



Pollination Ecology of the Spring Wildflower Community of a Temperate Deciduous Forest

Author(s): Alexander F. Motten

Source: *Ecological Monographs*, Vol. 56, No. 1 (Mar., 1986), pp. 21-42

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/2937269>

Accessed: 17/07/2014 17:31

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecological Monographs*.

<http://www.jstor.org>

POLLINATION ECOLOGY OF THE SPRING WILDFLOWER COMMUNITY OF A TEMPERATE DECIDUOUS FOREST¹

ALEXANDER F. MOTTEN

Department of Botany, Duke University, Durham, North Carolina 27706 USA

Abstract. I studied the spring wildflower community of mesic deciduous forests in piedmont North Carolina to determine (a) the extent to which fecundity is pollination-limited in the community, (b) the importance of competition for pollination in affecting seed-set, and (c) the characteristics of plants and their floral visitors that most contribute to full pollination. Although inadequate pollination seems likely in the community, supplemental hand-pollination significantly improved fecundity in just 3 of the 12 species I examined. Pollination-limited reproductive success was evident only in a distinctive subset of the community, species pollinated primarily by queen bumble bees. The majority of wildflower species are pollinated by flies and solitary bees. Measurements of visitation rates and pollinator effectiveness on these plants confirmed that they are usually adequately pollinated in spite of a short blooming season, considerable overlap in flowering times, extensive pollinator sharing by concurrently blooming species, and inclement weather that frequently interrupts insect activity. Many of the flies and solitary bees are inconstant foragers, yet competition for pollination among wildflower species through differential pollinator attraction or interspecific pollinator movements usually does not significantly decrease the seed-set of plants with shared visitors. Competition may act with other causes of insufficient pollination, however, as a selective force to maintain a characteristic set of floral biology traits within the community, including autogamy and self-compatibility, extended receptivity, and pollination by a variety of visitor types. That these floral traits contribute significantly to the successful pollination of vernal herbs was demonstrated by observations of visitor behavior, plant caging experiments that excluded visitors or restricted their access to selected flowers, and measurements of floral lifetimes and seed-set for individual plants. These traits are effective regardless of the source of pollination-limited fecundity, and it is the prevalence of such traits, rather than floral specialization or character displacement, that distinguishes the forest spring wildflower community from other communities with potentially inadequate pollinator service.

Key words: *bees; Bombylius major; competition; deciduous forest; floral biology; forest herbs; North Carolina; plant community; pollination; seed-set; spring wildflowers.*

INTRODUCTION

Pollination studies have traditionally concentrated on one or a few closely related plant or pollinator species. Pollinators and plants, however, rarely occur as isolated pairs. Studies at the level of the whole community can consider the relationship between flowers and their visitors in a more complex and ecologically realistic setting and can be used to examine interspecific interactions within groups of plants and pollinators. Most community pollination studies have sought evolutionary explanations for patterns of plant community structure and have emphasized the ways that plant species may have partitioned the visitor resource to reduce competition for pollination (e.g., Macior 1970a, Heithaus 1974, Percival 1974, Frankie 1975, Heinrich 1975, Moldenke 1975, Ostler and Harper 1978, del Moral and Standley 1979, Parrish and Bazzaz 1979, Thomson 1980). Such studies have described interspecific differences in floral rewards, color, or morphology and have especially noted staggered flowering phenologies (e.g., Mosquin 1971, Frankie et al. 1974, Heithaus 1974, Pojar 1974, Reader 1975, Stiles 1975, 1977, Heinrich 1976a, Pleasants 1980; but see Brown and Kodric-Brown 1979).

In contrast to the inferred evolutionary consequences of flower-visitor interactions in community-wide studies, the ecological implications have received less attention even though they are much more tractable experimentally. Ecological aspects include the importance of different floral visitors to various plant species, the dependence of pollinator effectiveness on the diversity and spatial patterns of plants in bloom, and especially the causes and extent of pollinator-limited plant reproductive success. Because reproductive success is an important component of plant fitness, ecological factors contributing to pollinator-limited seed-set can be potent selective forces on plant reproductive biology and breeding systems (e.g., Levin 1971, Lloyd 1980, Bierzychudek 1981, Stephenson 1981, Wyatt 1982). Despite their importance, direct studies of inadequate pollination in perennial plant populations or communities are uncommon. The very few demonstrations of reduction in reproductive output caused by competition for pollinators are based on studies of a single species (Zimmerman 1980) or two species of coexisting plants (Waser 1978, Campbell 1985). A few community pollination studies consider the relative contribution of different pollinators or describe competitive relationships among plant species (e.g., Hocking 1966, Feinsinger 1978, Brown and Kodric-Brown 1979, O'Brien 1980, Pleasants 1980,

¹ Manuscript received 16 August 1984; revised 29 March 1985; accepted 17 April 1985.

Thomson 1982). Fewer studies report rates of reproductive success for more than one or two species in a community or consider pollinator-limited fruit- or seed-set (Kevan 1972, Macior 1978a, Schemske et al. 1978, Gross and Werner 1983).

I examined pollinator-limited reproductive success in the spring wildflower community of deciduous forests in the piedmont of North Carolina. This community should be particularly susceptible to inadequate pollination for several reasons: its high diversity of entomophilous species, a short blooming season confined to the period of suitably warm temperatures before canopy closure (Gleason and Cronquist 1963), and frequently inclement weather that interrupts pollinator activity. Despite the widespread distribution of temperate deciduous forests, the pollination ecology of their spring wildflower communities has been little studied. Separate studies of the pollination biology of one or a few vernal herbs from many different localities (e.g., Lovell 1942, Macior 1970b, 1975, 1978a, Whigham 1974, Utech and Kawano 1975, Bernhardt 1976, 1977, Swanson and Sohmer 1976, Schemske 1977, 1978, Lindsey 1979) have provided no consensus on factors limiting fecundity in the forest spring wildflower community (Bierzuchudek 1982) nor has any consistent pattern among species emerged. Broader scale studies of the community have concentrated on species pollinated by queen bumble bees (Macior 1978b), phenological patterns and descriptions of floral visitors (Robertson 1895, 1924, Antonova 1973), or interactions between blooming time and pollination (Schemske et al. 1978).

My study used an observational and experimental approach to answer the following questions:

- 1) Is seed-set in forest spring wildflowers limited by pollinators, and if so, how strongly does inadequate pollination affect fecundity?
- 2) What characteristics of the plants and their floral visitors promote full pollination?
- 3) To what extent do plant species share pollinators, and how much does competition for pollinator service affect seed-set in pollinator-limited species?

STUDY SITES

I conducted the study from 1977–1982 on field sites in Durham and Orange counties, North Carolina, primarily the Oosting Natural Area and the Rhododendron Bluff and Gate 24 access areas of Duke Forest. Preliminary work was performed near the Eno River State Park in Durham County and in the North Carolina Botanical Garden. All sites were within 12 km of Duke University and consisted of mesic, lowland deciduous forest on north- or northwest-facing rocky slopes extending onto level, alluvial ground. The diagnostic species of rich, moist forest in piedmont North Carolina, *Fagus grandifolia* (Oosting 1942), occurred on all sites. Study areas ranged in area from ≈ 0.2 ha at the Botanical Garden to >0.6 ha at the Gate 24 and

Natural Area sites. At these latter two locations and Rhododendron Bluff, suitable wildflower habitat extended continuously over >5 ha. Spring wildflower associations were very similar throughout, with 11 of the 13 most common species represented at each location. A description of the flora of the Natural Area is given by Bornkamm (1975). Further description of the sites is contained in Motten (1982a).

METHODS

Measurements of the physical environment

I measured two physical factors likely to affect the reproduction of spring wildflowers: light and temperature. I measured light levels on the forest floor at the Gate 24 and Natural Area sites in 1979 using a Weston illumination meter. Near noon on completely cloudless or uniformly overcast days, I took readings at 10-m intervals along a 100-m transect through each site. Two transects were followed later in the season, when shadows became more pronounced. Immediately preceding and following these measurements, readings were taken in an adjacent open area fully exposed to the sun. Forest floor light intensity as a percentage of full sunlight was calculated from the means of the forest and open area measurements. I also determined relative light levels with a pair of Belfort Instrument Company pyrliographs, one placed on a study site, the other in full sunlight on the roof of a building on the Duke University campus. The two instruments were calibrated by putting them together for a day in full sunlight. In all years of the study I visually estimated the progress of canopy closure.

To assess the amount of time suitable for pollinator flight, I monitored the air temperature 10 cm above the ground and recorded cloud cover at hourly intervals on each day I was in the field.

Flowering phenologies and floral biology of common species

I recorded flowering dates for all herbaceous species each year by noting when species were coming into bloom, in full bloom, or going out of bloom (Anderson and Hubricht 1940). Populations were evaluated at 2–3 d intervals. Because the durations of peak bloom were not based on quantitative sampling, they were used only as qualitative descriptions of the intensity of flowering overlap through the season. Dates of first and last flowering of the entomophilous shrubs and understory trees blooming concurrently with the vernal herbs were also noted.

I made detailed observations of the floral biology of the 12 most common spring herbs. Species that were either too rare for experimental manipulation or had flowering periods extending into the summer were excluded. Lifetimes of individual flowers were measured by examining marked plants at 1–3 d intervals and recording the dates of floral anthesis, pollen release, and perianth withering. I estimated the timing of stig-

ma receptivity by noting when the stigmatic surface was exposed and pollen adhered to it and by examining pistils microscopically (at 100 ×) for enlarged stigmatic papillae. To determine whether seed-set depended on insect visitation, I covered plants bearing unopened flower buds with insect-exclusion cages in the form of cylinders constructed of aluminum window screening (7 × 7 meshes/cm²) with nylon mesh tops (9 × 10 meshes/cm²). I tested for self-compatibility by artificially self-pollinating flowers on caged plants. Geitonogamous pollinations were performed on *Claytonia virginica*, *Stellaria pubera*, *Cardamine angustata*, and *Tiarella cordifolia*; all other species were self-pollinated intraflorally. As an additional test of self-compatibility in *Erythronium umbilicatum*, *Cardamine angustata*, *Uvularia sessilifolia*, and *Trillium catesbaei*, I hand-pollinated flowers and after 48 h collected the pistils and examined them for pollen grain germination and pollen tube growth using fluorescence microscopy (Martin 1959). Presence of nectar was determined by direct observation with a 10 × hand lens on flowers kept caged for 24 h. The number of ovules per flower was obtained by dissecting ovaries or by examining fruit contents under a dissecting microscope while counting seeds.

Collection of floral visitors and measurements of visitation rates

I collected insect visitors to flowers in all years of the study and on all field sites, concentrating on the 12 most common herb species. Collections were made throughout the blooming period of each species. All insects were individually captured and killed to avoid contamination of their pollen loads by contact with other specimens. For each specimen I recorded the time and date of capture, the study site, and the species it was visiting. Bees emerging very early in the spring when few flowers were open were collected in pan traps.

I measured insect visitation rates on most of the common herb species in all years except 1977. Measurements were made throughout the blooming period of each species and at different times of the day whenever the weather was suitable for pollinator activity. Most observation plots were 1 m² (range: 0.25–4.00 m²) and were usually watched for 30-min intervals. Both single-species and mixed-species plots were used, the latter to note fine-scale foraging preferences of the visitors. I counted all open flowers of each species in the plot, then recorded the identity of each visitor entering the plot and the number of flowers of each species that it visited. Visitation rates were calculated in units of visits per flower per hour to standardize for differences in floral abundance. Common visitors were identified on sight; unfamiliar visitors were collected immediately after they left the plot.

Pollen load analysis

To supplement observations of visitor foraging behavior made while collecting specimens or measuring

visitation rates, I examined the pollen loads of selected visitors. The intent of the pollen analyses was to determine whether multiple floral records of visitor species were the result of individuals foraging on several hosts or of different individuals maintaining floral constancy but preferring separate hosts. Consequently, I only included specimens collected on days when at least two potential host species were in flower. Insects were examined under a dissecting microscope (40 ×), and ones with <25 grains were rejected as having too little pollen to estimate foraging preferences reliably. Pollen was removed from all parts of the insect by dabbing it with cubes of agar (each ≈ 1 mm³), then dissolving the agar in a drop of lacto-phenol with cotton blue stain on a glass slide. Subsamples were taken for specimens with very large amounts of pollen, particularly in corbicular or scopal loads. Pollen grains were identified by comparing them to a reference collection prepared from all entomophilous herbs, shrubs, and trees on the study sites. At least 200 grains were counted on each slide (or, if <200 grains were present, all were counted) and classified as host species (i.e., the flower the insect was collected on), other identifiable species, or unknown.

Measurements of pollination and reproductive success

To determine whether reproductive success was limited by insufficient pollinator service, I compared the fruit- and seed-set of supplementally hand-outcrossed flowers with those of naturally pollinated control flowers. Hand-pollinated plants were randomly selected from all reproductive individuals occurring within plots (usually 1 m² in area) or along transects located in representative areas of a population. The remaining individuals were the controls. For two species with small population sizes, *Uvularia sessilifolia* and *Iris cristata*, I marked all flowering individuals. On plants with multiple-flowered inflorescences, all the flowers of an inflorescence were pollinated. Flowers of early blooming species with persistence times longer than 7 d (see Table 1) were examined every 2–3 d and hand-pollinated at least twice. Flowers of *Sanguinaria canadensis* were treated once, on the day they first opened. Inflorescences of *Claytonia virginica* and *Stellaria pubera* were examined daily, and all flowers appearing receptive were treated. Flowers still open the next day were pollinated again. On the congested inflorescences of *Cardamine angustata* and *Tiarella cordifolia*, I pollinated all open flowers every other day. Flowers of all other species I pollinated once, shortly after they became receptive. To test the effectiveness of my supplemental pollination procedures, I also hand-outcrossed flowers from caged plants of most species.

I performed supplemental hand-pollinations for one year on the highly autogamous species, *Hepatica* and *Sanguinaria* (Table 1), and on two frequently visited species, *Claytonia* and *Cardamine*. I measured the reproductive success of control flowers for an additional

TABLE 1. Summary of floral characteristics of herb species used in the pollination experiments; species are listed by order of flowering. Entries are based on observations combined from different sites and years and are given as $\bar{X} \pm 1$ SD, followed by range (in parentheses) and sample size.

Species (family)	Description of flowers and inflorescence	No. ovules per flower	Nectar
<i>Hepatica americana</i> (Ranunculaceae)	flowers blue to mauve, of upturned bowl form, 1.5–2.0 cm wide, solitary, but most plants produce several flowers ($\bar{X} = 3.1$, range 1–13, $n = 92$ plants)	14.9 ± 3.35 (5–26) 385	no
<i>Erythronium umbilicatum</i> (Liliaceae)	flower yellow with red streaks at base of recurved perianth segments, of hanging bell form, 2–4 cm wide, solitary	29.2 ± 10.57 (5–72) 278	yes
<i>Sanguinaria canadensis</i> (Papaveraceae)	flower white, of upturned bowl form, 5–10 cm wide, solitary	25.3 ± 6.10 (8–38) 59	no
<i>Thalictrum thalictroides</i> (Ranunculaceae)	flowers white, of upturned bowl form, 1.0–2.5 cm wide, usually 3 per stem (range 1–5)	5.70 ± 2.01 (3–14) 92	no
<i>Claytonia virginica</i> (Portulacaceae)	flowers white or pink, with pink stripes on petals, of upturned bowl form, 1.0–1.5 cm wide, 6–17 per inflorescence	6	yes
<i>Cardamine (Dentaria)</i> <i>angustata</i> (Brassicaceae)	flowers white to pale pink, 8–10 mm long, bases of petals overlapping to form tube 4–6 mm long, 6–18 per inflorescence	6.9 ± 1.69 (4–12) 36	yes
<i>Stellaria pubera</i> (Caryophyllaceae)	flowers white with deeply notched petals, of upturned bowl form, 0.8–1.2 cm wide, 7–22 per inflorescence	12.8 ± 2.30 (5–22) 512	yes
<i>Uvularia sessilifolia</i> (Liliaceae)	flower pale yellow, of hanging bell form, 2.0–2.5 cm long, solitary	6.7 ± 1.67 (3–11)	yes
<i>Tiarella cordifolia</i> (Saxifragaceae)	flowers white ≈ 5 mm wide, many per inflorescence ($\bar{X} = 37$, range 17–70, $n = 61$ inflorescences) with 10–20 flowers open simultaneously	...†	no
<i>Trillium catesbaei</i> (Liliaceae)	flower white to pink, petals recurved forming open bell, 4–6 cm wide and nodding or nearly horizontal, solitary	24.0 ± 7.33 (2–41) 75	no
<i>Podophyllum peltatum</i> (Berberidaceae)	flower white, of shallow open bowl form, ≈ 5 cm wide and held horizontally, solitary	...	no
<i>Iris cristata</i> (Iridaceae)	flowers purple with orange stripes on sepals, 5 cm wide, 10–14 cm long, 1 (occasionally 2) flowers per stem	46.8 ± 3.02 (36–62) 47	yes

** Indicates that the mean life-span of insect-excluded flowers was significantly longer ($P < .01$) than that of naturally pollinated flowers, as determined by a t test or approximate t test if variances were unequal.

† No data collected.

‡ Control flowers that did not set fruit (and hence were probably unvisited) lasted the same number of days as hand-pollinated flowers and controls that did set fruit.

year on *Sanguinaria* and *Cardamine* and for two more years on *Hepatica* and *Claytonia*, with an emphasis on detecting changes in seed set during the blooming season. All other species I hand-pollinated during at least two field seasons.

I measured fruit-set by examining flowers weekly for ovary enlargement and counting only ovaries that reached the size typical of a fruit containing mature seeds. Seed-set of most species was determined by examining the fruit contents in the laboratory under a dissecting microscope. Seeds of *Claytonia* were counted in the field. I counted all ovules and assigned them to four categories: mature and fully developed, mostly

(> 50%) enlarged and partly filled, slightly enlarged and unfilled, or apparently undeveloped. Seed-set was defined as the sum of the numbers of ovules in the first two categories. Mostly filled seeds constituted < 10% of the seed-set in most fruits; the most notable exceptions were capsules of *Claytonia* near the end of the blooming season, when the proportion of incompletely filled seeds rose to > 50% per capsule. Percent seed-set per fruit was calculated as: (seed-set/total number of ovules in all categories) \times 100. Unfilled and undeveloped ovules were difficult to distinguish reliably because the two classes formed a continuum in most species. For this reason, and because undeveloped

TABLE 1. Continued.

Protogynous or protandrous	Life-span (d)	
	Naturally pollinated flowers	Insect-excluded flowers
protogynous	10.2 ± 2.05 (3-18) 87	10.8 ± 2.27 (4-21) 49
weakly protogynous	8.1 ± 1.17 (4-12) 58	10.4 ± 1.17 (6-13) 43
protogynous	7.8 ± 2.66 (4-12) 37	7.8 ± 2.58 (5-12) 17
protogynous	10.4 ± 1.36 (9-14) 21	10.8 ± 1.72 (9-15) 21
protandrous	2.3 ± 1.66 (2-5) 340	2.9 ± 0.98 (2-7) 69
weakly protogynous	3.6 ± 0.68 (3-6) 147	4.3 ± 0.76 (3-6) 96
protandrous	3.6 ± 0.79 (3-5) 94	5.1 ± 1.10 (4-7) 53
weakly protogynous	5.7 ± 1.37 (3-9) 17	...†
protogynous	6.2 ± 0.96 (5-9) 42 flowers, 20 inflor.	6.8 ± 0.87 (5-9) 33 flowers, 13 inflor.
protandrous	16.5 ± 2.42 (12-21) 21	...
weakly protandrous	6.0 ± 2.28 (3-8) 20	...
neither	3.1 ± 0.65 (2-4) 24	‡

ovules occurred in fruits of both hand-pollinated and control flowers, it was not possible to designate unambiguously a class of unfertilized ovules.

Measurements of pollinator effectiveness

To determine the relative importance of various insects as pollinators and to corroborate data from the hand-pollination experiments, I measured the pollination effectiveness of frequent visitors to *Erythronium*, *Claytonia*, and *Stellaria*. I also determined whether an especially common generalist visitor, *Bombylus major*, could pollinate *Thalictrum* and *Cardamine*. Plants used for effectiveness measurements were kept under insect-exclusion cages except while visits were being monitored. All receptive flowers under the cage were individually numbered. After the cage was removed, I noted the identity of each visitor and re-

corded the numbers of the receptive flowers it visited. Later, seeds were counted from each flower producing a fruit. The seed-set of uncaged flowers near the effectiveness plots was measured to estimate the seed-set potential of flowers with unrestricted pollinator access.

Because of the considerable variation in ovule number and seed-set per fruit in *Erythronium*, I also measured pollinator effectiveness on this species with counts of the pollen tubes that reached the base of the style following a single insect visit. Pistils were harvested 24-48 h after a flower was visited, then examined by fluorescence microscopy. Pollinator effectiveness measurements on *Thalictrum* were based on counts of pollen tubes in flowers with unopened anthers rather than seed-set, to avoid the confounding effect of autogamy.

RESULTS

Physical environment

Canopy closure began consistently between 4 and 9 April. Light levels declined steadily after the first week in April until canopy closure was complete about 1 May (Fig. 1). The maximum intensity was 57% of full sunlight at Gate 24 and 52% at the Natural Area, falling to 17% and 15%, respectively.

March was characterized by increasing temperature, as evident in Fig. 2, showing mean "pollinator-hours," the number of hours a day with temperatures > 12°C, the minimum for flight by many solitary bees (Abraham 1975) and other pollinators of vernal herbs (Schemske et al. 1978). The large confidence intervals during March reflect the variability of early spring weather. Between 1977 and 1981, 93% of the 5-d intervals before 2 April had at least one day with 0-1 pollinator-hours, but no such cold days occurred dur-

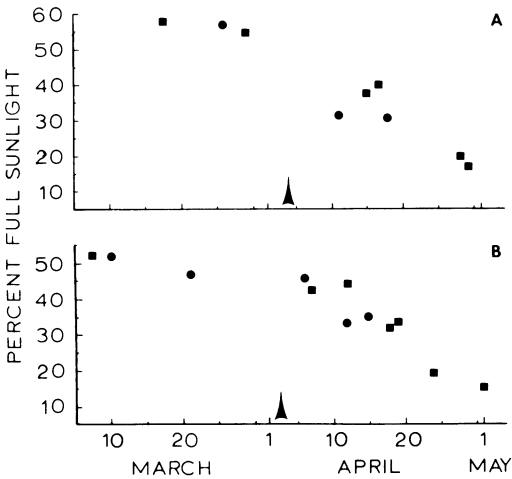


FIG. 1. Light levels in 1979 at the Gate 24 (A) and Natural Area (B) sites, expressed as percentages of full sunlight. ■ measurements made with pyrlieliographs; ● measurements made with the illumination meter. Arrows indicate when canopy trees first started to leaf out.

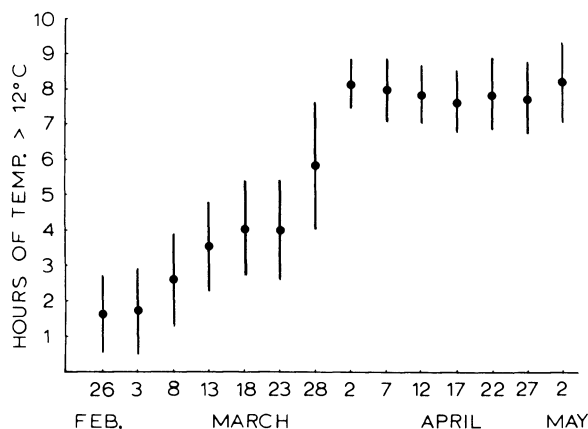


FIG. 2. Mean number of hours per day with temperatures above 12°C from 1978 to 1981. Each dot represents a 5-d interval, whose midpoint is marked on the ordinate. Vertical lines are 95% confidence intervals. Only observations between 0800 and 1700 are included, as floral visitors were rarely active beyond those hours.

ing the intervals after 2 April. Temperature varied considerably not only within years but also among years, especially early in the season. Differences between years in the number of pollinator-hours were much less pronounced after 28 March.

Mostly cloudy days were equally common in March and April, and during the study ranged from 11 to 15 in March and from 10 to 12 in April. The 30-yr averages for the weather station at the Raleigh/Durham airport (≈ 30 km from the study sites) for these months are 14 and 11 d, respectively. Although cold weather probably places the greatest constraint on pollinator activity in March, overcast skies may further reduce flower visiting. During the warmer month of April, pollinator activity is most strongly limited by cloudy or rainy weather.

Flowering phenology and floral biology

The flowering phenologies were characterized by extensive overlap, concentrated in April (Fig. 3). Five species bloomed consistently in March, and three reached their peak bloom then. In April as many as eight herbaceous species and three entomophilous tree and shrub species flowered simultaneously. This basic pattern remained unchanged despite some variations between years or sites. At the Natural Area, early spring species began flowering sooner than at Gate 24 in the same year, and several species (e.g., *Claytonia* and *Thalictrum*) had longer flowering periods, probably because of larger population sizes. Flowering phenologies were sensitive to annual differences in weather. The cold weather in March 1978 compressed the total blooming period of the three earliest species by at least 25% and shifted the dates of first flowering of all species blooming in March ≈ 2 wk later than in 1979. In con-

trast, a week of cold and snowy weather in early March 1980 made the blooming periods of *Hepatica* and *Erythronium* longer than in 1979.

Several floral traits were widespread in the spring wildflower community. A characteristic particularly noticeable during the height of the blooming season was the preponderance of white flowers. Seven of the species listed in Table 1 had mostly white flowers, and occasional plants of *Hepatica* also produced flowers that were very pale blue or lavender. Schemske et al. (1978) have also noted an abundance of white-flowered spring woodland herbs. Most species were highly dependent on insect pollination for sexual reproduction, with half of them largely self-incompatible (Table 2). Based on breeding system, floral morphology, and visitor rewards (i.e., their pollination syndromes; Faegri and van der Pijl 1979), and on the kinds of potential pollinators they attract, the species in Table 1 can be assigned to five categories. Two categories include flowers with an open, upturned bowl form: the nectarless, largely autogamous species (*Hepatica*, *Sanguinaria*, and *Thalictrum*) and the nectar-producing, self-compatible but nonautogamous species (*Claytonia* and *Stellaria*). Flowers of both groups were accessible to nearly all floral visitors and attracted a diverse assortment of bees and flies (Table 3). The autogamous species were among the earliest flowering members of the community (Fig. 3). Members of a third category, the nectar-producing, hanging-bell species (*Erythronium* and *Uvularia*), were visited only by bees, although these visitors included species of different sizes and tongue lengths. The fourth and most morphologically heterogeneous category consists of species visited primarily by very large bees, especially queen bumble bees. One species, *Iris*, had flowers that required a strong, large-bodied visitor for pollination. *Trillium* and *Podophyllum* had more open flowers that did not exclude smaller visitors but attracted bumble bee queens because of their large size and pollen reward. The attractive unit of *Tiarella* was the entire inflorescence, a brush-like mass of small, nectarless flowers. The species visited by queen bumble bees were among the latest blooming members of the community, and except for *Iris*, which had high fruit-set but very low seed-set when self-pollinated, all were self-incompatible. The fifth category consists of tubular or spurred flowers that were visited by long-tongued bees (e.g., megachilids) and flies (e.g., *Bombylus major*). Species in this group included *Viola* and *Cardamine*, which had a corolla sufficiently open to admit some short-tongued andrenids as well. The five categories overlap considerably with respect to floral visitors and differ more in degree than kind. With the exception of some queen bumble bee-pollinated species, there is rather little specialization among species in the potential pollinators they attract.

Two particularly noteworthy floral traits of spring wildflowers were the long persistence times of individual flowers—durations of a week or more were typi-

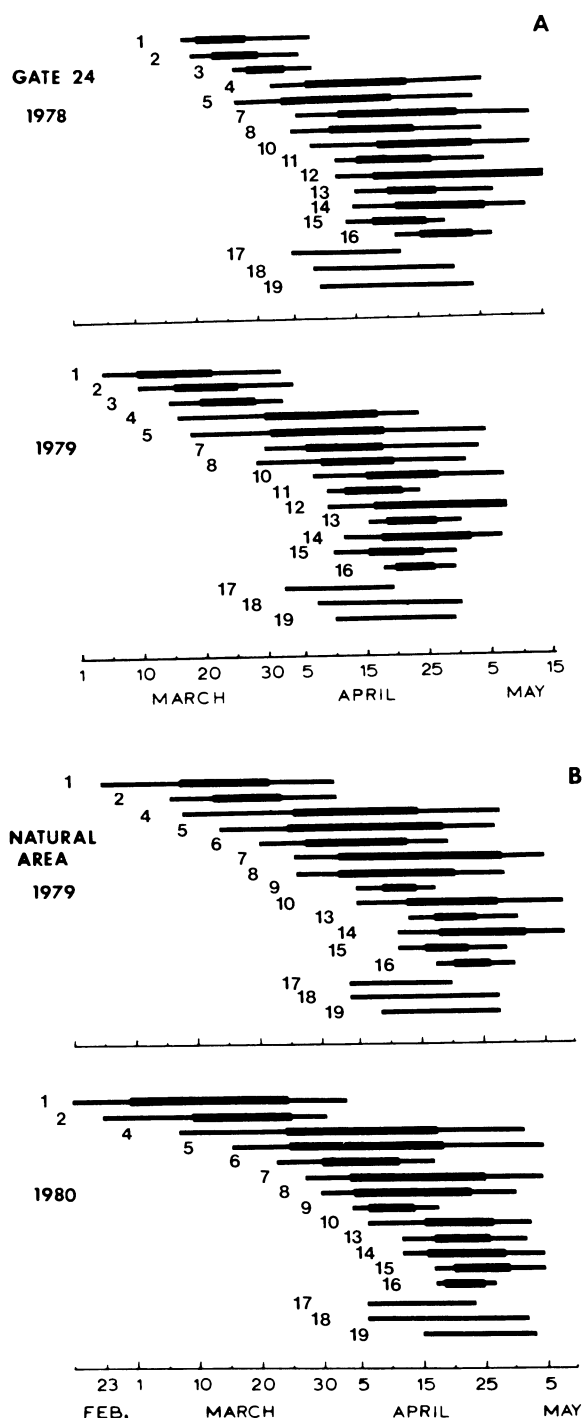


FIG. 3. Flowering phenologies of the spring blooming entomophilous herbs, shrubs, and understory trees (A) at the Gate 24 site in 1978 and 1979 and (B) at the Natural Area site in 1979 and 1980. Thickened bars represent estimated periods of full bloom for herb species. Numbers identifying herb species are as follows: 1. *Hepatica americana* (DC.) Ker; 2. *Erythronium umbilicatum* subsp. *umbilicatum* Parks and Hardin; 3. *Sanguinaria canadensis* L.; 4. *Claytonia virginica* L.; 5. *Thalictrum thalictroides* (L.) Boivin; 6. *Cardamine* (*Dentaria*) *angustata* O. E. Schulz; 7. *Stellaria pubera* Michaux; 8. *Viola papilionacea* Pursh; 9. *Uvularia sessilifolia* L.;

cal—and the negative correlation between floral duration and pollination success in many species. *Claytonia* had the shortest floral lifetime, a minimum of 2 d, but caged flowers persisted up to 7 d. Protogynous species generally had longer floral life-spans, and some, such as *Erythronium*, *Cardamine*, and *Tiarella*, had significantly longer lifetimes when insects were excluded (Table 1). The only species with a mean floral lifetime shorter than 4 d and no apparent trend toward increased persistence in the absence of pollination was *Iris*.

Description of visitor fauna

The most abundant floral visitors were solitary bees (Table 3), including short-tongued andrenids, halictids, and anthophorids (*Nomada*) and long-tongued megachilids. The dominant family by both number of individuals and species was the Andrenidae. Social bees were represented by honey bees (*Apis mellifera*) and queens of *Bombus bimaculatus*. Honey bees, unlike other highly visible floral visitors in the habitat, varied markedly in abundance among years and sites. Fewer than 20 honey bees were seen on all sites in 1977 and 1978, but in 1979 and 1980 they were the dominant visitors to *Erythronium* at the Natural Area site. At the Gate 24 site in 1979 and 1980 honey bees were common for only ≈ 10 d, mostly as visitors to *Erythronium*.

The most abundant visitor was the bee fly *Bombylius major*. This ubiquitous species was the most common visitor to *Thalictrum*, *Cardamine*, and *Stellaria* and was as numerous on *Claytonia* as *Andrena erigeniae*. Syrphid flies were uncommon, although they are important visitors to spring wildflowers in Illinois (e.g., Robertson 1929a, Schemske et al. 1978). Lepidoptera were also only occasional visitors. All visitor species recorded at least four times occurred on more than one site, and of all species recorded at least 10 times, only one (*Andrena nasonii*) occurred on fewer than three sites. Because of differences in collection intensity, the numbers of visitors listed in Table 3 provide only approximate estimates of relative pollinator abundance, and are less appropriate indicators of the attractiveness of frequently visited plant species than the measurements of visitation rates (Table 6).

The diversity of the spring pollinator fauna exhibited a distinctive seasonal pattern (Fig. 4). In late February or early March when *Erythronium* and *Hepatica* start-

10. *Tiarella cordifolia* var. *collina* Wherry; 11. *Uvularia perfoliata* L.; 12. *Chrysogonum virginianum* L.; 13. *Podophyllum peltatum* L.; 14. *Trillium catesbaei* Elliot; 15. *Amsonia tabernaemontana* Walter; 16. *Iris cristata* Aiton. Numbers identifying trees and shrubs are: 17. *Cercis canadensis* L.; 18. *Aesculus sylvatica* Bartram; 19. *Cornus florida* L. Nomenclature of these and all other North Carolina plant species referred to in the text follows Radford et al. (1968) except for *Erythronium umbilicatum* (see Parks and Hardin 1963).

TABLE 2. Fruit- and seed-set, with insects excluded, of hand self-pollinated, hand outcrossed, and unmanipulated flowers.

Species	Hand self-pollinated				Hand outcrossed				Unmanipulated			
	Fruit-set (%)	No. flrs	Seeds set per fruit ($\bar{X} \pm 1$ SD)	No. frts	Fruit-set (%)	No. flrs	Seeds set per fruit ($\bar{X} \pm 1$ SD)	No. frts	Fruit-set (%)	No. flrs	Seeds set per fruit ($\bar{X} \pm 1$ SD)	No. frts
<i>Hepatica americana</i> *	100	43	13.5 \pm 4.45	43	100	17	13.2 \pm 3.30	17	100	76	10.6 \pm 4.48	76
<i>Erythronium umbilicatum</i>	10	29	...†		91	86	12.4 \pm 5.05	74	6	105	7.2 \pm 5.04	6
<i>Sanguinaria canadensis</i>	89	18	15.7 \pm 8.31	16	94	17	11.6 \pm 7.68	16	94	18	11.7 \pm 5.14	17
<i>Thalictrum thalictroides</i> *	98	42	4.8 \pm 2.03	41		80	85	2.8 \pm 1.65	70
<i>Claytonia virginica</i>	91	44		6	187	3.5 \pm 1.87	6
<i>Cardamine angustata</i>	8	149	...		30	67	...		3	36	...	
<i>Stellaria pubera</i>	90	163	3.7 \pm 1.64	75	94	225	3.8 \pm 1.43	82	5	156	1.8 \pm 0.84	15
<i>Uvularia sessilifolia</i>	8	12	1.0	1	83	12	4.6 \pm 1.68	5	
<i>Tiarella cordifolia</i>	4	564	...		57	405	...		0	340		
<i>Trillium catesbaei</i>	31	13	2.0 \pm 2.00	4		19	22	2.2 \pm 2.33	3
<i>Podophyllum peltatum</i>	0	12	
<i>Iris cristata</i>	78	20	6.9 \pm 2.83	7	75	12	9.2 \pm 3.90	9	0	10		

* Fruit is an achene; fruit-set entries are percentages of flowers with at least one achene, and entries for seeds set per fruit are mean numbers of achenes per flower for all flowers that produced at least one achene.
† No data available.

ed to flower, males of *Andrena nigrihirta* and *A. tridens* were virtually the only pollinators. Females emerged up to a week later and were sometimes joined by honey bees after 2–3 wk. Although *Nomada* was collected in pan traps in early March, it was rarely seen on flowers until the end of the month. Flies in the genera *Gonia* and *Hylemya* were the only other early-season floral visitors. By late March both halictids and megachilids were present, as were several additional species of *Andrena*. *Bombylius* appeared consistently within 3 d of 21 March and within a day of the first appearance of *A. erigeniae*. Pollinator diversity was highest between the last week of March and the third week of April, the period during which the majority of the spring wildflowers were in peak bloom (Fig. 3). Queens of *Bombus bimaculatus* were the last spring pollinators to emerge and were the most visible floral visitors in the first week of May. By then, *Bombylius* and the early-season andrenids had disappeared and only occasional halictids or individuals of *Nomada* were collected as visitors to scattered flowers of *Stellaria*.

Vistor foraging behavior and
floral constancy

Most individual floral visitors foraged on more than one host, as is evident both from direct observation of visitor behavior (Table 4) and, for the solitary bees, from analysis of pollen loads (Table 5). *Bombylius* was by far the least discriminating visitor in the pollinator fauna. It was not unusual for a bee fly to visit *Car-*

damine, *Claytonia*, *Stellaria*, and *Thalictrum* in a 1 m² plot containing all four species. Of 51 bee flies making at least four visits in plots with three or four of these species, only 6 visited a single species, and 20 visited more than two species. No attempt was made to analyze pollen loads on *Bombylius* because many individuals carried <25 grains, usually on the legs, proboscis, and face, where they could be lost when the fly was collected.

Bees exhibited somewhat more host fidelity than flies, but most did not maintain consistent preferences within a foraging trip. The most constant foragers (other than oligoleges, such as *A. erigeniae* on *Claytonia*; Davis and LaBerge 1975) were honey bees and the early-season andrenids. In mixed-species plots, both *Erythronium* and *Sanguinaria* were visited by honey bees, but by different individuals. The host fidelity of andrenids in early spring was enforced by the abundance of *Erythronium* and the paucity of other, concurrently blooming nectar sources. After *Erythronium* finished blooming, *A. nigrihirta* and *A. tridens* foraged on a variety of nectar-producing species, as did the later appearing *A. carlini* and *A. nasonii*. Most individuals of these four andrenids visited more than one host during a foraging bout (Table 5). Of 66 specimens examined, 45 carried substantial (>10%) fractions of nonhost pollen, and 38 bore pollen from at least two nonhost species. Even with the exclusion of individuals collected on *Uvularia*, a relatively uncommon host that attracted no consistent foragers, the majority of the

andrenids examined had mixed pollen loads. After *Erythronium*, *Cardamine* was the species most likely to be visited by constant-foraging andrenids, probably because the inflorescences occurred in clumps and each had several flowers offering both pollen and nectar.

Solitary bees other than andrenids also had multiple host preferences. For *Nomada* and halictids, almost 50% of the individuals visited two or more kinds of flowers in mixed-species plots (Table 4), while 53% of the halictids ($n = 19$) and 76% of the *Nomada* ($n = 17$) had pollen loads that were $\leq 90\%$ pure (Table 5). Megachilids were even less constant, with only 5% of the individuals carrying host pollen nearly exclusively. Unknown and tree grains (especially *Cercis*) were common in the pollen loads of this group, suggesting that megachilids were foraging somewhat sporadically in the herb community.

Too few data are available on queen bumble bees to evaluate their behavior reliably. They were often seen flying from one clump of *Aesculus sylvatica* to another, and several individuals were seen moving consistently among racemes of *Tiarella*. The single pollen load taken from a specimen collected on *Tiarella*, however, contained 25% unknown foreign pollen.

Visitation rates

Differences in mean visitation rates among wildflower species were mainly due to differences in time of flowering, rewards offered, and kinds of visitors attracted. The common, early-blooming species, *Hepatica* and *Erythronium*, were visited much less frequently than equally abundant, later-blooming species (Table 6). Forty percent of the 30-min observation bouts on *Hepatica* and *Erythronium* ended without a visit, but

TABLE 3. Summary of insect visitors to spring wildflowers in piedmont North Carolina. Floral hosts are designated by the first 3–4 letters of the genus name.

Visitor*	Floral host									
	HEP	ERY	SANG	CLAY	THAL	CARD	STEL	VIOL	UVUL	TIA
Hymenoptera										
Andrenidae										
<i>Andrena carlini</i>	1	4	2	1		7	2			
<i>A. erigeniae</i>				378	1	2	3			
<i>A. nasonii</i>				3		2	8			
<i>A. nigrihirta</i>	27	273		13		16	6		15	
<i>A. tridens</i>	9	72		2		4			2	
<i>A. violae</i>								4		
Other <i>Andrena</i> (6 spp.)				3		1	1		1	
Anthophoridae										
<i>Ceratina calcarata</i>				3	3	2				
<i>Nomada</i> (5 spp.)	4	9		46	1	5	57			
<i>Xylocopa virginica</i>		2	1	1		1				
Apidae										
<i>Apis mellifera</i>	4	52	21	4		5				1
<i>Bombus bimaculatus</i>	2		1			5				18
Halictidae										
<i>Augochlorella</i> (2 spp.)		2		2		3	3			
<i>Dialictus</i> (3 spp.)	6	3	1	34	15		3			3
<i>Evylaeus macoupinensis</i>	5			4	1				1	1
Megachilidae										
<i>Osmia conjuncta</i>		4		7		1	7	2		1
<i>O. lignaria</i>		4		3		2				
Other <i>Osmia</i> (3 spp.)		7		4	1	1	6	4		
Diptera										
Anthomyiidae										
<i>Hylemya platura</i>	8			16						
Bombyliidae										
<i>Bombylius major</i>	20	2	20	418	130	79	122	17		8
Syrphidae (2 spp.)			1	14	2	4	4			
Tachinidae										
<i>Gonia</i> sp.	4			37	8	2	4			
Lepidoptera										
Pieridae										
<i>Euchlo creusa lotta</i>				5		2				

* Species names are given only for visitors with at least four visit records. No visitors to *Iris* were observed on the study sites, but queens of *Bombus bimaculatus* were noted on this species nearby. The only visitors observed on *Podophyllum* were 3 *B. bimaculatus* queens and 1 *Xylocopa virginica*. The sole visitors noted on *Trillium* were 2 *B. bimaculatus*, 1 *X. virginica*, and 1 *Andrena carlini*. For a more complete listing of visitors see Motten (1982a).

only 5% of the bouts on any of the later-blooming species were without visits, although floral densities in the plots remained about the same. The maximum visitation rates to both *Hepatica* and *Erythronium* occurred in late March and early April, after visitor abundance and diversity had increased markedly.

Nectarless species received fewer visits than concurrently blooming, nectar-producing species. The visitation rate on *Erythronium* was significantly higher than on *Hepatica* ($t = 1.89$, $n_1 = 65$, $n_2 = 24$; $P = .031$; one-tailed Wilcoxon two-sample test). Similarly, no visitors were seen on *Sanguinaria* until it reached full bloom and attracted honey bees. At that time the mean visitation rate by all visitors was $0.44 \text{ visits} \cdot \text{flower}^{-1} \cdot \text{h}^{-1}$ (4 observation periods, 55 flower/h), while during the same period the visitation rate on *Erythronium* was $2.11 \text{ visits} \cdot \text{flower}^{-1} \cdot \text{h}^{-1}$. Later in the season, visitation rates were significantly higher on *Cardamine*, *Claytonia*, and *Stellaria* than on the nectarless *Thalictrum* ($t = 1.93$, $n_1 = 17$, $n_2 = 26$, $P = .027$ for the smallest difference, between *Cardamine* and *Thalictrum*). The higher visitation rate on *Claytonia* than on *Cardamine*, which bloomed concurrently, reflects the added contribution of the oligolectic *A. erigeniae*.

Species blooming near the end of the season and pollinated primarily by queen bumble bees all had low visitation rates. Very few insects were observed on *Trillium* during the study, and none was seen during attempts to measure visitation rates. The same was true of *Podophyllum* although I watched for visitors to this species and *Trillium* whenever possible while on the study sites. No nocturnal visitors were observed on these or concurrently blooming species during the early evening hours, when air temperatures were favorable for insect activity. I did not measure visitation rates to *Tiarella*, but collection and observation efforts on this species were approximately equal to those ex-

TABLE 4. Constancy of floral visitors in plots of mixed species composition. Entries are based on observations of visitors that landed on 3 or more flowers.

Visitor*	Number of individuals visiting	
	1 species	≥ 2 species
<i>Andrena tridens</i> and <i>A. nigrihirta</i> †	18	6
<i>Nomada</i> spp.	9	8
<i>Apis mellifera</i>	24	3
Halictids	6	6
<i>Bombylius major</i>	22	99
Other Diptera	7	3

* Data were collected for a visitor species or group only if the plot contained two or more plant species typically used by the visitor according to Table 3.

† From observations made in plots containing *Hepatica* and *Erythronium* only.

ended on *Trillium* and *Podophyllum* and yielded many more visitor records, which suggests that *Tiarella* was visited more frequently.

Pollination success

Inadequate pollination can reduce reproductive success either by decreasing the number of flowers that set fruit or by decreasing seed-set per fruit. The first effect is a result of flowers remaining unvisited or unpollinated, while the second is a result of pollen transfers that do not fertilize all of the ovules that could have matured into seeds. For the eight species pollinated by solitary bees and flies, supplemental hand-pollination did not significantly increase any of the measures of reproductive success (Table 7), despite values of fruit-set and percent seed-set per fruit for untreated flowers of most species of <90% and as low as 28%. Hand pollinations of caged flowers of these species were generally quite successful (>80% fruit-set; Table 2), indicating that the hand-pollination treatment was capable of supplementing natural pollination. The exception was *Cardamine*, which consistently had low fruit-set regardless of treatment (Tables 2 and 7).

Supplemental hand-pollinations significantly improved the reproductive success of only three or possibly four species, all visited predominantly by queen bumble bees. Pollination deficiency in these plants reduced the percentage of flowers setting fruit but did not significantly decrease seed-set or percent seed-set per fruit in *Trillium* or *Iris* (seed-set was not measured for *Podophyllum* and *Tiarella*). Even among these four pollinator-limited species, only *Podophyllum* and *Iris* exhibited markedly higher fruit sets with hand-pollination. *Tiarella* and *Trillium* both registered much smaller increases in the percentage of flowers forming fruits, ≈9%.

Although there was no overall or consistent effect of inadequate pollination for most species, corresponding

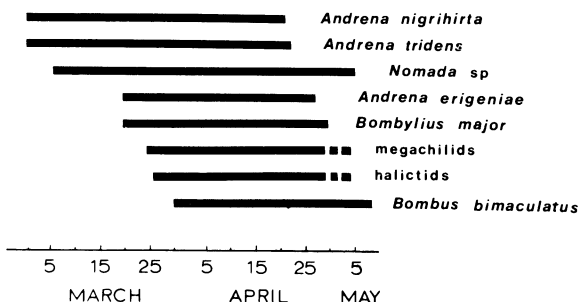


FIG. 4. Approximate periods of flower-visiting activity of the most abundant or most conspicuous groups and species of native pollinators. Halictids and megachilids were less common than other species shown, and uncertainty in their presence near the end of the season when visitation rates were low is indicated by dashed bars. Honey bees (*Apis mellifera*), when present, were most common during the last 2 wk of March. Scattered individuals were also observed at the Natural Area during early April 1980.

trends in the reproductive success of control flowers and patterns of visitor activity or availability indicated intervals of increased susceptibility. The time of greatest risk of insufficient pollination varied from one species to another. For *Claytonia*, the occasional flowers that became receptive early in the season, before *Bombylius* or *A. erigeniae* appeared, were the most likely to remain unvisited (Motten et al. 1981). For *Erythronium*, flowers opening near the peak of the blooming season, particularly in large populations serviced initially by native andrenids, may not have been fully pollinated (Motten 1983). Fruit-set in *Uvularia* was lower for early-blooming plants (40% vs. 75%, $n_1 = 52$, $n_2 = 60$), which bloomed when the bees were frequent visitors to *Cardamine*. For *Tiarella*, inflorescences flowering during the first half of the blooming period, when queen bumble bees were primarily visiting *Aesculus*, may not have been as completely pollinated as later flowering inflorescences. Mean percent fruit-set was lower for the early control inflorescences than for the early hand-pollinated ones (58.0% vs. 75.8%, $t = 1.685$, $df = 28$, $P = .054$, one-tailed test). Later blooming inflorescences had quite similar fruit-sets in both treatments: 69.0% for hand-pollinated ones ($n = 11$) and 66.2% for controls ($n = 24$). Combining the results from early- and later-blooming inflorescences in a two-way analysis of variance did not yield a significant treatment effect ($F = 1.82$, $df = 1, 61$, $P = .18$) or a significant treatment \times flowering time interaction ($F = 0.95$, $df = 1, 61$, $P = .33$).

Pollinator effectiveness

Floral visitors that differed greatly in body size and foraging preferences served as effective pollinators of spring wildflowers (Table 8). Both honey bees and native andrenids pollinated *Erythronium*. Although the andrenids are about one-third the size of honey bees, they deposited compatible pollen on the stigma nearly as often as the honey bees and in one visit could account for nearly half of the expected seed-set of a fully pollinated flower. Three very different insects were excellent pollinators of *Claytonia*: the oligolectic *A. erigeniae*; the generalist *Bombylius*, which fed while hovering; and *Gonia*, a generalist that landed on the flower to feed. More than 60% of the visits by each of these pollinators led to capsule formation. Similarly, *Stellaria* was successfully pollinated by both of its principal visitors, *Bombylius* and the generalist nectar forager *Nomada*. *Thalictrum* was pollinated both by the ubiquitous *Bombylius* and by halictids.

The effectiveness measurements can be used not only to determine whether a floral visitor is a potential pollinator but also to estimate the number of visits a flower must receive to be adequately pollinated. The appropriate method for estimating visit requirements depends on whether seed-set increases with repeated visits, a response that is more likely in species with large ovule numbers. *Erythronium* flowers visited twice by andrenids set significantly more seeds per fruit ($\bar{X} \pm SE$: 11.4 ± 2.49 seeds, $n = 5$ flowers) than did singly visited ones (one-tailed Wilcoxon Rank Sum Test, $T =$

TABLE 5. Proportion of host pollen (i.e., pollen of the plant species collected from) on the bodies of solitary bees captured while visiting spring wildflowers.

Visitor	Host	% of host pollen in pollen load				Number of bees with pollen of ≥ 2 spp. other than host	Nonhost pollen in mixed loads*
		91–100	50–90	11–49	0–10		
		Number of bees					
<i>Andrena nigrihirta</i>	<i>Claytonia</i>		1	1	3	3	Ca, E, S
	<i>Cardamine</i>	7	6	3		6	C, E, S, U
	<i>Uvularia</i>		5	4	4	12	C, Ca, S, T, X
	<i>Stellaria</i>	1	2	1	1	3	C, Ca, X
Other andrenids†	<i>Claytonia</i>			1	3	3	Ca, S, X
	<i>Cardamine</i>	9	3	1		5	C, S, U, X
	<i>Stellaria</i>	4	3		1	4	C, Ca, T, X
	<i>Uvularia</i>				2	2	Ca, S, X
Halictids	<i>Hepatica</i>	2	2		1		T, C
	<i>Thalictrum</i>	5		1			H, C
	<i>Claytonia</i>		2		3	2	Ca, S, T, X
	<i>Tiarella</i>	2	1			1	S, X
<i>Nomada</i> spp.	<i>Claytonia</i>		1	2	4	3	E, S, X
	<i>Stellaria</i>	4	6			4	C, Ca, T, X
<i>Osmia</i> spp.	<i>Claytonia</i>		1		5	3	Ca, Ce, S, X
	<i>Viola</i>		1	2	2	5	Ca, Ce, S, X
	<i>Stellaria</i>	1	5	4	3	7	Ca, T, U, V, X

* Abbreviations for nonhost pollen species present in mixed loads: C = *Claytonia*, Ca = *Cardamine*, Ce = *Cercis*, E = *Erythronium*, H = *Hepatica*, S = *Stellaria*, T = *Thalictrum*, U = *Uvularia*, V = *Viola*, X = other.

† Excluding the known oligolectic species *A. erigeniae* and *A. violae*. Individuals of these species captured on their preferred hosts consistently had >90% host pollen loads.

TABLE 6. Visitation rates to common spring wildflowers by all insect species combined.

Plant species	Visits · flower ⁻¹ · h ⁻¹		No. 30-min observation periods	Total no. flower · h
	Mean ± SD	Range		
<i>Hepatica</i>	0.30 ± 0.40	0.00–1.29	40	503
<i>Erythronium</i>	0.53 ± 0.92	0.00–5.56	110	1193
<i>Thalictrum</i> *	1.25 ± 0.88	0.00–3.47	26	281
<i>Claytonia</i>	2.66 ± 1.94	0.00–7.27	85	1044
<i>Cardamine</i>	1.86 ± 1.04	0.14–3.25	17	225
<i>Stellaria</i>	2.72 ± 1.97	0.00–6.60	27	211

* Approximately 25% of visits were brief (<1 s) “touches” by *Bombylius* during which no feeding activity was observed.

113.5, $P < .025$). A similar response was observed in *Stellaria* flowers visited twice by *Bombylius* ($\bar{X} \pm \text{SE}$: 3.2 ± 1.07 seeds, $n = 7$ flowers; $T = 342$, $P < .01$). *Claytonia* flowers, however, contain only six ovules each, and the seed-set per capsule for flowers visited repeatedly by either *Bombylius* or *A. erigeniae* did not increase significantly with repeated visits (Motten et al. 1981).

The number of visits needed to yield the seed-set of control flowers of *Erythronium* and *Stellaria* was estimated from measurements of seed-set per visit for different pollinators. Seed-set per visit was calculated as the product of the probability of visit success and the number of seeds set per successful visit, i.e., mean seed-set per fruit. A successful visit to *Stellaria* was one that resulted in capsule formation. A visit to *Erythronium* was considered successful if it resulted in at least one fully grown pollen tube; fruit-set was not used as the criterion of success because ovaries with too few fertilized ovules may have aborted (Motten 1982a). The calculations indicate that *Erythronium* requires 2 visits by honey bees or 2–3 visits by andrenids, while *Stellaria* needs 4–5 visits by *Bombylius* or 3 by *Nomada*. Because repeat visits to *Claytonia* did not significantly enhance seed-set, each visit can be considered an independent, “all or nothing” event in terms of its effect on pollination. The visit requirement for this species can thus be calculated from the probability that a single visit will be successful and result in fruit formation, using the expression $(1 - p)^n$, where p = probability of visit success and n = number of visits. A flower visited four times by either *Bombylius* or *A. erigeniae* has a $>.98$ probability of being pollinated.

DISCUSSION

Insufficient pollination is not a major cause of reduced seed- or fruit-set in the forest spring wildflower community of piedmont North Carolina, even though most of the 12 species examined had fruit- or seed-sets much lower than 100%. Evidence for pollination-limited fecundity from supplemental hand-pollination was restricted to a well-defined subset of the community, the four species pollinated primarily by queen bumble bees. Inadequate pollination was the primary source of reproductive failure for two of these, *Iris* and *Podophyllum*. For the two other bumble bee–pollinated

herbs, *Tiarella* and *Trillium*, pollinator-limited fruit-set was restricted to part of the blooming season or occurred at a low, consistent level for several years. None of the eight species pollinated by flies or solitary bees was significantly pollinator-limited. This difference in susceptibility between species visited by flies and solitary bees and those relying on queen bumble bees is corroborated by other studies of forest vernal herbs in the eastern United States. Small bee- and fly-pollinated species in which high (>90%) fruit-set has been observed include *Erythronium americanum* (Bernhardt 1977), *Uvularia perfoliata* (Whigham 1974), *Camassia scilloides*, *Hydrophyllum appendiculatum* (Macior 1978b), *Claytonia virginica*, and *Dentaria laciniata* (Macior 1978a, b). Seed-set measurements indicative of adequate pollination have also been reported for *D. laciniata*, *Sanguinaria canadensis* (Schemske et al. 1978), and *Hepatica acutiloba* (Bernhardt 1976). In contrast, much lower fruit-set (33–79%) has been observed in such typically queen bumble bee–pollinated species as *Mertensia virginica* (Macior 1978b), *Podophyllum peltatum* (Swanson and Sohmer 1976), and, repeatedly, *Dicentra canadensis* and *D. cucullaria* (Macior 1978a, b, Schemske et al. 1978). Hand-pollination experiments on the last three species indicated that inadequate pollination was at least partially responsible for the lower fruit production.

That the fecundity of most forest spring wildflowers is not strongly pollinator-limited was unexpected in view of the factors likely to produce such a result. For the first half of the blooming season low temperatures greatly restricted pollinator activity (Fig. 2), a pattern also observed by Schemske et al. (1978), and during the second half of the season one in three days was rainy or overcast. Moreover, strong competition for pollinator service seems probable because many species overlap in flowering periods and share inconstant floral visitors. While climatic variability and competition undoubtedly influence the pollination success of spring herbs, several characteristics of these plants promote successful pollination. These include (a) autogamy and self-compatibility, (b) extended floral life-span and stigma receptivity, and (c) the capacity to be fully pollinated in a few visits by a wide variety of floral visitors. In the following sections I discuss each of these traits as applied primarily to the bee- and fly-pollinated

species, then consider why the queen bumble bee–pollinated species as a group may be more susceptible to pollinator limitation.

Autogamy

Unreliable pollinator service can be a potent selective force and has been invoked to explain the high proportion of autogamous species in several habitats with frequently inclement weather (Hagerup 1951, Kevan 1972, Moldenke 1975), despite the generally low incidence of self-pollination in most perennial plant communities (Stebbins 1957). In piedmont North Carolina, the three autogamous wildflowers (*Hepatica*, *Sanguinaria*, and *Thalictrum*) all lacked nectar and were less frequently visited than nectar-producing species (Table 6). All three species also bloomed in early spring, when fewer pollinators were available and interruptions of visitor activity were most likely.

Schemske (1978) has also noted self-pollination in *Sanguinaria*, and suggests that a paucity of pollinators promotes autogamy. Macior (1978b) implies that self-pollination in the woodland annual *Corydalis flavula* may be favored by competition with *Dicentra* for bumble bee visits. I have proposed (Motten 1982b) that competition with *Erythronium* for visits by andrenids may intensify selection for autogamy in *Hepatica*. Without autogamy, seed-set in *Hepatica* would be pollinator-limited for much of the blooming period.

Variation in the degree of autogamy in spring wildflowers may reflect variation in opportunities for insect pollination. Lloyd (1965) observed that the races of the cedar glade species *Leavenworthia crassa* and *L. alabamica* that bloomed later in the spring attracted more pollinators and were less self-compatible than early-blooming ones. Bernhardt (1976) found that *Hepatica acutiloba*, although flowering very early, was only

TABLE 7. Summary of reproductive success of control (c) and supplementarily hand-pollinated (hp) flowers.‡ Sample sizes for fruit-set exceed those for seed-set in some species because seed-set was not measured in all years and seeds were occasionally lost to herbivory.

Species	Treatment	Fruit-set (per inflorescence)§			Seed-set per fruit per inflorescence		% seed-set per fruit per inflorescence¶		
		Mean (%)	No. infl.	95% CI	$\bar{X} \pm 1$ SD (no. seeds)	No. infl.	\bar{X} (%)	No. infl.	95% CI
<i>Hepatica americana</i> #	c	98.0	153		12.5 ± 4.29	150	88.5	145	85.5–91.1%
	hp	100	69		12.5 ± 4.46	69	87.1	68	81.6–91.7%
<i>Erythronium umbilicatum</i>	c	89.0	281		16.3 ± 8.45	166	53.7	166	48.6–58.8%
	hp	90.3	237		15.1 ± 7.33	181	55.2	181	51.9–58.4%
<i>Sanguinaria canadensis</i>	c	96.9	31		12.6 ± 5.56	10	66.6	10	52.3–79.5%
	hp	94.1	34		13.4 ± 7.94	32	69.1	32	58.2–79.1%
<i>Thalictrum thalictroides</i> #	c	98.0	55		5.2 ± 1.51	55	82.8	30	76.9–88.0%
	hp	100	46		4.9 ± 1.50	46	81.5	30	75.2–87.1%
<i>Cardamine angustata</i>	c	17.5	94		...††		...		
	hp	18.8	19			
<i>Claytonia virginica</i>	c	84.4	55	79.1–89.1%	4.3 ± 1.15	55	71.7	55	66.0–77.0%
	hp	86.4	10	74.0–95.1%	4.1 ± 0.98	10	69.7	10	63.9–75.2%
<i>Stellaria pubera</i>	c	86.5	55	80.9–91.3%	3.5 ± 1.18	54	28.2	52	25.5–31.0%
	hp	82.1	30	72.3–90.1%	3.2 ± 1.21	29	29.0	27	24.8–33.3%
<i>Uvularia sessilifolia</i>	c	58.0	131		4.6 ± 1.68	42	74.9	42	65.0–83.6%
	hp	64.5	62		4.2 ± 1.82	20	65.2	20	57.9–72.1%
<i>Tiarella cordifolia</i>	c	59.7	64	52.4–66.7%		
	hp	68.1†	32	61.1–74.7%		
<i>Trillium catesbaei</i>	c	79.6	157		7.6 ± 3.54	105	43.7	79	38.2–49.6%
	hp	88.3*	128		8.4 ± 3.66	91	43.9	62	39.9–47.9%
<i>Podophyllum peltatum</i>	c	9.4	32			
	hp	31.3*	32			
<i>Iris cristata</i>	c	56.5	84		7.4 ± 2.43	23	10.7	22	8.9–12.6%
	hp	93.1*	47		7.8 ± 3.42	19	8.2	10	8.3–13.4%

‡ Except for fruit-set values of species with a single flower per inflorescence, all percentage entries were calculated using arcsine square root–transformed values. Mean % fruit-set values for single-flowered species were compared with a *G* test; all other comparisons between treatments were made with one-tailed *t* tests (H_1 :hp > c). Tests on mean percentage values were made using transformed data.

§ For single-flowered species, entries are the overall percentage of flowers setting fruit, hence no confidence intervals are given.

|| (Total seed-set per inflorescence) ÷ (number of flowers on inflorescence that set fruit).

¶ (Total seed-set per inflorescence) ÷ (total number of ovules of flowers setting fruit) × 100.

Fruit is an achene; mean seed-set per fruit and mean % seed-set per fruit entries based on seed (achene) set per flower for all flowers producing at least one achene.

†† No data collected.

* $P < .05$ for comparison of control and hand-pollinated treatment.

† $.05 < P < .10$ for comparison of control and hand-pollinated treatment.

TABLE 8. Summary of pollination effectiveness measurements for common floral visitors to four spring wildflowers. All flowers were visited once.

Plant species	Visitor species	Pollina- tion effective- ness	No. flowers	No. seeds set per fruit		Mean no. seeds set per fruit, controls
				$\bar{X} \pm 1 \text{ SD}$	No. flowers	
		% styles with fully grown pollen tubes				
<i>Erythronium umbilicatum</i>	<i>Apis mellifera</i>	93	30	10.3 \pm 4.65	15	15.3
	<i>Andrena tridens</i> , <i>A. nigrihirta</i>	88	43	6.4 \pm 3.34	23	13.2
<i>Thalictrum thalictroides</i>	<i>Bombylius major</i>	44	17 (88 ovaries)	...†		...
	halictids	100	3 (14 ovaries)
		% fruit-set				
<i>Claytonia virginica</i>	<i>Andrena erigeniae</i> females	69	35	4.0 \pm 1.69	21	4.5
	<i>Bombylius major</i>	64	33	3.4 \pm 1.93	18	4.5
	<i>Gonia</i> sp.	83	6	3.4 \pm 2.07	5	4.5
<i>Stellaria pubera</i>	<i>Bombylius major</i>	55	51	2.6 \pm 1.14	28	4.4
	<i>Nomada</i> sp.	100	11	2.8 \pm 1.17	7	4.4

† No data collected.

slightly autogamous yet fully pollinated. The visitors he recorded correspond to those I observed on late-flowering *H. americana* (Motten 1982b) and on *Thalictrum* (Table 3). *Thalictrum* was much less autogamous than *Hepatica* and *Sanguinaria* (Table 2), reached peak bloom later, i.e., when pollinator diversity was higher, and was more frequently visited (Table 6). Individual plants in the *Thalictrum* populations I examined were also quite variable in the degree of autogamy; the proportion of seed produced under insect exclusion cages ranged from 21 to 86%. If this variation has a heritable component, the level of self-pollination in the population could change rapidly under the selective pressure of different levels of insect pollination.

Pollination and floral life-spans

A trait of particular importance to the pollination of spring wildflowers is extended floral life-span. This characteristic is a distinctive feature of the community, as noted by Antonova (1973) and Schemske et al. (1978). Floral lifetimes in another temperate herb community, the tallgrass prairie, are much shorter, averaging 2.4 d for early spring-blooming species (Parrish and Bazzaz 1979). The average life-span of forest wildflowers is ≈ 7 d (Table 1). Species flowering in March tended to have longer floral life-spans than ones flowering in April; this difference may be due in part to increasing temperatures, since life-spans within a species generally decreased as the season progressed. A negative correlation between floral life-span and air temperature means that flowers opening in cool weather, when insects are less active, are available to pollinators longer. Measurements of visitation rates to *Erythro-*

nium throughout the blooming season indicated that many flowers open in mid-March would not have received the 2–3 visits necessary for full seed-set had they not been open for at least a week (Motten 1983).

Floral life-span was also related to reproductive output in the later spring blooming, queen bumble bee-pollinated species. *Trillium*, with flowers lasting up to 3 wk, had a much higher fruit-set than *Podophyllum* and *Iris*, with flowers lasting no more than 8 and 4 d, respectively. The value of a long floral life-span to *Trillium* was evident in 1980, when 25% of the control flowers still had uncollected pollen a week after opening and had apparently not been visited. Most of the flowers were eventually pollinated, as 92% of them set fruit.

Extended floral persistence may also promote outcrossing in the three autogamous species, all of which are protogynous. In *Hepatica* and *Thalictrum* the outer whorl of anthers usually did not dehisce until the flowers had been open 2–4 d, and in both species some ovaries were likely to remain available for outcrossing throughout the lifetime of the flower, an additional 5–7 d. In *Sanguinaria* 3–5 d elapsed before the anthers converged on the pistil. In years when honey bees were active in the population, many anthers were stripped of pollen before contacting the stigma, and the flowers were presumably insect-pollinated. The behavior of the *Sanguinaria* flowers I examined differed from those studied by Schemske (1978), who observed self-pollination within hours after anthesis and a total floral lifetime of <3 d.

Many spring wildflowers exhibited extended receptivity in the absence of pollination. This response occurred in some long-lived flowers (e.g., *Hepatica* and

Erythronium), but was most well-developed in the strongly protandrous species, *Claytonia* and *Stellaria*. While a protogynous flower can continue to function as a pollen donor after the ovules are fertilized, both the male and female functions of a protandrous flower are reduced after pollination. For self-compatible plants in which the flowers on an inflorescence open sequentially, like *Claytonia* and *Stellaria*, short floral lifetimes decrease flowering overlap and may reduce self-pollination. When insect visits are scarce, however, the increase in fecundity from flowers that remain open and receptive may outweigh the disadvantages of possible geitonogamy. Flowers of *Claytonia* and *Stellaria* are staminate for 1 and 2–3 d, respectively, but once they become pistillate they wither within hours after pollination. Because they can remain pistillate for several days, the flowers of these species can last through short cold or rainy periods while pollinators are inactive. Such a response was observed in *Claytonia* (Motten et al. 1981). Similarly, early control flowers of *Stellaria* often were not pollinated when they first opened, probably because of competition with *Claytonia* (Campbell 1985), and had an average life-span 0.5 d longer than hand-pollinated flowers.

Pollination by diverse visitor types

The characteristic most responsible for the pollination success of forest spring wildflowers is their accessibility to different kinds of floral visitors that serve as effective pollinators. Bees as disparate in size as honey bees and andrenids pollinate *Erythronium*. The foraging behavior and size of megachilids indicate they are also likely pollinators of this species. Visitors with foraging behaviors and preferences as dissimilar as those of *Andrena erigeniae* and *Bombylius* are nearly equivalently effective pollinators of *Claytonia*. *Bombylius* also pollinates other open-bowl flowers, *Thalictrum* and *Stellaria*. In addition, these two species are pollinated by halictids and *Nomada*, respectively. *Cardamine* is probably pollinated by *Bombylius* and is undoubtedly well-served by andrenids, given their relatively high constancy on its flowers (Table 5) and their success in pollinating the much larger flowers of *Erythronium*.

Many zoophilous plants have a variety of potential pollinators, although this characteristic has been most frequently noted for species occurring outside the range of their "usual" pollinators or having widespread distributions (e.g., Grant and Grant 1965, Baker and Hurd 1968). Beattie (1971), however, has emphasized the importance of such diverse visitors as bumble bees, short-tongued bees, and syrphid flies within single populations of *Viola*. The same principle holds for most members of the forest spring wildflower community. One advantage of an open pollination syndrome is the reduced susceptibility to changes in the visitor fauna during the season. Very early spring flowers of *Hepatica*

are pollinated by male andrenids, while late-opening flowers are pollinated by halictids and *Bombylius*. Similarly, flowers of *Claytonia* that open before *A. erigeniae* and *Bombylius* appear are pollinated by *Gonia* and *Nomada*. When pollinators are scarce or inactive, visits by any insect capable of transferring pollen may improve seed-set.

The success of forest vernal herbs in utilizing diverse visitors depends on the pollination efficiency of the generalist, non-host specific foragers that dominate the pollinator fauna. Several characteristics of spring wildflowers promote pollination by such visitors. Foremost among these is the small number of visits required for full fruit- or seed-set (i.e., a yield equal to that of fully hand-pollinated flowers). Four visits were sufficient in all the plant-pollinator combinations examined in the effectiveness measurements (Table 8). This low required number of visits supports the conclusion from the supplemental hand-pollination experiments that pollinator service is not a major source of reduced fecundity. The mean visitation rates (Table 6) are far more than sufficient to ensure full pollination within a single day on days when pollinators are active. Only if visitation rates remain quite low throughout a flower's lifetime or pollinator visits remain consistently ineffective is seed-set likely to be affected. One reason so few visits are required may be the low ovule number of most spring wildflowers, particularly in species with multiple-flower inflorescences. Although single-flowered species tend to have larger ovule numbers, the larger-sized visitors these flowers attract also carry more pollen. *Iris* has the highest number of ovules per flower and is the species most dependent on queen bumble bees. Smaller, andrenid-pollinated single flowers, like those of *Uvularia*, have many fewer ovules (Table 1). In addition, because many spring wildflowers mature only a portion of their ovules into seeds even when fully hand-pollinated, the effective number of ovules is decreased and the actual pollination requirements are reduced.

A second trait facilitating pollination by generalists is self-compatibility since visitors need not move between separate, compatible plants. Self-compatibility is well-represented in the spring wildflower community; six of the species in Table 2 are mostly self-compatible, as are five of the seven species considered by Schemske et al. (1978). Insect-mediated self-pollination within a flower is quite likely in *Hepatica* and *Thalictrum*. Geitonogamy is common in *Stellaria* (Campbell 1983) and probably in *Claytonia* because *Bombylius* often visits flowers of the same or a nearby inflorescence.

The pollination efficiency of generalist visitors in the spring wildflower community is further enhanced by the large population sizes and clumped distributions of many vernal herbs. Pollinator movements are more likely to be intraspecific, thereby reducing the loss or

contamination of pollen loads that can occur with interspecific movements. Larger populations may also attract wide-ranging floral visitors and concentrate their foraging activity. A showy floral display is important in attracting pollinators, especially honey bees, to spring herbs in Russian broadleaf forests (Antonova 1973). In piedmont North Carolina, extensive flowering populations are characteristic of *Erythronium* and *Claytonia*. *Thalictrum*, *Sanguinaria*, and *Trillium* typically have patchy distributions. Uneven distributions in understory herbs have also been described by Struik and Curtis (1962) and Schemske et al. (1978).

*Floral biology and pollination of
queen bumble bee-visited flowers*

Many of the floral characteristics associated with successful pollination of the species pollinated by solitary bees and flies are not shared by the queen bumble bee-pollinated species. One difference is a floral morphology that restricts access to large, strong bees. Such extreme specialization in the spring wildflower community is uncommon; only 1 of 12 species I examined and 3 of the 21 species considered by Schemske et al. (1978) and Macior (1978a), two *Dicentra* species and *Mertensia*, are so highly specialized. Dependence on a visitor type that is not abundant or always available makes these species much more susceptible to pollination failure than species with more diverse floral visitors, and has been cited as a cause of low fruit-set in *Dicentra* (Macior 1978a, Schemske et al. 1978). Queen bumble bee-visited species are also likely to be pollinator-limited because most of them are self-incompatible (Table 2; see also Macior 1978a, Schemske et al. 1978). Pollen transfers between neighboring plants of *Dicentra canadensis* produce few fruits (Macior 1978a), while in *Podophyllum* fruit-set occurs only if pollination is between clones, and the infrequent bumble bee visits are often ineffective unless clones grow intermingled (Swanson and Sohmer 1976). Self-incompatibility may also affect the reproductive success of *Tiarella*. Bumble bees do not visit this species until it is in full bloom, and the alternative earlier season visitors like *Bombylius* and halictids are less effective pollinators because they often forage extensively on a single inflorescence. Although accessibility to solitary bees and flies may make *Tiarella* less dependent on bumble bees than *Iris* or *Dicentra*, self-incompatibility and a mass inflorescence attractive to large visitors make it less likely that the smaller visitors alone can fully pollinate the early-opening flowers.

*Constraints on fecundity other than
insufficient pollination*

For most spring wildflowers far fewer than 100% of the ovules mature into seeds (Table 7), yet insufficient pollination accounts for only a small portion of this deficit. Other potential causes of reduced fecundity include physical factors, resource limitation, and the

quality of pollination. The seed-set of *Hepatica* and *Erythronium* was sharply reduced following unusually cold weather in March 1980 (Motten 1982b, 1983), and 10% of the *Sanguinaria* flowers withered without producing fruits following a cold period in mid-March 1981. In April, falling light levels may depress seed-set. Many vernal herbs have high light requirements (Sparling 1967, Taylor and Percy 1976), and under low light intensity might be expected to produce less photosynthate and hence fewer seeds. The proportion of obviously aborted seeds in *Claytonia* increased steadily during canopy development (Motten et al. 1981), a pattern also noted by Schemske (1977). In *Stellaria*, which started flowering just before the canopy started to close, percent seed-set declined continuously through the blooming season (Campbell 1985). While fecundity is correlated with light availability in these two species, there is no experimental evidence that low light intensity is directly responsible for the lower seed-set. Exhaustion of stored reserves or diversion of photosynthate to future year's growth and reproduction could also reduce seed output near the end of a plant's flowering period, coincident with canopy closure. Lubbers (1982) has determined that seed production in *Thalictrum* during late spring involves an interaction between both light intensity and source-sink relationships within the plant.

Seed production in spring wildflowers may also be sensitive to the quality of pollination, i.e., the identity of the pollen parent. In a completely self-sterile species like *Podophyllum*, fruit-set depends on the extent of interclonal pollen transfer (Swanson and Sohmer 1976). Lower fertility of intraclonal pollinations may also partially account for the poor ($\approx 10\%$) seed-set per capsule in *Iris*, another clonal species. A potential selective force favoring pollination of *Iris* and *Podophyllum* by queen bumble bees is the greater energetic requirements of these large pollinators and the longer distances they fly to exploit a host (Heinrich 1977). Many non-clonal spring wildflowers also produce more ovules than seeds, even when fruit-set is higher as in *Erythronium*, *Trillium*, and *Stellaria*. This unused ovule capacity may be partially due to variability in the resources available for reproduction, but may also be a way of responding to variability in the quality of pollination. The amount of pollen a flower receives and the number of different genotypes represented depend on the activity of pollinators, the number and spatial distribution of other flowers in bloom, and the visitor species delivering the pollen. Provided the cost of unused ovules is not too high, this uncertainty may select for individuals that form more ovules than can usually be converted into seeds but which can thereby take advantage of the occasional years with a favorable combination of sufficient resources and high quality pollination (Wyatt 1981). There is indirect evidence that bet-hedging through increased ovule number may have been selected for in the spring wildflower com-

munity: percent seed-set per flower is highest in the species with the least uncertainty in pollination, the three autogamous species, and is next highest in *Claytonia*, a species with a fixed, low number of ovules and a specialist pollinator. Preliminary results of detailed pollination experiments with *Stellaria*, a self-compatible species in which geitonogamy is frequent (Campbell 1983), suggest greater resource allocation to fruits containing outcrossed rather than selfed seeds (A. Motten, *personal observation*).

Role of generalist pollinators

By any standard, pollination in the forest spring wildflower community of piedmont North Carolina is dominated by generalist floral visitors. Only three of the bee species in Table 3 are listed as oligolectic by Robertson (1929a, b) or Mitchell (1960): *Andrena erigeniae*, *A. violae*, and *A. arabis* (collected on *Cardamine*). Of these, only *A. erigeniae* was a prominent component of the pollinator fauna; the other two were rare, and neither was the most common visitor to its host. Not only do most visitor species have more than one host, but many individuals visit several hosts during a foraging bout. These inconstant visitors are nevertheless essential to pollination of spring wildflowers. None of the bees collected on *Uvularia*, and only 35% of those collected on *Stellaria*, had pure loads. Bees collecting pollen from *Thalictrum* and *Hepatica* did not visit these flowers exclusively, but also visited *Claytonia* and *Stellaria* for nectar. For many plants, any constancy by their solitary bee visitors is eclipsed by the dominance of *Bombylius*, whose degree of floral constancy is determined much more by plant spatial pattern than by innate preferences among flower types. Because of its ubiquity, effectiveness, and abundance, *Bombylius* is a dominant pollinator in the community. It substantially supplements *A. erigeniae* on *Claytonia* (Motten et al. 1981). From 1979–1981 it accounted for 59% of the visits to *Stellaria* ($n = 63$ visits). During 1979 and 1980 *Bombylius* accounted for 52% of the visits observed on *Cardamine* ($n = 106$) and 60% of those on *Thalictrum* ($n = 67$), while in 1981 the proportion increased to 89% of the visits to both species ($n = 152$ for *Cardamine*, $n = 160$ for *Thalictrum*).

Generalist, inconstant visitors appear to have a more prominent role in the forest spring wildflower community than in other communities with similar visitor faunas (e.g., Kevan 1972, Moldenke, 1975, O'Brien 1980). Bernhardt (1977), too, has described modest fidelity among solitary bees captured on *Erythronium americanum*, a species ecologically and florally quite similar to *E. umbilicatum*. Schemske et al. (1978), however, reported 81% constancy in the foraging series of visitors to forest spring wildflowers in Illinois. This high value probably reflects the absence on their sites of *Bombylius major*, an otherwise common and widely distributed species (Painter 1939), and the local dom-

inance of honey bees, which tend to be very constant foragers (Grant 1950) that can affect the foraging behavior of native bees (Eickwort and Ginsberg 1980).

Competition for pollination among spring wildflowers

Interspecific competition for pollination can occur either by differential attraction between competing species or by interspecific pollinator movements (Kordic-Brown and Brown 1979, Waser 1983). The first mechanism results in a diminished number of visits to the poorer competitor, while the second mechanism lowers pollinator effectiveness by blockage of the stigma with foreign pollen (Waser 1978), contamination of the stigma with foreign pollen that inhibits the germination of conspecific grains (Thomson et al. 1982), or loss of pollen to nonconspecific flowers. The data on pollinator activity (Table 6) and foraging behavior (Tables 4 and 5) suggest considerable potential for both forms of competition among spring wildflowers, but the hand-pollination experiments and pollinator effectiveness measurements indicate that their effect is usually not sufficiently strong to significantly decrease total seed or fruit production except in some of the queen bumble bee-pollinated species.

Differential attractiveness is most likely with the nectarless, early-blooming species. Although seed-set was unaffected in the highly autogamous species *Hepatica* or *Sanguinaria*, the loss of potential visitors to the preferred, nectar-producing *Erythronium* could reduce the amount of outcrossing. *Thalictrum*, despite attracting a diverse visitor assemblage during its later blooming period, was less frequently visited than common nectar producers like *Claytonia* and *Cardamine*. Such discrimination may not be experienced by all plants in a *Thalictrum* population, however. Individuals occurring intermingled with *Claytonia* are visited more frequently by *Bombylius* than individuals occurring in single-species patches (A. Motten, *personal observation*).

Competition by differential pollinator preference can also affect *Tiarella*, *Trillium*, and *Podophyllum*. All are nectarless and less attractive to queen bumble bees requiring nectar as they search for nest sites. Queen bumble bees preferred the shrub *Aesculus sylvatica*, which started blooming early in April, when the queens emerged. To the extent that bumble bees also visited *Aesculus* for pollen in mid-April (their corbiculae were sometimes packed with its distinctive orange pollen), *Aesculus* competed with the later-blooming, pollen-only herbs. Lower percent fruit-set for earlier-blooming inflorescences of *Tiarella* may be due to such competition. *Aesculus*, however, could also benefit the nectarless species by supporting newly emerged queens with nectar until they require pollen to found a colony, about the time the herbaceous species reach peak bloom. *Aesculus* could also benefit *Iris*, an apparently less pre-

ferred nectar source, by increasing the local density of queen bumble bees and increasing the probability that individuals "majoring" on *Aesculus* (sensu Heinrich 1976b) would use *Iris* as a "minor" host.

The inconstancy of floral visitors makes competition by interspecific pollinator movements particularly likely in the spring wildflower community. Low pollen carryover and decreased pollination effectiveness due to pollen loss during interspecific movements have been observed in *Bombus* and *Nomada* (Campbell and Motten 1985). Campbell (1985) has detected depressed seed-set in *Stellaria* plants growing adjacent to patches of *Claytonia* shortly after *Stellaria* begins blooming and is at the greatest minority disadvantage relative to *Claytonia*. Pollinator sharing by species of disparate abundance may also contribute to the lower fruit-set of early-flowering individuals of *Uvularia*, which bloomed during the flowering peak of the much more numerous *Cardamine*.

Another potential consequence of interspecific visits is reduction in seed quality. Mulcahy and Mulcahy (1975) have correlated offspring vigor with competition among pollen tubes, and a decrease in the number of pollen grains deposited could reduce the intensity of such competition. Gene flow and neighborhood size are decreased by pollen loss during interspecific flower visits (Campbell 1983), which could lead to a less than optimal outcrossing distance and less favorable matches of pollen and ovule genomes (Price and Waser 1979, Waser and Price 1983).

The most direct effect of interspecific pollinator movements is the loss of pollen, which may be a strong selective force since male function (pollen dispersal) as well as female function (ovule production) contribute to the fitness of a hermaphrodite plant (cf. Charnov 1979). Although pollen is lost to nonconspecifics through the activity of some common pollinators (Campbell and Motten 1985), the difficulty of determining the contribution to fecundity of pollen grains rather than ovules precluded a more thorough evaluation of the effect of pollinator sharing on male function.

Ecological consequences and evolutionary trends

The results of this study support several broad conclusions concerning the spring wildflower community of temperate deciduous forests: (a) many of the floral characteristics of its members are adaptive under a regime of potentially pollinator-limited fecundity, (b) the abundance and distribution of most species in the community are probably limited by factors other than inadequate pollination, and (c) despite considerable potential for interspecific competition for pollination, there is little evidence of well-defined partitioning of the pollinator resource by most species.

The suite of floral traits described above clearly pro-

mote full pollination. While it is unknown whether these traits in fact evolved in response to a prior history of low pollination, their current contribution to fruit- and seed-set is essential, as demonstrated by a combination of experimental manipulations (e.g., emasculation of autogamous flowers, control of visitor access to measure pollinator effectiveness) and interspecific comparisons (e.g., small bee- and fly-pollinated species vs. queen bumble bee-pollinated ones). Waser (1983) has recommended such a two-fold method to determine whether floral traits are selected for by competition, and the approach is equally appropriate for any cause of inadequate pollination.

Measurements of pollination success based on reproductive output make it feasible to infer effects of pollination on plant population sizes and species diversity. Such ecological properties are rarely considered in community pollination studies, which have stressed evolutionary outcomes of competition (e.g., Mosquin 1971, Heithaus 1974, Pojar 1974, Parrish and Bazzaz 1979, Pleasants 1980, Bauer 1983; but see Kevan 1972, Feinsinger et al. 1982) or relied on indirect estimates of pollination success that may not accurately reflect seed- or fruit-set (e.g., Hocking 1966, O'Brien 1980, Thomson 1982). The prevailing absence of pollination-limited seed-set among solitary bee- and fly-pollinated species, together with generalized pollination requirements that do not involve closely ordered blooming sequences or specialized visitors, suggests that the abundance and diversity of these plants is not constrained by inadequate pollination. Among less successfully pollinated, queen bumble bee-dependent species, persistence and increase may be due in part to asexual reproduction. Indeed, the most pollinator-limited species are also capable of extensive asexual reproduction; *Iris* and *Podophyllum* both spread rhizomatously, and *Dicentra cucullaris* and *D. canadensis* both produce bulbets. A similar trend in greater asexual reproduction among more pollinator-limited species also occurs in subalpine and boreal forest herb communities (Pleasants 1980, Barrett 1982). The potential longevity of such populations may actually increase the likelihood of detecting inadequate pollination, since low seed-set is less likely to result in extinction. It thus seems likely that the species diversity and distribution in the deciduous forest spring wildflower community are not principally determined by inadequate pollination; edaphic factors are probably more important (Rogers 1982).

The floral traits most typical of the spring wildflower community do not produce the partitioning of the pollinator resource that might be expected as a result of interspecific competition. Rather, autogamy, extended floral life-span, and unspecialized pollinator requirements all act to increase the likelihood of eventual pollination regardless of which plants bloom together or which visitors they share. In this respect the community is unlike most communities whose pollination

ecology has been studied (e.g., Mosquin 1971, Heithaus 1974, Percival 1974, Pojar 1974, Stiles 1975, 1977, Heinrich 1976a, Feinsinger 1978, Parrish and Bazzaz 1979, Pleasants 1980). Opportunities for niche specialization by spring wildflowers are limited. Of an already short (8–9 wk) flowering season, the most favorable period is the last 6 wk, making significant displacement in flowering periods unlikely. Heinrich (1976a) noted this restriction in his comparison of the flowering phenologies of a Maine woodland and bog. Moreover, the temperature cues that initiate flowering produce year-to-year differences in flowering dates, duration, and occasionally sequence (Fig. 3; Jackson 1966, Macior 1978b), which may preclude flowering at an apparently optimal time for pollination (Schemske et al. 1978). Diurnal separation of flowering time is not favored, because of uncertainty in visitation rates. Selection for morphologically restrictive flowers is also not likely to be strong, since the most prominent pollinators in the community are solitary bees and flies with labile foraging habits, and the more specialized queen bumble bees are not always available.

The alternative to utilizing separate pollinators is for taxonomically unrelated species to share an adequate, common supply of visitors (Baker 1963). One manifestation of this in the forest spring wildflower community is the prevalence of white, open-bowl flowers. The pattern is pronounced in the mountains of North Carolina, where *Anemone quinquefolia*, *Diphylleia cymosa*, and *Hepatica acutiloba* as well as *Claytonia*, *Thalictrum*, *Sanguinaria*, and *Stellaria* have flowers of this form (A. Motten, *personal observation*). The latter five species and several species of *Dentaria* (*Cardamine*) also contain similar ultraviolet-absorbing flavonoids whose absorption peak is close to the peak sensitivity of honey bees (Schilling and Calie 1982). White may be particularly visible in forests (Baker and Hurd 1968), and its general appropriateness in the habitat as a common color among flowers with similar morphologies and visitors would be particularly beneficial to nectarless species in obtaining extra visits by less discriminating visitors, as I have observed in mixed patches of *Thalictrum* and *Claytonia* (A. Motten, *personal observation*) and has been noted in subalpine species (Proctor and Yeo 1972, Thomson 1982).

Several investigators have reported instances of convergence in blooming time, floral morphology, or pollinator usage in communities generally thought to be dominated by partitioning of pollinator services (Thomson 1978, Brown and Kodric-Brown 1979, Parrish and Bazzaz 1979, Bauer 1983). Such observations, in addition to the results of this study, argue against uncritical application of competition theory and assumptions about niche partitioning to pollinator service, an atypical biotic "resource" that is not consumed by potential competition (Kodric-Brown and Brown 1979). A close examination of plant species sharing pollinators is likely to reveal mutualistic as well as

competitive interactions. Indeed, within the spring wildflower community (and others, e.g., Thomson 1982, Gross and Werner 1983, Rathcke 1983) the form of the relationship between species changes with plant spatial arrangements or the time in the blooming season.

Further tests of two major predictions generated by this study—(a) that plant species in a community characterized by extensive sharing of generalist visitors need not experience extensive pollinator-limited seed-set and (b) that coexistence is possible for groups of zoophilous species that show very little partitioning of a pollinator resource—will require additional community-wide pollination studies. Investigation of plant-pollinator relationships in other deciduous forest settings, such as the cove forests of the southern Appalachian Mountains (where the high species diversity should intensify competitive interactions) and disjunct stands with unusual floral or pollinator compositions, or in more distant community types with pollinator regimes similar to those of the deciduous forest in early spring, such as some alpine or arctic communities (S. Armbruster, *personal communication*), should prove rewarding.

ACKNOWLEDGMENTS

This paper is based on a dissertation submitted in partial fulfillment of the requirements for the Ph.D. at Duke University. I thank Henry M. Wilbur, Donald E. Stone, H. Fredrik Nijhout, and Daniel A. Livingstone for their support, and am grateful to C. Ritchie Bell for his encouragement and permission to work in the North Carolina Botanical Garden. Anne Lindsey graciously shared techniques in pollination biology. My research benefited from discussions with Diane Campbell, Anne Lubbers, Peter Morin, Bruce Saunders, and Helen M. Alexander. Many hours of insect watching were provided by David Alexander, Helen M. Alexander, Diane Campbell, Amy Hurst, Susan Muska, and John Sperry. For identification of insect specimens I appreciate the assistance of Lloyd Knutson of the U.S. Department of Agriculture, F. C. Thompson (Diptera), and S. W. T. Batra (Megachilidae and Anthophoridae). Additional determinations were provided by David Stephens (Anthophoridae), George Eickwort (Halictidae), and especially Wallace LaBerge (Andrenidae). Helpful comments on drafts of the paper were provided by Paulette Bierzychudek and Diane Campbell. This study was partially supported by a Research Award from the Graduate School, Duke University.

LITERATURE CITED

- Abraham, R. 1975. Recording the flight activity of insects with a time-sorting trap with special regard to climatic data. *Faunistisch-oekologische Mitteilungen* 5:11–22.
- Anderson, E., and L. Hubricht. 1940. A method for describing and comparing blooming-seasons. *Bulletin of the Torrey Botanical Club* 67:639–648.
- Antonova, L. A. 1973. Ecology of prevernal ephemerals in the broad-leaved forest. *Vestnik Leningradskogo Universiteta Seriya Biologii Geografii i Geologii* 28:28–35.
- Baker, H. G. 1963. Evolutionary mechanisms in pollination biology. *Science* 139:877–883.
- Baker, H. G., and P. D. Hurd. 1968. Intrafloral ecology. *Annual Review of Entomology* 13:385–414.
- Barrett, S. C. H. 1982. Breeding systems and flowering phenology of boreal herbs. *Miscellaneous Series Publication*

- 162, Botanical Society of America, Bloomington, Indiana, USA.
- Bauer, P. J. 1983. Bumblebee pollination relationships on the Beartooth Plateau tundra of southern Montana. *American Journal of Botany* **70**:134–144.
- Beattie, A. J. 1971. Pollination mechanisms in *Viola*. *New Phytologist* **70**:343–360.
- Bernhardt, P. 1976. The pollination ecology of *Hepatica acutiloba* DC. (Ranunculaceae). *Bulletin of the Torrey Botanical Club* **103**:255–258.
- . 1977. The pollination ecology of a population of *Erythronium americanum* Ker. (Liliaceae). *Rhodora* **79**:278–282.
- Bierzychudek, P. 1981. Pollinator limitation of plant reproductive effort. *American Naturalist* **117**:838–840.
- . 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. *New Phytologist* **90**:757–776.
- Bornkamm, R. 1975. A vegetation map of the Henry J. Oosting Natural Area, Orange County, North Carolina. Technical Bulletin Number 3, Duke University School of Forestry and Environmental Studies, Durham, North Carolina, USA.
- Brown, J. H., and A. Kodric-Brown. 1979. Convergence, competition, and mimicry in a temperate community of hummingbird-pollinated flowers. *Ecology* **60**:1022–1035.
- Campbell, D. R. 1983. Pollinator sharing and reproduction in a forest herb. Dissertation. Duke University, Durham, North Carolina, USA.
- . 1985. Pollinator sharing and seed set of *Stellaria pubera*: field experiments on competition for pollination. *Ecology* **66**:544–553.
- Campbell, D. R., and A. F. Motten. 1985. The mechanism of competition for pollination between two woodland herbs. *Ecology* **66**:554–563.
- Charnov, E. L. 1979. Simultaneous hermaphroditism and sexual selection. *Proceedings of the National Academy of Sciences (USA)* **76**:2480–2484.
- Davis, R. L., Jr., and W. E. LaBerge. 1975. The nest biology of the bee *Andrena (Ptilandrena) erigeniae* Robertson (Hymenoptera: Andrenidae). *Illinois Natural History Survey Biological Notes* **95**.
- del Moral, R., and L. A. Standley. 1979. Pollination of angiosperms in contrasting coniferous forests. *American Journal of Botany* **66**:26–35.
- Eickwort, G. C., and H. S. Ginsberg. 1980. Foraging and mating behavior in Apoidea. *Annual Review of Entomology* **25**:421–446.
- Faegri, K., and L. van der Pijl. 1979. *The principles of pollination ecology*. Third revised edition. Pergamon, Oxford, England.
- Feinsinger, P. 1978. Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecological Monographs* **48**:269–287.
- Feinsinger, P., J. A. Wolfe, and L. A. Swam. 1982. Island ecology: reduced hummingbird diversity and the pollination of plants, Trinidad and Tobago, West Indies. *Ecology* **63**:494–506.
- Frankie, G. W. 1975. Tropical forest phenology and pollinator plant coevolution. Pages 192–209 in L. C. Gilbert and P. H. Raven, editors. *Coevolution of animals and plants*. University of Texas Press, Austin, Texas, USA.
- Frankie, G. W., H. G. Baker, and P. A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests of lowland Costa Rica. *Journal of Ecology* **62**:881–919.
- Gleason, H. A., and A. Cronquist. 1963. *Manual of vascular plants of Northeastern United States and adjacent Canada*. Van Nostrand Reinhold, New York, New York, USA.
- Grant, V. 1950. The flower constancy of bees. *Botanical Review* **16**:379–398.
- Grant, V., and K. Grant. 1965. *Flower pollination in the Phlox family*. Columbia University Press, New York, New York, USA.
- Gross, R. S., and P. A. Werner. 1983. Relationships among flowering phenology, insect visitors, and seed set of individuals: experimental studies on four co-occurring species of goldenrod (*Solidago*: Compositae). *Ecological Monographs* **53**:95–117.
- Hagerup, O. 1951. Pollination in the Faroes—in spite of rain and poverty of insects. *Biologiske Meddelelser Kongelige Danske Videnskaberne Selskab* **18**:1–48.
- Heinrich, B. 1975. Bee flowers: a hypothesis on flower variety and blooming times. *Evolution* **29**:325–334.
- . 1976a. Flowering phenologies: bog, woodland, and disturbed habitats. *Ecology* **57**:890–899.
- . 1976b. The foraging specializations of individual bumblebees. *Ecological Monographs* **46**:105–128.
- . 1977. Pollination energetics: an ecosystem approach. Pages 41–46 in W. J. Mattson, editor. *The role of arthropods in forest ecosystems*. Springer-Verlag, New York, New York, USA.
- Heithaus, E. R. 1974. The role of plant-pollinator interactions in determining community structure. *Annals of the Missouri Botanical Garden* **61**:675–691.
- Hocking, B. 1966. Insect-flower associations in the high Arctic with special reference to nectar. *Oikos* **19**:359–387.
- Jackson, M. T. 1966. Effects of microclimate on spring flowering phenology. *Ecology* **47**:407–415.
- Kevan, P. G. 1972. Insect pollination of high arctic flowers. *Journal of Ecology* **60**:831–847.
- Kodric-Brown, A., and J. H. Brown. 1979. Competition between distantly related taxa in the coevolution of plants and pollinators. *American Zoologist* **19**:1115–1127.
- Levin, D. A. 1971. The origin of reproductive isolating mechanisms in flowering plants. *Taxon* **20**:91–113.
- Lindsey, A. H. 1979. *Pollination in Thaspium and Zizia*. Dissertation. University of North Carolina, Chapel Hill, North Carolina, USA.
- Lloyd, D. G. 1965. Evolution of self-compatibility and racial differentiation in *Leavenworthia* (Cruciferae). *Contributions from the Gray Herbarium of Harvard University* **195**:3–134.
- . 1980. Sexual strategies in plants I. An hypothesis of serial adjustment of maternal investment during one reproductive session. *New Phytologist* **86**:67–79.
- Lovell, H. B. 1942. The life story of three spring wildflowers. *Wild Flower* **19**:60–65.
- Lubbers, A. 1982. Spatial and temporal variation in the reproductive characteristics of *Thalictrum thalictroides* (L.) Eames and Boivin, a forest herbaceous perennial. Dissertation. Duke University, Durham, North Carolina, USA.
- Macior, L. W. 1970a. The pollination of *Pedicularis* in Colorado. *American Journal of Botany* **57**:716–728.
- . 1970b. The pollination of *Dicentra cucullaria*. *American Journal of Botany* **57**:6–11.
- . 1975. The pollination of *Delphinium tricornis* (Ranunculaceae). *American Journal of Botany* **62**:1009–1016.
- . 1978a. Pollination interactions in sympatric *Dicentra* species. *American Journal of Botany* **65**:57–62.
- . 1978b. The pollination of vernal angiosperms. *Oikos* **30**:452–460.
- Martin, F. W. 1959. Staining and observing pollen tubes in the style by means of fluorescence. *Stain Technology* **34**:125–128.
- Mitchell, T. B. 1960. *Bees of the eastern United States, Volume I*. Technical Bulletin Number 141, North Carolina

- Agricultural Experimental Station, Raleigh, North Carolina, USA.
- Moldenke, A. 1975. Niche specialization and species diversity along a California transect. *Oecologia* (Berlin) **21**: 219–242.
- Mosquin, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos* **22**:398–402.
- Motten, A. F. 1982a. Pollination ecology of the spring wildflower community in the deciduous forests of piedmont North Carolina. Dissertation. Duke University, Durham, North Carolina, USA.
- . 1982b. Autogamy and competition for pollinators in *Hepatica americana* (Ranunculaceae). *American Journal of Botany* **69**:1296–1305.
- . 1983. Reproduction of *Erythronium umbilicatum* (Liliaceae): pollination success and pollinator effectiveness. *Oecologia* (Berlin) **59**:351–359.
- Motten, A. F., D. R. Campbell, D. E. Alexander, and H. L. Miller. 1981. Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica*. *Ecology* **62**:1278–1287.
- Mulcahy, D. L., and G. B. Mulcahy. 1975. The influence of gametophytic competition on sporophytic quality of *Dianthus chinensis*. *Theoretical and Applied Genetics* **46**: 277–280.
- O'Brien, M. H. 1980. The pollination biology of a pavement plain: pollinator visitation patterns. *Oecologia* (Berlin) **47**: 213–218.
- Oosting, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *American Midland Naturalist* **28**:1–126.
- Ostler, W. K., and K. T. Harper. 1978. Floral ecology in relation to plant species diversity in the Wasatch Mountains of Utah and Idaho. *Ecology* **59**:848–861.
- Painter, R. H. 1939. Notes on type specimens and descriptions of new North American Bombyliidae. *Transactions of the Kansas Academy of Science* **42**:267–301.
- Parks, C. R., and J. W. Hardin. 1963. Yellow erythroniums of the eastern United States. *Brittonia* **15**:245–259.
- Parrish, J. A. D., and F. A. Bazzaz. 1979. Differences in pollination niche relationships in early and late successional plant communities. *Ecology* **60**:597–610.
- Percival, M. 1974. Floral ecology of coastal scrub in south-east Jamaica. *Biotropica* **6**:104–129.
- Pleasants, J. M. 1980. Competition for bumblebee pollinators in Rocky Mountain plant communities. *Ecology* **61**: 1446–1459.
- Pojar, J. 1974. Reproductive dynamics of four plant communities of southwestern British Columbia. *Canadian Journal of Botany* **52**:1819–1834.
- Price, M. V., and N. M. Waser. 1979. Pollen dispersal and optimal outcrossing in *Delphinium nelsoni*. *Nature* **277**: 294–296.
- Proctor, M., and P. Yeo. 1972. *The pollination of flowers*. Taplinger, New York, New York, USA.
- Radford, A. E., H. E. Ahles, and C. R. Bell. 1968. *Manual of the vascular flora of the Carolinas*. University of North Carolina Press, Chapel Hill, North Carolina, USA.
- Rathcke, B. 1983. Competition and facilitation among plants for pollination. Pages 305–329 in L. Real, editor. *Pollination biology*. Academic Press, Orlando, Florida, USA.
- Reader, R. J. 1975. Competitive relationships of some bog ericads for major insect pollinators. *Canadian Journal of Botany* **53**:1300–1305.
- Robertson, C. 1895. The philosophy of flower seasons, and the phænological relations of the entomophilous flora and the anthophilous insect fauna. *American Naturalist* **29**:97–117.
- . 1924. Phenology of entomophilous flowers. *Ecology* **5**:393–407.
- . 1929a. *Flowers and insects*. Science Press, Lancaster, Pennsylvania, USA.
- . 1929b. Phenology of oligolectic bees and favorite flowers. *Psyche* **36**:112–118.
- Rogers, R. S. 1982. Early spring communities in mesophytic forests of the Great Lakes region. *Ecology* **63**:1050–1063.
- Schemske, D. W. 1977. Flowering phenology and seed set in *Claytonia virginica* (Portulacaceae). *Bulletin of the Torrey Botanical Club* **104**:254–263.
- . 1978. Sexual reproduction in an Illinois population of *Sanguinaria canadensis* L. *American Midland Naturalist* **100**:261–268.
- Schemske, D. W., M. F. Willson, M. N. Melampy, L. J. Miller, L. Verner, K. M. Schemske, and L. B. Best. 1978. Flowering ecology of some spring woodland herbs. *Ecology* **59**: 351–366.
- Schilling, E. E., and P. J. Calie. 1982. Petal flavonoids of white-flowered spring ephemerals. *Bulletin of the Torrey Botanical Club* **109**:7–12.
- Sparling, J. H. 1967. Assimilation rates of some woodland herbs in Ontario. *Botanical Gazette* **128**:160–168.
- Stebbins, G. L. 1957. Self fertilization and population variability in the higher plants. *American Naturalist* **91**:337–354.
- Stephenson, A. G. 1981. Flower and fruit abortion: proximal causes and ultimate function. *Annual Review of Ecology and Systematics* **12**:253–279.
- Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* **56**:285–301.
- . 1977. Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science* **198**:1177–1178.
- Struik, G. J., and J. T. Curtis. 1962. Herb distribution in an *Acer saccharum* forest. *American Midland Naturalist* **68**:285–296.
- Swanson, S. D., and S. H. Sohmer. 1976. The biology of *Podophyllum peltatum* L. (Berberidaceae), the may apple. II. The transfer of pollen and success of sexual reproduction. *Bulletin of the Torrey Botanical Club* **103**:223–226.
- Taylor, R. J., and R. W. Pearcy. 1976. Seasonal patterns of the CO₂ exchange characteristics of understory plants from a deciduous forest. *Canadian Journal of Botany* **54**:1094–1103.
- Thomson, J. D. 1978. Competition and cooperation in plant-pollinator systems. Dissertation. University of Wisconsin-Madison, Madison, Wisconsin, USA.
- . 1980. Skewed flowering distributions and pollinator attraction. *Ecology* **61**:572–579.
- . 1982. Patterns of visitation by animal pollinators. *Oikos* **39**:241–250.
- Thomson, J. D., B. J. Andrews, and R. C. Plowright. 1982. The effects of a foreign pollen on ovule development in *Diervilla lonicera* (Caprifoliaceae). *New Phytologist* **90**:777–783.
- Utech, F. H., and S. Kawano. 1975. Biosystematic studies in *Erythronium* (Liliaceae-Tulipae): I. Floral biology of *E. japonicum* Decne. *Botanical Magazine* (Tokyo) **88**:163–176.
- Waser, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* **59**:934–944.
- . 1983. Competition for pollination and floral character differences among sympatric plant species: a review of evidence. Pages 277–293 in C. E. Jones and R. J. Little, editors. *Handbook of experimental pollination biology*. Van Nostrand Reinhold, New York, New York, USA.
- Waser, N. M., and M. V. Price. 1983. Optimal and actual

- outcrossing in plants, and the nature of plant-pollinator interaction. Pages 341–359 in C. E. Jones and R. J. Little, editors. Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, New York, USA.
- Whigham, D. 1974. An ecological life history study of *Uvularia perfoliata*. *American Midland Naturalist* **91**:343–359.
- Wyatt, R. 1981. Components of reproductive output in five tropical legumes. *Bulletin of the Torrey Botanical Club* **108**: 67–75.
- . 1982. Inflorescence architecture: how flower number, arrangement, and phenology affect pollination and fruit-set. *American Journal of Botany* **69**:585–594.
- Zimmerman, M. 1980. Reproduction in *Polemonium*: competition for pollinators. *Ecology* **61**:497–501.