Flowering Ecology of Some Spring Woodland Herbs

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FLOWERING ECOLOGY OF SOME SPRING WOODLAND HERBS[1]

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Abstract. Fecundity characteristics, phenology, and behavior of insect flower-visitors were studied for 7 early flowering woodland herbs: *Claytonia virginica*, *Dentaria laciniata*, *Dicentra canadensis*, *Dicentra cucullaria*, *Erythronium albidum*, *Isopyrum biternatum*, and *Sanguinaria canadensis*. *Sanguinaria canadensis* is facultatively autogamous, the *Dicentras* are obligate outcrossers, and the remainder are self-compatible, at least within a stem. All are insect pollinated except sometimes *S. canadensis*. The numbers of ovules per flower and flowers per stem tended to be inversely correlated, and large-seeded species (*S. canadensis*, *E. albidum*, *I. biternatum*) had lower numbers of potential seeds per stem than did small-seeded species.

Flowering of all species typically occurred during the first prolonged period of weather suitable for pollinator activity and ceased by the time the canopy closed. Annual differences in flowering times were associated with differences in average temperatures (i.e., early blooming in a warm, early spring), but cumulative degree-hours or degree-days of air or soil temperatures were not well correlated with flowering times. Other constraints on flowering phenology are discussed, including the predictability of suitable conditions, a proposed "fail-safe" mechanism that may assure flowering before canopy closure even if temperatures are abnormally low, and the importance of nontemperature factors in defining suitable conditions. Flowering time was not very finely tuned to the temperature regime and pollinator activity; flowers blooming during the flowering peak often had low seed production and the fertilization rate of most species was low. Evidence that seed production may have been pollinator limited for several species was obtained by comparing the success of hand pollination and of natural pollination, rarity of certain specialized pollinators, and estimates of the abortion rates of fertilized ovules. We suggest that flowering in early spring is a high-risk option in terms of insect-mediated sexual reproduction.

Certain flower-visiting insects favored *D. laciniata* out of proportion to its abundance, but no effect on seed set of other species was detectable. Honeybees were abundant and active flower visitors with the potential for disrupting ecological/evolutionary relationshps between native insects and flowers.

Key words: *Breeding systems*; Claytonia virginica; *competition*; Dentaria laciniata; Dicentra canadensis; Dicentra cucullaria; Erythronium albidum; *Illinois*; Isopyrum biternatum; *phenology*; *pollination*; *seed production*; *temperature*; *woodland herbs*.

INTRODUCTION

Among the first spring flowers to bloom in the deciduous forests of eastern North America are several "ephemeral" herbs with white or whitish flowers. Early flowering means that both the risk of encountering weather conditions unsuitable for plant growth and for pollinator activity and light availability, before closure of the canopy, is relatively high. Many studies have indicated that early spring flowering of herbaceous forest species typically occurs before canopy closure and as soon as suitable temperatures permit (Salisbury 1916, Robertson 1924, Leopold and Jones 1947, Lindsey and Newman 1956, Kieckhefer 1962, Vezina and Grandtner 1965, Jackson 1966, Castelli 1970, Bazzaz and Bliss 1971, Schemske 1977). However, no published studies have quantified variation in both temperature and light conditions with respect to flowering phenology for the entire subcommunity of early flowering herbs. Reproductive success is the evolutionary assay of adaptations, and permits investigation of the relative success of phenological variations. In addition, the occurrence of a common flower color may suggest convergence as well as competition among these plants for pollinators. Competition for pollinators is frequently discussed, but seldom demonstrated; in fact, whether seed production is even pollinator limited is little studied.

We chose the early flowering forest herbs for study because they are a suitable and natural subset of a whole community, a subset defined by the shared habitat and flowering season and composed of enough species for interesting comparisons, but not too many to monitor. Our interest in this group centered on a series of related questions: (1) What conditions delimit

the flowering season for these species; (2) How variable is flowering phenology from year to year; (3) How does seed production vary with phenology; (4) Is flowering somehow timed to occur when conditions for pollination for each species are optimal and seed production is greatest; and (5) Is there competition among simultaneously blooming species for pollinators?

Early flowering species that we studied are *Claytonia virginica* L. (Portulacaceae), *Dentaria laciniata* Muhl. (Cruciferae), *Dicentra canadensis* (Goldie) Walp. and *Dicentra cucullaria* (L.) Bernh. (Fumariaceae), *Erythronium albidum* L. (Liliaceae), *Isopyrum biternatum* (Raf.) T. & G. (Ranunculaceae), and *Sanguinaria canadensis* L. (Papaveraceae). These 7 species were the earliest flowering herbs to bloom in Brownfield Woods.

STUDY AREA

Brownfield Woods, ≈7 kilometres NE of Urbana, Illinois, provided a convenient study area with populations of 7 early flowering woodland herbs. This 24-ha site is dominated by sugar maple (*Acer saccharum*) and red oak (*Quercus rubra*) in the canopy and is bisected by a seasonal stream flanked by dead elm (*Ulmus* sp.) stubs and some burr oak (*Quercus macrocarpa*). Further description of the woods can be found in Boggess and Bailey (1964).

METHODS

Seventy-eight permanent quadrats, 1 m², were located at 25-metre intervals on 6 parallel transects 50 metres apart. We quantified flowering phenology by counting the number of flowering stems in these quadrats, usually every 3 days, during the springs of 1974, 1975, and 1976. The relative abundances of these 7 species, each at their flowering peak in the 78 regular census quadrats, demonstrated the necessity of additional quadrats for some species: *C. virginica* (range for 3 yr: 2,218–3,277 stems), *S. canadensis* (10–25), *D. laciniata* (200–356), *D. canadensis* (23–27), *D. cucullaria* (102–151), *I. biternatum* (0), and *E. albidum* (0). Additional census quadrats were located in dense stands of each species, as follows: *S. canadensis* 8, *I. biternatum* 8, *D. canadensis* 16, *D. cucullaria* 13. *Erythronium albidum* was censused along a 40-metre transect and in 3 patches (probably clones) in 1975, and in 6 1-metre² quadrats in 1976.

The behavior of insect flower visitors was quantified in several ways. The sequence and variety of flowers visited by individual insects were recorded for the first foraging insect observed in a randomly selected, 1-m² quadrat located within a 10 × 10-metre grid that included representatives of several flower species. Additional observations were made on plots that presented different proportions of flowering stems of several species; the frequency of visits was compared to the frequency of each flower species in the plot. Flower visitors were collected frequently, and identi-

fications confirmed. Not all flower-visiting insects are effective pollinators but, for our purposes, the flower visitors were viewed as possible pollinators and referred to as such.

Ultraviolet (UV) photographs of flowers from each plant species were taken under black light illumination with a 2.25–2.75 camera, using a Wratton 18.A filter on Tri X Pan® film exposed for 10 s at F.11. Although improvements in technique may refine our descriptions, this method allows at least a first-level description of the UV appearance of the flowers.

Breeding systems were determined for 5 of the 7 species. Dialysis tubing fastened over flowers in the bud stage prevented pollination from external vectors. The following treatments were performed: (1) Flowers unmanipulated; (2) Self-pollinations, within a flower; (3) Geitonogamous pollinations, between flowers on a single inflorescence; and (4) Cross-pollination between flowers on different stems, both adjacent (and possibly closely related genetically) and distant. Records of treatments 2 and 3 on *D. laciniata* were pooled and treatment 3 did not apply to *E. albidum* and *S. canadensis*. Presence or absence of nectar was determined from bagged flowers by treating the flowers or a distilled H_2O rinse from the flowers with a few drops of concentrated H_2SO_4 followed by a few drops of a 5% phenol solution. If sugar is present, this solution (H_2SO_4+phenol) becomes orange (Clark 1964).

The reproductive characteristics and fruiting success of each species were determined from marked plants and collection of ripened fruits from both marked and unmarked flowers. Phenology of marked plants was recorded at least every third day during each species' flowering period in 1975 and 1976. Ripened fruits were collected prior to their dehiscence and dissected in the field (*C. virginica* and *D. laciniata* stems) or stored at −20°C for later dissection. We recorded the number of flowers per stem, number of ovules per flower, and the number of aborted and mature seeds per fruit for each species. The percentage of total biomass allocated to sexual reproduction (including flower stems) was determined from ovendried weights of plant parts taken at time of flowering for all species and at time of fruiting for all but *E. albidum* and *Dicentra* spp. The clumped nature of *I. biternatum* made it difficult to separate individual stems and their roots. Therefore, a metal cylinder (15-centimetre diameter) was used to remove cores that included several stems and their roots, which were then partitioned into reproductive and nonreproductive parts, dried and weighed. Seed weight was determined for ovendried specimens.

Air and soil temperature data for 1974–1976 were provided by the Illinois State Water Survey, which maintains a National Weather Service station on the University of Illinois-Urbana campus. Johnson et al. (1975) have shown that mean monthly air and soil temperatures taken in woodlands outside of Urbana

closely paralleled those recorded at the Univ. of Illinois station, but were 2–4°C lower. Because our study depended only on comparison of heat sums between years, the absolute difference between urban and forest temperatures does not affect the results. Cumulative degree-hours were calculated as the summation of 0.5-h intervals recorded for each 3°C air-temperature increment $\geq$4°C for the months of February, March, and April, 1964–1973. This threshold (4°C) has been associated with flowering phenology of several early spring species (e.g., Lindsey and Newman 1956). The number of 0.5-h intervals that daylight temperatures exceeded 13°C during the flowering season of each year was determined as an indicator of potential pollinator activity. Temperatures suitable for the activity of early spring pollinators generally must be at least 13°C (L. Davis, *personal communication*), although flies may be active at slightly lower temperatures. We observed few flights below 13°C, and then, only in sun flecks, where the local temperature was higher. Each such interval is called a ''pollinator interval,'' and each day on which at least 1 such interval occurred is called a ''pollinator day.'' Soil temperature at 10 centimetres was expressed as the mean of the daily minimum and maximum reading, and degree-days accumulated above a temperature of 0°C or 4°C. The higher threshold was chosen in parallel with that for air temperature, and the lower one represents a level often important for biological activity such as the development of plant parts underground (e.g., Risser and Cottam 1967, Kimball and Salisbury 1974). Other thresholds for heat sums were tried also, but did not change the results.

Canopy development was monitored by recording light intensity levels throughout the study area each spring. Data collection was restricted to early afternoon of overcast days to avoid the intensity extremes present on clear days. This criterion precluded a rigid sampling schedule, and readings in all years were taken opportunistically. Values were obtained by measuring light intensity with a Weston Illumination Meter®, 1 metre above every other phenology plot (N = 42), and dividing each by a base reading taken in an open site adjacent to the woods. When radiation was relatively constant, an average of base readings taken immediately prior to and following sampling in the woods was employed. On days of fluctuating radiation, base readings were taken synchronously with a second light meter (A LI-COR® meter was used for this purpose in 1976).

The 5% level of rejection was used in all statistical decisions.

RESULTS
The plants

All 7 species are low-growing, herbaceous perennials with broadly overlapping ranges in northeastern and/or north-central United States and southeastern Canada. All have whitish, usually UV-absorptive flowers (see also Kevan 1972, Guldberg and Atsatt 1975). A brief description of each species is given below, and some salient reproductive features are summarized in Table 1.

Claytonia virginica (spring beauty). The dish-shaped, protandrous flowers, with 5 stamens and a single ovary, are borne in racemes. They are white to pale pink, with darker pink veins and stamens; UV radiation is reflected from the filaments. Flowers last an average of 3 days (range 1–8), and were staminate for 1 day (Schemske 1977). Seeds are scattered when the capsule dehisces. *Claytonia virginica* is the only 1 of the 7 species that was frequently observed growing in disturbed, nonforest sites, such as lawns and cemeteries.

Dentaria laciniata (cut-leaf toothwort). The white-petalled, bell-shaped flowers are protogynous, with 6 stamens and a single ovary, and are borne in a corymb. UV radiation is reflected from a spot at the base of each petal and sepal. Flower life is $\approx$4 days (range 1–7), and is slightly but significantly shorter if the flowers are not pollinated ($\bar{x}$ = 3.4 days); the female phase lasts an average of 2.7 days (range 0.5–7.0). *Dentaria laciniata* reportedly has the capacity for autogamy (Harriman 1965); however, bagged and unmanipulated flowers produced no seeds in our study. The fruit, a silique, is elastically dehiscent.

Dicentra canadensis (squirrel corn). The bilaterally symmetrical flowers are borne in racemes. The petals are white, tipped with yellow, and UV reflectance is indicated only at the petal tips. The petals completely enclose the ovary and 6 stamens, and pollination can only be effected when the pollinator forces apart the petal tips. This species and *D. cucullaria* are the only obligate outcrossers of the group (Macior 1970). Flowers last an average of 12 days (range 9–15). The fruit is a capsule; the seeds bear an elaiosome, and are probably ant dispersed (Berg 1969).

Dicentra cucullaria (Dutchman's breeches). This species is similar to squirrel corn, although the shape of the flower is different. Flowers last an average of 11 days (range 9–14) and the seeds are ant dispersed (Stern 1961, Berg 1969).

Erythronium albidum (white dog-tooth violet). The single flower has a pale lavender or dusky white perianth in the human visual spectrum and the UV pattern indicates absorptance except for some faintly reflectant areas on the outer side of the perianth. The petals are much recurved, so that the 6 stamens and single ovary protrude well beyond the perianth on the nodding flower. Unpollinated flowers typically last 11–13 days; pollinated flowers usually last 7–8 days. When the protandrous flowers open, anthers cover the stigma but they dehisce and shrivel back within a day, exposing the stigma. The fruit is a capsule, containing seeds that bear appendages like those of ant-dispersed species. However, we observed only crickets and cara-

TABLE 1. Summary of reproductive features of 7 species of spring herbs

A. Flower, ovule, and seed production: x̄, (range), N; N.D. = no data

Taxa	Flowers/stem			Ovules/flower		
	1974	1975	1976	1974	1975	1976
Claytonia virginica	13.9 (7–24) 110	14.5 (8–26) 107	12.5 (5–24) 143	6 (0)[1] 1,275	6 (0) 550	6 (0) 1,022
Dentaria laciniata	9.4 (3–16) 294	10.9 (3–15) 79	10.1 (3–17) 99	11.6 (1–18) 2,175	12.1 (6–20) 790	10.6 (2–19) 979
Dicentra canadensis	4.8 (2–8) 119	5.3 (3–8) 80	N.D.	17.5 (11–23) 79	16.2 (10–21) 370	N.D.
Dicentra cucullaria	6.2 (2–12) 252	6.8 (5–16) 77	N.D.	14.7 (6–23) 348	16.0 (9–25) 490	N.D.
Erythronium albidum	1 (0)	1 (0)	1 (0)	37.8 (12–88) 285	31.1 (14–64) 68	N.D.
Isopyrum biternatum	3.1 (1–7) 422	3.3 (1–9) 289	3.1 (1–7) 510	8.1 (4–14) 451	9.3 (4–15) 369	8.8 (1–13) 392
Sanguinaria canadensis	1 (0)	1 (0)	1 (0)	35.9 (13–62) 296	N.D.	29.0 (12–48) 150

Taxa	Seeds/flower		
	1974	1975	1976
Claytonia virginica	3.4 (0–6) 1,275	2.0 (0–6) 550	3.0 (0–6) 1,022
Dentaria laciniata	4.9 (0–16) 2,175	6.1 (0–15) 790	4.9 (0–15) 979
Dicentra canadensis	1.4 (0–4) 61	0.4 (0–4) 370	N.D.
Dicentra cucullaria	8.4 (0–21) 270	8.4 (0–20) 486	N.D.
Erythronium albidum	N.D.	0.5 (0–7) 277	1.0 (0–6) 224
Isopyrum biternatum	1.8 (0–10) 454	1.3 (0–6) 369	2.8 (0–9) 392
Sanguinaria canadensis	28.9 (9–54) 225	N.D.	24.7 (7–44) 80

[1] Rare ovaries contained 8 or 10 ovules.

B. Breeding systems, nectar production (+ or −) and reproductive effort: S = self-compatible, A = autogamous, O = obligate outcrossing

Taxa	Breeding system	Nectar production	Mean seed wt (mg)[2]	Reproductive effort	
				Flowering (N)	Fruiting (N)
Claytonia virginica	S	+	1.16 (50)	27% (10)	24% (9)
Dentaria laciniata	S	+	1.8 (359)	9% (15)	18% (13)
Dicentra canadensis	O	+	0.96 (50)	14% (13)	...
Dicentra cucullaria	O	+	1.24 (50)	8% (10)	...
Erythronium albidum	S	−	9.69 (60)	14% (7)	...
Isopyrum biternatum	S[1]	−	2.2 (100)	1% (10)	4% (10)
Sanguinaria canadensis	A	−	7.05 (30)	4% (12)	11% (17)

[1] Strongly protogynous and does not self within a flower, but flowers on the same stem are compatible, which is genetically equivalent.

[2] Seed only, minus elaiosome for ant-dispersed seeds. Elaiosome dry weights (x̄) were very small (erythronium 0.37 mg, Dicentra canadensis 0.16 mg, Dicentra cucullaria 0.08 mg) except in Sanguinaria (4.9 mg).

Each seed weighed individually except for Dentaria (359 seeds in 5 lots of different sizes) and Isopyrum (100 seeds, weighed as 10 groups of 10).

TABLE 2. Average percentages of ovules fertilized (F) and matured (M) per fruit. * = incidental abortion of ovules, too infrequent to change the percent matured

Taxa	Con-di-tion	1974	1975	1976
Claytonia virginica	F	. . .	36	48
	M	. . .	30	44
Dentaria laciniata[1]	F	87	96	97
	M	60 (63)	61 (61)	66 (67)
Dicentra canadensis	F	7	2	. . .
	M	7*	2*	. . .
Dicentra cucullaria	F	54	52	. . .
	M	54*	50	. . .
Erythronium albidum	F	19	9	. . .
	M	11	6	. . .
Isopyrum biternatum	F	28	18	36
	M	22	14	33
Sanguinaria canadensis	F	81	. . .	85
	M	81*	. . .	85*

[1] Numbers in parentheses exclude the effects of predation on seeds. Predispersal seed predation was negligible for all other species.

bid beetles moving the seeds, at night. This species is unusually patchy in distribution, forming large, almost monospecific clumps in our study area. Vegetative propagation by several means is well developed (Robertson 1966).

Isopyrum biternatum (false rue anemone). The white, UV-absorptive, flowers are dish shaped with yellow anthers and are born in a panicle; they are protogynous, have numerous stamens, and are unique among the species we have studied in having several ovaries, usually 4 or 5. Flowers last 7–10 days, of which 3–4 days are in the female phase. The fruit is a follicle and the seeds have no known special means of dispersal. Like *E. albidum*, this species is extraordinarily patchy in space, being found only in dense, monospecific stands in our study area.

Sanguinaria canadensis (bloodroot). A single, white, dish-shaped flower bears numerous stamens and a single ovary. UV light is completely absorbed. This is the only species of the 7 capable of autogamy; after a brief protogynous period during which outcrossing may occur, the anthers collapse on the stigma (Schemske, *In press*). The total life of the flower is ≈2 days. The fruit is a capsule, bearing ant-dispersed seeds. The leaves are unique in this group for they persist well into the summer, long after the capsule dehisces.

Fecundity characteristics

Reproductive effort, as indexed by the percent of total biomass allocated to sexual reproduction, was highest for *C. virginica* and was <20% for all other species (Table 1).

The breeding systems of the 7 species varied from facultative autogamy (*S. canadensis*), to possible selfing within a flower by means of an insect visitor (*C. virginica*, *D. laciniata*, *E. albidum*) to possible selfing among flowers on a stem, with marked protogyny (*I. biternatum* and *D. laciniata*), to obligate outcrossing (*Dicentra* spp.). The percent of ovules producing mature seeds was highest in *S. canadensis*, as expected from the capacity for autogamy. However, among the species requiring insect visitation for pollen transfer, the probability of fertilization (see below and Table 2) varied greatly, and showed no relationship to breeding system, nectar production or seed weight (Table 1).

Interspecific differences in the number of flowers per stem was marked (Table 1). The number of ovules per flower also differed greatly among species (Table 1). Mean ovule number was inversely correlated with mean flower number per stem in 1974 (Spearman rank correlation, $n = 7$, $r_s = -.768$), although not in 1975 ($r_s = -.657$, with data for only 6 species). All species possess considerable variability in potential seed output, but may have adopted partially compensating means of achieving this. The average potential seed output per stem (mean ovule number × mean flower number) for *C. virginica*, *D. laciniata*, *D. canadensis*, and *D. cucullaria* all fall between 83 and 108 in 1974 or 86 and 132 in 1975, but potential outputs for *S. canadensis*, *E. albidum*, and *I. biternatum* are all much lower (for 1974: 36, 38, and 27, respectively; for 1975: no data [ND], 31, 31). Although a stem is not equivalent to an individual, it may be no coincidence that these 3 species produce the largest seeds of this group (Table 1); those of *S. canadensis* and *E. albidum* are especially large.

Few published records for seed set in these species seem to be available; Struik and Curtis (1962) recorded 2 seeds per stem [=per flower] in *E. albidum* and 25 for *S. canadensis*. Low seed set for *E. albidum* therefore appears not to be simply a local phenomenon.

Flowering phenology

Seasonal flowering patterns for all 7 species in 1974, 1975, and 1976 are shown in Fig. 1. Four things are immediately evident from the figure. (1) Marked overlap of the flowering period of all species during the period from mid-March to early May. (2) Large annual variation, which affects all species in the same direction but not to the same degree. All species flowered latest in 1975 and earliest in 1976. (3) A few consistent phenological differences among the 7 species. *Sanguinaria canadensis* always reached its flowering peak earliest; *I. biternatum* peaked latest in all 3 years. The remaining 6 species showed no regular temporal partitioning. *Claytonia virginica* and *S. canadensis* typically were the earliest to begin flowering (Anderson and Hubricht 1940), and *D. canadensis* always began last. (4) Large differences in the shapes of the curves among species but little between years for the same species. Some species regularly bloomed over a long
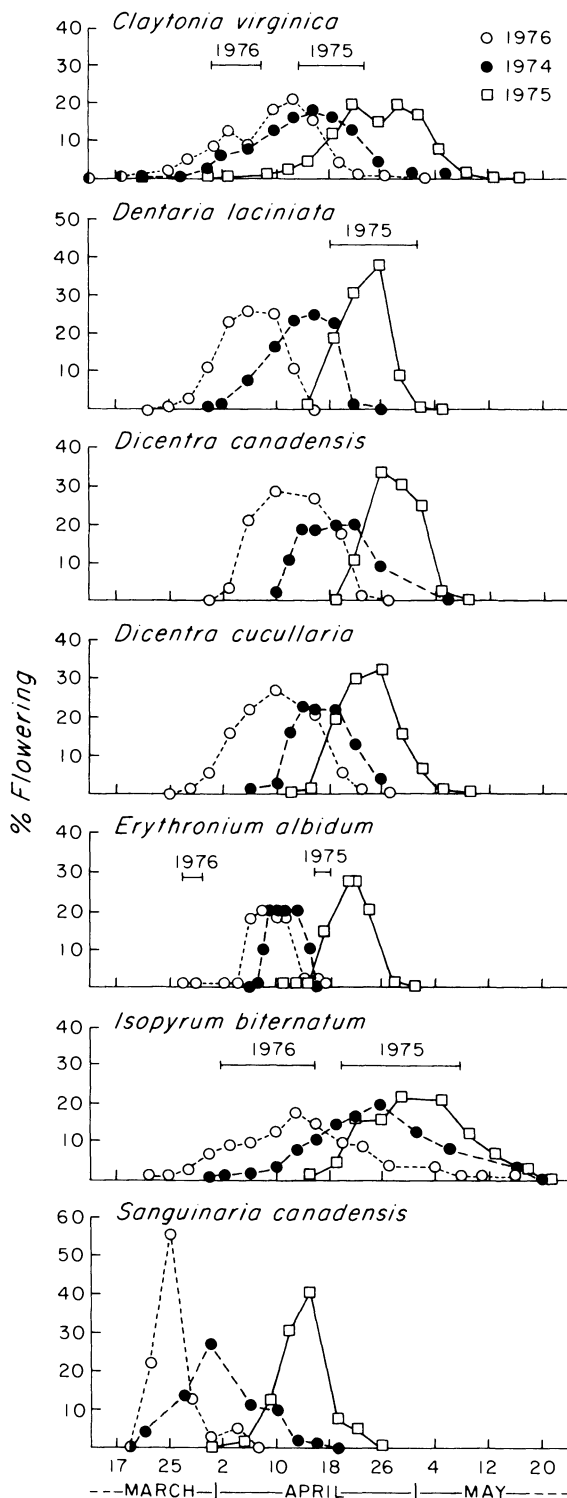
FIG. 1. Flowering phenology of 7 spring woodland ephemeral herbs in 3 yr. Data plotted as percent of all flowering stems in the census plots that bore flowers on the indicated days. Dated horizontal bars indicate period of statistically significant maximum seed set/flower for indicated year (data not available for all species or years).
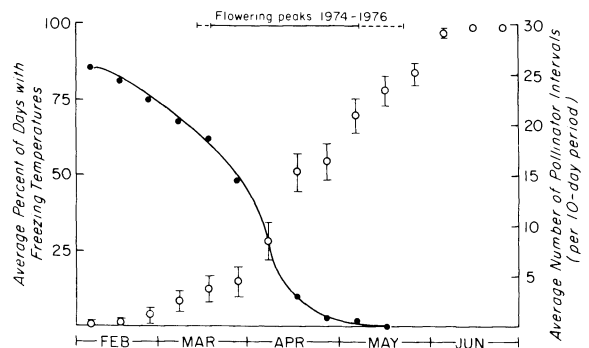

FIG. 2. Average seasonal decrease in the probability of freezing temperatures occurring during the indicated 10-day periods (data for 23 years, 1951–1973) (dots and curve); the average number of pollinator intervals per 10-day period ($\overline{X}$ ± 2 SE indicated) for 10 years, 1964–1973. The limits of the 1974–1976 flowering seasons and peaks (all species and years combined) are indicated at the top: range of flowering (dotted line), flowering peak (solid line).

period with long tails on the curve (*C. virginica*, *I. biternatum*), others began and/or ended suddenly with a fairly broad peak (*Dicentra* spp., *D. laciniata*, *E. albidum*), or had a sharp peak between gradual beginning and end (*S. canadensis*). The visibility of tails on the curve is partly dependent on sample size.

Flowering season in general.—By the end of March, on the average, <50% of the days in east-central Illinois are subject to freezing, and by mid-April, only ≈10% (Fig. 2). Furthermore, the average occurrence of conditions suitable for pollinator activity increased markedly in early April (Fig. 2). Between the end of March and mid-April, the average number of pollinator intervals jumped from <5 (per 10 days) to >15, and >50% of the days offered 1 or more pollinator intervals. Flowering peaks for our 7 species began when the average probability of freezing temperatures was lower than ≈65% and the average number of pollinator intervals per 10-day period was ≈4. Flowering peaks terminated before all the daylight hours became suitable for pollinator activity (in May). Therefore, flowering typically occurred almost as soon as the average probability of suitable pollinator conditions exceeded 0 and at a time when the risk of unsuitable conditions was often still high.

The amount of available light dropped from 50% of incident radiation during most of March to ≈32% in mid-April to <10% in early May (Fig. 3) as the canopy closed; complete canopy closure was effected before the end of May in all 3 years (Bazzaz and Bliss 1971, Morgan 1971). All of the 7 species terminated flowering before canopy closure. No annual variation in the time of canopy closure was detected (Fig. 3).

Annual variation.—Variation among years in flowering phenology showed that all species began flowering later and peaked later in 1975 than in 1976 or 1974 (Fig. 1). Mean March and April temperatures
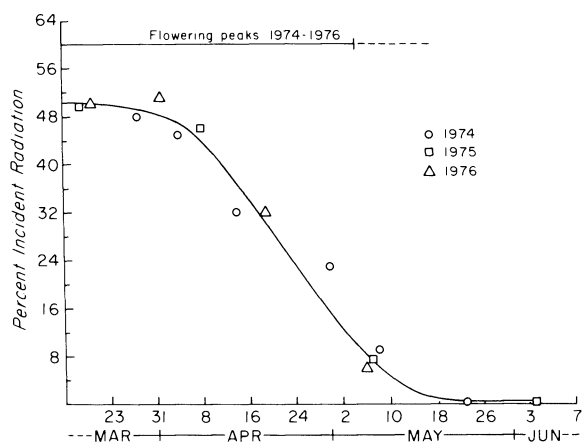
FIG. 3. Seasonal change in light penetration to the herbaceous layer. The duration of the 1974–1976 flowering seasons is indicated at the top (Fig. 2).

were considerably warmer than "normal" in 1976 and 1974, but equally colder than normal in 1975 (Fig. 4). More specifically, the first flowering peak for any of the 7 species occurred 17–20 days after an early period of 5 days or more of warm temperatures (Fig. 4) and the first flower was observed shortly after such a warm spell. This usually resulted in peak flowering for the group as a whole during the first period that consistently provided at least some pollinator intervals on many days (Fig. 4). Clearly, flowering times shifted to earlier dates when weather was warmer and were postponed in colder temperatures.

However, direct temperature effects may be restricted by other factor(s) (Fig. 4). In 1976, February was unusually warm, but flowering did not begin until mid-March. Furthermore, the cumulative degree-hours (air temperatures) before the flowering season began were quite different among years (Fig. 5) (the same was true for each species taken separately also,
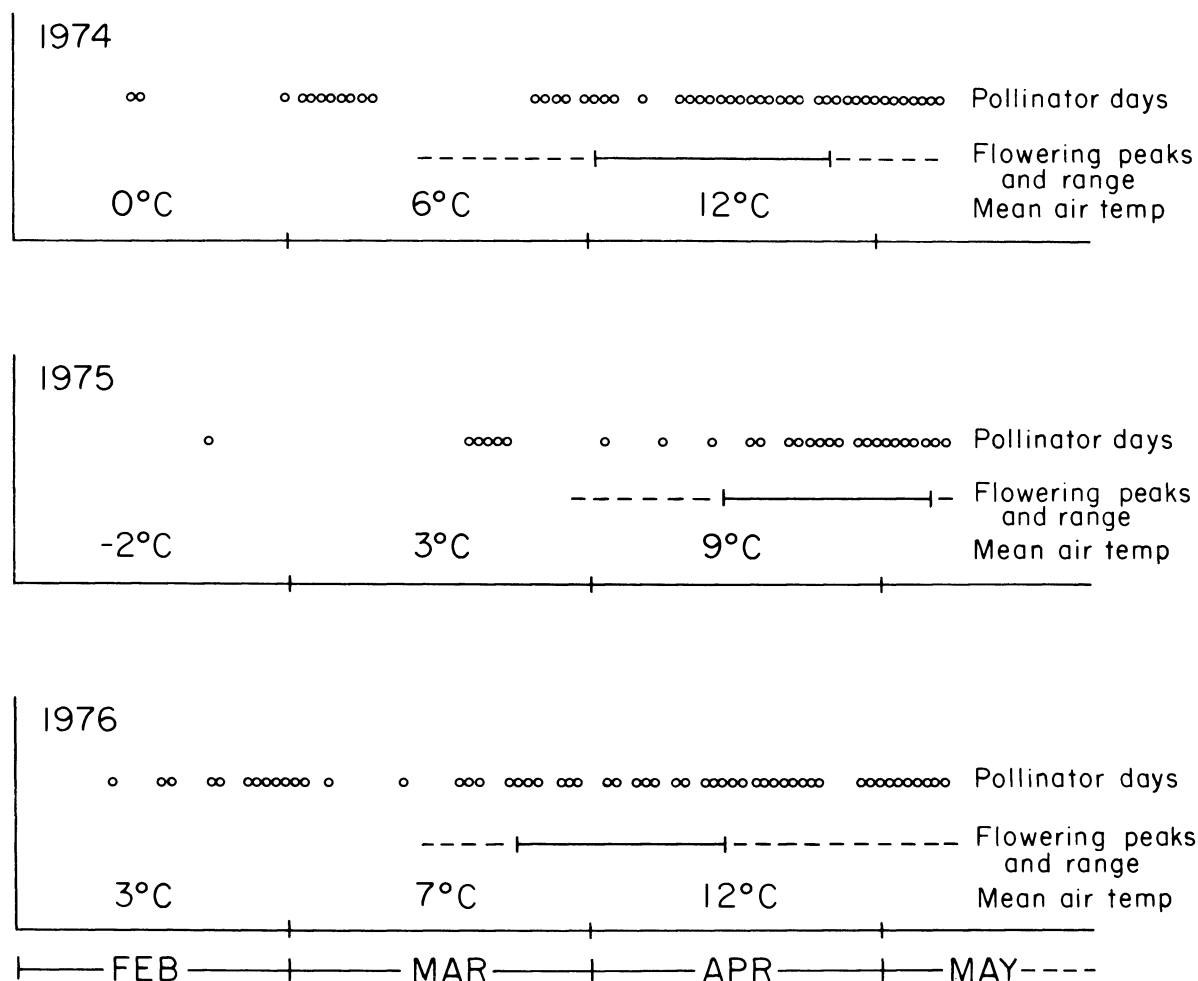

FIG. 4. Mean monthly air temperatures (February–April), duration of flowering seasons, and occurrence of warm diurnal temperatures (here indicated as at least 1 pollinator interval per day) for 1974–1976.
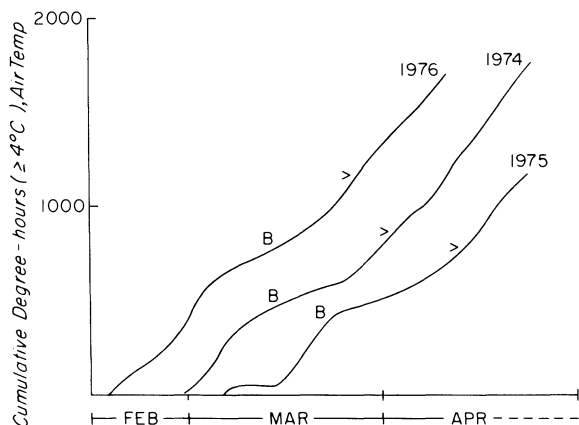
FIG. 5. Cumulative number of degree-hours per 24 h (threshold = 4°C, air temperature). The beginning of each flowering season (all species combined) is indicated on each annual curve by "B", the first flowering peak (*Sanguinaria canadensis*) by a caret. Only days after soil temperature (at 10 centimetre) exceeded 0°C are considered in the accumulation, because most plant development occurs above freezing.
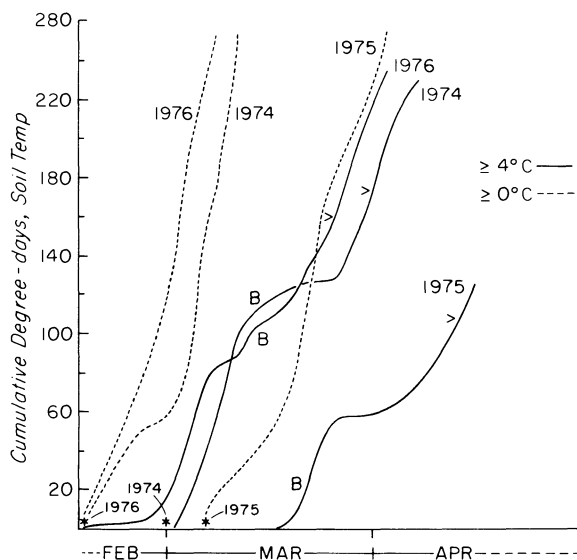

FIG. 6. Cumulative number of degree-days: soil temperatures. The beginning of each flowering season (all species combined) is indicated on each annual curve by "B", the first flowering peak by a caret. The last day of average soil temperatures below freezing is indicated by an asterisk for each year. The 0°C summations for 1974 and 1976 climb so rapidly that they are cropped short of flowering times. However, they differ so clearly from the summation for 1975 that the lack of simple relationship between soil temperatures and flowering is adequately demonstrated.

see below), indicating that the proximate control of flowering is probably more complicated than implied by earlier work (e.g., Lindsey and Newman 1956, Jackson 1966, but see Reader 1975b). Because soil temperatures are likely to be important in determining when plant growth and development can begin (e.g., Lettau 1965), we plotted cumulative degree-days at the 10-centimetre level for each of the 3 yr (Fig. 6). 1974 and 1976 showed both similar patterns and cumulative degree-days preceded the first flowering peak. The 1975 level was well below the other years; the first flowering peak occurred at ≈0.67 of the cumulative degree-days of the other 2 yr, and the flowering began at ≈0.2 of the level of the other years (Fig. 6). Similar differences appeared for each species considered separately (see below). Again, proximate control of flowering seems not to be a simple function of temperature.

Interspecific differences.—Although all 7 species responded to annual differences in temperature by temporal shifts in the same direction, some differences among the species in the degree of response may be seen in Fig. 1. Initiation of blooming varied least in *C. virginica*, 8 days difference among years, compared to ≈22 days for *D. laciniata* and *I. biternatum*. Initiation of flowering peaks shifted least for *C. viriginica* and *E. albidum*, ≈14 days difference among years, compared to ≈20 days for *I. biternatum* and *S. canadensis*.

Large differences in degree-hours or degree-days accumulated before flowering starts or peaks were evident for all species. For example, *C. viriginica*, reported to be rather closely tied to annual temperature variations by Lindsey and Newman (1956), began flowering after 1,200 degree-hours in 1975 but after

10,000 in 1976; the flowering peak began after 8,000 degree-hours in 1975 but after 18,000 in 1976. Similar differences were observed for the other species.

Temporal shifts in flowering are likely to be regulated proximately (in part) by temperature effects on plant growth. For 6 of these 7 species, seed production requires an insect pollen vector; the exception is *S. canadensis*, which characteristically has the earliest peak of blooming and hence, the highest risk of unsuitable weather for pollinators (Schemske, *In press*). The other 6 species, requiring pollinators, may be more highly adapted to respond to proximate temperature cues for growth and development in such a way that flowers are produced at times with a high probability of suitable weather for flying insect pollinators (Robertson 1895). We might therefore expect to find some correlation between the occurrence of early temperatures suitable for growth and later ones suitable for pollination, especially in species other than *S. canadensis*.

However, no association was apparent between the cumulative degree-hours (air temperature) or degree-days (soil temperature) and the occurrence or frequency of pollinator intervals during the flowering peak or total flowering season of any species. Early temperatures were, therefore, not precise predictors of the length of time for pollination during the flowering peak.

TABLE 3. Number of native flower visitors to each of the flowering species. Capture records from 1974 and 1975. An asterisk indicates visitation by honeybees, which were seldom collected

Taxa	Claytonia virginica	Dentaria laciniata	Dicentra canadensis	Dicentra cucullaria	Erythronium albidum	Isopyrum biternatum	Sanguinaria canadensis	Total
Andrenidae								
Andrena carlini	32	18			14	8		72
Andrena cressoni	1					1		2
Andrena erigeniae	57	1			1	2		61
Andrena erythronii					4			4
Andrena forbesii	6				1	3		10
Andrena masonii	11				5	7		23
Andrena miserabilis	5					1		6
Andrena personata						1		1
Andrena rugosa	2	1				2		5
Andrena sp. n.	4							4
Anthophoridae								
Ceratina metallica	1							1
Nomada luteola	1							1
Apidae								
Bombus griseocollis	1	3	10	6				20
Apis mellifera	*	*		*	*	*	*	*
Halictidae								
Augochlora pura						1		1
Augochlorella striata						1		1
Dialictus coeruleus	1							1
Dialictus oblongus						4		4
Dialictus obscurus	1							1
Dialictus imitatus						1		1
Dialictus zephyrus						1		1
Erylaeus macroupinensis						1		1
Halictus confusus		1						1
Lasioglossum forbesii	1							1
Syrphidae								
Carposcalis obscura	1							1
Eristalis dimidiatus	13	1						14
Helophilus fasciatus	20	4				2		26
Melanostoma sp.	1	2				2		5
Mesograpta marginata	1							1
Metasyrphus americanus	15					3	1	19
Syrphus torvus	2	1				2		5
Syrphus sp.	3	1						4
Xylota nemorum						1		1
Total species	22	10	1	1	5	19	1	32
Total individuals	180	32	10	6	25	44	1	298

The consequences of seasonal shifts in flowering can be examined in terms of seed production. Differences between means were compared by t-test; all differences reported below are statistically significant. Data are available for all 3 years for only 3 species (Table 1). Of these, *C. virginica* produced the most seeds per flower in 1974 and fewest in 1975 (the cold, late year). *Isopyrum biternatum* reached its highest average seed set in 1976 (the warmest year) and its lowest in 1975, and *D. laciniata* perversely reached its maximum in 1975. Of the others, *S. canadensis* set more seeds per flower in 1974 than in 1976, *E. albidum* produced more in 1976 than in 1975, *D. canadensis* did better in 1974 than in 1975; and *D. cucullaria* seed set was equal in 1974 and 1975. Thus, shifts in flowering phenology were not usually successful in maintaining levels of seed set, although it is possible that seed set might have been worse in the absence of such shifts. Furthermore, although several species were more successful in seed production in a warmer, earlier spring, this was not true for *C. virginica*, *D. laciniata*, or *S. canadensis*. Delayed flowering peaks were detrimental to seed set, especially for *I. biternatum*, *E. albidum*, and *D. canadensis*. These results suggest that temporal shifts are only imperfect responses to varying environmental conditions.

If the precise timing of flowering is adaptive in terms of sexual reproduction, we would expect maximum seed set to be achieved by flowers that bloom at the flowering peak. We have data for some species and

years that permit this comparison (Fig. 1). Peak seed set in 1975 was achieved by flowers open during peak flowering in *D. laciniata* and *I. biternatum*, but preceded peak flowering of *C. virginica* and *E. albidum*. In 1976, peak seed set tended to occur in flowers blooming just ahead of peak flowering in *I. biternatum* and *C. virginica*, and occurred markedly earlier in *E. albidum*. These results further substantiate the idea that perfect timing of flowering is seldom achieved.

In addition, flowering peaks of no species (or sets of species) coincided consistently with depressions of seed set (per flower or per ovule) in any other species. Therefore, any effects of possible competition for pollinators did not account for temporal displacements of peak seed set.

The frequent asynchrony of flowering and seeding peaks also allows comparison of the number of pollinator days during both peaks. The number of pollinator intervals and days was slightly greater during flowering peaks than during seed set peaks, except for *E. albidum*.

Interspecific differences in the shape of the flowering-phenology curve were marked and, in general, long-blooming species had broader peaks, but the ecological importance of these differences is not clear. No association of total length of flowering nor of relative height of the peak with floral longevity, pollinator specialization, efficiency of seed set, or other possibly relevant factors for which we have data was evident.

Flower visitors: constancy, selectivity, and visitation rates

The major flower visitors and possible pollinators were bees (families Apidae and Andrenidae) and flies (family Syrphidae), with occasional visits by small halictid and anthophorid bees. The alien honeybee (*Apis mellifera*) was common and was observed on all species except *D. canadensis*. The honeybee visited each of the remaining 6 species more frequently than any native visitor and, in most cases, more frequently than all native visitors combined. Although the population size of *Apis mellifera* undoubtedly varies annually with the activity of local beekeepers, the high frequency of honeybee visits to 6 of our 7 species suggests that coevolutionary relationships among the natives may well be disturbed, although the 300 yr or so of honeybee occupancy of North America ($\approx$130 yr in the Illinois area; Jaycox 1976) is potentially sufficient time for significant evolutionary adjustments to have been made.

Claytonia virginica was visited by a variety of native pollinators, predominately *Andrena erigeniae* (Andrenidae), a specialist on this species (Davis and LaBerge 1975; this study, Table 3). *Dicentra canadensis* and *D. cucullaria* were visited only by *Bombus griseocollis* (Apidae) of the native flower visitors; Macior (1970) found that *D. cucullaria* was pollinated by *Bombus* spp. Reportedly *E. albidum* has a special pol-

linator, *Andrena erythronii* (Michener and Rettenmeyer 1956), but was visited mainly by *A. carlini* in our survey. *Dentaria laciniata* was visited primarily by andrenids, especially *A. carlini*, and assorted syrphids. *Isopyrum biternatum* received a fairly wide diversity of regular visitors (Table 3).

Seven of the most common native flower visitors visited *C. virginica* more frequently than the remaining 6 flower species (Table 3); only *B. griseocollis* centered its foraging elsewhere (on *Dicentra* spp.). The frequency of insect visitation to *C. virginica* can be accounted for, in most cases, by the great relative abundance of this species in the woods and hence does not index insect "preference" for this species.

Floral preferences can be determined by comparing relative visitation rates to the relative availability of different flowers. Combining all observations for 3 plant species for which we have sufficient information, insects generally selected *D. laciniata* and *C. virginica* out of proportion to their abundance, and *I. biternatum* less (Table 4). On the plots containing just *C. virginica* and *D. laciniata*, the latter was heavily favored. Most of this preference is accounted for by the foraging of honeybees, which invariably preferred *D. laciniata* to *C. virginica* to *I. biternatum*. Syrphid flies, on the other hand, tended to prefer *C. virginica*, visited *D. laciniata* about as often as expected on the basis of relative abundance and tended to avoid *I. biternatum* (Table 4). *Andrena* spp. (except *A. erigeniae*) preferred *D. laciniata* to *C. virginica*, but did not show preferences between *C. virginica* and *I. biternatum*. *Bombus griseocollis* selected *D. canadensis* over *D. cucullaria*.

Most flower visitors were "constant" foragers, visiting only 1 species of flower during a foraging trip. We recorded flower visitations for 109 individual foraging insects (mostly *Apis*, *Andrena* spp. and syrphids), and found that 81% of these foraging series were to a single kind of flower. No differences in relative constancy of these 3 insect categories were apparent. The observed preferences indicated above must therefore result largely from foraging preferences of new recruits (possible for *Apis*) or preference changes between trips.

We estimated the total visitation rates to several species of flowers from the data obtained on plots of known floral abundances. *Claytonia virginica* received an average of 0.14 visits per stem per 10 min. (max = 0.62, n = 24 10-min intervals), *D. laciniata* 0.23 (max = 0.37, n = 15), and *E. albidum* 0.71 (max = 1.5, n = 8). *Isopyrum biternatum* received an average of only 0.03 visits per flower per 10 min (max = 0.1, n = 18). (Data for the other species are inadequate for these purposes.) Although the foraging rate on *I. biternatum* was determined on a per-flower basis, we can approximate a per-stem rate. Only rarely were more than 2 flowers open on an *I. biternatum* stem. By multiplying the per-flower visitation rate by 2, we

TABLE 4. Foraging preferences of insects: relative frequency of visitation compared to relative abundance of flowering stems in plots (data in parentheses were collected in separate observation periods on the basis of relative abundance of open flowers). Differences tested by χ^2; the frequency of observed visits is different from expected in all cases except those marked by a dagger (†)

A. All insects

	Frequency	
	Flowering stems	Visits
Claytonia virginica	78% (20%)	39% (53%)
Dentaria laciniata	20% (3%)	53% (8%)
Isopyrum biternatum	(76%)	(35%)
		[N = 501 (363)]

B. *Apis* only (additional observations on *S. canadensis*: 39 visits to 17 flowers compared to 20 visits to 40 *C. virginica* flowering stems in the same plot).

	Frequency	
	Flowering stems	Visits
Claytonia virginica	78% (38%)	20% (52%)
Dentaria laciniata	22% (3%)	80% (19%)
Isopyrum biternatum	(59%)	(29%)
		[N = 275 (128)]

C. Syrphids only

	Frequency	
	Flowering stems	Visits
Claytonia virginica	78% (30%)	73%† (61%)
Dentaria laciniatum	22% (3%)	27%† (2%)
Isopyrum biternatum	(67%)	(37%)
		[N = 92 (152)]

D. *Andrena* (except *A. erigeniae*)

	Frequency	
	Flowering stems	Visits
Claytonia virginica	74% (26%)	36% (14%†)
Dentaria laciniata	25%	56%
Isopyrum biternatum	(74%)	(86%†)

E. *Bombus griseocollis* (The relative frequencies of the plants in these plots are not representative of the whole study area, where *Dicentra cucullaria* outnumbered *Dicentra canadensis* 4:1)

Dicentra canadensis	67%	86%
Dicentra cucullaria	33%	14%
		(N = 43)

arrive at a stem visitation rate of 0.06 visits/stem/10 min, which is still quite low compared to the other species.

DISCUSSION AND CONCLUSIONS

Fecundity characteristics

Reproductive effort of these 7 species of woodland herbaceous perennials tended to fall within the ranges for other perennial herbs (Struik 1965, Anderson and Loucks 1973, Gaines et al. 1974, Ogden 1974). That

for *C. virginica* was relatively high (within the range depicted for an annual *Helianthus*, Gaines et al. 1974) and is perhaps related to *C. virginica's* ability to colonize other habitats.

Breeding systems of our early flowering herbs varied from facultative autogamy to obligate outcrossing, and thus showed no common adaptations to early blooming. Seed set was not related to breeding system except in the autogamous *S. canadensis*, with a typically high proportion of ovules maturing into seeds. The average number of flowers per stem tended to be inversely correlated (among species) with the number of ovules per flower, such that the maximum potential seed output per flowering stem was quite high for the relatively small-seeded *C. virginica*, *D. laciniata*, and *Dicentra* spp., but lower for the large seeded *S. canadensis*, *E. albidum*, and *I. biternatum*. Thus, within some constraints imposed by selection for seed size, it appears that trade-offs between flower number and ovule number have resulted in similar reproductive potentials. The largest ovule numbers (per flower) are found in the species that are probably ant dispersed (*E. albidum*, *S. canadensis*, *Dicentra* spp.). To the extent that large ovule number permits large numbers of seeds to be matured at a given time, a large number of seeds in one spot might be an adaptation facilitating ant dispersal; the results of Beattie and Lyons (1975) for *Viola* were inconclusive.

The selection pressures emphasizing ovule number at the expense of flower number might also involve the ability of pollinators to deliver relatively large pollen loads or to make repeated visits which are most feasible if flower longevity is great. Of the species with larger numbers of ovules, *S. canadensis* is facultatively autogamous and receives much pollen, *E. albidum* has a very long flower life, and *Dicentra* spp. have long flower life and are pollinated primarily by large bees, capable of carrying much pollen. A long pistillate phase is not characteristic of the species with smaller ovule numbers.

Phenology variations

Flowering of all 7 species began as soon as temperatures were apparently suitable for plant growth and for pollinator activity and ended before closure of the canopy. All species bloomed earlier during a warm, early spring than a cold, late spring, and the first species (*S. canadensis*) typically began flowering shortly after the first period of several consecutive days of warm weather. Flowering peaks for all species thus occurred during the first period of weather consistently suitable for insect pollinators.

Closer inspection of the relationship between spring temperature and flowering, however, showed that the association may not be as close as is often claimed. First, unusually warm weather in early spring (February) did not induce flowering as early as might have been expected. Furthermore, unusually cold weather

in March and April did not prevent flowering. Second, neither cumulative degree-hours (air temperature) nor degree-days (soil temperature) were good predictors of flowering times for the group or for species taken singly, especially in an unusually cold spring (1975). Third, although *S. canadensis* always reached its flowering peak first and *I. biternatum* last, the remaining species peaked at different times, relative to each other and to the temperature regime, in different years. These observations suggest the importance of additional factors regulating flowering phenology, including: (1) a low probability of warm weather (and thawed soil) in February may select against the capacity to respond to unusually warm temperatures in early spring. The number of 0.5-h daylight intervals suitable for pollinator activity occurring in February is usually very low (<1 in 10 days, Fig. 2). Temperatures favorable for plant growth and flowering are often lower than those for insect flight (e.g., Lindsey and Newman 1956, Risser and Cottam 1967, Caldwell 1969), and Urbana weather records for the 87 yr since 1889 indicate that in only 14 yr did the February average temperature equal or exceed 2°C (as in 1976), but equalled or exceeded −1°C (as in 1974) in 42 yr. Thus, weather warm enough for pollinator activity or plant growth has occurred rather infrequently in February, so we would guess that the high risk of unsuitable weather may have selected against even earlier flowering. (2) Canopy closure occurred at a consistent time in all 3 yr, clearly defining the later limit of the flowering season for all our species, and thus providing an end point beyond which flowering may not be postponed. In addition, the leaves of *C. virginica*, *Dicentra* spp., and a different species of *Erythronium* (*americanum*), have high light-compensation points and are shade intolerant; *D. laciniata* leaves are somewhat less so (Sparling 1967). Sparling also noted that leaf development of these species was complete before the canopy closed. *Sanguinaria canadensis* leaves have lower compensation points (Sparling 1967) and persist well into summer, in deep shade. Canopy closure was correlated with increased abortion rates of fertilized ovules in *C. virginica* (Schemske 1977). Perhaps in an unusually cold spring such as 1975, a fail-safe mechanism operates to permit flowering before the canopy closes. Given that these species are apparently committed to early spring flowering, the disadvantages of flowering during a cold, late spring are probably less than those of flowering as the canopy closes. Such a suggestion assumes that annual flowering is the rule. (3) Conditions during the dormant period may be critical proximate factors (Risser and Cottam 1967), uncorrelated with temperatures for growth and flowering. Risser and Cottam (1967) reported that rates of shoot development of *Erythronium* spp. and *Dicentra cucullaria* increased with increasing duration of the cold treatment to which dormant bulbs/corms were subjected, and that the duration of life for the above-ground parts

decreased. This response is exactly what is expected from the hypothetical fail-safe mechanism: when development is delayed, growth is rapid once it becomes possible, and the aboveground part of the cycle is speedily completed (e.g., before the canopy closes). (4) The critical thermal thresholds and optima of each species are likely to be different (e.g., Lindsey and Newman 1956, Risser and Cottam 1967, Anderson and Loucks 1973), perhaps for historical reasons as much as present ecological ones. (5) Other ultimate or proximate factors, perhaps important in regulating flowering phenology, might be nutrient availability (Muller and Bormann 1976), throughfall precipitation (Anderson et al. 1969), photoperiod (Bliss 1971), and conditions for production and storage of photosynthate the previous year.

Annual differences of phenology were associated with differences in average seed production per flower for all species except *D. cucullaria*. Seed production was lowest for 4 species in 1975, the cold, late spring, when *D. laciniata* achieved its highest seed production. *Claytonia virginica* and *S. canadensis* reached their maximum seed output in 1974, the intermediate year. Phenological shifts therefore did not usually result in equal annual seed production, and different species produced their maximum numbers of seeds/flower in different years. All 7 species are perennials with considerable vegetative propagation; the requirements of this aspect of growth may place constraints on temporal shifts in flowering, and diminish to some extent the importance of high seed production in any one year.

All species except *S. canadensis* depend entirely on insects for pollination. We might therefore expect to find that these species respond to proximate cues for growth and development such that flowering occurs at a time of maximum suitability for pollinator activity. In general, flowering peaks occurred during the first protracted period that offered temperatures suitable for pollinator activity. If the entire flowering season in 1975 had occurred at the same time as in 1974, the number of days with suitable pollinator intervals would have been only 38–73% (depending on the species) of the 1974 level. By blooming late, most species spanned similar numbers of pollinator days in both years (*D. laciniata* and *E. albidum* did not). The number of pollinator days during the 1976 flowering season of all species would have been very similar to that of 1974 if flowering had occurred at the same time; but the early 1976 season also included a similar number of pollinator days. Furthermore, a forward shift of the flowering peak for each species in any year to the period immediately preceding the observed peak usually would have resulted in a decrease in the number of pollinator days. Backward shifts of the flowering peak to the period immediately following the observed peak seldom would have increased the number of pollinator days, although the duration of suitable intervals during

those days would often have increased. These observations provide evidence that these plants can successfully shift their flowering times to occur during the first consistently suitable period.

However, heat sums early in the season, before flowering, were not correlated with the occurrence of conditions suitable for pollinator activity during flowering. Furthermore, seasonal maxima of seed production per flower were frequently nonsynchronous with the flowering peaks of each species, suggesting that peak flowering was often not *precisely* timed to coincide with seemingly optimal pollinator conditions. Because the duration of suitable pollinator conditions differed little between the times of peak flowering and of peak seed production, we infer that long series of hours or days with suitable conditions for pollinator activity are not necessary for the observed rates of successful pollination. The insect pollinators can apparently service the flowers during short, rather unpredictable interludes of suitable conditions for activity. As a consequence, it seems that these plant species may not possess any great capacity for fine tuning of their flowering peaks to pollinator conditions. Rather, they may flower as soon as possible each spring, after the first warm spell, and essentially gamble on the presence of adequate pollinator conditions on particular days during that first period in which pollinator activity is possible. Therefore, due to the erratic weather of early spring or to other factors, optimal pollinator conditions may often be missed, with resultant displacement of flowering and seed-production peaks and, for some species, annual differences in reproductive output. The low fertilization rate estimated for most species indicates that viewing the phenology of these species as something of a gamble may not be far wrong. The possibility of other constraints on flowering phenology (see above) does not alter this argument. We are suggesting that conditions suitable for pollination may not be of overriding importance in determining the *precise* timing of flowering *within* the early spring period. Hence, other constraints may be so.

Particularly for very patchily distributed species, another explanation of the asynchrony of flowering and seed set peaks is possible. Microspatial variation in climatic conditions (e.g., Anderson et al. 1969, Beattie 1971, Bliss 1971) for different individuals could produce locally different optima for flowering that become obscured in consideration of a population average, unless the number of patches was large compared to the microclimatic variations (which was probably not true in our study, at least for *E. albidum*).

Jaques and Hilleary (1945) and Leopold and Jones (1947) stated that the earliest-blooming species are likely to show the most annual variation in the start of flowering. However, this does not appear to be true *within* the group of early flowering species, judging from our data, as well as those of Leopold and Jones

(1947), Lindsey and Newman (1956), and Jackson (1966).

Flower visitors, pollinator limitations, and interactions among plant species

Some observations indicated that competition for pollinators was potentially important. Competition in the past may have selected for early flowering (e.g., Robertson 1895, 1924, Levin and Anderson 1970, Mosquin 1971, Heithaus 1974, Reader 1975a) and perhaps autogamy (Levin 1972c) in *S. canadensis*, and may have contributed to the evolution of specialist pollinators (e.g., *A. erigeniae*, *A. erythronii*, and to some extent *Bombus* with respect to this group of plants) on some other species. Such evidence for competition is, of necessity, largely inferential.

The blooming period of 6 of the species we studied were not regularly staggered, but overlapped extensively, and to somewhat different degrees in different years, and thus temporal displacement was not evident (for these 6 species). *Sanguinaria canadensis* consistently preceded the others in peak blooming.

Although *D. laciniata* attracted certain flower visitors out of proportion to its abundance in the woods, no depression of seed set of simultaneously blooming species was evident. Strong seasonal changes in seed set per flower made it impossible to demonstrate competitive effects. Although peak flowering of *D. laciniata* did not coincide with depressions of seed set in other species, it is possible that overall seed set might have been higher in the absence of *D. laciniata*. Individual insects with preference for *C. virginica*, for instance, may have continued to forage on *C. virginica*; visitors to *D. laciniata* may have been primarily additional individuals. If this were the case, then the flowering of *D. laciniata* would not remove pollinators from *C. virginica* but would simply reduce the additions to the pool of individuals visiting *C. virginica*.

That competition for pollinators is of considerable potential importance in determining seed production is supported by evidence for pollinator limitations on seed set for 6 of the 7 species. First, for *E. albidum* an average of 78% of the hand-pollinated flowers outcrossed between "clones" produced seed, compared to an average of 33% of the flowers available for natural pollination. *Erythronium albidum's* special pollinator (*A. erythronii*) was rare in Brownfield Woods, and although *Apis* visited *E. albidum* frequently, it seems to have been ineffective as a pollinator. Second, bumblebees were also present in low numbers, and their preference for *D. canadensis* was insufficient to compensate for the absolute rarity of pollinator visits. Third, we estimated whether ovules had been successfully fertilized by observing if any size increase had occurred as the fruit began to mature. If abortion of fertilized ovules occurred before a size increase became apparent, both fertilization and abortion rates would be underestimated. The percent of ovules ap-

parently fertilized was quite low for all species except *S. canadensis* and *D. laciniata* (Table 2). That for *D. canadensis* reflected the low rate of *Bombus* visitation, and that for *E. albidum*, the ineffectiveness of *Apis* as a pollinator. The figures for *I. biternatum* tend to be somewhat lower than for *C. virginica*, but not as low as the low visitation rate would have suggested. Fourth, we can compare the number of ovules per fruit with the number of ovules fertilized and matured. If failure of fertilization accounts for a greater portion of ovule loss than failure to mature, we can infer that pollinators provide important limitations on seed production. On the other hand, if abortion of fertilized ovules is relatively great, pollinator limitation is less likely to be of major importance to seed set. For 5 of the 6 species requiring insect vectors of pollen, the abortion rate (the difference between percent fertilized and matured) was low compared to the rate of fertilization (Table 2), supporting the hypothesis of the general importance of pollinator limitation. Even the autogamous breeding of *S. canadensis* did not result in 100% seed set. However, marked increases in ovule-abortion rates for late-blooming *C. virginica* (Schemske 1977), *D. laciniata*, and *E. albidum* flowers show that the relative importance of pollinator limitation may vary seasonally. *Dentaria laciniata* was the only species with a consistently high level of fertilization and a relatively high abortion rate.

The alien and ubiquitous honeybee had strong foraging preferences and the potential for effecting marked changes in the relationships among certain of these plant species. The extent to which this potential is realized depends on the extent to which pollinators have limited the distribution and abundance of these plant species.

Another kind of interspecific relationship involving pollinators is floral mimicry. Nectar-poor species might be mimics of species offering richer, more copious nectar rewards (e.g., Macior 1968, 1971, Heinrich 1975). The white coloration common to all 7 species might suggest that a mimicry system is operating within this group; in addition, most largely or totally absorb UV light (Jones and Buchmann 1974, Utech and Kawano 1975). However, flower shapes are quite distinctive except in *I. biternatum* and *C. virginica* which are both saucer shaped. *Isopyrum biternatum* produces no nectar, *C. virginica* does, but these 2 species are readily distinguished in both the visible and the UV portions of the spectrum. Therefore, the morphological characteristics do not strongly suggest mimicry, although floral form sometimes may be quite unimportant for some pollinators (e.g., *Bombus*, Macior 1974). Nectarless mimics may commonly follow their nectar-bearing models in flowering time (Heinrich 1975) or bloom sporadically during the more extended flowering season of the supposed model (Gentry 1974), thus capitalizing on established foraging habits of the pollinators. Among our species, the peak

bloom of the nectarless *I. biternatum* consistently followed that of the nectar-rich *D. laciniata*, and in 1975 and 1976 peak seed set for *I. biternatum* tended to occur both during and after peak flowering of *D. laciniata*. However, *I. biternatum* has a far more extended season than *D. laciniata*, though they begin at about the same time, so a strong case for mimicry of *D. laciniata* by *I. biternatum* is hard to claim.

Convergence of floral morphology or colors and sharing of pollinators has been suggested (Macior 1974, Watt et al. 1974), but pollinator sharing seems likely only if pollinators were not limiting to seed set or in mimicry systems. Competitive use of the same pollinators does not qualify as sharing in this sense. Therefore, this form of interspecific interaction is unlikely in our system.

The possibility that rare species in a community may suffer "minority disadvantage" from pollinators favoring more common species has been discussed by Levin (1972a,b), Straw (1972), and Bobisud and Neuhaus (1975). Straw concluded that species present in low frequencies could overcome their minority disadvantage if their pollinators were relatively constant. As we have seen, both rare and common species in our study possessed very constant flower visitors and thus the rarer species appear to have overcome their potential disadvantage relative to the common species.

That the common flower color for all 7 species is white remains to be explained. The use of flowers as basking sites for insects that may then pollinate the flower (e.g., Hocking and Sharplin 1965, Kevan 1975) is a possibility, as yet untested. However, the bilaterally symmetrical shape of the pendant *Dicentra* flowers suggests that such an explanation probably can't be a general one for this group of species. White is probably 1 of the most conspicuous colors, viewed against a brown or green background of leaf litter or foliage. If the background reflected UV radiation, the contrast with UV-absorbing flowers would be enhanced (Frohlich 1976), but samples of litter and fresh foliage indicate little background reflection. High visibility of flowers might be particularly important to insects that fly early in the year, because the brief interludes of suitable flight conditions that often prevail at that season may place a premium on rapid location of food resources by the insects.

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