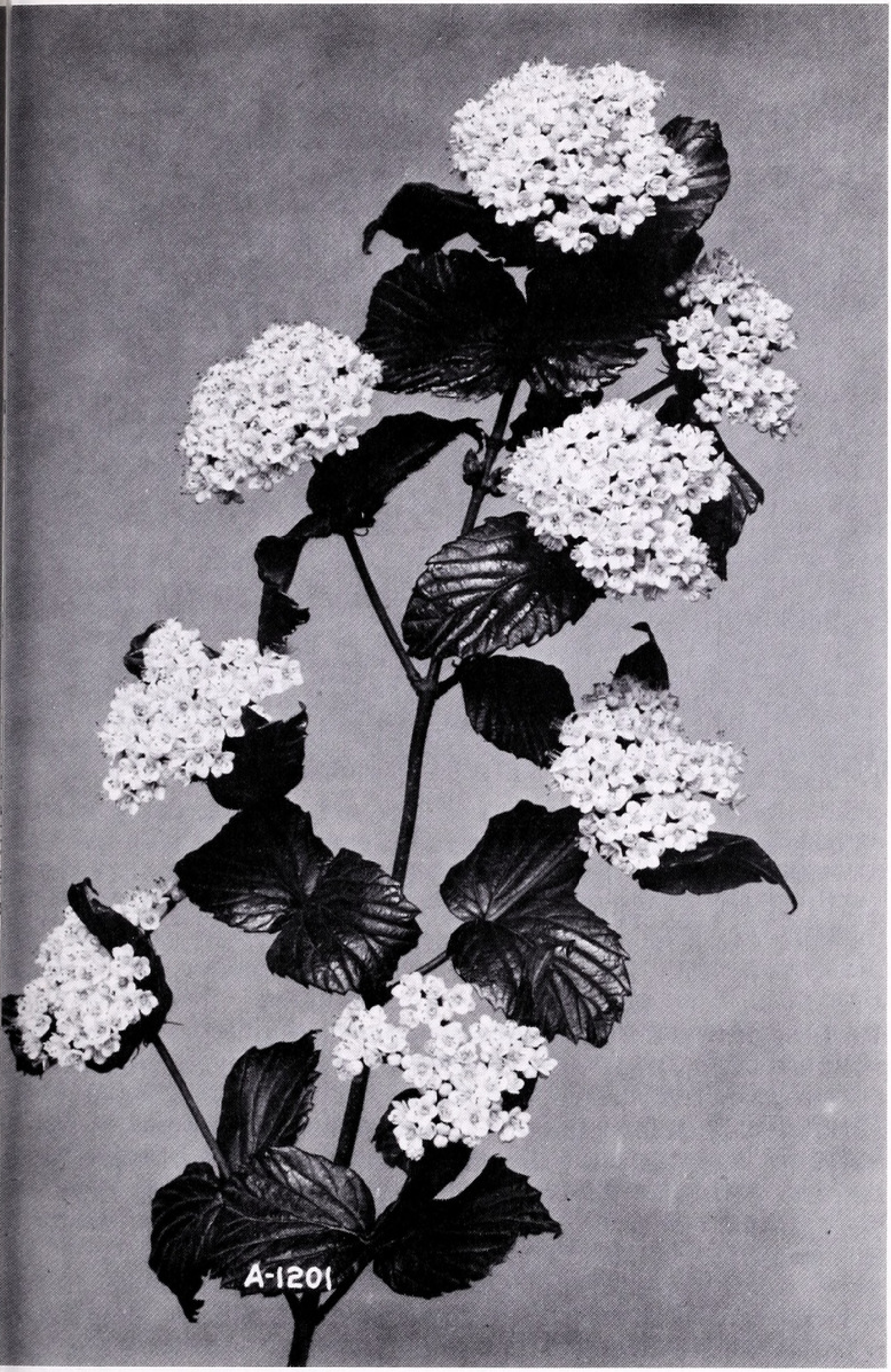
Flowering Times In *Viburnum*

by Michael Donoghue

That plants of different species flower at different times during the year is well known to everyone. But for many plants we have very little reliable data concerning flowering times, and even when we do have this information, we often know very little about what triggers flowering and what physiological changes are involved, let alone the evolutionary explanations for such timing differences.

Botanists are approaching these questions in a number of different ways. One approach is to record, over a number of years, the flowering times of all the plants in a given community (such as a tropical rain forest in Malaya (Medway, 1972) or a forest understory in New England (Lyon, 1922)) and to try to make sense of any patterns which emerge. Other botanists study variation in flowering periods within a single species and try to explain this in physiological, ecological, and evolutionary terms (Goodwin, 1941; Olmstead, 1944; Ray & Alexander, 1966). Another approach is to study flowering times in some broader taxonomic context, for example, by comparing the flowering times of the species within a genus. This approach has rarely been pursued very rigorously, although sometimes lists of flowering times are produced for seed manuals (e.g., Gill & Pogge, 1974) or in studies of wildlife food plants (e.g., Rollins, 1974). Plant sys-

Michael Donoghue is a graduate student in biology at Harvard University. He is writing his doctoral dissertation on the systematics of the genus Viburnum, *especially the Mexican and Central American species.*



photograph of Viburnum rafinesquianum *taken in May 1903 by Alfred Rehder, no devoted considerable time to the study of viburnums, especially the Asian embers of the genus. Though the size of* Viburnum *inflorescences varies con-derably, most of them are constructed very much like those shown here. The otograph also shows the simple, opposite leaves characteristic of the genus.*

tematists have long made a habit of noting the flowering periods of the plants they study, but unfortunately this information is rarely very precise. For example, we often read in monographs or in field guides that species *A* flowers in mid-spring, while its relative, species *B*, flowers in mid- to late spring. Because these records are for species throughout their geographical ranges, this information may obscure important differences in flowering times, particularly where two species happen to grow together, i.e., where they are sympatric.

An arboretum is an ideal place to begin a comparative study of the flowering times of woody plants, especially for those genera which are taxonomically well represented in the living collections. A comparative survey of flowering phenology conducted in one spot is certainly of interest to those who wish to plan their gardens and grounds so that plants are always in flower or who wish to have flowers of a similar kind over as long a period as possible. In addition, this kind of survey, when properly interpreted, can provide important insights into the biology of the plants concerned. On the basis of such studies alone we cannot hope to answer fully why related plant species differ in flowering times, but we may uncover patterns which suggest possible answers and discover problems which deserve further study.

The Arnold Arboretum has a long history of keeping records of flowering times. Professor J. G. Jack kept detailed records of blooming dates in the Boston area between 1887 and 1893. Later, Donald Wyman, horticulturist of the Arboretum for many years, listed the order of bloom of a wide variety of trees and shrubs in the Arboretum (1939a). These early lists were subsequently revised and expanded for various genera, among them *Viburnum*. Wyman (1937, 1945, 1959) placed 47 *Viburnum* taxa into flowering categories such as mid-May, late May, and early June. While his records are sufficient for most horticultural purposes, they are not very precise and in a few cases (e.g., *V. prunifolium*) seem to be inaccurate. Although he listed the order of bloom, he indicated nothing about the length of the flowering period or any overlap in flowering times.

During 1978 and 1979 I conducted a study of the different ways *Viburnum* plants grow from year to year once they become of flowering age. This required regularly visiting the Arnold Arboretum, especially during the spring and summer. In conjunction with this study I kept a record of the dates when plants of many *Viburnum* species were in flower. These observations reveal what seems to be a consistent order in which different species begin and end their flowering periods. But before discussing flowering times, we should first consider the structure of *Viburnum* flowers and inflorescences.

Flowers and Inflorescences

Viburnum is a genus of about 135 species. It is widely distributed in the Northern Hemisphere and extends into the Southern Hemisphere in the Andes of South America and in Malesia. Viburnums are

An especially large plant of Viburnum dentatum *at the Arnold Arboretum. The dense, rounded shape is typical of old viburnums grown in the open. Note the very large number of inflorescences on this one plant. William H. Judd, standing next to the plant, was propagator at the Arnold Arboretum from 1916 to 1946. For many years he kept records of the onset of flowering in a variety of early blooming plants, including* V. farreri. *Photograph by R. W. Curtis, June 1922.*

most abundant and diverse in eastern Asia, while eastern North America and the mountains of Mexico and Central America are also areas of high diversity. The genus is generally divided into nine sections. Alfred Rehder, who worked for many years at the Arnold Arboretum, is responsible for this subgeneric classification of *Viburnum* (1908, 1940). The sections differ principally in fruit and leaf characters but also in growth pattern. Egolf (1956) carried out an extensive program of controlled hybridizations in *Viburnum* and found that species within sections are commonly interfertile and produce viable seed, while crosses between species belonging to different sections yield very little seed.

The flowers of most *Viburnum* species are borne in rather complex inflorescences which are properly described as umbel-like, compound corymbs (Figure 1:a). These are often flat-topped and resemble the compound umbels of the Umbelliferae (the carrot family). In most species the inflorescence has a stalk, but some taxa produce sessile

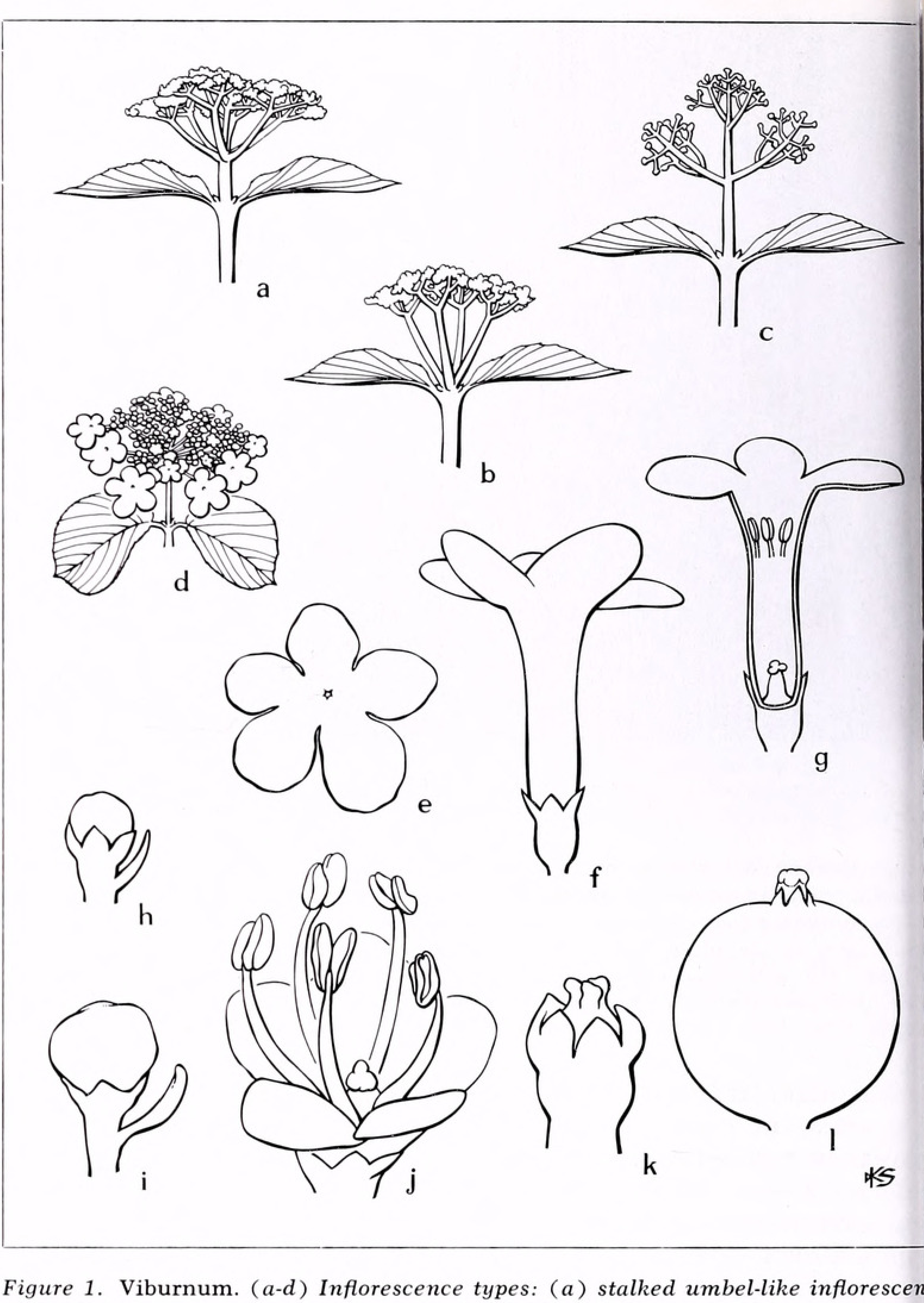


Figure 1. Viburnum. *(a-d) Inflorescence types: (a) stalked umbel-like inflorescen with all its branches originating at one level; (b) stalkless umbel-like inflorescen (c) paniculate inflorescence with its branches originating at different levels; (d) florescence with sterile marginal flowers. (e-g) Flower types: (e) close-up of a ster marginal flower; (f) a tubular flower with its corolla tube much longer than its rolla lobes; (g) the inside of a tubular flower showing the attachment of the s mens to the corolla tube, the inferior ovary, and the short style. (h-l) Developme of a flower from young bud through fruit: (h) very young flower bud; (i) old flower bud just prior to opening; (j) an open flower with a short corolla tube showi the five stamens which alternate with the five corolla lobes; (k) a flower from whi the corolla and its attached stamens have fallen, leaving the sepals and the sty (l) the fruit (ripened ovary), which contains one seed.*

Left: *A picture of* Viburnum furcatum *taken in the winter. In this and some other species the vegetative buds and the well developed inflorescence "buds", such as the one shown, are not enclosed by bud scales. Plants with these so-called naked buds tend to flower earlier in the spring than those with bud scales.* Right: *Most viburnums have flowers very much like those of* Viburnum prunifolium *shown here. The five minute sepals are not visible in this picture, but note the five fused petals, the five stamens which alternate with the petals and shed their pollen inwardly, and the small style in the center of the flower. The flower buds also shown here would probably have opened within a day (see Figure 1:i,j). Photographs by M. Donoghue.*

(stalk-less) inflorescences (in this study, V. *furcatum*, V. *lentago*, V. *prunifolium*, and V. *rufidulum* (Figure 1:b)). Some Asian species produce paniculate inflorescences with opposite branches (in this study, V. *farreri* and V. *sieboldii* (Figure 1:c)). The inflorescence is always terminal on a portion of stem, but it is sometimes borne on a short lateral shoot (in this study, V. *plicatum*) or sometimes on a shoot which dies back at the end of the season (in this study, V. *opulus* and V. *sargentii*). In some species the inflorescences overwinter in an exposed state as well-developed "buds" (photograph above). These are the taxa with naked buds (in this study, V. × *burkwoodii*, V. *carlesii*, V. *furcatum*, V. *lantana*, and V. × *rhytidophylloides*). In most species the next year's leaves and inflorescences overwinter enclosed by bud scales. In V. *cassinoides*, V. *lentago*, V. *plicatum*, V. *prunifolium*, and V. *rufidulum* one pair of bud scales is generally produced, while in the remaining species considered in this study, there are two (or rarely more) pairs of scales.

Plants of different species produce different numbers of flowers per inflorescence, from about 15 to over 500. The number of inflorescences per plant depends largely on the size of the plant, but there are often hundreds. This makes the flowering of viburnums quite spectacular and in part accounts for their horticultural importance.

The fertile flowers of nearly all viburnums are strikingly uniform in morphology, although they may differ slightly in size and hairiness. They are usually small (between 4 and 10 mm. across) and by themselves not very conspicuous. There are five persistent, small, green calyx lobes at the summit of the ovary. The corolla consists of five fused petals, i.e., it is sympetalous, and is white or cream-colored or rarely slightly pink. In most species the corolla tube is shallow (about 2 to 3 mm.) and the flowers are saucer-shaped or bell-shaped (Figure 1:j). In a few Asian species (in this study, *Viburnum carlesii* and *V. farreri*) the corolla is elongate and tubular and can be up to 15 mm. long. The five stamens are attached generally near the base of the corolla tube and are alternate with its lobes. The anthers are borne on slender filaments which usually project out of the throat of the corolla (Figure 1:j), but in those species with tubular corollas the anthers are borne within the tube near its opening (Figure 1:g). The anthers split open longitudinally and release the yellow-colored pollen. The pistil is constructed of three carpels, but only one large seed is developed in each fruit (see Wilkinson, 1948, for details of ovary construction and development). The ovary is inferior or nearly so, and the cone-shaped style is very short (usually about 1–1.5 mm. long (Figure 1:k)). The stigma, which is white in color in most species, but red in some, is usually slightly tri-lobed and fairly broad. When it is receptive to pollen it appears somewhat shiny. It seems that in most viburnums the pollen begins to be shed before the stigma is receptive, i.e., they are slightly protandrous, but this has never been experimentally confirmed.

In a few species (in this study, *Viburnum furcatum, V. opulus, V. plicatum*, and *V. sargentii*) sterile flowers are produced around the periphery of the inflorescence (Figure 1:d and photograph opposite). The corollas of these flowers are quite large and showy (to about 30 mm. across (Figure 1:e)). Occasionally one finds remnants of stamens and a style in the center of the flattened corolla. These showy marginal flowers are presumed to function in attracting insect pollinators, thereby increasing the number or the quality of the fruits that are produced, but this has never been tested. Cultivars of several species produce inflorescences with only sterile flowers. These so-called "snowball" forms occur in *V. opulus, V. plicatum, V. macrocephalum*, and *V. cordifolium* (Egolf, 1962).

Most viburnums seem to be pollinated effectively by a variety of insects. I have noted bees and wasps (Hymenoptera), flies (Diptera), butterflies and moths (Lepidoptera), and beetles (Coleoptera) visiting viburnums and presumably effecting at least some pollination.

p: *Large sterile flowers surround the numerous small, perfect flowers in these* *lorescences of* Viburnum sargentii. *This condition occurs in five other* Viburnum *ecies in four different sections of the genus and may have evolved independently* *veral times.* Bottom: *All of the flowers are enlarged and sterile in the inflores-* *nces of the form of* Viburnum plicatum *shown here and known as the Japanese* *owball. Snowball forms occur in three other species. Such plants cannot pro-* *ce fruits and seeds and therefore must be propagated by cuttings. Photographs* *M. Donoghue.*

In addition Gould (1966) reported that ruby-throated hummingbirds occasionally visit the flowers of *Viburnum lantanoides* (the hobble-bush, formerly known as *V. alnifolium*). The species with short corolla tubes often have a musky odor and probably are pollinated mostly by small bees and by flies. Species with long corolla tubes tend to have a strong, sweet odor, especially towards sundown, and may be visited most commonly by Lepidoptera, perhaps nocturnal moths. Viburnums produce very little nectar and only for a short time. Bees seem attracted to *Viburnum* flowers principally as a source of pollen.

Flowering Times

The timing of flowering varies considerably among *Viburnum* species. Some of the species that grow in tropical latitudes flower nearly continuously throughout the year and one can often find mature flowers and fruits at the same time on the same plant. *Viburnum sambucinum* in Malesia (Kern, 1951) and *V. hartwegii* in Mexico and Central America are examples. On the other hand, in some tropical species flowering is limited to a given season, although plants of this sort may go through two or more flowering flushes during this period. In the New World tropics many such species flower during the summer months, which is the wet season in most areas, but others flower during the drier winter months (e.g., *V. blandum* and *V. venustum* in Central America). Most viburnums of temperate regions have very restricted and well-defined flowering periods, mostly during the spring and early summer. Flowering in these species is highly synchronized on single plants, as well as between plants of the same species. Generally only one period of flowering (and consequently of fruiting) occurs per year.

Plants of *Viburnum* species from the Temperate Zone flower for approximately seven to twelve days. Inflorescences near the top of the plant often come into flower slightly before inflorescences lower on the plant, but generally there is a period during which flowers are open in nearly all the inflorescences at once. All the flowers in an inflorescence open usually within two to four days of each other. Because of the large number of flowers that open during this short period, the exact sequence of flower opening is very difficult to determine; however, sterile marginal flowers, if present, open usually one to four days before any of the perfect flowers.

Each flower begins its development in the spring as a compact green bud (Figure 1:h). As the bud expands, the corolla begins to turn white and becomes inflated (Figure 1:i). The flower opens (Figure 1:j) and then remains open until the corolla withers and falls off, usually within four or five days. The flowers do not close at night nor in bad weather as in some other plants. When the corolla falls, only the calyx lobes and the tiny style are left at the top of the

TABLE I: WEATHER STATION DATA RECORDED AT THE DANA GREENHOUSES

1978	Avg. Max. Temp. (°F)	Avg. Min. Temp. (°F)	Precipitation (inches)	1979	Avg. Max. Temp. (°F)	Avg. Min. Temp. (°F)	Precipitation (inches)
March	45	24	3.21	March	49	33	2.83
April	54	36	1.93	April	57	37	4.44
May	69	46	5.25	May	70	52	4.12
June	81	55	0.40	June	81	54	0.96

ovary (Figure 1:k), which if fertilization has occurred, begins to enlarge and mature into a fruit (Figure 1:l).

Methods and Results

Viburnums from Asia, Europe, and North America are well represented in the Arnold Arboretum. Some 40 species and numerous varieties and cultivars, representing seven of the nine sections of the genus, are currently in cultivation in the living collections. The Arboretum thus provides a good spot to begin to investigate flowering behavior in Temperate Zone viburnums. The present study reports on 21 *Viburnum* taxa, including representatives of each of the seven sections present (Appendix). The plants I followed grow in or near the main *Viburnum* collection, which is located near the Centre Street entrance behind the Dana Greenhouses. All the plants are thus exposed to nearly the same temperature regime and receive the same amounts of sunlight and precipitation, although, to be sure, there are some micro-climatic differences. A summary of climatological data for the spring and early summer of 1978 and 1979, as recorded at the Dana Greenhouses, is presented in Table I.

The *Viburnum* collection was visited somewhat irregularly at intervals of about seven to twelve days throughout the spring and summer. On each visit I recorded the condition with respect to flowering for each plant and checked usually two or more plants of each taxon. The results are shown in Tables II and III. Since the observations were not continuous, some inferences about when a species began and ended its flowering period were necessary. If a plant were in bud on one visit, in full flower the next visit, and past flower on a third visit, it obviously began to flower between visits one and two and ended flowering between visits two and three, but the exact timing is not known. In tabulating flowering times I have made the assumption that plants flowered over ten consecutive days unless the observations actually indicated a longer time. Thus I marked the time of full flowering and then marked five days on both sides of this. For some taxa an assumed flowering period of ten days was actually too long. If ten days were assumed in these cases, plants would have to have developed from the early bud stage to full flower in one or two days, while this development usually would take from three to five days. These special cases are indicated in Table III by an asterisk.

The tables of flowering times illustrate some interesting points. First, a glance at Table II shows that viburnums flower over a two- to three-month period, depending on the weather during a particular year. The first species begins flowering around mid-April and the last species ends by July. During this period different species flower at different times. The overall sequence of flowering in viburnums is almost identical in 1978 and 1979. Differences between these years are most notable among the species that flower earliest. For example, *Viburnum farreri* began flowering much earlier and its flowering period was longer in 1979 than in 1978. Mr. W. H. Judd, a former propagator at the Arnold Arboretum, kept records of the onset of flowering in a number of early flowering plants (Wyman, 1939b). He recorded considerable variation for *V. farreri* (then called *V. fragrans*) from January 14, 1932, through April 20, 1939. This variation clearly relates to differences in the weather, which is especially unpredictable during the early spring. As shown in Table I, the winter was milder and it was warmer earlier in the spring of 1979 than in 1978, and this appears to account for shifts in the onset of flowering. Flowering times of the early-flowering species were advanced by about a week in 1979, but species that flower later began flowering at about the same time in 1978 and 1979. While the exact dates of flowering fluctuate from year to year, the times that species flower relative to one another appear to fluctuate very little. Thus, presumably, the dates of flowering would change with locality, for example, between the southern and the northern United States, but the relative sequence of flowering probably would not change with locality very much. A species constancy resulting in a predictable sequence of flowering is clearly of interest to horticulturists.

The Biological Importance of Flowering Times

The observation that plants of a particular *Viburnum* species flower during nearly the same period every year suggests that there is a genetic basis for the timing of flowering, although a range of expressions is possible owing to environmental differences from year to year or in different localities. There also seem to be genetic differences within what are recognized as species, as illustrated by *V. dentatum*, within which var. *pubescens* and var. *scabrellum* tend to flower a week later than var. *dentatum*. Other evidence of variation within a taxon is provided by *V. × burkwoodii*, which had an extended flowering period in 1978 and a somewhat extended period in 1979. As Egolf (1962) points out, there are cultivars of *V. × burk-*

TABLE II: *Viburnum* FLOWERING TIMES

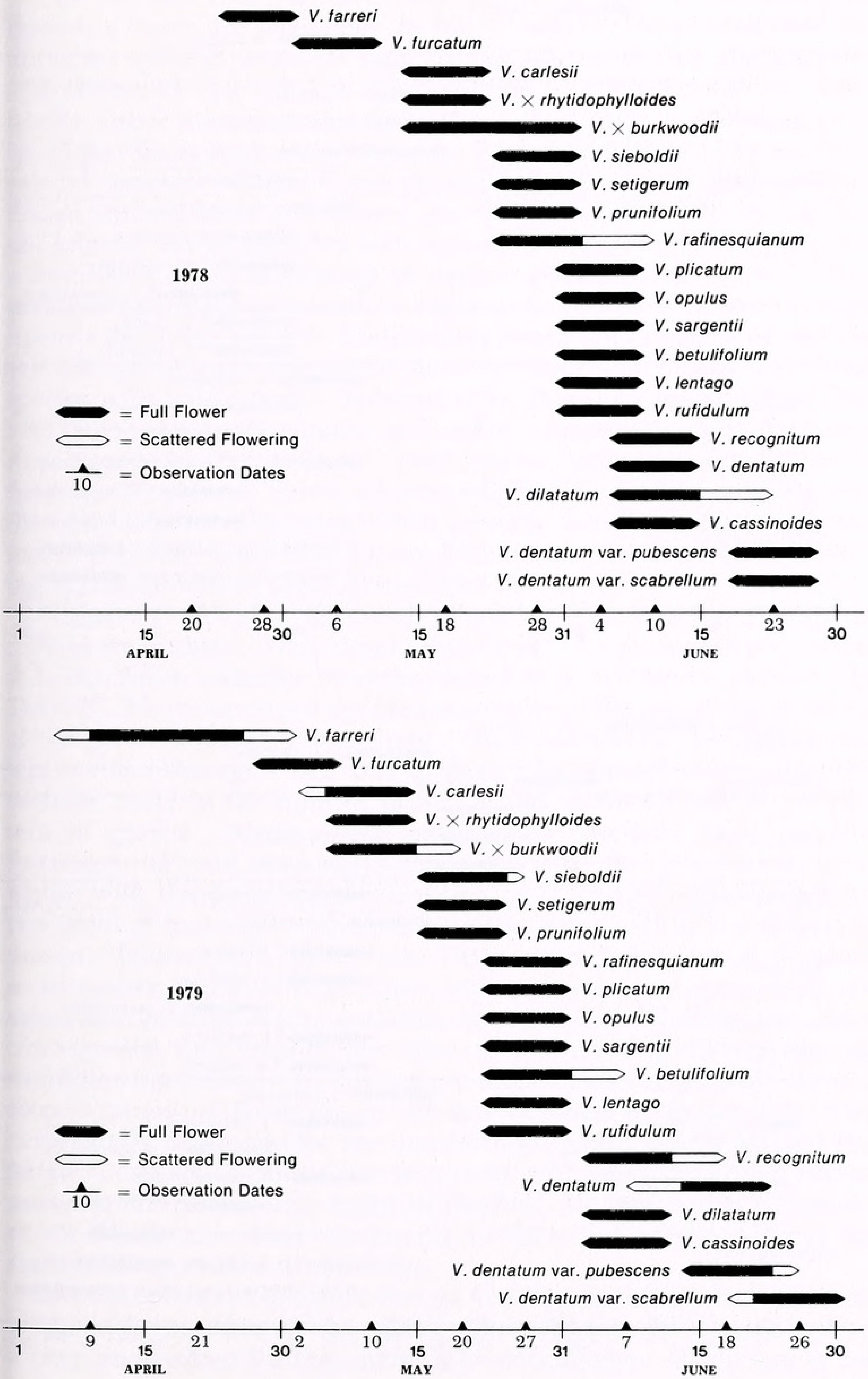
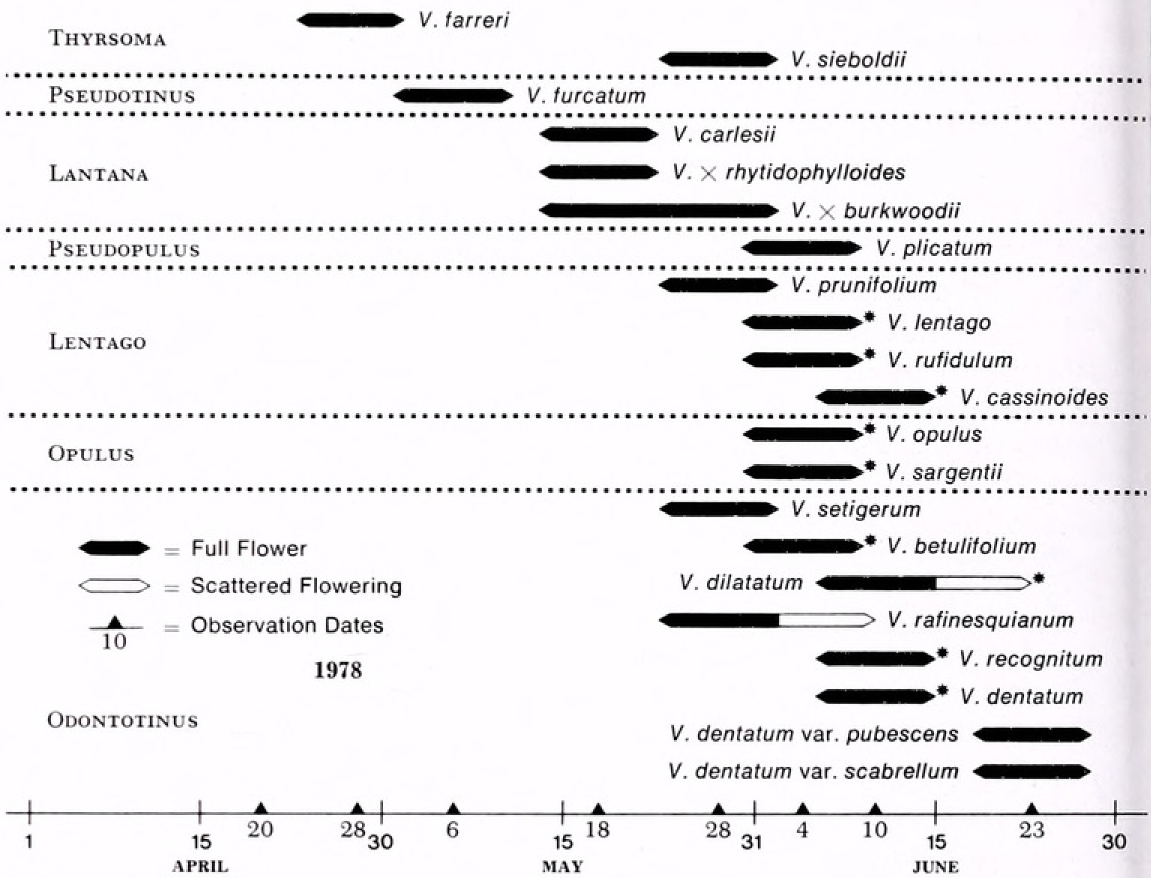
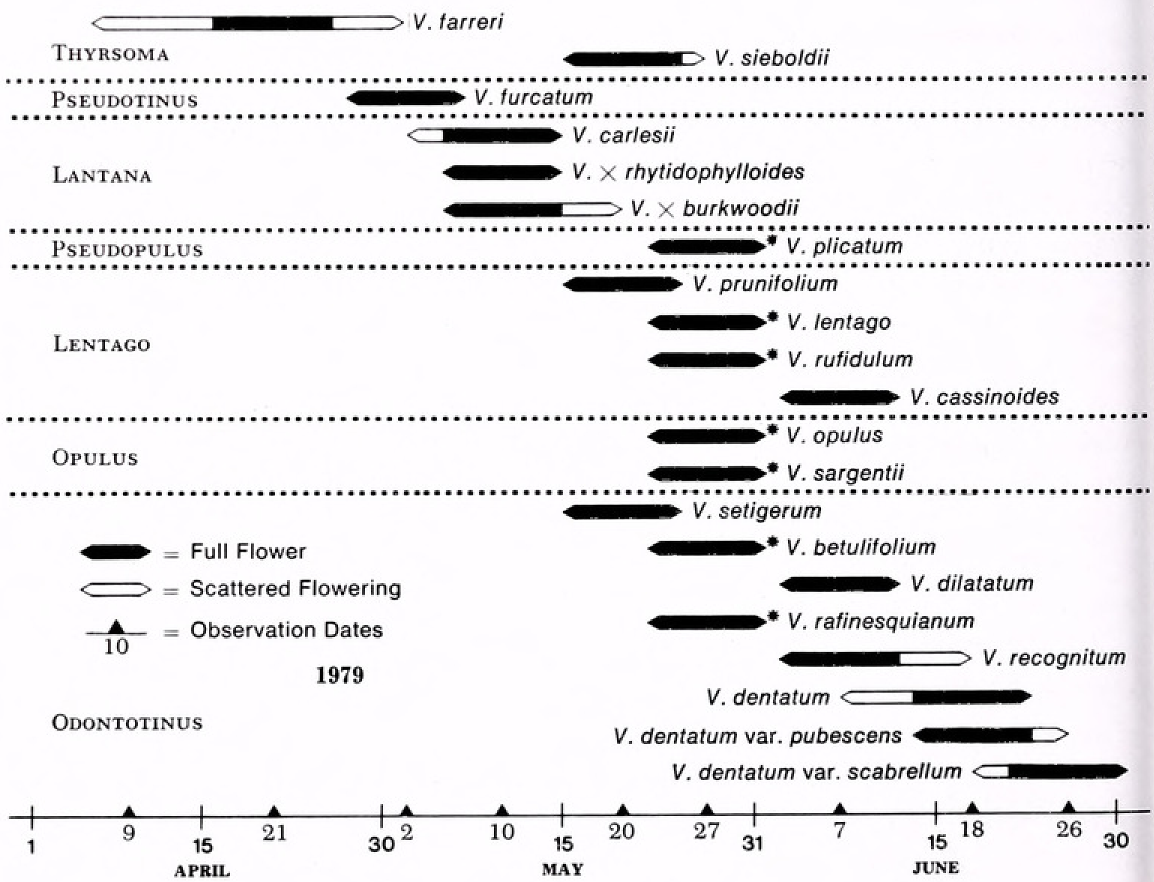


TABLE III: *Viburnum* Flowering Times by Section





woodii ('Fulbrook' and 'Anne Russell') that differ markedly and consistently from one another in flowering times.

One question raised by these observations is how the differences in flowering times are mediated. In the viburnums considered here the initiation of inflorescences and flowers begins during the summer and continues through the early autumn. The inflorescences overwinter either as tiny primordia within a bud or in a relatively well-developed form in those species that have naked buds. The environmental cues that initiate flower production and those that trigger continued inflorescence and flower growth during the next spring are not known, but presumably a combination of factors is involved (for a discussion of the physiology of flowering see Bidwell, 1974). Temperature and available moisture seem to be the most important cues in early-flowering species. Consecutive warm days in the early spring are enough to swell the flower buds of *Viburnum farreri* and those species with naked buds. Unfortunately, this early growth often dies back when the weather turns cold again, and consequently flowering may be very spotty. As Egolf (1962) notes, "almost invariably the *V. fragrans* [*V. farreri*] flower clusters will be damaged by a freeze and the early blooms obliterated." It is possible that some day-length (or more accurately, dark-length) requirement may be involved in initiating spring growth in those species that flower later in the season.

Whatever the cues, different *Viburnum* species clearly respond differently to them. Why should this be so? To answer this question it is helpful to consider flowering times in a taxonomic context. In Table III, I have arranged the taxa according to the taxonomic sections of the genus to which they belong. There are several interesting patterns which emerge when this is done. As pointed out earlier, the sections differ in the number of bud scales produced and in the pattern of growth. Species with naked buds (sections LANTANA and PSEUDOTINUS) are invariably among the early flowering viburnums, while, with the conspicuous exception of *V. farreri*, all species with two pairs of bud scales flower during the latter half of the flowering season. Plants with naked buds begin their inflorescence development earlier and overwinter their inflorescences in a more fully developed state than plants with one or two pairs of bud scales. As a consequence they require less time to mature their flowers during the following season. In our area some species occasionally have a second period of flowering in the late summer or in the fall. Not surprisingly, these species are mostly those with naked buds, but the Asian *V. erosum* (section ODONTOTINUS), with two pairs of bud scales, seems to flower regularly again in the fall. McAtee, in his treatment of the North American viburnums (1956), has recorded many instances of sporadic fall flowering.

The exceptional *Viburnum farreri* develops an inflorescence within a bud with two pairs of bud scales. The inflorescence is produced on a very small, often leafless, stem. The development of the bud is not


Left: *In this species of* Viburnum, V. farreri, *the flowers have tubular corollas with five spreading lobes. The stamens are not visible here because they are contained within the tube. This species and several others bear their flowers in paniculate rather than umbel-like inflorescences. Photograph by A. Bussewitz.* Right: *A photograph of* Viburnum farreri *taken by Oakes Ames on April 16, 1931. Plants of this species are the first viburnums to bloom in our area. The inflorescences are well developed in winter buds and expand rapidly following a warm spell in the early spring. The flowers open well before the leaves expand.*

much arrested, and it may even begin to swell and open during the fall or during warm spells in the winter. When spring comes, the inflorescences are quite well developed, and the flowers mature while the plant is essentially leafless (photograph above). Although there is a marked correlation between growth pattern and flowering time, it is obvious that considerable variation is possible even within the constraints of a single pattern of growth (e.g., sections LENTAGO, ODONTOTINUS, and THYRSOMA), so other explanations for flowering time differences are needed.

One possible explanation is that flowering time differences originated while different *Viburnum* populations were growing in different regions, i.e., while they were allopatric. Allopatric divergence in flowering times could result from natural selection or from what is known as genetic drift.

Natural selection occurs when organisms with a particular heritable trait leave more offspring than organisms that lack the trait. This process results in a larger percentage of organisms with the favored trait in succeeding generations. For example, imagine that a population of a particular *Viburnum* species is subjected to a new environment. Further suppose that there is some genetically determined variation in flowering time in this population. If in the new environment those plants that flowered somewhat earlier produced more offspring, then in succeeding generations we would notice that more of the plants in the population would flower earlier. Over a period of time, the result would be a shift in the flowering period in this population.

Genetic drift is the process whereby certain genes, and hence traits, are fixed in small populations due to chance alone. This could result in a shift in flowering time if, for example, all the plants that flower late in a particular population die, leaving only early flowering individuals.

If a shift in flowering time (either due to natural selection or genetic drift) were to occur in one of two populations growing in different areas and if at some later time the geographic ranges of these populations were to overlap, we would observe a flowering time difference between them. This difference might even prevent members of one population from interbreeding with members of the other population, i.e., they would be reproductively isolated.

A second explanation for the origin of flowering time differences is that divergence may have been the result of two (or more) similar species growing together in the same area. This could occur in several ways. Suppose that plants of two very closely related species happen to be growing together. Under these circumstances hybridization between plants of the different species might occur. If the hybrids were inviable or in some way less fit than either of the parental species, then any plants that did not hybridize would produce more viable seed and leave more offspring than those plants that did hybridize. As a result of this natural selection, any mechanism that would limit hybridization would become more common in succeeding generations. Hybridization would be limited, or impossible, if plants of the different species were to flower at different times. Therefore, given that there was genetically determined variation in flowering times in these populations, selection could result in a divergence in flowering times.

It is not necessary that two species be able to hybridize for there to be selection for a divergence in flowering times. Imagine two species that grow in the same area and have very similar flowers pollinated by the same kind of insect. If there were a limited number of pollinators in this environment and if plants of the two species flowered simultaneously, the plants would compete for the services of the pollinators. On the other hand, if the flowering times of the two species did not overlap, they could both more effectively utilize the pollinators and (all other things being equal) would set more fruit and produce greater numbers of offspring. In this way natural selection might result in divergence in flowering times to minimize the competition for pollinators (see Robertson, 1924; Levin & Anderson, 1970; Mosquin, 1971; Heinrich, 1975; Frankie, 1975; and Stiles, 1978, for the development of this fascinating idea).

In the last two examples divergence was the result of two similar species growing together in the same area. As we have seen, under these circumstances natural selection could result in divergence (1) to prevent the production of hybrids and/or (2) to reduce competition between individuals of different species for some limited resource, such as pollinators. These phenomena are known as character displacement, a name which refers to the character differences between species which result when their geographic ranges overlap (see Grant, 1972, and Levin, 1978, for reviews of the history of this concept). It is very difficult to show that character displacement has occurred, and very few (if any) unequivocal cases have been documented. The problem is that all other possible explanations for divergence (for example, allopatric divergence) must be ruled out, and this is usually very difficult to do. In general, if we find that two species differ in flowering times or in some other way in the region where they are sympatric, but that they are the same in this regard where they do not grow together, then we can entertain the possibility that character displacement has occurred.

Now we can ask which of these explanations account for the flowering time differences we find in *Viburnum*. To answer this question we have to consider those instances where two or more *Viburnum* species grow together. Usually when different viburnums grow in the same region, they have different ecological preferences and so rarely grow side by side. But it is not too difficult to find several species growing close enough together that hybridization between them could occur. Often the viburnums involved are members of different sections of the genus and often they flower at different times. An example of this pattern in New England is provided by *V. lantanoides* (section PSEUDOTINUS, flowering in mid-May), *V. cassinoides* (section LENTAGO, flowering in late May), and *V. acerifolium* (section ODONTOTINUS, flowering in mid-June). In this case and in others like it, it is very difficult to decide upon the cause of the flowering time differences. Timing differences may have resulted from divergence at some period when the species did not grow together or from character displacement to minimize competition for the same pollinators. As noted earlier, Egolf (1956) has shown that hybridizations between species in different sections are usually unsuccessful. Therefore, if the flowering time differences are the result of character displacement to limit hybridization, then it must have occurred in the distant past, before these species were genetically reproductively isolated, i.e., at a time when they could hybridize.

Sometimes species that belong to the same section can be found

e honey bee shown here is collecting pollen from the flowers of a plant of Vi-
rnum farreri *at the Arnold Arboretum. She packs moistened pollen into the pol-*
ı baskets on her hind legs for transport. Because of the length of the corolla
be in V. farreri, *honey bees rarely reach the stigmas and are not effective polli-*
tors. In the wild this and other species of Viburnum *with tubular corollas may*
visited by a wide variety of insects, but probably are mostly pollinated by moths
d butterflies. Photograph by M. Donoghue.

growing close together. In such cases there generally are flowering time differences which effectively prevent hybridization between the species. In some of these cases differences in flowering times could have arisen by character displacement, perhaps to minimize the production of inferior hybrid plants. Possible examples of this are provided by species of the section LENTAGO. *Viburnum lentago* grows mostly in northern parts of eastern North America, while *V. rufidulum* grows mostly in the southeastern United States. The ranges of these species overlap a little in the central eastern United States. *Viburnum prunifolium* ranges through the central eastern states and frequently overlaps the ranges of both *V. lentago* and *V. rufidulum*.

As indicated in Table III, in both 1978 and 1979 *Viburnum prunifolium* flowered about a week before *V. lentago* and *V. rufidulum*. By the time the latter were in full flower *V. prunifolium* was completely past flowering. These species were recently studied by Rader (1976), who noted that "the flowering time of *V. prunifolium* was observed to be approximately two weeks earlier than *V. rufidulum*." She also noted that *V. lentago* flowered somewhat before *V. rufidulum*, an observation which my study does not corroborate.

It is possible to obtain hybrids between these species, and a few populations are known in which natural hybridization between species appears to be occurring (Brumbaugh & Guard, 1956; Rader, 1976). Rader even suggested that hybridization between *Viburnum lentago* and *V. rufidulum* may have given rise to *V. prunifolium*. But she also recognized that the "difference in flowering time poses a barrier to crossing, thereby reducing the incidence of successful hybrid populations." A fuller understanding of the cause(s) of these flowering time differences will require accurate observations of flowering times in the field, under natural conditions, throughout the ranges of these species. But the observations reported here provide the necessary groundwork upon which further studies can build.

The timing of flowering is affected by a variety of factors including the climate, plant architecture, pollinator availability, and the presence (or absence) of related or similar plants in the same environment. Sorting out the ultimate causes of flowering time differences is a very difficult task. Comparative studies of flowering times, both in the Arboretum and in the field, can help us to begin to understand the reasons for the differences in flowering times that are everywhere so apparent to us.

Acknowledgements

I thank Marion Carter, Norton Batkin, Elizabeth Taylor, and Drs. Peter Stevens, Carroll Wood, Jr., and Richard Weaver, Jr., for helpful discussion and advice. I am especially grateful to Paul Groff for his assistance in recording flowering times in 1979 and to Karen Stoutsenberger for drawing Figure 1.

Appendix

Viburnum *Taxa Included in this Study of Flowering Times*

V. betulifolium Batalin

V. × *burkwoodii* Burkwood (*V. carlesii* Hemsley × *V. utile* Hemsley)

V. cassinoides Linnaeus

V. dentatum Linnaeus

V. dentatum var. *pubescens* Aiton

V. dentatum var. *scabrellum* Torrey & Gray

V. dilatatum Thunberg

V. farreri Stearn

V. furcatum Blume

V. lentago Linnaeus

V. opulus Linnaeus

V. plicatum Miquel

V. prunifolium Linnaeus

V. rafinesquianum Schultes

V. recognitum Fernald

V. × *rhytidophylloides* Suringar (*V. rhytidophyllum* Hemsley × *V. lantana* Linnaeus)

V. rufidulum Rafinesque

V. sargentii Koehne

V. setigerum Hance

V. sieboldii Miquel

Viburnum *Sections Included in this Study of Flowering Times*

LANTANA Spach

LENTAGO DeCandolle

ODONTOTINUS Rehder

OPULUS DeCandolle

PSEUDOPULUS Dippel

PSEUDOTINUS Clarke

THYRSOMA (Rafinesque) Rehder

Voucher specimens will be deposited in the herbarium of the Arnold Arboretum (Jamaica Plain).

References

Bidwell, R. G. S. 1974. Plant physiology. Macmillan Publishing Co., Inc., New York.

Brumbaugh, J. H., & A. T. Guard. 1956. A study of evidences of introgression among *Viburnum lentago, V. prunifolium,* and *V. rufidulum* based on leaf characteristics. Abstract in *Proc. Indiana Acad. Sci.* 66: 300.

Egolf, D. R. 1956. Cytological and interspecific hybridization studies in the genus *Viburnum.* Unpubl. Ph.D. thesis, Cornell University.

———. 1962. Ornamental deciduous flowering viburnums. *Amer. Hort. Mag.* 41: 139–155.

Frankie, G. W. 1975. Tropical forest phenology and pollinator plant coevolution, *in* L. E. Gilbert & P. H. Raven, eds., Coevolution of animals and plants. University of Texas Press.

Gill, J. D., & F. L. Pogge. 1974. *Viburnum* L., *in* Seeds of woody plants in the United States, pp. 844–850. U. S. D. A. Agr. Handb. No. 450.

Goodwin, R. H. 1941. The selective effect of climate on the flowering behavior of *Solidago sempervirens* L. *Proc. Rochester Acad. Sci.* 8: 22–27.

Grant, P. R. 1972. Convergent and divergent character displacement. *J. Linn. Soc., Biol.* 4:39–68.

Gould, W. P. 1966. The ecology of *Viburnum alnifolium* Marsh. Unpubl. Ph.D. thesis, State University of New York, College of Forestry at Syracuse University.

Heinrich, B. 1975. Bee flowers: a hypothesis on flower variety and blooming times. *Evolution* 29:325–334.

Kern, J. H. 1951. The genus *Viburnum* (Caprifoliaceae) in Malaysia. *Reinwardtia* 1:107–170.

Levin, D. A. 1978. The origin of isolating mechanisms in flowering plants. *Evol. Biol.* 11:185–317.

———, & W. W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. *Amer. Naturalist* 104:455–467.

Lyon, C. J. 1922. A phaenological study in New England. *Torreya* 22:19–28.

McAtee, W. L. 1956. A review of the neartic *Viburnum*. Privately printed, Chapel Hill, North Carolina.

Medway, L. 1972. Phenology of a tropical rain forest in Malaya. *J. Linn. Soc., Biol.* 4:117–146.

Mosquin, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos* 22:398–402.

Olmsted, C. E. 1944. Growth and development in range grasses. IV. Photoperiodic responses in twelve geographic strains of side-oats grama. *Bot. Gaz.* 106:46–74.

Rader, L. L. 1976. A biosystematic study of *Viburnum prunifolium* and *Viburnum rufidulum* (Caprifoliaceae). Unpubl. Ms. thesis, University of Tennessee, Knoxville.

Ray, P. M., & W. E. Alexander. 1966. Photoperiodic adaptations to latitude in *Xanthium strumarium* L. *Amer. J. Bot.* 53:806–816.

Rehder, A. 1908. The viburnums of eastern Asia, *in* C. S. Sargent, ed., Trees and shrubs, pp. 105–116. Houghton Mifflin and Company, Boston.

———. 1940. Manual of cultivated trees and shrubs, 2nd ed. The Macmillan Company, New York.

Robertson, C. 1924. Phenology of entomophilous flowers. *Ecology* 5:393–407.

Rollins, J. A. 1974. Viburnums, *in* J. D. Gill & W. M. Healy, eds., Shrubs and vines for north-eastern wildlife, pp. 140–146. U. S. D. A. Forest Service General Technical Report NE–9.

Stiles, F. G. 1978. Temporal organization of flowering among the hummingbird food plants of a tropical wet forest. *Biotropica* 10:194–210.

Wilkinson, A. M. 1948. Floral anatomy and morphology of some species of the genus *Viburnum* of the Caprifoliaceae. *Amer. J. Bot.* 35:455–465.

Wyman, D. 1937. Viburnums. *Bull. Popular Inform. Arnold Arbor.* 5:73–79.

———. 1939a. The order of bloom of trees and shrubs at the Arnold Arboretum. *Ibid.* 7:53–64.

———. 1939b. This hesitant spring. *Ibid.* 7:13–16.

———. 1945. Viburnums for the northern United States. *Arnoldia* 5:57–63.

———. 1959. Viburnums. *Ibid.* 19:47–56.