The Pollination Ecology of Four Species of Local Vernal Herbaceous Angiosperms

by

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ABSTRACT

The pollination ecology of four populations of vernal herbaceous angiosperms representing four locally common species of plants in the Central New York State area were studied. Three study sites were selected and research was conducted in the field by personal observation and accepted experimental methods. Four experimental categories were established for each species at their study sites. One group of plants represented controls, the second groups had their anthers excised at anthesis, the third were isolated from foreign pollen by placing them in plastic bags and the fourth were both isolated and emasculated. By controlling pollen influx in each category, the main mode of reproduction could be determined on the basis of fruit and seed production. Visiting insects were captured on blossoms, checked for the presence of host plant pollen and identified to species (in most cases).

Hepatica acutiloba DC. showed a trend towards xenogamy favoring an entomphilous syndrome although a small percentage of seeds appeared to be produced by autogamy through a mechanical syndrome. Short-tongued flies and solitary Apoidea were common pollinators. Erythronium americanum Ker. also showed a trend towards xenogamy, but pollination was accomplished

by large heavy Apoidea. Trillium grandiflorum (Michx.) Salisb. is agamospermic, but not unless abortive tubes are produced in the pistil. Under experimental conditions in the field, pollen deposition on the stigma was the result of an entomphilous syndrome that appeared to favor xenogamous transmission. Podophyllum peltatum L. was the only species studied, which reproduced entirely without insect vectors. Fruit production was the result of succesful agamospermy. In other populations P. peltatum may be a typical xenogamous Bombus pendant flower, but agamospermy appears to dominate the Brockport population, which seems to be the result of intraspecific competition with invasive field species.

The morphology, phenology, and ecology of the four species studied reflected the coevolution of blossoms and vector. Discrepancies existed between the biology of the populations and the information present in some field guides, suggesting that enviromental barriers result in different evolutionary trends between populations.

INTRODUCTION

From the end of March until the first week in June, the northeastern forests of the United States are known for their populations of vernal flowering herbaceous angiosperms. The number of species may differ according to the region, but the major families are represented in the herbaceous spring flora of the Northeast (Gleason & Cronquist, 1963).

Despite the great difference in phylogeny and morphology, several general statements may be applied to the anthesis of most vernal flowering harbaceous angiosperms. Since subtle climatic, edaphic and biotic differences appear to exist throughout the Northeast, the blooming period of a single species is not homogeneous and may occur sporadically throughout the entire spring season (Hylander, 1954). However, the phenology of any particular colony is rarely longer than two to four weeks (Seymour, 1969). Anthesis is usually completed just prior to the production of leaves in the forest's population of woody angiosperms. Most forest herbs are perennials and their anthesis is generally earlier than those herbs found in other habitats, with a few exceptions (Gleason and Cronquist, 1963). Most forest herbaceous angiosperms have completed anthesis just prior to the June anthesis of nonforest pecies. That is, the flowers of the forest herbs have already vithered and set fruit during the height of the so-called oney flows of June (Free, 1970).

Within the last fifteen to twenty years, greater attention has been paid to the pollination ecology of familiar vernal herbaceous species. In several cases, apomictic modes have been documented under laboratory conditions, but the true role of pollination in the natural habitat has been forgotten. Considering the highly modified life cycle, mentioned above, a series of intriguing questions are left to the interested botanist.

What research has been conducted in the field leaves a rather complicated picture. Some species are apparently dependent on autogamy as the dominant mode of seed production (Wildman, 1950), others show a trend towards agamospermy, but only after abortive pollen tubes are produced in the pistil (Jeffrey, 1948). Some are autogamous, but they require insect vectors to transport pollen to the stigma (Beattie, 1969). True xenogamous species appear to rely on the early emerging insects as vectors (Macior, 1970; Grant & Grant, 1965). Where species are entirely entomophilous their blossoms may be deficient in floral nutrients like nectar (Beattie, 1971; Macior, 1970), suggesting the evolution of exclusive vector mechanisms.

Hepatica acutiloba D.C. (Ranunculaceae), Erythronium americanum Ker. (Liliaceae), Trillium grandiflorum (Michx.) Salisb. (Liliaceae), and Podophyllum peltatum L. (Berberidaceae) are all familiar spring perennial herbaceous angiosperms of Northeastern forests. Their pollination ecology is largely unknown. This study has two objectives. First, what is the dominant mode or modes of reproduction that lead to the development of viable seeds and mature fruit? Second, what are the pollinating vectors (if any) of their blossoms?

FLORAL BIOLOGY

I. Hepatica acutiloba DC.:

Phenology: Colonies flower throughout the Northeast from March to April according to Gleason and Cronquist (1963). However, records exist which may show that anthesis may be delayed until late May following severe cold spells (Seymour,1969).

Floral Morphology: There is no infloresence. Each mature plant produces from one to several villous scapes, each about 5-15 cm long. Each scape terminates in a solitary flower that is subtended by a calyzlike involucre consisting of three pointed bracts. There are six or seven petallike sepals from 12-25 mm wide. There is no corolla but the calyx is a showy mauve, blue, purple, white or pink. Stamens are small and numerous, and there are several short-styled, hypogynous pistils. The overall advertising form would probably be described as bowl to salverlike, according to Faegri and van der Pijl (1971). The fruit is an oblong, hairy achene. Nectaries may be lacking since _H. acutiloba_ lacks staminodes and Brown (1938) states that the outer ring of stamens are modified to act as nectar glands in ranunculacean plants that lack a corolla.

Ecology: In western New York, this species appears to prefer dry, mature woods of calcareous soils (Gleason and Cronquist,1963). References to hybridization with _Hepatica_ americana (DC.) Kers. appear throughout the literature of the late nineteenth and early twentieth century (House, 1918) suggesting possible introgression through xenogamy.

II. Erythronium americanum Ker.:

Phenology: Most authorities agree that anthesis occurs from late April through late May in the Northeast.

Floral Morphology: Each two-leaved plant produced a single stout peduncle (1-2 dm) that terminates in a solitary nodding, or pendant, flower. The perianth is composed of six tepals (24-50 mm) that are bright yellow at anthesis. There are six red or yellow stamens with elongate filaments that are flattened below. Anthers are linear to oblong, basifixed and either bright yellow or dull red. The single, superior pistil is composed of three erect nonseparate stigmas and a triangular style. Since the flower nods and the perianth recurves, the floral advertising form is more bell that funnellike (Faegri and van der Pijl, 1971). The fruit is an obovoid loculicidal capsule. Torrey (1853) stated that, while seeds are numerous, many are abortive. Since Erythronium belongs to the tribe Tulipae, its nectaries may be corollar rather than septal (Brown, 1938).

Ecology: This species prefers moist, rich woods and grows in large colonies that commomly consist of one or two two-leaved flowering plants and many nonflowering one-leaved plants. Controversey surrounds tha fate of the one-leaf plant.

Gleason and Cronquist (1963) state that the vegetativity produced, one-leaf plant never flowers. Arthur Cronquist (personal communication) adds that if the one-leaved plants were to mature to become fertile two-leaved plants then the life span of a two-leaved plant is only one of two years. Otherwise, each colony would gradually have more than one or two flowering specimens. Smith (1961), on the other hand, states that it may take up to six years before a seed-grown plant will set flower.

III. <u>Trillium grandiflorum</u> (Michx.) Salisb.:

Phenology: Anthesis of a colony generally occurs throughout May (Gleason and Cronquist, 1963) or from May through mid-June (Seymour, 1969).

Floral morphology: A 5-8 cm long erect peduncle terminates into a solitary flower, 5-7.5 cm broad. The calyx is composed of three, green lanceolate sepals, 3-5 cm long. The corolla consists of three obovate petals 4-6 cm acute. Petals are white, fading to pink. There are six stamens, 15-25 mm long, with pale yellow anthers and short, stout filaments. The pistil is solitary, straight, superior and styleless. The floral advertising form is typically funnellike (Faegri and van der Pijl, 1971). The fruit is a globose, many-seeded, blueblack berry; nectaries are probably septal (Brown, 1938). Agamospermy may be the major mode of reproduction for seed production, but it never occurs unless abortive pollen tubes are produced in the pistil.

Ecology: This species also prefers moist, rich woods. The plants reproduce vegetatively from rootstocks to form dense carpets on the forest floor. Ants have been observed disseminating seeds (Gates, 1941). Citations of floral anomalies are very old in the literature suggesting considerable genetic variation between sexually isolated colonies.

IV. Podophyllum peltatum L.:

Phenology: According to Fernald (1950), anthesis may occur as early as April. Gleason and Cronquist (1963) state that populations flower in May. House (1918) extends it through June in New York State.

Floral Morphology: Each mature plant produces a single nodding scape, 5-10 cm long, that terminates in a solitary (Pendant) flower. The flower bud is subtended by three green, fugacious sepals. The waxy white corolla consists of six to nine obovate petals and is from three to five cm wide. The The stamens are yellow, linear-oblong, open longitudinally, and are always double the number of petals. There is one hypogynous pistil with a sessile stigma and a thick-ovoid ovary. The floral advertising from is bell-like (Faegri and van der Pijl, 1971). The fruit is a lemon yellow berry four to five cm long. Seeds cover the very large placenta in many rows, each seed enclosed in a pulpy aril. Ripening occurs from late June through August. Rickett (1966) described the floral frangence as "too sweet." Dana (1918) found it malodorous. Nectaries in the Berberidaceae are typically corollar (Brown, 1938), but Mathews (1912) states that this species is nectarless.

Ecology: Dense colonies frequently appear in open stretches of wet rich woods. Such colonies are the result of clonal reproduction by creeping rhizomes. Immature, non-flowering plants produce a solitary, stemlike petiole that terminates in a peltate eight-lobed blade. Mathews (1912) believed that the plants were cross-pollinated by bumblebees and early bees, but did not rule out autogamy as he observed anthers touching the stigma.

METHODS AND MATERIALS

Study Sites:

Hepatica acutiloba: This population was located on the north-facing slope of the Niagara escarpment on dolestone at 198 m facing McCargo Lake on the Fancher Campus of the State University College At Brockport, town of Murray in Orleans County, New York. Duration of the study was from April 15, 1975 to May 30, 1975.

Erythronium americanum and Trillium grandiflorum: Both populations were located in Swartout's woods of the S.U.C. Brockport campus, in the town of Sweden, the village of Brockport in Monroe County, New York. The study began on April 20, 1975 and terminated June 7, 1975.

Podophyllum peltatum: The population was located in the college swamp woods of the S.U.C. Brockport campus, in the village of Brockport, of the town of Sweden, Monroe County, New York. The study lasted from May 18, 1975 to June 15, 1975.

Observations Regarding the Floral Biology of the Four Populations: Notes were taken in the field regarding the phenology, morphology and ecology of the four populations on a daily basis. Photographs were taken to record the biological characteristics.

Experimental Procedure to Discern the Dominant Modes of Reproduction: In each population, plants were chosen at random according to approved methods (Solbrig, 1970) and, in the case of H. acutiloba, the flower buds of each plant were selected at random to represent four experimental groups. Just prior to anthesis, each bud selected was placed in a transparent plastic bag and sealed with thread. Following anthesis, the blossom was placed in one of four experimental categories:

Group A, Controls: Following anthesis, the bag was removed. Fruit produced in this category should give a natural indication of the rate of fruit production in the population.

Group B, Emasculates: Following anthesis, the bag was removed and the anthers excised. If fruit is produced in this category, then foreign pollen is transmitted by a vector.

Group C, Isolates: The bag was not removed following anthesis. If those blossoms that are denied access to foreign pollen set fruit, then pollination should be autogamous.

Group D. Isolated Emasculates: Following anthesis, the bag was removed, the anthers were excised, and the bag was replaced. Blossoms that set fruit without either foreign pollen or their own are agamospermic.

Two weeks after floral withering of the entire population, the flowers were harvested and checked for the presence of fruit and seed. One hundred and twenty buds of H. acutiloba were bagged; ultimately representing thirty plants per category. Sixty buds were bagged for each species in the remaining three populations, representing fifteen plants for each category in each species.

Herbarium Samples: Specimens representative of each population were collected, pressed and mounted to serve as a record for the study.

Insect Observation and Collection: Behavior of insect species, in relation to the flowers of the populations studied, was noted in the field during morning, afternoon and crepuscular periods. Insects were caught selectively when they were observed collecting floral nutrients or lighting on the blossoms. insect was placed in a separate vial containing 75% ethanol, and examined for the presence of pollen from the host flower. Insects were keyed to species when possible.

RESULTS

I. Observations Regarding the Floral Biology of the Four Populations

Hepatica acutiloba

Phenology: The earliest recorded flower blossomed on April 16, 1975. Floral withering of the population was completed by the end of the second week in May.

Floral Morphology: All perianth color variations were represented within the population. The calyx color of an individual blossom often varied during the floral life. Mauve buds often produced white blossoms. Purple blossoms faded to blue, while white blossoms faded to pink. The number of sepals per calyx varied from six to twelve. Partially opened buds, or buds forced open just prior to anthesis, displayed anthers that touched the stigmas of the gynoecium.

Ecology: The forest canopy consisted of mature ironwood (*Ostrya*) with an understory of beech seedlings and shadbush. The *H. acutiloba* population grew in the outcroppings of Lockport Dolomite. *H. acutiloba* was the earliest flowering herb on the north slope. However, the phenology of the population overlapped with the anthesis of local populations of *Thalictrum* spp., *Viola* spp., *Trillium grandiflorum, Erythronium americanum, Dentaria laciniata* and *Caulophyllum thalictroides.* Perianths remained closed when the temperature dropped to the low fifties and below. Many buds were lost to rabbits.

Erythronium americanum

Phenology: Blossomed from about April 25, 1975 to May 10, 1975.

Floral Morphology: In this population, flowers with red stamens were less common than those with yellow stamens. Mature capsules contained the remains of many unfertilized ovules as well as mature seed.

Ecology: The population was located in a moist woodlot with a canopy of mature silver maples and an understory of beech seedlings. Erythronium americanum formed a living carpet of one- and two leaved plants across the forest floor. Groups of from twelve to twenty flowering plants were clumped together in dells created by the roots of the silver maples. Anthesis of the population overlapped with local populations of Trillium grandiflorum, Hepatica acutiloba, Dicentra cucullaria, Dentaria laciniata, Trillium arectum and Caulophyllum thalictroides.

Trillium grandiflorum:

Phenology: First flowering plants appeared on May 2, 1975, while floral withering of the entire population was completed by May 14, 1975.

Floral Morphology: Some flowers displayed partially bent scapes which led to horizontal funnel bloosoms. Blossoms whose stamens were fused to the corolla represented the typical anomaly.

Ecology: Occupied the same habitat as Erythronium americanum, but distributed in colonies from six to thirty or more flowering plants, surrounded by immature seedlings. Anthesis overlapped that of E. americanum, T. erectum, De. Laciniata, Di. cucullaria, C. thalictroides, Asarum canadense L., Actaea spp. and Lonicera oblongifloia (Goldie) Hook. Blossoms fade just prior to leaf production in the canopy and understory.

Podophyllum peltatum:

Phenology: First opened on May 20, 1975. The floral withering of the colony occured by June 2, 1975.

Floral Morphology: The corolla may recurve as the individual blossom matures.

Ecology: The habitat was a heavily cut-over swamp forest now supporting invading weed tree species and much willow and ash. Colonies of Podophyllum peltatum grew on drained hillocks above areas of standing water and muddy soil. The colonies were so dense that nodding flowers were often occluded by the umbrella-like leaves. Anthesis overlapped with Ranunculus acris, Lonicera hirsuta, Chimaphila umbellata, Geranium Robertianum and Hesperis matronalis.

II. Fruit and Seed Production

TABLE I

Flower vs. Fruit Turnout in Hepatica acutiloba

Category	# flrs. set out	# withered flrs. recovered	# flrs. with fruit
A. Controls	30	17	17
B. Emasculates	30	14	14
C. Isolates	30	16	12
D. Iso. Emasc.	30	13	9

Table I is inconclusive although fruit production appears to drop in categories C and D. Since a single blossom of *H. acutiloba* normally bears several fruits the determination of the dominant mode of reproduction can not be made on the basis of blossoms with fruit vs. blossoms without fruit. Therefore, we must compare the number of achenes on each blossom in each category.

TABLE II

Achene Number of Each Blossom in Each Category for H. Acutiloba

	A	B	C	D
	6	7	0	0
	14	12	6	11
	14	12	4	4
	6	18	0	0
	12	17	1	5
	14	12	5	15
	17	12	0	5
	16	15	0	0
	11	13	5	7
	10	17	1	3
	15	11	14	8
	28	15	15	0
	11	12	7	
	12	16	3	
	16		19	
	17		8	
	11			
ΣX =	230	189	88	63
ΣX^2=	3510	2667	1008	559
$\bar{X}$ =	13.529	13.5	5.5	4.8

To determine if there is any difference between the four categories we assume the Null Hypothesis that all four categories are equal and compute a Model I ANOVA.

Model I ANOVA Table:

Source of variation	d.f.	SS	MS	F
among groups	3	5098.8220	1699.6074	75.01
within groups	57	1291.4277	22.6566	
total	60	6390.35		

$F_{(3, 57)}$ is similar to 3.169 $\neq$ 75.01

Critical value for SS within = 3 (22.6566) (3.169) = 215.39629

A vs. B,C,D=1037.560$\neq$ Critical calue SS within

B vs. C,D=652.4$\neq$" " " "

A vs. C,D=746.06$\neq$" " " "

We reject the null hypothesis that all four categories are equal. We reject the null hypothesis that there is no difference between A, Controls and experimental groups B,C,D and C,D. We reject the null hypothesis that category B equals categories C and D. Therefore, xenogamy appears to be the dominant mode of reproduction.

TABLE III

Flower vs. Fruit Turnout in Erythronium americanum:

Category	#flrs. set out	# withered flrs. recovered	#flrs. with fruit
A. Controls	15	11	10
B. Emasculates	15	15	12
C. Isolates	15	12	0
D. Iso. Emasc.	15	11	0

The dominant mode of reproduction appears to be xenogamy in *E. americanum.* When the blossoms are denied access to the pollen of other plants they fail to set fruit. If autogamy occured via entomophily category B would not produce any fruit since the anthers had been excised prior to exposure.

TABLE IV

Flower vs. Fruit Turnout in *Trillium grandiflorum*:

Category	#flrs. set out	# withered flrs. recovered	# flrs. with fruit
A. Controls	15	10	7
B. Emasculates	15	12	10
C. Isolates	15	7	0
D. Iso. Emasc.	15	11	3

This species is known to reproduce primarily by agamospermy but apomixis will not occur unless abortive pollen tubes are produced in the pistil. Is pollen deposition mechanical? Since no fruits were produced in category C, I conclude that it is not. Under experimental field conditions fruit is produced following the xenogamous deposition of pollen in category B. Fruit production in category D is probably the result of error caused by the dislodgement of pollen while excising the anthers. Apparently, zoophilous autogamy can not be ruled out completely although fruit production in A is proportionately lower than in category B..

TABLE V

Flower vs. Fruit Turnout in Podophyllum peltatum:

Category	# flrs. set out	# withered flrs. recovered	# flrs. with fruit
A. Controls	15	13	12
B. Emasculates	15	15	14
C. Isolates	15	15	14
D. Iso. Emasc.	15	11	10

Anthers were not found touching the stigma, unlike H. acutiloba. Insect activity was practically non-existent (see next section). Considering this information and the fruit turn-out in category D, I conclude that this population is agamospermic. Similar turnouts in all four categories suggest that both alien and host pollen are superfluous and that the reproduction of seed occurs by apomixis. Otherwise, P. peltatum was capable of adjusting to each experimentally induced exclusive mechanism without influencing the ultimate rate of reproduction.

III. General Activity of Insect Visitor

Hepatica acutiloba: From April 18, 1975 to April 23, 1975, foraging was dominated by Diptera represented by Calliphoridae, Phoridae and Drosophilidae. From April 24, 1975 until the complete floral withering of the entire colony, the flowers were visited by families of solitary Apoidea and Diptera of the Syrphidae, Tachinidae and Bombyliidae. Apis mellifera L. regularly visited these flowers until the anthesis of Erythronium americanum and Dentaria laciniata. Bombus spp. were active in the woods by the end of April, but they totally ignored the colony. The Greatest amount of insect activity, both in number of insect species and insect foraging, was found in those plants bearing the greatest number of blossoms. No correlation could be made between foraging preference and perianth color.

Erythronium americanum: Comparatively few Diptera visited this species following anthesis. Calliphoridae were caught while foraging for nectar. Principle visitors belonged to local species of large, heavy Apoidea. The first Bombus queen was sighted on April 27, 1975, but the first queen was taken on a flower was caught on April 28, 1975. Bombus queens remained constant to E. americanum until the later anthesis of Dicentra cucullaria. The Oedemeridae was the only family of Coleoptera represented.

Trillium grandiflorum: Bees of the family Apidae proved to be the earliest foragers. Bombus sp. practically deserted the entire population following the anthesis of Di. cucullaria, De. laciniata and Lonicera oblongifolia, but Apis mellifera proved to be a constant visitor. Bombylliidar flies were common visitors. Following the desertion of Bombus queens, T. grandiflorum received a considerable amount of attention from families of solitary Apoidea like the Anthophoridae, Halictidae and Andrenidae.

Podophyllum peltatum: The blossoms received very little attention. Solitary Apoidea and Bombus queens were attracted to the flower, but continually refrained from foraging for pollen. Many species of insects were seen basking and resting on the leaves. P. peltatum shared the habitat with invasive field herbs which were flowering at the time. These species were always well attended by both large and small species of Hymenoptera, Diptera and Lepidoptera.

IV. Species Identification and Behavior

Coleoptera:

Oedemeridae-Asclera ruficollis (Say) was the only species of beetle found on H. acutiloba, E. americanum and T. grandiflorum. It was usually found chewing on the stamens or pistil of the blossoms and its dorsal and ventral sides were dusted with the host pollen. This beetle often damaged blossoms of H. acutiloba by devouring the gynoecium and chewing up the perianth. It was also observed chewing on the stigma of E. americanum, but not doing any considerable damage.

Homoptera:

Cicadellidae-Neokolla hieroglyphica (Say) was found within the blossom of T. grandiflorum sucking fluids from petals. Its body was devoid of pollen. Agallia quadripunctata (Procancher) was found in a blossom of P. peltatum following a rainstorm. Although it was the only insect found in this species for any length of time, it was also devoid of pollen.

Diptera:

Calliphoridae-Polenia rudis (Fab.) was the most common Dipteran on H. acutiloba. After it landed on the tip of the perianth, it extended its probocis to the base of the sepal, then walked through the androecium and gynoecium retracing and extending its procobis all the time. Once it reached the opposite side, it usually flew away. Pollen deposition was inconsistent. Some specimens were caught without any pollen at all. Others were found bearing grains of host pollen on the side of the thorax, abdomen and on the legs. Mixed loads of pollen, including host plant and pollen of other species, was found on one specimen. The foreign pollen turned out to be that of Tussilago Farfara L. Specimens of Polenia rudis were caught feeding on the nectar of E. americanum but they always lacked the host plant's pollen. A specimen of Phormia regina (Mg.) was collected on a blossom of H. acutiloba. It also lacked pollen of any kind.

Bombylliidae-Bombyllius major L. was a frequent visitor to H. acutiloba but never as common as Polenia rudis. Insects would land on the calyx and insert their long tongues at the base of the sepal. One specimen was caught bearing a mixed load of H. acutiloba and T. Farfara pollen. All other specimens of

B. major caught on Hapatica were devoid of all kinds of pollen. B. major foraged on T. grandiflorum following the anthesis of the colony. Here, the insects perched on the corolla and walked down the petals to the base of the blossom. Pollen deposition was typically nototribic and never contained alien loads.

Tachinidae-Gonia sp. was captured on H. acutiloba bearing mixed loads of pollen.

Syrphidae-Syrphus ribesii L. (male) was caught on H. acutiloba bearing mixed loads of pollen.

Phoridae-Several Megaselia were caught feeding on the anthers of H. acutiloba. Their bodies were always devoid of any pollen.

Drosophilidae-Drosophilia affinis Sturtevant was commonly found crawling among the stamens of H. acutiloba. They were never found bearing pollen on their backs.

Hymemoptera:

Apirae-Apis mellifera L. was a common visitor to H. acutiloba, E. americanum and T. grandiflorum. Honeybees bearing sternotribic depostitions of H. acutiloba pollen were frequently caught on the host plant flower where they foraged for nectar and pollen. This continued until the local anthesis of De. lacinitata and E. americanum. A. mellifera captured on E. americanum and T. grandiflorum usually carried only host plant pollen. Two specimens were caught on T. grandiflorum that also carried the pollen of De. laciniata. The pollen of E. americanum was distributed sternotribically while the pollen of T. grandiflorum was deposited nototribically. All Apis mellifera captured were worker caste imagoes. Conversely, the Bombus bimaculatus Cress.

captured on E. americanum and T. grandiflorum were all queen imagoes. Specimens bearing only sternotribic deposits of host plant pollen were consistently taken on E. americanum. Queens taken on T. grandiflorum commonly carried nototribically deposited host plant pollen in association with sternotribically deposited loads of De. laciniata, E. americanum and Di. cucullaria. The frequency of B. bimaculatus on T. grandiflorum definitely decreased when the anthesis of the populations of De. laciniata, Di. cucullaria and Lonicera oblongifolia were at their zenith.

Anthophoridae-Ceratina calcarata Robt. was a common visitor of T. grandiflorum. Most specimens captured were male although a pair of copulating adults were nototribic. Ceratina dupla Say was also taken on T. grandiflorum. As in the first species, it only bore nototribic loads of the host plant's pollen. Four specimens of the genus Nomada were taken on Erythronium americanum. Nomada sulphurata Sm. (male) was caught bearing alien loads of pollen. Two female Nomada sp. (probably N. dentariae Robt.) were caught bearing mixed loads and host loads, respectively. One unidentified Nomada sp. (female) carried mixed loads. Pollen deposition of host plant pollen was sternotribic.

Colletidae-Female Colletes thoracicus Sm. were caught on H. acutiloba bearing host plant pollen.

Halictidae-Augochlorella stricata (Prov.) and Augochlora pura (Say) were both taken on T. grandiflorum. Host plant pollen was deposited nototribically. Dialictus imitatus (Sm.) was collected on H. acutiloba. It did not carry any pollen deposits.

Dialictus coerulus (Robt.) was taken on H. acutiloba and E. americanum. In both cases, they were found carrying host plant pollen. A Dialidtus sp., probably D. pilosus (Sm.), and Dialictus versatus (Robt.) were taken on H. acutiloba. Both carried host plant pollen.

Megachilidae-Osmia atriventris Cr. was taken on E. americanum. Pollen deposition was sternotribic and composed entirely of plant pollen.

Andrenidae-Andrena carlini Ckll. was collected on E. americanum. It carried mixed loads of host plant pollen and De. laciniata pollen. Twenty-five unidentified Andrena spp. were taken on H. acutiloba, E. americanum and T. grandiflorum. Generally, those taken on E. americanum were large, hairy, bumblebeelike specimens while those taken on H. acutiloba and T. grandiflorum were smaller and less hairy. Pollen depositions were typically sternotribic on H. acutiloba and E. americanum while those taken on T. grandiflorum were nototribic. Mixed pollen loads were very common on Andrena spp. taken on all three flower species.

DISCUSSION

Unlike Viola spp. (Beattie,1971), under experimental conditions autogamous seeds of H. acutiloba are the result of a mechanical rather than a zoophilous syndrome. We can not reject the null hypothesis that achene production in category C is equal to achene production in category D. Anthers were removed following anthesis, although it was noted that anthers touched stigmas prior to the anthesis of the blossom. Considering the similarity between the mean of C and the mean of D, I suggest that non-xenogamously produced achenes are always the direct result of mechanical self-pollination prior to anthesis. If this is the case, then the number of autogamously produced seeds may increase during seasons with unprecedented cold snaps forcing perianths to remain closed while keeping vectors in a state of torpor. This would account for the distinctly similar achene turnout between category A, which retained antheers following anthesis, and category B, which lost its anthers right after anthesis.

Morphologically, the entomophilous syndrome in H. acutiloba is typified by the bowl-salver advertising form that generally suggests pollination by unspecialized vectors (Faegri and van der Pijl, 1971). Predictably, the pollen vectors of H. acutiloba were represented by the large short-tongued Diptera and the small, solitary, short-tongued Apoidea. Foraging by the principally nectar feeding Baombylius major, Halictidae, Andrenidae and Anthophoridae demonstrates that H. acutiloba probably bears nectaries at the base of the perianth. Despite pollination by Apis mellifera, H. acutiloba evolved in the absence of that genus, which was later introduced by American colonists. The species was tatally ignored by Bombus spp., but this behaviour has been recorded before (Macior, 1968).

Erythronium americanum appears to be a typical zoophilously xenogamous species like most of the Liliacae. The bell advertising form morphologically corresponds to the pendant blossom preferred by the large heavy Apoidea (Macior, 1966). Pollen transmission was relegated to the indigenous and introduced Apidae and the large solitary Apoidea species. Basal corollar nectaries encourage foraging by species representative of many families in the Apoidea. When local vernal Northeastern flora lack easily dislodged pollen and nectaries, Bombus become the exclusive pollinators (Macior, 1967). The anthesis of E. americanum coincided with the emergance of this season's Bombus queens, but preceded the anthesis of Dentaria spp., Lonicera oblongifolia and Dicentra cuccularia, which are all typical Bombus flowers (Macior, 1970).

The absence of fruit in category C demonstrates that abortive pollen tube induced agamospermy is the result of an entomophilous syndrome in Trillium grandiflorum. Denied insect vectors, this species failed to produce fruit by mechanical self-pollination.

The vertical, funnel shaped corolla provides a landing platform for vectors, encouraging nototribic deposition in insects capable of collecting nectar or pollen. Pollenination was accomplished by the ling-tongued Apis mellifera, Bombus bimaculatus, and Bombylius major, as well as the smaller shorter-tongued solitary bees. Since T. grandiflorum is regularly pollinated by morphologically diverse species the floral exclusive mechanisms are not as well defined as they are in species pollinated by one genus or by convergently modified vectors. The desertion of T. grandiflorum by Bombus, following the anthesis of Dicentra cucullaria, Lonicera oblongifolia and Dentaria spp. testifies to the lack of floral modification compared to other bell or funnel flowers (Faegri and van der Pijl, 1971). Where exclusive floral modification leads to specific vector pollen deposition the insect remains constant to the blossom population for the duration of floral anthesis. Incomplete vector attendence throughout the blossoming season discourages the co-evolution of exclusive mechanisms and encourages attraction and pollination by less specialized vectors. Unlike other Liliacae, T. grandiflorum lacks a yellow, or red and yellow, perianth. Also lacking are consistently nodding scapes and superior stigmas and stamen that typify the hummingbird, hawkmoth or Bombus pollinated species (Grant and Grant, 1965 and 1968). Entomophily in T. grandiflorum appears to fluctuate due to intraspecific competition with the more highly modified Bombus flowers that display the non-Bombus exclusive mechanisms that include nodding scapes, bell perianths, nectar spurs and anther cones.

Morphologically, Podophyllum peltatum bears all the characteristics of a pendant Bombus flower. The corolla recurves to expose the androecium and stigma, nectaries are absent although the flower is odorous and the peduncle is bent producing a nodding blossom. Although Bombus and other pollinating insects were plentiful within the population site, the flowers were ignored. Other species were visited consistently. Recent evidence exists whixh indicated that Wisconsin populations of P. peltatum are xenogamous and pollinated by Bombus (S. H. Sohmer, personal communication). Sohmer has also noted that his flowers fail to set fruit when enclosed in bags at anthesis. Why are the flowers of the Brockport population ignored by vectors? In the absence of well lighted areas, Bombus may ignore possible food flowers (Free and Butler, 1959). Bombus are not as constant a vector as Apis mellifera or territorial Trochilids (Free, 1970; Grant and Grant, 1967). Since Bombus queens collect nectar as well as pollen (Macior, 1964, 1973), nectarless species may be ignored in favor of general Apoidea flowers. The Brockport population exists in a cut-over woods where attractive invading, late spring flowering field herbs have become common. Apparently, Bombus queens find these herbs more attractive than P. peltatum. In the absence of vectors, natural selection has favored those plants that could produce viable seeds without pollen.

The phenology of vernal populations of herbaceous angiosperms serves a double role. Where the blooming period of various species is stratified throughout the season, introgression of populations in the same genus becomes difficult. Convergent evolution has produced non-phylogenetically related populations with similar exclusive mechanisms. Dissimilar phenology discourages intra-specific competition for vectors (Macior, 1973). In zoophilous angiosperms, nonrandom reproduction depends on the constancy of a population of vectors to a population of blossoms (Grant, 1950). Pollination efficiency can decrease when a single population of vectors must service two different populations at the same time.

Secondly, the phenology of plant populations must coincide with the emergence of the vector population in order to insure maximum population fertility. Where vector numbers are decreased by environmental pressures, the rate of fruit and seed production of the host plant population decreases (Free, 1970; Macior, 1973). The degree of floral modification depends exclusively on the constancy of the vector. Therefore, the co-evolution of imago-activity and flowering period definitely influences the current floral morphology of the species (Bell, 1969).

H. acutiloba was the earliest species to bloom. Although the population continued to bloom in the presence of specialized large and heavy Apoidea flowers the gross floral morphology is retained by selective vector pressure. The earliest insect vectors to emerge are the unspecialized short-tongued Diptera and Apoidea. By the time the specialized Bombus spp. and Lepidoptera appear, the antesis of the colony is past its zenith and other exclusive species, especially adapted to attract these vectors, have opened, so these later vectors tend to ignore what's left of the population.

E. americanum, a haevy Hymenopterous pendant flower, follows. It is the earliest Bombus flower and it precedes the Bombus specialized Di. cucullaria, De. spp. and Lonicera oblongifolia. Since Bombus will desert E. americanum while the population still blooms, co-evolution remains incomplete and other large and heavy Apoidea are capable of pollinating the flower.

Trillium grandiflorum blossoms concurrently with several species of vernal Bombus flowers. Although Bombus will transmit Trillium grandiflorum pollen, entire colonies may be neglected in favor of other flowers. Morphologically, T. grandiflorum is still capable of being pollinated by both the long-tongued Bombus spp. and Bombyllius spp., and the short-tongued, smaller Apoidea.

The present population of Podophyllum peltatum remains agamospermic due to selective biotic pressures. Trees in leaf cut down on the quantities of light reaching the forest floor, discouraging field Hymenoptera. In well lighted areas, invasive species like Hesperis matronalis and early flowering honeysuckles attract Bombus queens, which require nectar for incipient colonies (Macior, 1973). The floral modifications of the P. peltatum blossom tend to exclude vectors that cannot feed in an inverted position and/or require nectar as their primary floral nutrient. Therefore, it seems likely that the agamospermic trend will continue as long as the concurrently flowering invasive species remain to distract principle pollinators.

Although Apis mellifera is an introduced species, there is no reason to suspect that it might not influence the development of indigenous vernal flora. Since Apis mellifera is more constant than Bombus (Free, 1970), it may play a larger role in the non-random reproduction of populations of general Hymenoptera and Diptera flowers. Bombus may desert E. americanum midway through the blooming season or totally ignore T. grandiflorum, when other species are available, but A. mellifera continues to return to the same colony year after year, and from the beginning to the end of the blooming season (Grant, 1950). Since the introduction of A. mellifera, vernal flora may have come to depend less on Bombus and more on Apis. The constancy of Apis to E. americanum and T. grandiflorum may have resulted, or will result, in the alteration of floral morphology and in the extension of population phenology. If Apis mellifera continues to pollinate vernal flora, natural selection would tend to favor those plants with longer flowering seasons. A. mellifera pollinates H. acutiloba prior to the anthesis of large Hymenoptera flowers. This could definitely influence floral variation in this species as well as in more modified ranunculacean plants (Bell, 1969).

In closing, it is interesting to note that the discrepancies between the literature sources and the actual observations in the field. The Swartout's wood population of E. americanum grew differently than those described by Gleason and Cronquist (1963). The population of H. acutiloba displayed all the possible perianth color variations, while the population of T. grandiflorum displayed bent scapes and the colonies of P. peltatum were totally ignored by bees and had recurved corollas. Considerable variation is to be expected in Northeastern populations. The Northeast is no longer an expense of unbroken forest. Therefore, populations of species od herbaceous vernal flora are no longer continuous. Where geographical, edaphic, climatic and biotic differences exist, isolated populations will tend to vary from each other. The biology of species of vernal flora should not be considered to be continuous from place to place, or even from year to year. Where man interferes with the ecosystem, populations of angiosperms are treated to new selective pressures and must continue to evolve or vanish completely.

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APPENDICES

GLOSSARY

Achene: A small, dry indehiscent fruit with a relatively thin wall containing a single seed.

Agamospermy: Seed production by parthenogenesis.

Androecium: The whorl of stamens.

Apomixis: The substitution for sexual reproduction of an asexual process which does not involve any unclear fusion.

Autogamy: Self-pollination from self-compatability.

Berry: A fruit with a fleshy meso- and endocarp.

Bract: Modified leaf that subtends a flower or an infloresence.

Calyx: Whorl of sepals.

Capsule: A dry, dehiscent fruit developed from a compound ovary containing two or more seeds.

Corolla: Whorl of petals.

Entomophily: Pollination via insect vectors.

Floral Advertising Form: Description of the gross morphology of floral parts modified for pollination by animal vectors.

Gynoecium: Whorl of pistils.

Nectar: Diluted carbohydrates secreted by nectaries.

Nectary: A gland or modified structure embedded or attached to the surface of a plant that secretes nectar.

Nototribic: Pollen is deposited on the dorsal side of the vector. Typical in crawl-in funnel and gullet flowers.

Peduncle: A stem of stalk that bears flowers.

Perianth: Synonym for the calyx or the corolla, or the calyx and the corolla.

Pollination: The deposition of pollen on to the stigma of a pistil, invariably leading to the formation of a viable seed.

Scape: A peduncle that terminates in a solitary flower.

Staminode: A sterile structure occupying the position of a stamen often acting as a nectary.

Sternotribic: Pollen is deposited on the ventral side of the of the vector. Typical in bowl-bell flowers.

Tepal: A member of an undifferentiated perianth bearing characteristics of both sepal and petal.

Xenogamy: Cross-pollination because of self-incompatability.

IDENTIFICATIONS

Partial Report - material submitted May 11, 1975.

COLEOPTERA
Oedemeridae
E1-P,H28-P,H45-MP - Asclera ruficollis (Say) 10
Determined by T. J. Spilman

DIPTERA
Calliphoridae
H2-N,H9-N,H29-N,H4-N,H12-P,H33-N,H6-N,H21-P,H43-MP, H8-N,H22-N,E7-N - Polenia rudis (Fab.) 12
H5-N - Phormia regina (Mg.) 1
Determined by R. J. Gagne

Bombyliidae
427-MP,H48-W - Bombylius major L. 2
Determined by L. Knutson

Tachinidae
H20-MP - Gonia sp. 1
Determined by C. W. Sabrosky

Syrphidae
H44-MP - Syrphus ribesii L. 1♂
Determined by F. E. Thompson

Phoridae
H3-W,H1-n - Megaselia sp. 1
Drosophilidae
H1-N - Drosophila affinis Sturtevant 1
Determined by W. W. Wirth

Partial Report - material submitted June 3, 1975.

COLEOPTERA
Oedemeridae
T22 - Ascera ruficollis (Say) 1
Determined by T. J. Spilman

DIPTERA
Bombyliidae
T11-P - Bombylius major L. 1
Determined by L. Knutson

HEMIPTERA-HOMOPTERA
Cicadellidae
T7-N - Neokolla hieroglyphica (Say) 1
P1-N - Agallia quadripunctata (Provancher) 1
Determined by J. P. Kramer

HYMENOPTERA

Apidae

T8-MP, T6-P, T15-P, E22-P, T23-P, T21-P, T13-P, T10-P, T25-P, T9-MP - Apis mellifera L. — 10 workers

T14-MP - Bombus bimaculatus Cress. — 1♀

Note: Please send bees pinned in the future.

Anthrophoridae

T27-P, T20-P, T26-P - Ceratina calcarata Robt. — 1♀, 2♂♂

T16-P - Ceratina calcarata Robt. in copula — 1♂&1♀, kept.

T17-P - Certina dupla (Say) — 1♂

Halictidae

T24-P - Augochlorella stricata (Prov.) — 1♀

T19-P - Augochlora pura (Say) — 1♀

Andrenidae

T15-MP - Andrena. sp. — 1♂

Megachilidae

E22-P - Osmia atriventris Cr. — 1♂

Determined by S.W.T. Batra

IDENTIFICATIONS

HYMENOPTERA

Apidae

E2-P, H31-M, H10-P, H11-MP, T4-P, T2-P, H24-P, D1-MP, T3-P, H25-P, E6-P, H19-MP, H18-MP, T5-P, H16-P, H26-P, H14-MP - Apis mellifera L. — 20 workers

E11-P, E16-P, E12-P, T1-M, E13-P, E20-MP - Bombus bimaculatus Cr. — 6♀♀

Halictidae

H7-N - Dialictus imitatus (Sm.) — 1♀

H46-P, E9-P - Dialictus coerulus (Robt.) — 2♀♀

H34-P - Dialictus sp. near pilosus (Sm.) — 1♀

\- Dialictus versatus (Robt.) — 1♀

Andrenidae

D2-MP, E17-MP, D4-MP, D3-MP - Andrena carlini Ckll. — 4♀♀, 1♂. kept 1

E3-P, E4-p, H15-P, E10-MP, E5-NP, E19-MP, H35-P, H38-MP, H30-P, H40-P, H36-P, H47-P, H41-P, E8-MP, H23-N, H37-P, H42-MP, H32-MP, H39-P - Andrena spp. — 22♂♀

(I suggest that you dry and pin these and send to the specialist in this large genus:
Dr. W.E. LaBerge
Illinois Natural History Survey
Urbana, Illinois 61801)

Colletidae

H17-P, H13-P - Colletes thoracicus Sm. — 2♂♂

Anthophoridae

E14-M - Nomada sulphurata Sm. — 1♂

E18-MP - Nomada sp. — 1♂

E15-MP, D5-P - Nomada sp., near dentariae Robt. — 2♀♀

Determined by S.W.T. Batra
Systematic Entomology Laboratory, IIBIII