

4-1936

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### Recommended Citation

Rosendahl, C. O., & Dahl, A. O. (1936). Rhythm In Blossoming. *Journal of the Minnesota Academy of Science*, Vol. 5 No.6, 7-15.

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paper is not for summaries of science in the making, but rather for concentrates of the reasonably well established broader generalizations, concepts, and viewpoints. Naturally, any such brief would be tentative and require continued revision, because one of the best established principles is that our concept of truth changes.

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## RHYTHM IN BLOSSOMING

*With Special Reference to Hayfever*

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Everyone acquainted with things in nature has observed that certain phenomena of plant life are periodic. It is also obvious to most of us that these manifestations are seasonal. In our latitude, the trees and shrubs leaf-out in April and early May; lilacs bloom in late May, roses in June, asters and goldenrod delay their floral display until July and August. These are familiar facts, and it is well known that many of the successional phenomena of plant behavior are closely correlated with the gradually rising temperatures of spring and early summer. One can also safely assume that a more or less definite periodicity has become established for each species through hundreds and thousands of years of adjustment to its environment, but this does not answer the question as to why species of different families, or of different genera, or different species of one genus, bloom at different times of the season. Neither does it account for the definiteness of the rhythm, which in some cases is so precise that the opening day of bloom may fall on the same date year after year. Many other phenomena of plant behavior are tied up with this general problem, and it is necessary to cite only a few examples to emphasize the complexity of it and to point out how remarkably well means have been adjusted to ends.

If we take a census of all our native wind-pollinated trees and shrubs, we find that practically all of them blossom before the leaf-buds have opened or while the leaves are only in the early stages of unfolding. Among these are the Alders, Hazel, Birches, Silver Maple, Box Elder, Poplars, Cottonwoods, Elms, Oaks, Ash, Hackberry, Hickory, Butternut, and Walnut. These are the hayfever species of the spring season. It does not seem reasonable to assume that all these species bloom early in order to allow enough time for the proper maturation of the fruit because some of them develop their seeds in a few weeks, others in one to two months, while some of the Oaks require 15 to 16 months. More likely, it is directly correlated with the method of wind pollination. If the blooming were delayed until the full development of the leaves, pollination would be greatly interfered with by the leaf canopy. Blossoming before foliation is, therefore, an efficiency measure, designed to ensure fertilization of the greatest possible number of flowers. The flowering rhythm is adjusted to conform to this fundamental biological law.

In considering the native woody plants among which insect pollination obtains, our hypothesis may appear on first sight not to hold because there are both early and later blooming species. However, in the light of the increasingly accepted viewpoint among students of Plant Phylogeny that the wind-pollinated condition among Angiosperms is the later or derived one, the situation is readily understandable. Undoubtedly, both early and late blooming insect pollinated species occurred in the earlier history of flowering plants. Only those that retained insect pollination would be favored to survive if the habit of blossoming late in the season persisted. It is, therefore, interesting to note that among our native woody species that bloom after they are in full foliage, practically every species is insect pollinated. Familiar examples of these are certain species of Willow, Black Locust, Honey Locust, Kentucky Coffee Tree, Thorn Apples, Black and Choke Cherry, Blackberries, Raspberries, Currants, Bittersweet, Holly, Buckthorn, Mountain Maple, Sumac, Basswood, Dogwoods, Viburnums, and Buttonbush. We are familiar with only one or two cases of wind-pollinated woody species that bloom when in foliage, one of which (the Grape) is somewhat doubtful, the other (the Mulberry) which has explosive flowers that propel the pollen to considerable distances. The cases of insect-pollinated plants of our region that blossom before the leaves are unfolded are comparatively rare and their occurrence does not necessarily affect the general principle here set forth. They belong mostly to the Rose family, a group of plants that has been singularly stable in retaining the primitive pollinating habit of Angiosperms.

In the case of herbaceous wind-pollinated plants, there is no leaf canopy to interfere with the pollen being carried from flower to flower. Almost invariably, the inflorescences overtop the foliage; and where the monoecious or dioecious condition obtains, the pollen flowers occupy the most advantageous position with respect to the air currents.

Another aspect of periodicity in blooming is illustrated by a large number of our common woodland flowers. Everyone who wants to gather Hepaticas, Bloodroots, Dutchman's Breeches, Wood Anemones, Mayflowers, Toothworts, Mertensias, Adder's Tongue, and many other familiar species knows that he must get out in April or early May in order to find them. If he should go back to the same woods three or four weeks after the high tide of blossoming, he would encounter no late stragglers, and in the case of several of the more conspicuous species, he would seek in vain for a leaf or any other trace of the plants. Species of this type have become attuned to a short vegetative as well as blossoming period, definitely correlated with the development of the leafy canopy of the hardwood forest. They prefer a forest soil and at the same time they require a certain optimum of light for reproduction and vegetative growth. In meeting these two demands, they have adjusted themselves to a short period of life activity, after which they re-

main dormant in the dense shade of the forest for the greater part of the year.

We have tried by experiments to induce these native plants to blossom at other than their accustomed time but have succeeded only when the sequence of events in nature is duplicated as nearly as possible. That is to say, there must be a period of rest, then freezing, followed by thawing, and, lastly, a sufficiently high temperature. It is possible in this way to shift the period of blossoming of some of our common wild flowers from early spring to mid-winter. However, all species do not respond, and in such cases, the length-of-day factor is likely to be the limiting one. Another manifestation of periodicity in the life activity of plants is so commonplace that it attracts but little attention, nor does it appear to have been deemed worthy of serious investigation. We refer, namely, to the daily opening and closing of flowers. There are numerous species whose flowers open once and remain in that condition until they wither, but there are also many that open and close successively for a dozen days or more. Most of these bloom by day, some by night only. Obviously, the phenomenon is related to light intensity, but this does not explain why the opening and closing occur at definite times of the twenty-four hour period. Some bloom with the first glint of dawn, others at sunrise, and so on through the succeeding hours of daylight to twilight and darkness. This procession of blossoming induced Linnaeus to construct the famous flower clock at Upsala which registered the hours of the day like some giant sundial. Not only are the periods of opening for some species definite, but, also, those of closing, and we have repeatedly seen the African Daisy in our garden fold up its rays promptly at two o'clock in the afternoon no matter whether the sun were shining or not. The time of bloom and its duration can, no doubt, be correlated to some extent with the time of flight of the insects upon which the species depends for its pollination, but there is still much left to conjecture as to how this adjustment has come about.

This marked periodicity in the occurrence of certain major events in the life cycle of plants has been emphasized by data we have gathered over a period of years. First is a record we have kept continuously since 1923 of the earliest pollination dates of over one hundred native species of plants, and, second, the pollen statistics we have gathered during the last three years in connection with the study of the hayfever problem.

A comment that one frequently hears as regularly as the vernal season returns is that, "Spring is later this year than usual." Fortunately, human memory is very faulty; otherwise, our summers would be growing alarmingly shorter. Our records reveal that there are variations in the advent of the blossoming of our vernal plants, but they are oscillations rather than tendencies in one or the other direction. Furthermore, the variations are really less marked than would be expected on the basis of actual fluctuations in temperature from one season to another.

TABLE I. EARLIEST POLLINATION DATES OF FIVE REPRESENTATIVE TREES IN THE MINNEAPOLIS AREA

Species	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934
1. Soft Maple..... ( <i>Acer saccharinum</i> )	Apr. 18	Apr. 6	Mar. 26	Apr. 9	Mar. 17	Mar. 25	Mar. 29	Mar. 12	Apr. 3	Apr. 8*	Apr. 6*	Apr. 6
2. Elm..... ( <i>Ulmus americana</i> )	Apr. 20*	Apr. 23*	Apr. 3	Apr. 20*	Apr. 15	Apr. 4	Apr. 4	Apr. 3- 4	.....	Apr. 18*	Apr. 21*	Apr. 17*
3. Cottonwood..... ( <i>Populus deltoides</i> )	Apr. 27*	Apr. 28*	Apr. 8	Apr. 21*	Apr. 18*	.....	Apr. 16*	Apr. 10	Apr. 13	Apr. 21*	Apr. 22*	Apr. 23*
4. Box Elder..... ( <i>Acer Negundo</i> )	Apr. 30*	Apr. 30*	Apr. 12	Apr. 24*	.....	May 8	Apr. 20	Apr. 10	Apr. 13	Apr. 21*	Apr. 21*	Apr. 26*
5. Bur Oak..... ( <i>Quercus macrocarpa</i> )	May 21*	May 29*	Apr. 30	.....	May 21*	May 15*	.....	.....	.....	.....	May 17*	.....

\* These dates appear especially significant when compared with dates based on the pollen content of the air.

This latter fact becomes more evident when we study some pollination data collected in the field and, especially, when we examine data based upon actual atmospheric pollen counts. From Table I we note that the species that regularly ushers in the spring season for this locality is the Soft Maple. The earliest date on record is March 12 in 1930. This year (1935), pollination began on the same date (Mar. 26) as in 1925. The starred dates indicate those which appear to be especially significant from our air-pollen data. The Elm begins to shed pollen as early as April 3, although, as will be evident from air-pollen graphs later, the period of April 17 to the 23rd represents the peak of pollen production. The earliness of the 1925 and 1930 seasons is also visible in the pollination behavior of Cottonwood, Box Elder, and Bur Oak. Cottonwood was recorded as pollinating as early as April 8 in 1925. As with the Elm, the period centering around April 20 to April 23 is important in connection with our air data. Practically the same set-up is seen with respect to the Box Elder. Bur Oak is somewhat later in shedding pollen than the four trees just considered, the height of its flowering season being observed about May 15-17.

If we turn to the atmospheric data, the dates of pollination take on a greater significance. Records of the pollen content of the air have been obtained by exposing an oil-coated microscope slide out of doors for twenty-four hours. Air-carried particles including pollen grains are ever settling, and some of these will adhere to the slide's sticky surface. A slide so exposed is subsequently examined under the microscope, and the pollen grains observed in twenty-five systematically distributed fields are recorded both as to kind and number of each. The approximate number of pollen grains per cubic yard of air can be calculated from such counts by use of formulae devised by physicists. Simply, these formulae are based on the obvious fact that more small pollen grains can occupy a cubic yard of air than can large ones. The data are put on such a basis for the reason that it gives a measure of the actual conditions to which the hayfever patient is exposed—a measure which is of prime importance in diagnosis and treatment of hayfever.

These pollen data have been graphically summarized, Figure 1 presenting the total "Tree Pollen" content of the air for the years 1932, 1933, and 1934. The daily quantities indicated in this graph were obtained by simply totaling the pollen count for the various component species, thereby giving a compact summary of this somewhat varied group. The components of the group (arranged chronologically according to time of pollination) are as follows:—Maple, Elm, Cottonwood, Poplar, Box Elder, Hazel, Birch, Ash, Juniper, Tamarack, Ironwood, Oak, Willow, Mulberry, Pine, Hackberry, Butternut, Walnut, Fir, Spruce, and Hickory. In Figure 1, the coincidence of peaks on April 23 for the years 1932 and 1933 is quite striking, and it serves as a good example of the existence of a definite pollination rhythm. But the vernal season, during which the temperature factor is the most important, is not the best time



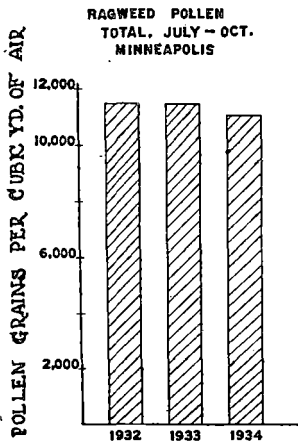


FIGURE 3

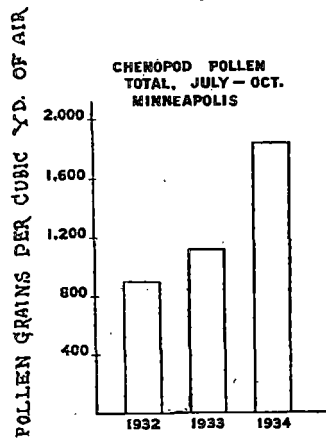


FIGURE 4

CORRELATION COEFFICIENTS OF  
TOTAL POLLEN CONTENT OF AIR  
AND MEAN TEMPERATURE ( $r_{xy}$ ).  
MINNEAPOLIS

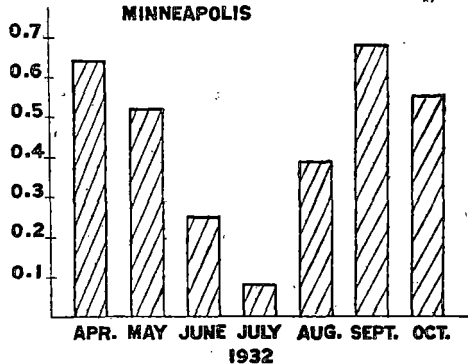


FIGURE 5

tration seen on April 23 in 1932 and 1933. However, the season speeded up, so to speak, causing the Oak peak to occur about a week earlier than in the two previous years. This Oak pollen peak came at about the same time as the memorable dust storms of that year.

During August and September, as reference to Figure 2 will demonstrate, there is marked stability as to the time of pollen production in the Ragweed Group. (Incorporated in this group are the closely allied Common, Giant, and Western Ragweeds; Marsh Elder; and Cocklebur.) Striking similarity of behavior as to consecutive seasons is seen when curves for the three years' data are shown simultaneously. For example, both in 1932 and 1933, August 15th



was the first day to show a pollen count of 100 or more. In 1934, this same rise came on August 14th. Such data give a quantitative basis for the commonly observed fact of hayfever cases starting their first marked symptoms during the middle of August. Close scrutiny of the curves, reveals numerous coincidental peaks and of these, those representing the highest pollen concentration of the entire season are of greatest significance. Such peaks are consistently noted within the period August 29-30th. This stability of pollination behavior comes at a time when summer heat is established—*i.e.* when temperature has become fairly uniform; and at a time during which other factors besides temperature are operative. It is truly during such a period that this rhythmic behavior is best seen. There is a remarkable stability even with respect to total amount of pollen produced as evidenced by the Ragweeds. For example, the total amount of pollen for 1934 was only 3.86% lower than in 1932 as is evident in Figure 3.

Turning to the Chenopod Group (Figure 4), we are met with the reverse of the conditions just seen in the Ragweeds—*i.e.* 1934 shows a tremendous increase in total pollen production over 1932. This fact finds explanation in the severe droughts of 1933 and 1934 which caused devastation of our pastures and thereby opened up much territory for the not too exacting Russian Thistle.

The status of temperature as an involved factor becomes somewhat more clear from correlation studies of daily pollen concentration and mean daily temperature (from U. S. Weather Bureau reports). As one would expect, the highest correlation between pollen count (which is a measure of pollen production) and temperature is shown at those times when temperature is most important—namely, in spring and in late summer and fall. The decrease in amount of correlation seen in October (Figure 5) is explained on the basis that during this month the end of the growing season is reached.

Somewhat earlier in this discussion reference was made to the length-of-day factor in connection with the manifestation of periodicity in plant behavior. It is a pretty well established fact, though perhaps not generally known, that certain late summer and autumn species blossom progressively later as one observes them from north to south in their range. This phenomenon is clearly shown by studies based on the series of slides exposed for us by the various Weather Bureau Stations that have kindly cooperated. Thus, Duluth, our most northerly station, shows the earliest peak in Ragweed pollen production, while Springfield, Mo., our most southerly station, shows the latest peak. Of similar interest is the fact that as one goes south the amount of ragweed pollen produced in September increases until it actually exceeds the quantity observed during August for such stations as Madison, Wisconsin; Wheaton, Illinois; Des Moines, Iowa; and Springfield, Missouri.

The seasonal aspect of hayfever causes complicates the clinical

and etiological phases of the problem (cf. Ellis & Rosendahl).<sup>1</sup> It is becoming more and more clear that in order to insure proper diagnosis and treatment there must be adequate and reliable pollen data available, and it is only by means of field and air studies, carried on throughout the season from early spring until late fall that such information can be obtained. An important part of such data is the demonstration of a high degree of precision in the rhythmic recurrence of vital phenomena in the activities of the plant species involved.

## SOIL EROSION DEMONSTRATION AREAS IN SOUTHERN MINNESOTA

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The evil of soil erosion, by both wind and water, is not only a live issue of the day, but is one of our most important agricultural problems. It is a problem that should have been vigorously attacked fifty or one hundred years ago, but it is the American custom to wait until a problem reaches the verge of being a calamity before any action is taken to improve the situation. This has been true with regard to all our natural resources. We have stripped off our vast areas of virgin timber, with only very meager attempts at reforestation. We have drained swamps that should never have been drained. We have killed off much of our wildlife, and to make matters even worse, we have destroyed much of the natural habitat of this wild life. We have more or less mined our soils and allowed them to wash away, without doing anything to restore their fertility.

In addition to the actual loss of these resources, the cost of our wasteful methods is today being expressed in terms of human misery for thousands who are choking in dust storms of the drought-stricken plains region, and other thousands who have been made homeless by floods in the lower Mississippi Valley. Also, scattered throughout our land there are more thousands of families who, even in normal times, could barely eke out a living from their once fertile fields now impoverished by unrestrained erosion.

All of these problems are a direct result of the misuse of our land, and of our failure to have a long-time plan of use for the greatest good of the majority. The adjustments necessitated by our past mistakes are going to be expensive and will require many years to accomplish, but these adjustments must be made if we are to have a stabilized agriculture.

<sup>1</sup> Ellis, R. V. and Rosendahl, C. O., *Minn. Med.* XVI: 379-389, 1933; *Ibid.* XVII: 378-392, 1934.