BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 87, NO. 5, pp. 348–360 SEPTEMBER, 1960

TORREYA

Studies on the Ecological Life History of Saxifraga virginiensis

MICHAEL H. LEVIN

Saxifraga virginiensis Michx., the Early Saxifrage, is a spring flowering plant which has a wide distribution in the eastern United States and adjacent Canada. According to Fernald (1950) the plant is found on dry or wet rocks, and gravelly open or shaded slopes, from Saguenay County, Quebec to Minnesota and south to Georgia.

The objective of the present study is to explain the life cycle of *S. virginiensis*. The approach followed in general is that suggested by the work of Stevens and Rock (1952). This study which began in February 1959 was terminated in May 1960 and, unless stated otherwise, the field work was carried out in the William L. Hutcheson Memorial Forest, a mature oak forest (Buell, 1957) located one mile east of East Millstone, New Jersey, on the Piedmont Plateau. The study area is located 30 feet from the north forest edge approximately 50 feet west of Spooky Brook, and was occupied by a population of approximately 100 mature plants.

Weekly observations were made between February 1959 and May 1960. When observations began the leaves on each plant revealed a deep red pigmentation. The majority of the leaves exhibited injury at the margins where the red pigmentation was most intense. By April 15 the pigmentation had almost entirely left the leaves. The flower buds began to show signs of enlarging in their position at the center of the rosette on April 8. Scapes began to elongate on April 8, and by April 15 white petals were showing through the sepals of buds in clusters on elongated scapes. Most of the plants were in flower on April 22. The height of flowering was attained between April 29 and May 6. By May 6 the inflorescence was a loosely spreading panicle of cymes. After this date the carpels began to enlarge, and the stigmas diverged. Seeds began to fall from the split follicles approximately May 20, and by May 27 most of the follicles were open. On June 10 seeds had completely shed and nearly all scapes collapsed. After this the plants became a less conspicuous part of the ground cover.

During periods of dry hot summer weather, usually after a period when little rain had fallen, nearly all leaves curled from the tips and margins, drying to approximately the thickness of a petiole, and rolling toward the center of the leaf and toward the center of the rosette. As a result of rainfall most of the leaves unrolled to approximately their former size and turgidity. Some leaves, however, never unrolled and these eventually dropped off. Flower buds were first visible in the center of the rosettes of most plants on November 11. These flower buds enlarged very slowly during the winter.

Leaf litter from the canopy of white oak (*Quercus alba*), black oak (*Q. velutina*), and red oak (*Q. rubra*), understory of flowering dogwood (*Cornus florida*), and shrub layer of maple-leaved viburnum (*Viburnum acerifolium*) was deepest over the study plot on November 11, but by February 10 most of the litter had been blown from the wind-swept study area.

The root system of a specimen of *S. virginiensis* arose from two knobby vertical rhizomes located at or slightly below the soil surface, and from a horizontal rhizome located 0.25 inch below the soil surface which connected the two above ground shoots. Several thick brown roots extending to a maximum depth of 4 inches bore numerous fine white roots. Although the fine white roots branched considerably, the thick brown ones appeared not to branch to any great extent.

The perennating buds are located below the caudex on the vertical part of the rhizome but still very close to the soil surface. The plant may therefore be classed as a hemicryptophyte.

Germination. Seeds were collected from mature open follicles on May 27. The seeds were stored dry in a refrigerator at 41° F until germination tests were initiated.

In order to determine whether the seeds would germinate in darkness at low temperature, 100 seeds were counted into each of 12 petri dishes on August 25. Six dishes contained only moist germination blotter paper and the remaining six contained a peat moss substrate below the blotter paper. The 12 dishes were placed in a dark refrigerator at 41°F. Percentage of germination was determined on February 22 by counting seedlings with extruded radicles and cotyledons which had emerged from the seed coats.

Dr. Lela V. Barton of Boyce Thompson Institute for Plant Research, Yonkers, New York, has informed the author that a mixed lot of *Saxifraga* spp. seeds germinated 62% in red light at 77°F. Two weeks were required for emergence of radicles. Tests were initiated on November 16 to determine whether *S. virginiensis* would show a similar response.

Four petri dishes were filled with fine sand with a piece of finely woven cloth placed on top of the sand. Fifty seeds were counted into each dish. Two dishes of seeds were then placed (1) at room temperature in full sunlight, and (2) wrapped in paper and in a dark chamber also at room temperature. Percentage of germination (appearance of true leaves in this and the following experiment) was recorded after two months.

Since the seeds did not germinate in the dark at room temperature, tests were begun to determine whether seeds placed below the soil surface would germinate. A quantity of seeds was placed 0.5 inch below the surface of finely sieved soil in a small pot. Seeds were scattered on the soil surface of another small pot. Both clay pots received seasonal sunlight at room temperature, and moisture by means of a wick inserted through the bottom holes of the pots and extending into a shallow dish of water.

Of the 600 seeds receiving moist low temperature stratification on blotter paper substrate, the germination mean for the six dishes was 63%. Maximum and minimum germination percentages were, respectively, 68% and 54%. None of the seeds stratified on peat moss (pH 3.5) germinated even though the seed coats had ruptured.

Seeds placed in full sunlight at room temperature on November 16 germinated 65% in two months. Seedlings began to appear after two weeks. Not a single seed in the dishes placed in the dark chamber at room temperature germinated. After one month in darkness a dish of seeds was placed in full sunlight where they began to germinate after two weeks.

Seeds buried 0.5 inch below the soil surface failed to germinate when the pots were placed in full sunlight. Seeds placed on the surface of the soil germinated. The surface of the soil in the pot in which the seeds had been buried was loosened and turned over with a spatula on December 14, and seedlings appeared on January 1. The seeds collected in 1959 were viable in tests conducted in April 1960.

Carleton (1937) has suggested stratifying *Saxifraga* seeds during the winter in a refrigerator and planting them in their permanent location in the spring, and Pearce (1936) recommends late-autumn sowing of *Saxifraga* seeds. Both of these treatments provide moist low temperature stratification, and the germination of seeds in the spring indicates the importance of moist low temperature.

Seedling Establishment. Although seedlings with at least two true leaves were first observed on August 5, 1959, in 1960 small seedlings, with only cotyledons, were seen on April 4. The difference between these dates is probably to be reconciled to the untrained eye of the author in 1959. Since the seedlings are extremely small in April they may go unnoticed until a summer rain enables them to grow to an easily seen size and density.

Fifty-nine seedlings were counted in one six-inch square quadrat on August 5. Fig. 1 illustrates the density and morphological characteristics of seedlings on August 26. By September 5, 57 plants remained in the plot. Attrition takes place gradually with the root systems of the young plants becoming exposed, and by November 11, 34 seedlings were found in the quadrat. On December 16, six seedlings were observed in the quadrat, and by February 10 only three remained. These did not flower the spring following germination.

The establishment of young plants depends upon a suitable habitat not covered by litter (Fig. 1). The plants develop too slowly and are too small to be successful in a

habitat that is litter-covered. It is probably for this reason that *S. virginiensis* occupies the wind-swept study area, and not the surrounding litter-covered forest floor. Observations made after rainfalls give evidence that droplets of rain pock the soil (Fig. 1) and uproot the young plants. During the winter following establishment of the seedlings,

FIG. 1. Photograph taken August 26, showing density and morphology of seedlings. Note the relative absence of litter. One inch is equal to 2.54 gradations of the stake.

frost heaving of the upper layer of the soil uprooted many of the remaining small plants. In this connection, Grullemans (1930) noted that fallen leaves or straw will ultimately kill *Saxifraga hypnoides*, but a snow cover will not injure the plant.

Photoperiod. S. virginiensis flowers during a short period (approximately five weeks) in the spring of the year. During the period when the plants flowered in 1959, daylengths in the natural habitat at latitude 41°N were between 12 and 14 hours. This phase of the investigation was initiated to determine whether *S. virginiensis* would exhibit a photoperiod response to: (1) a short daylength of 8 hours, (2) a long day of 16 hours, (3) seasonal greenhouse conditions. The following approaches to this problem were employed: (1) keeping the plants in the greenhouse for the duration of the study, and (2) exposing the plants to prevailing weather conditions outside the greenhouse and bringing them in on predetermined dates.

Plants were collected on July 25, 1959, from an open, south-facing habitat near the banks of the Delaware River, two and one-half miles south of Riegelsville, Pennsylvania. Thirty plants were transplanted to plastic pots containing a mixture of topsoil and humus in the proportion 1 : 1. The 42 remaining plants were planted in metal flats and placed outside the greenhouse. The care that these plants in flats received was daily watering.

The long and short daylight periods were controlled automatically by an electric time switch. Both chambers opened at 8 a.m. and closed at 4 p.m. thus utilizing insolation. Extended periods of light (an additional eight hours) in the long day chamber were supplied by four 60-watt cool white fluorescent lights. The intensity of artificial light reaching the plants was 100 foot candles.

Temperature was measured in the long and short day chambers by placing standard Weather Bureau maximum and minimum thermometers with the plants. The thermometers were read each week, and the temperatures compared with greenhouse temperatures recorded by a thermograph.

On September 10 ten plants were placed under the three distinct photoperiods in the greenhouse. Two plants in each group received complete nutrient solution (Robbins, 1953).

All plants receiving short day conditions from September 10 to January 8 failed to flower (Fig. 2—1). Of the plants receiving long day conditions continuously only two produced weak few-flowered scapes, flowering on January 27. The remaining six plants did not flower. Plants receiving prevailing greenhouse conditions produced a few flowers at the center of the rosette about January 13, but failed to produce a scape. The two plants in each environmental condition receiving complete nutrient solution did not exhibit a marked increase in size, but did show an increased vigor over those plants not receiving complete nutrient solution.

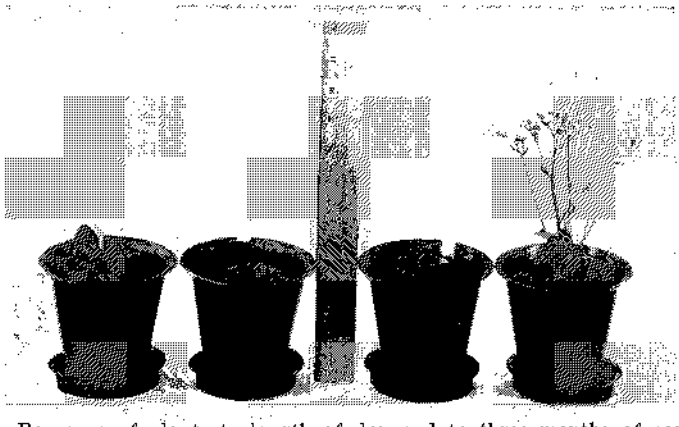

FIG. 2. Response of plants to length of day and to three months of seasonal cold treatment. Left to right:

(1) short day—greenhouse September 10–January 8
(2) short day—introduction from outdoors on December 11
(3) long day—greenhouse September 10–January 8
(4) long day—introduction from outdoors on December 11

Photograph taken January 8, 1960.

Two plants from each of the three flats outside the greenhouse were brought into the greenhouse and placed under each of the three photoperiods on December 11.

The two plants introduced on December 11 and placed under short day conditions failed to flower (Fig. 2—2). Those introduced from outdoors and receiving long day conditions flowered vigorously (Fig. 2—4) and by January 4 were at the height of flow-

ering. The two plants introduced to prevailing greenhouse conditions flowered weakly from January 8 to the termination of the experiment on February 16. One of the latter plants had produced a short scape by February 16.

All of the remaining plants in the flats in which they were growing were brought into the greenhouse, after an additional month of cold treatment outdoors, on January 10. One flat was placed in each environmental condition on that date.

Plants in the flat placed under short day conditions did not flower even though small flower buds had formed deep in the center of the rosette. All 12 plants receiving long day conditions flowered vigorously, attaining the height of flowering on February 2.

Plants in the flat placed at prevailing greenhouse conditions began to flower weakly about February 14. These did not produce scapes by the 16th of February.

The minimum greenhouse temperature during the study period was 52°F and the maximum 100°F. Minimum temperatures recorded in the chambers were identical with that recorded by the thermograph, but the maximum temperature recorded in the short day chamber was 8 degrees higher than the maximum greenhouse temperature.

In the forest, the mature plants probably flower for consecutive years.

Vegetative Multiplication. Observations of plants growing on steep banks near Washington Valley Reservoir in Somerset County, New Jersey revealed that two large clones were present. Fourteen plants comprising one clone were collected and brought to the greenhouse where the soil around the roots and rhizomes was sluiced away with a jet of water. The curvature of the rhizomes at the edge of the clone appeared to indicate that most, if not all, of the plants had originated from some plant near the center of the clone, but most were not connected by rhizomes. To determine whether rhizomes which are detached from the parent plant can grow a shoot portion, the rhizomes of 14 plants were removed from the shoots and roots and planted 0.25 inch below the soil surface in a clay pot. The pot was watered each day. Rhizomes were removed from the soil on May 16, 12 days after burial and examined for buds, leaves, and turgidity.

Four rhizomes had at least one bud with tiny green leaves, eight rhizomes had buds that appeared to be enlarged, and two rhizomes had no buds visible. Only one of the rhizomes showed signs of decaying, and this only in a small portion.

It would seem probable that these plants can spread vegetatively by sending forth a rhizome which grows a short distance beneath the soil surface, produce a rosette of leaves at the surface, may in some cases detach from the parent plant through mechanical injury such as frost heaving, and that the plants once detached can maintain themselves independently of the parent plant.

Leaf Appearance. The number of new leaves added to the rosette was recorded weekly from the last week in June to the second week in February on each of six plants marked with numbered stakes. Temperature and precipitation were recorded weekly in the study area. The largest mean number of leaves appearing in the rosettes of six plants in any one week was 1.2 recorded on August 12 after a period of heavy rainfall. During the latter part of August and early September when temperatures were highest and precipitation lowest, leaf appearance took place slowly. At this time the influence of drought was evidenced by curling and drying of the leaves. Leaves appeared four out of five weeks during the period from October 7 to November 4. This was the most rapid rate of appearance recorded. After the first week in November the rate of appearance decreased as the minimum temperature went below 34°F. During the spring flowering period there is also a burst of leaf appearance.

Seed Dispersal. Within the forest, the minutely papillate seeds are dispersed during late May and early June. There are probably two agents: (1) wind, and (2) tracking in earth on the feet of animals. The seeds are dispersed as the panicle branches vibrate in the wind, dislodging the seeds from the urn-shaped open follicles. Dr. D. B. O. Savile of the Canada Department of Agriculture, Research Branch, Plant Research Institute, Central Experimental Farm, Ottawa, Canada, has suggested in personal correspondence in 1959 that this "censer mechanism" is effective only in the open where strong winds occur. Wind dispersal of seeds is probably reduced within the forest. Seedlings were observed only in small areas around the mature plants; not one was found outside the study area.

even by a diligent search. Long distances are probably traversed in clods of earth on the feet of animals.

Biotic Influence. Many leaves are lost during the spring before and during the time that the plants flower. Several plants had lost flowers and part of the scapes. Loss of leaves also takes place during the fall. This appears to be due to small mammals foraging on the forest floor. Evidence seems to point to a rodent such as the rabbit or squirrel because open flowers at the top of a 10- to 12-inch scape were, on two occasions, eaten completely without damage to the scape.

Savile (personal correspondence, 1959) has suggested that "the genus *Saxifraga* is primarily adapted to arctic-alpine situations, and those species that have spread into temperate lowlands retain many of the characters that fit them for arctic-alpine survival." He states that "the small white flowers are specifically adapted to dipterous pollinators, but that it is quite possible that other insects may visit them in temperate areas." Five insects were collected on May 3, 1960 from flowers growing on banks near the Washington Valley Reservoir. These belonged to two orders: Hymenoptera and Diptera. P. W. Oman of the United States Department of Agriculture, Agricultural Research Service, Entomology Research Division, Beltsville, Maryland, reported the Hymenoptera of the family Halictidae as: *Augochlorella striata* (Prov.) and *Halictus (Chloralictus)* spp. The Diptera taken from the flowers were reported as *Gonia frontosa* Say, of the family Tachinidae. Chapman (1933) noted in the outer ovary tissue of *S. virginiensis*, a short distance above the point where the carpels separate, a darkly staining group of cells, rich in contents which probably serve as nectaries. The representative of the order Diptera which was collected on May 3 was observed probing that area of two flowers for periods of several seconds each.

Habitats. During the first week of May 1960 observations were made of two habitats in Somerset County, New Jersey, near the Washington Valley Reservoir: (1) Chimney Rock Road 0.75 mile above the quarry, and (2) East Branch Middle Brook at the intersection with Gilbright Road. Plants growing in both habitats extend out as far on the rock as there is moss and soil to provide the substrate, but as one progresses back from these areas of primary exerarch succession into more established vegetation, *S. virginiensis* disappears abruptly. The areas which the plants inhabit were moist that spring due to water running along the slope between basalt and the shallow soil. The plants which had established themselves in habitats that were not moist with runoff had withered flowers, which upon examination were without seeds, and dried scapes. Apparently, there is little competition for space, light, water or a combination of these with the mosses which comprise the mat, for young seedlings, though not prolific, were seen in the moss mat. The moss probably serves to stabilize the surface not making it as subject to frost heaving, and pocking by raindrops. Once other plants establish themselves, *S. virginiensis* does not find it as easy to maintain itself, and produce seedlings. The nature of this competition would be an area for further experimentation.

Salisbury (1942) states that "in general, the larger the supply of food material in the seed, the more advanced the phase of succession that the species can normally occupy." [Small seeded plants normally occupy early stages of succession]. He gives the weight of a single seed of *Saxifraga oppositifolia* as 0.00008916 gms. The weight of 50 seeds of *S. virginiensis* as determined by the author was approximately 0.00005 gms. If small seeded plants normally occupy early stages of succession, why is the plant to be found in the mature oak forest on the Piedmont of New Jersey? The answer is that the study area at the William L. Hutcheson Memorial Forest is one that has probably been disturbed. With this suspicion in mind, the author and Dr. B. B. Stout, of the Forestry Department of Rutgers–The State University, examined the area at the forest. After examination of the site Dr. Stout suggested that the area had probably been the location of a tree that had blown down. His explanation was based upon examination of the soil which showed that many fragments of shale were near the surface of the soil, and that this had probably been the result of shale being brought up when the roots of the tree were heaved above the surface. The area is slightly concave now, indicating that many years have passed since this occurred. The moss growing on the site is *Mnium cuspi-*

datum. Examination of more recent blowdown mounds failed to reveal *M. cuspidatum*. Dr. E. T. Moul of the Botany Department at Rutgers–The State University, in personal conversation in 1960 suggested that the mosses *Pogonatum* spp. or *Dicranella* spp. grow first on these blowdown mounds and that *Atrichum* spp. and *Mnium* spp. establish themselves later. Studies of succession of mosses and higher plants on blowdown mounds would provide information of great value in piecing together the story of secondary succession within this mature forest.

The assistance and encouragement of Professor Murray F. Buell, Mrs. Helen F. Buell, and Dr. John A. Small is gratefully acknowledged.

SUMMARY

1. A 16 month study of the ecology and periodicity of *Saxifraga virginiensis* in a single colony, possibly a clone, was supplemented with observations, laboratory and greenhouse studies of plants from other areas.

2. Seeds germinated both at 41°F in darkness and at room temperature in sunlight. Spring germination, in the natural habitat, points to moist low temperature as being of prime importance.

3. Normal flowering occurred only with those plants which received seasonal cold treatment to December 11, and long days after introduction to the greenhouse.

4. Rhizomes are capable of producing new shoot portions and presumably a new plant.

5. The largest mean number of leaves appearing in a single week appeared in early August after a period of heavy rainfall. Weekly rate of leaf appearance was most rapid between October 7 and November 4. Leaves appeared four out of five weeks during that time.

6. In a habitat investigated in New Jersey, both dipterous and hymenopterous insects visited the flowers.

DEPARTMENT OF BOTANY
RUTGERS—THE STATE UNIVERSITY OF NEW JERSEY
NEW BRUNSWICK, NEW JERSEY

Literature Cited

Buell, M. F. 1957. The mature oak forest of Mettler's Woods. William L. Hutcheson Memorial Forest Bull. **1**(1): 16–19.

Carleton, R. M. 1937. The refrigerator as a garden tool. Hort. **15**: 412.

Chapman, M. 1933. The ovule and embryo sac of *Saxifraga virginiensis*. Amer. Jour. Bot. **20**(3): 151–158.

Fernald, M. L. 1950. Gray's manual of botany, 8th ed. American Book Company, New York.

Grullemans, J. J. 1930. Rock garden plants. Minnesota Horticulturalist **58**(4): 103–112.

Pearce, R. D. 1936. Late autumn sowing of seeds. Flower Grower **23**(10): 514.

Robbins, W. R. 1953. Formula for nutrient solution. Errett C. Albritton, Ed., values in nutrition and metabolism. McGregor and Werner Inc., Dayton, Ohio.

Salisbury, E. J. 1942. The reproductive capacity of plants. G. Bell and Sons, Ltd., London.

Stevens, O. A. and L. F. Rock. 1952. Outline for ecological life history studies of herbaceous plants. Ecology **33**: 415–422.

Alexander William Evans

MASON E. HALE

On December 6, 1959, Dr. Alexander William Evans died at the age of 91 of pneumonia contracted while he was recovering from a hip injury. This unfortunate illness