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MANY TO FLOWER, FEW TO FRUIT: THE REPRODUCTIVE BIOLOGY OF *HAMAMELIS VIRGINIANA* (HAMAMELIDACEAE)[1]

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Hamamelis virginiana flowers from late September to late November. In 1977, we began studying the reproductive biology of this eastern North American arborescent shrub by examining floral phenology and rewards, pollen-ovule ratios, breeding system, pollination, pollinator and resource limitation, and seed dispersal. The homogamous, self-incompatible flowers emit a faint odor, bear nectar with sucrose ratios typical of bee- and fly-pollinated flowers, and produce abundant sticky pollen. Flowers were visited infrequently by insects representing six orders. Flies were the most common floral visitors, specifically members of the genus *Bradysia*, but small bees also carried high percentages of *Hamamelis* pollen. Despite high pollen/ovule ratios (11 445 grains/ovule), bees and flies are likely pollinators, as experiments indicate wind pollination is less likely. Pollen quantity and resource availability did not appear to limit reproductive output, but pollen quality did. Tests of >40 000 flowers showed natural fruit set to be <1%. The flowering time, breeding system, and clumped distribution of plants, likely due in part to limited seed dispersal, combine to yield this remarkably low fruit set. Because all other species of *Hamamelis* flower from late winter to early summer, it may be that *H. virginiana* evolved a fall flowering phenology to avoid competition for pollinators with the closely related *H. vernalis*.

Key words: breeding system; floral phenology; fruit/flower ratios; Hamamelidaceae; *Hamamelis*, pollen/ovule ratios; pollination; pollinator limitation; reproductive limitations.

Many factors affect the reproductive success of flowering plants. Among these factors, the timing, frequency, and duration of the flowering period (collectively referred to here as phenology) is obviously of great importance (Rathcke and Lacey, 1985). The phenology of a species not only encompasses when, how often, and how long reproduction takes place but also determines the degree of reproductive synchrony with other plant species (Rathcke, 1988a, b). Synchrony among species might be advantageous if the presence of one species facilitates increases in pollinator visitation and thus fruit/seed set in another species (Thomson, 1980, 1982; Rathcke and Lacey, 1985). Conversely, in the case of wind-pollinated species or species sharing generalist biotic pollinators, there might be divergence in flowering times, presumably to reduce interspecific pollen collection and possible ''stigma clogging'' (e.g., Waser, 1978a, b). Perhaps similarly, competition for biotic pollinator visits favors divergence, given that reduced visitation rates due to competition among simultaneously flowering species can result in lower pollen transfer and thus lower fruit/seed set (Mosquin, 1971; Rathcke and Lacey, 1985).

Despite seasonality, there is substantial overlap in the timing and duration of flowering among plant species (e.g., Rathcke, 1988a, b; Gross, MacKay, and Whalen, 2000). However, there are examples of phenological patterns that result in little or no overlap with other species or result in reproduction during climatically unfavorable periods. For example, in neotropical dry forests, many trees flower during the dry period (Bullock and Solis-Magallanes, 1990) rather than the perhaps climatically more favorable growing season. Similarly, in the case of arctic plants, there are several examples of species that flower during periods of subfreezing temperatures and that, in some cases, even flower beneath the snow (Molau, 1997). These phenologies may or may not be favorable for pollination and reproduction. Thus, flowering at the extremes raises the following interesting questions about the reproductive success of these species: (1) How is reproduction possible under such adverse conditions? (2) Are these plant species reproductively successful? (3) How are these plants pollinated and what is their breeding system? (4) Is pollen transfer sufficient for fruit and seed production?

A good example of a species flowering in seemingly nonoptimal periods from the northeastern United States and southeastern Canada is *Hamamelis virginiana* (witch hazel, Hamamelidaceae). It is one of two or four species of the genus, depending on the taxonomy (Wen and Shi, 1999; Li et al., 2000), native to North and South America. All the other species, including two disjunct species in Asia, flower from early spring to early summer. *Hamamelis virginiana* flowers in late autumn, usually after leaf drop, and during periods of frost and subfreezing temperatures. Our study attempts to determine how a species that flowers under such extreme conditions succeeds reproductively at a time when there are very few pol-

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linators and most other plants presumably have shut down physiologically for the winter.

Hamamelis virginina is a common arborescent shrub in eastern deciduous forests, ranging from Nova Scotia to Wisconsin and south to northern Florida and eastern Texas (Meyer, 1997). Individuals often form dense clumps and have the potential to produce sucker sprouts from the base (De Steven, 1983). Mature reproductive plants range from 3 to 5 m in height, with mildly fragrant flowers that appear in autumn (Meyer, 1997). Inflorescences usually consist of three flowers. Flowers are bisexual and consist of four, long, slender, yellow petals, alternating with four short stamens (Meehan, 1890). Each petal is circinately vernate in bud. Alternating with the stamens are four oblong, shiny staminodia that ''shine'' from the film of nectar on their upper surface (Graenicher, 1906). Anther valves open toward the carpels, offering the potential to deposit pollen onto the bodies of visiting insects (Shoemaker, 1905). The two styles, with their often red-tipped stigmas, point outward, and the bicarpellate, semi-inferior ovary contains two ovules (Endress, 1977).

One of the more intriguing aspects of the reproductive biology of *H. virginiana* is the temporal separation of pollination and fertilization (Shoemaker, 1905; Flint, 1957). Pollen transfer and some pollen tube growth occur during the flowering period in the autumn, but fertilization does not occur until the following spring, around the time new leaves are produced. The capsular fruits develop during the growing season, reach maturity (10–14 mm in length) in late August, and remain on the plant even after the next year's flowering commences. The two seeds (5–9 mm) are ballistically ejected as the capsule dries and dehisces (Berry, 1923).

There have been some studies of the breeding system of *H. virginiana* in other localities. De Steven (1983), working with Michigan populations, concluded that witch hazel was autogamous and self-compatible. In contrast, Sommer (1986), working with Maryland populations, concluded that witch hazel was an obligate outcrosser and self-incompatible. We add here intensive studies of the breeding system and reproductive biology of *H. virginiana* in New England. We have been studying *H. virginiana* populations in Connecticut and some plants from other New England states since the mid-1970s. We have examined the pollination biology of these arborescent shrubs, carrying out a large number of hand-pollinations, following the fate of tens of thousands of marked flowers, and assaying natural pollination. Lastly, we explored the likelihood of pollen limitation to reproductive output using supplemental pollinations, and resource limitation to reproductive output using floral density manipulations.

MATERIALS AND METHODS

Floral biology—*Phenology and floral maturation*—In Mansfield, Connecticut in both 1977 and 1978, 60 flower buds on 10–11 plants were tracked to document the floral phenology. More information on this and other field sites is given at the end of Table 2. Ten unique phenological stages were recognized, including the following: floral bud opening (BO), corolla 100% unrolled (BU), one anther open (AO1), two anthers open (AO2), three anthers open (AO3), four anthers open (AO4), stigma color change (SCC), anthers wilted (AW), petals gone (PG), and flowers off (FO). The phenological stage was recorded daily for each flower. From these data, we determined the pattern of floral maturation including the timing of male and female function. The mean duration of flowering, as well as the degree of overlap in male and female function, was derived from these data.

Floral rewards—Nectar is exuded as a thin film on the adaxial surface of the staminodes. The quantity is small, in fact too small to be taken in a micropipette. To obtain sufficient quantities of nectar for compositional analysis, staminodes of 100 flowers (4 staminodes/flower), all from Mansfield, Connecticut, were touched to filter paper. The sugar, lipid, and amino acid content of the extracted solution was analyzed in the laboratory of Herbert and Irene Baker at the University of California at Berkeley in July of 1978.

Pollen/ovule ratios (P/O)—In 1977 (in Mansfield, Connecticut), 1988 (in Mansfield, Connecticut and Newmarket, New Hampshire), and 1998 (in Mansfield, Connecticut) pollen/ovule ratios were estimated. Flowers were collected with the anther valves still closed and placed in Carnoy's solution. Using a haemocytometer and averaging the counts of five grid cells on each slide, pollen counts were performed for each flower (Lloyd, 1965). The mean pollen quantity was determined across the flowers from each individual and the P/O calculated by dividing by two, the number of ovules per ovary.

Breeding system—*Compatibility*—In 1998, for each of four groups (treatments), we collected 25 flowers in Mansfield, Connecticut (five flowers per plant, five plants). The treatments consisted of hand self-pollinations, hand outcross pollinations, controls (no pollination, bagged), and open-pollinated flowers. The flowers were dissected to remove the entire pistil, and each pistil was subsequently fixed in Carnoy's solution. The fixed pistils were placed in 0.8 N NaOH at 60° for 2 h, then stained with aniline blue for 1 h. After pollen tubes were mounted and gently squashed on a glass microscope slide in aniline blue in glycerine (Martin, 1959), the number of pollen tubes present and their position in the style were recorded using a fluorescence microscope.

Hand pollinations—To achieve successful hand pollinations, we went to great extremes. We used large sample sizes, mounted dissecting microscopes on tripods to guarantee effective hand-pollination in the field, collected pollen from distant parts of Connecticut and from New Hampshire, employed many experienced plant breeders (e.g., G. J. Anderson, G. Bernardello, M. Cleland, T. Philbrick), and performed pollination experiments spanning three decades.

We also assessed the occurrence of natural pollen transfer in 1978, 1983, and 1988. In 1978 and 1988, branches with unopened flowers were brought into the laboratory and observed through anthesis in this wind- and pollinator-free environment for >1 wk to determine the deposition of pollen on the stigmas of flowers with opened and closed anther valves. In 1983, post-pollination (petals abscised) flowers that had either dropped from or still remained on the plants were collected, and the presence of pollen tubes in styles was assessed (fluorescence microscopy).

To further explore the breeding system of *H. virginiana* and to explore the possiblity of pollen limitation of fruit set, hand outcross pollinations, non-pollinated flowers (bagged controls), naturally pollinated (open-pollinated) flowers, and hand self-pollinated flowers were tracked through fruit set. Pollinations were conducted in the fall and fruit set was assessed the following fall. These manipulations and assessments were peformed in 1977–1978 (N = 23 747 flowers), 1978–1979 (N = 23 366), 1981–1982 (N = 193 flowers), 1982–1983 (N = 146 flowers), 1983–1984 (N = 1014), 1988–1989 (N = 75 flowers), and 1998–1999 (N = 2793 flowers). For example, in the 1977–1978 pollinations, ~24 000 flowers were tracked from the time of initial pollination (September or October 1977) through the following flowering season (September 1978). Censuses were made on 23 December 1977, 29 March 1978, 1 June 1978, 10 June 1978, 19 June 1978, 14 July 1978, 14 August 1978 and 18 September 1978 to track flower retention (pre-fertilization) and fruit development and retention (post-fertilization).

Hand self-pollinations allowed us to further test for self-compatibility. Autogamy was explored using bags constructed of twisted nylon organza fabric placed over branchlets with unopened floral buds. Control flowers were left unbagged and pollinated by natural vectors. The percentage fruit set was determined for each treatment. A similar protocol was used in all years.

Sink-source manipulations—To test whether resources limit reproductive output, we performed a series of floral density manipulations. On 3 October 1988, we removed large numbers of flowers from various branches, counted

the remaining flowers, and tracked fruit set until November 1989 on manipulated and control plants. Two branches on each of five plants were selected for study. On one branch all flowers were counted, then most of the flowers were removed. Between 1000 and 4500 flowers were removed, leaving only 15–18% of the flowers on the five manipulated branches. On the second branch on each plant, all flowers were counted and left intact. Mean fruit set was compared for the two treatments using a paired *t* test.

Pollination and pollinators—To address the question of how plants that begin flowering in late September, very near the first frost, are pollinated, we studied the insect visitors and assayed their pollen loads and performed two experiments to assess the likelihood of wind pollination. We logged hundreds of hours observing flowers and recording biotic visitors. Most of these observations were diurnal, but some nocturnal observations were made as well. We also took vouchers of the visitors (all of which were diurnal) and examined body parts for pollen loads in 1977 and 1978. Floral visitors were identified by entomologists at the University of Connecticut and the USDA Systematic Entomology Laboratory. Pollen from the insects was identified as from either *H. virginiana* or other species, and thus the percentage of *Hamamelis* pollen being carried by the insect could be calculated.

To assess the likelihood of wind pollination, we used screen bags constructed of fiberglass window screen with openings large enough to allow pollen in, but small enough to exclude insect floral visitors (mean width of pores = 1.21 mm). The screen in the bags may well introduce a boundary layer effect, preventing some airborne pollen from passing through the mesh. However, past bioassays showed sufficient fruit set with flowers of another anemophilous species (*Fraxinus americana*) enclosed in the screen bags (Anderson, 1976). Tests by others (Sacchi and Price, 1988; Kearns and Inouye, 1993) have also confirmed the efficacy of screen bags utilized in this way. The experiments with *Hamamelis virginiana* were conducted in 1977–1978 (N = 3731 flowers) and 1978–1979 (N = 4268 flowers) in Mansfield, Connecticut. We tracked flowers for 1 yr in 1977–1978, but for only 6 mo in 1978–1979. Control flowers were marked and counted in each experimental array. To further examine the likelihood of wind pollination, we tested for free pollen in the air within a dense population of *H. virginiana* plants. Four microscope slides covered with a thin layer of petroleum jelly were placed within the canopy of the cluster of plants. These ''pollen traps'' were set out for 24 h on 21 October 1988, when climatic conditions were favorable (no rain). The presence/absence of witch hazel pollen on these slides was recorded.

Seed dispersal—In 1978, 60 fruits were collected and brought into the laboratory to assess the dispersal distance of seeds. *Hamamelis* seeds are expelled via a ballistic mechanism as the capsule dehisces (Berry, 1923; Meyer, 1997). The pedicel ends of fruits were mounted in modeling clay and placed on a step ladder 30–60 cm above the ground at a 45° angle, which is similar to the way the fruits are held on the shrubs. The horizontal distance that seeds traveled was recorded.

RESULTS

Floral biology—*Flowering phenology*—Flowering began on 27 September 1977, and on 25 September 1978, occurring ~10–12 d before the average date of first frost in central Connecticut (7 October; R. Steinen, University of Connecticut, personal communication) and corresponding roughly to the time of leaf abscission in *H. virginiana*. The flowering period lasts 3–4 wk (1977: N = 48 flowers, mean = 21 d, SE = 1.6; 1978: N = 35 flowers, mean = 29 d, SE = 2.0) before most floral parts abscise. In New England during this time, there is little else in flower.

Floral maturation—Once the floral bud begins opening, it takes an average of 4 d for the corolla to be fully open (Fig. 1; 1977: N = 35, SE = 0.27; 1978: N = 33, SE = 0.49). Anthers open, making pollen available, a mean of 4 d after the corolla begins to open and last for a period of ~8 d total before withering. Very soon after all pollen is released, the anthers wilt (~11–12 d after corolla unrolling begins) (Fig. 1; 1977: N = 37 flowers, mean = 11 d, SE = 0.49; 1978: N = 31 flowers, mean = 12 d, SE = 0.60). The stigmas are receptive at approximately the same time as anthers are open, with a color change from greenish yellow to light red occurring in the stigma an average of 8 d after corolla unrolling begins (1977: N = 25 flowers, mean = 8 d, SE = 0.6; 1978: N = 26 flowers, mean = 8 d, SE = 0.8). All petals abscise an average of 20 d after corolla unrolling begins (Fig. 1; 1978: N = 25 flowers, mean = 20 d, SE = 0.79).

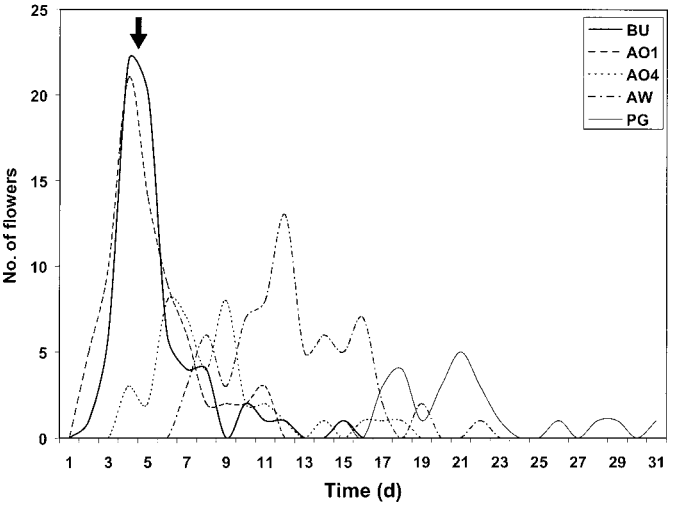

Fig. 1. The floral phenology of *Hamamelis virginiana* depicted as the number of flowers (N = 120) at any particular stage. Time 0 = anthesis. Arrow represents point at which stigmas are receptive (see text for further discussion). BU = corolla bud 100% unrolled, AO1 = one anther open, AO4 = four anthers open, AW = anthers wilted, and PG = petals gone.

Fruit maturation—Approximately 80% of flowers fall off the plants by December, the end of the flowering period (Fig. 2A). After December, there are some small differences among years in flower retention: 1998 had the lowest retention (15%), whereas 1977 had the highest retention (23%). Roughly 8% of the initial flowers are retained on the plants through March of the following spring, prior to fertilization (Fig. 2A). For the flowers surviving until March, the majority of loss occurs in the first 2 mo following fertilization; from 72% (1977–1978) to 90% (1998–1999) of those fruits/flowers on the plants in March are lost before early July (see Fig. 2B). Most of the fruits that have not aborted by this time continue to develop on the plants through the subsequent fall flowering period.

Floral rewards—The pollen of *H. virginiana* is sticky, small-grained (15–20 μm), and abundant (see below). Given these characteristics, pollen might serve as a reward to insect visitors. Nectar is exuded in tiny droplets, forming a film on the adaxial surface of the staminodes. The quantity is small. Analysis of nectar constituents indicated an amino acid concentration of 121 μg/mL, with proteins present in low amounts. Arginine, aspartic acid, cysteine, isoleucine, leucine, methionine, and threonine were present in low (1 on Baker Scale) concentrations. Alanine, glutamic acid, serine, tryptophan, and valine were present in low to moderate (2 on Baker

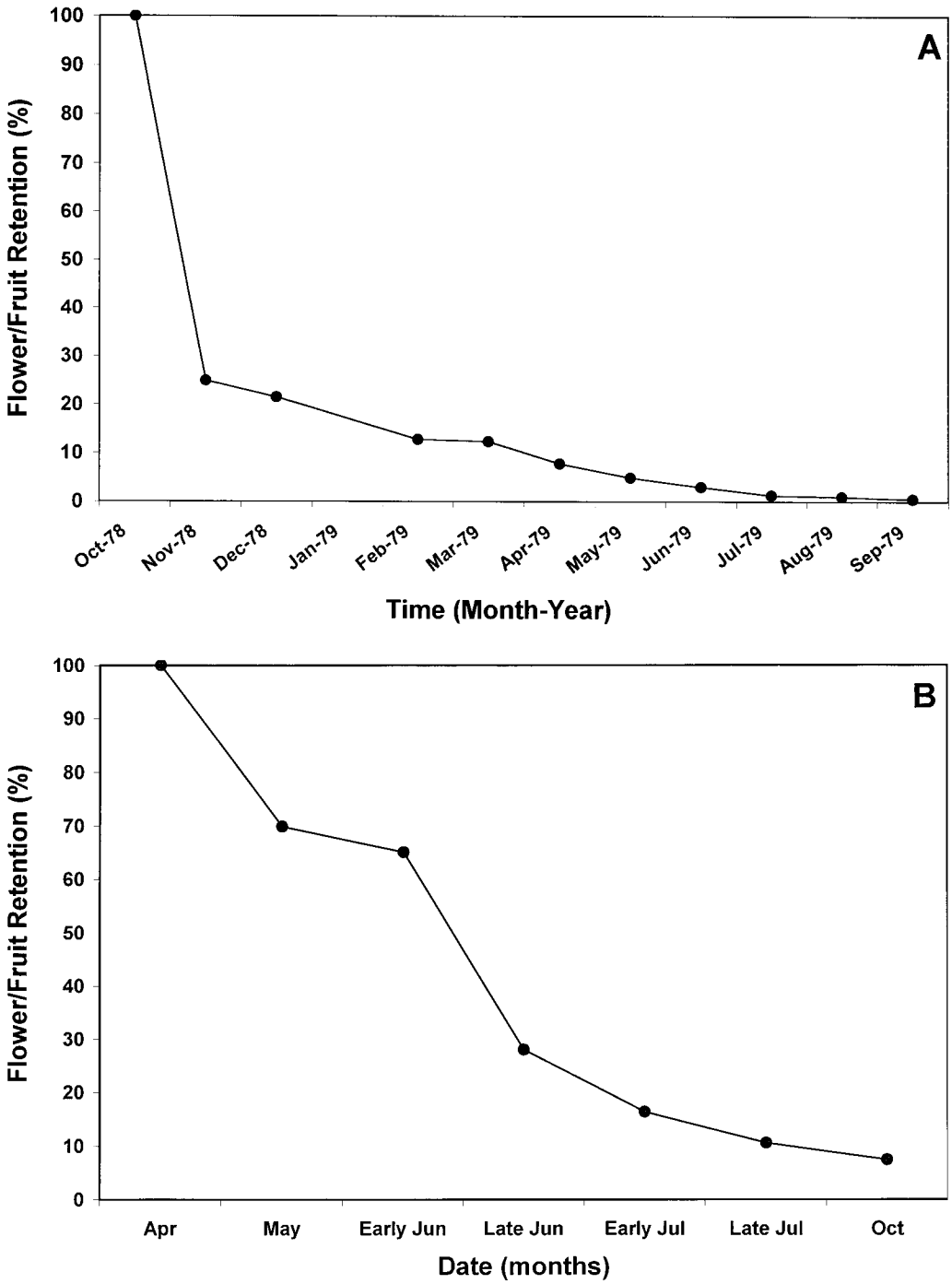

Fig. 2. (A) The percentage of flowers/fruits retained over the course of fruit development (1978–1979 data set). Pollination occurs in the late fall, with fertilization occurring around mid-April. (B) Percentage of fruits retained over a period just prior to fertilization through flowering for the subsequent season (October) (1998–1999 data set). The number of fruits/flowers present in mid-April was treated as the 100% value.

Scale) concentrations. Asparagine, glycine, phenylalanine, and proline were present in high (3 on Baker Scale) concentrations. There was also a high concentration of lipids, as indicated by the presence of osmic acid (1.6 mg/mL). Phenols (p-nitraniline) and organic acids were also recorded. Saccharide presence included sucrose (0–20% of saccharide content), glucose (41–44% of saccharide content) and fructose (36–60% of saccharide content) with a ratio of sucrose (S) to glucose (G) and fructose (F) [S/(G+F)] of 0.251.

Pollen/ovule ratios—Counts of pollen quantity were made on three separate occasions. In 1977, pollen/ovule ratios (P/O) in *H. virginiana* averaged 14 144 pollen grains/ovule ($N = 4$ plants, mean = 14 144, SE = 329), whereas in 1998, the P/O ranged from 4600 to 12 850 pollen grains/ovule ($N = 10$ plants [50 flowers], mean = 9015 pollen grains/ovule, SE = 853). In 1988, P/O estimates were made on two geographically distinct populations, Connecticut and New Hampshire. Estimates of P/O were significantly higher for the New Hampshire pop-

TABLE 1. Summary of experimental results on the breeding system of *Hamamelis virginiana*. Studies were conducted over several different time intervals from 1977 through 1999. Numbers indicate sample sizes for various treatments, numbers of fruits set, and the percentage of fruits set.

Year	Treatment	Purpose: test for	No. of flowers	No. of fruits	Fruit set (%)
1977–1978	OP	control	19 710	93	0.47
	B	autogamy	3558	8	0.22
	W	wind-pollination	3731	7	0.19
	X	hand self-pollination	235	0	0.00
	O	hand outcrossed pollination	244	0	0.00
1978–1979	OP	control	19 261	127	0.66
	B	autogamy	3835	4	0.10
	W	wind-pollination	4268	10	0.23
	X	hand self-pollination	134	3	2.23
	O	hand outcrossed pollination	136	3	2.21
1981–1982	O	hand outcrossed pollination	193	0	0.00
1982–1983	O	hand outcrossed pollination	146	8	5.48
1983–1984	O	hand outcrossed pollination	577	4	0.70
	OP	control	437	1	0.23
1988–1989	O	hand outcrossed pollination	75	0	0.00
1998–1999	OP	control	2234	2	0.09
	B	autogamy	254	1	0.39
	X	hand self-pollination	170	0	0.00
	O	hand outcrossed pollination	135	3	2.22

Note: Treatment abbreviations are as follows: OP = open-pollinated controls, B = bagged, W = screened, wind-pollinated, X = hand self-pollinated, and O = hand outcross-pollinated. Fruit set was assessed on 19 September 1978 for 1977–1978 experiment, 15 June 1979 for 1978–1979 experiment, and 14 October 1999 for 1998–1999 experiment.

ulation ($N = 3$ plants, mean = 16 493 grains/ovule, SE = 1137) than the Connecticut population ($N = 7$ plants, mean = 11 209 grains/ovule, SE = 876; Mann-Whitney U test, $W = 27.0$, $P < 0.03$). The combined mean P/O was 11 445 grains/ovule ($N = 24$ plants, SE = 143).

Breeding system—*Compatibility*—Of the 25 hand self-pollinated flowers examined in 1998 with fluorescence microscopy, 23 had pollen tubes present and the remaining two had pollen grains present but no evidence of pollen tube growth. Of the 25 bagged, control flowers, only 6 had pollen grains present, and 4 of these had pistils with pollen tubes.

In spite of the evidence for successful self-pollination, the summary of all hand self-pollinations (see Table 1) indicates that subsequent fruit set and maturation are quite rare; in fact, in both 1977–1978 and 1998–1999, no hand self-pollinated flowers matured fruits. An additional 134 flowers were hand self-pollinated in 1978, but were only tracked until June 1979, a somewhat early fruit set assessment date (see *Fruit maturation* above). Only three flowers in the 1978 self-pollinations had enlarged ovaries in June of 1979, also indicating a very low likelihood of fruit set.

Observations indicate that self-pollen is deposited on an overwhelming proportion of the flowers. A 1978 examination of stigmas on 100 open-pollinated flowers brought into the laboratory indicated that 80% of those flowers that had open anther valves also had pollen present on their stigmas, whereas only 17% of flowers ($N = 18$) without open anther valves had pollen present on their stigmas. Thus, the flowers with open anther valves had a higher than expected occurrence of pollen on their stigmas, whereas the flowers with closed anther valves had a lower than expected occurrence of pollen on their stigmas ($\chi^2 = 29.33$, df = 1, $P < 0.000$). An additional analysis was performed in 1988 ($N = 54$ open-anther valve flowers; $N = 23$ closed-anther valve flowers) with similar results ($\chi^2 = 42.987$, df = 1, $P < 0.0000$). Overall, these data indicate the great likelihood of self-pollination (but not self-*fertilization*; see more below) in flowers with open anthers.

Hand pollinations—Experiments involving hand outcross pollinations, nonpollinated flowers (bagged controls), and naturally pollinated (open-pollinated) flowers were used to further explore the breeding system of *H. virginiana* and to test the possibility of pollen limitation of fruit production. In one experiment in 1998, 24 of the 25 hand-outcrossed flowers had both pollen grains and tubes present, and only one flower had neither grains nor tubes present. Open-pollinated flowers were taken from 10 sites with five individuals/site and five flowers/individual (1998, $N = 241$ flowers) and used to tally pollen grain and tube presence and quantity. About 84% (203 flowers) had many (>100) pollen grains present on the stigmatic surface, 9% (22 flowers) had some (<50) pollen grains present, and only 7% (16 flowers) had no pollen on the stigmatic surface. Regardless of number of pollen grains in open-pollinated flowers, if pollen was present, pollen tubes grew roughly halfway down the style, with a few reaching all the way to the top of the ovary. Although pollen tube growth was not tested, the 1978 and 1988 studies of pollen on stigmas of flowers with open or closed anthers also strongly support the contention that open flowers (especially those with anthers open)

have pollen on the stigmas. Stigmas may be clogged with self-pollen that is incompatible, thus posing yet another limitation to fruit set.

Despite successful hand outcross pollination and strong evidence of natural pollen distribution, overall fruit set was extremely low (Table 1). Only 93 (0.47%) of the 19 710 open-pollinated flowers assayed in the 1977–1978 experiment matured fruits. Similarly, only 0.66 and 0.09% of the open-pollinated flowers in the 1978–1979 and 1998–1999 experiments, respectively, developed into fruit. Even with very careful application of pollen, supplementing pollen loads through outcrossing did not result in dramatic increases in fruit set for any of the experiments. However, small (nonsignificant) increases in fruit set did result from hand outcrosses for the 1998–1999 study.

Evidence from fluorescence microscopy on a set of open-pollinated flowers in 1983 also argues against pollen limitation. An analysis of 53 flowers still on the plants and 30 flowers that had naturally abscised from the shrubs (collected from the ground) showed pollen grains and pollen tubes in all 83 pistils.

Pollination and pollinators—*Entomophily*—We noted floral visitors and collected pollen from insects that had visited *H. virginiana* in the fall of 1977 and 1978. A total of 298 specimens representing six orders were collected, including 34 identified to genus and 36 identified to species (Table 2). Of these visitors, the flies (order Diptera) were most prevalent, comprising 73% (216 of 298) of all floral visitors and 52% of the identified species (Table 2). A species of dark-winged fungus gnat in the genus *Bradysia* constituted 42% of all flies collected. Hymenoptera constituted 18% (53 of 298) of the visitors and 32% of the identified species visiting witch hazel. Coleoptera represented 3% (8 of 298) of the floral visitors (Table 2). The Diptera were highly diverse (24 families) and showed wide ranges in the quantity of pollen found on their bodies (0–1254 pollen grains) and in the percentage of pollen that was *Hamamelis* (0–100%). The extreme range in pollen loads likely reflects the small stature of many of these flies and the fact that most of these insects are not primarily pollinators and thus do not have bodies well equipped to carry pollen. Although individuals of *Bradysia* had small pollen loads (mean = 23 grains), 70% of the pollen was *Hamamelis*. Eight of the 10 individual Hymenoptera from which pollen was collected had exclusively *Hamamelis* pollen, which is not surprising for a group that is constituted of species often dependent on floral rewards. Only a few pollen grains were collected on four of the five Coleoptera specimens, but most of this pollen was exclusively *H. virginiana* (Table 2).

Anemophily—Only seven (0.19%) of the 3731 flowers enclosed in screen bags in 1977 set fruit (Table 1). Thus, fruit set in ''wind''-pollinated flowers was less than half that of the control flowers. Only one of the four microscope slides with petroleum jelly set out in a dense stand of *H. virginiana* contained witch hazel pollen, and even on this slide, only a few grains were present.

Sink-source manipulations—As previously discussed, the remarkably low fruit set of *H. virginiana* appears not to be pollen limited. As a test of whether resources may be limiting reproductive output, we dramatically reduced the number of flowers on large branches to assay the effect on subsequent fruit ''load.'' Despite 70–85% reductions in flowers, average fruit set for the flowers remaining on these five branches studied ($N = 2381$) was only 2.5%, a value even lower than the 3.5% ($N = 2469$ flowers) fruit set among flowers on nonmanipulated branches (paired t test, $P > 0.05$, df = 7).

Seed dispersal—Average seed dispersal distance was 3.45 m ($N = 45$, SE = 0.18), with a range of 0.6–4.9 m. However, the distribution of distances was skewed with nearly 45% of seeds traveling a horizontal distance of 3.9 m or greater.

DISCUSSION

Phenology and floral maturation—Witch hazel flowers in the autumn after leaf drop and during a period when the temperature drops below freezing most nights and is at or below freezing for many days. This autumn-flowering period is strikingly different than the phenology of other species that also occur in the temperate deciduous forest. For example, Sommer (1986) sampled 24 species flowering in similar habitats as *Hamamelis*, and found only one species, *Desmodium pauciflorum*, that showed any degree of overlap with witch hazel flowering. In general, the genus *Hamamelis* is characterized by flowering at extreme times, but all other species of *Hamamelis* flower from very early spring to early summer, rather than in the fall (J. Li, Harvard University, personal communication).

Duration of flowering is ~3–4 wk for individual flowers (our study) and spans 4–5 wk for individual plants (De Steven, 1983). There is no evidence from our work nor from that of others (Meehan, 1890; Graenicher, 1906; De Steven, 1983) for the temporal separation (dichogamy) of male and female function or the spatial separation (herkogamy) of male and female floral parts. In fact, we noted the deposition of self-pollen on the stigmas of flowers that were isolated from pollinators and wind (i.e., flowers opened on large branches removed to the lab). Our results show that self-deposited pollen is not compatible; thus, stigmas may become coated with incompatible pollen. This obviously reduces the area available on the tiny stigmas for viable compatible pollen (stigma ''clogging''). Although there are no morphological features that indicate differences in receptivity of stigmas as they mature, there could be nonmorphological, and thus cryptic, differences in stigmatic receptivity that we did not observe.

Reproductive biology—*Breeding system and compatibility*—Based on fluorescence and fruit set studies and many controlled pollinations, we conclude that *H. virginiana* is not self-compatible and thus not autogamous, but rather an obligate outcrosser. Although pollen tubes were actually observed growing at least partway down the styles of self-pollinated flowers, the very low fruit set indicates that there is little or no effective fertilization. Sommer (1986, Maryland populations) reached similar conclusions. In contrast, De Steven (1983, Michigan populations) concluded that *H. virginiana* was self-compatible and autogamous. These divergent conclusions might be explained by differences in methodological approaches. As a result of using a September assessment date, our fruit set data were conservative, whereas De Steven's 1983 conclusions were based on a much earlier date. Her final fruit counts were made sometime in early June. Our data, with thousands of flowers over many seasons in Connecticut, showed a consistent regular fruit drop through early July (Fig. 2).

TABLE 2. Flora visitors of *Hamamelis virginiana* collected over two flowering seasons. Data consist of (1) the number of individuals of each order, family and, where possible, genus observed on flowers, (2) the year in which the insects were collected and the locality of these collections, and (3) information on the pollen carried on some of these insects. Pollen data consist of the percentage of pollen that was *Hamamelis* found on the insect, the number of other species of pollen observed on the insect, and counts/estimates of the quantity of *Hamamelis* pollen on the insect.

Floral visitors	No. of individuals	Year collected	Locality	Pollen load		
				Hamamelis (%)	No. of other species	No. of grains
COLEOPTERA	8					
Carabidae	1					
Lebia ornata Say	1	1978	CV	100	0	45
Chrysomelidae	2					
Cryptocephalus tinctus LeConte	1	1978	PR	—[a]	—	—
Diabrotica longicornis (Say)	1	1977	CV	100	0	2
Coccinellidae	1					
Scymnus (Pullus) sp.	1	1978	CV	—	—	—
Curculiondiae	1					
Anthonomus sp.	1	1978	CV	—	—	—
Lampyridae	1					
Ellychnia sp.	1	1978	CV	88	2	17
Lathridiidae	1					
Melanopthalma pumila LeConte	1	1977	—	—	—	—
Staphylinidae	1					
Omalium sp.	1	1977	CV	100	0	251
DIPTERA	216					
Anisopodidae	4					
Sylvicola fuscatus (Fabr.)	4	1977	PR, NER, PSR	75 ± 25 (N = 4)[b]	0 ± 0	36 ± 28
Anthomyiidae	5					
Not identified to species	2	1978	PR, CV	99	6	1254
Anthomyia pluvialis L.	1	1977	—	0	1	0
Hylemya sp.	1	1977	CV	0	0	0
Scatophaga stercoraria L.	1	1978	CV	100	0	127
Bibionidae	7					
Bibio longipes Loew	7	1977 (1), 1978 (6)	PR, PSR	1977: 100; 1978: 98 ± 1.4 (N = 4)	1977: 0; 1978: 1.8 ± 1.2	1977: 8; 1978: 120 ± 60
Calliphoridae	14					
Not identified to species	4	1977 (10), 1978 (4)	SER, PR, NER, PSR, CV	1977: 65 ± 15 (N = 8); 1978: 87 ± 12 (N = 4)	1977: 0.9 ± 0.3; 1978: 2.3 ± 1.7	1977: 5.3 ± 2.3; 1978: 349 ± 247
Lucilia illustris (Meigen)	1					
Melanomya serva (Walker)	2	1977	AM	90 ± 10 (N = 2)	0.5 ± 0.5	5 ± 1
Pollenia rudis (Fab.)	7					
Ceratopogonidae	11					
Forcipomyia spp.	7	1978	PSR, PR, CV	—	—	—
Forcipomyia bipunctata (L.)	1					
Forcipomyia brevipennis (Macq.)	3	1977 (2), 1978 (1)	PR, CV	—	—	—
Chironomidae	22					
Cricotopus sp.	20	1978	CV, PR	—	—	—
Cricotopus cricotopus	2	1978	CV	—	—	—
Chloropidae	2					
Tricimba sp.	1	1977	AM	0	0	0
Tricimba lineella (Fallen)	1	1978	CV	—	—	—
Drosophilidae	3					
Chymomyza amoena Loew	3	1977 (2), 1978	CV, NER, AM	1977: 100; 1978: —	1977: 0; 1978: —	1977: 11; 1978: —

TABLE 2. Continued.

Floral visitors	No. of individuals	Year collected	Locality	Pollen load		
				Hamamelis (%)	No. of other species	No. of grains
Ephydridae	1					
Discocerina obscurella (Fallen)	1	1978	CV	—	—	—
Lonchaeidae	1					
Lonchaea sp.	1	1977	—	50	1	1
Muscidae	17					
Not identified to species	3	1977 (2), 1978 (1)	PSR, PR	1977: 51 ± 37 (N = 2)	4 ± 2	7.5 ± 6.5
Coenosia sp.	1					
Helina sp.	1					
Muscina assimilis (Fallen)	2					
Musca autumnalis DeGeer	2					
Musca domestica (L.)	1					
Orthellia caesarion (Meigen)	1					
Phaonia sp.	2					
Pyrellia cyanicolora	3	1978	—	100%	0	4
Zetterstedt						
Spilogona sp.	1					
Muscoideae	2					
Not identified to species	2	1977	SER, NER, PSR	90 ± 11 (N = 2)	1 ± 1	506 ± 495
Mycetophilidae	3					
Not identified to species	2	1977, 1978	AM, PSR	0	0	0
Leia sp.	1					
Otitidae	1					
Pseudotephritis vau (Say)	1	1978	CV	99	1	174
Phoridae	2					
Megaselia sp.	1	1977	PR	100	0	18
Megaselia megaselia	1	1978	CV	—	—	—
Psychodidae	2					
Psychoda sp.	2	1977	—	—	—	—
Sarcophagidae	2					
Sarcophaga sp.	2	1978	PR	92	4	49
Sciaridae	86					
Bradysia spp.	86	1977 (78), 1978 (8)	PR, SER, AM, NER, PSR, CV	1977: 69 ± 8 (N = 26)	0.5 ± 0.1	22.6 ± 11.5
Sciomyzidae	1					
Not identified to species	1	1977	RED	66	1	34
Sepsidae	2					
Sepsis punctum (Fabricius)	2	1977	NER, PSR, CV	50 ± 50 (N = 2)	0	3
Simulidae	2					
Not identified to species	2	1977	CV	—	—	—
Syrphidae	22					
Not identified to species	5	1977 (3), 1978 (2)	PR, CV	1977: 100; 1978: 56 ± 31 (N = 2)	1977: 0; 1978, 60 ± 46	1977: 185; 1978: 60 ± 25
Metasyrphus americanus (Wied.)	3	1977 (2), 1978 (1)	PR, NER, PSR, CV	1977: 97; 1978: 42	1977: 2; 198: 105	1977: 70; 1978: 75
Syrphus torvus O. S.	4	1977 (2), 1978 (2)	PSR, PR, CV	1977: 46.5 ± 46.5 (N = 2); 1978: 96	1977: 1 ± 0; 1978: 7	1977: 6.5 ± 6.5; 1978: 181
Syrphus vitripennis (Meigen)	6	1977 (6)	PR, SER	89 ± 6 (N = 7)	1.8 ± 0.99	31 ± 8.7
Toxomerus geminatus Say	4	1977 (2), 19 1978 (2)	AM, PR	1977: 43 ± 43 (N = 2); 1978: 86 ± 15 (N = 2)	1977: 0.5 ± 0.5; 1978: 2.5 ± 2.5	1977: 3 ± 3; 1978: 9 ± 3
Tachinidae	4					
Admontia degeerioides Cog.	1	1977	SER	94	1	78

TABLE 2. Continued.

Floral visitors	No. of individuals	Year collected	Locality	Pollen load		
				Hamamelis (%)	No. of other species	No. of grains
Compsilura concinnata (Mg.)	2	1977	NER, PSR	0	2	0
Trichopoda pennipes (F.)	1	1978	CV	<1	28	1
HOMOPTERA	4					
Aphididae	1					
Not identified to species	1	1978	CV	—	—	—
Cicadellidae	1					
Graphocephala coccinea (Forster)	1	1978	CV	—	—	—
HYMENOPTERA	53					
Apidae	1					
Aphidius sp.	1	1977	CV	100	0	198
Braconidae	5					
Aspilota sp.	3	1977	—	90 ± 10 (N = 2)	0.5 ± 0.5	3.5 ± 0.5
Rogas sp.	1	1977	PR	100	0	25
Spathius sp.	1	1978	CV	—	—	—
Ceraphronidae	2					
Dendrocerus sp.	2	1978	CV, PSR	—	—	—
Chrysidae	1					
Omalus sp.	1	1978	CV	—	—	—
Cynipidae	2					
Not identified to species	2	1978	PR, CV	—	—	—
Diaysriidae	4					
Not identified to species	4	1978	CV	—	—	—
Eucoilidae	1					
Eucoila sp.	1	1978	PR	—	—	—
Eulophidae	7					
Tetrastichus sp.	7	1977 (4), 1978 (3)	SER, PR	100	0	48
Figitidae	1					
Xyalaspis sp.	1	1977	PR	0	1	0
Halictidae	6					
Augochlora pura Say	1	1977	—	100	0	1
Dialictus sp.	1	1978	—	50	3	6
Dialictus tegularis (Robt.)	1	1977	—	—	—	—
Ichneamonidae	3					
Not identified to species	1	1978	CV	—	—	—
Coccygomimus sp.	1	1977	NER, PSR	100	0	5
Cratichneumon sp.	1	1977	—	100	0	200
Ormyridae	2					
Ormyrus sp.	2	1978	CV, PR	—	—	—
Perilampidae	2					
Not identified to species	2	1978	CV, PSR	—	—	—
Platygastridae	4					
Platygaster sp.	1	1978	PSR	—	—	—
Synopeas sp.	3	1978	PSR, CV	—	—	—
Pteromalidae	10					
Not identified to species	10	1977 (3), 1978 (7)	PR, NER, PSR, CV	1977: 50 ± 50 (N = 2); 1978: —	1977: 0.5 ± 0.5; 1978: —	1977: 9 ± 9; 1978: —
Scelionidae	1					
Telenomus sp.	1	1978	CV	—	—	—
Torymidae	1					
Torymus sp.	1	1978	PR	—	—	—
Trichogrammatidae	1					
Not identified to species	1	1978	PSR	—	—	—
NEUROPTERA	1					
Hemerobiidae	1					

TABLE 2. Continued.

Floral visitors	No. of individuals	Year collected	Locality	Pollen load		
				Hamamelis (%)	No. of other species	No. of grains
Not identified to species	1	1978	CV	—	—	—
HETEROPTERA	15					
Anthocoridae	15					
Not identified to species	8	1977	PSR, SER, NER, CV	67 ± 21 (N = 6)	0.5 ± 0.3	7.8 ± 3.4
Orius insidiosus	7	1978	CV	—	—	—
Reduviidae	2					
Not identified to species	2	1978	CV	56	122	154
THYSANOPTERA						
Not identified to species	1	1978	CV	—	—	—

Note: Abbreviations for localities as follows: AM = Ayer's Mountain, Franklin, Connecticut; CV = Off Route 275, Coventry, Connecticut; NER = Off North Eagleville Road, Mansfield, Connecticut; PR = Pink Ravine, Mansfield, Connecticut; PSR = Pumping Station Road, Mansfield, Connecticut; RED = Redding, Connecticut; SER = Off South Eagleville Road, Mansfield, Connecticut.

[a] = no data.

[b] Mean and SE are presented.

It is possible that *H. virginiana* shows variation in compatibility. For example, Rathcke and Real (1993), working with the temperate forest shrub *Kalmia latifolia*, concluded that plants in Virginia populations were autogamous, whereas those in Rhode Island populations were not. Similarly, there may be some fruits produced by self-pollination in plants that are largely self-incompatible; for example, the self-incompatible woodland herb *Anemone nemorosa* produces some fruit from self-pollinations (Muller, Schneller, and Holderegger, 2000). Although such variable compatibility is a possibility, the data we have imply that fruit set in this species cannot be assessed accurately before late August or September; the data assessed at or after that time indicate self-incompatibility.

Pollination—*Floral rewards*—*Hamamelis virginiana* nectar contains16 amino acids and possesses a sugar ratio [S/(G+F)] of ~0.25. In a survey of 948 plant species, Baker and Baker (1983a, b) reported that species with a sugar ratio in the range of 0.1–0.5 were most frequently pollinated by short-tongued bees (35% of the species), long-tongued bees (25% of species), and flies (9% of species). In addition, the pollen is moderately abundant, small, sticky, and readily available, and thus could also serve as part of the reward system.

Entomophily and anemophily—Diptera were the most frequent floral visitors in our study (73% of all visitors and 52% of the species diversity), but there was a wide range in pollen quantity on the bodies of these insects. On the other hand, the hymenopteran visitors (18% of all visitors, 35% of identified species) carried high percentages of *Hamamelis* pollen on their bodies, suggesting more fidelity to *Hamamelis* flowers. Both DeSteven (1983) and Sommer (1986) also documented a high frequency of fly visits to *H. virginiana* flowers. Sommer (1986) indicated that Diptera (63%) and Hymenoptera (22%) were the primary floral visitors and pollen carriers. Similarly, De Steven (1983) reported that Diptera comprised 73% of all floral visitors. We also find it interesting that the most prevalent species visiting *H. virginiana* flowers in Michigan and Connecticut are dark-winged fungus gnats of the genus *Bradysia* (present study; De Steven, 1983), an insect not usually considered a pollinator because of its small size. Thus, these small flies may indeed—as a swarm, a group—constitute significant witch hazel pollinators. The variation in pollen load carried by flies in general, and by the fungus gnats specifically, suggests that most of the fly visitors likely do not function particularly effectively as pollinators. Given the morphology of *H. virginiana* flowers, the exposed glistening staminodes where a thin film of nectar is produced, the small exposed floral parts, the sugar ratio, and documented visits to some of the flowers open in late September or early October, small bees are also potential pollinators.

The pollen/ovule ratios we measured in *H. virginiana* are within the range for wind pollination (Cruden, 1977). In addition, the small quantities of nectar and the paucity of insects at this time of the year argue against entomophily, and the occurrence of flowering after leaf drop suggests the possibility of anemophily (Rathcke and Lacey, 1985). However, we conclude that there is little evidence for wind pollination in *H. virginiana* for several reasons. First, the stigmas are not conducive to capturing airborne pollen: they are tiny, almost devoid of three-dimensional structures (papillae), and not particularly wet. Second, the pollen is sticky and released from anthers in a way that would not promote dispersion into the air. Third, our tests for the presence of airborne pollen with slides in dense clusters of plants captured little or no pollen. Finally, bagging experiments designed to test for wind-pollination yielded little fruit set. These patterns, combined with the bright coloration and mild, pleasant odor of the flowers suggest that, unlikely and ineffective as it is, an insect pollination syndrome is more plausible. Clearly, there would not seem to be specialized insect pollinators for this late-autumn-flowering species. But it is much more likely that the pollen yielding effective fruit set is transmitted by bees and flies than by the wind.

Limits on reproductive output—Overall, fruit set was very low in populations of *H. virginiana* in northeastern Connecticut (usually <1% fruit set in open-pollinated control flowers). Neither supplemental pollinations nor reduction of floral sinks resulted in significant increases in fruit set. Our fluorescence studies indicate the presence and germination of pollen on most stigmas. We also observed pollen on stigmas of flowers that aborted (1983). These results, in combination with results

from supplemental hand pollinations, indicate little if any evidence of pollen limitation: pollen reaches stigmas, germinates, and pollen tube growth occurs. Although the quantity of pollen per se does not seem to be limiting reproductive success, the source of the pollen may well be. Self-pollen is not effective, i.e., we found no evidence for self-compatibility in *H. virginiana* populations in Connecticut. On the other hand, if there is a complicated self-incompatibility system, the combinations correct for effecting fruit set may be rare. The longer season in more southerly sites (see below) may provide more opportunity for bees or flies to transmit effective pollen that is not swamped out on the self-pollen-clogged stigmas. Additionally, fruit set does not seem to be resource limited. We removed thousands of flowers (amounting to >70% of the standing crop of flowers) from plants and found no increase in the fruit set among the remaining flowers. Perhaps more experiments or even larger sample sizes are needed. However, we have gone to great lengths to insure both of these. The fruit set of witch hazel, even at the low values we have recorded, may simply be at its maximum. Fruit set this low is not unknown, as the results of Sutherland and Delph's (1984) survey show (e.g., there are several species with fruit set at or below 1%).

Our estimates of natural (open, naturally pollinated flowers) fruit set are lower than those published by other authors. Sommer (1986) found 18% of flowers set fruit. Our lower estimates may reflect our more conservative assessment of fruit set or perhaps the less climatically favorable conditions in Connecticut than in Maryland. Late fall and winter conditions in Connecticut are likely to be less hospitable for pollination than those in Maryland. Thus, flowers and pollinators may be less abundant toward the northern edge of *H. virginiana*'s range, and harsher winter conditions perhaps may result in more overwinter mortality of flowers. Given the 5–7 mo delay between pollination and fertilization (Shoemaker, 1905; Flint, 1957), this prefertilization stage is likely critical to the reproductive success of *H. virginiana*.

De Steven (1983) found that 6% of inflorescences in 1977 and 43% of inflorescences in 1979 set fruit. At three flowers per inflorescence, and assuming an average of one fruit per inflorescence, this gives 2–14% fruit set per flower. Our data show that the majority of fruit abortion occurs between May and July. This abortion might be explained by a lack of fertilization, post-fertilizaton mortality cued by physiological factors (both intrinsic mortality/abortion factors), or by extrinsic factors such as fruit predation and parasitism (De Steven, 1982). Since DeSteven (1983) scored fruit set much earlier than we did (early June), it may well be that her assessments missed the majority of fruit abortion that occurs during the early growing season through early July. In fact, in another study, De Steven (1982) reported that the majority of fruit loss due to physiological abortion occurred in mid-June through July. Thus, our estimates of fruit set are more conservative and take into account this initial fruit loss.

Extreme phenologies and reproduction—Overall, it appears that the reproductive success of *H. virginiana*, a species blooming at the marginal extreme of the growing season, is very limited indeed. Fruit set is remarkably low in Connecticut populations, and supplemental pollinations and sink-source manipulations resulted in no significant increases in reproductive output. Even when fruits do mature and produce seeds, they are dispersed only a short distance (an average of ~3.5 m). Thus, populations of *H. virginiana* possibly often consist of highly clumped, (likely) closely related individuals, increasing the likelihood of incompatibility limiting reproduction. The self-incompatibility system, as well as the paucity of insect visitors, at least in Connecticut populations, contribute to limited fruit set.

In general, angiosperms often have a low fruit/flower ratio (e.g., <25% of flowers set fruit in outcrossing hermaphrodites; Sutherland and Delph, 1984). *Hamamelis virginiana* has extremely low fruit set (<1% of flowers set fruit). There are a number of explanations for the disparity between number of flowers produced and fruit set, each presuming a selective advantage to overproduction of flowers. For example, if the maternal parent can select which fruits to mature based on the quality or quantity of pollen deposited (Bertin, 1990), higher quality offspring should result. Similarly, overproduction might allow for plants to take advantage of resource-rich or environmentally favorable conditions, thus matching fruit production with resource availability (Stephenson, 1981). Another explanation for overproduction of flowers is pollinator attraction. A large floral display might promote a greater number of pollinator visits and thus possibly increase the amount of compatible pollen reaching the styles (Stephenson, 1979). In a 1986 study, Sommer evaluated five hypotheses concerning the overproduction of flowers in *H. virginiana* and concluded that attraction of pollinators was the likely cause for such overproduction in witch hazel. Given the paucity of insect visitors, and the timing of flowering in this species, overproduction of flowers to attract pollinators seems a likely explanation, within the context of a self-incompatibility system (the latter constituting selection among pollen tubes).

The question of why *H. virginiana* has a fall flowering phenology remains open. All other species of *Hamamelis*, including the closely related *H. vernalis* of the southeastern United States, flower in early spring or summer (Li et al., 2000). Based on the distributions of extant species and putative *Hamamelis*-like fossils, Berry (1923) considers the current Asian-North American disjunction of the genus a good example of an ancient distribution. Molecular studies of the phylogenetic relationships of the North American species of *Hamamelis* are incongruent in terms of the number of species supported, ranging from two (Wen and Shi, 1999) to four (Li et al., 2000), but agree with Berry's conclusions regarding the disjunct distributions. Furthermore, the molecular studies agree that one of the Asian species (*H. japonica*) is more closely related to the North American species than to its Asian relative (*H. mollis*). Both phylogenetic studies also place *H. virginiana* as basal to *H. vernalis* (which is linked to the other two North American species, if they are treated as distinct). All the other species, both Asian and North American, flower in early spring to early summer. Thus, *H. virginiana* stands alone in its fall-winter flowering time.

In a study of limited scope in the Ozarks of Missouri, USA, where *H. virginiana* and *H. vernalis* occur sympatrically, Bradford and Marsh (1977) observed that in unusual years when *H. virginiana* flowered late and *H. vernalis* early, the flowering times of the species overlapped. In such instances, there was a strong pollinator preference for *H. vernalis*. This suggests the possibility that *H. virginiana* may have acquired a different flowering phenology via displacement of flowering time. The temporal separation of pollination (fall) and fertilization (spring) in *H. virginiana* (Shoemaker, 1905; Flint, 1957) also supports the argument of a shift from spring to fall flowering in *H. virginiana*. It is thus possible that the fall flow-

ering of *H. virginiana* may have evolved in part as a means of avoiding competition for pollinators with the closely related *H. vernalis*. Regardless of the selective mechanisms involved, *H. virginiana* certainly has very few to no competitors for pollinators when it flowers late into the fall and early winter in New England. Individuals often produce a very large number of flowers, but have a small number of floral visitors and a remarkably low fruit set.

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