185–192.

Voss, E.G. 1985. Michigan flora. Part II. Dicots (Saururaceae – Cornaceae). Cranbrook Institute of Science (Bulletin 59) and University of Michigan Herbarium, Ann Arbor.

Wagner, W.L., Herbst, D.R., and Sohmer, S.H. 1999. Manual of the flowering plants of Hawaii. 2nd ed. Vol. 1. University of Hawaii Press and Bishop Museum Press, Honolulu.

Weldy, T., Mitchell, R., and Ingalls, R. 2002. New York flora atlas [online]. Available from http://nyflora.org/atlas/atlas.htm [cited 10 January 2003].

Williams, C.F., and Guries, R.P. 1994. Genetic consequences of seed dispersal in three sympatric forest herbs. I. Hierarchical population-genetic structure. Evolution, **48**: 791–805.

Wunderlin, R.P., and Hansen, B.F. 2002. Atlas of Florida vascular plants [online]. Available from http://www.plantatlas.usf.edu. [cited 10 January 2003].

Zangerl, A.R., and Bazzaz, F.A. 1983. Responses of an early and late successional species of *Polygonum* to variations in resource availability. Oecologia, **56**: 397–404.

Zar, J.H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, Upper Saddle River, N.J.